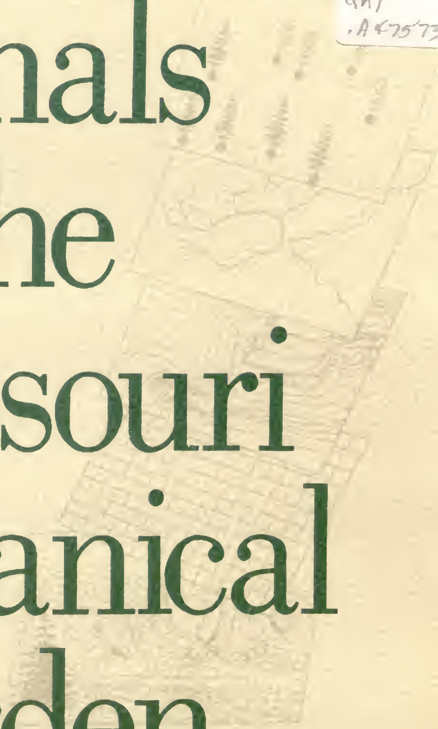

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NEW TOOLS FOR INVESTIGATING BIODIVERSITY SYMPOSIUM: INTRODUCTION[1]

P. Mick Richardson[2]

The ready availability of cheaper, faster computers and large amounts of ever-cheaper memory has opened up new possibilities in the study of the vast diversity of living organisms. The 43rd Annual Systematics Symposium introduced a variety of these possibilities to the occupants of an auditorium filled to capacity by the 449 registered participants representing 11 countries and 35 of the U.S. states. Mike Austin started the morning off with a fine talk about Australian eucalypt forests. After the coffee break, Deborah Clark described some of the studies she and her coworkers have undertaken at La Selva in Costa Rica. The morning session was rounded out by Charles Convis's talk on the past and future of Geographic Information Systems (GIS) in the biological sciences. GIS are what we now use to study how things occur in space. Amazingly, I saw my first ever GIS system in the middle of a forest in Panama. It was, of course, the machine at La Selva mentioned above.

After lunch, David Mladenoff described how GIS, radio collars, and regional databases were being used to define favorable wolf habitat in the Northern Great Lakes region. This was followed by a talk on large-area mapping of biodiversity presented by J. Michael Scott and Michael D. Jennings. The final talk of the afternoon was a presentation by Hanna Tuomisto about satellite imagery and field studies in Amazonian forests. The after-dinner address, co-authored by Andrew D. Weiss, Claire Kremen, and George E. Schatz, was about GIS and a new national park in Madagascar. Four of the talks are represented by the papers following this introduction. The contents of the other talks have been published elsewhere and can readily be found in various databases via the names of the authors.

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[1] This and the four articles that follow it are the proceedings of the 43rd Annual Systematics Symposium of the Missouri Botanical Garden, *New Tools for Investigating Biodiversity*. The symposium was held 4–5 October 1996 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

The symposium was supported in part by the National Science Foundation under grant number DEB-9420140. I thank Bette Loiselle and George Schatz for helping to select a fine diversity of speakers, Kathy Hurlbert and her expert staff for wonderful help in organizing and administrating the symposium, John Myers for his fine illustration for the cover of the symposium brochure, and the symposium registrants for being such a pleasant group of scientists.

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AN ECOLOGICAL PERSPECTIVE ON BIODIVERSITY INVESTIGATIONS: EXAMPLES FROM AUSTRALIAN EUCALYPT FORESTS[1]

Mike P. Austin[2]

ABSTRACT

Australia is a large continent with a relatively small population, and government agencies and research institutions are devoting considerable resources to the development of new approaches and tools for conserving and managing Australia's biodiversity. Issues of data quality, choice of analysis method, ecological theory, and GIS (geographic information system) use are discussed using examples from recent Australian studies with emphasis on the scientific components. The problem of data quality is examined in terms of a suitable minimum data set and the need for a survey design for representative sampling using results from a survey of 24,000 km^2 in northeastern New South Wales. Examples of analytical tools for modeling species distribution, e.g., generalized linear models (GLM) and generalized additive models (GAM), are presented using data from a database of 9537 plots and 273 tree species for an area of 40,000 km^2 in southeastern New South Wales. The necessity for ecological theory, in particular continuum theory as opposed to community concepts, is examined in the context of these results. The interface between ecological and evolutionary theory is discussed drawing on the results of statistical modeling (GLM) of species richness patterns of *Eucalyptus* subgenera in the same area. The predictive use of GIS in mapping vegetation, using statistical modeling (GAM) and multivariate classification techniques, is demonstrated with an application to a comprehensive regional assessment (CRA) process for establishing a regional conservation plan. These methods and analytical tools have been collated into a package, BioRap, which also includes methods for the selection of priority areas for conservation. Rapid progress is being made in developing new tools. However, theory for ecological, statistical, environmental, and evolutionary processes is urgently needed to ensure effective use of these emerging tools for investigating and managing biodiversity.

A key issue facing society is how to conserve our global biodiversity. There is need to use the currently available information now in order to fill the gaps in our conservation strategies. Areas with complementary suites of species and/or representative types of ecosystems are required. There is also a need to constantly examine how to make better use of available data and to find better methods to convert data into useful information for policy decisions on conservation. Scott & Jennings (1998, this issue) presents a detailed account of one of the most comprehensive approaches so far.

Australia is a large continent with a small population, and government agencies and research institutions are devoting considerable resources to the development of new approaches for conserving and managing Australia's biodiversity. To do this, Commonwealth and State governments have developed major databases and Geographic Information Systems (GIS) to provide biodiversity information on the location, abundance, and dynamics of Australia's native flora and fauna, e.g., the Environmental Resource Information Network (ERIN, Chapman & Busby, 1994). Key issues arising from the use of these tools are how best to answer policy questions, data quality, the suitability of analytic tools, the role of ecological theory, the predictive success of GIS, and how best to make methods available to the wider community of users.

This paper focuses on Australian research in this area, in particular on improving information provision methods using modern computer technology. The topics considered are: use of available data, such as herbarium records and vegetation survey data; design of surveys to obtain more cost-effective data; use of statistical modeling and GIS to predict species distributions and richness patterns from survey data; and the need to evaluate methodology against existing theory.

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[1] I thank those colleagues in the Division of Wildlife and Ecology and in other Australian organizations whose work has made this review possible. I also thank J. A. Meyers, N. C. Coops, and G. B. Barnett for preparing the figures.

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ANN. MISSOURI BOT. GARD. 85: 2–17. 1998.

DATA

Most developed countries are establishing databases of biotic data for creating and evaluating conservation policies (Chapman & Busby, 1994; Scott & Jennings, 1998; Soberón et al., 1996). Similar methods are also being adopted for developing countries (Hall, 1994). The data are usually based on herbarium or museum records. In Australia, the federal government has established the Environmental Resources Information Network (ERIN) to collate, organize, and provide access to the available data. Maximizing the use of existing data is now critical as resources to re-collect data by means of surveys are very limited. As part of this effort the principal herbaria and botanic gardens in Australia have cooperated to produce a common standard for computer-based records systems for specimens. There is a working group that meets regularly to address ongoing applications issues. It is estimated to cost $6 Australian to database a single herbarium or museum record, but several times that to collect specimens using professional staff (Chapman & Busby, 1994). ERIN has developed an extensive hardware and software system to support the aim of providing primary data to identify and characterize regional environmental patterns for use in environmental assessment and planning. For handling taxonomic data, ERIN has developed modules for managing taxon names and easily updating them (*Taxon*), managing individual records of specimens *(Specimen)*, and a *Data Dictionary and catalogue* module for managing data sets including custodianship. These modules and others are linked to a GIS to form what ERIN terms a Spatial Information System (SIS). Chapman and Busby (1994) provided further details of the system, and there is a website (http://www.erin.gov.au) that also provides a public access system for plant records. The system provides for all types of data and remote-sensing coverage of Australia, but the primary taxonomic record data are a key component.

It is important, however, to recognize that herbarium records suffer from several weaknesses (Hall, 1994; Margules & Austin, 1994; Soberón et al., 1996): the records record presence only, and there is no information about absence; the locations are often poorly recorded; the presence of other species and of environmental variables is inconsistently recorded; and the spatial distribution of specimens is highly biased. Figure 1 exemplifies the location bias of museum records; it shows the distribution of all suitable records of elapid snakes in Australia (Longmore, 1986). The major roads in remote areas of the continent are clearly outlined by the record locations. With hindsight it is easy to be critical, and such records were not intended to provide definitive data for regional biogeographic or conservation studies. However, when used for analysis of areas of high biodiversity or endemism, problems can arise; see Tuomisto (1998, this issue) for an example from Amazonia. The minimum data set needed for analysis is presence/absence data and an accurate location for which environmental data can be obtained via a map or GIS. Statistical analysis is precluded by the lack of absence data. How to use presence-only data is a serious problem not always recognized by systematists (Soberón et al., 1996; Margules & Redhead, 1995) when considering conservation issues. However, herbarium collections provide taxonomic precision and verifiable voucher specimens, which vegetation surveys usually lack.

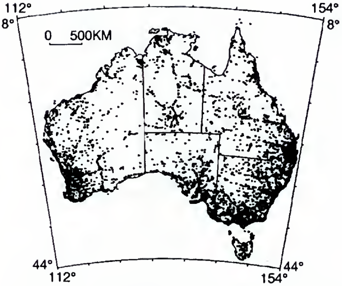

Figure 1. Collection sites for all species in the *Atlas of Elapid Snakes of Australia* (Longmore, 1986). Note the alignment of sites along major roads, especially in the Northern Territory. Reprinted with permission.

This has led to the development in Australia of two heuristic methods to make maximum use of presence data. The first, BIOCLIM (Nix, 1986; Busby, 1986, 1991; now termed BIOMAP (Hutchinson et al., 1997)), uses geocoded specimen records together with estimates of a selected set of bioclimatic variables for the location. The estimates are derived from climatic surfaces calculated using records from climatic stations. These specimen records are used to estimate the range of each bioclimatic variable within which the species is found. For each location where a specimen of a species is recorded, the climatic estimates are aggregated to provide a "climate profile" of the taxon. The values for each estimate are ranked in increasing order such that the minimum value, the 5th percentile, and 95th percentiles, etc., can be defined. This has been done for 12 bioclimatic variables to define the climatic profile (Busby, 1986). By describing the climatic profile for a species as the combination of climatic conditions lying between the 5th and 95th percentiles for 16 climatic variables, a climatic envelope for the *potential* occurrence of a species is defined. From this profile, together with a grid of predictions of the bioclimatic variables for a region or continent, a map of the potential occurrence of a species can be generated based on climatic information (Longmore, 1986; Hutchinson et al., 1997). The prediction map is only of potential occurrence because no information on absence is used, and there is no information on other environmental or historical factors that might control species occurrence.

There are four essential components to the procedure: (1) a method to produce climatic estimates from the records of climate stations and measurements of latitude, longitude, and elevation (see Wahba & Wendelburger, 1980; Hutchinson & Bischof, 1983; Hutchinson, 1984); (2) existence of a digital elevation model which can be used to generate the climatic predictions for all points in the region; (3) a conceptual model for deciding on an appropriate set of bioclimatic variables relevant to the organisms being studied (Nix, 1986); and (4) a classification algorithm to define the bioclimatic envelope. Hutchinson et al. (1997) provided an up-to-date presentation of all stages of the approach. Examples of the application of this method are Longmore (1986), for a continental study of elapid snakes; Nix and Switzer (1991), on the potential regional distribution of Australia's rainforest vertebrate fauna; Busby (1986) on distribution of *Nothofagus cunninghamiana* (Fagaceae); and Busby (1988) on the impact of climate change on Australia's flora and fauna.

A revised method, HABITAT, has been published (Walker & Cocks, 1991) that uses a polygonal rather than the cruder multidimensional rectangular definition of the climatic envelope used by BIOCLIM. This procedure provides a more conservative (smaller) envelope that takes more account of the actual distribution of presence records in the climate space. It has been applied to estimating the continental distribution of kangaroos (Walker & Cocks, 1991). However, BIOCLIM (now BIOMAP) remains the most extensively used of heuristic methods for presence data. See Austin et al. (1994a) for a further review of presence methods.

To provide better data, herbarium records should contain precise locations and consistent environmental information. A preferable minimum data set is presence/absence data for all species in a standard set of taxa from plots collected as part of a vegetation survey. In any survey, absence is conditional on the sampling effort made at a site. Large databases that are capable of supporting statistical modeling can be built up by collating such data from existing surveys (Austin et al., 1990; Leathwick & Mitchell, 1992). The principal weakness in such data sets is the unknown sampling bias in the original selection of the plots. To make most use of databases they should be ecological in nature rather than taxonomic. Margules and Austin (1994) have discussed the requirements for establishing such a database, listing four requirements: (a) a conceptual framework based on ecological theory; (b) field data obtained from sites using survey design principles based explicitly on the conceptual framework; (c) a rationale for determining which measurements should be made at the chosen sites in addition to the floristic records; and (d) appropriate statistical methods for analyzing survey data and predicting (extrapolating) the regional distribution of species from the point records. These authors failed to emphasize that this is only possible if the database is linked to a GIS.

SURVEY DESIGN

How to obtain a representative sample of the vegetation variation in a region is a central question for conservation evaluation. Vegetation surveys of large areas are expensive and time-consuming, particularly if random or systematic sampling is undertaken in rugged or inaccessible regions (Burbidge, 1991; see also Tuomisto, 1998). Cost-effective methods are required. In Australia, modifications by Austin and Heyligers (1989, 1991) of the gradsect sampling approach first proposed by Gillison and Brewer (1985) provide an example of an explicit, consistent, and repeatable method. Unlike many sampling strategies that produce unbiased estimates of some mean value, e.g., basal area of timber per unit area in the region, vegetation surveys should be directed toward obtaining a representative sample of the **range of variation** in vegetation composition. The detection of unusual combinations of species is as important as accurate estimates of the average composition of the commonest forest types. The method proposed by Austin and Heyligers (1989) is based on sampling vegetation from all possible combinations of selected environmental variables. The logistics of surveys, e.g., travel time between sampling sites, add considerably to the costs. Sampling along a transect is very cost-effective in travel time. If the transect is oriented along the steepest environmental gradient in

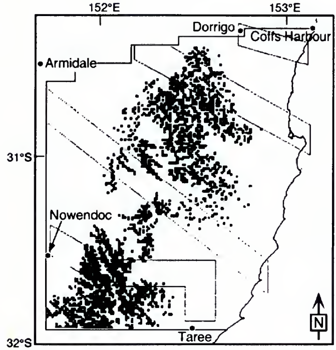

Figure 2. The position of four gradsects selected for a region of the north coast of New South Wales, showing the extent to which they sample a particular altitude/rainfall class (mean annual rainfall 1000–1399 mm and altitude 180–540 m). Individual squares represent 1 km². Redrawn from Austin and Heyligers (1991).

a region (i.e., a gradsect), then different environments can be sampled with less effort. Where such a gradsect is positioned along an access route, then a very cost-effective although biased survey is obtained.

Austin and Heyligers (1989, 1991) designed a survey of the forest vegetation of coastal northern New South Wales (NSW) based on the principles outlined above. The area surveyed was 24,000 km², and the floristic data consisted of presence/absence data of tree species recorded from a 50 × 20 m plot oriented along the contour with estimates of the ranking of the dominant species. The protocol used consisted of seven steps: (1) Identify the major environmental variables influencing the distribution patterns of the vegetation in the study region. For their region these were temperature, rainfall, radiation, and nutrients. (2) Recognize a set of variables best suited because of their availability and practicality to determine the position and direction of the gradsects. For the north coast region these were altitude (an easily measured and highly correlated surrogate for temperature), mean annual rainfall, and lithology (crude surrogate for soil nutrient content). (3) Select gradsects using these variables and the best available technology. Figure 2 shows the extent to which the four selected gradsects sample one particular combination of altitude and rainfall. (4) Stratify the gradsects into geographical segments and stratify the environment within segments to provide replicate sampling of different environmental combinations at different locations (Fig. 2). (5) Stratify at the local scale, i.e., within the 1-km resolution used in positioning the gradsects to take account of other important environmental determinants of vegetation. In this case five topographic positions as a surrogate for solar radiation were sampled within each 1-km gridcell selected. (6) Decide the effort to be spent sampling the rarest environmental combinations as compared with increased replication of the commonest combinations. Determine the location of samples by selecting random coordinates and taking the closest suitable cell with adequate access. Table 1 shows an example of the survey design for a particular segment. (7) Review assumptions regarding importance of environmental variables on which the survey was designed and modify if necessary before completing the survey. Austin and Heyligers (1989) modified the survey design after finding that depth to water table had an overriding influence in the coastal lowlands.

Table 1. Example of survey design for a segment. Size of the environmental cells and their sampling frequency for the middle segment of the southern segment. Reproduced from Austin & Heyligers (1989).

Rock-type	Altitude classes	Rainfall classes				
		2	3	4	5	6
3	1					
	2				4 (x)	
	3				3 (1)	45 (1)
	4					2 (x)
	5					
6	1					
	2					
	3			1 (0)		
	4			1 (0)		
	5					
8	1	2 (1)	15 (1)	26 (1)		
	2		16 (1)	37 (1)	38 (1)	1 (0)
	3		1 (0)	34 (1)	22 (1)	12 (1)
	4					1 (0)
	5					
9	1		11 (1)	30 (1)	2 (x)	
	2		55 (2)	17 (1)	28 (1)	1 (0)
	3		86 (2)	75 (2)	4 (x)	2 (1)
	4		1 (0)	26 (1)		
	5			1 (0)		

The plain numbers refer to the total number of pixels in an environmental cell. The numbers in parentheses refer to the number of samples (a sample may consist of up to 5 plots each from different topographic positions) to be sampled in each cell. An "x" indicates that these cells were not easily accessible and no sample was to be taken.

The approach of Austin and Heyligers (1989) can be summarized as an **SR**^{3} strategy, that is, **S**tratification, **R**epresentation, **R**eplication, and **R**andomization. It represents one realization of the first two requirements of Margules and Austin (1994) for establishing a database. A total of 1025 plots were sampled by Austin and Heyligers (1989) equal to an area of 1.025 km^2, or approximately 1/24,000th of the study area. The restriction of sampling to gradsects means that not all locations have an equal chance of being selected in the sample, and therefore the sample obtained is highly biased. However, the sample is representative, and the design is explicit, consistent, and repeatable, which is not always the case with biodiversity surveys at the present time. While it is possible to design an SR^3 survey without a GIS, it is much easier if one is available. Modifications of it have since been used in northern NSW, Australia (Ferrier, pers. comm.), in Sri Lanka (Green & Gunawardena, 1993), and in South Africa (Wessels et al., in press). The approach makes two ecological assumptions. First, that vegetation varies continuously with environment, forming a continuum rather than discrete communities (Austin & Smith, 1989), and therefore all combinations of environmental conditions should be sampled. Second, it assumes that the major environmental gradients in any given region are known or can reasonably be hypothesized.

The comparative performance of gradsect sampling has been evaluated by Austin and Cawsey (1991) with artificial data and by Wessels et al. (in press) with survey data for birds and dung beetles in South Africa. Both studies support the cost-effectiveness of gradsect sampling against systematic, random, and various purposive methods. Detailed attention has been given to this example of survey design because vegetation survey methods appears to be a neglected topic (Greig-Smith, 1983; Jongman et al., 1987; Kent & Coker, 1992), though see Noy-Meir (1971) for an early Australian example. A variety of alternative designs have been developed in Australia; see Noy-Meir (1971), Austin and Basinski (1979), Margules and Nicholls (1987), Prober and Austin (1990), McKenzie et al. (1991), and Neave et al. (1996).

STATISTICAL MODELING

Availability of survey data consisting of presence/absence for species plus information on environmental variables from a GIS allows the prediction of species distributions using statistical modeling. Statistical modeling is no longer restricted to quantitative data with normal errors (McCullagh & Nelder, 1989), as many botanists assume. There is currently a wide variety of prediction methods extending well beyond the usual statistical methods to neural nets (Aleksander & Morton, 1990; Fitzgerald & Lees, 1992), genetic algorithms (Holland, 1992; Lees, 1994), and decision trees (Breiman et al., 1984; Lees & Ritman, 1991). A recent evaluation of many of these methods (Austin et al., 1994a, 1995; Austin & Meyers, 1996) for analyzing plant ecological data concluded that while most techniques can be found to have advantages under certain circumstances, statistical models perform better with typical vegetation survey data. Franklin (1995) provided review of recent work from a geographer's perspective. The two statistical modeling methods that are currently being actively used are Generalized Linear Models (GLM; McCullagh & Nelder, 1989) and Generalized Additive Models (GAM; Hastie & Tibshirani, 1990). Examples of the use of GLM with vegetation data are Austin et al. (1990, 1994b) and Leathwick and Mitchell (1992). Nicholls (1989, 1991) provided a detailed discussion with examples of how to use GLM with vegetation survey data. The more recent technique of GAM was introduced to plant ecology by Yee and Mitchell (1991). Leathwick (1995) used it to study the climatic relationships of New Zealand tree species. Austin and Meyers (1996) compared GLM and GAM for *Eucalyptus* forest species and discussed their role in the management of forest biodiversity. Recently GAMs have been used for predicting flora and fauna distributions for a large area of northwestern NSW (NSW NPWS, 1994a, b) and to derive predicted vegetation communities for the south coast of NSW in an unpublished CSIRO consultancy report in 1996.

Statistical models such as GLM are used for the prediction of a response variable (or dependent variable) from a set of predictor (or independent) variables. One advantage of GLM over the classical regression method is that it allows error functions other than the normal, and hence the use of density or even binary data is possible. GAM, a non-parametric technique, has the additional advantage that the mathematical function describing the shape of the curve relating the response variable to a predictor variable need not be specified precisely. A smoothing spline is fitted to the data, and only the number of inflections in the curve need be specified, not whether it is a polynomial or exponential function.

The key problem in the model-building process for GLM use with vegetation data has been the shape of the response of a plant species to environmental predictors. Ecological theory is needed to define a reasonable set of potential responses. The evidence regarding the existence of the bell-shaped response usually presented in textbooks is ambiguous (Austin & Smith, 1989), and more flexible curves need to be considered. The β-function is one complex function that has been proposed (Austin et al., 1994b). It requires definition of the limits of a species distribution along an environmental gradient within which a variety of skewed or symmetric curves can be represented by β-functions with different parameter values. Austin et al. (1994b) fitted a β-function for temperature to data for nine species of *Eucalyptus* (Myrtaceae). No species had a symmetric response shape; all were skewed and the patterns of skewness were dependent on position along the environmental gradient of mean annual temperature (Austin et al., 1994b). The results were confirmed for a larger set of *Eucalyptus* species (Austin & Gaywood, 1994). Their conclusions suggest that species distributions along gradients have well-specified skewed shapes and nonrandom patterns. If these patterns are found in other suitable data sets, then it may be possible to propose rules regarding the biodiversity patterns to be found in vegetation. Data sets are needed where the length of the environmental gradient sampled clearly exceeds the width of the environmental niche of the individual species, otherwise the species limits cannot be specified. Failure to appreciate this limitation to the use of β-functions has resulted in controversy (Oksanen, 1997; Austin & Nicholls, 1997; see also Austin & Meyers, 1996).

It is the difficulty of specifying the exact form of the response shape that has led several researchers to use GAM (Yee & Mitchell, 1991; Norton & Mitchell, 1993; NSW NPWS, 1994a, 1994b; Leathwick, 1995). GAM, while conferring the advantage of a non-parametric smoothing function, is not without problems, e.g., the sensitivity of significance tests (Austin et al., 1995; Austin & Meyers, 1996), and is certainly not without assumptions as asserted by Norton and Mitchell (1993). It is a "current best practice method" for biodiversity analysis but is likely to undergo significant modifications in the near future as further evaluation is done.

Eucalyptus fastigata: A Case Study in GAM Prediction of Species Distribution

The steps in modeling the distribution of a species based on available plot data from a region in southeastern NSW, Australia, are presented here. The details of the study area have been published previously (Austin et al., 1990; Austin et al., 1994b). Briefly, it is approximately 40,000 km² in area and runs from just north of latitude 35°S to the Victorian border, and from longitude 148°E to the east coast of Australia. The climate varies considerably across the region: mean annual temperature ranges from 2.5°C on Mt. Kosciusko at 2200 m to 16.9°C on the northern coastal plain, while mean annual rainfall varies from 480 mm to more than 2000 mm, with marked seasonal differences in rainfall patterns. *Eucalyptus fastigata* H. Deane & Maiden is a species characteristic of the coastal scarp forests between 400 m and 800 m (Fig. 3), and results of statistical models of its distribution using GLM have been published (Austin, 1992; Austin et al., 1994b).

MODELING STEPS

1. Collate available plot data for the defined region. Details of the database and the contributors can be found in Austin et al. (1994b). The current database has 9537 plots with records of the presence/absence for 273 tree species, and the geographical distribution of the plots is shown in Figure 3.
2. Select and generate a set of appropriate environmental predictors. Climatic variables have been generated from a digital elevation model (DEM) using a variety of packages now incorporated into BioRap (Hutchinson et al., 1997), and values for the plots obtained using a GIS. Those variables based on lithology were derived from a lithology GIS layer. Eleven environmental variables were selected as potential predictors. These included eight continuous variables: average summer rainfall, average winter rainfall and rainfall seasonality (ratio of summer/winter rainfall), mean annual temperature, temperature of the hottest month and winter cold index, average summer radiation and average winter radiation (kj/m²/day adjusted for slope and aspect); and three factor or categorical variables: topographic position (6), lithology class (6), and nutrient index (5) (figure in parentheses is the number of classes in the factor). Figure 4 shows the plots mapped into a climate space equivalent to the geographical space shown in Figure 3.
3. Restrict the data, where the data extend well beyond the environmental niche of a species. For example, *E. fastigata* does not occur below 7°C or above 16°C mean annual temperature (Fig. 4). Inclusion of those zero values beyond these limits can complicate the analysis and lead to poor prediction of the occurrence of the species near the limits (Austin & Meyers, 1996). The data are therefore restricted to those observations that occur within limits set by having

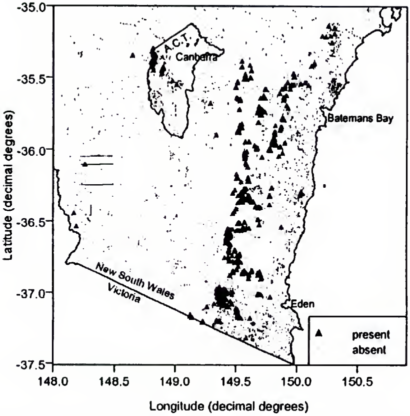

Figure 3. The geographical distribution of *Eucalyptus fastigata* as determined from the database of 9537 plots for southeast NSW. Triangles indicate *E. fastigata* present; dots indicate plots without *E. fastigata.*

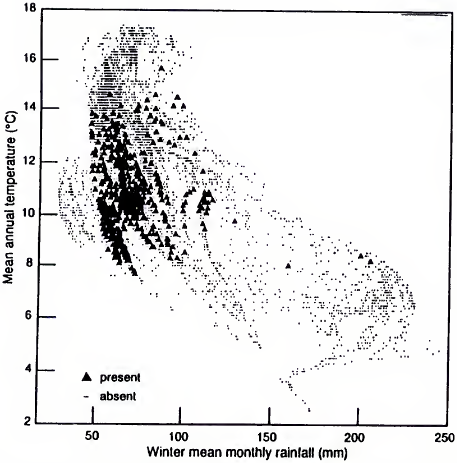

Figure 4. The distribution of *Eucalyptus fastigata* in a climate space defined by mean annual temperature and mean monthly winter rainfall. Note *E. fastigata* is absent below 7° and above 16°C mean annual temperature, with numerous plots above and below those limits.

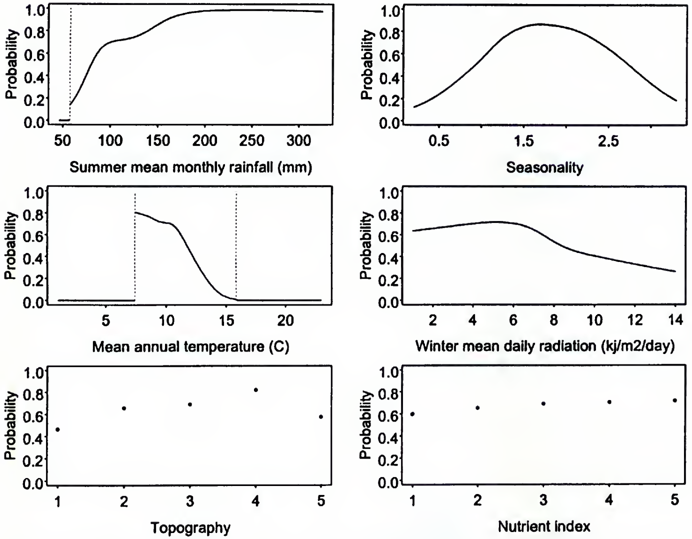

Figure 5. The shape of the GAM response functions for 6 of the 11 predictors for *Eucalyptus fastigata.* Note that the functions have been fitted only within limits for mean annual temperature and summer mean monthly rainfall.

100 zero values above and below the last positive observation, provided there are additional observations beyond the limits; see Austin and Meyers (1996) for further details.

4. Fit a GAM. The model was derived for presence/absence data for *E. fastigata,* as predicted from the 11 environmental variables using S-Plus package (Statistical Sciences, 1993), with four degrees of freedom for the continuous predictors. All eleven predictors were included in the model. The shapes of the responses differ markedly for the different predictors (Fig. 5).
5. Use GIS to predict the distribution of the species for unsampled areas in the region. This was done using the predictive functions derived from GAMs. The predicted distribution of *E. fastigata* clearly shows the major zone of occurrence along the coastal scarp (Fig. 6; cf. Fig. 3).

These models can be used to investigate current ecological problems of relevance to our future management of biodiversity. For example, where would *Eucalyptus fastigata* occur if global warming resulted in a 2°C rise in regional temperature and local increases in rainfall? The predicted geographical distribution after such a change is shown in Figure 7. *Eucalyptus fastigata* would undergo a substantial reduction in occurrence on the coastal scarp under such a scenario. Note that this is a static analysis ignoring problems of dispersal, time to equilibrium, and changed competitive interactions. The role of environmental niche models in relation to climate change models and physiological growth models was reviewed by Austin (1992), with particular reference to *E. fastigata.*

The above procedure is explicit, repeatable, and consistent. There are both statistical and ecological research issues still to be resolved about the best procedure. Austin and Meyers (1996; Austin et al., 1995) have examined the performance of GLM, GAM, and regression trees on both real data and simulated data where truth is known. They conclude that a mixed strategy using both GLM and GAM functions is desirable. They suggest that the best results are as dependent on the availability of suitable ecological and statistical skills as on the particular procedure used. The explicit nature of

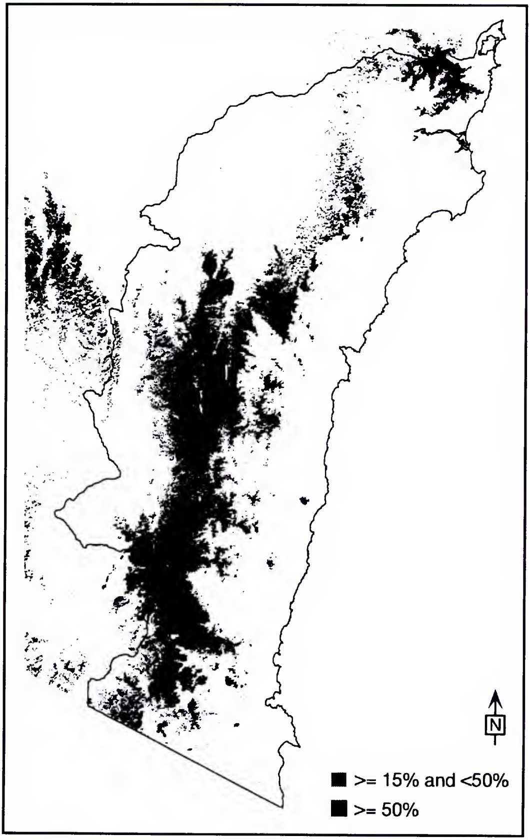

Figure 6. The predicted geographical distribution of *Eucalyptus fastigata* in terms of probability of occurrence using the GAM functions and a GIS for the coastal zone (outlined area) of New South Wales.

the models for individual species provides a firm basis on which to build an improved understanding of species distribution patterns. The *ad hoc* mapping of vegetation and species based on unknown mental models derived from an unknown arbitrary database imperfectly remembered is no longer adequate. However, it must also be remembered that these models are only as good as the data, and the ecological assumptions on which the predictors are selected, and are based on correlation, not causation.

SPECIES RICHNESS

Statistical models like GLM can be used in other contexts more relevant to evolutionary botany and

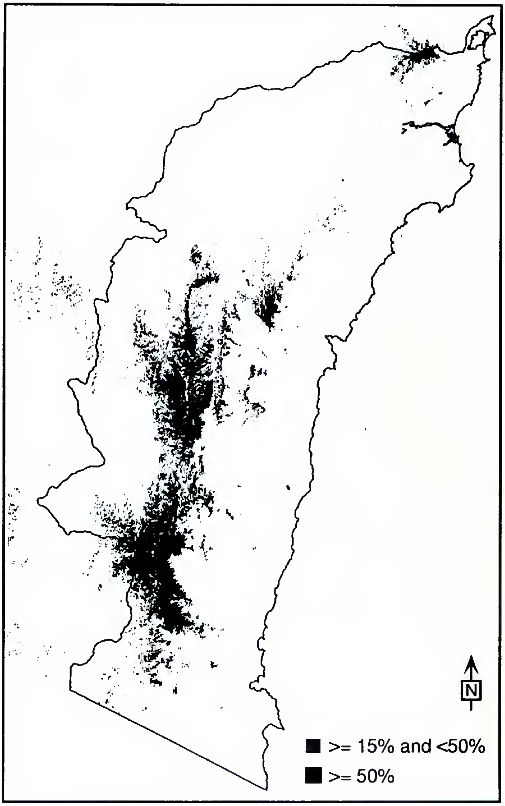

Figure 7. The predicted distribution of *Eucalyptus fastigata* if mean annual temperature increased by two degrees and rainfall by 20% in coastal and tableland regions and 10% in the western region for the same region as Figure 6.

its interface with ecology (Currie, 1991). Austin et al. (1996) investigated patterns of tree species richness in southern NSW using a similar but smaller data set (7208 plots) than that used for *Eucalyptus fastigata* above. Similar predictors to those of Austin et al. (1994b) were used, namely mean annual temperature, mean annual rainfall, mean annual daily radiation, and four categorical variables (topographic position, lithology, nutrient index, and rainfall seasonality). Total tree-species richness for 0.1-ha plots was predicted as the dependent or response variable using GLM, with cubic polynomial functions for the continuous variables and interaction terms for temperature and rainfall. Regional scale patterns of species richness are predictable from the environment, with mean annual temperature the most important predictor. Maximum species richness for trees was found in protected gullies at temperatures >16°C, with rainfall >900 mm, on volcanic soils with intermediate or high nu-

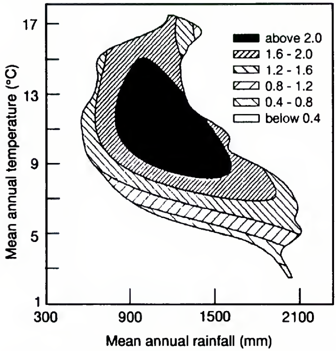

Figure 8. The predicted distribution of species richness for *Eucalyptus* subg. *Monocalyptus* in relation to climatic predictors on exposed ridges with high radiation and low nutrients, with soft sedimentary lithology.

trient levels (Austin et al., 1996). This habitat represents the limited conditions under which the species-rich warm temperate rainforest species can survive in the fire-prone eucalypt-dominated forests of the region. Various components of tree-species richness can be recognized. For example, there are numerous species of *Eucalyptus* in the region, and analyses of the species richness patterns were made for two of the subgenera, *Monocalyptus* and *Symphyomyrtus*. All predictors except seasonality of rainfall were significant for the subgenus *Monocalyptus*, and there was a complex skewed response to temperature and rainfall (Fig. 8). Maximum species richness for *Monocalyptus* was predicted for exposed ridges on sediments or granites under low nutrient conditions in temperate climatic conditions. The other subgenus, *Symphyomyrtus*, showed a distinct complementary pattern and insensitivity to radiation and topographic position, but species richness also varied with seasonality of rainfall. High species richness was associated with fertile soils (Austin et al., 1996). There has been considerable discussion about the differential behavior of species from these two subgenera and their ability to co-occur (Noble, 1989). The descriptive models obtained by GLM analysis are consistent with the conclusions reached in the literature review of Noble (1989).

For the evolutionary botanist these results pose the question of why there are more species of subgenus *Monocalyptus* co-occurring in some environments than others. Figure 8 shows that there is an optimum environment for numbers of species of *Monocalyptus*; any theory of biodiversity and evolution should be able to explain the existence of such a pattern in environmental space. Managers of biodiversity also need to understand the relationship between species richness and environment. If individual species and species richness are both strongly related to environment, then the concept of a regional species pool needs to be re-examined.

APPLICATIONS

An example of the use to which these computer-based tools are being put in Australia is an unpublished consultancy report by the CSIRO Division of Wildlife and Ecology for the NSW National Parks and Wildlife Service. The objective of the consultancy was to map the pre-European forest vegetation (pre-1750) at the scale of 1 : 100,000, such that the percentage of the pre-European communities still surviving could be estimated. This information would then be used to determine which currently forested areas should be conserved, which logged, and which require further detailed examination. The region concerned was the Southern Coastal Zone of NSW. There was only a limited time available to complete the study. However, the existing database and modeling studies described above, plus an appropriate GIS, provided a suitable basis for undertaking the study using modern methods.

The ecological theory on which the study was based assumed that the vegetation formed a continuum such that the precise composition of the vegetation varied continuously, and communities were a function of the frequency of particular environmental combinations in the landscape (Austin & Smith, 1989). Estimating individual species distributions using GAMs from existing data for relevant environments would allow spatial predictions of distributions for cleared areas. Combining the predictions for individual species for each cell of a GIS gives an expected but continuously varying community composition. This composition data can then be classified using numerical methods to give a consistent description of forest communities for the entire region.

The steps involved practical decisions at each stage. These are dependent on the particular features of each project. These are briefly described here to indicate the types of problems that arise.

1. Data. The existing database consisted of 8377 plots. No data were recorded in the database for the northeastern area of the zone. Additional data were collated from that and other regions

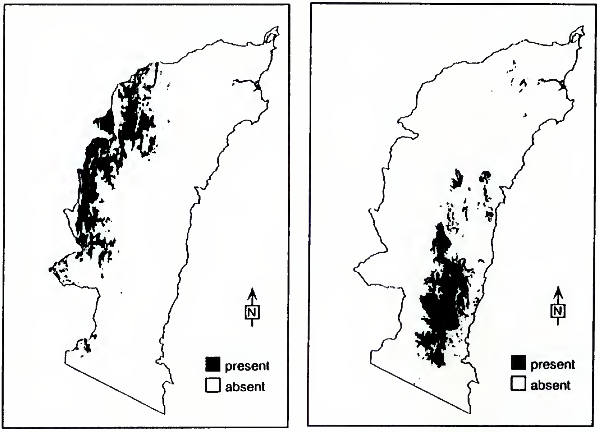

Figure 9. Pre-1750 mapping units. —a (left). Savannah Woodlands (*Eucalyptus melliodora/E. bridgesiana* group). —b (right). Lowland Granite Communities *(E. tereticornis* group).

in the zone. However, this was found to give a very biased sample from the northeastern region; most plots were from warm temperate rainforest in gullies. An additional survey of the northeastern region was necessary.

2. Survey. The design was based on the **SR³** strategy, described previously. The gradsect approach was not used, as access was not a major limiting factor and distances were small. Each of the three 1 : 100,000 maps containing parts of the northeastern area were used as geographical strata within which environmental combinations based on mean annual temperature, mean annual rainfall, and lithology were mapped with a GIS. Sites were selected for second stage sampling by topographic position, as previously described (Austin & Heyligers, 1989).
3. Modeling. The data finally consisted of 9537 plots. After setting an acceptance criterion of at least 50 presence observations in order to include a species in the GAM modeling, 88 tree species were modeled. To reduce the time taken to model the species, the same model was fitted to all species. The eleven predictors used for *E. fastigata* (see above) were used. Use of such a generic model ignoring significance levels will result in overspecification. The degree to which this reduces the accuracy of the models is the subject of current research.
4. GIS. A GIS with a 1-ha resolution was available containing all the necessary predictor variables, so predictions for each of the 88 species was possible for each of the 2.7 million cells in the GIS in the 27,000 km² zone.
5. Classification. To provide a community classification of the zone, the 2.7 million pixels, each characterized by the probability of occurrence of 88 tree species, were used in a numerical classification using ALOC and UPGMA procedures in the package PATN (Belbin, 1995). The available computer facilities and time imposed major limitations on the analysis of the large species by pixel matrix.

The final stage was a manual reorganization of the classification dendrogram to provide mappable units. Vegetation composition is strongly controlled by aspect in the area, and classification units were grouped into catenary sequences to give spatially coherent units for mapping. Two levels of vegetation classification were recognized: classes roughly corresponding to formations or alliances, and units approximating communities. Figure 9 gives examples of the class maps obtained. These maps at the finer scale of units, when combined with a land-cover map showing remaining forest areas, were used to decide that a further 100,000 ha of forest needed to be reserved in order to conserve an adequate representation of the pre-1750 forest communities. Pressey (in press) discusses the relationship between the scientific analysis and the political process for a similar exercise for northern NSW.

When information of this kind is available, then a further stage is reached where methods are needed to determine biodiversity priority areas. Explicit criteria are required, but the particular techniques are dependent on the available data. In general terms there are two classes of methods: (1) those that identify a set of areas in which all selected biodiversity attributes (e.g., species) are represented a specified number of times, e.g., once, twice, or three times; (2) those that maximize the amount of biodiversity represented by a given number of areas (Margules & Redhead, 1995). In the first the level of representation is specified arbitrarily, while in the second it is the number of areas that is fixed. This has become a major area of research and innovation where numerous constraints and trade-offs have been incorporated into the computer algorithms. In Australia, Margules and Nicholls (1987) pioneered an effective computer algorithm for the attribute-representation approach. Subsequently these authors with Pressey explored a number of the options with this approach (Nicholls & Margules, 1993; Pressey & Nicholls, 1989a, b; Pressey, 1994). Faith (1994) has developed a number of approaches to the second class of methods, using measures of dissimilarity and ordination techniques (Faith & Walker, 1994, 1997; Faith & Nicholls, 1997). Two features of the work by these authors are worthy of comment. First, the recognition that species richness per se is not a good criterion for conserving representative biodiversity; it is easily shown with simple examples that selecting the richest site of three may result in conserving fewer species than selecting the two sites each with fewer species. Complementarity of site composition is more important than maximal richness of individual sites. Second, the recognition that sophisticated algorithms are only valuable if they can be used with the limited and arbitrary data sets currently available and enhance those data rather than hide their inadequacies. The BioRap manuals (Margules & Redhead, 1995; Boston, 1997; Hutchinson et al., 1997; Faith & Nicholls, 1997; Noble, 1997) provide case studies of the use of alternative methods with various types of data.

DISCUSSION

Herbarium records, while a primary source of data, have their limitations for analysis of species distributions (Hall, 1994; Austin et al., 1994a; Soberón et al., 1996). Data quality is a key issue, and computer routines for examining records of a species' distribution are an important first step (Chapman & Busby, 1994). New approaches such as BIOCLIM (Nix, 1986; Busby, 1991) and HABITAT (Walker & Cocks, 1991) are examples of heuristic methods designed to overcome the limitations of presence data. One difficulty is that survey data will age taxonomically. Without voucher specimens, it will not be possible to update survey records to take account of taxonomic revisions. However, managing biological diversity will require better data than herbarium presence records provide. Haila and Margules (1996) argued strongly that a necessary component of any practicable strategy for preserving the biological diversity of the earth is systematic field survey. They noted, however, that modern theoretical ecologists regard surveys as tedious, mundane activities; yet such data are essential to testing theory. Any survey has implicit in its design a set of ecological assumptions and a set of statistical assumptions; if these are not recognized and progressively improved upon, then maximum use will not be made of our limited survey resources. This paper has attempted to present some of the Australian experience in this area, but rapid changes are occurring as a result of society's demands that decisions be made on the inadequate database that currently exists. Poor survey design and predictive modeling techniques are adding to the difficulties. A major reason for this is that much of the work is appearing in the "gray" literature, and is inaccessible to many conservation scientists who might otherwise use the improved methods and techniques if they were aware of them. This review suffers from this problem in that much of the Australian work, good and bad, has yet to be published in the international literature and only exists in internal reports or reports published with small numbers of copies. Electronic publication may solve this problem of access to the literature.

Computer technology in various forms, remote-sensing, GIS, and statistical software are being used to create new tools for the study of biodiversity. What is more important is that we are finding new ways of thinking about the problems of studying biodiversity, whether it is how to design surveys or to develop new theories integrating ecology and evolution to better conserve our flora. Each stage in the study of biodiversity is now the subject of intense investigation in terms of basic research, conservation application, and cost-effectiveness (Margules & Austin, 1991). In addition, the results of such biodiversity studies are being incorporated into computer packages designed to facilitate community decision-making in regional land-use plans (Cocks et al., 1995) and are being actively used in conservation planning (Pressey, in press). A period of evaluation is now needed to determine which of these methods or tools are the best.

At the present time our immediate pragmatic concern is to make the best possible use of the biodiversity data we currently have to make sensible conservation decisions. Margules and his colleagues, in putting together the BioRap manuals and software for rapid assessment of biodiversity priority areas for the World Bank (with funding from AustAid), have shown how to make use of available data. The opportunity to constantly reiterate the processes is one of the strongest arguments for having computer-based tools for all aspects of biodiversity study: they can be repeated when necessary.

Literature Cited

Aleksander, I. & H. Morton. 1990. An Introduction to Neural Computing. Chapman & Hall, London.

Austin, M. P. 1992. Modeling the environmental niche of plants: Implications for plant community response to elevated CO_2 levels. Austral. J. Bot. 40: 615–630.

——— & J. J. Basinski. 1979. Bio-physical survey techniques. Pp. 24–42 *in* M. P. Austin & K. D. Cocks (general editors), Land Use on the South Coast of New South Wales, Vol. 1. CSIRO, Melbourne.

——— & E. M. Cawsey. 1991. Sampling strategies costed by simulation. Pp. 167–175 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

——— & M. J. Gaywood. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. J. Veg. Sci. 5: 473–482.

——— & P. C. Heyligers. 1989. Vegetation survey design for conservation: Gradsect sampling of forests in North-eastern New South Wales. Biol. Conservation 50: 13–32.

——— & ———. 1991. Vegetation survey design, a new approach: Gradsect sampling. Pp. 31–36 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

——— & J. A. Meyers. 1995. Modeling of Landscape Patterns and Processes Using Biological Data. Subproject 4: Real Data Dase Study. Consultancy Report for ERIN, CSIRO Division of Wildlife & Ecology, Canberra.

——— & ———. 1996. Current approaches to modeling the environmental niche of eucalypts: Implications for management of forest biodiversity. Forest Ecol. Managem. 85: 95–106.

——— & A. O. Nicholls. 1997. To fix or not to fix the species limits, that is the ecological question: Response to Jari Oksanen. J. Veg. Sci. 8: 743–748.

——— & T. M. Smith. 1989. A new model for the continuum concept. Vegetatio 83: 35–47.

———, A. O. Nicholls & C. R. Margules. 1990. Measurement of the realized qualitative niche: Environmental niches of five *Eucalyptus* species. Ecol. Monogr. 60: 161–177.

———, J. A. Meyers & M. D. Doherty. 1994a. Modeling of Landscape Patterns and Processes using Biological Data. Sub-project 2: Predictive Models for Landscape Patterns and Processes. Consultancy Report for ERIN, CSIRO Division of Wildlife and Ecology, Canberra.

———, J. G. Pausas & A. O. Nicholls. 1996. Patterns of tree species richness in relation to environment in south–eastern New South Wales, Australia. Austral. J. Ecol. 21: 154–164.

———, A. O. Nicholls, M. D. Doherty & J. A. Meyers. 1994b. Determining species response functions to an environmental gradient by means of a ß-function. J. Veg. Sci. 5: 215–228.

———, J. A. Meyers, D. L. Belbin & M. D. Doherty. 1995. Modeling of Landscape Patterns and Processes using Biological Data. Subproject 5: Simulated Data Case Study. Consultancy Report for ERIN, CSIRO Division of Wildlife & Ecology, Canberra.

Belbin, D. L. 1995. PATN Users Guide and Technical References. CSIRO Division of Wildlife and Ecology, Canberra.

Boston, A. N. 1997. BioRap. Rapid Assessment of Biodiversity. Vol. 1. The BioRap Biological Database. Australian BioRap Consortium, CSIRO, Canberra.

Breiman, L., J. H. Friedman, R. A. Olshen & C. J. Stone. 1984. Classification and Regression Trees. Wadsworth International Group, Belmont, California.

Burbidge, A. A. 1991. Cost constraints on surveys for nature conservation. Pp. 3–6 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

Busby, J. R. 1986. A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. Austral. J. Ecol. 11: 1–7.

———. 1988. Potential impacts of climate change on Australia's flora and fauna. Pp. 387–398 *in* G. I. Pearman (editor), Greenhouse: Planning for Climate Change. CSIRO, Melbourne.

———. 1991. BIOCLIM—A bioclimate analysis and prediction system. Pp. 64–68 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

Chapman, A. D. & J. R. Busby. 1994. Linking plant species information to continental biodiversity inventory, climate modeling and environmental monitoring. Pp. 179–195 *in* R. I. Miller (editor), Mapping the Diversity of Nature. Chapman & Hall, London.

Cocks, K. D., J. R. Ive & J. L. Clark. 1995. Forest Issues. Processes and Tools for Inventory, Evaluation, Mediation and Allocation. Report of a Case-study of the Bateman's Bay Area, New South Wales, Australia. CSIRO Division of Wildlife and Ecology Project Report, Canberra.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. Amer. Naturalist 137: 27–49.

Faith, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. Philos. Trans., Ser. B. 345: 45–58.

——— & P. A. Walker. 1994. DIVERSITY: A Software Package for Sampling Phylogenetic and Environmental Diversity. Reference Manual and User's Guide. v.2.1. CSIRO Division of Wildlife and Ecology, Canberra.

——— & ———. 1997. Environmental diversity: On the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. Biodiversity & Conservation 5: 399–415.

——— & A. O. Nicholls. 1997. BioRap Rapid Assessment of Biodiversity, Vol. 3. Tools for Assessing Biodiversity Priority Areas. Australian BioRap Consortium. CSIRO, Canberra.

Fitzgerald, R. W. & B. G. Lees. 1992. The Application of Neural Networks to the Floristic Classification of Remote Sensing and GIS Data in Complex Terrain. Proceedings of the XVII Congress of the International Society for Photogrammetry and Remote Sensing, Washington, D.C.

Franklin, J. 1995. Predictive vegetation mapping: Geographic modeling of biospatial patterns in relation to environmental gradients. Progr. Phys. Geogr. 19: 474–499.

Gillison, A. N. & K. R. W. Brewer. 1985. The use of gradient directed transects or gradsects in natural resource survey. J. Environm. Managem. 20: 103–127.

Green, M. J. B. & E. R. N. Gunawardena. 1993. Conservation Evaluation of Some Natural Forests in Sri Lanka. Forestry Department, Sri Lanka, in assocation with UNDP, FAO, and IUCN.

Greig-Smith, P. 1983. Quantitative Plant Ecology, 3rd. ed. Blackwell Scientific Publications, Oxford.

Hall, J. B. 1994. Mapping for monographs: Baselines for resource development. Pp. 21–35 *in* R. I. Miller (editor), Mapping the Diversity of Nature. Chapman & Hall, London.

Haila, Y. & C. R. Margules. 1996. Survey research in conservation biology. Ecography 19: 323–331.

Hastie, T. & R. Tibshirani. 1990. Generalised Additive Models. Chapman & Hall, London.

Holland, J. H. 1992. Genetic algorithms. Sci. Amer. 267(1): 44–50.

Hutchinson, M. F. 1984. A Summary of Some Surface Fitting and Contouring Programs for Noisy Data. Consulting Report No. ACT 84/6, CSIRO Division of Mathematics and Statistics and Division of Water and Land Resources. CSIRO, Canberra.

——— & R. J. Bischof. 1983. A new method for estimating the spatial distribution of mean seasonal and annual rainfall applied to the Hunter Valley, New South Wales. Austral. Meteorol. Mag. 31: 179–184.

———, L. Belbin, A. O. Nicholls, H. A. Nix, J. P. McMahon & K. D. Ord. 1997. BioRap Rapid Assessment of Biodiversity, Vol. 2. Spatial Modeling Tools. Australian BioRap Consortium, CSIRO, Canberra.

Jongman, R. G. H., C. J. F. ter Braak & O. F. van Tongeren. 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen.

Kent, M. & P. Coker. 1992. Vegetation Description and Analysis: A Practical Approach. Belhaven Press, London.

Leathwick, J. R. 1995. Climatic relationships of some New Zealand forest tree species. J. Veg. Sci. 6: 237–248.

——— & N. D. Mitchell. 1992. Forest pattern, climate and vulcanism in central North Island, New Zealand. J. Veg. Sci. 3: 603–616.

Lees, B. G. 1994. Decision Trees, Artificial Neural Networks and Genetic Algorithms for Classification of Remotely Sensed and Ancillary Data. 7th Australian Remote Sensing Conference Proceedings, Melbourne, Australia, March 1994.

——— & K. Ritman. 1991. Decision-tree and rule-induction approach to integration of remotely sensed and GIS data in mapping vegetation in disturbed or hilly environments. Environm. Managem. 15: 823–831.

Longmore, R. (editor). 1986. Atlas of Elapid Snakes of Australia. Australian Flora and Fauna Series, Number 7. Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra.

McCullagh, P. & J. A. Nelder. 1989. Generalized Linear Models, 2nd ed. Chapman & Hall, London.

McKenzie, N. L., A. C. Robinson & L. Belbin. 1991. Biogeographic survey of the Nullarbor District, Australia. Pp. 54–63 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

Margules, C. R. & M. P. Austin (editors). 1991. Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne, Australia.

——— & ———. 1994. Biological models for monitoring species decline: The construction and use of data bases. Philos.Trans., Ser. B 344: 69–75.

——— & A. O. Nicholls. 1987. Assessing the conservation value of remnant habitat 'islands': Mallee patches on the western Erye Peninsula, South Australia. Pp. 89–102 *in* D. A. Saunders, G. W. Arnold, A. A. Burbidge & A. J. M. Hopkins (editors), Nature Conservation: The Role of Remnant Vegetation. Surrey Beatty and Sons, Sydney.

——— & T. R. Redhead. 1995. BioRap. Guidelines for Using the BioRap Methodology and Tools. CSIRO Dickson, Canberra.

Neave, H. M., T. W. Norton, R. B. Cunningham & H. A. Nix. 1996. Biological inventory for conservation evaluation: I. Design of a field survey for diurnal, terrestrial birds in southern Australia. Forest. Ecol. Managem. 85: 107–122.

Nicholls, A. O. 1989. How to make biological surveys go further with Generalised Linear Models. Biol. Conservation. 50: 51–75.

———. 1991. Examples of the use of generalized linear models in analysis of survey data for conservation evaluation. Pp.191–201 *in* C. R. Margules & M. P. Austin (editors), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.

——— & C. R. Margules. 1993. An upgraded reserve selection algorithm. Biol. Conservation 64: 165–169.

Nix, H. 1986. A biogeographic analysis of Australian elapid snakes. Pp. 4–15 *in* R. Longmore (editor), Atlas of Elapid Snakes of Australia. Australian Flora and Fauna Series, Number 7. Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra.

——— & M. A. Switzer (editors). 1991. Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics. Kowari No. 1. Australian National Parks and Wildlife Service, Canberra.

Noble, I. R. 1989. Ecological traits of *Eucalyptus* L'Herit. subgenera *Monocalyptus* and *Symphyomyrtus*. Austral. J. Bot. 37: 207–224.

Noble, S. J. 1997. BioRap Rapid Assessment of Biodiversity, Vol. 4. Tools for Storing and Mapping Spatial Data. Australian BioRap Consortium, CSIRO, Canberra.

Norton, T. W. & N. D. Mitchell. 1993. Application of generalised additive models to wildlife modeling and population viability analysis. *In:* Proceedings of the 7th Annual Symposium on Geographic Information Systems in Forestry, Environments and Natural Resources. Vancouver, Canada, February 1993. Ministry of Supply and Services, Vancouver, Canada.

Noy-Meir, I. 1971. Multivariate analysis of the semi-arid vegetation in south-eastern Australia: Nodal Ordination by Components Analysis. Quantifying Ecology. Proc. Ecol. Soc. Australia 6: 159–193.

NSW NPWS (New South Wales National Parks and Wildlife Service). 1994a. Fauna of North-east NSW Forests. North-east Forests Biodiversity Study Report No. 3. Internal Report NSW National Parks and Wildlife Service.

———. 1994b. Flora of North-east NSW Forests. North-east Forests Biodiversity Study Report No. 4. Internal Report NSW National Parks and Wildlife Service.

Oksanen, J. 1997. Why the beta-function cannot be used to estimate skewness of species responses. J. Veg. Sci. 8: 147–152.

Pressey, R. L. 1994. Ad hoc reservations: Forward or backward steps in developing representative reserve systems. Conservation Biol. 8: 662–668.

———. Algorithms, politics and timber: An example of the role of science in a public, political negotiation process over new conservation areas in production forests. *In* R. T. Wills, R. J. Hobbs & M. D. Fox (editors), Ecology for Everyone: Communicating Ecology to Scientists, the Public and the Politicians. Surrey Beatty and Sons, Sydney (in press).

——— & A. O. Nicholls. 1989a. Efficiency in conservation evaluation: Scoring versus iterative approaches. Biol. Conservation 50: 199–218.

——— & ———. 1989b. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. Biol. Conservation 50: 263–278.

Prober, S. M. & M. P. Austin. 1990. Habitat peculiarity as a cause of rarity in *Eucalyptus paliformis.* Austral. J. Ecol. 176: 189–205.

Statistical Sciences. 1993. S-PLUS. Version 3.2. Math-Soft, Seattle, Washington.

Scott, J. M. & M. D. Jennings. 1998. Large-area mapping of biodiversity. Ann. Missouri Bot. Gard. 85: 34–47.

Tuomisto, H. 1998. What satellite imagery and large-scale field studies can tell about biodiversity patterns in Amazonian forests. Ann. Missouri Bot. Gard. 85: 48–62.

Soberón, J., J. Llorente & H. Benítez. 1996. An international view of biological surveys. Ann. Missouri Bot. Gard. 83: 562–573.

Wahba, G. & J. Wendelberger. 1980. Some new mathematical methods for variational objective analysis using splines and cross-validation. Monthly Weath. Rev. 108: 1122–1143.

Walker, P. A. & K. D. Cocks. 1991. HABITAT: A procedure for modeling a disjoint environmental envelope for a plant or animal species. Global Ecol. Biogeogr. Lett. 1: 108–118.

Wessels, K. J., J. D. Grimbeek, M. J. Van der Linde & A. S. Van Jaarsveld. An evaluation of the gradsect biological survey method. Biodiversity & Conservation (in press).

Yee, T. W. & N. D. Mitchell. 1991. Generalised additive models in plant ecology. J. Veg. Sci. 2: 587–602.

DECIPHERING LANDSCAPE MOSAICS OF NEOTROPICAL TREES: GIS AND SYSTEMATIC SAMPLING PROVIDE NEW VIEWS OF TROPICAL RAINFOREST DIVERSITY[1]

Deborah A. Clark[2, 3]

ABSTRACT

How are tree species within tropical rainforests distributed at the landscape scale? One research site, the La Selva Biological Station in Costa Rica, offers exceptional tools for addressing this question: a documented flora, soil and topographic maps, a reserve-wide grid, and a Geographical Information System (GIS). My colleagues and I have combined these tools with highly replicated systematic sampling over 600 ha of old growth to investigate patterns of forest composition within this lowland tropical wet forest. This approach has revealed features of within-forest heterogeneity that had remained "invisible" during extensive fieldwork by many researchers at La Selva. Examples are: a doubling in density of the guild of subcanopy and canopy palms between flat terrain and increasingly steep topography; strong shifts in density of many palm and tree species over La Selva's limited gradients of soils and topography; evidence of human harvesting of one palm species from old-growth forest; and evidence suggesting indigenous human activity deep within the reserve (the co-occurrence of a previously unrecognized zone of alluvial soil, buried charcoal, and an avocado tree). These studies have also added 15 tree species to the known flora of this intensively researched forest. Although La Selva's support for such landscape-scale studies is exceptional, even in remote tropical forests it is now possible to systematically sample and geo-reference information on site variation and species distributions using newly available Global Positioning Systems. Findings can then be cross-referenced with current and future site data, using a GIS. Although such efforts, especially the development of a GIS, require considerable investments of time and expertise, the payoff can be a more robust understanding of the distribution of tree diversity and species abundances over tropical rainforest landscapes.

How many tree species exist in tropical rainforests? Where are they found, and how and why do their abundances vary spatially? Such information is critical for understanding the biodiversity, structure, and function of this biome and for conserving representative sites into the future. Unfortunately, these superficially simple and basic questions about the world's tropical rainforests are currently unanswerable.

One reason for this situation is extreme species richness. Those carrying out inventories of lowland forest in the wet Neotropics typically find 80–300+ species of trees $\geq$ 10 cm in diameter co-occurring in a single hectare (Valencia et al., 1994; Gentry, 1988; Foster & Hubbell, 1990; Lieberman et al., 1985a). In addition to the sheer numbers of taxa, identification is made challenging by the sterile condition of most trees at any given time. Many

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[1] I thank the Andrew W. Mellon Foundation, the National Science Foundation (BSR89-18185 and DEB94-07581), and the Organization for Tropical Studies (OTS) for financial support of this research. The La Selva Geographic Information System and reserve-wide grid were made possible by donations to OTS from the National Science Foundation, the Environmental Systems Research Institute, Sun Microsystems, Inc., and the Andrew W. Mellon Foundation. OTS also provided invaluable research and logistical support. David B. Clark was co-investigator for all the research summarized here and provided many key ideas and constructive criticism for this paper. Phil Sollins introduced us to La Selva's soil variability. Leonel Campos, William Brenes, and Rosa Sandoval carried out fieldwork and data management with care and expertise. Marco Vinicio Castro, Jenny Juárez, and Jane Read helped with GIS mapping. On-site expertise in tree identification was provided by Orlando Vargas. The collections of the Herbario Nacional de Costa Rica and the Instituto Nacional de Biodiversidad de Costa Rica (INBio), and taxonomic expertise contributed by the Manual to the Plants of Costa Rica Project (B. E. Hammel, M. H. Grayum) and INBio (N. Zamora) were key for this study, as was Alwyn Gentry's (1993) guide to the woody plants of northwest South America.

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[3] This paper is dedicated to the memory of Alwyn H. Gentry (1945–1993), who made extraordinary contributions to the current understanding of the world's tropical forests.

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tropical wet forest plants only fruit and flower episodically, some even supra-annually (cf. Newstrom et al., 1994; Appanah, 1990), and in addition any plot includes many immature stems. Even when reproductive specimens can be obtained, identifying tropical rainforest trees is often not straightforward. Reference collections, keys, and treatments are incomplete and constantly evolving, as are the accepted names for given taxa. Much of the tree diversity occurs in problematic families, such as Sapotaceae, Myrtaceae, and Lauraceae, with difficult-to-separate species. For these and many other groups, any hope of definitive identification often rests with a few contemporary specialists, who are usually halfway around the world from the study site. Finally, as Gentry (1994) and others have pointed out, whenever a great investment of time and personnel results in distinguishing all tree species in a tropical rainforest plot, some to many of these turn out to be new to science. The bottom line is that, for most tropical forests, the tree flora remains poorly known. Only a handful of tropical forests have been well studied floristically (e.g., sites in Gentry, 1990; Condit, 1995). Even in the exceptional sites with long histories of plant collecting and well developed florulas, new species of trees keep turning up as researchers look carefully at the forest.

Deciphering the nature and determinants of tree distributions within the world's tropical rainforests is clearly going to be difficult, but not simply because of these issues of taxonomic complexity and incomplete collecting and monographing (Gentry, 1992). A second obstacle, a corollary to the richness of these tree communities, is the local rarity of most species. For example, in a Costa Rican lowland wet forest (La Selva), 81% of the tree species inventoried had densities of ≤ 1 individual ≥ 10 cm in diameter per ha (data from Lieberman et al., 1985b). The resulting sample-size limitations mandate innovative approaches for studying the distributions of most tree species within these forests.

A third challenge is presented by another kind of diversity, the abiotic heterogeneity of tropical forest landscapes. Those monotonous expanses of green viewed from overflying planes are actually complex mosaics of forest types. Underlying the species-rich tree communities are landscapes of interdigitated terrain types. The component patches differ among themselves in many ways: topography, soil nutrients, and hydrology (Ashton, 1964; Austin et al., 1972; Baillie et al., 1987; Kahn, 1987; Gentry & Ortiz S., 1993; Ruokolainen & Tuomisto, 1993; Tuomisto et al., 1995; Clark et al., 1995; Duivenvoorden, 1996), disturbance histories (e.g., very large blowdowns; Nelson et al., 1994), flooding regimes (Salo & Rasanen, 1989; Foster, 1990), and histories of human intervention (Gordon, 1982; Gómez-Pompa & Kaus, 1990; Anderson, 1990; Bush & Colinvaux, 1994). In tandem with the incomplete knowledge of floristics goes a poor understanding of this spatial heterogeneity in tropical rainforest landscapes. Part of this has simply been due to the difficult logistics and the size of the problem—for many areas of tropical rainforest, studies of all of the above factors are still lacking. Efforts to discern the spatial mosaics within these forests will greatly benefit from an interdisciplinary approach. Tropical forest ecologists and plant systematists, particularly those trained in North America, often have little training in soils and geomorphology. Soil scientists and geologists are well prepared to evaluate the spatial variation in these site factors, but usually lack any knowledge of plant systematics. Similarly, anthropologists, historical geographers, and archaeologists have special skills for assessing current and historical potential human impacts within a forest. Understanding the patterns and causes of tree distributions within tropical rainforests will require pooling information and insights from these disparate disciplines.

In this paper, I describe in-progress research at a rainforest site that offers an unparalleled set of tools for deciphering the spatial mosaics within the tree community. This work has built on three key elements: an extensive site database generated through decades of research in many disciplines; the use of highly replicated, systematic sampling to study the forest at the landscape scale; and synthetic analysis of complementary types of spatial information, made possible by a Geographical Information System (GIS). I show how this combined approach is revealing levels of spatial heterogeneity within this forest that were previously unrecognized, in spite of the extensive research history of the site. I review the process of developing these research tools and then assess the potential applicability of these and other promising new methods for extending such studies more generally in tropical rainforest.

An Exceptional Site for Assessing Rainforest Landscapes

This research was carried out at the La Selva Biological Station of the Organization for Tropical Studies (OTS), an international consortium of universities and research institutions. La Selva (Fig. 1) is a 1550-ha reserve located in the Caribbean lowlands of northeast Costa Rica, Central America

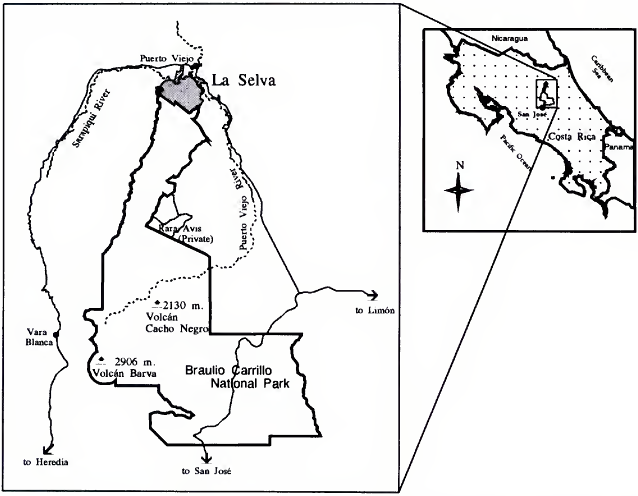

Figure 1. Location of the La Selva Biological Station, Costa Rica, Central America (map produced by J. Juárez, OTS).

(10°26′N, 84°00′W; elevation 37–150 m). It is contiguous with Braulio Carrillo National Park (47,000 ha), which protects a forested transect extending from the lowlands to 2900 m above sea level. La Selva is classified in the Holdridge Life Zone System as Tropical Wet Forest (Hartshorn & Hammel, 1994). Mean temperature is 26°C, and mean annual rainfall is 4 m, with every month averaging at least 100 mm of rain (Sanford et al., 1994). Detailed site information is given in McDade et al. (1994).

Due to a combination of factors, La Selva offers exceptional research support for landscape-scale studies in tropical rainforest (Clark, 1990). Over nearly 30 years, the station has evolved from a rustic farmhouse at the edge of a remote lowland forest into one of the most intensively studied tropical rainforests worldwide. Currently more than 250 researchers a year at La Selva carry out studies in the fields of systematics, evolutionary ecology, long-term population dynamics, conservation biology, soil science, forestry, ecosystem ecology, and atmospheric chemistry. This multifaceted research activity has built up a rich site database and creates opportunities for interdisciplinary studies. The station's research infrastructure includes four additional elements that have been critical for our studies of the spatial heterogeneity of tree distributions: a documented flora, a reserve-wide grid system, a detailed soils map, and a site GIS.

PLANT IDENTIFICATION

For the non-specialist, identifying plants is easier at La Selva than at most tropical rainforest sites. The in-progress La Selva Flora Project (Wilbur, 1986) has produced a checklist of 1852 vascular plant species (R. Wilbur, pers. comm.), including 323 species of trees ≥ 10 cm in diameter (Hartshorn & Hammel, 1994). Several treatments have been published (see Hartshorn & Hammel, 1994), and the full flora is nearing completion. The station has a small reference herbarium, plus a collection of ca. 4000 plasticized high-contrast xeroxes (method developed by R. B. Foster) of La Selva specimens deposited at Duke University Herbarium, headquarters of the La Selva Flora Project. The site's arboretum includes more than 1300 trees of 230 species. The Station Naturalist (O. Vargas) can provide preliminary identifications for sterile material of much of the flora. Equally important, at only 1.5–2 hrs. from La Selva, the principal investigators of the "Manual to the Plants of Costa Rica" project (B. E. Hammel and M. H. Grayum, with collaborator N. Zamora) are based at Costa Rica's National Biodiversity Institute (INBio) and have generously helped with identification of problematic taxa. Costa Rica's national herbarium (CR) also maintains a large curated collection in San José.

THE LA SELVA GRID

In 1991, a remarkable tool for spatially referenced field research was installed at La Selva: a reserve-wide grid system. Covering all 1550 ha of La Selva, the grid consists of permanent marker posts at 50 m × 100 m spacing, surveyed (x, y, and z) to decimeter accuracy. The 6000+ points surveyed during the installation of the grid also provided the means to generate a topographic map of the entire reserve. We know of no other tropical rainforest with anything approaching this level of baseline spatial information (the closest would be the growing world network of 50-ha tropical forest plots [Condit, 1995], which are gridded at a 5 m × 5 m spacing). Scientists working in temperate forests are likely to take for granted the availability of topographic maps such as the U.S. Geological Survey quadrangles for the United States. Virtually all tropical forest sites, however, lack such fundamental site data. For this reason, there has been very little spatial referencing and analysis of landscape composition in tropical field studies.

The grid has revolutionized how researchers design and carry out their field studies at La Selva. Now, any organism or observation can be mapped within the forest simply by measuring to the nearest grid post. Most La Selva researchers currently spatially reference their field data. This makes it possible to relate their findings to data from other projects and to baseline site information. In addition, the grid provides a basis for systematic, highly replicated sampling over large expanses of forest, a prerequisite for assessing how species vary across the landscape.

A RESERVE-WIDE SOILS MAP

In the early years of research at La Selva, the reserve was considered to include four broad soil types (cf. Hartshorn, 1983): "Recent Alluvium," the most fertile sites, currently episodically flooded by the major rivers; "Old Alluvium," higher areas of intermediate fertility interpreted to be river terraces from the Pleistocene; "Swamp," the permanently or seasonally wet zones within La Selva; and "Residual," the largest portion of the reserve, with broken topography and infertile soils produced by in-place weathering of the underlying lava flows. This broad classification scheme, however, was unsupported by landscape-scale soil chemical studies or soil mapping. It is perhaps not surprising that most research at La Selva was carried out without regard to the forest's edaphic variation.

In 1987, however, this situation was radically changed when a professional soil survey was carried out. The resulting 1:10,000 soil map of La Selva (Sancho & Mata, 1987) may be the most intensive soil mapping available for any comparable area of tropical forest worldwide (P. Sollins, pers. comm.). Sancho and Mata used extensive field reconnaissance, analysis of large numbers of grab samples, and more detailed analysis of soil profiles to demarcate 23 soil consociations and 1 complex. La Selva's soils were shown to range from infertile ultisols, a dominant soil type of the world's tropics (Richter & Babbar, 1991), to relatively fertile entisols and inceptisols (Sollins et al., 1994). The advent of the soils map and considerable "consciousness-raising" of the researcher community by resident soil scientists and ecosystem ecologists have stimulated most current field researchers to factor La Selva's edaphic variation into their studies, just as they stimulated us to investigate the landscape-scale mosaics of tree community composition within the forest.

As valuable as it is, the La Selva soils map is not a static, definitive resource. It is, and should be, constantly evolving as new information comes in. Further, as found for soil maps in other parts of the world (cf. Lathrop et al., 1995; Oberthur et al., 1996), it will always incorporate uncertainties at some scales. Sancho and Mata (1987) did their soil survey before there was a grid, a topographic map, or a reliably surveyed map of the reserve; thus, there were bound to be errors in their delimitation of soil units. Second, their map depicted patterns at a scale of 1:10,000. Such a map inherently involves uncertainty at the finer scales of the phenomena studied by most field researchers. Soil map units by definition have inclusions of other soil types, and this is necessarily the case in sites like La Selva with substantial soil variation at the very local scale, a condition likely to be general within tropical soils (Richter & Babbar, 1991). Sancho and Mata's consociations are defined as mapping units within which ≥ 75% of the area is the described soil type. Finally, as in plant taxonomy, there are soil splitters and lumpers. Whether La Selva's important soil variation comprises 24 units or many fewer ones (or many more) is a matter for researcher evaluation, and the answer is likely to vary with the organism or phenomenon being studied. For our studies of tree distributions within La Selva, David

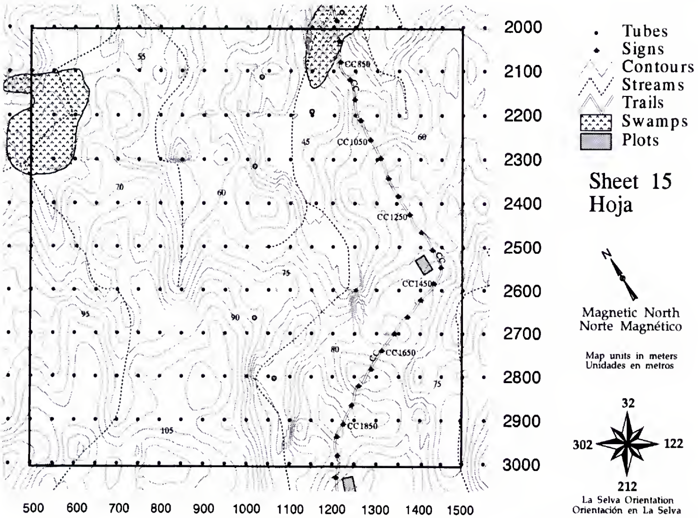

Figure 2. An example of a field map detailing GIS data for one quadrangle within La Selva (map produced by J. Juárez, OTS).

Clark and I modified the soils map both by aggregating consociations and by refining Sancho and Mata's (1987) consociation boundaries after carrying out intensive grid-based soil sampling (see below).

THE LA SELVA GIS

In 1989 OTS initiated a GIS for the station. The on-site GIS lab includes two Sun workstations that run the GIS software ARC/INFO, a large-format plotter, and a digitizer. Early system development involved major donations of equipment and financial support,[1] as well as an extensive investment of time in design and set-up by experienced GIS personnel. The station now maintains a full-time GIS manager for data updating and maintenance and to help individual system users. General-use data layers that have been incorporated into the GIS (e.g., Fig. 2) include site topography, stream and river courses, boundaries and trails, the soils map, current and past land use, locations of study plots, and the 3000+ grid posts. Remote-sensed imagery of the reserve and surrounding region is also being incorporated. Researchers are increasingly using the grid to spatially reference their field data, incorporate them into the La Selva GIS, and then relate them to the other available data layers. For our studies of tree distributions within La Selva, the GIS was a critical resource.

GIS AND SYSTEMATIC SAMPLING REVEAL MOSAICS OF TREE DIVERSITY WITHIN A TROPICAL RAINFOREST

Over the last several years, David Clark and I and several collaborators have taken advantage of the research tools at La Selva to investigate how tree community composition varies within the old-growth forest landscape. We began with a study focusing on the large palms, then used the grid and GIS to assess the distributions of a core set of tree species under long-term study, and most recently have scaled up to study the spatial variation of overall tree floristics. In all three cases we have evaluated patterns at the scale of multiple 100s of hectares. This landscape-scale focus and an integration of site data with tree distributions have revealed previously unrecognized levels of internal heterogeneity within this forest.

Table 1. The seven taxa of canopy and subcanopy palms (Arecaceae, subfamily Arecoideae) in old-growth forest at La Selva. Tribes and species names from Henderson et al. (1995). Vouchers are specimens in the Costa Rican National Herbarium (CR). Summary relationships are from analyses in Clark et al. (1995).

Tribe	Species [Voucher No.]	Association between:[1]			
		Density (stems/ha) and soil type	Occurrence (presence/absence) and:		
			Soil/ topography		Harvesting
Iriarteeae					
	Iriartea deltoidea Ruiz & Pav. [*Chacón et al. 1968*]	+	−	[local absence]	+
	Socratea exorrhiza (Mart.) H. Wendl. [*Stevens 24559*]	+	−	[everywhere]	−
Areceae					
	Prestoea decurrens (H. Wendl. ex Burret) H. E. Moore [*Grayum & Jermy 6783*]	+	+	[alluvial/flat]	−
	Euterpe precatoria Mart. var. *longevaginata*[2] (Mart.) Andrew Hend. [*Grayum 7813*]	+	+	[residual/slopes]	−
Geonomeae					
	Welfia regia H. Wendl. ex André[3] [*Wiemann & Rich 137*]	+	−	[everywhere]	−
Cocoeae					
	Astrocaryum confertum H. Wendl. ex Burret [*de Nevers & Hammel 7820*]	rare in upland			
	Astrocaryum alatum H. F. Loomis [*Stevens 24625*]	rare in upland			

[1] + a significant association; − no such association (from Clark et al., 1995).

[2] "*Euterpe macrospadix* Oersted" in Clark et al. (1995).

[3] "*Welfia georgii* Wendl. ex Burret" in Clark et al. (1995).

NON-RANDOM DISTRIBUTIONS OF THE LARGE PALMS

Palms are an important component of the La Selva old-growth forest. The seven species of subcanopy and canopy palms (Table 1, henceforth referred to by genus) comprise 25% of all woody stems ≥ 10 cm in diameter (Lieberman et al., 1985a). This abundant species group has significant impacts on forest structure—the large palms' dense canopies can strongly affect the distribution of light environments in the understory, and the senescing and falling of their massive leaves contributes to the high levels of physical damage to smaller plants below them (cf. Vandermeer, 1977; Clark & Clark, 1989). The fruits of several of these palm species are also important in the diets of diverse mammal species (Levey et al., 1994; Timm, 1994). For all these reasons, it is of interest to know how this guild of plants is distributed within La Selva. Does the group as a whole vary in density among different sectors of the landscape? Do any of the component species show non-uniform distributions within the old-growth forest?

Approaches to such questions about tropical forest composition have usually involved evaluating plant species abundances within one to a few plots or transects selected by the researcher as representative of the forest as a whole (a notable exception is the pioneering work of Ashton [1964, 1969] and Austin et al. [1972]). Such a design has been to a large degree mandated by both the lack of base maps of site variation and the difficult logistics within such forests. Although enumerating all species within a plot is indeed the only way to study numerous aspects of plant population structure and dynamics (cf. Dallmeier, 1992), this approach is not suited for generalization to the larger landscape, and the findings can be uninterpretable in terms of specific site variables, such as topography or soil type. One illustration of these issues is given by data from three upland forest inventory plots within La Selva (Hartshorn, 1983), which provided striking evidence of non-uniform distributions of the large palms. In all three plots (2, 4, and 4 ha), the second most abundant tree species ≥ 10 cm in diameter was a palm, but the species was different in each plot (*Iriartea* in Plot IIb [Alluvial Soil]; *Welfia* in Plot I [Alluvial Soil plus some Swamp; and *Iriartea* was absent from this plot; Hartshorn & Hammel, 1994]; *Socratea* in Plot III [Residual Soil]; species names of the single representative of each genus at La Selva are given in Table 1). Although these plot data demonstrate that the distribution of large palms varies markedly within La Selva, they are insufficient for assessing how these distributions relate to the forest's soil and topographic variation.

The advent of GIS and the grid at La Selva, however, made possible a radically different approach to assessing plant distributions within the old growth. The grid, with its 50 m × 100 m spacing, was a set of precisely located points spread over the entire forest. Using them as sample points, we could systematically sample a large landscape. By assessing palm distributions this way in many watersheds and terrain types, and in different forest stages (gap to mature forest) and topographies within each soil type, we could achieve a level of environmental replication difficult to achieve with other methods.

To investigate the landscape distributions of large palms at La Selva, we selected a 568-ha sector of the upland (non-swamp) old-growth forest. We then assessed the presence/absence and local abundance of the seven species at each of 516 grid intersections within this study area. We used our field notes regarding streams, swamps, and topography to refine the Sancho and Mata (1987) soils map, and we used the GIS to aggregate soil consociations into four contrasting units: Alluvium (most fertile, with gentle topography); Streams (the valley soils of the principal streams); Residual soils (broken terrain, soils weathered from lava); and Arboleda (a problematic area of steep topography, thought to be of intermediate fertility [Sollins et al., 1994]). In the field we also classified each sample point in terms of topographic position. The methods, results, and statistical analyses of this study are detailed by Clark et al. (1995). Here I highlight several findings that demonstrated a spatial substructuring of this forest previously invisible to us and dozens of others who have worked at the site for a decade or more.

We found that the total abundance of the canopy and subcanopy palms varies greatly across the landscape. Larger individuals of this guild (stems ≥ 10 m tall, all species combined) continuously decrease in density from slope crests, to slopes of decreasing steepness, to slope bases and flat terrain. Over this topographic gradient the density of large canopy and subcanopy palms declines by a factor of two. Such spatial heterogeneity in the abundance of these palms within La Selva must have widespread impacts on forest structure and on processes as diverse as mammal activity and understory light environments.

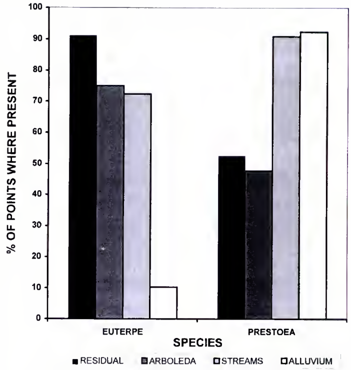

Figure 3. Contrasting soil affinities of *Euterpe precatoria* and *Prestoea decurrens* (from Clark et al., 1985). Data for each species are the percent of the sample points in each soil type at which any individual > 1 m tall was observed. Sample points per soil type (soil descriptions given in text): Residual, 329; Arboleda, 44; Streams, 65; Alluvium, 78. For both species the association between presence/absence patterns and soil type was highly significant (χ^2, df = 3, $P < 0.0001$).

The species-level distributions of these palms revealed further evidence of substructuring within the forest. All five of the species that were not rare in upland forest showed highly significant variation in local density or overall presence/absence patterns with respect to the spatial variation in topography and soils within La Selva (Table 1). One closely related species pair, La Selva's single species of *Prestoea* and single species of *Euterpe* (Table 1), showed strong but contrasting edaphic associations, both with soil type (Fig. 3) and with topographic position. *Euterpe* was strongly biased toward steep topography and the less fertile soils. *Prestoea,* in contrast, while nearly omnipresent on gentle topography, was absent at half the sample points on the soils with steep slopes. The most abundant large palm, the single *Welfia* species (Table 1), strongly varied in density across the four soil units although it was present everywhere (at 100% of the sample points).

The use of GIS to investigate the spatial distributions of these large palms revealed yet another striking feature of the La Selva old-growth forest that was previously unsuspected. From one sector of what had often been considered "virgin forest," the otherwise omnipresent canopy palm *Iriartea* (*deltoidea*; Table 1) is nearly completely absent. The most probable explanation for this anomalous distribution is local removal by historic human harvesting. Our analyses demonstrated that the patterns of presence/absence for both *Iriartea* and the closely related *Socratea* (*exorrhiza*; Table 1) were insensitive to both soil type and topographic position. *Socratea* was omnipresent within the old-growth forest. Similarly, *Iriartea* was omnipresent on all soil types, except in one zone of Alluvium close to former human habitation and easy river access. By interviewing local residents we found that *Iriartea* was the most sought-after native palm taxon for its large and tasty meristem ("heart-of-palm") and its robust, durable stems, which were used in construction. That *Socratea* remained in this sector of the forest is probably due both to the bitter taste of its meristem ("palmito amargo") and to its more slender stems, less useful for building. This evidence of prior human impact on tree floristics within this intensively studied sector of the La Selva old growth has changed how the forest is viewed. In addition to being key background information for many of the studies carried out in this particular sector, this finding has stimulated La Selva researchers to be on the alert for evidence of other human impacts within the old growth.

GIS REVEALS EDAPHIC ASSOCIATIONS OF CANOPY AND EMERGENT TREES UNDER LONG-TERM STUDY

When the grid and GIS were installed at La Selva, they offered an opportunity to investigate the spatial distributions of the tree species David Clark and I had under long-term demographic study in the old-growth forest. Since 1982 we have accumulated samples of individuals of all post-seedling life history stages (from 50-cm-tall saplings to adults) of nine ecologically contrasting species of canopy and emergent trees at La Selva (voucher numbers are for specimens deposited in the Herbario Nacional de Costa Rica): *Dipteryx panamensis* (Pittier) Record & Mell (Papilionaceae) [*R. Robles 1199*]; *Minquartia guianensis* Aubl. (Olacaceae) [*G. Herrera 2250*]; *Lecythis ampla* Miers (Lecythidaceae) [*R. Robles 2208*]; *Hymenolobium mesoamericanum* H. C. Lima (Papilionaceae) [*R. Aguilar 19*]; *Pithecellobium elegans* Ducke (Mimosaceae) [*B. Hammel 17319*]; *Hyeronima alchorneoides* Allemão (Euphorbiaceae) [*Chacón 751*]; *Simarouba amara* Aubl. (Simaroubaceae) [*R. Robles 1670*]; *Cecropia insignis* Liebm. (Cecropiaceae) [*W. Burger 11135*]; and *Cecropia obtusifolia* Bertol. (Cecropiaceae) [*R. Robles 1446*]). Our annual measurements of survival, growth, and microsite of > 2800 individuals have enabled us to evaluate these species' ontogenetic growth patterns, relation to light environments and forest dynamics, and sensitivity to yearly climatic variation (cf. Clark & Clark, 1992, 1994; Clark et al., 1993). Before the advent of the GIS and the grid, however, our understanding of these trees' relation to the edaphic variation within La Selva was limited to an intuitive sense that *Dipteryx* was associated with the Alluvium and *Pithecellobium* with the Residual soils. We have recently used the new spatial tools at La Selva to refine our understanding of edaphic variation within the forest and then to assess the distributions of our nine focal tree species with respect to this variation (D. B. Clark et al., 1998).

To refine the soils map, we used the grid intersections as a framework for systematically sampling the soils within a 573-ha section of the reserve (one soil sample from 50-cm depth at each of 1171 grid points). We arrayed the resulting soil samples geographically and then classified each into a soil type, following the concepts originally developed by Sancho and Mata (1987) and Sollins et al. (1994). For classification, we combined soil color with our field-collected data on each point's topographic position and slope angle and with GIS data for point elevation and surrounding terrain (from a kriged digital elevation model of La Selva based on the 6000+ surveyed points). We delimited polygons following elevational contour lines around the spatial groupings of soil units at grid points, and then digitized the resulting soils map into the La Selva GIS. Although our analysis largely confirmed the previous soil mapping of the reserve, it did result in some significant changes in unit boundaries and a more intuitive geographic relation between site geomorphology (Alvarado I., 1990) and the soils. It also significantly altered our understanding of soil variation in some areas that had been study sites for diverse research studies within La Selva (see below). For our study of the edaphic associations of the nine tree species, we aggregated the upland soil types into three broad units: Old Alluvium (excludes the currently floodable Recent Alluvium), Residual, and Stream Valley.

We had previously mapped our tree population samples into the GIS by referring each tree in the field to the grid (by measuring distance and compass bearing to the nearest grid post or to the nearest tree that had been so mapped), and then incor-

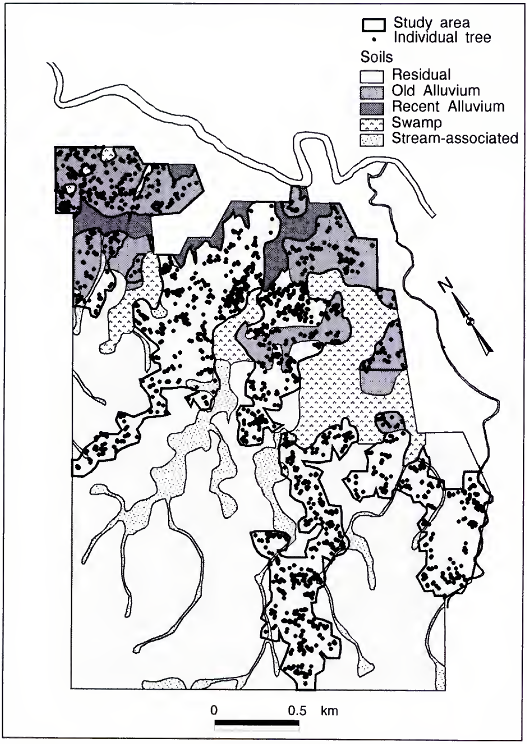

Figure 4. A GIS-generated map of the 216 ha area (demarcated by thick black border) encompassing the long-term study populations of our nine focal species of canopy and emergent trees at the La Selva Biological Station, Costa Rica. Individual trees are indicated by black dots. The underlying soil map (described in the text) is a refined version of the original (Sancho & Mata, 1987) La Selva map.

porating these tree location data into the GIS. Although this process was very time consuming (more than 1 person-year of work), it created a permanent spatially explicit data set for the long-term population ecology studies, and it was a prerequisite for a tree × soil analysis. For this analysis, we used the GIS to delimit the old-growth areas of La Selva containing our tree samples, overlaid this map on the new soils coverage (Fig. 4), and then used the included grid intersections to generate the expected (background) distributions of both soil and topography within our 216-ha study area.

This GIS analysis revealed that, in the upland old-growth forest, all nine of our study species had nonrandom distributions associated with one or more features of La Selva's edaphic variation. Most of the highly significant associations ($P < 0.005$) were with soil type (6 species). Within their preferred soil, three of the nine species also showed highly significant biases with respect to topographic position. As we had suspected, the distribution of *Pithecellobium elegans* was strongly skewed toward the Residual soils, and that of *Dipteryx panamensis* was biased toward the Alluvium. Both species, however, showed additional biases that we had not perceived during many years of fieldwork: *P. elegans* was preferentially on flat ridgetops and biased away from slope bases within the Residual soils, while the distribution of *D. panamensis* within the Alluvium was biased toward gentle slopes and away from flat terrain. Another discovery was that La Selva's two *Cecropia* species had strong, contrasting edaphic associations (*C. insignis:* Stream Valley soils, lower slope angles; *C. obtusifolia,* higher slope positions, but no bias regarding slope angle or soil type).

SCALING UP: THE EDAPHIC ASSOCIATIONS OF THE LA SELVA TREE FLORA

We have recently scaled up these approaches to analyze distribution patterns within the total La Selva tree community and their relation to soil type and topography. We once again have used the grid as a basis for systematic, highly replicated sampling of old-growth forest, this time including the swamps. At each grid intersection ($N = 1171$) in 573 ha of La Selva old growth, we established a 0.01-ha circular plot within which we measured and identified all tree stems of ≥ 10 cm diameter (5127 stems total).

This landscape-scale approach has provided new insights about how tree diversity is distributed within La Selva. The sample, which includes 253 of the 323 tree species known from La Selva, also resulted in the addition of 15 new species to the site's tree list. One of these, *Caryodendron angustifolium* Standl. (Euphorbiaceae), represents a genus new to Costa Rica. These finds are a result of the process of "ecological collecting," the challenging work of identifying all trees in a plot, including the non-reproductives. This approach to tropical forests is very different from that taken by taxonomic specialists, who naturally focus on the plants that are flowering or fruiting when they visit a site (Gentry, 1994). As Gentry pointed out, even some of the more common species found in an all-stem inventory in a given tropical forest can turn out to be new to the site or to science. Additionally, our sampling over the whole landscape turned up numerous examples from the "tail of the species distribution" (B. E. Hammel, pers. comm.)—those many tree taxa that are locally very rare within any tropical rainforest. Such discoveries improve understanding both of local site biodiversity and of species distributions at larger spatial scales within tropical forest regions.

In addition to these new finds, use of the GIS for spatial examination of the data set (D. B. Clark et al., unpublished data) has revealed extensive substructuring of the tree community across this rainforest landscape (Fig. 5). As with the guild of large palms, some other tree species are strongly associated with certain soils (e.g., Fig. 5A, *Castilla elastica* Sessé in the Old Alluvium and Recent Alluvium). Additional interesting distribution patterns are evident for many tree species. For example, *Lonchocarpus oliganthus* F. J. Herm. (Fig. 5B) is associated with the Recent Alluvium, the Swamp soils, and with the Stream Valley soils that meander through the Residual Soil region of La Selva. These soil units range from nutrient-rich (Recent Alluvium) to strongly infertile (Stream Valley soils); this species is able to grow over a wide range of soil fertility but only in sites that are wet or floodable. Another distribution pattern found for numerous species is that shown by one of the canopy-level *Matisia* species (Bombacaceae) at La Selva, *M. ochrocalyx* K. Schum.; although confined to the Residual soils in La Selva, this species occupies only a restricted area within this soil type (Fig. 5A). With this type of distribution, factors other than the variation among major soil units must be playing a role. One possibility is individualistic responses of tree species to combinations of particular soil characteristics, such as certain cations, P, N, pH, soil organic matter, or texture, coupled with substantial variation in these characteristics within soil units. Such complex idiosyncratic edaphic associations were found to characterize many tree species in tropical rainforest areas of Sarawak, Borneo (Baillie et al., 1987). To investigate this possibility, our next step will be to go beyond the "typic" characterization of soil variation so far used at La Selva and to measure and map individual soil properties across the landscape. We will analyze a large suite of soil characters from each of the sample points used in this study and then combine GIS and multivariate techniques to examine them for associations with the non-random distributions of trees within La Selva. This factor-level approach will greatly aid interpretation of the currently enigmatic distributions of many of the species.

In addition to revealing the mosaic nature of the tree community in this tropical rainforest, this GIS-based analysis has also produced new evidence suggestive of past human activity deep within the old-growth forest. Within one of our 0.01-ha tree inventory plots in well developed forest in La Selva's center, 80 m from the nearest trail and more than 1 km from any historic human habitation (Fig. 5a), we found a tree of the species of cultivated avocado, *Persea americana* Mill. (Lauraceae). This species has been found in very old archaeological deposits (7000 B.C.) in the Americas (Simpson & Connor Ogorzaly, 1986). The site where we encountered this tree is very close to where charcoal was found within the soil profile by researchers (R.

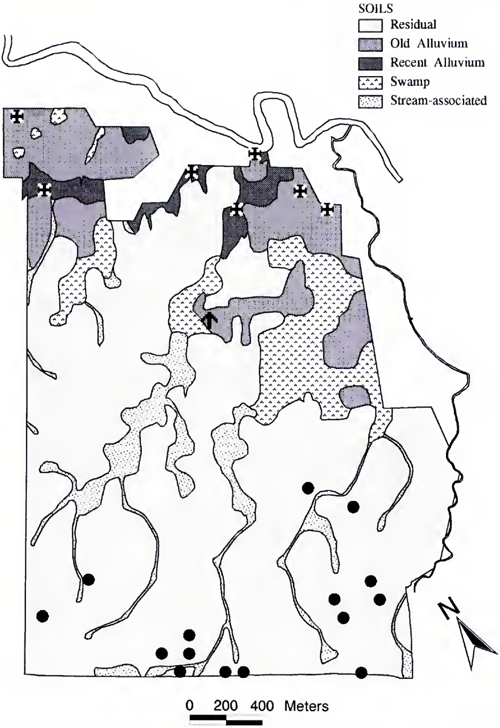

Figure 5. Examples of spatial substructuring of the tree community in upland old-growth forest at La Selva. Symbols indicate the occurrences of a given species in the 0.01-ha plots centered on all grid intersections (N = 1171) within this 573-ha sector of forest. The soil map is as in Figure 4. —A (this page). Three species' distributions in the sample plots: crosses, *Castilla elastica* (Moraceae); arrow, *Persea americana* (Lauraceae); dots, *Matisia ochrocalyx* (Bombaceae). —B (next page). Occurrences of *Lonchocarpus oliganthus* (Papilionaceae) in the sample plots (crosses).

Sanford, Jr. & S. Horn) investigating the reserve's history (Horn & Sanford, 1992, and unpublished). By the original soils map (Sancho & Mata, 1987), the site plots out within the infertile Residual soils that cover most of La Selva, a puzzling location for the kinds of indigenous human activity suggested by the tree and charcoal. However, when we overlaid this collection point on our refined soils map (based on grid-based soil collections, see above), we found this site to be within a previously unrecognized zone of (more fertile) Old Alluvium within the Residual soil region. This is a classic case of how such GIS data syntheses can enhance the results of individual studies. Taken by themselves, these lines of evidence are much less interesting than when combined through spatial referencing.

SCALES OF SPATIAL VARIATION WITHIN TROPICAL RAINFORESTS, AND THE TOOLS TO INVESTIGATE THEM

DIFFERENT LEVELS OF WITHIN-FOREST EDAPHIC MOSAICS

It is becoming increasingly clear that marked internal heterogeneity is an important characteristic of

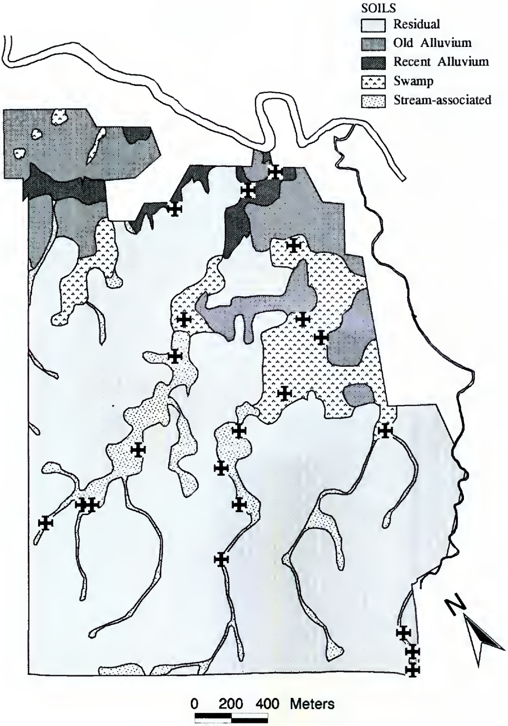

Figure 5. Continued.

the tropical rainforest biome (Ashton, 1964; Austin et al., 1972; Baillie et al., 1987; Kahn, 1987; Gentry & Ortiz S., 1993; Ruokolainen & Tuomisto, 1993; Tuomisto et al., 1995; Clark et al., 1995; Duivenvoorden, 1996; Clark, present study). Recognizing and interpreting the spatial mosaics within these forests will be fundamental to both understanding and conserving their great biodiversity. The markedly different scales of important spatial variation, however, will require distinct research approaches.

At one scale are structurally distinct forest types that can be distinguished by field reconnaissance, visual inspection from small planes, or interpretation of remote-sensed data. Examples of visually distinct patches that harbor particular floras are swamp forests dominated by a few species of large palms and the stands of low canopy and small-diameter trees found on very infertile white sands across Amazonia. Assessing how such strongly contrasting patches are distributed within tropical rainforest landscapes is a vital need for understanding the spatial distribution of biodiversity within the biome (cf. Tuomisto et al., 1995). Evaluation of the community-level biotic differences among these patch types is also needed. Given the dramatic vegetation shifts between these readily distinguishable forest types (cf. Tuomisto et al., 1995; Duivenvoorden, 1996; Terborgh et al., 1996), inventorying a few plots or transects within each should adequately indicate major distinctions among them.

A second level of tropical forest mosaics is of those occurring *within* one of these patch types and thus across much more limited gradients of environmental variation. This is the scale that we have been principally investigating within La Selva: the internal heterogeneity of an upland tropical forest landscape, in the absence of extreme intra-site contrasts such as those occurring on adjacent terraces within floodplains or where white sand and clay-dominated soils are interdigitated (cf. Duivenvoorden, 1996). As we have shown, even at this "within-patch" scale, the tree community composition of tropical moist forest can show marked spatial variation. We found much of the internal heterogeneity in the La Selva tree flora to be associated with local variation in soil types and topography, even though the total relief and the total range of soil characters were quite constrained subsets of those found more regionally in the lowland wet tropics. Most of these tree-site associations, even some of the most striking ones, were previously unrecognized, despite the long history of research at this site.

For our investigation at La Selva of this more local scale of internal variation within tropical rainforest, the combined use of landscape-scale systematic sampling and GIS proved to be critical. By spreading out the sampling over 100s of hectares of forest, we obtained highly replicated, spatially separated observations of tree floristics within each major soil unit and in each type of topographic situation (positions along the ridgetop-to-swale catena and different slope angles). Had we assessed these factors within a single plot or transect, even a very large one, we could not have generalized our findings to the larger landscape due to the possibility of sample bias from particular local edaphic or historic conditions. The 50 to 100 m intervals between neighboring sampling points also reduced the likelihood of spatial autocorrelation among samples (cf. Clark et al., 1996). Finally, the GIS enabled us to relate several classes of complementary site information to the patterns we discovered in the tree distributions. A particular additional strength brought by GIS to such work is that it provides an ongoing link to the site database, even as it is being expanded and refined through time. This combined research approach thus seems well suited to both assessing and interpreting the landscape-scale spatial variation in floristics within a given type of tropical rainforest. A further analytical step that could significantly enhance the data interpretation would be to use generalized linear modeling (GLM) to evaluate the simultaneous (combined) effect of multiple site factors (e.g., soil type, topography, and disturbance history) on the tree species' distribution patterns (cf. Austin et al., 1996).

RECOGNIZING HUMAN "FOOTPRINTS"

In addition to edaphic variation, past human interventions, from silviculture to swidden agriculture to selective cutting, are an important potential source of within-landscape heterogeneity in tropical rainforest. This is true even in stands considered old growth, as we found at La Selva. Indeed, an accumulating body of research findings indicates that most tropical forests are likely to have been affected this way (e.g., Gordon, 1982; Anderson, 1990; Gómez-Pompa & Kaus, 1990; Brown et al., 1991; Bush & Colinvaux, 1994; Garcia-Montiel & Scatena, 1994). Given the likely pervasiveness of such impacts, researchers studying the distribution of biodiversity within these forests should explicitly seek indications of human activities in their study sites (Hamburg & Sanford, 1986). As we found at La Selva, evidence of such anthropogenic impacts can emerge when landscape-scale floristic patterns are assessed for non-random distributions beyond those attributable to the site's edaphic variation. For this kind of question, the combined use of GIS, edaphic surveys, and systematic replicated vegetation sampling seems a useful approach.

CAN IT BE DONE ELSEWHERE?

Is this La Selva experience translatable to other, less developed sites in the tropics? One newly available research tool makes the answer to this increasingly yes. The Global Positioning System (GPS) is a technology for field determination of locations by interpretation of satellite signals. A field researcher in any tropical forest can now use a portable GPS receiver with extendable antenna, run in parallel with a GPS station at their base site, to measure field locations with good to excellent accuracy (recent trials under canopy in a suite of U.S. forests produced accuracies of ca. 2–8 m; Deckert & Bolstad, 1996). This technology will also rapidly become both less expensive and more effective (the U.S. administration recently resolved to remove the current system of signal degradation, probably within 10 years). Although using GPS requires significant training and equipment, the benefits are immense for field researchers.

Now, any tree or vegetation type encountered in the most remote tropical forests can be spatially referenced so as to be relocatable by anyone. Thus "ecological collecting," the inventorying and identification of even non-reproductive plants, becomes feasible anywhere, because sterile plants can be precisely mapped for repeated visits until found fruiting or flowering. Well documented location data made generally available to the research community will maximize the current and future value of the very limited systematic and ecological work within these forests. We should begin to think of the entire tropical forest biome as a "permanent study plot."

This new tool also makes feasible in any tropical rainforest the type of landscape-scale/GIS research we used at La Selva. With GPS any field researcher can carry out highly replicated, systematic sampling over 100s of hectares, without depending on a very expensive physical grid such as La Selva's. When site variables as well as vegetation are assessed at all sample points, the ground is laid for a synthetic GIS analysis of the relation between floristic patterns and site conditions at the landscape scale. None of these elements, however, are easy to attain. Those starting from ground zero in a tropical forest site will find that considerable effort is involved in achieving each component of such an approach: the use of GPS in the field; the determination of site factors, particularly soil characteristics; plant identification; and the analysis of the resulting data with GIS. Our strongest recommendation based on our experiences at La Selva is to build multidisciplinary research teams incorporating expertise in all these fields, rather than having individual researchers trying to develop all the necessary skills. Such a team brings in the needed levels of prior training and experience in these new areas, and thus ensures the quality of data produced.

CONCLUSIONS

The biodiversity of the world's tropical rainforests is still largely unstudied and unprotected. These are compelling reasons for increasing current research efforts to understand the geographic and local variation of the biota within these ecosystems. Recent studies in different parts of the tropics have demonstrated a high level of within-forest mosaicism. This is an important new dimension of complexity that must be understood if current conservation efforts in this biome are to be effective. As shown by our research experiences in one Central American forest site, the combined use of GIS and highly replicated systematic sampling of site and biotic variables over meso-scale landscapes (100–10,000 ha) is one promising strategy for deepening current understanding of the great spatial variation within the world's tropical rainforests.

Literature Cited

Alvarado I., G. E. 1990. Características geológicas de la Estación Biológica La Selva, Costa Rica. Tecnol. en Marcha 10: 11–22.

Anderson, A. B. 1990. Extraction and forest management by rural inhabitants in the Amazon estuary. Pp. 65–85 *in* A. B. Anderson (editor), Alternatives to Deforestation. Columbia Univ. Press, New York.

Appanah, S. 1990. Plant-pollinator interactions in Malaysian rain forests. Pp. 85–101 *in* K. S. Bawa & M. Hadley (editors), Reproductive Ecology of Tropical Forest Plants. MAB/UNESCO/Parthenon Press, Paris.

Ashton, P. S. 1964. Ecological Studies in the Mixed Dipterocarp Forests of Brunei State. Oxford Forest. Mem. 25, Oxford Univ. Press, Oxford.

———. 1969. Speciation among tropical forest trees: Some deductions in the light of recent evidence. Biol. J. Linn. Soc. 1: 155–196.

Austin, M. P., P. S. Ashton & P. Greig-Smith. 1972. The application of quantitative methods to vegetation survey III. A re-examination of rain forest data from Brunei. J. Ecol. 60: 305–324.

———, J. S. Pausas & A. O. Nicholls. 1996. Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. Austral. J. Ecol. 21: 154–164.

Baillie, I. C., P. S. Ashton, M. N. Court, J. A. R. Anderson, E. A. Fitzpatrick & J. Tinsley. 1987. Site characteristics and the distribution of tree species in Mixed Dipterocarp Forest on Tertiary sediments in central Sarawak, Malaysia. J. Trop. Ecol. 3: 201–220.

Brown, S., A. J. R. Gillespie & A. E. Lugo. 1991. Biomass of tropical forests of south and southeast Asia. Canad. J. Forest Res. 21: 111–117.

Bush, M. B. & P. A. Colinvaux. 1994. Tropical forest disturbance: Paleoecological records from Darien, Panama. Ecology 75: 1761–1768.

Clark, D. A. & D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rainforest. Ecol. Monogr. 62: 315–344.

——— & ———. 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. J. Ecol. 82: 865–872.

———, ———, R. Sandoval M. & M. V. Castro C. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology 76: 2581–2594.

Clark, D. B. 1990. La Selva Biological Station: A blueprint for stimulating tropical research. Pp. 9–27 *in* A. Gentry (editor), Four Neotropical Rainforests. Yale Univ. Press, New Haven, Connecticut.

——— & D. A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. Oikos 55: 225–230.

———, ——— & J. M. Read. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. J. Ecol. 86: 101–112.

———, ——— & P. M. Rich. 1993. Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. Biotropica 25: 397–407.

———, ———, ———, S. Weiss & S. F. Oberbauer. 1996. Landscape-scale distribution of understory light and forest structure in a neotropical lowland rain forest. Canad. J. Forest Res. 26: 747–757.

Condit, R. 1995. Research in large, long-term tropical forest plots. Trends Ecol. Evol. 10: 18–22.

Dallmeier, F. (editor). 1992. Long-term monitoring of biological diversity in tropical forest areas. UNESCO, Paris.

Deckert, C. & P. V. Bolstad. 1996. Forest canopy, terrain, and distance effects on global positioning system point accuracy. Photogramm. Engin. Remote Sensing 62: 317–321.

Duivenvoorden, J. F. 1996. Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. Biotropica 28: 142–158.

Foster, R. B. 1990. Long-term change in the successional forest community of the Rio Manu floodplain. Pp. 565–572 *in* A. H. Gentry (editor), Four Neotropical Rainforests. Yale Univ. Press, New Haven, Connecticut.

——— & S. P. Hubbell. 1990. The floristic composition of the Barro Colorado Island forest. Pp. 85–98 *in* A. H. Gentry (editor), Four Neotropical Rainforests. Yale Univ. Press, New Haven, Connecticut.

Garcia-Montiel, D. C. & F. N. Scatena. 1994. The effect of human activities on the structure and composition of a tropical forest in Puerto Rico. Forest Ecol. Managem. 63: 57–78.

Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. Proc. Natl. Acad. Sci. U.S.A. 85: 156–159.

——— (editor). 1990. Four Neotropical Rainforests. Yale Univ. Press, New Haven, Connecticut.

———. 1992. Tropical forest biodiversity: Distributional patterns and their conservational significance. Oikos 63: 19–28.

———. 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru). Conservation International, Washington, D.C.

———. 1994. Importance of the Explorer's Inn Reserve permanent plots. Pp. 55–57 *in* R. B. Foster, T. A. Parker III, A. H. Gentry et al. (editors), The Tambopata-Candamo Reserved Zone of Southeastern Peru: A Biological Assessment. Conservation International, Washington, D.C.

——— & R. Ortiz S. 1993. Patrones de composición florística en la Amazonia Peruana. Pp. 155–166 *in* R. Kalliola, M. Puhakka & W. Danjoy (editors), Amazonia Peruana. PAUT and ONERN, Jyvaskyla, Finland.

Gómez-Pompa, A. & A. Kaus. 1990. Traditional management of tropical forests in Mexico. Pp. 45–64 *in* A. B. Anderson (editor), Alternatives to Deforestation. Columbia Univ. Press, New York.

Gordon, B. L. 1982. A Panama Forest and Shore. The Boxwood Press, Pacific Grove, California.

Hamburg, S. P. & R. L. Sanford, Jr. 1986. Disturbance, Homo sapiens, and ecology. Bull. Ecol. Soc. Amer. 67: 169–171.

Hartshorn, G. S. 1983. Plants. Pp. 118–157 *in* D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago.

——— & B. E. Hammel. 1994. Vegetation types and floristic patterns. Pp. 73–89 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Henderson, A., G. Galeano & R. Bernal. 1995. Field Guide to the Palms of the Americas. Princeton Univ. Press, Princeton, New Jersey.

Horn, S. P. & R. L. Sanford, Jr. 1992. Holocene fires in Costa Rica. Biotropica 24: 354–361.

Kahn, F. 1987. The distribution of palms as a function of local topography in Amazonian terra-firme forests. Experientia 43: 251–259.

Lathrop, R. G., Jr., J. D. Aber & J. A. Bognar. 1995. Spatial variability of digital soil maps and its impact on regional ecosystem modeling. Ecol. Modelling. 82: 1–10.

Levey, D. J., T. C. Moermond & J. S. Denslow. 1994. Frugivory: An overview. Pp. 282–294 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Lieberman, D., M. Lieberman, G. S. Hartshorn & R. Peralta. 1985b. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. J. Trop. Ecol. 1(2): 97–109.

Lieberman, M., D. Lieberman, G. S. Hartshorn & R. Peralta. 1985a. Small-scale altitudinal variation in lowland wet tropical forest vegetation. J. Ecol. 73: 505–516.

McDade, L. A., K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors). 1994. La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Nelson, B. W., V. Kapos, J. B. Adams, W. J. Oliveira, O. P. G. Braun & I. L. Doamaral. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. Ecology 75: 853–858.

Newstrom, L. E., G. W. Frankie, H. G. Baker & R. K. Colwell. 1994. Diversity of long-term flowering patterns. Pp. 142–160 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Oberthur, T., A. Dobermann & H. U. Neue. 1996. How good is a reconnaissance soil map for agronomic purposes? Soil Use & Managem. 12: 33–43.

Richter, D. D. & L. I. Babbar. 1991. Soil diversity in the tropics. Advances Ecol. Res. 21: 315–389.

Ruokolainen, K. & H. Tuomisto. 1993. La vegetación de terrenos no inundables (tierra firme) en la selva baja de la Amazonia Peruana. Pp. 139–153 *in* R. Kalliola, M. Puhakka & W. Danjoy (editors), Amazonia Peruana. PAUT and ONERN, Jyvaskyla, Finland.

Salo, J. & M. Rasanen. 1989. Hierarchy of landscape patterns in western Amazon. Pp. 35–45 *in* L. B. Holm-Nielsen, I. C. Nielsen & H. Balslev (editors), Tropical Forests: Botanical Dynamics, Speciation and Diversity. Academic Press, New York.

Sancho M., F. & R. Mata Ch. 1987. Estudio detallado de suelos, Estación Biológica "La Selva." Organization for Tropical Studies, San José, Costa Rica.

Sanford, R. L., Jr., P. Paaby, J. C. Luvall & E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pp. 19–33 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Simpson, B. B. & M. Connor Ogorzaly. 1986. Economic Botany: Plants in Our World. McGraw-Hill, New York.

Sollins, P., F. Sancho M., R. Mata Ch. & R. L. Sanford, Jr. 1994. Soils and soil process research. Pp. 34–53 *in* L. A. McDade, K. S. Bawa, H. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Terborgh, J., R. B. Foster & P. Nunez V. 1996. Tropical tree communities: A test of the nonequilibrium hypothesis. Ecology 77: 561–567.

Timm, R. M. 1994. The mammal fauna. Pp. 229–237 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (editors), La Selva: Ecology and Natural History of a Neotropical Rain Forest. Univ. Chicago Press, Chicago.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy & Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

Valencia, R., H. Balslev & G. Paz y Mino C. 1994. High tree alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation 3: 21–28.

Vandermeer, J. H. 1977. Notes on density dependence in *Welfia georgii* Wendl. ex Burret (Palmae), a lowland rainforest species in Costa Rica. Brenesia 10/11: 9–15.

Wilbur, R. L. 1986. The vascular flora of La Selva Biological Station, Costa Rica—Introduction. Selbyana 9: 191.

LARGE-AREA MAPPING OF BIODIVERSITY[1]

J. Michael Scott[2] and Michael D. Jennings[3]

ABSTRACT

The age of discovery, description, and classification of biodiversity is entering a new phase. In responding to the conservation imperative, we can now supplement the essential work of systematics with spatially explicit information on species and assemblages of species. This is possible because of recent conceptual, technical, and organizational progress in generating synoptic views of the earth's surface and a great deal of its biological content, at multiple scales of thematic as well as geographic resolution. The development of extensive spatial data on species distributions and vegetation types provides us with a framework for: (a) assessing what we know and where we know it at meso-scales, and (b) stratifying the biological universe so that higher-resolution surveys can be more efficiently implemented, covering, for example, geographic adequacy of specimen collections, population abundance, reproductive success, and genetic dynamics. The land areas involved are very large, and the questions, such as resolution, scale, classification, and accuracy, are complex. In this paper, we provide examples from the United States Gap Analysis Program on the advantages and limitations of mapping the occurrence of terrestrial vertebrate species and dominant land-cover types over large areas as joint ventures and in multi-organizational partnerships, and how these cooperative efforts can be designed to implement results from data development and analyses as on-the-ground actions. Clearly, new frameworks for thinking about biogeographic information as well as organizational cooperation are needed if we are to have any hope of documenting the full range of species occurrences and ecological processes in ways meaningful to their management. The Gap Analysis experience provides one model for achieving these new frameworks.

Systematics is the science of describing the fundamental units that make up the diversity of life, classifying organisms in a way that indicates their natural relationships. The age of discovery, description, and classification of biological diversity is far from over. New species of chordates, the most thoroughly described phylum, are still being discovered. However, we are entering a new phase of characterizing biological diversity. This new phase is distinguished on the one hand by: (a) progress in applying concepts relating spatial scale to the hierarchy of biotic organization and more cooperative relationships among institutions that conduct research, planning, and management of biological resources; and (b) new and powerful technologies for inventorying and monitoring biological diversity. On the other hand there are setbacks due to financial limitations and a lack of societal support for the management practices that it will actually take to maintain the natural diversity of life on earth.

Clearly, the level of effort being invested in completing the description of most species and subspecies is orders of magnitude less than the level of human enterprise that results in the collateral damage of extinction and extirpation (Hawken, 1993). In order to make progress in managing for biological diversity we need to know: what species there are (systematics), how they function (behavioral and ecosystem science), how they are distributed in space (biogeography), time (population ecology), and how they are presently managed (wildlife and conservation biology). One distinct problem is that the properties of biological diversity change as the objects (individuals, populations, species, assemblages of species) are aggregated or disaggregated (Allen & Starr, 1982).

A complete biological inventory of a large area may involve, for example, describing the genetic structure of a species, its behavior, population sizes, and other metrics such as reproductive success, mortality, and mutation rates. It must describe the species' ecological positions in multiple dimensions (e.g., trophic, community affiliations, habitat, etc.) as well as the processes that maintain the ecosystems in which a species occurs. The undertaking must include studies of the biogeography of the species and the biogeography of its habitats. Finally, it must include an assessment of the current conservation status of the species and its habitats. The challenge is no less daunting than launching a 19th-century expedition to describe the flora and fauna of the Amazon Basin.

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[1] We thank the many partners of GAP for their efforts to provide biologically defensible databases that can be used in more effective interagency efforts at managing biodiversity.

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So far, we have been able to document habitat-specific distributions and have obtained some sense of reproductive success over space and time for only a very few species—those that are important recreationally or commercially, or those that are rare and popular such as the California condor (*Gymnogyps californianus*) or whooping crane (*Grus canadensis*). Even for a group as intensively studied as the birds of North America, there are hundreds of species reported in fewer than ten studies in the primary ornithological literature (J. Ratti & J. M. Scott, unpublished ms.). We have just begun to study the earth as a biosphere, and the tools we are using, such as remote sensing and geographic information systems, are still developing. The challenge is to think hierarchically (Wiens, 1989) and to link the tools of geographers with those of classical taxonomists and naturalists by building two-way bridges among the disciplines. Only by increased interdisciplinary cooperation are we to have some hope of describing and understanding the complexity of nature's diversity and how to better manage our natural heritage for future generations.

We describe a method and its implementation that complements the work of systematics by focusing on two other specific parts of the biodiversity issue: biogeography and land management. The method we describe is now being carried out in the United States as the Gap Analysis Program under the Biological Resources Division of the U.S. Geological Survey (Scott et al., 1993, 1996). We present some background, methods, and results to date. Then we discuss opportunities for improving biodiversity information through better integration of systematics, ecosystem science, and biogeography.

BACKGROUND

BIODIVERSITY AND SPATIAL SCALE

Biodiversity is ". . . the variability among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems" (1993 Convention on Biological Diversity, Article 2, as cited in Heywood, 1995: 8). By this view, biodiversity is complex and deals with composition, structure, and process of its component parts (Noss & Cooperrider, 1994). Its characterization necessitates a synthetic hierarchical construct. Additionally, when dealing with the spatial or geographic aspects of biological diversity, clear labels and definitions for units that relate biological diversity to geographic extent are necessary.

The four basic principles that underpin the concept of hierarchy for ecology are: (1) that systems are defined by measures of their structural components and by the rates of their processes; (2) systems are ordered according to both their occurrences in space and the frequencies or rates of their processes over time; (3) larger/slower systems constrain the occurrences and behaviors of smaller/faster systems, providing the context within which the smaller/faster systems operate; and (4) the mechanisms or properties by which a system operates may not be determined only by a simple aggregation of its smaller/faster components, nor by a reduction of its larger/slower components (O'Neill et al., 1986).

When mapping elements of biodiversity over large areas, the relationships among and between the pattern of dominant land-cover types, species diversity, and spatial scale are critical. Measures of species diversity must be expressed relative to biogeographic units of a determined spatial scale if they are to be meaningful (Levin, 1981). However, confusion about the differences between types of diversity ("thematic resolution") and cartographic scale is persistent (e.g., Short & Hestbeck, 1995; Davis, 1995; Edwards, 1995; Scott et al., 1995). We suggest using seven categories as a framework for describing species diversity in relation to ecological patterns and spatial scale (Table 1; Whittaker, 1960, 1977).

The linkage between types of diversity and spatial scale makes this framework especially useful. Figure 1 (Stoms & Estes, 1993) shows how four of these categories ("inventory diversities") are used to describe species diversity *within* sampling units of four approximate sequential sizes and corresponding with four hierarchical levels of biotic organization: a single ground sampling point (*point diversity*), a natural community (*alpha diversity*), a landscape (*gamma diversity*), and a large geographic region (*epsilon diversity*). Three other terms ("differentiation diversities") are used when comparing the amount of change in species composition *between* individual sampling points (*pattern diversity*), natural communities (*beta diversity*), and landscapes (*delta diversity*) (Whittaker, 1977).

The critical point here is that the magnitude of alterations to land and water characteristics, formerly limited in spatial extent and pattern so as to be manifest at the levels of populations and species, is now so extensive that changes are manifest at the levels of natural communities, landscape ecosystems, and global ecosystems (Heywood, 1995;

Table 1. Spatial categories of species diversity (Whittaker, 1977; Stoms & Estes, 1993).

Inventory diversities	Differentiation diversities
1. *Point diversity:* A small, or microhabitat, sample of species diversity from within an alpha unit. Generally 10 to 100 square meters.	
	2. *Pattern diversity:* The change in diversity between points within a community.
3. *Alpha diversity:* A single within-habitat measure of species diversity regardless of internal pattern. Generally 0.1 to 1000 hectares.	
	4. *Beta diversity:* The change in diversity among different communities of a landscape; an index of between-habitat diversity.
5. *Gamma diversity:* The species diversity of a landscape made up of more than one kind of natural community. Generally, 1000 to 1,000,000 hectares.	
	6. *Delta diversity:* The change in diversity between landscapes along major climatic or physiographic gradients.
7. *Epsilon diversity:* The species diversity of a broad region of differing landscapes. Generally 1,000,000 to 100,000,000 hectares.	

Vitousek et al., 1996; Vitousek et al., 1997). Conservation efforts implemented at the population and species level alone may no longer be effective when system-wide changes are being forced at the landscape and global levels of ecosystem functioning. Furthermore, the properties by which a system interacts with the agents of change may not be readily identified by an aggregation of a system's smaller components or by a reduction of its larger components. Information derived from synoptic observations of both the level of biotic organization and the geographic extent at which the changes are being induced is needed (Jennings & Scott, 1993).

We believe that providing a rangewide elemental basis for assessing biodiversity conservation using maps of vegetation types and vertebrate species distributions creates sampling frameworks from which unbiased samples for more detailed studies of species occurrences, density, and viability may be made. For the first time, we can be spatially explicit about a suite of species that co-occur in a repeating pattern across the landscape, for example, those characterized by the dominance of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson). We can understand the extent of its occurrence as context, examine its landscape position, and make inferences about composition, structure, and function that are rangewide. The result is a significant advancement over being limited to conclusions about the ponderosa pine vegetation alliance only from stand-level examinations.

In a similar fashion, we may use the distribution map, for example, of a wolverine (*Gulo gulo*) to ask questions about the representativeness of extant collection records, or view it as a testable hypothesis and conduct wolverine surveys to document not only presence/absence but also abundance and reproductive success. We may also use these maps to make more detailed descriptions of its habitat from an unbiased sample of its entire range, all in such a manner that inferences may be made about the wolverine or its habitat (or in the earlier case, ponderosa pine) rather than simply the study site we chose to sample.

PURPOSE

The purpose of gap analysis is twofold. The first is to provide regional conservation assessments of native vertebrate species and natural land-cover types. The second is to facilitate the application of this information to land-management activities. These goals are accomplished by (a) mapping the vegetation alliances (FGDC, 1996; Grossman et al., 1994) of the United States; (b) mapping predicted distributions of each native vertebrate species; (c) mapping the existing conservation lands and ranking them by their management status; (d) determining the degree of representation that vertebrate species and land-cover types have in conservation lands; (e) providing this information to the public and those entities charged with land-use research, policy, planning, and management; and (f) building institutional cooperation in the application of this information to state and regional management activities. This, then, provides an objective database of biogeographic information that allows researchers, planners, and managers to stratify the land surface for work at higher resolutions (Scott et al., 1993, 1996), and to understand the regional and continental context of higher-resolution information from smaller areas (Jennings, 1995).

DEVELOPMENT

The term "gap analysis" refers to the process by which species and natural communities not adequately represented in conservation lands are identified. These are the "gaps" in our present-day efforts to maintain biological diversity, and it is these that are most likely to become endangered with extinction in the future. By understanding what these gaps are and where they are, future conservation crises and conflicts may be avoided.

The development of the Gap Analysis Program (GAP) began in 1987 in response to the need to complement species-by-species management of endangered species in dealing with broad-spectrum habitat loss (Scott et al., 1987, 1993, 1996). There was a need for synoptic and spatially explicit information on the distribution of each native vertebrate species and natural community, and their management status. At the time, there were no readily available, consistent data that could provide for an understanding of either the context of a single land management decision or the occurrence of a species' habitat in the ecological contexts of landscapes or bioregions.

There are many other uses for these data. Most states do not have current maps of land cover, and GAP is the first state- and national-level effort to produce this information at resolutions usable by land managers, planners, scientists, and policy makers (Scott et al., 1987, 1993, 1996). Maps showing the distributions of land cover, habitat type, vertebrate species, land management, or combinations thereof can be generated regionally or nationally. Such information may be used to identify areas that are suitable for development and where other land-use conflicts may be avoided, as well as those areas important for meeting conservation needs.

In the years since 1987, significant barriers to mapping elements of biological diversity across large areas have been overcome (Scott et al., 1996). A wide range of tools for mapping natural land-cover and habitat types and predicting vertebrate species distributions has emerged, and procedures have been refined, tested, and further refined. There is still room for improvements; additional development and testing of some methods at varying spatial and thematic scales (for example, accuracy assessment) and land-cover mapping is still needed.

COOPERATION

The U.S. Geological Survey's GAP is conducted as state-level projects, and currently there are 46 active or completed projects. Although coordinated and primarily funded by the U.S. Geological Survey's Biological Resources Division (formerly the National Biological Service), GAP is made up of over 450 cooperating organizations, including universities, businesses, and state and federal agencies.

Of equal importance to the technical progress is the way natural resources institutions (private and public) are coalescing around the concept of a standard large-area information base (one way this may be seen is through the "bottom-up" organization (and funding) that characterizes the program). GAP, the largest effort ever mounted to map selected (i.e., vertebrate species and vegetation types) biological resources of the United States, is being carried out cooperatively by state-level projects.

The importance of having data sets that are comparable across state boundaries is in revealing actual patterns of species and vegetation community distribution at scales relevant to both the magnitude of present-day changes and the multiple levels of biological organization. Such information may be used to identify areas that are suitable for development and where land-use conflicts may be avoided, as well as those areas important for meeting conservation needs. New frameworks are emerging for both in the new type of information being developed and in the convergent way it is being developed.

There is now convergence on mutually recognized and systematic definitions for natural communities as intrinsic entities and as habitat types, for example, as indicated by the land-cover classification system being proposed for adoption by the Federal Geographic Data Committee (FGDC) and by formation of the Ecological Society of America's Vegetation Classification Panel. There has been substantial recent progress on methods for mapping alliances of natural communities, as represented by dominant natural vegetation or non-vegetated land-cover types, though it appears that no single method will suffice for all environments (Caicco et al., 1995; Stoms, 1994). There is increasingly more common ground on methods for predicting the dis-

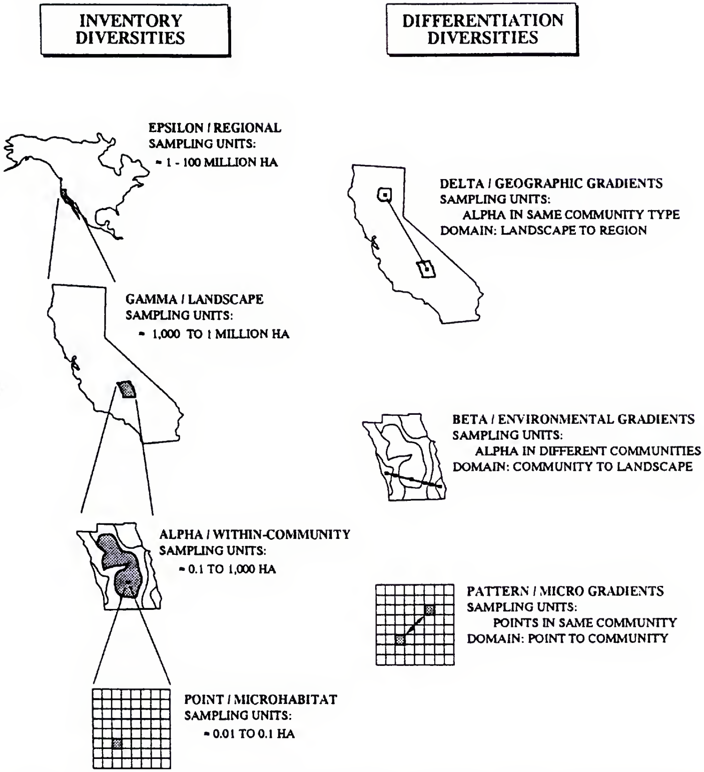

Figure 1. Diagram showing seven spatial levels of species diversity defined by Whittaker (1977). The lefthand column represents levels of diversity within a spatially sequential set of sample units, or "Inventory Diversities." The righthand column represents categories of species change in composition between or among sample units of the same spatial level. (From Stoms & Estes, 1993, reprinted with permission.)

tribution of native vertebrate species (Butterfield et al., 1994; Edwards et al., 1995). And, much experience has been gained in the mapping of areas that are managed for biodiversity (Beardsley & Stoms, 1993). Although many issues remain, such as accuracy assessment and appropriate scale and resolution, much attention is being brought to bear on them, and the trends are quite positive.

Frameworks are now in place in GAP, as well as in other large-scale biological assessments, for generating, archiving, distributing, querying, and experimenting with biological data that cover large areas, and there is a great deal of interest in improving the science of these efforts. What might be of greater significance is that consensus on these issues is taking place among state-level institutions as well as among the state and national interests who have responsibility for research and management of natural resources.

The concept underlying this dynamic is that it is far more important now, while land use decisions concerning millions of hectares are being made daily, to begin with an accounting of the conservation status for the mappable elements of biological diversity than to put off any real action until perfect methods have been conceptualized, and all elements of biodiversity have been identified and mapped, tested, published, replicated, adopted, diffused, and applied. There is simply not the time, money, nor political will to take that path. Today we have the capabilities to build powerful sets of information, imperfect though they may be, that correspond to the multiple levels of biotic organization. And we have the ability to foster the application of that information, by all concerned, to solve the seemingly inexorable problems of maintaining our biological heritage. It requires that professionals and their institutions put aside their past disciplinary and institutional differences, assume some risk, and commit to work together with whatever resources they have. This can result in a leveraging of funds and minimizing of duplicate efforts.

METHODS

GAP requires computer-based (digital) maps of: (a) existing natural or semi-natural land cover to the level of community alliances (vegetation types characterized according to their dominant or co-dominant plant species or, in the absence of a dominant vegetation species, dominant land-cover feature (Grossman et al., 1994)); (b) predicted present-day distributions of native vertebrate species; and (c) public land ownership and private conservation lands. These data layers are analyzed to compare distributions of each native vertebrate species, group of species, and community alliance with the existing network of conservation lands. Results show where the conservation "gaps" are in both land management and in the body of knowledge about species and natural communities. An overview of the methods for developing each of these three data sets is presented below (see also Scott et al., 1993; Jennings et al., 1996; Gap Analysis Program World Wide Web home page http://www.gap.uidaho.edu/gap).

LAND COVER

Generally, the mapping of land cover is done by delineating areas of relative homogeneity (basic cartographic "objects"), then labeling these areas using categories defined by a land-cover classification system. More detailed attributes of the individual areas are added as more information becomes available, and a process of validating both polygon patterns and labels is applied for editing and revising the map. This is done in an iterative fashion, with the results from one step causing reevaluation of results from another step. For example, the discovery of attributes for a given mapped polygon may result in adjustment of its boundary. Finally, an assessment of the overall accuracy of the data is conducted. Where the database is appropriately maintained, the final assessment of accuracy will show where improvements should be made in the next update (Davis et al., 1995).

Some of the problems with efficient mapping of large areas at the desired spatial and thematic resolutions (i.e., 1:100,000-scale and community alliance theme) that have been overcome are: (a) classification of land cover, (b) data acquisition, (c) delineation of land-cover pattern, (d) object interpretation (Orians, 1993), and (e) assessment of final map accuracy. In order to provide meaningful comparisons across large areas, a consistent land-cover classification system is needed. Land-cover classifications must rely on specified attributes such as the structural features of plants, their floristic composition, or environmental conditions to differentiate categories evenly (Küchler & Zonneveld, 1988). Although there has been much effort devoted to the classification of vegetation, there has been no previous attempt to apply a detailed classification of natural land cover across the contiguous 48 United States at a 1:100,000 scale, although Crumpacker et al. (1988), assessed the occurrence of 135 potential vegetation types on federal and Indian lands. In mapping land cover, GAP uses the National Vegetation Classification (FGDC, 1996, 1997; Grossman et al., 1994; Bourgeron & Engelking et al., 1994; Sneddon et al., 1994; Weakley et al., 1996; Loucks, 1995, 1996).

The minimum thematic object that Gap Analysis is mapping is the community alliance (Grossman et al., 1994; see Appendix 1 for a sample description of a community alliance), although in practice for some areas, mosaics of undifferentiated alliances (e.g., "oak woodlands" rather than "*Quercus garryana* alliance") represent the limit of current capabilities to map land cover across ecoregions and biomes. The alliance corresponds most closely with the units of alpha diversity (a sample representing a community regarded as homogeneous despite its internal pattern) in order to conduct analyses at the beta, gamma, delta, and epsilon levels. A spatial depiction of beta diversity (between-habitat diversity) represents the pattern of landscape, or gamma, heterogeneity. For Gap Analysis, the central concept is that the structural and floristic characteristics of dominant vegetation or (in the absence of vegetation) dominant land features, can be used systematically to delineate and map patterns of beta and gamma diversity. Models of these patterns are important for generating and evaluating landscape-level conservation options.

For the delineation of land-cover patterns, the Landsat Thematic Mapper (TM) satellite images serve both as a base map and as a source of spectral information for discriminating among land-cover types. Although methods for preprocessing the basic TM product used in mapping land cover were variable at the earlier stages, currently state projects use a standard TM product that is geographically registered to within 30 m, corrected for terrain distortion and systems errors, and spectrally classified into 240 classes using bands 1, 2, 3, 4, 5, and 7 (see Bara, 1994).

No single procedure is appropriate for the delineation of land-cover patterns in all environments of the United States (Davis et al., 1995), and a variety of methods are used to delineate land-cover patterns by the GAP state project analysts (Davis et al., 1991; Davis & Stoms, 1996; Davis et al., 1995; Edwards et al., 1995; Lillisand, 1996; Scott et al., 1993; Slaymaker et al., 1996). As pattern is delineated, the resulting objects are interpreted and labeled in an iterative fashion. To recognize vegetation alliances, training images of each type are identified on the ground. Air photos or air videos are being used to train analysts. Additional data sets, such as digital elevation models, temperature and precipitation patterns, and soils maps, are also used. A single, precisely standardized method for pattern delineation is not possible because: (a) vegetation characteristics differ substantially among biogeographic regions, requiring different approaches, especially for interpretation of remotely sensed data; for example, the use of TM imagery from different seasons may be used singularly in a false color composite format and interpreted visually, or their spectral values may be transformed in a specific way and merged together to reveal patterns based on phenotypic distinction (the possible variations are almost endless); (b) the expertise for vegetation typing and mapping is itself also regional in nature, resulting in different approaches by the state project scientists; (c) many different sources of information are used to render the maps (for example, variability in the date of imaging among TM scenes within a state and wide variation in the availability of information about the occurrence of dominant cover types from state to state), introducing variability into the product; (d) the current mapping work is a first generation effort, with significant improvements to the technology being made by the state GAP projects; there is a need to try different methods because an effort of this magnitude, extent, and degree of resolution has not been undertaken before; (e) of necessity, GAP is a collaborative "bottom-up" effort focused on pragmatic, near-term conservation, and at present there is neither the institutional support nor the time to research and develop a single method, achieve consensus on such a method, then implement a large "top-down" program.

Each map class of the state-level spatial data sets is tested for accuracy, using independent field data, with the confidence interval carried through further transformations with that data set's metadata. A detailed review of data quality is undertaken when edge-matching data from adjacent states. Since the present effort is a first generation one, improved methods are expected to dampen the amplitude of inter-state variation in later generations as well as increase thematic resolution and accuracy. A number of land-cover data sets from states that used different methods have been edge-matched with good results (M. Murray, Idaho Cooperative Fish and Wildlife Research Unit, C. Homer, Utah Cooperative Fish and Wildlife Research Unit, and R. Redmond, Montana Gap Analysis Project, Missoula, pers. comm.).

VERTEBRATE SPECIES DISTRIBUTIONS

The objectives for mapping the distributions of vertebrate species are to provide maps of known confidence in order to support analysis of conservation status to develop a database of locational records, geographic range, wildlife habitat associations, and predicted distribution of each vertebrate species for the long-term utility for GAP and its cooperators.

Most existing information on species distribution has typically been collected at the scale of individual field sites and extrapolated to small-scale range maps for state, regional, or national references and field guides. Lacking for most biogeographic information on species is a meso-scale expression (e.g., 1:100,000) of a detailed distribution map, as compared with a general range map depicting broad regional or continental limits.

The basic assumption of GAP's predicted species distribution maps is that a species has a high probability of occurring in appropriate habitat types that are within its predicted range. GAP links species' general ranges to large-area land-cover maps and other physical data, which are intermediate in scale between a known specimen collection site and a field guide range map (see Edwards et al., 1996;

Scott et al., 1993). This approach is derived from the assumption that, for large areas such as states or nations, it is impractical to map the distribution of species at a nominal scale of 1:100,000 only from intensive field surveys. GAP therefore makes use of existing information on range limits and refines it to develop spatial statements of the presence and absence of a species in map polygons that represent appropriate habitat as understood from current knowledge of the species and the ability to map its habitat (Scott et al., 1993; Butterfield et al., 1994; Edwards et al., 1995).

Predicting species distributions by relating them to environmental features that can be mapped from remotely sensed data is an efficient approach to estimating the distribution and management status of elements of biodiversity. However, no matter what their scale, *all* range and distribution maps are predictions about the presence of a species in a particular geographic area. The accuracy of those predictions generally improves as the size of the area, length of the sampling period, and intensity of sampling are expanded because greater temporal scale as well as heterogeneity of large areas make it more likely that a species will be found to occur there. GAP maps of predicted distributions are currently intended for use and validation at the landscape, or gamma, level of diversity (an area made up of more than one kind of natural community, generally, 1000 to 1,000,000 ha; Whittaker, 1977), but new efforts are able to attribute species to "patches" as small as 2 hectares. For some species, such resolution may be desirable to allow more precise estimation of habitat area, while for other species, such small patches may be biologically meaningless. For the majority of species, the ability to map at this resolution probably exceeds our knowledge of their ecology.

We mapped predicted vertebrate species' occurrences by first obtaining specimen collections and verified sighting records for specific known locations for each species and entering this information into a database. These records are considered as either current (within the past 10 years) or historical (> 10 years old). Second, the general range extent for each species is established from the best available information—frequently field guides. Third, an exhaustive literature search is done to establish the known habitat relationships (vegetation, elevation, lakes, etc.) for each species. Fourth, a habitat relationship model for each species is constructed for use in a geographic information system (GIS). Fifth, the range units and habitat associations are integrated into a predicted species-distribution map, with areas attributed by known versus predicted occurrences. Sixth, an expert review of the draft maps is conducted, the maps are edited, and all changes are documented (Csuti & Crist, in prep.). The resulting maps are testable hypotheses, predictions we hope will be improved with better information over time (Fig. 2). This type of database bootstrapping is critical if we are to overcome both sparse data and funding constraints. At the landscape level of resolution, GAP predictions of accuracy have ranged from 70% to over 90% for birds, mammals, amphibians, and reptiles (Edwards et al., 1996; Scott et al., 1993; C. Peterson, Idaho State University, pers. comm.). The procedure works best for species with habitat preferences that can be described in terms of land cover and other mapped features or characteristics. It works for habitat specialists only if their specific habitat requirements are available as mapped features or are well associated with other mapped characteristics such as land-cover types. An additional caution is that species with very restricted distributions cannot reliably be predicted to occur in seemingly appropriate habitat within their general distributional limits. Because of their rarity, these species are often the subject of special attention from state and federal resource agencies. The specific locations where they are known to occur are usually tracked by Natural Heritage Programs (NHPs) and Conservation Data Centers (CDCs). GAP makes use of the data from Heritage Programs and CDCs to report the presence of populations of such species within a mapped unit. For security purposes, the exact locations of these populations are distributed only by the NHPs or CDCs.

LAND-OWNERSHIP AND LAND-MANAGEMENT MAPS

Since one purpose of GAP is to provide an assessment of the conservation status of species and their habitats, maps of lands that are managed for conservation must be compared with the distributions of species and habitats. Most states, however, do not have a current inventory of land-management status. The first step toward developing a map of conservation lands is to map land-ownership by the major categories of (1) public lands by managing agency, (2) voluntarily identified privately owned conservation lands, and (3) all other privately owned lands. Then, as a second step, the attributes for land-management categories are added to these tracts. All non-conservation privately owned lands (category 3 above) are simply labeled "private," and individual parcel boundaries are not delineated.

Land-ownership and land-management maps in-

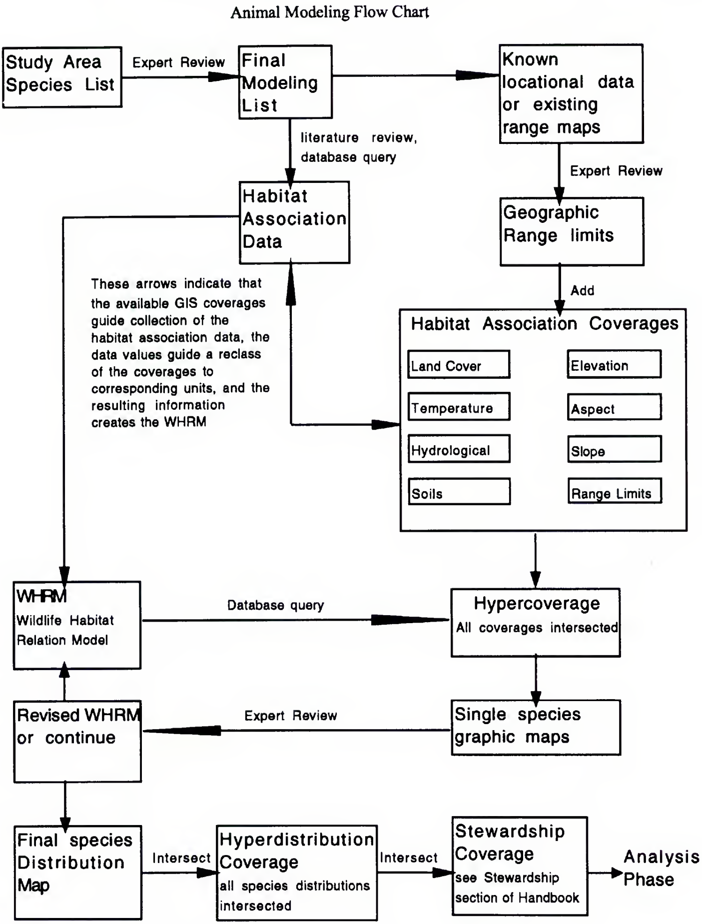

Figure 2. The gap analysis wildlife habitat relationship model.

clude land parcels that can be reasonably resolved at a 1:100,000 scale. Commonly this is 1 ha, which is equivalent to 1 mm² on a 1:100,000 scale map. Descriptions of how the land-management maps are developed are provided by Scott et al. (1993), Beardsley and Stoms (1993), and Edwards et al. (1995). Land-management is ranked by the four levels shown in Table 2.

Over the past year, there has been an ongoing discussion among GAP participants about the ad-

Table 2. The four levels of land management and their definitions.

Level	Definition
1.	Areas having a management plan in operation to maintain a natural state and within which natural disturbance events are allowed to proceed without interference.
2.	Areas generally managed for natural values, but which may receive uses that degrade the quality of existing natural communities.
3.	Areas for which legal mandates generally prevent permanent land cover conversions from natural or semi-natural habitats to anthropogenic habitats, such as conversions to agriculture, but which are subject to extractive uses such as silviculture or mining.
4.	Areas managed for intensive human uses.

equacy of these definitions. Many feel a larger number of categories that use a wider variety of management activities undertaken on behalf of native species and ecosystems would be more useful. When a greater number of management categories was recognized during the Sierra Nevada ecosystem project and species were rated differently within these categories because of their varying responses to management practices, communication among cooperators was greatly improved (F. Davis, University of California, Santa Barbara, pers. comm.). As a result, GAP is exploring a land-management scheme having greater thematic resolution.

ANALYSES

While there are many ways that the three basic data sets of land cover, vertebrate distributions, and land management may be analyzed, the primary purpose is to identify potential gaps in the existing network of conservation lands. The identification of conservation gaps is intended to provide land stewards with the information needed to modify their plans and practices in order to maintain our natural biodiversity and the processes that sustain it, and to avoid conflicts with other uses of the land.

The analysis presented here focuses on the basic requirements for a state gap analysis project. These call only for identification of those biotic elements that lack adequate representation in conservation lands rather than the identification of specific geographic locations needed to "plug" the gaps. The latter is the selection phase of reserve design and requires detailed on-the-ground information concerning habitat quality and demographics of the species of interest. The first objective is to determine the representation of each mapped alliance and vertebrate species in each category of land ownership and management status. The second objective is to interpret the analysis in a way that is useful for land stewards in land-use planning and management for conserving those biotic elements. The program provides the data sets and the analyses in forms suitable for additional modeling, biodiversity assessment, and planning activities.

These objectives are met by intersecting the land-cover and animal ("element") distribution GIS coverages with the land-ownership and land-management coverage so that the element coverages incorporate the stewardship boundaries. Then, the statistics from that intersection are used to generate a table reporting the representation of individual elements (species and dominant cover types) in each ownership and management category. Finally, these results are used to generate maps of those elements found to be lacking in their representation in conservation lands, and they are incorporated into a standard final report. Each species and plant community alliance is identified and analyzed separately. Selected groups of elements of interest may also be analyzed. For example, a spatial analysis of species having less than 10%, 20%, and 50% of their distributions in status 1 or 2 (Table 2) land-management areas is provided. Other groups of species of special interest (e.g., endangered species or declining neotropical migrant bird species, and endemic species, etc.) may also be analyzed for their representation in conservation lands.

There are clearly some limitations to this approach. One is that the historical distributions of elements are usually poorly known; measures of present-day distributions usually cannot indicate the extent of loss in historical range (but see Noss et al., 1995). For example, if an element has already been reduced by 90% from its historic distribution, and gap analysis indicates a 50% occurrence in management status 1 or 2 areas, the result is that only 4.5% of its historic distribution is represented. Another limitation is that GAP currently does not predict element viability. For most species and plant communities, viability measures such as habitat quality, species abundance, population trends, reproductive success, and mortality at a site are unknown and cannot be assessed given current knowledge. Therefore, GAP only provides information on representation with the objective of highlighting at-risk species and vegetation types that should undergo viability analysis as a next step. GAP is the first phase of identifying a three-part process that also includes reserve selection and design. Generally, conservation assessment of animal species must be used with more caution than assessment of land-cover types because land-cover maps are actual, typically with a statistically valid accuracy assessment, while animal distributions are predicted and difficult to validate. Land-cover types are more stationary and change slowly, while animal species are mobile and can expand and contract ranges over relatively short time spans; effects of management status on land-cover types are generally easier to predict than effects on animal species.

RESULTS AND DISCUSSION

Prior to the development of spatial data by GAP, the information needed to assess the conservation status of all but a few of the most popular vertebrate species was not available in the United States. There were no geographically extensive maps or databases of species distributions or actual dominant vegetation types at cartographic scales usable by local land managers. For example, Klopatek et al. (1979) estimated that 34% of the land surface in the United States was subject to some form of intensive land use. The authors concluded that 23 of the 106 types of potential (or original) vegetation may have been reduced by over 50%. Much more significantly, though, they concluded that there were major drawbacks and limitations to their findings because no inventory of actual vegetation existed at that time. They relied on general predictions of the occurrence and extent of potential vegetation for baseline data and compared those hypothetical data with nonstandardized estimates of county-level land-use practices. The critical information has, until now, been unavailable at the level of resolution necessary for large-area management of ecological systems.

We believe that a comprehensive plan for protecting our nation's biodiversity must include a representation of species and vegetation communities across their full range of geographical occurrence and ecological expression. The latter is being made possible by the development of standard catalogs and classification of the nation's vegetation types (Bourgeron & Engelking, 1994; Sneddon et al., 1994; Weakley et al., 1997; Drake & Faber-Langendoen, 1997; FGDC, 1997; ESA Vegetation Classification Panel, in prep.), which is overcoming the lack of a standardized system of vegetation classification (Orians, 1993). There is some confusion as to what represents a reasonable target for species or community conservation. The Endangered Species Act (ESA) currently stipulates species, subspecies, or distinctive population units. Much of the current debate over reauthorization of the ESA concerns the unit of protection, with many asking that we be more restrictive and protect only species or populations for which it can be demonstrated there is no gene flow with other populations. It is the belief of many that we have spent an inordinate amount of effort protecting subspecies and populations, although this is not borne out by the facts (Tear et al., 1993). One suggested conservation target is the natural community or the association in the National Vegetation Classification (FGDC, 1997; Jennings, 1993). However, we are currently unable to synoptically map that level of detail across physiographic provinces, ecoregions, or biomes. Examination of coarser levels such as mosaics of dominant vegetation types suggests that 16 of 30 plant communities evaluated in Utah were at risk (Edwards et al., 1995), and 32 of 71 in Idaho were considered vulnerable (Caicco et al., 1995). Thus, even at this coarser level of the GAP mapping effort, we found perhaps 25–40% of mapped vegetation types were at risk, and with them, other associated elements of biodiversity. This suggests that major progress toward protecting biodiversity could be made by simply insuring that viable examples of each of the vegetation alliances in North America be managed for their long-term viability.

However, we must be cautious. In interior maritime coniferous forest in the Pacific Northwest (Scott et al., unpublished ms.) we found the Western Red Cedar had 36% of its acreage in special management status. However, when examining the evenness of the Western Red Cedar forest alliance across its full range of ecological and geographical expression, we found its occurrence in special management areas was biased elevationally and geographically. When we examined the representation of the 16 identified and mapped natural community associations of the Western Red Cedar alliance in Idaho, we found eight with no acreage in special management areas and several with more than 80%. Thus, the more detail we have, the more informed the decision-making process of how to proceed with management. This just serves to emphasize the need for a hierarchical approach, spatially and thematically, for evaluating the effectiveness of current conservation efforts.

To date, results from Gap Analysis projects have been reported from Utah, Wyoming, Arkansas, California, Idaho, Oregon, Massachusetts, and Maine. Information from these areas has been used for land-use planning at several locations in southern California (Crowe, 1996), including Camp Pendleton and the Mojave Desert (T. Edwards, pers. comm.). It has been used to assess the contribution of proposed wilderness areas and new national parks to the further protection of biodiversity (Wright et al., 1994). Other uses include identification of new research sites and species and vegetation types at risk. But perhaps more importantly, it has served as the catalyst for new partnerships, often among individuals and organizations who had little or no history of working together. Partnerships (e.g., Crowe, 1996) forged in the data acquisition and analysis phase of the individual Gap Analysis projects have continued on into the implementation phase of GAP and into other endeavors as well.

These partnerships are deepening as we periodically update the thematic layers of GAP, and their application for more informed land-use decisions becomes an ordinary feature of natural resources management. Additional information on Gap Analysis can be found at http://gap.uidaho.edu/gap.

Literature Cited

Allen, T. F. & T. B. Starr. 1982. Hierarchy: Perspectives for Ecological Theory. Univ. Chicago Press, Chicago.

Bara, T. J. (editor). 1994. Multi-resolution Land Characteristics Consortium Documentation Notebook. EMAP-Landscape Characterization, EPA Office of Research and Development, Research Triangle Park, North Carolina. See also, the MRLC home page on the World Wide Web at http://www.epa.gov/grd/mrlc.

Beardsley, K. & D. M. Stoms. 1993. Compiling a digital map of areas managed for biodiversity in California. Nat. Areas J. 1: 177–190.

Bourgeron, P. S. & L. D. Engelking. 1994. A Preliminary Vegetation Classification of the Western United States. A report prepared by the Western Heritage Taskforce and The Nature Conservancy for the University of Idaho Cooperative Fish and Wildlife Research Unit. The Nature Conservancy Western Regional Office, Boulder, Colorado.

Butterfield, B. R., B. Csuti & J. M. Scott. 1994. Modeling vertebrate distributions for gap analysis. Pp. 53–68 *in* R. I. Miller (editor), Mapping the Diversity of Nature. Chapman and Hall, London.

Caicco, S. L., J. M. Scott, B. Butterfield & B. Csuti. 1995. A gap analysis management status of the vegetation of Idaho. Conservation of Biological Diversity 9: 498–511.

Crowe, R. E. 1996. Use of gap analysis in regional planning in southern California. Pp. 221–238 *in* J. M. Scott, T. H. Tear & F. W. Davis (editors), Gap Analysis, A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Crumpacker, D. W., S. W. Hodge, D. Friedley & W. P. Greg, Jr. 1988. A preliminary assessment of the status of major terrestrial and wetland ecosystems of federal and Indian lands in the United States. Conservation Biol. 2(1): 103–115.

Davis, F. W. 1995. The nature of gap analysis. Letter. BioScience 46: 74–75.

——— & D. M. Stoms. 1996. Geographic Information Systems Analysis of Biodiversity in California. Final report. University of California, Santa Barbara, Department of Geography.

———, J. E. Estes, B. Csuti, J. M. Scott, D. Stoms, M. Painho, P. Stine, A. Hollander, R. Walker, M. Bueno. C. Cogan & V. Gray. 1991. Geographic Information Systems Analysis of Biodiversity in California. Final Report—Year I. Department of Geography, University of California, Santa Barbara.

———, P. A. Stine, D. M. Stoms, M. I. Borchert & A. D. Hollander. 1995. Gap analysis of the actual vegetation of California: 1. The southwest region. Madroño 42: 40–78.

Drake, J. & D. Faber-Langendoen. 1997. An Alliance Level Classification of the Vegetation of the Midwestern United States. A report prepared by The Nature Conservancy Midwest Conservation Science Department for the University of Idaho Cooperative Fish and Wildlife Research Unit. The Nature Conservancy Midwest Regional Office, Minneapolis, Minnesota.

Edwards, T. C., Jr. 1995. Data defensibility and gap analysis. Letter. BioScience 46: 74–75.

———, C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey & D. W. Wight. 1995. Utah Gap Analysis: An Environmental Information System. Final project report 95-1. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

———, ———, ———, A. Falconer, R. D. Ramsey & D. W. Wright. 1996. Adequacy of wildlife habitat relationships models estimating spatial distributions on terrestrial vertebrates. Conservation. Biol. 10: 63–270.

Eyre, F. H. (editor). 1980. Forest Cover Types of the United States and Canada. Society of American Foresters, Washington, D.C.

FGDC (Federal Geographic Data Committee). 1996. FGDC Vegetation Classification and Information Standards. U.S. Geological Survey, MS 590 National Center, Reston, Virginia.

———. 1997. FGDC Vegetation Classification and Information Standards. Federal Geographic Data Committee, U.S. Geological Survey, Reston, Virginia.

Grossman, D., K. L. Goodin, X. Li, C. Wisnewski, D. Faber-Langendoen, M. Anderson, L. Sneddon, D. Allard, M. Gallyoun & A. Weakley. 1994. Standardized National Vegetation Classification System. Report by The Nature Conservancy and Environmental Systems Research Institute for the NBS/NPS Vegetation Mapping Program. National Biological Service, Denver, Colorado.

Hawken, P. 1993. The Ecology of Commerce. Harper Collins, New York.

Heywood, V. H. (editor). 1995. Global Biodiversity Assessment. Cambridge Univ. Press, Cambridge.

Jennings, M. D. 1993. Natural Terrestrial Cover Classification: Assumptions and Definitions. Gap Analysis Technical Bulletin 2. Idaho Cooperative Fish and Wildlife Research Unit, Moscow, Idaho.

———. 1995. A confluence of biology, ecology, and geography for the management of biological resources. Wildlife Soc. Bull. 23(4): 658–662.

——— & J. M. Scott. 1993. Building a macroscope: How well do places managed for biodiversity match reality? Renewable Resources J. 11: 16–20.

———, E. Brackney, P. Crist & R. Sorbel. 1996. Gap Analysis Program 1995 and 1995 Status Report. USGS Gap Analysis Program, Moscow, Idaho.

Klopatek, J. M., R. J. Olson, C. J. Emerson & J. C. Jones. 1979. Land-use conflicts with natural vegetation in the United States. Environm. Conservation 6: 191–199.

Küchler, A. W. & I. S. Zonneveld (editors). 1988. Vegetation Mapping. Kluwer Academic Publishers, Boston.

Levin, S. A. 1981. The problem of pattern and scale in ecology. Ecology 73: 1942–1968.

Lillisand, T. M. 1996. A protocol for satellite-based land-cover classification in the upper Midwest. Pp. 103–118 *in* J. M. Scott, T. H. Tear & F. W. Davis (editors), Gap Analysis, A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Loucks, O. L. 1995. Special committee on vegetation classification annual report. Bull. Ecol. Soc. Amer. 76: 221–223.

———. 1996. 100 years after Colles: A national classification for vegetation. Bull. Ecol. Soc. Amer. 77: 75–76.

Noss, R. F. & A. Y. Cooperrider. 1994. Saving Nature's Legacy. Island Press, Washington, D.C.

———, T. E. LaRoe III & J. M. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biol. Rep. 28. U.S. Dept. of the Interior. National Biological Service, Washington, D.C.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide & T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Monographs in Population Biology No. 23. Princeton Univ. Press, Princeton.

Orians, G. H. 1993. Endangered at what level? Ecol. Applications 20: 206–208.

Scott, J. M., B. Csuti, J. D. Jacobi & J. E. Estes. 1987. Species richness: A geographical approach to protecting biodiversity. BioScience 37: 782–788.

———, F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, Jr., J. Ulliman & G. Wright. 1993. Gap analysis: A geographic approach to protection of biological diversity. Wildlife Monogr. 123.

———, M. D. Jennings, R. G. Wright & B. Csuti. 1995. Landscape approaches to mapping biodiversity. Letter. BioScience 46: 74–75.

———, T. H. Tear & F. W. Davis (editors). 1996. Gap Analysis, A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Short, H. L. & J. B. Hestbeck. 1995. National biotic resource inventories and GAP analysis. BioScience 45: 535–539.

Slaymaker, D. M., K. M. L. Jones, C. R. Griffin & J. T. Finn. 1996. Mapping deciduous forests in southern New England using aerial videography and hyper clustered multitemporal landsat TM imagery. Pp. 87–101 *in* J. M. Scott, T. H. Tear & F. W. Davis (editors), Gap Analysis, A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Sneddon, L., M. Anderson & K. Metzler. 1994. A Classification and Description of Terrestrial Community Alliances in The Nature Conservancy's Eastern Region: First Approximation. A report prepared for the National Gap Analysis Program, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow.

Stoms, D. M. 1994. Scale dependence of species richness maps. The Professional Geographer 46: 346–358.

——— & J. E. Estes. 1993. A remote sensing research agenda for mapping and monitoring biodiversity. Int. J. Remote Sensing 14: 1839–1860.

Tear, T. H., J. M. Scott, P. Hayward & B. Griffith. 1993. Status and prospects for success of the Endangered Species Act: A look at recovery plans. Science 262: 976–977.

Thomas, K. A. & F. W. Davis. 1996. Applications of gap analysis data in the Mojave Desert of California. Pp. 209–220 *in* J. M. Scott, T. H. Tear & F. W. Davis (editors), Gap Analysis, A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope & R. Westbrooks. 1996. Biological invasions as global environmental change. Amer. Sci. 84: 486–478.

———, H. A. Mooney, J. Lubchenco & J. M. Melillo. 1997. Human domination of earth's ecosystems. Science 277: 494–499.

Weakley, A. S., K. D. Patterson, S. Landaal & M. Gallyoun. 1996. International Classification of Ecological Communities: Terrestrial Vegetation of the Southeastern United States. Working draft of April 1966. The Nature Conservancy, Southeastern Regional Office, Chapel Hill, North Carolina.

———, ———, ——— & ———. 1997. An Alliance Level Classification of the Vegetation of the Southeastern United States. A report prepared by The Nature Conservancy Southeastern Regional Office for the University of Idaho Cooperative Fish and Wildlife Research Unit. The Nature Conservancy Southeastern Regional Office, Chapel Hill, North Carolina.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279–338.

———. 1977. Species diversity in land communities. Evol. Biol. 10: 1–67.

Wiens, J. A. 1989. The Ecology of Bird Communities. Vol 2. Processes and Variations. Cambridge Univ. Press, New York.

Wright, R. G., J. L. MacCracken & J. Hall. 1994. An ecological evaluation of proposed new conservation areas in Idaho: Evaluating proposed Idaho national parks. Conservation Biol. 8: 207–216.

Appendix 1. A Sample Description of a Community Alliance Vegetation Type (from Sneddon, 1994)

I. Class: Forest
  I.C. Subclass: Mixed evergreen and deciduous forest
    I.C.3. Group: Mixed needle-leaved evergreen and cold deciduous forest
      I.C.3.N. Subgroup: Natural/Seminatural vegetation (not cultivated)
        I.C.3.N.a. Formation: Mixed needle-leaved evergreen and cold deciduous upland forest
          I.C.3.N.a.b. Community Alliance: *Tsuga canadensis–Acer saccharum–Betula alleghaniensis* Forest Alliance

Description: Eastern hemlock, sugar maple, yellow birch, forest alliance: Forests of this alliance include mesic communities known as "hemlock ravine" and "hemlock-northern hardwoods." Communities of this alliance generally occur in mesic ravines, north-facing slopes, and other cool, moist habitats. They contain substantial amounts of *Tsuga canadensis*, as well as other components of the northern hardwood forest, most commonly *Betula allegheniensis*, as well as *Acer saccharum* and *Fagus grandifolia*. *Tsuga* may be dominant, particularly in ravines, and *Prunis serotina* is a major component in the Allegheny Mountains. Other canopy associates include *Betula lenta*, occasional *Pinus strobus*, and *Picea rubens* in northern New England. *Viburnum alnifolium*, *Diervilla lonicera*, *Sambucus pubens*, and *Taxus canadensis* occur in these communities; *Rhododendron maximum* is particularly characteristic in southern representatives of this alliance. Herbaceous flora may be sparse, but generally includes *Mitchella repens*, *Oxalis montana*, *Lycopodium lucidulum*, *Streptopus roseus*, *Medeola virginiana*, *Epigaea repens*, and *Maianthemum canadense*.

SAF type 24, Hemlock,—Yellow Birch is more or less synonymous with this alliance.

Regional Distribution: This alliance occurs in all Eastern Region states except Delaware. It also occurs in the Midwest Region and locally at higher elevations in the Southeast Region. The full range of this alliance is quite broad and is likely to be more or less coincident of that given for SAF type 24, Hemlock–Yellow Birch: central and southern Ontario, southern Quebec, south to Wisconsin and Michigan, and Cape Breton, south on the Allegheny and Catskill Mountains, central New England and the Appalachians, south discontinuously on the southern Appalachians (Eyre, 1980).

WHAT SATELLITE IMAGERY AND LARGE-SCALE FIELD STUDIES CAN TELL ABOUT BIODIVERSITY PATTERNS IN AMAZONIAN FORESTS[1]

Hanna Tuomisto[2]

ABSTRACT

The great problem in biodiversity studies in Amazonia is that the existing data are regionally very biased, whether the question is about species distribution patterns, local species diversity levels, or differences in species diversity and species composition among sites. The surroundings of a few cities and biological stations are relatively well inventoried, while most of Amazonia still remains unknown in these respects. The essential questions are, to what extent can these data be extrapolated, and from where do we most urgently need more data? Quantifying biodiversity is not just a question of how many species there are in one hectare. It is also a question of how many different habitats there are, how much the floras of the different habitats differ from each other, and how many species there are in a given region as a whole. Satellite images are invaluable in studying such regional variability, because they provide an overview of wide areas, even inaccessible ones. The color patterns in satellite imagery enable one to identify and map areas that differ in some way; field studies are then needed to find out whether these differences are significant in ecological and floristic terms. Satellite imagery from Peruvian Amazonia shows variation to such an extent that hundreds of sites need to be studied to document and understand it. Because it would take too much time to identify the thousand or so plant species that can be found in a single hectare of forest, we have developed an inventory method based on indicator species. This makes it possible to monitor large areas relatively rapidly and has revealed some intriguing ecological and biodiversity patterns in Amazonia.

Amazonia comprises a huge block of tropical rainforest, and in spite of the relatively dense network of navigable rivers and the active roadbuilding in some areas, most parts of it are practically inaccessible, at least within the time and budget limits of an average biological field trip. No wonder, therefore, that biological inventories have been heavily concentrated on very few spots, which have then become famous inventory sites that everyone working in Amazonia wishes to visit. In southern Peru we have Cocha Cashu and Tambopata biological stations, with high levels of bird and butterfly species richness. In northern Peru we have the Mishana and Yanamono sites, which had the highest tree species diversity per hectare (Gentry, 1988) until a few years ago, when the 1-ha tree inventory in Cuyabeno (eastern Ecuador) was completed and set the new world record, 307 species (> 10 cm DBH; Valencia et al., 1994). Ecuador also hosts the second 50-ha tree plot in the Neotropics, which is now being established in the Yasuni National Park and is surpassing diversity estimates (Robin B. Foster, pers. comm.). In Colombian Amazonia there is Araracuara with impressive bird and tree diversities, and in central Brazil there is Manaus, with a high species richness in all groups. These are just a few of the most important sites.

In spite of the dedicated efforts of many field biologists, the total area of forest that has been thoroughly inventoried at these sites is vanishingly small, only a few square kilometers out of the 5 million in Amazonia, and no one knows what there is between these well-visited sites. The situation is like having to map plant diversity of North America on the basis of a few tree inventory plots made, say, in northern California, Yellowstone National Park, and the surroundings of the Niagara Falls, plus some general collections concentrated along the road between New York City and Washington, D.C. So what can we really learn about biodiversity in

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Amazonia on such a basis? Are the established sites truly the hotspots of biodiversity, or is the high number of species found in them only a function of the high amount of collecting effort that has been invested (Nelson et al., 1990)?

In a situation like this, there are many questions one would like to get an answer for. The most fundamental of all is: To what extent can we generalize the results from the sites we know something about? In the case of plant diversity, this translates into finding out whether there are floristically different vegetation types involved, and if so, how these can be characterized and mapped. Quantifying biodiversity in general is not just a question of how many species there are in a hectare. It is also a question of how many different habitats there are, how much the floras of the different habitats differ from each other, and how many species there are in a given region as a whole.

This is where satellite imagery comes into the picture. Since satellite images cover practically the whole earth, they can provide information on even the most remote rainforest areas, and in such a way that an overview of wide areas can be obtained at a glance. The color patterns in the satellite images are created by local differences in how the ground cover reflects sunlight, which depends on many physical properties, such as vegetation structure, color of plant leaves, presence of surface water, presence of bare soil or rock, and many more. Because of this physical basis, it is a relatively safe assumption that whenever there is a color difference between two parts of a single satellite image, there is also some physical difference between the corresponding sites in the field. This is the good news. The bad news is that it is usually impossible to know what these physical differences are unless one has visited the sites in the field. In Amazonia, the only easily recognizable ground cover categories are rivers, cities, roads, and vegetation; also cultivated areas can usually be recognized by their characteristic shape. But to find out more detailed properties of the vegetation (natural or cultivated) at a given site, one needs ground truthing or aerial photographs. Even such a trivial question as whether the vegetation is forest or not cannot be solved on the basis of a satellite image alone; the spatial resolution of the images is not detailed enough to show structural details like trees.

This is why large-scale field studies are needed. Properly processed satellite images soon reveal that even the continuous rainforest is not homogeneous, but rather shows itself as a bewildering mosaic of patches that come in different colors, sizes, and shapes. It is the task of the field studies to find out how each of the reflectance patterns can be interpreted in ecological and floristic terms. Do the differences in reflectance correspond to floristic differences? Does the degree of reflectance difference reveal the degree of floristic difference? Which are the species that actually occur in each of the recognizable patches? How many different habitats are there in the area as a whole? How many species are there in the area as a whole? How are the different habitats distributed? How restricted are the distributions of the plant species in relation to the habitats?

All these questions can be answered, at least to some degree, if the field studies cover enough area and are carefully planned with the help of the satellite imagery. Field inventories need to include sites in landscape patches with different reflectances to document the differences, but they also need to include some sites in similar patches to document how homogeneous these are. And the inventories need to be rapid; it is not feasible to spend several months at a single site, if there are hundreds of sites to be inventoried. This paper will present results of studies that have been conducted in the northern part of Peruvian Amazonia with these objectives in mind.

BASICS OF SATELLITE IMAGERY

There is an ever-growing body of literature about satellites and satellite images, but much of it is rather technical and therefore alien to the majority of botanists who are not specialized in this particular field. The purpose of this paper is to give the reader an idea of the potential and the problems involved in the use of satellite imagery in vegetation and biodiversity studies by giving a short introduction to those aspects of satellite images that are most relevant in this context. More complete technical accounts can be found in, for example, Harris (1987), Mather (1987), and Lillesand and Kiefer (1994).

The physical basis of satellite images is quite simple: the satellite carries sensors that scan the ground and record the intensity of reflected sunlight. The smallest unit of observation is a pixel, the size of which depends on the kind of satellite and sensor used. In Landsat satellites, which are the most widely used satellites in vegetation studies, each pixel roughly corresponds to a square 80 m by 80 m on the ground when MSS (multispectral scanner) sensors are used, and to 30 m by 30 m when the more advanced TM (thematic mapper) sensors are used. While scanning the terrain, the sensors essentially measure the average reflectance

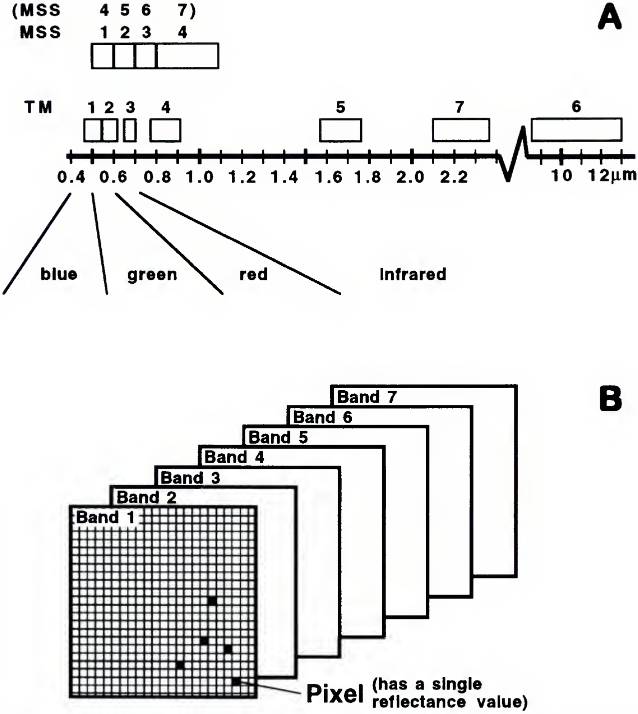

Figure 1. —A. The bands in Landsat MSS and TM data. The numbering of MSS bands has been changed, and therefore older images use a different numbering system (shown in parenthesis) than more recent images. —B. Schematic representation of the data structure in Landsat TM imagery, where each of the seven wavelength bands is recorded in its own data file.

of each pixel on a relative scale and store the measured value into the cell corresponding to that pixel in a spreadsheet database (Fig. 1). In the process, any details smaller than the pixel are lost, and afterward it is impossible to see on the image if a particular pixel contained, say, a house or a group of trees or open field. If such details are needed, they have to be obtained from other sources, like field studies or aerial photographs.

In the satellite, there are several spreadsheets being filled in simultaneously, each by its own sensor that records the reflectance in a certain wavelength band. The MSS is equipped with sensors to observe four bands, and the TM has sensors for seven bands, including both visible and infrared wavelengths (Fig. 1). Any of the bands in a satellite image can be viewed on a computer screen with the help of an image analysis program. The computer is then told to use the spreadsheet corresponding to the desired band, for example, the one recording green, and to convert the numerical information back to light intensities, in this case to the intensity of illumination of the pixels on a computer screen. The result is a map where those pixels that had a high reflectance for green on the ground are displayed bright on the computer screen, and those that had low reflectance are displayed dark. At this stage, it is possible to choose any color for the display. The original green can be displayed as green, but it can equally well be displayed as red or blue or (most commonly) gray. It is irrelevant which color is chosen, because the information is here conveyed by the relative brightness of the pixels, not their hue.

Different bands show somewhat different information, because not all surfaces reflect the different wavelengths in a similar way. For example, water tends to absorb infrared, but to have a high reflectance for visible wavelengths, especially blue. Therefore open water areas can appear almost black in images created using the infrared bands, but very bright in images that use the bands of visible wavelengths. Vegetation, on the other hand, has high reflectance for infrared, but very low reflectance for visible wavelengths, especially red and blue, because these are absorbed and used in photosynthesis. Because of these differences, it is usually desirable to view several bands at once to get a better idea of the overall spectral variation in the study area. The easiest way of doing this is to make a color composite using three of the available wavelength bands.

Three bands can be used simultaneously because each pixel on a color computer screen can be thought of as a group of three lamps: red, green, and blue. The hue and brightness of a pixel depend on which of these lamps are lit and how brightly they shine. For example, if only blue is lit, the pixel will appear blue; if red and green shine at equal intensities but blue is not lit at all, the result is yellow, and if the intensity of red is increased relative to the intensity of green, the hue becomes progressively more orange and finally red.

In the process of making a color composite, the computer produces a map with each of the desired bands, assigns each of these to its own color on the screen, and displays the three maps simultaneously on top of each other to produce a full-color image. On displaying a TM image, for example, the reflectance values of band 3 can control the intensities of red on the screen; band 4 can control green, and band 5 can control blue. Obviously there are many other possible combinations that can be used. In fact, because different bands convey different information and hence show partly different patterns in the image, the choice of the band combination is very important. Patterns in an image created with bands 4, 5, and 7 are somewhat different than those in an image created with bands 1, 2, and 3. For vegetation studies, the most useful color composites are often obtained by combining two near-infrared bands with one visible-light band.

It is important to keep in mind that the actual colors of the final satellite image product have no absolute meaning: they depend on the arbitrary decision on which of the chosen bands was assigned to which of the colors on the computer screen, and as long as the same band combination is used, changing the color assignments makes no difference for the information content of the image although the overall color of the image may change drastically. Of course some color combinations look more pleasing than others and are therefore more commonly used.

In densely vegetated areas with little surface relief, such as lowland Amazonia, most of the surface is green. From an airplane, such areas look rather monotonous with few eye-catching features, and so they look from a satellite, too. This is because there are no big differences in surface reflectance from one site to another, and therefore most of the pixels have reflectance values that are very similar and only represent a narrow range of the possible intensities that the satellite sensor is capable of recording. Consequently, a color composite created with the original satellite data looks relatively homogeneous: there may be a hint of a pattern there, but if the differences in intensity are not big enough, they cannot be confidently recognized or mapped.

Image enhancement is the solution to this problem. There are several ways of enhancing an image, but the main purpose of all of them is to make more efficient use of the different light intensities a computer is able to display. Instead of using just the narrow range of intensities that were recorded in the original spreadsheets of the satellite image, the computer recalculates the reflectance value for each pixel in such a way that the differences are exaggerated and a wider range of possible intensities is used on the computer screen. The process can be compared to adjusting the contrast on a TV screen: if contrast is too low, all patterns on the screen seem fuzzy; if contrast is too high, details are lost; when contrast is optimized, the patterns become clear and easy to recognize.

A more advanced phase in the digital analysis of satellite imagery is the automatic classification of the image to different ground-cover types. There are two principally different methods that can be used to obtain a computer-classified image: supervised and unsupervised classification procedures. In supervised classification, the user selects groups of pixels that represent the different ground-cover types in the area, and the computer then assigns each of the remaining pixels to one of these classes. In unsupervised classification, the user defines either the number of classes she wants to obtain, or the amount of variation to be allowed within any one class. The computer then creates as many classes as are needed and assigns each pixel to one of these.

Unfortunately, a general drawback of digital classification is the very low reliability of classification within the rainforest realm (see discussion in Tuomisto et al., 1994). Relatively good results can be obtained in areas where there are clear structural differences among the ground-cover types, such as exist among savannas, swamps, and closed-canopy forests. However, distinguishing among different kinds of closed-canopy forest is much more difficult, and hence the degree of error is higher. Another source of error is that, even if the study area is unexplored in the field and it is unknown how many vegetation types there are, the user has to define either the number of classes or the variation allowed within each class prior to analysis. In this way, user-induced bias is easily incorporated into the results, although digital analysis is often advocated as an "objective" method.

A great advantage of unclassified images is that the researcher can be fairly certain that all the patterns that are visible in the product really exist in nature. Fieldwork may later show that not all of them are relevant for the questions at hand, or that some true differences were not recognized, but the risk of creating artificial patterns is small.

Indeed, unclassified but enhanced image products have proved especially useful for the monitoring of large and unexplored rainforest areas, since they are able to reveal spatial patterns whose existence has previously been unknown (Townshend et al., 1987; Kalliola et al., 1991; Tuomisto et al., 1994; Tuomisto et al., 1995). Consequently, such satellite images can be efficiently used in fieldwork planning: they can help in locating sites that represent formerly uninventoried or otherwise interesting vegetation, and they can also indicate to what extent results of fieldwork at any given location can be extrapolated to other locations. For these reasons, the term "satellite imagery" is used in the following text to mean "enhanced, unclassified satellite imagery."

MATERIAL AND METHODS

A preliminary interpretation of satellite imagery was used to identify units that were suspected to harbor different kinds of rainforest vegetation in the northern part of Peruvian Amazonia. An attempt was then made to select field study sites so that as many of these units as possible were sampled, while attention was also paid to the adequate geographical distribution of the samples. Initially the satellite image interpretation was based on a Landsat MSS scene from 1983 centered around the city of Iquitos (published in Tuomisto et al., 1994), but later a more recent TM scene (from 1993, to be published elsewhere) became available, as well as TM scenes for adjacent areas. The scale of the images used in the visual interpretation was 1:250,000.

The exact locations of the field study sites were chosen with the help of the satellite imagery so as to be both representative of interesting-looking landscape patches (or border zones between patches) and practically accessible by roads or navigable rivers. The primary purpose of the study was to document variation within *tierra firme* (non-inundated) forests, so swamps and seasonally inundated areas were excluded from the sampling whenever they were large enough to be identifiable in the satellite images. However, small swamps in depressions between adjacent hills and floodplains of small creeks occur throughout *tierra firme*, and these were included as a part of the natural variation within the landscape.

The present paper will concentrate on documenting distribution patterns of pteridophytes. In earlier studies (Tuomisto et al., 1995; Ruokolainen et al., 1997) we have found that pteridophytes and the Melastomataceae can be used as indicators of more general floristic patterns, because the floristic similarities among sites as measured with either pteridophytes or the Melastomataceae show a very high correlation with the floristic similarities as measured with trees: the correlation between pteridophytes and trees can exceed 0.8 (Mantel test, $P < 0.001$; Ruokolainen et al., 1997). This is very practical for large-scale vegetation studies, where it is necessary that the sampling at any one site is floristically representative enough to justify regional comparisons. Both pteridophytes and the Melastomataceae are easy to identify and collect compared to trees, because they are smaller in size and include far fewer species. Indeed, the high species diversity of trees makes tree sampling and identification especially laborious, and the number of individuals observed per tree species in any one sample plot is often low (Campbell et al., 1986; Balslev et al., 1987; Gentry, 1988; Valencia et al., 1994; Duivenvoorden & Lips, 1993, 1995; Ruokolainen et al., 1997; see also Clark, 1998, this volume). Consequently, chance can have a great impact on the observed floristic composition, and it is difficult

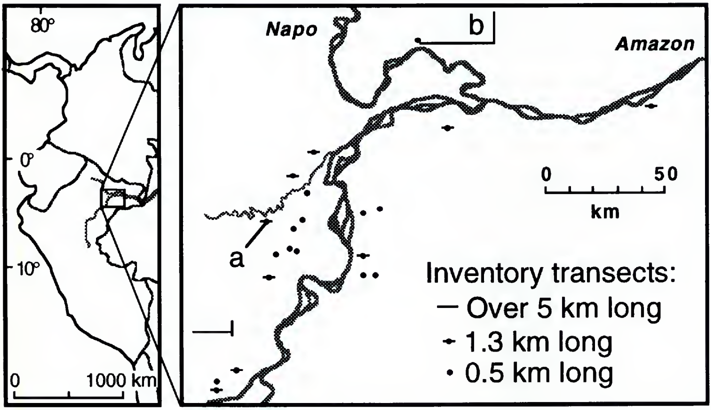

Figure 2. Map of the study area in Peruvian Amazonia with the locations of 23 inventory transects. The transects in Mishana (a) and Sucusari (b) are discussed in detail in the text.

to unravel ecological patterns in the tree species distributions. Focusing the inventories on suitable indicator species makes it possible to sample larger areas and more individuals per species in a shorter time, and consequently it becomes more feasible to work out the possible edaphic preferences of each species. It also becomes possible to evaluate with a higher certainty whether two samples actually belong to the same forest type or not, because each sample contains a higher proportion of the local species pool and the observed similarity patterns are hence more robust.

Because the study was aimed at finding out to what extent edaphic conditions influence the distribution of plant species, sampling was done along continuous, finely subdivided transects. This made it possible to directly compare the changes in floristic composition, species abundance patterns, and environmental variables (such as the nutrient content, texture, and drainage of the soil). Several soil samples were taken from each site for chemical analyses in order to quantify the edaphic differences among and within sites. Details on these analyses will be published elsewhere (Ruokolainen et al., 1997, in prep.).

In all, 23 transects were sampled (Fig. 2), totaling almost 83 km or 22 ha. In most cases, the transects were selected within a uniform area of rainforest as judged from the satellite imagery, but four of the transects were placed so that they crossed one or several boundaries that were visible in the imagery. These were Mishana (marked with "a" in Fig. 2), Trece de Febrero (15 km S of Mishana), Sucusari (marked with "b" in Fig. 2) and Carbajal (> 20-km transect in the SW corner of the study area).

At each of the fieldwork sites, one of four alternative sampling procedures was followed, depending on the degree of detail required and the time available for studying the site. The field procedures were (1) 500-m-long qualitative transect, (2) 500-m-long quantitative transect, (3) 1300-m-long quantitative transect, and (4) several-km-long semiquantitative transect. In all procedures, the baseline followed a predetermined compass direction (with allowance made for a 90° angle in four cases). The short transects (less than 2 km long) were 5 m wide, and the longer transects were 2 m wide. In the qualitative transects, a list was obtained of those pteridophyte species that occurred within an estimated 2.5 m on either side of the baseline. The quantitative transects were subdivided into contiguous 5 m by 5 m subunits, and the corners of each subunit were marked; within each subunit, the individuals of each pteridophyte species were counted. The semiquantitative transects were divided into subunits 100 m long, and for each subunit the presence of pteridophytes within an estimated 2 m on the left side of the baseline was recorded. In the first transect (Mishana, marked with "a" in Fig. 2), no size limit was applied to the pteridophytes, but in the subsequent transects only pteridophytes with at least one leaf longer than 10 cm were taken into account in order to reduce the time spent on looking for and identifying tiny plantlets. Pteridophytes with leaves less than 5 cm long were excluded from the Mishana data before analysis for the present paper. Epiphytes and climbers were only included if they had green leaves at a height less than 2 m above ground.

Nomenclature of the pteridophyte species is mainly in accordance with the revision of the genus *Lindsaea* (Kramer, 1957) and *Pteridophyta of Peru* (Tryon & Stolze, 1989–1994). However, *Lindsaea lancea* (L.) Bedd. var. *lancea* and *L. lancea* var. *falcata* (Dryand.) Rosenst. are in the present paper treated as good species rather than varieties, because (1) they are easy to recognize in the field at any size > 3 cm, (2) they differ ecologically (*L. falcata* Dryand. grows mainly on decaying wood or litter while *L. lancea* is mainly terrestrial), and (3) they maintain their distinctness even when occurring at the same site and on the same substrate.

RESULTS AND DISCUSSION

DIVERSITY PATTERNS IN PTERIDOPHYTES

The fern genus *Lindsaea* provides an interesting example of diversity patterns at different spatial scales. The 23 transects (Fig. 2) harbored a total of 11 *Lindsaea* species, all of which occurred at more than one site. The number of species at any one site ranged between zero and six, and up to nine species were found in the very long transects (Fig. 3A). Transect length obviously contributed to the high *Lindsaea* species richness of the two longest transects, but among the 0.5–1.3-km-long transects there was no consistent relationship between sample size and number of species found. If only the geographical distribution of the diversity values is observed, it is hard to find any regular pattern in the species richness patterns.

A much clearer picture emerges when the soil characteristics of the sites are also taken into account, because these were clearly related to whether a particular species was present or absent at a given site. One of the species thrives on clay soils that are rich in nutrients (*Lindsaea phassa* K. U. Kramer; Fig. 3B), while two species are restricted to nutrient-poor sandy soils (*L. hemiglossa* K. U. Kramer and *L. tetraptera* K. U. Kramer; Fig. 3K, L). One species can be characterized as a generalist (*L. divaricata* Klotzsch; Fig. 3C), as it can be found almost anywhere save the very poorest and the very richest soils of the region (however, there is some indication that there are actually two closely related forms with different edaphic preferences involved). All the other species are confined to the relatively poor loamy soils, but even among these species there are some interesting differences in distribution patterns. For example, *Lindsaea bolivarensis* V. Marcano and *L. taeniata* K. U. Kramer are both relatively frequent at some loamy soil sites, but they rarely occur at the same site (Fig. 3H, I).

The general ecological pattern that arises is that there are more *Lindsaea* species adapted to poor soils than to rich soils, and that the genus is also locally most diverse on relatively poor loamy soils. Indeed, the only site with no *Lindsaea* species at all has the richest soils of the 23 sites, and the 3 sites that only had one species each (this species was invariably *L. phassa*) are all among the rich-soil sites. All sites with intermediate to poor soils had more than two species each.

It is important to notice here that terms such as "poor" and "rich" should be understood so that they only refer to the relative soil fertility of the 23 sites reported here, and that they do not imply "poorness" or "richness" in a wider context. The present study was conducted in a limited geographical area, and the sampling is far from complete even for that area. Therefore, it is almost certain that the sites discussed here do not represent the full range of existing soil variation in Western Amazonia, so no matter whether the sites are here called poor or rich, they might all just become "intermediate" if more sites were to be included in the comparison.

In some cases it is obvious that internal heterogeneity within a single transect contributed to the high number of species present. Among the short transects, the most obvious example of this phenomenon is the transect close to the village of Mishana (marked "a" in Fig. 2). This transect crossed the boundary between intermediate loamy-clayey soil to poor sandy soil at about 600 m from the beginning of the transect (Fig. 4; further details on floristic and soil changes at this edaphic boundary have been published in Tuomisto & Ruokolainen, 1994). At that same point, the dominant *Lindsaea* species changed from *L. lancea* (on loamy soil) to *L. divaricata* (on sandy soil). *Lindsaea falcata* was abundant close to the transition zone, with a few individuals at the end of the sandy part. The favored substrate of this species appears to be dead plant material, as it is usually found either on decaying wood or on microsites with thick litter and humus layers. The same is true for *L. guianensis* (Aubl.) Dryand., which is most commonly found on decaying tree trunks. This behavior may explain

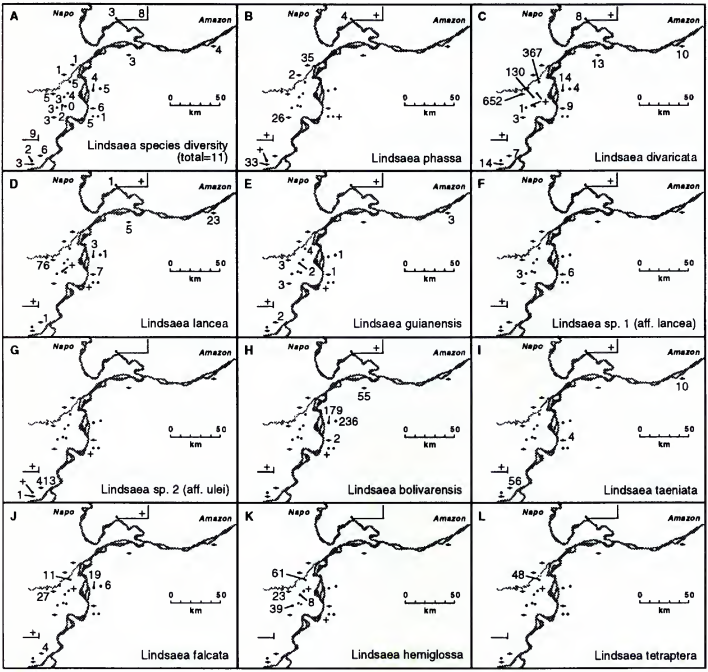

Figure 3. —A. Number of *Lindsaea* species in each of 23 inventory transects. —B–L. Number of individuals of each *Lindsaea* species found in the transects. + indicates that the species was present but the number of individuals was not recorded. The species are shown approximately in the order of decreasing requirements for soil fertility.

why *L. guianensis* is found at sites with widely different soil characteristics and can co-occur with such ecologically different species as *L. phassa* and *L. hemiglossa* (compare Fig. 3E with 3B and 3K). The fifth species found in Mishana was *L. hemiglossa*, which was restricted to the sandy soil at the end of the transect in accordance with its preference for sandy soils at other sites (Figs. 3K, 4).

At a wider scale, spatial variation in species composition can be observed along a 43-km-long transect starting from the river Sucusari (marked "b" in Fig. 2). The most eye-catching feature of the satellite image covering the area is the alteration of lighter and darker patches, which corresponds roughly to the alteration of topographies with lower and higher hills, respectively. The transect harbored a total of eight *Lindsaea* species, the distributions of which are shown in Figure 5. As it turned out, transect sections with lower topography tended to have clayey soils, while in the more hilly sections the soils were loamy and poorer in nutrients (the satellite image and the details of the soil analyses will be published elsewhere; Ruokolainen et al., in prep.).

The soil differences were clearly reflected in the species distribution patterns. The distribution of *Lindsaea phassa* was again unlike those of the other species: it was relatively frequent in the beginning and the end of the transect, but entirely lacking in the hilly stretch between km 23 and 38. *Lindsaea taeniata, L. lancea,* and *L. divaricata* were also uncommon in this area, but showed otherwise more

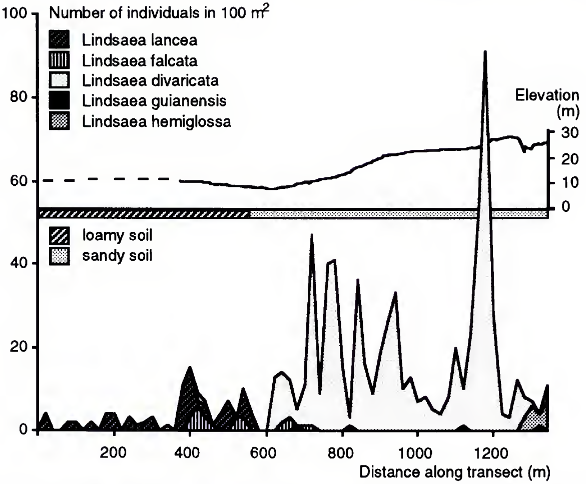

Figure 4. Spatial variation in the abundance of the *Lindsaea* species that were found in the transect in Mishana (for geographic location, see Fig. 2).

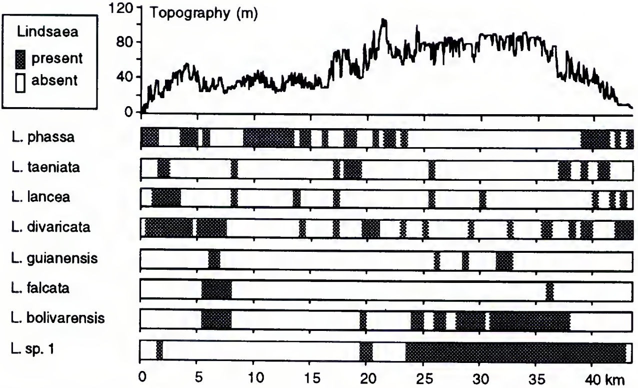

Figure 5. Spatial variation in the occurrence of the *Lindsaea* species that were found in the transect in Sucusari (for geographic location, see Fig. 2).

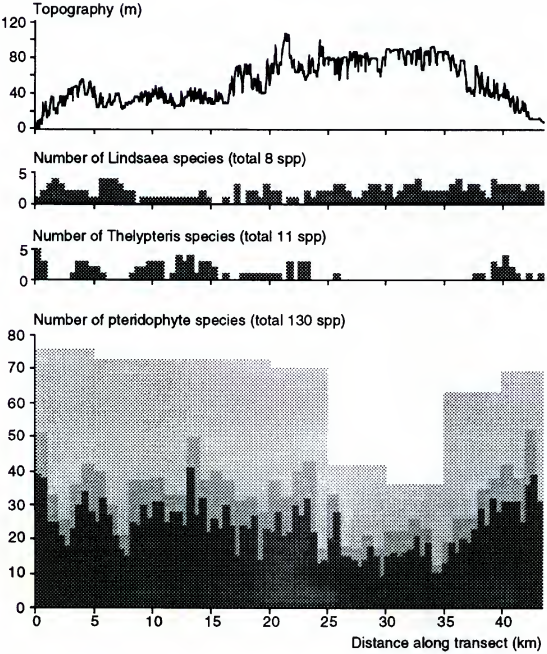

Figure 6. Spatial variation in the species diversity of *Lindsaea*, *Thelypteris*, and pteridophytes in general along the transect in Sucusari (for geographic location, see Fig. 2). For *Lindsaea* and *Thelypteris*, species richness is calculated in sample units 500 m long, and for overall pteridophyte species richness in units 500 m, 1000 m, and 5000 m long.

scattered distributions, and were often present in subunits where *L. phassa* was lacking. The remaining four species were essentially present where *L. phassa* was absent, i.e., in the loamy-soil sections of the transect. *Lindsaea bolivarensis* and an unidentified species of *Lindsaea* were almost confined to the high hills around km 30.

Although the local species richness of the genus *Lindsaea* tends to be higher on poor soils than on rich soils, this is by no means a universal pattern. For example *Thelypteris*, another species-rich fern genus, shows the opposite trend. In the Sucusari transect, *Thelypteris* had no species at all on poor soils, and by far most of the species were found on rich soils (Fig. 6).

The diversity pattern of *Thelypteris* was paralleled by many other fern genera, with the result that the overall species richness of pteridophytes was clearly higher in rich-soil sections than in poor-soil sections of the Sucusari transect (Fig. 6). This result was found at several different spatial scales. When subunits of 500 m were analyzed, the number of species per subunit ranged between 9 and 41, which is from less than a tenth to almost a third of the total of 130 species in the transect. Obviously the number of species increases with the size of the observed subunits, but even with subunits as long as 5 km, the number of species never exceeded 76 (just over half of the total). In the least species-rich 5-km subunit the number of species was only 36, i.e., less than in the most species-rich 500-m subunits. This shows that diversity patterns depend on local site conditions as much as they do on sampling scales.

The overall tendency for pteridophytes, that species diversity is positively correlated with soil fertility, explains why species diversity and local elevation appear negatively correlated in Figure 6. The geological setting at this particular site is simply such that the poorest soils are found at the highest elevations. Because the Sucusari transect lies entirely within the lowland forest zone (about 100–200 m above sea level), this pattern cannot be explained by the elevation gradient itself: a vertical distance of 120 m is not big enough to cause such elevation-dependent patterns that are found on mountain slopes. The topography is sufficient, however, to expose sediments of different origins and thereby to give rise to significant spatial variation in soils.

ON THE HOMOGENEITY OF THE RAINFOREST

Most *tierra firme* forests are structurally uniform, which is reflected in the paucity of vegetation types recognized for non-inundated areas in Amazonia (e.g., Prance, 1989). Even when this broad category of rainforest is subdivided, attention is usually paid to geomorphology rather than the vegetation itself for the simple reason that geomorphological data are readily available by remote sensing methods, whereas obtaining floristic data requires fieldwork (for examples, see Malleux, 1975; Encarnación, 1985; Duivenvoorden & Lips, 1993; Tuomisto et al., 1994; INRENA, 1995).

When no obvious regional differences have been apparent in *tierra firme*, researchers have tended to assume that these forests are ecologically uniform at broad spatial scales. Therefore, most theories that have attempted to explain the origin and maintenance of Amazonian biodiversity have concentrated on a variety of mainly historical factors. Examples include cyclical changes in climate (Haffer, 1969, 1993; contributions in Prance, 1982; Whitmore & Prance, 1987), intermediate disturbance (Connell, 1978; Salo et al., 1986), random walk (Hubbell & Foster, 1986), and distribution barriers caused by rivers (Hershkovitz, 1968; Salo et al., 1986; Capparella, 1988; Ayres & Clutton-Brock, 1992; Haffer, 1992).

Some researchers have stressed the role of edaphic specialization of plant species in promoting beta-diversity (Gentry, 1981; Young & León, 1989; van der Werff, 1992; Kalliola et al., 1993; Tuomisto & Ruokolainen, 1994; Tuomisto & Poulsen, 1996), but others have argued that the evidence is not yet sufficient to distinguish between random dispersal and edaphic influences (Condit, 1996).

Evidence supporting the ecological differentiation model is accumulating, however. The *Lindsaea* results documented above show that there is systematic floristic variation within the rainforest that can be explained by edaphic specialization of plant species and their differentiated occurrence in different habitats. The pronounced variation in pteridophyte species richness within the Sucusari transect shows also that alpha-diversity can vary considerably among adjacent sites in a predictable manner, even in the absence of physical dispersal barriers. Furthermore, the relationships that were found between local diversity and soils in the plant groups dealt with here (*Lindsaea*, *Thelypteris*, and the pteridoflora in general) seem also to hold for these groups at the continental scale (Tuomisto & Poulsen, 1996). This underlines the difficulty in explaining these patterns by chance alone (cf. Linhart & Grant, 1996).

ESTIMATING SPECIES DIVERSITY

If one wishes to use measured alpha-diversities (species diversity within habitat) to yield estimates of gamma-diversity (species diversity at the regional scale), it is especially important to have a good estimate of beta-diversity (habitat diversity). Reported gamma-diversity (known number of species) in western Amazonia is not strikingly high in relation to the large area involved. The Amazonian lowlands of Ecuador and Peru together cover an area of almost 600,000 km^2, but only 3100 flowering plants are known from Amazonian Ecuador (Renner et al., 1990) and 7000 from Amazonian Peru (Brako & Zarucchi, 1993). However, the three most species-rich 1-ha tree plots in the world are all situated in this region (Cuyabeno: Valencia et al., 1994; Mishana and Yanamono: Gentry, 1988), and they have about 300 tree species each (> 10 cm DBH).

What is the explanation for this discrepancy between spectacularly high alpha-diversity and much more everyday gamma-diversity? Is the forest so homogeneous that species are hyperdispersed, with beta-diversity being very low, or are so many of the existing habitats unknown that a high proportion of the species have remained undiscovered because their habitats have never been inventoried?

Some species have certainly escaped discovery, which is obvious from the fact that new plant species are continuously being described from Amazonia. In the present study, 2 probably undescribed species were found among the total of 11 *Lindsaea* species, which increases the number of known species by 22%. For several reasons, this may not be a very good estimate of the overall proportion of undescribed plant species. The fern flora of the Iquitos region is already relatively well collected and known, so in less well-known areas the proportion of undescribed species may be higher. This assumption is supported by the observation that the sites where the two undescribed species were found have not been included in earlier inventories. Furthermore, fern species are generally widespread and relatively well known in comparison with most other plant groups, and therefore the proportion of undescribed species is probably higher among flowering plants than ferns. Finally, different genera must hide different proportions of undescribed species because of differences in their taxonomic complexity and the unequal taxonomic attention that has been paid to them, and we do not know whether *Lindsaea* gives an overestimate or an underestimate of the average among ferns.

What the *Lindsaea* and other fern data (Tuomisto & Poulsen, 1996) do show quite conclusively is that the species are not hyperdispersed; instead, their distributions reflect edaphic conditions. To some degree similar behavior has been shown among trees, but the tree data are less conclusive because tree sample sizes have been too small to represent the local flora well (e.g., Duivenvoorden & Lips, 1993, 1995; Tuomisto et al., 1995; Ruokolainen et al., 1997).

This being the situation, it can be asked how representative the existing herbarium collections are of the overall regional flora. Only a few sites have been studied intensively enough to warrant the claim that their floras are well known, and even though species typical of the vegetation types found at these sites would be well represented in herbaria, species typical of other vegetation types may be entirely absent. Furthermore, many of the existing data come from general collecting trips, which are concentrated along rivers and roads for obvious reasons of accessibility (Renner et al., 1990), so riparian and pioneer species are probably well represented, while species of the forest interior may be much less collected. Other reasons for missing species include preferred sizes of the plants (shrubs are easy to collect whereas lianas are not) and preferred seasons (plants that are not fertile during the collecting trip are ignored). Also, species that have showy flowers and long flowering or fruiting seasons may be collected with a high frequency, while species with infrequent or inconspicuous flowering tend to go unnoticed. All these sources of error need to be controlled if reliable estimates of species numbers are to be obtained.

It is a general problem in large-scale biodiversity studies in Amazonia and elsewhere that the available herbarium data are not presence-absence data, but rather presence-only data. If a species was found and collected at a given site, it is documented as a herbarium specimen. But if a species was found but not collected at the site, no record of it remains. Therefore it is impossible to distinguish between real absence of a species and apparent absence due to non-collection, which has led to serious biases in defining biodiversity centers in Amazonia (Nelson et al., 1990). This problem can only be solved by systematic sampling efforts that use study plots or other quantifiable methods that provide comparable data for the different sites.

HOW MANY KINDS OF RAINFOREST ARE THERE?

In general, earlier studies have discussed three habitat types within *tierra firme*, differentiated by whether the soil is sand, loam, or clay (Tuomisto et al., 1995; Tuomisto & Poulsen, 1996; Ruokolainen et al., 1997). The same basic division is used in the present paper, with some additional variation being recognized within each of the three main types. The next question is, how well does this represent the variation found in the region? In other words, can we assume "three" to be a reasonable estimate of habitat diversity, or should we expect to find many more habitats if more sites were inventoried? This is a crucial question for biodiversity assessments, but an answer cannot be obtained just by field inventories: the huge amount of work involved especially in tree sampling makes it impossible to establish enough plots to obtain conclusive answers by field surveys alone.

Satellite imagery can efficiently be used to target field inventories, because it reveals both the existing patterns in the landscape, and the easiest ways to access each of the landscape types. Thereby field sampling can be planned so that the amount of effort invested remains reasonable, while the amount of landscape variation that is covered by field inventories is maximized, and unnecessary repetitive sampling within the same landscape type is minimized.

Satellite images give a clear impression of widespread habitat heterogeneity: on the basis of Landsat TM images we have estimated that many more than a hundred biotopes exist in Peruvian Amazonia alone (Tuomisto et al., 1995; see also Kalliola et al., 1991; Räsänen et al., 1993; Tuomisto et al., 1994). The exact number of vegetation types can never be objectively counted (cf. Webb, 1954; Webb et al., 1970; Austin, 1985), but the importance of obtaining some estimate for the number of habitats and the degree of floristic difference among them can hardly be overestimated in studies that aim at assessing total biodiversity of a given region (see, for example, the discussion in Campbell et al., 1986). The number of habitats can be estimated from satellite imagery, but the degree of difference between them can only be established by field surveys. Both components need to be known in order to estimate how high beta-diversity really is.

Gamma-diversity is essentially the product of alpha-diversity and beta-diversity, so it should be obvious that it cannot be reliably estimated unless both of these components are satisfactorily known. Given the current world-wide interest in biodiversity, it is surprising how little attention the problem of estimating beta-diversity has attracted.

It is noteworthy that, in spite of their clear differences, the 23 fern transects reported in the present paper are according to satellite imagery situated in the most uniform part of Peruvian Amazonia (PAUT, 1993; Räsänen et al., 1993; Tuomisto et al., 1995). The reason that the study was initiated there rather than in one of the more heterogeneous areas is that complete satellite imagery was not available at the time when the work was started, and the northern part of the country was the only area where we knew of any edaphic variation at all in the *tierra firme* forests: we were attracted there by the famous white-sand forests of Iquitos (Gentry, 1981; Encarnación, 1985). Since then, it has gradually become obvious that the white sands form only a very small part of the ecological spectrum in the area, and that most of the variation is actually found within the forests on non-sandy soils.

Within Peruvian Amazonia, Landsat images show both general regional patterns and detailed local patterns, all of which can be postulated to represent ecological and floristic variation in the forest. Obviously only a minute part of the variation has been field verified, but to date we have discovered nothing that would contradict this interpretation. It is interesting to note that changes between the biotopes may take place gradually over long distances or more abruptly, and regional variation is found in the relative abundances of the different kinds of ecotones (Tuomisto et al., 1995). In some inundated areas the vegetation patches are elongated in shape and have a uniform general orientation, in others they are narrow and aligned according to the river courses. In *tierra firme* areas, large smooth-edged patches are typical in northern Peru, while smaller and more abrupt patches are frequent in the central to southern parts of the country (Tuomisto et al., 1995). Such differences in landscape structure may have important implications for the biota (Dunning et al., 1992; Taylor et al., 1993), but they have not been paid attention to in either the planning or the interpreting of ecological, floristic, and biodiversity studies in Amazonia.

GEOECOLOGICAL CONSIDERATIONS

Western Amazonia has been the scene of a wide variety of geological events during different eras, which has resulted in considerable heterogeneity of terrain at different hierarchical levels (Salo & Räsänen, 1989; PAUT, 1993; Räsänen et al., 1993). For example, large parts of Peruvian Amazonia have been influenced by sea incursions and fluvial dynamics since the late Cretaceous, and therefore the region consists of a mosaic of edaphically and geomorphologically different areas (Salo et al., 1986; Hoorn, 1993; Räsänen et al., 1987, 1992, 1995). Soil characteristics such as nutrient content, texture, and water permeability are determined, among other things, by the geological formations from which the soils are derived, and by the length of time they have been subject to weathering.

Because of the apparent edaphic specificity of many plant species and habitat types, geological formations with special geochemical characteristics and different ages are especially interesting from ecological and biogeographical points of view. Examples include the Pastaza fan with its Holocene (younger than 10,000 years) volcanoclastic material (Räsänen et al., 1990, 1992) and the Pebas formation with its marine or brackish sediments from the Miocene (Hoorn, 1993; Räsänen et al., 1995). Both of these formations can give rise to soils that are chemically unlike anything else in Amazonia and can therefore be expected to harbor edaphically specialized plant endemics.

It is noteworthy in this context that the Pastaza fan area has been designated an uninteresting area for biodiversity conservation by a workgroup that selected priority areas on the basis of known endemism and diversity centers (Workshop 90, 1991). Very few biological specimens have been collected in the Pastaza swamplands, which has resulted in a low number of known species. However, the geological characteristics of the area suggest that it is ecologically unique and should be prioritized in conservation planning (Kalliola et al., 1996). At the very least, the area should be given special attention when biological collection trips are planned in the future.

CONCLUSIONS

Satellite imagery can be efficiently used in rainforest studies to recognize different habitats and to map their extent even in areas that are difficult to get to in the field. This provides an unparalleled tool for studies whose aim is to reach regional conclusions on species diversity. For this purpose, all the habitats that are recognized in satellite imagery have to be field-documented in order to verify to what degree they are floristically distinct, and to quantify species diversity within each of them. Neither local nor regional species diversity can be read directly from satellite imagery, but once the species composition of each of the different habitats has been clarified, diversity estimates for unvisited areas can be obtained by using satellite imagery to correlate them with one of the already field-documented habitat types.

Indicator species can be used with great success to facilitate recognizing floristically different habitats. Thereby they can also be used to predict distribution and diversity patterns of other plants and animals, but only when it has been clarified by field surveys how these relate to the defined habitats. It is not possible to predict the diversity of such organisms for which this background information is lacking, because different plant and animal groups can show opposing diversity patterns.

Only about a dozen vegetation types are usually recognized in Amazonia, and consequently ecological research results are often generalized as representative of "the tropical rainforest." Satellite image analyses show that the extent of heterogeneity in Peruvian Amazonia is such that extrapolations of field results are not warranted without more detailed vegetation mapping, and there obviously is a great need for well-planned work in this field. It is almost ironic that the digital phase in satellite image analysis can be reduced to running a spectral enhancement and printing a hardcopy of the result, which can be accomplished by an experienced analyst in a few hours. Thereafter, it can easily take an experienced botanist a lifetime to finish the fieldwork needed in order to find out what the different color patterns really mean in terms of the diversity of habitats and species.

Literature Cited

Austin, M. P. 1985. Continuum concept, ordination methods and niche theory. Annual Rev. Ecol. Syst. 16: 39–61.

Ayres, J. M. & T. H. Clutton-Brock. 1992. River boundaries and species range size in Amazonian primates. Amer. Naturalist 140: 531–537.

Balslev, H., J. Luteyn, B. Øllgaard & L. B. Holm-Nielsen. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. Opera Bot. 92: 37–57.

Brako, L. & J. L. Zarucchi. 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru. Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1–1286.

Campbell, D. G., D. C. Daly, G. T. Prance & U. N. Maciel. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. Brittonia 38: 369–393.

Capparella, A. P. 1988. Genetic variation in neotropical birds: Implications for the speciation process. Acta Congr. Int. Ornith. 19: 1658–1664.

Clark, D. A. 1998. Deciphering landscape mosaics of neotropical trees: GIS and systematic sampling provide new views of tropical rainforest diversity. Ann. Missouri Bot. Gard. 85: 18–33.

Condit, R. 1996. Defining and mapping vegetation types in mega-diverse tropical forests. Trends Ecol. Evol. 11: 4–5.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Duivenvoorden, J. F. & J. M. Lips. 1993. Landscape Ecology of the Middle Caqueta Basin. Explanatory notes to the maps. Studies on the Colombian Amazonia III A. Tropenbos Colombia.

——— & ———. 1995. A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. Tropenbos Series 12, 1–438.

Dunning, J. B., B. J. Danielson & H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Encarnación, F. 1985. Introducción a la flora y vegetación de la Amazonia peruana: Estado actual de los estudios, medio natural y ensayo de una clave de determinación de las formaciones vegetales en la llanura amazónica. Candollea 40: 237–252.

Gentry, A. H. 1981. Distributional patterns and an additional species of the *Passiflora vitifolia* complex: Amazonian species diversity due to edaphically differentiated communities. Pl. Syst. Evol. 137: 95–105.

———. 1988. Tree species richness of upper Amazonian forests. Proc. Natl. Acad. Sci. U.S.A. 85: 156–159.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165: 131–137.

———. 1992. On the "river effect" in some forest birds of southern Amazonia. Bol. Mus. Paraense Emilio Goeldi 8: 217–245.

———. 1993. Time's cycle and time's arrow in the history of Amazonia. Biogeographica (The Hague) 69: 15–45.

Harris, R. 1987. Satellite Remote Sensing: An Introduction. Routledge & Kegan Paul, London, New York.

Hershkovitz, P. 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colors. Evolution 22: 556–575.

Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. Palaeogeogr., Palaeoclimatol., Palaeoecol. 105: 267–309.

Hubbell, S. P. & R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pp. 314–329 *in* J. Diamond & T. J. Case (editors), Community Ecology. Harper and Row, New York.

INRENA. 1995. Mapa forestal del Perú 1 : 1,000,000. Ministerio de Agricultura, Dirección General Forestal, Lima.

Kalliola, R., H. Tuomisto & K. Ruokolainen. 1996. Areas importantes para la conservación de la selva baja peruana desde el punto de vista geoecológico. Pp. 127–132 *in* L. O. Rodriguez (editor), Diversidad Biológica del Peru: Zonas Prioritarias para su Conservación. GTZ & INRENA, Lima.

———, A. Linna, M. Puhakka, J. Salo & M. Räsänen. 1993. Mineral nutrients from fluvial sediments in the Peruvian Amazon. Catena 20: 333–349.

———, M. Puhakka, J. Salo, H. Tuomisto & K. Ruokolainen. 1991. The dynamics, distribution and classification of swamp vegetation in Peruvian Amazonia. Ann. Bot. Fenn. 28: 225–239.

Kramer, K. U. 1957. A revision of the genus Lindsaea in the New World. North-Holland Publishing, Amsterdam.

Lillesand, T. M. & R. W. Kiefer. 1994. Remote Sensing and Image Interpretation, 3rd ed. John Wiley & Sons, New York.

Linhart, Y. B. & M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Rev. Ecol. Syst. 27: 237–277.

Malleux, J. 1975. Mapa forestal del Peru (Memoria explicativa). Universidad Nacional Agraria, Lima.

Mather, P. M. 1987. Computer Processing of Remotely-Sensed Images: An Introduction. John Wiley & Sons, New York.

Nelson, B. W., C. A. Ferreira, M. F. Da Silva & M. L. Kawasaki. 1990. Refugia, endemism centers and collecting density in Brazilian Amazonia. Nature 345: 714–716.

PAUT (Proyecto Amazonia de la Universidad de Turku). 1993. Mapa geoecológico de selva baja de la Amazonia peruana. PAUT, Helsinki.

Prance, G. T. (editor). 1982. Biological Diversification in the Tropics. Columbia Univ. Press, New York.

———. 1989. American tropical forests. Pp. 99–132 *in* H. Lieth & M. J. A. Werger (editors), Ecosystems of the World 14B. Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Elsevier, Amsterdam.

Renner, S. S., H. Balslev & L. B. Holm-Nielsen. 1990. Flowering plants of Amazonian Ecuador—A checklist. AAU Reports 24: 1–241.

Ruokolainen, K., A. Linna & H. Tuomisto. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographic patterns in Amazonian rain forests. J. Trop. Ecol. 13: 243–256.

Räsänen, M., R. Kalliola & M. Puhakka. 1993. Mapa geoecológico de la selva baja peruana: Explicaciones. Pp. 207–216 *in* R. Kalliola, M. Puhakka & W. Danjoy (editors), Amazonia Peruana: Vegetación Húmeda Tropical en el Llano Subandino. PAUT and ONERN, Jyväskylä, Finland.

———, J. S. Salo & R. J. Kalliola. 1987. Fluvial perturbance in the Western Amazon basin: Regulation by long-term sub-Andean tectonics. Science 238: 1398–1401.

———, A. M. Linna, J. C. R. Santos & F. R. Negri. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269: 386–390.

———, R. Neller, J. Salo & H. Jungner. 1992. Recent and ancient fluvial deposition systems in the Amazonian foreland basin. Geol. Mag. 129: 293–306.

———, J. S. Salo, H. Jungner & L. Romero Pittman. 1990. Evolution of the Western Amazon lowland relief: Impact of Andean foreland dynamics. Terra Nova 2: 320–332.

Salo, J. & M. Räsänen. 1989. Hierarchy of landscape patterns in western Amazon. Pp. 35–45 *in* L. B. Holm-Nielsen, I. C. Nielsen & H. Balslev (editors), Tropical Forests: Botanical Dynamics, Speciation and Diversity. Academic Press, London.

———, R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka & P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322: 254–258.

Taylor, P. D., L. Fahring, K. Henein & G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571–573.

Townshend, J. R. G., C. O. Justice & V. Kalb. 1987. Characterization and classification of South American land cover types using satellite data. Int. J. Remote Sensing 8: 1189–1207.

Tryon, R. M. & R. G. Stolze. 1989–1994. Pteridophyta of Peru. Fieldiana, Bot. n.s. 20, 22, 27, 29, 32, 34.

Tuomisto, H. & A. D. Poulsen. 1996. Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. J. Biogeogr. 23: 283–293.

——— & K. Ruokolainen. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. J. Veg. Sci. 5: 25–34.

———, A. Linna & R. Kalliola. 1994. Use of digitally processed satellite images in studies of tropical rain forest vegetation. Int. J. Remote Sensing 15: 1595–1610.

———, K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy & Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

Valencia, R., H. Balslev & G. Paz y Miño. 1994. High tree alpha-diversity in Amazonian Ecuador. Biodiversity & Conservation 3: 21–28.

Webb, D. A. 1954. Is the classification of plant communities either possible or desirable? Bot. Tidsskr. 51: 362–370.

Webb, L. J., J. G. Tracey, W. T. Williams & G. N. Lance. 1970. Studies in the numerical analysis of complex rain-forest communities. V. A comparison of the properties of floristic and physiognomic-structural data. J. Ecol. 58: 203–232.

Werff, H. van der. 1992. Substrate preference of Lauraceae and ferns in the Iquitos area, Peru. Candollea 47: 11–20.

Whitmore, T. C. & G. T. Prance. 1987. Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford.

Workshop 90. 1991. Biological Priorities for Conservation in Amazonia. Map produced by Conservation International, Washington, D.C.

Young, K. R. & B. León. 1989. Pteridophyte species diversity in the central Peruvian Amazon: Importance of edaphic specialization. Brittonia 41: 388–395.

SELECTED PROCEEDINGS FROM THE 1997 MIDWESTERN RARE PLANT CONFERENCE: INTRODUCTION

Kayri Havens[1]

The Center for Plant Conservation, headquartered at the Missouri Botanical Garden, is a national network of 28 botanical gardens and arboreta, each of which is responsible for preserving rare plants within its biogeographical region through protective cultivation and seed banking. The Missouri Botanical Garden is a member of this network, thereby engaged in protecting some of the rarest plant species from Missouri and five nearby states. As part of the Garden's commitment to regional rare plant conservation, it hosted the first Midwestern Rare Plant Conference in February 1997. The conference will be a biennial event, to be held at one of five regional botanical gardens and arboreta on a rotating basis. The 1997 meeting provided a forum for exchanging research results on rare Midwestern plants, for setting regional plant conservation priorities, and for developing and implementing collaborative plant conservation projects in the Midwest. The meeting consisted of two days of scientific paper and poster presentations followed by a one day conservation task force meeting organized by the Center for Plant Conservation.

Topics covered at the 1997 Midwestern Rare Plant Conference included population biology and genetics, reproductive biology, demography, systematics, autecology, and monitoring and recovery strategies for rare taxa from the upper and lower Midwest as well as the Great Plains. The following collection of papers are a subset of the over 35 invited and contributed presentations given at the meeting. Two of the papers focus on a rare grass, *Calamagrostis porteri* subsp. *insperata*. Because the taxon consistently fails to set viable seed, Havens and Holland examined genetic and environmental factors affecting its reproductive failure. In a field study, Bittner and Gibson looked at the taxon's vegetative performance in relation to a number of environmental variables. Three of the papers focus on the population genetics of rare species. Crawford et al. studied genetic variation in *Trifolium stoloniferum* using randomly amplified polymorphic DNA (RAPD) markers. In contrast to an earlier allozyme study, they found that even small populations contained a number of different genets and are worthy of conservation consideration. Baskauf and Snapp examined isozyme variation in the highly restricted cedar glade endemic *Astragalus bibullatus*. They found little differentiation between populations, suggesting that local adaptation may not be a critical concern when selecting propagules for reintroduction projects. In the self-incompatible prairie forb *Asclepias meadii*, Tecic et al. compared allozyme variation between sites managed by mowing and by fire. They found less variation in the mowed populations, perhaps because annual summer mowing prevents sexual reproduction. In a second paper on *Asclepias meadii*, Bowles et al. look at habitat differences between populations, discuss how fire and mowing affect population structure, and examine a number of factors that affect outplanting success in restoration projects. Finally, a paper by Clinebell and Bernhardt looks at the pollination ecology of five tallgrass prairie *Penstemon* species. They found that the assemblage of pollinators present at a site varied with population size. This may have interesting implications for patterns of gene flow in natural and reintroduced populations.

The conference and task force meeting was made possible through the generosity of the following sponsors and co-organizers: Center for Plant Conservation, Chicago Botanic Garden, Missouri Botanical Garden, Missouri Department of Conservation, The George Gund Foundation, The Holden Arboretum, The Morton Arboretum, The Nebraska Statewide Arboretum, and the U.S. Fish and Wildlife Service, Region 3.

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FACTORS AFFECTING REPRODUCTIVE SUCCESS IN A RARE GRASS, *CALAMAGROSTIS PORTERI* SUBSP. *INSPERATA*[1]

Kayri Havens[2] *and Douglas L. Holland*[3]

ABSTRACT

Calamagrostis porteri A. Gray subsp. *insperata* (Swallen) C. W. Greene is a rare grass that is currently treated as a "species of concern" by the U.S. Fish and Wildlife Service. Production of viable seed had never been observed, and little was known about the factors affecting this reproductive failure. In this study we examined the effects of maternal genotype, pollen source, and light intensity on caryopsis (the single-seeded fruit produced in grasses) production. Maternal genotype and pollen source (self vs. outcross) significantly affected the number of caryopses initiated, while light intensity had no significant effect. However, nearly all of the caryopses initiated aborted late in development. In the 2000+ florets we examined, only one fully filled, viable caryopsis was found. The conditions under which this caryopsis was produced suggest future courses of management.

Calamagrostis porteri A. Gray subsp. *insperata* (Swallen) C. Greene is a rare grass currently known from approximately 80 populations in five Midwestern states: Illinois, Indiana, Kentucky, Missouri, and Ohio. It was discovered in 1934 in Jackson Co., Ohio, and was originally described as *C. insperata* (Swallen, J. Wash. Acad. Sci. 25: 413. 1935). It was formerly a Category 2 federal candidate for listing as endangered or threatened due in part to its extremely patchy distribution throughout its range (Drewry, 1993), and is now, like all former Category 2 candidates, called a "species of concern" by the U.S. Fish and Wildlife Service (Drewry & Sayers, 1996). It grows primarily in forest openings and along edges of upland woods (Spooner et al., 1983).

Calamagrostis porteri subsp. *insperata* was reported by Greene (1980) to be octoploid ($2n = 56$), although a related species, *Calamagrostis canadensis,* also $2n = 56$, is reported to be tetraploid and has allozyme banding patterns typical of those expected in tetrasomic inheritance (Macdonald & Lieffers, 1991). Diploids ($2n = 14$) are not known in *Calamagrostis,* indicating that the genus is quite old and polyploidization occurred early in its evolutionary history (Greene, 1980). Although apomixis is prevalent in the genus, Greene (1984) postulated that *Calamagrostis porteri* subsp. *insperata* reproduced sexually due to the presence of sexual megagametophytes produced from reduced megaspores, as well as normal microsporogenesis and pollen formation. However, it has never, to our knowledge, been observed to set viable seed, which probably contributes to its rarity. Several hypotheses have been proposed to explain this reproductive failure. First, encroachment of woody vegetation and subsequent shading may inhibit flowering. Flowering tillers are very rare in most populations and are most often seen on plants in relatively sunny areas (Greene, 1984; Bittner & Gibson, 1993). Second, *C. porteri* subsp. *insperata* may be self-incompatible (Greene, 1980), and if so, reproduction may be limited by lack of compatible mates. Many populations consist of only a few plants, which could be vegetative clones, given that *C. porteri* can reproduce asexually via rhizomes (Greene, 1984). In addition, many plants lack viable pollen, as estimated by stainability with cotton blue (Greene, 1980).

Information regarding reproduction of many rare or endangered taxa, including *C. porteri* subsp. *insperata,* is scanty, but vitally important for management and recovery plans. The purpose of this study was to investigate the effects of light intensity, pollen source, maternal genotype and pollen viability on reproductive success in *Calamagrostis porteri*

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Table 1. Provenance (county and state of collection, voucher number and location, and Missouri Botanical Garden accession number), treatment, and pollen viability for the four genotypes used.

Genotype	Provenance	Treatment	Pollen viability
1	Jackson Co., OH, Subpopulation C Voucher: *Weiland 29* (MO) Accession # 901734	Sun—"Female" Shade—"Female"	0% 95%
2	Jackson Co., OH, Subpopulation B Voucher: *Weiland 29* (MO) Accession # 901733	Sun—"Female" Shade—"Female"	98% 20%
3	Vinton Co., OH Voucher: *Rogers 345* (MO) Accession # 872392	Sun—"Female" Shade—"Female"	99% 98%
4	Texas Co., MO Voucher: *Summers 3631* (MO) Accession # 902331	Sun—"Male"	99%

subsp. *insperata.* We examined caryopsis (single-seeded fruits produced in grasses; functionally analogous to seeds in most other species of flowering plants) production and viability in two different light regimes and with three pollination treatments: self-pollination, natural crossing, and hand-outcrossed pollinations.

MATERIALS AND METHODS

Specimens of *Calamagrostis porteri* subsp. *insperata* were field-collected in 1987 and 1990 from Jackson and Vinton Cos., Ohio, and Texas Co., Missouri (Table 1). The plants are maintained in protective cultivation at the Missouri Botanical Garden as part of its cooperative agreement with the Center for Plant Conservation. The Center for Plant Conservation is an organization dedicated to preserving rare plants in the United States primarily through ex situ cultivation and seed banking.

Only four genotypes were included in this experiment. These were the only genotypes that flowered in the ex situ collection. Since viable seed production has never been observed in natural populations, growing plants from seed was not an option. Three sets of two genetically identical clones were used as pollen recipients (hereafter "females"; it should be noted that although plants are hermaphroditic, we are referring only to their functional gender in this study). The female plants were collected from three different populations or subpopulations in Ohio. The three clumps of tillers were divided and potted separately to produce the pairs of clones. The pollen donor (hereafter "male") was collected in Missouri and is presumably genetically distinct from all of the females. All plants were grown in a shaded lath house until flowering culm initiation. Upon flowering, in mid June 1994, one member of each pair of clones was placed in full sun, the other member remaining in the shaded lath house for the duration of the experiment. Inflorescence number varied on the female plants from 1 to 65. Two to four of the inflorescences on each female were bagged with nylon stockings prior to anthesis to test for self-compatibility. Approximately half of the remaining inflorescences were hand-pollinated by shaking one of the male's inflorescences over the female inflorescence. The remaining inflorescences were not manipulated and allowed to outcross or self-pollinate naturally. Hence, each female plant received three treatments, except one plant from genotype #1 that had only one flowering culm, and it received the hand-pollination treatment. Inflorescences were harvested 22 August 1994 after they had turned brown. Approximately 100 florets were randomly selected and removed from each inflorescence. These florets were scored for the presence or absence of caryopses and, when present, their developmental stage. To assess viability, caryopses were placed in petri dishes on moist filter paper in an incubator at 22°C under long day conditions (16/8 photoperiod) and monitored for germination for one month. Half of the caryopses from each treatment were given a cold treatment (12 weeks at 4°C) prior to incubation.

All plants in the study were tested for pollen viability using Alexander's stain (Alexander, 1969). Pollen grains that stained dark red were presumed to be viable.

SYSTAT 5 computer software (Systat, Inc., SPSS, Chicago, IL) was used for all the statistical analyses. A three-way mixed model ANOVA was used to

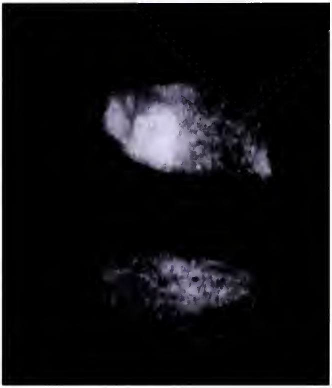

Figure 1. Micrograph of aborted, non-viable caryopses.

partition variance in the number of caryopses initiated into components due to genotype, a random effect, and pollen source and light treatment, both fixed effects. Univariate analyses were done using one-way ANOVAs with post hoc Tukey mean comparisons after significant differences were found in the multivariate analysis (Dowdy & Wearden, 1983).

RESULTS

All but one plant produced viable pollen. Viable pollen was not observed in any of the approximately 20 anthers examined in one of the plants of genotype #1 (sun treatment). A second plant (genotype #2, shade) produced only approximately 20% stainable pollen. The rest of the plants, including the plant used as a male for hand-pollinations, produced abundant, viable pollen. Pollen stainability for these plants ranged from 95 to 100% (Table 1).

Some caryopses were initiated in all plants; however, nearly all of these were shriveled at the basal end and did not germinate (Fig. 1). These caryopses contained endosperm and were easily distinguished from the uniovulate ovaries that did not initiate fruit development. Only one fully filled caryopsis was found, and it germinated after three days on moist filter paper without pretreatment. It was found on the plant that also initiated the most caryopses (genotype #2, sun, hand-pollination).

Caryopsis initiation varied within and among plants. One genotype (#3) was less successful in initiating caryopses across all treatments. There were also significant differences between the pollen-source treatments. Both hand- and open-pollination treatments initiated significantly more caryopses than the selfing treatment. Light intensity did not have a significant effect on the number of caryopses initiated (Table 2, Fig. 2).

Table 2. Results of ANOVA showing the magnitude of variance in number of caryopses initiated attributable to maternal genotype, pollen source, and light treatment.

Source	d.f.	Mean square	F-ratio	Probability
Genotype	2	7512.3	33.0	$P < 0.001$
Pollen source	2	5511.2	24.2	$P < 0.001$
Light treatment	1	57.0	0.3	n.s.
Error	26	227.4		

DISCUSSION

Reproductive failure in plants can occur at any of several serial stages: flower production, gametophyte development, pollination, fertilization, and seed/fruit maturation. In *Calamagrostis porteri* subsp. *insperata*, limited success in many of these stages contributes to the extremely low seed set overall. In native populations, flowering tillers are very rare and most often seen in areas of relatively high light (Bittner & Gibson, 1993). While light intensity does not appear to be important at the stages of seed initiation and development, our experiment did not address the effect of light intensity on flower production. All plants were grown in the semi-shaded lath house until flowering tillers were initiated; at that point, half of the plants were moved to full sun. Although our plants flowered in the lath house, light intensity in densely shaded woods may be low enough to preclude flowering in many populations.

Viable gametophyte production is also problematic in this taxon. This may be due to meiotic difficulties caused by polyploidy. A shift toward asexual reproduction is frequently seen in polyploid species (Levin, 1983). Maternal genotypes varied significantly in the number of caryopses initiated. This probably reflects differences in megagametophyte production or viability, rather than pollen or resource limitation. Genotypic differences in caryopsis initiation were consistent across all pollination treatments including hand-pollinated plants which received abundant pollen, and all plants received adequate amounts of water and fertilizer. Genetic effects on seed set have been documented in several studies (Mazer et al., 1986; Geber, 1990;

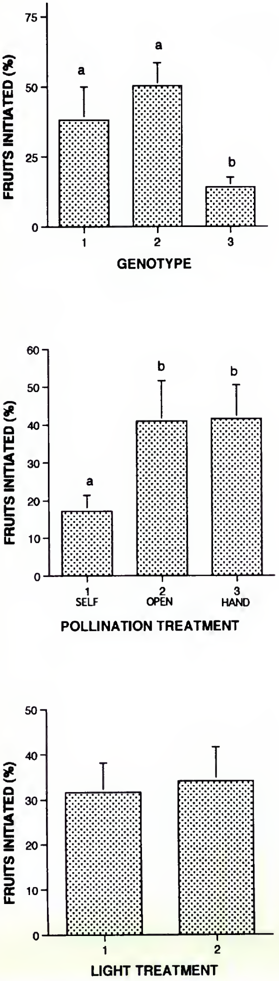

Figure 2. Mean number of caryopses (fruits) initiated (± SE) for the three maternal genotypes, the three pollen treatments, and the two light treatments. Significant differences between means are indicated by different letters ($P < 0.05$).

Sultan, 1990). Problems with male gametophyte production were also evident; two of the seven plants produced little or no viable pollen. However, the variation in pollen production was not explained by genotype or light treatment. Although chromosome counts were not done on our plants, differences in chromosome number between plants would not completely explain the variation seen in gametophyte production for two reasons. First, clones varied in their pollen production, and second, individuals that failed to produce viable pollen made viable female gametophytes and vice versa.

This taxon also has limited success at the reproductive stages of fertilization, seed/fruit initiation, and seed/fruit maturation. Plants that potentially received outcrossed pollen, either from open pollinations or from hand pollinations, were significantly more successful in initiating caryopses than plants that received only self pollen. Nevertheless, plants that were bagged to prevent outcrossing did initiate some caryopses. Although Greene (1980) postulated the taxon was genetically self-incompatible, observing caryopsis initiation in bagged inflorescences suggests the grass is self-compatible. Grasses that exhibit self-incompatibility typically have a two-locus, gametophytic system that causes pollen-tube growth to cease in the stigma, either when the tube first touches the stigmatic papillae or in the intercellular spaces of the stigma, prior to fertilization and seed initiation (Richards, 1986).

The failure of most self-pollinated ovules to initiate development as well as the extremely high rate of seed abortion in this taxon, even among outcrossed seeds, may be a reflection of a high genetic load. Although recent polyploids are not expected to carry a genetic load (Lande & Schemske, 1985; Hedrick, 1987), the long history of polyploidization in this taxon may have allowed a large genetic load to develop. A similarly high load has been documented in the tetraploid *Vaccinium corymbosum* L. (Ericaceae; Krebs & Hancock, 1991) and the diploid *Dedeckera eurekensis* Reveal & J. T. Howell (Polygonaceae; Wiens et al., 1989). As in *V. corymbosum* and *D. eurekensis,* we found embryo-lethal factors expressed in both selfed and outcrossed seeds, indicating dominant mutations may be present.

Of the 2000+ florets scored, we found only one fully filled, viable caryopsis. Perhaps most significantly, this finding demonstrates that sexual reproduction is possible in this taxon, although it is highly unlikely, especially in natural populations. In addition, the conditions under which this caryopsis was produced (pollen from another genotype, full sun) suggest courses of management for this rare species. A genetic survey would provide valuable information on the amount and pattern of genetic variation present in the taxon. An experimental population would allow us to test the effects of creating light gaps and introducing novel genotypes on flowering and seed set in a natural setting. Since seed banking is not currently a viable option for this taxon, ex situ conservation efforts are focusing on tissue culture and cryopreservation of vegetative plant parts, as well as investigating the feasibility of embryo rescue techniques.

Literature Cited

Alexander, M. P. 1969. Differential staining of aborted and non-aborted pollen. Stain Technol. 44: 117–122.

Bittner, R. T. & D. J. Gibson. 1993. Distribution and ecology of *Calamagrostis porteri* subsp. *insperata* (Swallen) C. Greene in southern Illinois. Report submitted to the Illinois Department of Conservation.

Dowdy, S. & S. Wearden. 1983. Statistics for Research. John Wiley & Sons, New York.

Drewry, G. 1993. Plant taxa for listing as endangered or threatened species: Proposed rules. Fed. Reg. 58: 51154.

——— & R. Sayers. 1996. Endangered and threatened wildlife and plants; Review of plant and animal taxa that are candidates for listing as endangered or threatened species. Fed. Reg., 50 CFR Part 17, 96: 4412.

Geber, M. A. 1990. The cost of meristem limitation in *Polygonum arenastrum*: Negative genetic correlations between fecundity and growth. Evolution 44: 799–819.

Greene, C. W. 1980. The Systematics of *Calamagrostis* (Gramineae) in Eastern North America. Unpublished Ph.D. Thesis, Harvard University, Cambridge.

———. 1984. Sexual and apomictic reproduction in *Calamagrostis* (Gramineae) from eastern North America. Amer. J. Bot. 71: 285–293.

Hedrick, P. W. 1987. Genetic load and the mating system in homosporous ferns. Evolution 41: 1282–1289.

Krebs, S. L. & J. F. Hancock. 1991. Embryonic genetic load in the highbush blueberry *Vaccinium corymbosum* (Ericaceae). Amer. J. Bot. 78: 1427–1437.

Lande, R. & D. W. Schemske. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. Evolution 39: 24–40.

Levin, D. A. 1983. Polyploidy and novelty in flowering plants. Amer. Midl. Naturalist 122: 1–25.

Macdonald, S. E. & V. J. Lieffers. 1991. Population variation, outcrossing, and colonization of disturbed areas by *Calamagrostis canadensis*: Evidence from allozyme analysis. Amer. J. Bot. 78: 1123–1129.

Mazer, S. J., A. A. Snow & M. L. Stanton. 1986. Fertilization dynamics and parental effects upon fruit development in *Raphanus raphanistrum*: Consequences for seed size variation. Amer. J. Bot. 73: 500–511.

Richards, A. J. 1986. Plant Breeding Systems. George Allen & Unwin, London.

Spooner, D. M., A. W. Cusick, B. Andreas & D. Anderson. 1983. Notes on Ohio vascular plants previously considered for listing as federally endangered or threatened species. Castanea 48: 250–258.

Sultan, S. 1990. Evolutionary implications of phenotypic plasticity: Genetic diversity for norms of reaction to resource gradients in *Polygonum persicaria* L. Unpublished Ph.D. Thesis, Harvard University, Cambridge.

Wiens, D., D. L. Nickrent, C. I. Davern, C. L. Calvin & N. J. Vivrette. 1989. Developmental failure and loss of reproductive capacity in the rare palaeoendemic shrub *Dedeckera eurekensis*. Nature 338: 65–67.

MICROHABITAT RELATIONS OF THE RARE REED BENT GRASS, *CALAMAGROSTIS PORTERI* SUBSP. *INSPERATA* (POACEAE), WITH IMPLICATIONS FOR ITS CONSERVATION[1]

R. Todd Bittner[2] *and David J. Gibson*[3]

Abstract

Calamagrostis porteri subsp. *insperata* was known from only two extant populations in Ohio prior to the late 1980s. Recent searching has documented more than 80 populations of this rare grass in five states. Although more populations exist than previously believed, the habitat requirements for this subspecies are still unknown. To quantify these requirements, data were collected on photosynthetic photo-flux density (PPFD), air and soil temperature, vapor-pressure deficits (VPD), soil moisture and depth, pH, percent organic matter, and associated species cover from three populations in southern Illinois. Leaf area, predicted total leaf area, and number of tillers per m^2 were measured to ascertain the relationship between vegetative performance and microenvironmental conditions. Detrended Canonical Correspondence Analysis (DCCA) was used to ordinate the samples using the cover of co-occurring species and the environmental variables. Leaf area, predicted total leaf area, and number of tillers were significantly related to the nine environmental variables at all three sites. The vegetative performance of this rare grass in southern Illinois seems to be determined by a complex suite of environmental factors, of which PPFD, VPD, and soil temperature are extremely influential, especially in the spring. The ordination shows that the three populations are distinctly separated, with total predicted leaf area, tiller density, soil moisture, soil temperature, air temperature, and pH being highly correlated to the ordination axes. Habitat modifications resulting in closed forest canopies detrimentally affect the vegetative performance of this taxon.

Conservation biologists, in attempting to evaluate the causes of endangerment to rare plant species in order to aid in their recovery, have employed ecological research to characterize biotic interactions and habitat requirements (Schemske et al., 1994). In particular, an understanding of the autecology and natural history of rare species is necessary (Brussard, 1991). A number of studies focusing on environmental conditions have led to a better understanding of limiting ecological factors responsible for rarity of endangered species (Gawler et al., 1987; Buchele et al., 1989; Boyd & Hilton, 1994; Vivian, 1967).

Lack of basic ecological information about the former Federal endangered species candidate (FWS, 1993) *Calamagrostis porteri* A. Gray subsp. *insperata* (Swallen) C. W. Greene (Poaceae) poses a problem to conservation biologists and land managers. As conservation measures are appropriately planned for this taxon, there is a need to better understand its microhabitat ecology.

Calamagrostis porteri subsp. *insperata* (reed bent grass) was first described from Ohio as *Calamagrostis insperata* (Swallen, 1935). Another Ohio population, three Missouri populations, and one Arkansas population (now believed extirpated) were documented in subsequent years. This grass is now known from more than 80 populations in five states: Illinois, Indiana, Kentucky, Missouri, and Ohio (Campbell et al., 1992; Homoya, 1995; Summers, 1993; Bittner, 1995b). Its habitats are extremely varied but are often located on cool, north-facing sandstone bluff edges and tree-fall gaps in dry-mesic upland forests found in unglaciated areas (Bittner, 1995a). This cool-season, rhizomatous grass rarely flowers and spreads almost exclusively through vegetative growth. It is a tufted perennial that can stand up to 1 m tall. Highly specific flowering conditions, self-incompatibility, and poor fruiting success contribute to the reproductive limitations of several taxa of *Calamagrostis*, including *C. porteri* subsp. *insperata* (Greene, 1980).

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The goals of this study were to determine how microhabitat conditions and ground cover of associated taxa are related to the vegetative performance of *Calamagrostis porteri* subsp. *insperata* in three of the five known southern Illinois populations (as of 1993), to contribute to the general information about this taxon, and to aid in evaluating its endangered status.

MATERIALS AND METHODS

STUDY SITES

The five Illinois populations of *Calamagrostis porteri* subsp. *insperata* are located in Pope County, southern Illinois, at Bell Smith Springs Ecological Area and Lusk Creek Canyon Natural Area (Fig. 1). All the populations are within the Shawnee National Forest and are managed by the U.S. Forest Service under prescription 8.2 (to protect, preserve, and enhance the unique scientific, educational, and natural values found within this National Natural Landmark and Ecological Area; USDA, 1992). Only three of the five populations were sizeable enough for the purposes of this research. Two populations were from Bell Smith Springs [BSS1, *Summers 4774* (MO); BSS2, *Bittner 347* (ILLS), *348* (SIUC)], and one population was from Lusk Creek Canyon [LC, *Bittner 350* (ILLS)]. These three populations were estimated to contain between 4000 and 18,000 tillers.

This unglaciated, predominantly forested area lies in the Greater Shawnee Hills Section of the Shawnee Hills Natural Division (Schwegman, 1973). The bedrock consists of massive Pennsylvanian sandstone strata, and the topography is rugged, with many canyons, bluffs, and ravines. The well-drained soils have low organic-matter content, moderate permeability, and moderate available water capacity (USDA, 1975).

The study populations of *Calamagrostis porteri* subsp. *insperata* are located predominantly within the dry-mesic, upland forest community. The habitat of *C. porteri* subsp. *insperata* in these populations is on cool, northwest- and northeast-facing bluff edges and hillsides with high species diversity and many rare, uncommon, and conservative plants (taxa with a high degree of habitat specificity) as associates. Tillers occur in both leaf-litter zones and moss- and lichen-dominated areas within dry-mesic, oak-hickory forests. Within two populations (LC and an unstudied BSS population), dense mats of *Sphagnum* species are present throughout large sections. Springs, intermittent streams, or seeps are also common within the study populations. The dominant overstory species association consists of *Quercus alba* L., *Q. rubra* L., *Q. velutina* Lam., *Carya glabra* (Mill.) Sweet, and *C. ovata* (Mill.) K. Koch (Voigt & Mohlenbrock, 1964).

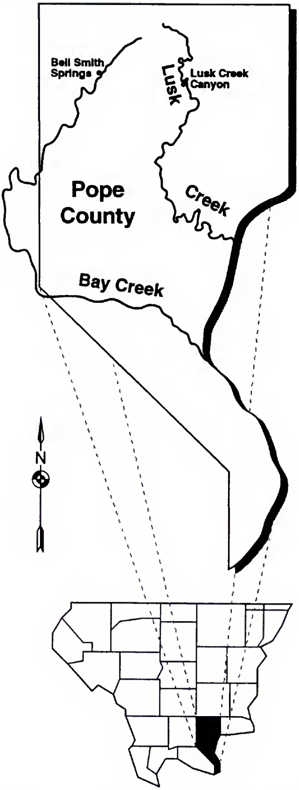

Figure 1. The location of *Calamagrostis porteri* subsp. *insperata* populations at Bell Smith Springs Ecological Area and Lusk Creek Canyon Natural Area in Pope County, southern Illinois.

FIELD PROCEDURES

In each of the three populations, fifteen 1-m^2 quadrats were located randomly and accepted if they contained tillers of *C. porteri* subsp. *insperata*. An additional four randomly selected 20-m transects of contiguous 1-m^2 quadrats were established perpendicular to the bluff edge within the BSS1 population (but did not necessarily contain tillers).

The number of tillers in each quadrat was sampled four times during the growing season of 1993 (April, May, July, and September). To calculate mean leaf area per quadrat, the lengths of all the leaves from five randomly chosen tillers, the numbers of leaves per tiller, and an estimated percent of living area per leaf were recorded twice (May and August). A regression developed from leaf tracings of 100 randomly selected leaves was used to predict leaf area from leaf length ($R^2 = 0.94$, $P < 0.0001$). Leaf area was calculated by multiplying the estimated leaf area (predicted from leaf length) by the percent living area per leaf. Mean leaf area per quadrat was calculated by multiplying the number of tillers from the previous month by the mean number of leaves per tiller by the mean leaf area.

Predicted total leaf area per quadrat was calculated by multiplying the mean leaf area for the season by the mean number of leaves per tiller by the mean number of tillers for the season.

Tiller survivorship was determined at each of the three populations by marking new tillers with plastic tags monthly throughout the growing season from April through September in three randomly selected 1-m^2 quadrats per population. Both new tillers and dead tillers (> 50% dead area) were recorded each month.

To determine which factors were related to the microdistribution of *C. porteri* subsp. *insperata*, environmental factors were measured twice a day at monthly intervals (April–September) throughout the growing season from 8:00 to 10:00 A.M. and 2:00 to 4:00 P.M.

At the midpoint of each quadrat, light intensity was measured with a line-quantum sensor, model LI-191SA (LICOR, Lincoln, NB) attached to a data logger (LICOR model 1000). The line-quantum sensor averages photosynthetic photon-flux density (PPFD) through 400–700 nm over 1 m. Total PPFD measurements were made in full sunlight throughout the data-collection period and used as a control. Available PPFD within each quadrat was calculated by dividing values for PPFD in each quadrat by control values to give a total light-intensity value.

Air, soil, and wet-bulb temperatures were collected similarly to PPFD in the individual quadrats, and at 5-m intervals along the transects. The wet- and dry-bulb temperatures were used with barometric pressure obtained from the nearby Carbondale airport weather station (approximately 65 km NE of the study sites) to calculate vapor-pressure deficit (VPD) values according to Cox (1990).

Within each quadrat, morning and afternoon observations of environmental data (PPFD, air, and soil temperature, and vapor pressure deficits) were averaged for each month to obtain six monthly observations. Several transformations were performed to normalize the data according to Sokal and Rohlf (1969). PPFD values were divided by 100 and arcsine transformed prior to analysis (arcsine $\sqrt{}$ (X * 100)). Vapor pressure deficit values were divided by 10 and arcsine transformed. Soil and air temperature values were log-base 10 transformed.

Soil moisture was measured by collecting soil samples in May and July from each individual quadrat, and in every fifth quadrat within each transect, following the procedures of Bannister (1986). The soil-moisture values were divided by 100, arcsine transformed, and averaged prior to analysis. Soil depth to bedrock was measured in each corner and midpoint for each quadrat with a steel probe, averaged, and log-base 10 transformed prior to analysis. Soil samples, previously dried for soil-moisture measurements, were used to determine the pH using a 1:5 soil-water slurry, and organic content using standard procedures (SPAC, 1992). Soil pH was converted to hydrogen-ion concentration for data analysis.

The canopy cover of all vascular plant species rooted in each quadrat was estimated in July using a modified Daubenmire scale (Abrams & Hulbert, 1987). Moss and lichen cover was recorded, but identification to species was not made. The midpoint values were used for the species-cover data in an ordination, and for total-cover calculations for each sample. Arcsine-transformed midpoint values were used for statistical analysis. The identity of canopy species immediately above each quadrat was also determined; nomenclature follows Mohlenbrock (1986).

ANALYTICAL METHODS

The following analyses were performed individually for each of the three populations using SAS, Version 6 (SASI, 1990). Simple and multiple regressions were performed to predict tiller densities, mean leaf area, and total predicted leaf area (performance) from air temperature, soil temperature, vapor-pressure deficit, PPFD, soil moisture, soil depth, pH, percent organic matter, and vegetation cover (environmental). For the simple and multiple monthly regressions, environmental variables (independent variables) from the previous month and the current month were tested against the performance of *C. porteri* subsp. *insperata* (dependent variables) for the current month. Mean variables

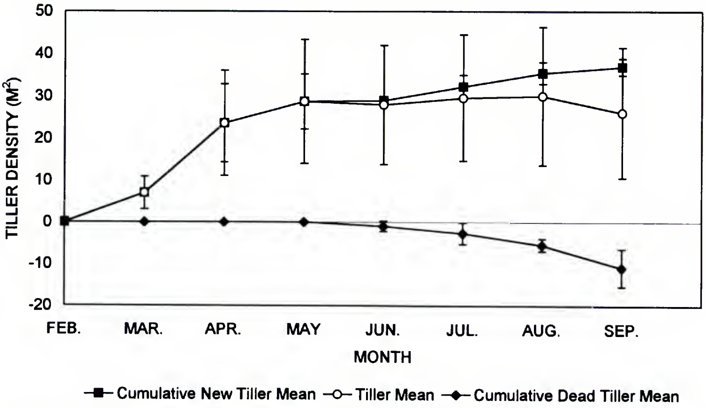

Figure 2. Net tiller density and cumulative number of new and dead tillers of *Calamagrostis porteri* subsp. *insperata* from BSS1, BSS2, and LC from February to September 1993 (mean of nine quadrats from the three sites).

were used for simple regressions. The pair of environmental variables with the lowest probabilities (*P*) for each month and mean were used for the multiple regressions, and for a simple regression of their cross-products, respectively.

Separate one-way ANOVAs were used to compare tiller presence/absence (dependent variable) at BSS1 for each month and mean using the environmental variables (independent variables). Similarly, environmental data from the previous month and the current month were tested against the performance data for the current month.

Detrended Canonical Correspondence Analysis (DCCA) was performed on the cover and environmental data matrices using CANOCO (ter Braak, 1988), in a manner similar to that of Gibson and Looney (1994), to determine the relationships among the 125 quadrats. The ordination was based upon the 59 quadrats that contained tillers of *C. porteri* subsp. *insperata* and from which environmental data were collected. The quadrats for which environmental data were not available were not used to construct the ordination axes, but were held "passive" in the analysis and added subsequently, after the axes were constructed on the basis of their cover data. Rare species were downweighted using the rare-species downweighting option (ter Braak, 1988). Reliability of the results was checked and found to be acceptable using Oksanen and Minchin's (1997) debugged and strict version of DECORANA.

The relationships between the measures of performance for *C. porteri* subsp. *insperata* (i.e., leaf area, predicted area, and tiller density) and the ordination axis-scores were determined using Spearman Rank Correlations (SASI, 1990).

Results

The highest number of new tillers was produced in April, with March and May yielding the second and third highest number of new tillers, respectively (Fig. 2). New tillers were produced each month, but to a lesser extent from June to September. Cumulative gains leveled off from May to June after a sharp increase. This plateau was followed by a more moderate increase. Mean tiller density remained relatively constant from April to September, with the highest mean in August. No tillers died until June, with the frequency increasing each month thereafter.

The mean percentage PPFD decreased markedly from April to May as the forest canopy closed, lowering the available PPFD on the forest floor to less than 5% (Table 1). Mean monthly temperature of both air and soil increased into the summer, as expected, with a high variation between months. Vapor-pressure deficit monthly means were highest in the late spring and early fall.

Mean tiller densities increased slightly from April to May and generally declined into September (Table 1). Tiller density was highly variable among

Table 1. Monthly means and standard deviations for environmental data and tiller densities in three populations (BSS1 = Bell Smith Springs 1, BSS2 = Bell Smith Springs 2, and LC = Lusk Creek) of *Calamagrostis porteri* subsp. *insperata*. (PPFD = photosynthetic photo flux density, AirT = air temp. (°C), SoilT = soil temp. (°C), VPD = vapor pressure deficit (mm Hg), Tlr = tillers per m²; LC and BSS2 have n = 15; BSS1 has n = 95 for PPFD and Tlr and n = 35 for AirT, SoilT, and VPD). No tiller density data collected for any population in June or August.

		April		May		June		July		August		September	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BSS1	PPFD	71.9	11.8	6.4	5.4	3.3	4.4	2.7	3.8	2.8	1.7	2.6	2.1
	AirT	13.3	1.3	22.3	0.6	26.9	0.8	29.8	0.5	28.4	0.7	21.2	0.4
	SoilT	12.8	0.4	14.9	0.7	18.4	0.8	22.7	0.9	22.1	0.8	18.8	0.5
	VPD	2.3	0.4	2.5	0.4	2.5	0.4	1.1	0.2	0.7	0.2	2.6	0.3
	Tlr	19.3	20.6	20.1	21.1	—	—	21.1	22.2	—	—	13.8	12.6
BSS2	PPFD	53.7	6.9	10.3	10.3	2.8	1.7	2.6	2.6	2.3	2.7	1.5	1.1
	AirT	17.4	0.9	20.2	0.5	29.6	0.5	28.3	0.2	25.6	0.4	20.7	0.3
	SoilT	10.2	0.4	14.7	0.3	18.7	0.4	22.7	0.4	21.8	0.4	17.0	0.6
	VPD	2.2	0.4	2.0	0.2	2.2	0.2	1.2	0.2	1.8	0.2	2.2	0.2
	Tlr	32.0	23.6	45.3	35.1	—	—	41.4	28.5	—	—	27.8	18.0
LC	PPFD	41.4	13.0	6.1	3.9	2.5	2.2	3.3	3.0	6.6	2.2	6.3	5.8
	AirT	24.7	1.8	18.3	0.6	28.4	0.3	30.3	0.2	30.3	0.4	26.9	0.3
	SoilT	9.8	0.5	13.2	0.3	19.3	0.4	22.0	0.5	22.3	0.4	17.8	0.4
	VPD	3.5	0.9	1.6	0.5	2.1	0.2	1.7	0.2	2.0	0.2	3.4	0.3
	Tlr	13.1	17.7	75.7	66.1	—	—	83.0	67.4	—	—	69.2	53.2

samples within the populations, ranging from 0 to almost 240 tillers per m². Mean leaf area declined throughout the year as well, due to leaf senescence. Both leaf area and total predicted leaf area were highly variable within the populations.

Five of the nine environmental variables were significantly different between quadrats with and without tillers of *C. porteri* subsp. *insperata* at different times throughout the year in population BSS1: VPD, air and soil temperature, PPFD, and soil depth (Table 2). Quadrats with tillers present had significantly lower VPD early in the season. Significantly higher soil temperature, air temperature, VPD, PPFD, and deeper soil were observed in quadrats with tillers of *C. porteri* subsp. *insperata* during the second half of the growing season.

Five of the nine environmental variables significantly predicted *C. porteri* subsp. *insperata* performance at BSS1: VPD, PPFD, pH, and soil organic matter (Table 3). VPD was negatively related to leaf area, and PPFD, pH, and organic matter were positively related to tiller density, leaf area, and total predicted leaf area, respectively.

Five of the nine environmental variables at BSS2 significantly predicted *C. porteri* subsp. *insperata* performance: VPD, PPFD, soil temperature, cover, and organic matter (Table 3). Leaf area was negatively related to soil temperature, but positively related to plant cover; tiller density was negatively related to VPD, but positively related to PPFD and soil temperature; total predicted leaf area was positively related to PPFD; tiller density for two monthly data combinations was positively related to soil temperature and PPFD combined; and mean leaf area was positively related to total cover and negatively related to soil temperature in combination. Predicted total leaf area was positively related to a simple regression interaction between PPFD and organic matter. The regression predicting tiller density in July from PPFD and soil temperature in June had the highest R^2 of all the regressions performed (0.80). Mean leaf area predicted from cover and soil temperature also had a high variance accounted for (R^2 = 0.74).

Five of the nine environmental variables at LC significantly predicted *C. porteri* subsp. *insperata* performance: VPD, PPFD, soil moisture, and soil and air temperature (Table 3). Leaf area was negatively related to soil temperature and positively related to soil moisture individually, combined, and by their interaction. Tiller density was positively related to VPD and PPFD. Total predicted leaf area was positively related to PPFD and air temperature. Mean soil temperature and moisture predicting leaf area accounted for the most variance (R^2 = 0.47).

A total of 113 species associated with *C. porteri* subsp. *insperata* was recorded from the quadrats within the three sites. There were 47 species with a frequency greater than 10% at any site. The woody species (woody vines, seedlings, saplings,

Table 2. ANOVA results from Bell Smith Springs (BSS1) listing significant relationships between the presence/absence of *Calamagrostis porteri* subsp. *insperata* and environmental variables. Given are the probability (*P*), variance accounted for (R^2), degrees of freedom (d.f.), mean value (Mean), number of occurrences (*N*), and standard error (s.e.) of each combination of months of measurement. (Environmental variable abbreviations are listed in Table 1. Depth = soil depth (cm), Dep.Var. = dependent performance variable, Ind.Var. = independent environmental variable.)

Month						Present			Absent		
Dep.Var.	Ind.Var.	Ind.Var.	*P*	R^2	d.f.	Mean	*N*	s.e.	Mean	*N*	s.e.
May	May	VPD	0.0122	0.18	1/34	2.44	28	0.08	2.91	7	0.10
July	May	VPD	0.0095	0.19	1/34	2.43	27	0.08	2.89	8	0.09
August	May	VPD	0.0095	0.19	1/34	2.43	27	0.08	2.90	8	0.09
July	July	SoilT	0.0308	0.13	1/34	22.89	27	0.19	22.11	8	0.12
August	July	SoilT	0.0308	0.13	1/34	22.90	27	0.19	22.11	8	0.12
August	August	PPFD	0.0003	0.14	1/90	3.18	66	0.23	1.90	25	0.15
August	August	AirT	0.0306	0.13	1/34	28.56	27	0.14	27.90	8	0.15
August	August	SoilT	0.0209	0.15	1/34	22.28	27	0.15	21.60	8	0.08
August	August	VPD	0.0060	0.21	1/34	0.74	27	0.05	0.54	8	0.06
September	August	PPFD	0.0008	0.12	1/90	3.17	65	0.23	1.98	26	0.17
September	August	AirT	0.0113	0.18	1/34	28.60	26	0.18	27.95	9	0.09
September	August	SoilT	0.0488	0.11	1/34	22.27	26	0.16	21.71	9	0.13
September	August	VPD	0.0207	0.15	1/34	0.74	26	0.05	0.60	9	0.06
September	September	PPFD	0.0002	0.14	1/90	2.94	65	0.22	1.63	26	0.51
September	September	SoilT	0.0094	0.19	1/34	18.94	26	0.10	18.44	9	0.11
Mean	Mean	Depth	0.0126	0.07	1/90	28.73	70	2.06	16.80	21	2.54

and shrubs) were, in descending order of dominance, *Parthenocissus quinquefolia* (L.) Planch., *Ostrya virginiana* (Mill.) K. Koch, *Toxicodendron radicans* (L.) Kuntze, *Sassafras albidum* (Nutt.) Nees, *Acer saccharum* Marshall, *Quercus rubra, Q. alba, Carya glabra, Vaccinium palludum* Aiton, *Fagus grandifolia* Ehrh., *Q. velutina*, and *C. ovata* (mean cover > 2% at any site). The herbaceous vascular and nonvascular species were, in descending order of dominance, mosses, *Polystichum acrostichoides* (Michx.) Schott, *Dichanthelium boscii* (Poir.) Gould & L. G. Clark, and *Luzula multiflora* (Retz.) Lej., (mean cover > 2% at any site).

The first, second, and third DCCA ordination axes cumulatively accounted for 21, 39, and 53% of the variance, respectively (the eigen values were 0.45, 0.41, and 0.30, respectively). Plots from the three sites (BSS1, BSS2, LC) were dissimilar to each other and clearly separated when plotted on DCCA axes 1 and 2 (Fig. 3). Only a small overlap is present between the LC and BSS2 samples. The LC samples had a higher tiller density and a greater predicted total leaf area than those from either BSS site. The two variables with the highest correlation to the first axis were soil temperature ($r = 0.69$) and soil moisture ($r = 0.53$; $P < 0.05$ for all correlations reported here). The two variables with the highest correlation to the second axis were air temperature ($r = 0.62$) and pH ($r = 0.53$). The variables with the highest correlation to the third axis were PPFD ($r = 0.53$) and soil depth ($r = -0.43$). Tiller density ($r = 0.34$) and total predicted leaf area ($r = 0.33$) of *C. porteri* subsp. *insperata* were highly correlated ($P < 0.001$) to the second axis, while no measures of performance were significantly related to the first axis.

The species-environmental data biplot shows the environmental variables and species (those with weightings > 50) ordination scores (Fig. 4). *Acer saccharum, Luzula multiflora, Ostrya virginiana, Parthenocissus quinquefolia, Quercus alba, Sassafras albidum, Toxicodendron radicans*, and mosses were highly weighted in the ordination (weight > 100). The LC samples have a higher air temperature and pH. The BSS2 samples have a higher VPD and soil depth. The BSS1 samples have higher organic matter, total cover, PPFD, soil moisture, and soil temperature.

DISCUSSION

The habitat conducive to supporting populations of *Calamagrostis porteri* subsp. *insperata* in the Greater Shawnee Hills Section of the Shawnee Hills Natural Division (Schwegman, 1973) of southern Illinois is comprised of high-quality (Grade A or B; White & Madany, 1978), dry-mesic, upland oak-hickory forest and bluff edge communities that have northeast- or northwest-facing aspects.

In determining the microhabitat requirements of

Table 3. Probability (*P*), variance accounted for (R^2), parameter estimate sign (+/−), and the significant independent variables predicting the performance (i.e., tiller density, leaf area, and predicted total leaf area) of *Calamagrostis porteri* subsp. *insperata* in month combinations from BSS1, BSS2, and LC are listed for the simple and multiple regressions. (Environmental variable abbreviations are listed in Tables 1 and 2. SoilMo = soil moisture, Organic = soil organic matter content, Cover = cover of associated species; LC & BSS2: for the simple and cross-product regressions d.f. = 1/13, for the multiple regressions d.f. = 2/12; BSS1: d.f. = 1/63 for PPFD, d.f. = 1/27 for Organic and pH, d.f. = 1/26 for VPD.)

Month		Simple regression				Multiple regression			
		Variables				Variables			
Dep.Var.	Ind.Var.	Dep.Var.	Ind.Var.	*P*	R^2	Dep.Var.	Ind.Var.	*P*	R^2
Population BSS1									
Aug.	Aug.	Leaf area	− VPD	0.0098	0.24	—	—	—	—
Sep.	Aug.	Tiller	+ PPFD	0.0075	0.11	—	—	—	—
Mean	Mean	Leaf area	+ pH	0.0188	0.19	—	—	—	—
Mean	Mean	Pred. area	+ Organic	0.0292	0.17	—	—	—	—
Population BSS2									
May	May	Tiller	− VPD	0.0066	0.45	—	—	—	—
July	May	Tiller	− VPD	0.0102	0.41	—	—	—	—
July	June	Tiller	+ PPFD	0.0003	0.64	Tiller	(+)PPFD + SoilT	0.0001	0.80
July	June	Tiller	+ SoilT	0.0377	0.29	—	—	—	—
July	July	Tiller	+ PPFD	0.0033	0.50	Tiller	(+)PPFD + SoilT	0.0011	0.68
July	July	Tiller	+ SoilT	0.0052	0.46	—	—	—	—
Aug.	July	Leaf area	− SoilT	0.0329	0.30	—	—	—	—
Mean	Mean	Tiller	+ PPFD	0.0025	0.52	Leaf area	(+/−)Cover + SoilT	0.0003	0.74
Mean	Mean	Leaf area	+ Cover	0.0110	0.40	—	—	—	—
Mean	Mean	Pred. area	+ PPFD	0.0025	0.52	—	—	—	—
Mean	Mean	Pred. area	+ PPFD * Organic	0.0309	0.31	—	—	—	—
Population LC									
Apr.	Apr.	Tiller	+ VPD	0.0135	0.39	—	—	—	—
July	June	Tiller	+ PPFD	0.0450	0.27	—	—	—	—
July	July	Tiller	+ PPFD	0.0486	0.27	—	—	—	—
Sep.	Aug.	Tiller	+ PPFD	0.0290	0.32	—	—	—	—
Mean	Mean	Tiller	+ PPFD	0.0434	0.28	Leaf area	(−/+)SoilT + SoilMo	0.0214	0.47
Mean	Mean	Leaf area	− SoilT	0.0287	0.32	—	—	—	—
Mean	Mean	Leaf area	+ SoilMo	0.0087	0.42	—	—	—	—
Mean	Mean	Pred. area	+ PPFD	0.0320	0.31	—	—	—	—
Mean	Mean	Pred. area	+ AirT	0.0496	0.26	—	—	—	—
Mean	Mean	Leaf area	− SoilT * SoilMo	0.0082	0.43	—	—	—	—

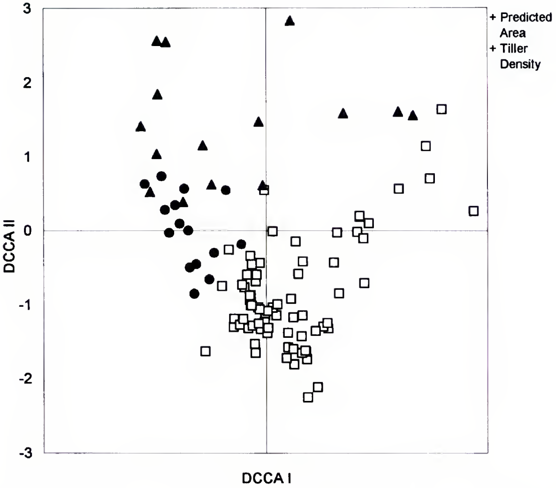

Figure 3. DCCA Axis I and II plot of quadrats containing *Calamagrostis porteri* subsp. *insperata* from sites BSS1 (□), BSS2 (●), and LC (▲). Dependent variables that are significantly ($P < 0.05$) correlated with each ordination axis are listed with their signs on the appropriate axis.

C. porteri subsp. *insperata,* we found that vegetative performance is related to a complex suite of environmental factors. All nine environmental variables tested were significantly related at one of the three sites (Table 3). Vapor pressure deficit and PPFD were related to the vegetative performance at all three sites. Additionally, vegetative performance was related to air and soil temperature and soil moisture at LC, cover, soil temperature and organic matter at BSS2, and organic matter and pH at BSS1. No single environmental factor seems to be responsible for vegetative performance. Similarly, no single environmental factor is related to the presence or absence of *C. porteri* subsp. *insperata.* Rather, as shown in studies of other taxa (e.g., Gibson & Good, 1987), it is the relative magnitude and importance of these limiting factors that provide an understanding of the subspecies' microhabitat requirements or realized niche.

Although these results show many shared trends between the populations with respect to the environmental variables as significant predictors of vegetative performance, the DCCA ordination shows the sites separated when plotted on two axes. It is clear that the ground cover of associated species and the microhabitat are not similar among the three sites (at the local level). At a broader level, this is also supported by a review of the literature that shows a wide range of plant associates (and habitats) for *C. porteri* subsp. *insperata* throughout its range (Ambrose et al., 1994; Campbell et al., 1992; Summers, 1993; Bittner, 1995a).

Although soil moisture, soil temperature, air temperature, and pH were highly correlated with the first two axes in the ordination, only 39% of the variance was accounted for. This demonstrates that more factors are involved with distribution and abundance of the associated species than were sampled. Total predicted leaf area and tiller density were both significantly related to the second axis. This was due to the much higher tiller densities and more robust leaves present at the LC population.

Leaf senescence contributed greatly to the decline in leaf area from May to August at each site. Because *C. porteri* subsp. *insperata* grows only on cool, northeast- or northwest-facing slopes, it is possible that there is an upper limiting temperature for growth. Temperature is frequently the main limiting factor for C_3 taxa (Ode et al., 1980; Barnes et al., 1983), such as *C. porteri* subsp. *insperata.* While high soil temperature is related to high per-

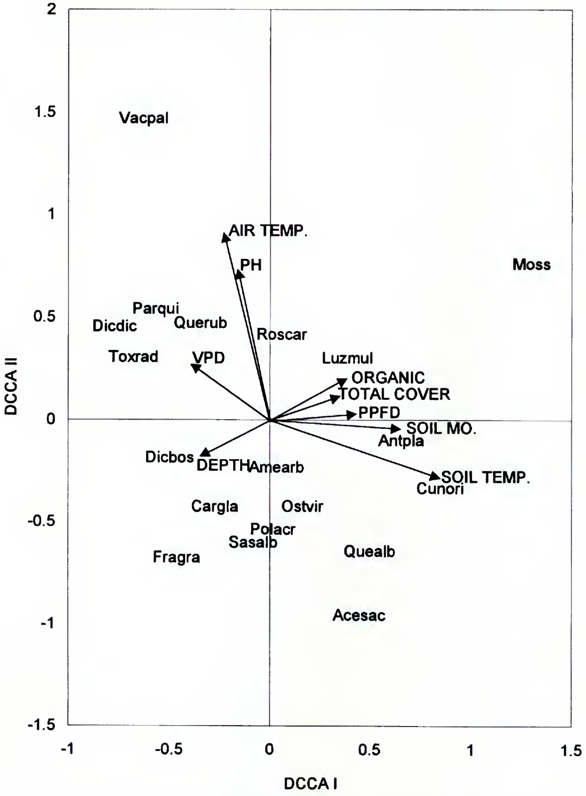

Figure 4. DCCA Axis I and II species cover–environmental variable biplot ordination. Environmental variables and species (those with weightings > 50) coordinates are plotted and labeled on Axes I and II. Acesac = *Acer saccharum*, Amearb = *Amelanchier arborea*, Antpla = *Antennaria plantaginifolia*, Cargla = *Carya glabra*, Cunori = *Cunila origanoides*, Dicbos = *Dicanthelium boscii*, Dicdic = *D. dichotomum*, Fragra = *Fagus grandifolia*, Luzmul = *Luzula multiflora*, Ostvir = *Ostrya virginiana*, Parqui = *Parthenocissus quinquefolia*, Polacr = *Polystichum acrostichoides*, Quealb = *Quercus alba*, Querub = *Q. rubra*, Roscar = *Rosa carolina*, Sasalb = *Sassafras albidum*, Toxrad = *Toxicodendron radicans*, Vacpal = *Vaccinium pallidum*.

formance early in the growing season, it may contribute to increased leaf senescence later in the season.

Calamagrostis porteri subsp. *insperata* seems to exhibit microhabitat selection similar to that of *Calamagrostis canadensis* (Michx.) P. Beauv., a boreal forest understory species. *Calamagrostis canadensis* exhibits an opportunistic "guerrilla" strategy for clonal foraging that allows the plants to vegetatively locate and exploit the most favorable microhabitats within the population by expanding rhizomes into conditions with warmer soil and higher light, as demonstrated in a glasshouse experiment (Macdonald & Lieffers, 1993). Field observations also documented that *C. canadensis* allocates resources to its rhizomes for the invasion of favorable microsites (e.g., treefall gaps). Rhizome expansion and exploitation in *C. canadensis* is influenced by soil temperature and cover, rather than PPFD alone (Macdonald & Lieffers, 1993). Tillers of *C. porteri* subsp. *insperata* at population BSS1 were present within the most favorable microhabitats (i.e., quadrats with higher soil temperature and PPFD; Table 2), as in *C. canadensis.*

Observations of tiller production suggest that there are two distinct periods of production, one in the spring and the second in mid to late summer, with the latter considerably lower. The performance of *C. porteri* subsp. *insperata*, especially in the early spring, may be the result of the microenvironmental conditions from the previous year. In *C. canadensis*, mobilization of rhizome carbohydrate reserves for shoot regrowth is responsible for tiller production in the spring (Hogg & Lieffers, 1991), and it is likely that the same is true for *C. porteri* subsp. *insperata*. The second production period may be the result of the photosynthetic output from the current year. The difficulty of understanding the performance of individual tillers is also compounded by the fact that not all photosynthetic products go into tiller production, but some are allocated for rhizome elongation and foraging (Macdonald & Lieffers, 1993).

Unfortunately, the present study was unable to determine the conditions favorable for sexual reproduction due to the low number of flowering tillers. Some states, such as Missouri, have seen prolific but sporadic flowering episodes in some populations (Summers, 1993). No such events have been noted in Illinois. However, from field observations and extrapolations from neighboring samples, inferences can be made to determine the microhabitat conditions most conducive to the production of flowering tillers. Two sterile flowering tillers (inflorescences without reproductive structures) were recorded in 1992, and one in 1993, from the same location (it is unknown if it was the same genet). This location in population BSS1, on a bluff edge under a small canopy gap along a hiking trail, allowed almost full sunlight to reach the tiller from early morning through midday. The northeast-facing aspect at this location allowed the soil and air to be heated by sunlight early in the day and remain warm throughout the day. In contrast, samples at BSS2 and LC had northwest-facing aspects, and did not have soil heated directly by sunlight until midday or the afternoon. Furthermore, soil temperature and PPFD were higher earlier in the year at BSS1 than at BSS2 or LC. These observations suggest an important role of early–mid growing season soil temperature and light on flowering. Late-season environmental factors may be less important for flowering as suggested by Havens and Holland (1998, this issue), who found no effect on sexual reproductive success from differences in late-season light. The flowering-tiller location was also wet for considerable parts of the year because of the presence of an intermittent stream.

Environmental data were collected for the entire growing season from a quadrat located less than 1 m from the flowering tiller (1993). This same quadrat was the DCCA ordination Axis I right endpoint. Axis I was positively correlated with soil temperature ($r = 0.69$) and soil moisture ($r = 0.53$). These data suggest that there is a very small window of appropriate microhabitat conditions conducive to producing flowering tillers that is dependent on a complex suite of environmental factors including soil temperature, soil moisture, and light. Of course, other environmental and genetic factors not examined may also be related to the ability of this genet to flower.

Establishment of new populations of *C. porteri* subsp. *insperata* via sexual means would be an unlikely event. It is extremely probable that each population consists of a single, fragmented genet. Because *C. porteri* subsp. *insperata* is supposedly self-incompatible (Greene, 1980), successful fertilization would require simultaneous flowering of two genetically dissimilar populations or genets (over 1 km apart at BSS and 50 m at LC). Many plants lack viable pollen (Greene, 1980) or lack sexual structures altogether (Summers, 1993; Bittner, 1995a). Even if fertilization occurs, successful seed production is still not ensured (Greene, 1980). The remote chance of successful sexual reproduction was demonstrated by Havens and Holland (1998) when they hand-crossed four presumably different genotypes and produced only one seed that germinated out of 2000+ fertilized florets examined. Because seed production and suitable habitat are not common, colonization via seed dispersal would be an extremely rare event. Undoubtedly, the infrequency of this occurrence contributes to the rarity of this taxon.

Calamagrostis porteri subsp. *insperata* maintains its populations primarily by vegetative means, especially in Illinois. The current populations appear to occupy islands of suitable habitat surrounded by ecologically unsuitable habitat. Therefore, it would be unlikely that a population would be able to expand to new sites via vegetative means, except locally through transport of vegetative fragments.

Two uncommon to rare associated species were discovered during the course of this study. At LC and an unsampled BSS population, over 10 m^2 were carpeted by *Sphagnum* spp. These areas also contained some of the highest densities of *C. porteri* subsp. *insperata* in southern Illinois. Another associate, *Carex willdenowii* Schuhr, is present in three of the populations. It is listed as an Illinois endangered species and is known from only three counties in the southern part of the state (Herkert, 1991). The presence of these species within suitable habitat might be a good indicator for the presence of *C. porteri* subsp. *insperata* in southern Illinois.

A limitation of the present investigation is that populations throughout the range of *C. porteri* subsp. *insperata* were not studied. Therefore, we are not able to fully document the variable habitats or climates in which this taxon occurs. Additionally, this research was not exhaustive in examining all possibilities that may have affected the rarity of this taxon. Nevertheless, the limiting factors of specificity of habitat, unsuccessful seed production (Greene, 1980; Havens & Holland, 1998), and limited colonization of new habitat are primarily responsible for the few populations present in southern Illinois, and are the most likely reasons why *C. porteri* subsp. *insperata* is rare.

The long-term survival of *C. porteri* subsp. *insperata* in southern Illinois is threatened in several ways. Natural disturbances, such as treefalls, may not create enough favorable microhabitats within extant populations to maintain viable populations indefinitely. Increased forest succession and closure of the tree canopy caused by fire suppression have likely affected this taxon adversely (Bittner, 1995a; Ambrose et al., 1994). Additionally, several populations are extremely small in area (80–120 m^2), which increases the chances of destruction of a population by a single stochastic event. These actions could eventually degrade or extirpate the current populations. Since it is extremely unlikely that new populations would be produced by either vegetative or sexual means, it is necessary that the existing populations be properly protected and managed to ensure their long-term survival.

Future research is needed to determine the effects of management on vegetative and sexual performance. Summers (1993; in Ambrose et al., 1994) has suggested that canopy gaps should be created within and around the populations to determine how the populations respond to such management. Only a small percentage of the canopy (10–25%) should be removed at first. Summers stated that too much disturbance (e.g., timber cuts) leads to rapid growth from nearby species that outcompete and choke out *C. porteri* subsp. *insperata*. He further added that prescribed burning should be conducted on an experimental basis and suggested that flowering events may be related to mild disturbance.

Literature Cited

Abrams, M. D. & L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. Amer. Midl. Naturalist 117: 442–445.

Ambrose, D. M., W. R. Ostilie, M. R. Penskar & D. W. Schuen. 1994. Element Stewardship Abstract for *Calamagrostis porteri* subsp. *insperata*, Reed Bent Grass. The Nature Conservancy, Arlington, Virginia.

Bannister, P. 1986. Water relations and stress. Pp. 73–144 *in* D. Moore & S. B. Chapman (editor), Methods in Plant Ecology. Blackwell Scientific, Oxford, England.

Barnes, P. W., L. L. Tieszen & D. J. Ode. 1983. Distribution, production, and diversity of C_3- and C_4-dominated communities in a mixed prairie. Canad. J. Bot. 61: 741–751.

Bittner, R. T. 1995a. Distribution and Microhabitat Relations of a Rare Grass, *Calamagrostis Porteri* subsp. *Insperata*, in Southern Illinois. Unpublished Master's Thesis, Southern Illinois University, Carbondale.

———. 1995b. New populations of rare species in Illinois. Erigenia 14: 59–60.

Boyd, R. S. & C. D. Hilton. 1994. Ecologic studies of the endangered species *Clematis socialis* Kral. Castanea 59: 31–40.

Braak, C. J. G. ter. 1988. CANOCO—A FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis, Principal Components Analysis, and Redundancy Analysis (Version 2.1). TNO Institute of Applied Computer Science, Wageningen, Netherlands.

Brussard, P. F. 1991. The role of ecology in biological conservation. Ecol. Applic. 1: 6–12.

Buchele, D. E., J. M. Baskin & C. C. Baskin. 1989. Ecology of the endangered species *Solidago shortii*. I. Geography, populations, and physical habitat. Bull. Torrey Bot. Club 116: 344–355.

Campbell, J. J. N., S. A. Bonney, J. D. Kiser, L. W. Kornman, J. R. MacGregor, L. E. Medley & A. C. Risk. 1992. Cooperative Inventory of Endangered, Threatened, Sensitive, and Rare Species, Daniel Boone National Forest, Morehead Ranger District. U.S. Forest Service.

Cox, G. W. 1990. Laboratory Manual of General Ecology, 6th ed. Wm. C. Brown, Dubuque, Iowa.

FWS (Fish and Wildlife Service). 1993. 50 CFR Part 17, Plant Taxa for Listing as Endangered or Threatened Species; Notice of Review. Part IV. Fed. Reg. 58: 51144–51190.

Gawler, S. C., D. M. Waller & E. S. Menges. 1987. Environmental factors affecting establishment and growth of *Pedicularis furbishiae*, a rare endemic of the St. John River Valley, Maine. Bull. Torrey Bot. Club 114: 280–292.

Gibson, D. J. & R. E. Good. 1987. The seedling habitat of *Pinus echinata* and *Melampyrum lineare* in oak-pine forest of the New Jersey Pinelands. Oikos 49: 91–100.

——— & P. B. Looney. 1994. Vegetation colonization of dredge spoil on Peridido Key, Florida. J. Coastal Res. 10: 133–143.

Greene, C. W. 1980. The Systematics of *Calamagrostis* (Gramineae) in Eastern North America. Unpublished Ph.D. Thesis, Harvard University, Cambridge, Massachusetts.

Havens, K. & D. L. Holland. 1998. Factors affecting reproductive success in a rare grass, *Calamagrostis porteri* subsp. *insperata*. Ann. Missouri Bot Gard. 85: 64–68.

Herkert, J. R. (editor). 1991. Endangered and Threatened Species of Illinois: Status and Distribution, Volume 1—Plants. Illinois Endangered Species Protection Board, Springfield, Illinois.

Hogg, E. H. & V. J. Lieffers. 1991. The relationship between seasonal changes in rhizome carbohydrate reserves and recovery following disturbance in *Calamagrostis canadensis*. Canad. J. Bot. 69: 641–646.

Homoya, M. 1995. New vascular plant records for Indiana. Indiana Academy of Science, 111th Annual meeting, Nov. 2–3, 1995. [Abstract.]

Macdonald, S. E. & V. J. Lieffers. 1993. Rhizome plasticity and clonal foraging of *Calamagrostis canadensis* in response to habitat heterogeneity. J. Ecol. 81: 769–776.

Mohlenbrock, R. H. 1986. Guide to the Vascular Flora of Illinois. Southern Illinois Univ. Press, Carbondale.

Ode, D. J., L. L. Tieszen & J. C. Lerman. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology 61: 1304–1311.

Oksanen, J. & P. R. Minchin. 1997. Instability of ordination results under changes in input data order: Explanations and remedies. J. Veg. Sci. 8: 447–454.

SASI (SAS Institute Inc.). 1990. SAS Language: Reference, Version 6, 1st ed. Cary, North Carolina.

Schemske, D. E., B. C. Husband, M. H. Ruckelshaus, C. Goodwille, I. M. Parker & J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75: 584–606.

Schwegman, J. 1973. Comprehensive Plan for the Illinois Nature Preserves System, Part 2. The Natural Divisions of Illinois. Illinois Nature Preserves Commission, Rockford.

Sokal, R. R. & F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.

SPAC (Soil and Plant Analysis Council, Inc.). 1992. Handbook on Reference Methods for Soil Analysis. Soil and Plant Analysis Council, Athens, Georgia.

Summers, B. 1993. Botanical Survey for Federal and State Listed Plant Species in Oregon and Shannon Counties, Eleven Point Ranger District, Mark Twain National Forest. U.S. Forest Service.

Swallen, J. R. 1935. Two new grasses from the United States and Mexico. J. Wash. Acad. Sci. 25: 413–414.

USDA. 1975. Soil Survey of Pope, Hardin, and Massac Counties, Illinois.

———. 1992. Final Supplemental Environmental Impact Statement: Amended Land and Resource Management Plan, Shawnee National Forest. USDA Forest Service Eastern Region.

Vivian, V. E. 1967. *Shortia galacifolia*: Its life history and microclimate requirements. Bull. Torrey Bot. Club 94: 369–387.

Voigt, J. W. & R. H. Mohlenbrock. 1964. Plant Communities of Southern Illinois. Southern Illinois Univ. Press, Carbondale.

White, J. & M. H. Madany. 1978. Classification of Natural Communities in Illinois. Pp. 310–405 *in* Illinois Natural Areas Inventory Technical Report.

GENETIC VARIATION IN RUNNING BUFFALO CLOVER (*TRIFOLIUM STOLONIFERUM*: FABACEAE) USING RANDOM AMPLIFIED POLYMORPHIC DNA MARKERS (RAPDs)[1]

Daniel J. Crawford[2], *Elizabeth J. Esselman*[3], *Jennifer L. Windus*[4], *and Carol S. Pabin*[5]

ABSTRACT

Trifolium stoloniferum Muhl. ex Eaton (Fabaceae), a perennial, stoloniferous herb commonly known as running buffalo clover, once occurred over a large area in the Midwest (U.S.A.) but is currently restricted to five states and is federally endangered. The purpose of this study was to examine genetic variation within and among populations of *T. stoloniferum* throughout its known geographic distribution using Random Amplified Polymorphic DNAs (RAPDs) as markers. The average within-population banding similarity values for 390 individuals from 21 populations are high, ranging from 0.920 to 0.984 (mean = 0.952). The mean banding similarities for comparisons between populations range from 0.856 to 0.902 (mean = 0.884), implying that much of the diversity resides among populations in this species. There are also differences in average similarities within and between patches at the population level, suggesting substructuring within populations. A large proportion of plants sampled within populations have different banding patterns, indicating that populations do not consist of one to several genets perpetuated vegetatively by stolons. Our results agree with those of previous workers using allozymes in showing relatively low levels of diversity within populations and in the species as a whole. However, in the present study RAPD-marker variation was detected in all populations, with levels of diversity in several smaller populations equal to those in larger ones; no allozyme variation was detected in half of the populations sampled, and smaller populations were often monomorphic. Two bands are unique to Missouri populations and one band was found only in Ohio populations. Allozyme data were used to suggest that conserving smaller populations could be of lower priority because they lack diversity; certain ones are identical to each other, and thus they may consist of single genets. By contrast, RAPDs show that even the smallest populations have a high proportion of different genets and thus are worthy of further consideration for conservation.

It is generally accepted that the long-term viability of a species is correlated with the levels of genetic variation it maintains (Vrijenhoek, 1994) because species with low levels of diversity may lack the ability to adapt to new and changing environments (Godt et al., 1996). It follows, therefore, that successful strategies for the maintenance of rare species must include an understanding of the levels and distribution of genetic diversity.

Population biologists have described levels of genetic variation in plant and animal populations primarily by utilizing allozymes (Hamrick & Godt, 1990). Enzyme electrophoresis has several advantages over other readily available methods for assessing genetic variation in most plant species (Hamrick et al., 1991). Allozymes exhibit Mendelian inheritance and thus are not subject to environmental effects on the phenotype as may occur for quantitative morphological or physiological traits. In addition, allozymes are inherited as codominants, allowing the identification of alleles and loci; the allelic frequency data may be used to calculate diversity at different hierarchical levels such as within and between populations, geographical areas, etc. (Nei, 1973). Although protein electrophoresis has several advantages, one shortcoming is that only a relatively small number of loci can be surveyed and only those encoding proteins are sampled. Also, rare plant species may have little or no detectable allozyme variation (Crawford et al., 1994; Lesica et al., 1988; Soltis et al., 1992) so that no assessment can be made

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ANN. MISSOURI BOT. GARD. 85: 81–89. 1998.

of how genetic diversity is apportioned within the species.

Random amplified polymorphic DNAs (RAPDs) have gained popularity as molecular markers in recent years, with Hadrys et al. (1992) providing an early perspective for the use of RAPDs in molecular ecology. RAPDs have both advantages and limitations relative to allozymes for the study of variation in rare plants. Advantages include the availability of hundreds of the 10-base primers used to generate the RAPD bands with PCR. This allows for the sampling of many more loci than is possible with allozymes, and parts of the genome in addition to those encoding soluble enzymes can be examined (Stewart & Porter, 1995; Whitkus et al., 1994). Use of additional primers will, in most instances, eventually reveal variation within populations and/or species of plants in which allozyme diversity is lacking or extremely low (Brauner et al., 1992; Crawford, 1997; Crawford et al., 1994; Meyer et al., 1993; Rieseberg & Gerber, 1995; Rieseberg et al., 1989).

The limitations of RAPDs fall into the two broad categories of reproducibility and interpretation of banding patterns on the one hand and analysis of the data on the other. The question of reproducing the same banding pattern for a given plant and primer in the present study will be discussed later. It is usually assumed that co-migrating bands in gels are homologous (represent the same segment of DNA), but there have been few studies to document this. The work of Rieseberg (1996) found that 79% of the RAPD bands were homologous for different species of *Helianthus*. While the level of error involved in assuming homology for co-migrating RAPD bands from different plants is not known, available data suggest that the assumption is valid in most cases for populations of the same species or closely related species (Lannér et al., 1996; Stammers et al., 1995). Because RAPDs are inherited primarily as dominants, the genetic basis of the banding patterns cannot be inferred, as is usually possible with allozymes, and this precludes the routine use of gene diversity statistics (Nei, 1973). If it is possible to assume from other information (such as allozymes) that populations are in Hardy-Weinberg equilibrium, then one can infer allelic frequencies from the absence of a given band in individuals (which are assumed to be homozygous recessive). However, rare plants often have little or no allozyme diversity within populations, and it is not possible to make assumptions about equilibrium within the very population where RAPDs represent an alternative to allozymes for assessing diversity. Various methods have been used for analyzing RAPD banding patterns, and several will be used in this study.

Trifolium stoloniferum Muhl. ex Eaton (Fabaceae: Papilionoideae), commonly known as running buffalo clover, is a rare, highly stoloniferous, perennial herb. The species is known historically from nine states in the midwestern United States and was thought to be extinct from 1940 until the early 1980s, when it was rediscovered in West Virginia (Brooks, 1983; Campbell et al., 1988; Homoya et al., 1989; Cusick, 1989). Subsequently, additional populations were discovered in Indiana, Kentucky, Ohio, West Virginia, and Missouri. Since then running buffalo clover has been listed as an endangered species by the U.S. Fish and Wildlife Service (FWS, 1987). Recently, a number of populations have been found, particularly in Kentucky and West Virginia. Most populations are small (10–200 plants), but several populations are known with more than 1000 rooted crowns.

Past genetic studies of *T. stoloniferum* using allozymes suggested low genetic diversity in this species (Hickey et al., 1991; Hickey & Vincent, 1992). These studies also indicated that smaller populations have lower levels of diversity than larger ones, the majority of the diversity occurs among populations, and that gene flow between populations is limited, even between those separated by short distances.

The purpose of this study was to assess genetic variation within and among *T. stoloniferum* populations throughout their known geographic distribution using RAPD markers. Specific questions examined include: (1) How much RAPD diversity exists in the species? (2) How is the diversity in the species distributed? (3) Do populations of *T. stoloniferum* consist of more than one genotype (genet)? (4) Do larger populations contain more genetic variation than smaller ones? (5) Is there genetic substructuring, or a spatial distribution of different genotypes within and among populations?

METHODS

POPULATIONS EXAMINED

DNA was extracted from the leaves of 390 individual plants from 21 populations in Ohio, Kentucky, West Virginia, Missouri, and Indiana. State and county locations for populations are shown in Figure 1 and Table 1. Estimated population sizes are indicated in Table 1. One to two leaves were collected from each plant in April 1994 through June 1996. In larger populations, leaves were collected along a randomly placed transect, while leaves were collected throughout the smaller pop-

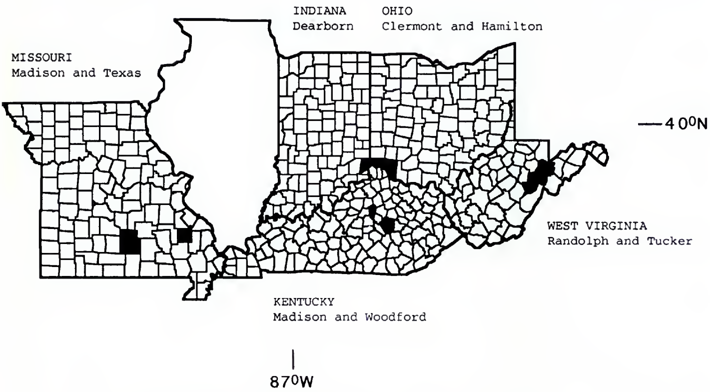

Figure 1. Map of state and county locations (in black) for populations of *Trifolium stoloniferum* examined in this study. County names are given below each state name. State and county locations for each population are listed in Table 1.

ulations. Twelve of the 21 populations sampled were examined for evidence of substructuring, either by comparing overall similarities within and between subpopulations or by determining the presence of unique RAPD markers between subpopulations. Voucher specimens for each population (e.g., *Crawford et al. 1601–1621*) are deposited at OS.

DNA EXTRACTIONS

Total DNA was extracted from 0.07–0.09 g (fresh weight) of mature leaf tissue following a miniprep extraction technique from Doyle and Doyle (1987). Leaf tissue was ground in 0.7 ml of 2 × CTAB isolation buffer [100mM Tris-HCl, pH 8, 1.4 M NaCl, 20 mM EDTA, 2% hexadecyltrimethylammonium bromide (CTAB), 1% Nabisulfite, 0.2% 2-mercaptoethanol]. The ground leaf tissue was incubated at 60°C for 30–60 min., extracted once with chloroform-isoamyl alcohol (24 : 1), centrifuged at high speed for 2 min., and the supernatant was collected. Nucleic acids were precipitated by adding 0.46 ml isopropanol, recovered by high-speed centrifugation for 2 min., washed in 0.8 ml 76% EtOH/0.01 M NH_4OAc, and resuspended in 0.1 ml 10 mM NH_4OAc/25mM EDTA.

RAPD PROTOCOL AND ANALYSIS

The protocol for amplifications is a modification of the procedure of Williams et al. (1990). Reactions were performed in volumes of 25 μl containing 1.5 mM MgCl, 100 μM each of dATP, dCTP, dGTP, and dTTP, 0.2 μM primer, 1.5 μl genomic DNA (an amount that gave reliable amplifications) and 0.75 unit of Taq polymerase. Amplifications were performed in a Perkin Elmer Cetus DNA Thermal Cycler programmed for 40 cycles of 1 min. at 94°C, 2 min. at 35°C, and 2 min. at 72°C. Amplifications were performed with five primers, A-3, A-4, A-7, A-8, and A-9 from Operon Technologies. Amplification products were analyzed by electrophoresis in a 1.5% agarose gel in 1 × TBE (tris-borate-EDTA) buffer, detected by staining with ethidium bromide, and photographed on a UV transilluminator. A 100 base-pair ladder of DNA fragments (BRL) was included on each gel as a size reference.

Amplification products from individuals of each population and each primer were initially electrophoresed in separate gels. One to three individuals that (either singly or collectively) contained all bands in a population were identified from these gels. These individuals were then amplified a second time and run together on a second gel along with individuals from every other population that had been judged to contain the same bands. This was done to ensure that the presumed similarities and differences in bands between populations were reproducible.

RAPD marker similarity was calculated by de-

Table 1. Population locations, number of individuals sampled, and average RAPD marker similarity comparisons within and among populations of *Trifolium stoloniferum*. The number of observed genotypes and genotypic diversity index values (Ellstrand & Roose, 1987) for each population are also included.

State/county locations and populations sampled	Estimated population size (number of rooted crowns)	Number of leaves sampled per population	Number of observed genotypes	Number of observed genotypes/number of plants sampled	Range of average similarity value with all other populations	Average similarity with all other populations	Average similarity within the population
Indiana							
Hidden Valley, Dearborn	2500	15	14	0.93	0.810–0.915	0.868	0.952
Kentucky							
Cane Forest, Madison	125	21	21	1.00	0.804–0.906	0.873	0.920
K-ridge, Madison	100	14	9	0.64	0.933–0.803	0.895	0.951
Otter Creek, Madison	200	27	22	0.81	0.843–0.929	0.896	0.945
Upper Viney Fork, Madison	150	21	18	0.86	0.848–0.914	0.892	0.954
Wilhoit, Woodford	75	15	14	0.93	0.793–0.926	0.890	0.959
Missouri							
Meagher, Madison	200	16	15	0.94	0.804–0.937	0.860	0.955
Tieslide, Texas	500	11	10	0.91	0.848–0.898	0.864	0.955
Ohio							
Congress Green, Hamilton	150	23	17	0.74	0.825–0.946	0.892	0.950
Miami, Hamilton	500	30	15	0.50	0.851–0.946	0.902	0.983
Milford, Clermont	20	10	7	0.70	0.874–0.914	0.886	0.939
Newberry, Hamilton	200	26	20	0.77	0.803–0.921	0.877	0.944
Niehaus, Hamilton	2500	46	45	0.98	0.810–0.920	0.881	0.935
West Virginia							
Crouch Knob, Randolph	3000	26	26	1.00	0.815–0.886	0.856	0.941
Ferno, Tucker	550–1000	20	17	0.85	0.856–0.920	0.889	0.964
Laural, Randolph	125	9	5	0.55	0.840–0.938	0.899	0.984
Rich Mountain, Randolph	150	14	12	0.86	0.850–0.929	0.894	0.960
Rock Camp Run, Randolph	1000–1500	14	13	0.93	0.846–0.910	0.887	0.949
Shaver's, Randolph	225–350	15	13	0.87	0.875–0.926	0.896	0.959
Snyder, Randolph	500	10	10	1.00	0.812–0.915	0.890	0.950
Upper John's Run, Randolph	230–1000	9	9	1.00	0.814–0.914	0.887	0.951

termining overall band similarity among all individuals and then calculating mean similarity for plants within and between populations. A second approach was to ascertain the number of different discrete banding patterns (multilocus genotypes) found within populations, and to assess the number and frequency of variable bands within and between populations.

Overall RAPD similarity within and between populations was calculated using a program written by Vera Ford, University of California, Davis (pers. comm.). Pair-wise individual similarity values for all plants were averaged for a measure of within-population similarity and again for between-population comparisons. Only bands that were scorable (1 or 0) in both individuals were used in this computation. Bands not clear or unscorable between individuals were not included.

The calculation for pair-wise individual similarity is:

$$S_{ij} = \frac{(2 \times B_{ij})}{(B_i + B_j)}$$

Where:

B_{ij} = the number of bands scored 1 for both individuals i and j.

B_i = the number of bands scored 1 for individual i and likewise for j.

The calculations and assumptions for average within and between-population or group similarity are as follows:

Assume the first population consists of individuals numbered n_1 to n_x, and the second population consists of individuals numbered m_1 to m_x.

Average pair-wise similarity of individuals in the first population is given by:

$$\frac{\Sigma\ S_{ij} \text{ for all i and j with } n_1 \leq i \leq j \leq n_x}{\dfrac{(1 + n_x - n_1) \times (n_x - n_1)}{2}}$$

Likewise, average similarity of individuals for the second population is calculated as:

$$\frac{\Sigma\ S_{ij} \text{ for all i and j with } m_1 \leq i \leq j \leq m_x}{\dfrac{(1 + m_x - m_1) \times (m_x - m_1)}{2}}$$

The average similarity for all individuals between groups 1 and 2 is given by:

$$\frac{\Sigma\ S_{ij} \text{ for all i and j with } n_1 \leq i \leq n_x,\ m_1 \leq j \leq m_x}{(1 + n_x - n_1) \times (1 + m_x - m_1)}$$

Similarity comparisons were made both within and among populations and subpopulations. The lower the similarity value within a population, between populations, etc., the higher the diversity. For example, if all plants within a population have identical banding patterns, then the similarity value would be 1.00 and there would be no diversity.

The number of discrete banding patterns or multilocus genotypes was determined for each population and then was divided by the number of plants sampled to produce a measure of genetic diversity (Ellstrand & Roose, 1987). The number and percentage of variable bands was determined for each population, and the mean value for all populations was calculated. Also, the number of bands variable between populations (bands not present in every population) was determined, and the average percentage of all populations in which these variable bands occur was calculated.

RESULTS

WITHIN- AND BETWEEN-POPULATION SIMILARITIES

The five primers produced a total of 59 different RAPD bands for all plants examined. Within-population similarity values ranged from 0.920 to 0.984 with a mean of 0.952 (Table 1). Lowest similarity (highest diversity) was seen at Cane Forest (0.920) and the highest (lowest diversity) in the Laural population (0.984). Genetic diversity within populations, as measured by the proportion of plants with different banding patterns, ranged from 0.50 for Miami to 1.00 in Cane Forest, Crouch Knob, Snyder, and Upper John's Run (Table 1) with a mean of 0.846 for all populations. The average percentage of variable bands within a population was 18.7, and an average of 46.3 percent of individuals within a population contained variable bands.

The average similarities of each population with all other populations ranged from 0.856 to 0.902, with the highest average for Miami (0.902) and the lowest for Crouch Knob (0.856). Average within-population similarities were always higher than any average between a given population and all other populations (Table 1); the mean value was 0.952 within and 0.884 between all populations.

Thirteen of the 59 bands (22.03%) were variable in between-population comparisons. These variable bands occurred in an average of 62.70% of the populations, and an average of 53% of the individuals within a population contained a variable band.

Overall similarity of plants between the four disjunct areas of Missouri, Indiana–Ohio, Kentucky, and West Virginia showed higher average values

Table 2. Subpopulation location, number of individuals sampled, and average RAPD marker similarity comparisons within and among subpopulations of *Trifolium stoloniferum*. The number of observed genotypes and genotypic diversity index values (Ellstrand & Roose, 1987) for each subpopulation are also included.

State and subpopulations examined	Estimated subpopulation sizes (number of rooted crowns)	Number of leaves sampled per subpopulation	Number of observed genotypes	Number of observed genotypes/ number of plants sampled	Range of average similarity values	Average similarity with other subpopulations	Average similarity within a subpopulation
Missouri							
Meagher 1	75	10	9	0.90	0.843–0.937	0.862	0.952
Meagher 2	125	6	6	1.00	0.804–0.937	0.857	0.957
Ohio							
Newberry 1	50	8	7	0.88	0.803–0.891	0.867	0.933
Newberry 2	200	18	13	0.72	0.835–0.921	0.887	0.955
Niehaus 1	1500	11	11	1.00	0.810–0.902	0.876	0.917
Niehaus 4	300	12	12	1.00	0.833–0.902	0.881	0.946
Niehaus 6	30	6	6	1.00	0.817–0.920	0.892	0.950
Niehaus 8	150	17	17	1.00	0.821–0.910	0.875	0.927
Miami B	200	14	8	0.57	0.854–0.946	0.900	0.982
Miami L	150	16	7	0.44	0.851–0.946	0.903	0.983
West Virginia							
Shaver's 1	50	7	6	0.86	0.880–0.926	0.897	0.959
Shaver's 2	300	8	7	0.86	0.875–0.924	0.895	0.958

within than between the areas (0.905 versus 0.868). Two bands were unique to the two Missouri populations, with frequencies of 0.693 and 0.940 in each. One band was unique to the five Ohio populations, and it occurred with a frequency of 0.707 for all plants studied.

POPULATION SIZE AND LEVEL OF DIVERSITY

The level of genetic diversity, whether measured by overall similarity or proportion of unique banding patterns, was sometimes but not invariably correlated with population size (Table 1). For example, Niehaus (mean similarity of 0.935; 0.980 of plants with different banding patterns) and Crouch Knob (0.941 and 1.00) were the two largest populations and contained relatively high levels of diversity, whereas the small Laural population had low diversity (Table 1). A notable exception to size and diversity was Cane Forest, which was one of the smaller populations, yet had high diversity (Table 1).

SUBPOPULATION DIVERSITY

For every population in which average similarities were calculated for subpopulations (defined as dense patches or clumps separated by more than 3 m), lower similarities (higher diversities) were found between rather than within the subpopulations (Table 2). The within-population similarities within Miami B and L were 0.982 and 0.983, respectively, while the similarity between them was 0.946. For Shaver's 1 and 2 the values were 0.959 and 0.958, with a between-subpopulation similarity of 0.925. For the four Niehaus subpopulations, the mean within-similarity was 0.935; the range of values between them was 0.859–0.920 with a mean of 0.901.

In 5 of the 12 subpopulations, all plants examined had different multilocus genotypes (Table 2). The lowest proportion of multilocus genotypes was found in the two Miami subpopulations; they also had the highest mean band similarity among individuals (Table 2).

For several populations, RAPD bands were found in one or more of the subpopulations but not in others. Newberry subpopulation 2 contained four bands not found in Newberry 1. Niehaus subpopulations 1, 4, and 8 had one band not present in Niehaus 6; Niehaus 1 and 8 had one band not found in 4 and 6, while Niehaus 1 had one band missing from the other subpopulations. Miami subpopulation B had two bands not detected in Miami subpopulation L, Shaver's 1 had one band missing in Shaver's 2, and Meagher 1 had four bands not found in Meagher 2. There was also evidence of substructuring in the Congress Green and Otter Creek populations. The Congress Green population consisted of six distinct patches, and 10 RAPD markers were restricted to one to four of the patches. The Otter Creek population consisted of three patches and had nine RAPD bands present in only one or two of the patches.

DISCUSSION

Trifolium stoloniferum, as the specific epithet implies, is a highly stoloniferous species that often occurs in relatively small populations with estimated sizes of 500 or fewer rooted crowns. These attributes suggest that it may be highly clonal with very few genets per population (see discussion in Ellstrand & Roose, 1987). An extensive study of allozymes (28 populations, 336 rooted crowns) in *T. stoloniferum* revealed low levels of diversity, with half of the populations displaying no variation (Hickey & Vincent, 1992). The allozyme data did not refute the hypothesis that populations of running buffalo clover are highly clonal and that certain ones may consist of one or a few genets. Given that allozyme diversity may be low or nonexistent in rare plants (see Crawford et al., 1994; Lesica et al., 1988; Soltis et al., 1992), enzyme electrophoresis may sometimes be inadequate for assessing the number of genets in a population and for apportioning diversity within and between populations.

Results from the present study using RAPD banding patterns reveal that a high proportion of the rooted crowns sampled within populations represent different genotypes. In addition to variation within populations, RAPDs indicate substructuring within populations. The allozyme results of Hickey et al. (1991) likewise indicated substructuring in certain populations of *T. stoloniferum*. Given the sometimes highly patchy distribution of plants, the presence of subpopulations is not unexpected.

The high proportion of different multilocus genotypes (banding patterns) within populations of *Trifolium stoloniferum* indicates that the species is not highly clonal despite its highly stoloniferous nature. Such a high proportion of different multilocus genotypes is concordant with the hypothesis of sexual reproduction and some level of outcrossing. High selfing in the very small populations (where we sampled a large percentage of the rooted crowns) should fix a few genotypes rather than allow for nearly every plant to have a different multilocus genotype. Preliminary results by Carolee Franklin (pers. comm.) indicate that running buffalo clover is self-compatible but, importantly, it is not autogamous. Determining its breeding system is the focus of her ongoing study.

Despite a high proportion of plants with different genotypes, RAPD diversity is still limited in populations. An average of 18.7% of the bands are variable within a population, or conversely, over 81% of the bands in a population are invariable. These variable bands occur in an average of 46% of the plants per population. Thus, in the average population, less than 20% of the bands are variable and occur in less than half the plants. This low variation in populations is also reflected in the high average overall similarity of banding patterns.

The lower average similarity of individuals between, compared to within, populations indicates higher diversity between populations; these results are concordant with those of Hickey and Vincent (1992), suggesting differentiation between populations. Among all populations examined in the present study, 22% of the bands were variable, and on the average these variable bands occurred in 62.7% of the populations, with a range of 9.5 to 95%. Thus, the percentage of variable bands is slightly lower within as compared to between populations (18.7 versus 22%).

Although RAPD diversity was detected in all populations of *T. stoloniferum* and even higher diversity occurred between populations, the level of diversity does not at first glance seem very high. However, it is of interest to compare the present results with those of the few other available studies that used similar methods of analysis. A study of RAPD diversity for ten populations and 129 individuals of the rare Kentucky endemic goldenrod *Solidago albopilosa* E. L. Braun (Asteraceae) (Esselman & Crawford, 1997) revealed an average within-population similarity of 0.702 and a value of 0.413 between populations. Thus, this highly localized species has over twice as much diversity between populations than the much more widely distributed *T. stoloniferum*. Also, the within-population diversity in *S. albopilosa* is about 20% higher than in running buffalo clover.

Calamagrostis porteri A. Gray subsp. *insperata* (Swallen) C. W. Greene (Poaceae) is another rare and highly restricted taxon that has been studied with RAPD markers, and thus can be used for comparison with *T. stoloniferum*. This subspecies rarely flowers and has been reported as self-incompatible, suggesting that reproduction by rhizomes is common (Greene, 1984). Six Ohio populations have average within-population similarity values ranging from 0.982 to 1.00 (mean = 0.995). The average similarity for between-population comparisons ranges from 0.842 to 0.963 (mean = 0.909) (J. Li et al., in litt.). The average similarity values seen in *Trifolium* (Table 1), although high, are lower than those found in *C. porteri* subsp. *insperata*, a species that reproduces almost exclusively vegetatively.

As shown in Figure 1, the distribution of running buffalo clover is disjunct, with populations in Kentucky, Missouri, Ohio–Indiana, and West Virginia. The higher similarity of plants within, compared to between, these four areas indicates slight geographic differentiation. However, the only areas containing unique bands (and thus unique multilocus genotypes) are Missouri and Ohio, with two bands in the former area and one in the latter.

CONCLUSIONS AND COMMENTS ON CONSERVATION

This study shows that a high percentage of plants in populations of *Trifolium stoloniferum* have different RAPD banding patterns, indicating that populations do not consist of one or a few genets perpetuated by stolons. Higher average diversity was detected between rather than within populations, and populations from the four disjunct areas in the distribution of *T. stoloniferum* are more similar than are those from different geographical areas. While these results show differentiation between populations, only 22% of the bands are variable between populations, and unique bands were limited to two in the Missouri populations and one in the Ohio populations. If one were to use RAPD banding patterns per se as a guide to the conservation of populations, then the Missouri populations and one or more of the Ohio populations should be preserved simply because they contain unique bands. RAPD bands (and banding patterns) alone should not be the basis for conserving (or not conserving) particular populations of *Trifolium stoloniferum*, but they can assist in formulating a more broadly based conservation plan for the species. The results of the present study suggest a different strategy for population preservation than that proposed by Hickey and Vincent (1992) on the basis of their extensive allozyme studies. They suggested that certain small populations in lawns might be accorded lower priority for protection because they exist in tenuous sites and show no genetic variation. Also, if different populations are identical at all allozyme loci, it is possible that only one genet is represented, and one population would preserve all the diversity present in all the populations. Our results demonstrate that even the smallest populations contain genetic diversity. Thus it cannot be assumed that populations are genetically uniform and are also identical to other small populations. The interpretation of Hickey and Vincent (1992) was reasonable based on their data, but the more variable RAPD bands provide a different picture.

Comparison of results demonstrates the problems inherent in making conservation decisions based on only one type of marker. By the same token, however, it is not advisable to base conservation decisions solely on the presence of RAPD data. Rather, it is preferable to use the data to infer certain aspects of the biology of running buffalo clover, and these inferences can provide some guidelines. Small populations, as well as larger ones, contain a high proportion of different multilocus genotypes. This suggests the possibility that different combinations of alleles and multilocus genotypes important for growth and reproduction (components of fitness) exist within populations, rather than populations consisting of one genotype. This argues for conserving small as well as large populations, and also for conserving as many populations as possible for subsequent studies of comparative reproductive biology, demography, etc.

Within all populations where different patches were examined, substructuring was detected with RAPDs. This may be the result of restricted gene flow and/or selection (not on the RAPD loci themselves) at a local level. Detailed studies of *T. stoloniferum* at the local level could help elucidate the causes of substructuring. The present study also indicates that as many populations as possible should be conserved if the factors shaping the variation and evolution in this fascinating species are to be understood.

Literature Cited

Brauner, S., D. J. Crawford & T. F. Stuessy. 1992. Ribosomal DNA and RAPD variation in the rare plant family Lactoridaceae. Amer. J. Bot. 79: 1436–1439.

Brooks, R. E. 1983. *Trifolium stoloniferum*, running buffalo clover: Description, distribution and current status. Rhodora 85: 343–353.

Campbell, J. J. N., M. Evans, M. E. Medley & N. L. Taylor. 1988. Buffalo clovers in Kentucky (*T. stoloniferum* and *T. reflexum*): Historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. Rhodora 90: 399–418.

Crawford, D. J. 1997. Molecular markers for the study of genetic variation within- and between-populations of rare plants. Opera Bot. 132: 149–157.

———, T. F. Stuessy, D. W. Haines, M. B. Cosner, D. Wiens & P. Lopez. 1994. *Lactoris fernandeziana* on the Juan Fernandez Islands: Allozyme uniformity and field observations. Conservation Biol. 8: 277–280.

Cusick, A. W. 1989. *Trifolium stoloniferum* (Fabaceae) in Ohio: History, habitats, decline and rediscovery. Sida 13: 467–480.

Doyle, J. J. & J. C. Doyle. 1987. A rapid DNA isolation procedure for small amounts of fresh leaf tissue. Phytochem. Bull. Bot. Soc. Amer. 19: 11–15.

Ellstrand, N. C. & M. K. Roose. 1987. Patterns of genotypic diversity in clonal plant species. Amer. J. Bot. 74: 123–131.

Esselman, E. J. & D. J. Crawford. 1997. Molecular and morphological evidence for the origin of *Solidago albopilosa* (Asteraceae), a rare endemic of Kentucky. Syst. Bot. 22: 1–13.

FWS (U.S. Fish and Wildlife Service). 1987. Endangered and threatened wildlife and plants: Determination of endangered status for *Trifolium stoloniferum* (running buffalo clover). Fed. Reg. 52: 21478–21480.

Godt, M. W., B. R. Johnson & J. L. Hamrick. 1996. Genetic diversity and population size in four rare southern Appalachian plant species. Conservation Biol. 10: 796–805.

Greene, C. W. 1984. Sexual and apomictic reproduction in *Calamagrostis* (Gramineae) from eastern North America. Amer. J. Bot. 71: 285–293.

Hadrys, H., M. Balick & B. Schierwater. 1992. Applications of random amplified polymorphic DNA (RAPD) in molecular ecology. Molec. Ecol. 1: 55–63.

Hamrick, J. L. & M. J. W. Godt. 1990. Allozyme diversity in plant species. Pp. 43–63 *in* A. H. D. Brown, M. T. Clegg, A. L. Kahler & B. S. Weir (editors), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer, Sunderland, Massachusetts.

———, ———, D. A. Murawski & M. D. Loveless. 1991. Correlations between species traits and allozyme diversity: Implications for conservation biology. Pp. 76–86 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Hickey, R. J. & M. A. Vincent. 1992. Application of isozyme techniques in native North American *T. stoloniferum* species. Pp. 15–17 *in* D. S. Woffard & K. H. Quesenberry (editors), Proceedings of the Twelfth *Trifolium stoloniferum* Conference. University of Florida, Gainsville.

———, ——— & S. I. Guttman. 1991. Genetic variation in running buffalo clover (*T. stoloniferum*, Fabaceae). Conservation Biol. 5: 309–316.

Homoya, M. A., J. A. Aldrichand & E. M. Jacquart. 1989. The rediscovery of the globally endangered clover, *Trifolium stoloniferum*, in Indiana. Rhodora 91: 207–212.

Lannér, C., T. Bryngelsson & M. Gustafsson. 1996. Genetic validity of RAPD markers at the intra- and interspecific level in wild *Brassica* species with n = 9. Theor. Appl. Genet. 93: 9–14.

Lesica, P., R. F. Leary, F. R. Allendorf & D. E. Bilderbeck. 1988. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. Conservation Biol. 2: 275–282.

Meyer, M. A., A. J. Shaw & J. J. Doyle. 1993. Analysis of genetic variation within and between-populations of *Scopelophia cantaratae* using RAPD's and isozyme patterns. Amer. J. Bot. 80: 165. [Abstract.]

Nei, M. 1973. Analysis of gene divesity in subdivided populations. Proc. Natl. Acad. U.S.A. 70: 3321–3323.

Rieseberg, L. H. 1996. Homology among RAPD fragments in interspecific comparisons. Molec. Ecol. 55: 99–105.

——— & D. Gerber. 1995. Hybridization in the Catalina Island mountain mahogany (*Cercocarpus traskiae*): RAPD evidence. Conservation Biol. 9: 199–203.

———, S. Zona, L. Aberbom & T. Martin. 1989. Hybridization in the island endemic, Catalina Mahogany. Conservation Biol. 3: 52–58.

Soltis, P. S., D. E. Soltis, T. L. Tucker & F. A. Lang. 1992. Allozyme variability is absent in the narrow endemic *Bensoniella oregona* (Saxifragaceae). Conservation Biol. 6: 131–134.

Stammers, M., J. Harris, G. M. Evans, M. D. Howard & J. W. Forster. 1995. Use of random PCR (RAPD) technology to analyse phylogenetic relationships in the *Lolium/Festuca* complex. Heredity 74: 19–27.

Stewart, C. N. & D. M. Porter. 1995. RAPD profiling in biological conservation: An application to estimating clonal variation in rare and endangered *Iliamna* in Virginia. Biol. Conservation 74: 135–142.

Vrijenhoek, R. C. 1994. Genetic diversity and fitness in small populations. Pp. 37–53 *in* V. Loeschcke, J. Tomiuk & S. K. Jain (editors), Conservation Genetics. Birkhauser Verlag, Basal, Switzerland.

Whitkus, R. J. Doebley & J. F. Wendel. 1994. Nuclear DNA markers in systematics and evolution. Pp. 116–141 *in* R. L. Phyllips & I. K. Vasil (editors), DNA-based Markers in Plants, Advances in Cellular and Molecular Biology of Plants, Vol. 1. Kluwer Academic Publishers, Netherlands.

Williams, J., A. R. Kubelik, K. Livak, J. A. Rafalski & S. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucl. Acids Res. 18: 6531–6535.

POPULATION GENETICS OF THE CEDAR-GLADE ENDEMIC *ASTRAGALUS BIBULLATUS* (FABACEAE) USING ISOZYMES[1]

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ABSTRACT

The rare cedar-glade endemic *Astragalus bibullatus* (Fabaceae) has low levels of genetic variability both within and among populations. Within-population means across 15 isozyme loci resulted in estimates of 1.4 alleles per locus, 25.6% polymorphic loci, and 0.064 for observed heterozygosity. Populations are genetically very similar, with a low F_{ST} and genetic identity values ranging from 0.981 to 1.000. Sites where this species naturally occurs should be protected, but, considering the low levels of population differentiation, the source of transplants or seeds needed to establish new populations may not be the most critical concern.

Astragalus bibullatus Barneby & E. L. Bridges (Fabaceae) is a rare plant endemic to the limestone ("cedar") glades of middle Tennessee's Central Basin. It is a perennial that overwinters as a rosette, flowers in April and May, and ripens fruits in June (Baskin & Baskin, 1989). *Astragalus bibullatus* was described as a new species in 1987, with the Great Plains taxon *A. crassicarpus* Nutt. var. *crassicarpus* considered to be its closest relative (Barneby & Bridges, 1987). Known from only a few sites, *A. bibullatus* is federally listed as endangered (FWS, 1991).

Conservation biologists are often concerned about levels of genetic variability present in rare species. Many authors have pointed out that species with little genetic variability would have limited evolutionary potential under heterogeneous or changing environments (e.g., Frankel, 1970, 1974; Franklin, 1980; Soulé, 1980; Beardmore, 1983; Bradshaw, 1984; Antonovics, 1984; Lande & Barrowclough, 1987; Huenneke, 1991). Compared with more geographically widespread species, rare and localized species often (but not always) have low levels of genetic variability (Hamrick & Godt, 1990; Hamrick et al., 1991; Karron, 1987, 1991). Such low levels of genetic variability could be the result of inbreeding and/or random genetic drift in small populations (chronically small, or small due to founder events or other genetic bottlenecks), or perhaps adaptation to a narrow set of environmental conditions.

When estimating the genetic diversity of a species, population genetic structure can be examined to evaluate the level at which most variability occurs (whether at the level of the individual, the population, or the entire species), and the genetic similarity of populations can be estimated. Such analyses can help in management decisions for rare species. For example, population "C" of *A. bibullatus* is located on private property the owner plans to bulldoze, so state conservation officials hoped to transplant most of these individuals to an *A. bibullatus* site on protected public land. Despite being protected, such a location could be unsuitable if the "C" population were genetically quite distinct from the resident plants. Possible negative effects could include reduced genetic diversity via local selection and random genetic drift, and poor growth of the transplants if genetic differences involve unique adaptations to local environmental conditions. Such possibilities raise the question of how genetically similar the *A. bibullatus* populations are.

This study examines the population genetic structure of *A. bibullatus*, using isozymes to estimate the genetic variability of this narrow endemic and the genetic similarity of its populations.

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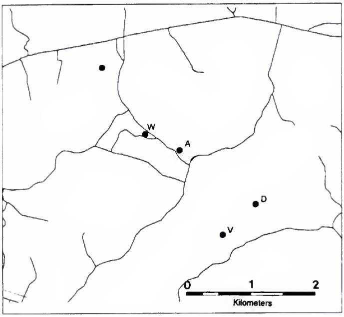

Figure 1. Relative positions of populations of *Astragalus bibullatus*. "W" represents both WO and WS. The unlabeled population was not sampled (see text). Population C (not shown) is about 20 km southwest of this area. Specific details about population locations have been omitted to protect this endangered species.

MATERIALS AND METHODS

COLLECTION OF SAMPLES

Populations of *Astragalus bibullatus* were sampled during the summer of 1995. Leaves were collected and refrigerated in moist reclosable bags. Those collected in the field were stored on ice for a few hours before they were refrigerated.

Spatially separated clusters of plants are referred to here as "populations" and labeled specifically by letters (A, C, D, V, WO, and WS). Population C is relatively isolated, being about 20 km from the other populations; on the other hand, WO and WS are only about 70 m apart. All populations then known for the species were sampled except one—a possibly artificially established colony with perhaps 60–100 plants (FWS, 1991) to which the landowner refused access. At the time of sampling, population C existed almost entirely as potted plants in the greenhouse because individuals had been dug up for transplanting. Figure 1 shows the relative positions of all populations except for C, with "W" representing both WO and WS.

Virtually all plants present were sampled for C, D, and V. Individuals were sampled haphazardly from A, WO, and WS, with a large fraction of the plants present included in the sampling. The holotype for *Astragalus bibullatus* was collected from population A and is deposited in VDB (see Barneby & Bridges, 1987).

ELECTROPHORESIS

Electrophoresis procedures generally followed Werth (1985). Leaves were homogenized on ice in the simple extraction buffer to which 10% polyvinylpyrrolidone and 0.6% mercaptoethanol had been added immediately before grinding. Crude homogenate was then adsorbed onto filter paper wicks and loaded onto 12% starch gels. Various individuals were used as marker genotypes on gels throughout this study.

Four buffer systems (three continuous and one discontinuous) were used to visualize 12 enzyme systems:

(1) tris-borate EDTA, pH 8, for alcohol dehydrogenase (ADH) (1.1.1.1), aldolase (ALD) (4.1.2.13), and glyceraldehyde-3-phosphate dehydrogenase (NAD-dependent form) (G3PDH) (1.2.1.12);
(2) tris-citrate, pH 8, for isocitrate dehydrogenase (NADP-dependent form) (IDH) (1.1.1.42), malate dehydrogenase (MDH) (1.1.1.37), and phosphoglucoisomerase (PGI) (5.3.1.9);
(3) histidine-citrate, pH 5.7 (Wendel & Weeden, 1989), for menadione reductase (MNR) (1.6.99.-), phosphoglucomutase (PGM) (5.4.2.2), phosphogluconate dehydrogenase (PGD) (1.1.1.44); and
(4) the discontinuous system from Ridgeway et al. (1970), pH 8.1, for aspartate aminotransferase (AAT) (2.6.1.1), leucine aminopeptidase (LAP) (3.4.11.1), and triose-phosphate isomerase (TPI) (5.3.1.1).

Staining protocols generally followed Wendel and Weeden (1989). Other staining solutions are described in Werth (1985) (IDH), Moran and Hopper (1983) (MNR), Soltis et al. (1983) (G3PDH), and Baskauf (1993) (LAP, MDH, PGM). Loci and alleles were numbered from the electrophoretically fastest to the slowest.

ANALYSIS

Allele frequencies, measures of genetic variability, and Nei's (1978) unbiased genetic identity were calculated using BIOSYS-1 (Swofford & Selander, 1989); χ^2 goodness-of-fit tests of genotype frequencies for deviations from Hardy-Weinberg expectations (using the Levene correction for small samples) and χ^2 contingency tests to examine the independence of allele frequencies among populations were performed. Hierarchical cluster analysis (UPGMA) (Sneath & Sokal, 1973) was used to group populations by genetic similarity using Nei's genetic identity. Wright's (1978) F-statistics (F_{IS} and F_{ST}) for evaluating within vs. among population

Table 1. Allele frequencies and sample size (N) for polymorphic loci in *Astragalus bibullatus.*

Locus/allele	Population					
	A	C	D	V	WO	WS
PGM-1 (N)	32	28	21	16	22	18
1	0.203	0.000	0.024	0.000	0.045	0.028
2	0.016	0.107	0.048	0.063	0.045	0.139
3	0.781	0.893	0.929	0.938	0.909	0.833
PGM-2 (N)	32	28	21	16	22	18
1	0.859	0.839	0.929	0.875	0.364	0.833
2	0.063	0.036	0.000	0.000	0.091	0.111
3	0.078	0.125	0.071	0.125	0.545	0.056
ADH-1 (N)	30	24	16	8	21	15
1	0.367	0.188	0.250	0.063	0.262	0.233
2	0.633	0.813	0.750	0.938	0.738	0.767
PGD-2 (N)	32	21	21	15	22	16
1	0.984	1.000	0.976	0.967	0.841	0.938
2	0.016	0.000	0.024	0.033	0.159	0.063

variability were calculated according to Weir and Cockerham's (1984) procedures, which correct for effects of sample size and provide a weighting system for multiple alleles at a locus. *t*-tests were used to determine whether the value of an *F*-statistic differs significantly from zero.

RESULTS

Fifteen putative loci were considered to have been resolved, coding for only 10 of the enzyme systems. This is because interpretation was at least partially unclear for MDH, PGI, PGM, PGD, and TPI, usually due to the presence of a larger number of invariant bands than could be accounted for by the typical number of loci found in diploid plant species. Crossing studies are not helpful in such a case involving invariant loci, and comparisons of banding patterns of leaf tissue versus soaked pollen (Weeden & Gottlieb, 1980) did not aid interpretation. Liston (1992) reported duplication of certain isozyme loci (PGI, PGD, TPI, perhaps MDH) for some *Astragalus* taxa, and it is possible that there may be several cases of gene duplication in *A. bibullatus* as well.

Of the 15 loci resolved, 11 appear to be invariant for this species (ALD, LAP, AAT, IDH, PGD-3, MDH-3, the two G3PDH loci, and all three MNR loci). Allele frequencies for the four polymorphic loci are given in Table 1.

Astragalus bibullatus does show some genetic variability for soluble enzymes, but at a low level (Table 2). Within populations, 20% to 27% of the loci included in this analysis are polymorphic (P). The mean number of alleles per locus (A) is 1.4. Observed heterozygosity (H_o) for these loci ranges from 0.038 (for V) to 0.099 (for WO), with a mean of 0.064. Species level estimates are similar, with A = 1.4 and P = 27%. These estimates of isozyme variability may be overestimates, considering that some unknown number of clearly invariant loci were excluded from the analysis.

As a whole, the populations are somewhat differentiated from one another at three of the four variable loci, as indicated by the significant ($P < 0.01$) χ^2 contingency tests of allele frequencies (Table 3). Further analysis revealed that despite being separated by only about 70 m, WO and WS show highly significant differences ($P < 0.001$) in allele frequencies at PGM-2. In fact, WO appears to be genetically the most distinctive population in the species.

Nonetheless, the populations of *A. bibullatus* are all very similar genetically. Genetic identity values among these populations are consistently high, ranging from 0.981 to 1.000 (Table 4, Fig. 2). An F_{ST} of 0.089 (Table 5) indicates that less than 10% of the total genetic variability of the species is the result of differences among populations, and in fact the jackknifed mean F_{ST} does not differ significantly from zero ($P > 0.05$). Therefore, most variability in this species is due to genetic heterogeneity within populations rather than genetic differentiation among populations.

Genotype frequencies for variable loci do not deviate significantly from the Hardy-Weinberg expectations within populations; thus expected heterozygosity values (H_e) are very close to observed values (H_o) for this species (Table 2). This situation

Table 2. Genetic variability* at 15 loci for *Astragalus bibullatus*.

Population	N	A	P	H_o	H_e
A	29.3 (0.7)	1.4 (0.2)	26.7	0.064 (0.034)	0.074 (0.040)
C	26.1 (0.7)	1.3 (0.2)	20.0	0.061 (0.033)	0.053 (0.029)
D	20.4 (0.4)	1.3 (0.2)	26.7	0.056 (0.034)	0.047 (0.027)
V	15.8 (0.8)	1.3 (0.1)	26.7	0.038 (0.019)	0.036 (0.018)
WO	21.3 (0.4)	1.4 (0.2)	26.7	0.099 (0.049)	0.095 (0.047)
WS	14.0 (1.0)	1.4 (0.2)	26.7	0.068 (0.032)	0.072 (0.034)
Mean (all populations)		1.4	25.6	0.064	0.063

* Mean sample size per locus (N), mean number of alleles per locus (A), percentage of loci polymorphic (P), observed heterozygosity (H_o), expected heterozygosity (H_e) as an unbiased estimate (Nei, 1978). Standard errors are indicated in parentheses.

is reflected in the fact that F_{IS} values are close to zero and the jackknifed mean does not differ significantly from zero (Table 5). These data suggest that *A. bibullatus* may be primarily an outcrossing species; however, this species' mating system has not been studied.

DISCUSSION

Although not completely lacking in genetic diversity at isozyme loci, the narrow endemic *Astragalus bibullatus* has low levels of variability. This is true for each population and for the species as a whole. In a compilation of plant isozyme studies, Hamrick and Godt (1990) reported population level means of A = 1.72, P = 43.0%, and H_e = 0.159 for 85 studies of widespread species, as opposed to A = 1.39, P = 26.3%, and H_e = 0.063 for 100 studies of narrowly endemic species. Thus means estimated for the rare *A. bibullatus* (A = 1.4, P = 25.6%, and H_e = 0.063) are comparable to those given for endemics in general. Low levels of variability at isozyme loci also have been reported for some western species of *Astragalus* with restricted geographic ranges (Karron, 1991; Liston, 1992). On the other hand, Travis et al. (1996) found 220 variable AFLP markers and substantial differentiation among populations for the rare *Astragalus cremnophylax* Barneby var. *cremnophylax*. These data are not directly comparable to isozyme data, however, and it is not known what levels of diversity or population differentiation would be detected by an isozyme survey of this taxon.

A few other species endemic or nearly endemic to the limestone glades of Tennessee have been assayed for variability at isozyme loci. Levels of genetic variability estimated for *Echinacea tennesseensis* (Beadle) Small (Asteraceae), another federally listed endangered species, were similar to those of *A. bibullatus*: A = 1.3, P = 23.0%, and H_e = 0.071 (Baskauf et al., 1994). A much less rare congener, *Astragalus tennesseensis* A. Gray, had relatively high estimates, with A = 1.71, P = 43.1%, and H_e = 0.148 (calculated from Wiltshire,

Table 3. Independence of allele frequencies for populations of *Astragalus bibullatus*: χ^2 contingency analyses.

Locus	# of alleles	DF	χ^2	P
PGM-1	3	10	36.263	0.00008
PGM-2	3	10	67.705	0.00000
ADH-1	2	5	8.312	0.13986
PGD-2	2	5	16.539	0.00546

Table 4. Genetic identities (Nei, 1978): pairwise comparisons for populations of *Astragalus bibullatus*.

Population	A	C	D	V	WO	WS
A	*****					
C	0.997	*****				
D	0.998	1.000	*****			
V	0.992	1.000	0.999	*****		
WO	0.981	0.985	0.981	0.982	*****	
WS	0.999	1.000	1.000	0.999	0.984	*****

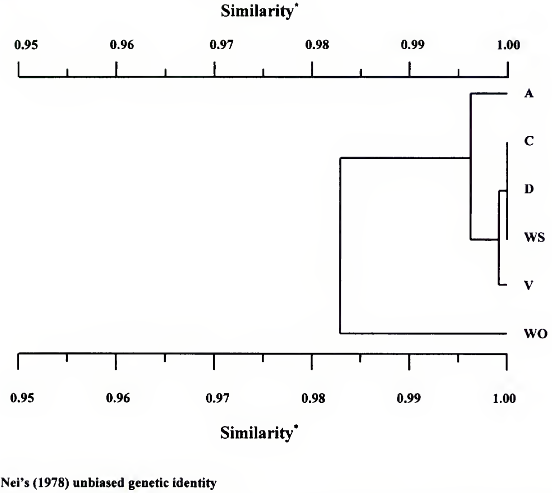

Figure 2. Populations of *Astragalus bibullatus* clustered according to genetic similarity. The similarity measure used is Nei's (1978) unbiased genetic identity.

1994). However, *Dalea foliosa* (A. Gray) Barneby, another legume federally listed as endangered, has much lower estimates, with A = 1.15, P = 13.8%, and H_e = 0.045 (calculated from Wiltshire, 1994).

Population sizes of *Astragalus bibullatus* appear to be quite variable among years and have been extremely small at times (Somers & Gunn, 1990; FWS, 1991), a factor that could contribute to low levels of genetic variability. For example, the "A" population was reported to consist of only a couple plants in 1979, but had increased to 171 plants by 1988 after the site had been cleared of woody vegetation. Such dramatic population fluctuations or extinction and recolonization events, even when rare, can greatly decrease effective population sizes and thus genetic variability (Wright, 1940; Nei et al., 1975; Lande & Barrowclough, 1987; McCauley, 1993). Such population crashes have been observed for some species showing no genetic variability at isozyme loci (Lesica et al., 1988; Waller et al., 1987), as well as some *Astragalus* species showing very low levels of variability (e.g., *A. clarianus* Jepson; Liston, 1992).

Table 5. *F*-statistics for polymorphic loci in *Astragalus bibullatus*.

Locus	F_{IS}	F_{ST}
PGM-1	−0.108	0.041
PGM-2	0.041	0.194
ADH-1	−0.029	0.019
PGD-2	0.090	0.053
Mean*	−0.009 NS (0.029)	0.089 NS (0.060)

* Means jackknifed over polymorphic loci (Weir & Cockerham, 1984), with standard errors indicated in parentheses. Neither mean differs significantly from zero (NS, $P > 0.05$).

"Genetic bottlenecks" resulting from population crashes are not the only factor that could affect genetic variability in *A. bibullatus*. Even at the best of times populations of this species are not large, and the smaller a population the more quickly random genetic drift is likely to erode variability. On the other hand, this plant is a perennial that probably has a long-term seed bank like many of its congeners (e.g., *A. tennesseensis*; Baskin & Baskin, 1989). Both of these features would favor the retention of genetic variability within the species.

The fine-scale differentiation observed between "populations" WO and WS, which are separated by only 70 m, was unexpected considering the great similarity among populations as a whole for this species. WO is also the population that displays the highest levels of heterozygosity. Of all populations, WO occurs in the most open habitat—a regularly mowed area along a private lane. The WS plants, on the other hand, grow in one of the most shaded spots among trees. Our isozyme data suggest that limited gene flow occurs between these two populations despite their close proximity. Gene flow could be restricted due to pollinator behavior, or could be ineffective due to differential selection pressures.

The most immediate threat to survival for *A. bibullatus* appears to be lack of protected habitat, with all populations but two occurring on privately owned land. The plight of the "C" site is a clear indication of this threat. WO could be a particularly good population to try to protect, given that it is genetically the most distinctive (indicated by genetic identity values) and the most variable (indicated by heterozygosity estimates); nevertheless, all of the populations are genetically quite similar. Extinction because of environmental stochasticity is a risk for any highly localized species limited to a few populations (Lande, 1988; Simberloff, 1988); thus the establishment of new populations of this species is advisable. A seed storage program is already in progress (K. Havens, pers. comm.). The low level of population differentiation observed for *A. bibullatus* suggests that the origin of seed used in establishing new populations probably is not a critical consideration. Similarly, these data provide no evidence of major genetic differences that might make inadvisable the transplanting of individuals from C to the V population.

Overall, it appears that protection of natural populations and the establishment of new populations are high priorities in alleviating the threat of extinction for this rare species. In addition, further research is needed. Little is known about the life cycle and ecology of *Astragalus bibullatus*, and any management plans would benefit from this type of information. Furthermore, it would be interesting to know how the genetic variability of this cedar-glade endemic compares with that of its widespread prairie relative, *A. crassicarpus* var. *crassicarpus*, and such a comparison is planned.

Literature Cited

Antonovics, J. 1984. Genetic variation within populations. Pp. 229–241 *in* R. Dirzo & J. Sarukhan (editors), Perspectives on Plant Population Ecology. Sinauer, Sunderland, Massachusetts.

Barneby, R. C. & E. L. Bridges. 1987. A new species of *Astragalus* (Fabaceae) from Tennessee's Central Basin. Brittonia 39: 358–363.

Baskauf, C. J. 1993. Comparative Population Genetics and Ecophysiology of a Rare and a Widespread Species of *Echinacea* (Asteraceae). Ph.D. Dissertation, Vanderbilt University, Nashville, Tennessee.

———, D. E. McCauley & W. G. Eickmeier. 1994. Genetic analysis of a rare and a widespread species of *Echinacea* (Asteraceae). Evolution 48: 180–188.

Baskin, J. M. & C. C. Baskin. 1989. Cedar glade endemics in Tennessee, and a review of their autecology. J. Tennessee Acad. Sci. 64: 63–74.

Beardmore, J. A. 1983. Extinction, survival, and genetic variation. Pp. 125–163 *in* C. M. Schonewald-Cox et al. (editors), Genetics and Conservation. Benjamin/Cummings, Menlo Park, California.

Bradshaw, A. D. 1984. Ecological significance of genetic variation between populations. Pp. 213–228 *in* R. Dirzo & J. Sarukhan (editors), Perspectives on Plant Population Ecology. Sinauer, Sunderland, Massachusetts.

FWS (U.S. Fish & Wildlife Service). 1991. Endangered and threatened wildlife and plants: *Astragalus bibullatus* (Guthrie's ground-plum) determined to be endangered. Fed. Reg. 56: 48748–48751.

Frankel, O. H. 1970. Variation, the essence of life. Sir William Macleay Memorial Lecture. Proc. Linn. Soc. Lond. 95: 158–169.

———. 1974. Genetic conservation: Our evolutionary responsibility. Genetics 78: 53–65.

Franklin, I. R. 1980. Evolutionary change in small populations. Pp. 135–149 *in* M. E. Soulé & B. A. Wilcox (editors), Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer, Sunderland, Massachusetts.

Hamrick, J. L. & M. J. W. Godt. 1990. Allozyme diversity in plant species. Pp. 43–63 *in* A. H. D. Brown et al. (editors), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer, Sunderland, Massachusetts.

———, ———, D. A. Murawski & M. D. Loveless. 1991. Correlations between species traits and allozyme diversity: Implications for conservation biology. Pp. 75–86 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Huenneke, L. F. 1991. Ecological implications of genetic variation in plant populations. Pp. 31–44 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Karron, J. D. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. Evol. Ecol. 1: 47–58.

———. 1991. Patterns of genetic variation and breeding systems in rare plant species. Pp. 87–98 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241: 1455–1460.

——— & G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pp. 87–124 *in* M. E. Soulé (editor), Viable Populations for Conservation. Cambridge Univ. Press, Cambridge, U.K.

Lesica, P. R., F. Leary, F. W. Allendorf & D. E. Bilderback. 1988. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. Conservation Biol. 2: 275–282.

Liston, A. 1992. Isozyme systematics of *Astragalus* sect.

Leptocarpi subsect. *Californici* (Fabaceae). Syst. Bot. 17: 367–379.

McCauley, D. E. 1993. Genetic consequences of extinction and recolonization in fragmented habitats. Pp. 217–233 *in* P. M. Kareiva et al. (editors), Biotic Interactions and Global Change. Sinauer, Sunderland, Massachusetts.

Moran, G. F. & S. D. Hopper. 1983. Genetic diversity and the insular population structure of the rare granite rock species, *Eucalyptis caesia* Benth. Austral. J. Bot. 31: 161–172.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

———, T. Maruyama & R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1–10.

Ridgeway, G. J., S. W. Sherburne & R. D. Lewis. 1970. Polymorphisms in the esterases of Atlantic herring. Trans. Amer. Fisheries Soc. 99: 147–151.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Rev. Ecol. Syst. 19: 473–511.

Sneath, P. H. A. & R. R. Sokal. 1973. Numerical Taxonomy. Freeman, San Francisco.

Soltis, D. E., C. H. Haufler, D. C. Darrow & G. V. Gastony. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73: 9–27.

Somers, P. & S. C. Gunn. 1990. Status report: *Astragalus bibullatus* Barneby & Bridges. Unpublished report, U.S. Fish & Wildlife Service.

Soulé, M. E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. Pp. 151–169 *in* M. E. Soulé & B. A. Wilcox (editors), Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer, Sunderland, Massachusetts.

Swofford, D. L. & R. K. Selander. 1989. BIOSYS-1, a Computer Program for the Analysis of Allelic Variation in Genetics. Release 1.7. User's Manual. University of Illinois, Urbana, Illinois.

Travis, S. E., J. Maschinski & P. Keim. 1996. An analysis of genetic variation in *Astragalus cremnophylax* var. *cremnophylax*, a critically endangered plant, using AFLP markers. Molec. Ecol. 5: 735–745.

Waller, D. M., D. M. O'Malley & S. C. Gawler. 1987. Genetic variation in the extreme endemic *Pedicularis furbishiae* (Scrophulariaceae). Conservation Biol. 1: 335–340.

Weeden, N. F. & L. D. Gottlieb. 1980. Isolation of cytoplasmic enzymes from pollen. Pl. Physiol. 66: 400–403.

Weir, B. S. & C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Wendel, J. F. & N. F. Weeden. 1989. Visualization and interpretation of plant isozymes. Pp. 6–45 *in* D. E. Soltis & P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Werth, C. R. 1985. Implementing an isozyme laboratory at a field station. Virginia J. Sci. 36: 53–73.

Wiltshire, B. 1994. Assessment of genetic diversity in *Astragalus tennesseensis* and the federal endangered *Dalea foliosa.* Unpublished Master's Thesis, Southern Illinois University, Carbondale, Illinois.

Wright, S. 1940. Breeding structure of populations in relation to speciation. Amer. Naturalist 74: 232–248.

———. 1978. Variability Within and Among Natural Populations, Vol. 4. Evolution and the Genetics of Populations. Univ. Chicago Press, Chicago.

GENETIC VARIABILITY IN THE FEDERAL THREATENED MEAD'S MILKWEED, *ASCLEPIAS MEADII* TORREY (ASCLEPIADACEAE), AS DETERMINED BY ALLOZYME ELECTROPHORESIS[1]

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ABSTRACT

Most populations of the federal threatened Mead's milkweed, *Asclepias meadii* Torr. (Asclepiadaceae), occur primarily in prairie haymeadows in Kansas and Missouri, where annual summer mowing prevents seed production. Exceptions are large populations in fire-managed habitats at the Rockefeller Prairie, a former Kansas haymeadow, and at Weimer Hill, a glade complex in southeastern Missouri. This perennial rhizomatous species is self-incompatible. The few remaining small populations in Illinois, Iowa, and northern Missouri persist vegetatively but no longer produce seeds and are vulnerable to stochastic extinction processes. Allozyme electrophoresis was used to measure the amount and distribution of genetic variation in *A. meadii* and to provide guidance for its recovery and restoration. Samples were obtained from 19 populations encompassing the extant range of the species in Kansas, Missouri, Iowa, and Illinois. *Asclepias meadii* was genetically variable for most of the 12 loci examined, with a mean of 1.53 alleles per locus, 40.8% polymorphic loci, and observed heterozygosity of 0.158. These values are comparable to published values for other milkweed species. More than half of the total 42 alleles were rare, with 15 alleles unique to single populations. About 74% of the genetic variation in *A. meadii* occurs within populations ($F_{ST} = 0.261$), and analyses do not provide conclusive evidence for a geographic pattern in genetic variation among populations. The two fire-managed populations had more genotypes and fewer ramets per genet than the haymeadows. For the latter, inhibition of sexual reproduction may have resulted in clonal spread and attrition of genotypes, thus exacerbating the effects of sexual incompatibility and inbreeding. These factors suggest that multiple propagule sources would maximize genetic diversity for recovering depauperate populations or for restoring new populations; however, sampling from a few larger, genetically diverse populations would provide much of the species' genetic diversity. Such sources would include the large fire-managed populations. Empirical data are needed to determine the population-genetic consequences of long-distance crosses and introductions that are apparently needed to restore viable populations of this species in the eastern part of its range.

The restoration of declining species enters a realm of conservation biology in which environmental, demographic, and genetic factors limit the survival and growth of populations (Shaffer, 1981; Wilcox & Murphy, 1985; Gilpin & Soulé, 1986). When once widespread self-incompatible or outcrossing plant species have reduced population sizes, forced inbreeding can result in either total reproductive failure or lower reproductive fitness with increased homozygosity and lower evolutionary potential (Menges, 1991; Schaal et al., 1991; Weller, 1994). Thus, restored populations of plants must be large enough to withstand loss from environmental or demographic events, and populations of either self-incompatible or outcrossing species must also contain sufficient numbers of genetically

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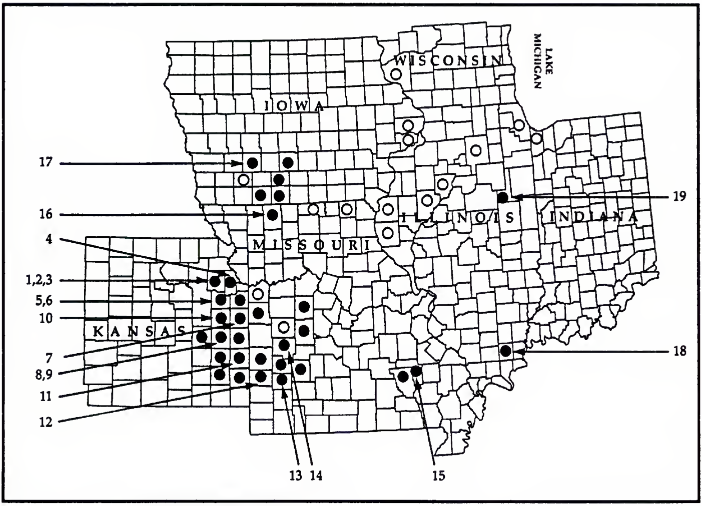

Site Number, Name & State

1	Rockefeller, KS	6	Jack's, KS	11	Hinton Creek, KS	16	Helton, MO
2	Dog Leg, KS	7	Osawatomie, KS	12	Cook Meadow, MO	17	Woodside, IA
3	French Creek, KS	8	Garnett, KS	13	Niawathe, MO	18	Saline, IL
4	High, KS	9	Sunset, KS	14	Wah-kon-tah, MO	19	Ford, IL
5	Colyer, KS	10	Fowler Hill, KS	15	Weimer Hill, MO		

Figure 1. Distribution by county of *Asclepias meadii*. Closed circles are counties with extant populations; open circles are counties from which populations have been extirpated. Allozyme study-site locations are numbered corresponding to Table 1.

different individuals to allow reproduction, avoid inbreeding, and have evolutionary potential (Les et al., 1991; DeMauro, 1993, 1994).

Understanding and resolving genetic problems is an important need in the conservation and recovery of declining plant species (Asins & Carbonnell, 1987; Barrett & Kohn, 1991; Falk & Holsinger, 1991; Amos & Hoelzel, 1992; Fenster & Dudash, 1994). This need is exemplified for the federal threatened (Harrison, 1988) Mead's milkweed, *Asclepias meadii* Torr. (Asclepiadaceae). This species is an obligate outcrossing, long-lived, late-successional perennial that is restricted to virgin tallgrass prairies, prairie haymeadows, and glades (Betz, 1989). The plant is pollinated by small bumblebees (*Bombus*) and miner bees (*Anthophora*) and, like all milkweeds, its pollen is dispersed in pollinia and its seeds are wind-dispersed from follicles (Betz & Lamp, 1992; Betz et al., 1994). Plants have an underground rootstock that produces multiple ramets, and from which rhizomes up to 1 m long have been observed in the field and in potted plants (M. L. Bowles, pers. obs.).

Asclepias meadii formerly ranged from Kansas eastward through Missouri and Illinois to northwest Indiana, and north into southern Iowa and northwest Wisconsin (Fig. 1). The origin of *A. meadii* is speculative. Gleason (1922) indicated that it was derived from the more eastern *A. amplexicaulis* Sm., and Fernald (1925) suggested it survived glaciation in the driftless area of Wisconsin and adjacent states. Woodson (1954) and Noamesi and Iltis (1957) proposed a more likely post-glacial migration from the Ozark uplands similar to that proposed for *Silene regia*, a prairie species whose highest genetic diversity is in the Missouri Ozarks (Dolan, 1994).

When *A. meadii* was discovered in 1843, it may not have been rare. Owing to habitat destruction and fragmentation, this species is presently known from a total of just 31 counties in parts of its former range in Illinois, Iowa, Missouri, and Kansas, the latter of which contains the largest number of populations. In Iowa, small populations, each with relatively few plants, are found in prairie remnants in four counties. Of the two known Illinois "populations," one is represented by only a single plant from a railroad prairie in Ford Co. The other occurs in the Shawnee Hills, Saline Co. This population comprises four colonies fragmented by forest encroachment among four small glades, one of which is isolated from the others by more than a kilometer. The largest colony has 17 ramets, and the others have only a few ramets. In the southwestern and west–central part of Missouri, *A. meadii* occurs in small populations within remnant prairies. It is also locally abundant in large glades of the St. Francis mountain system of the Ozark Plateau in Iron and Reynolds Cos., Missouri.

Although *A. meadii* is locally abundant in Kansas and Missouri, most suitable habitats were converted to native prairie haymeadows nearly a century ago (Fitch & Hall, 1978). This cultural management practice removes developing seed pods (follicles), thereby eliminating pollen-mediated gene flow and sexual reproduction (McGregor, 1977; Betz, 1989). In such populations, reproduction is limited to vegetative spread of rhizomes. One exception is Kansas University's Rockefeller Prairie, Jefferson Co., Kansas, which was converted from annual haymowing to a two- or three-year burning rotation in about 1956 (Fitch & Kettle, 1988). Because *A. meadii* is a long-lived perennial (Betz, 1989), it can survive decades of haymowing and reproductive failure, and may increase ramet (but not genet) numbers by rhizomatous spread. In a seven-year demographic study of 140 ramets in unmowed railroad prairies, Betz (1989) annually removed all mature seed pods and found a 9.3% decline in ramet numbers, suggesting that some sexual reproduction is required for long-term maintenance of natural populations. This life-history strategy correlates with low levels of follicle production reported for most milkweeds (Wyatt, 1976; Wyatt & Broyles, 1994). For example, although 77% of 140 ramets studied by Betz (1989) flowered annually, less than six follicles matured annually.

The glade populations of *A. meadii* in the Ozark Mountains of Missouri have escaped conversion to agriculture and haymowing but, as in Illinois, appear to be fragmented by forest encroachment resulting from fire suppression (Guyette & McGinnes, 1982; Guyette & Cutter, 1991; Ladd, 1991). The greatest concentration of these plants occurs in Iron Co. at Weimer Hill and in adjacent Reynolds Co. on Proffit Mountain, both of which are fire-managed natural areas. The Weimer Hill population contains 100 or more plants distributed among numerous glade openings (each less than 1 ha in area) that occur along a kilometer of bluff line habitat.

As with most milkweeds, *A. meadii* appears to be self-incompatible, as selfed garden plants do not produce follicles (M. L. Bowles, pers. obs.). Incompatibility in *Asclepias* appears to involve a late-acting ovarian system, and is not thoroughly understood (Seavey & Bawa, 1986; Shannon & Wyatt, 1986; Broyles & Wyatt, 1991; Kahn & Morse, 1991; Karron, 1991; Broyles & Wyatt, 1993a; Wyatt & Broyles, 1994). This life-history characteristic, combined with low effective population sizes (in some cases so low as to prevent sexual reproduction), impacts directly upon federal recovery planning to recover or restore sustainable populations of *A. meadii* (M. L. Bowles, pers. obs.). Furthermore, it is critical to assess the amount of genetic variation among populations to determine how genetic differentiation should be managed in recovery or restoration operations. This information may be especially important for restorations, where limited habitat size may require metapopulation management in which translocation of genetic material is required to maintain a high level of genetic diversity among populations (Bowles et al., 1998).

The purpose of this research was to determine the amount and distribution of genetic variation within and among *A. meadii* populations, and to compare the effects of management (burning versus mowing) on this variation. Allozymes provide a relatively rapid means to assess neutral genetic variation within and among populations of rare, endangered and/or threatened plant species (Waller et al., 1987; Lesica et al., 1988; Nickrent & Wiens, 1989; Billington, 1991; Hickey et al., 1991; Schaal et al., 1991; Godt & Hamrick, 1996a, 1996b), and multilocus genotypic diversity within populations (Sipes & Wolf, 1997). Detection of genetic diversity by DNA-based methods such as RAPDs (random amplified polymorphic DNA) is gaining use, especially when allozyme variability is low (e.g., Rieseberg et

Table 1. Mead's milkweed study sites sampled for allozymes (see Fig. 1 for site locations). Population sizes obtained from Kansas and Missouri Natural Heritage Program census data or M. L. Bowles (pers. obs.).

Population number	Population name	State	County	Habitat or management	Population size (approx. no. indiv.)
1.	Rockefeller	Kansas	Jefferson	former haymeadow[a]	200
2.	Dog Leg	Kansas	Jefferson	former haymeadow	< 20
3.	French Creek	Kansas	Jefferson	haymeadow	< 25
4.	High	Kansas	Leavenworth	haymeadow	< 25
5.	Colyer	Kansas	Douglas	haymeadow	< 25
6.	Jack's	Kansas	Douglas	haymeadow	> 300
7.	Osawatomie	Kansas	Miami	roadside	< 10
8.	Garnett	Kansas	Anderson	haymeadow	> 100
9.	Sunset	Kansas	Anderson	haymeadow	> 100
10.	Fowler Hill	Kansas	Franklin	haymeadow	< 25
11.	Hinton Creek	Kansas	Bourbon	former haymeadow	> 400
12.	Cook Meadow	Missouri	Barton	rotation[b]	< 25
13.	Niawathe	Missouri	Dade	rotation[c]	< 300
14.	Wah-kon-tah	Missouri	St. Clair	rotation[c]	< 20
15.	Weimer Hill	Missouri	Iron	glades[d]	100
16.	Helton	Missouri	Harrison	preserve/burned	< 5
17.	Woodside	Iowa	Adair	haymeadow (mowed late)	< 30
18.	Saline	Illinois	Saline	glades	< 40
19.	Ford	Illinois	Ford	railroad prairie	< 5

[a] Burned every 2 or 3 years since 1956.
[b] Former haymeadow, unmowed when milkweeds flower since ca. 1990.
[c] Burn/hay/rest since ca. 1980.
[d] Metapopulation managed by burning.

al., 1989; Rieseberg & Gerber, 1995). However, when the resolution of this genetic variation is fine-scale, such as genotypic variation within populations, allozyme variation may provide a more conservative system that is useful across a broader range of genetic diversity within and among populations (Swensen et al., 1995). Allozymes have already proven useful in population-level studies of relatively common (Broyles & Wyatt, 1990, 1991, 1993b; Foré & Guttman, 1996) as well as rare milkweeds (Edwards & Wyatt, 1994).

MATERIALS AND METHODS

POPULATION SAMPLING

Leaf samples were collected in 1992 from individual ramets of *Asclepias meadii* from 19 populations throughout the extant range of the species; supplemental collections were made from the Weimer Hill study site in 1993 (Table 1, Fig. 1). When possible, at least 20 individuals were sampled from each population. However, this number was sometimes not achieved because of the limited number of individuals located during this study. This was despite previous censuses of larger populations at some large sites, and no doubt was due to difficulties in locating small vegetative plants when flowering individuals were absent (Alexander et al., 1997). Sampling was minimally destructive, and consisted of removing one or two leaves from the lower nodes of the stem. Samples were individually numbered and labeled by population name, sealed in a plastic bag, and stored on ice until returned to the lab. Samples that were not extracted immediately were quickly frozen with liquid nitrogen, then maintained at −75°C until extraction.

ISOZYME ELECTROPHORESIS

Enzymes were extracted by using a Polytron homogenizer (Brinkman Industries, Westbury, NY) to grind the leaf tissue in ca. 2.0 ml of "microbuffer" pH 7.5 (Werth, 1985) supplemented with 5% (w/vol) polyvinylpyrrolidone (MW 40,000) and 0.1% 2-mercaptoethanol. For extremely small samples, hand-held glass homogenizers were used with varying amounts of extraction buffer (less than 1.0 ml). Samples were kept on ice throughout the extraction process. Cellular debris was pelleted via centrifugation at 10,000 rpm for 10 minutes, and the supernatant was poured into a microcentrifuge tube and stored at −75°C.

For electrophoresis, the extract was absorbed onto 6 × 19 mm Whatman #3 filter paper wicks and loaded into 13% starch gels (Starch Art, Smithville, Texas) for typical horizontal starch gel electrophoresis (Wendel & Weeden, 1989). Ten enzyme systems representing 12 putative loci were assayed using three gel electrode buffer systems. Alcohol dehydrogenase (Adh-2), isocitrate dehydrogenase (Idh-1), glutamate dehydrogenase (Gdh-2), and shikimate dehydrogenase (Skdh) were resolved using the Tris-citrate pH 7.5 buffer (Soltis et al., 1983). Aspartate aminotransferase (Aat-2, -3), glucose phosphate isomerase (Gpi-2), malic enzyme (Me-1), menadione reductase (Mnr), phosphoglucomutase (Pgm-1), and triose phosphate isomerase (Tpi-1, -2) were resolved using a lithium hydroxide buffer (Ridgeway et al., 1970). Finally, malate dehydrogenase (Mdh-2) and 6-phosphogluconate dehydrogenase (6-Pgd) were resolved with a pH 6.0 histidine citrate (Olmstead, 1989). Enzyme-staining protocols were essentially as reported in Soltis and Soltis (1989). Shikimate dehydrogenase showed activity but was not resolved for all populations; hence it was excluded from analysis. Menadione reductase (Mnr-2) showed high levels of variability within and between populations, but resolution was inadequate; hence this system was also excluded from analysis.

GEL SCORING AND ANALYSIS

Gel banding patterns were recorded photographically and genotypes were inferred based upon knowledge of enzyme subunit composition and the number of loci per enzyme system commonly seen in other plants (Gottlieb & Weeden, 1981; Weeden & Wendel, 1989). Enzyme patterns previously documented for other species of *Asclepias* were also consulted. Allelic isozymes were measured and recorded as relative mobilities using the most common allele as the standard (relative mobility of 100). When more than one locus appeared for an enzyme system, the most anodal one was designated "locus one."

Relative mobility numbers were converted to alphabetic genotypes prior to entry into BIOSYS-1 (Swofford & Selander, 1981). This program was used to calculate genetic variability measures by population, such as mean sample size per locus (*N*), mean number of alleles per locus (A), percentage of polymorphic loci (P), direct-count heterozygosity (H_o), expected heterozygosity given Hardy-Weinberg equilibrium (H_e), and chord and arc genetic distances between populations (Cavalli-Sforza & Edwards, 1967). To analyze partitioning of genetic variability within and among populations, the fixation index (Wright, 1978) was used. Because of its small sample size, the subdivided Saline Co., Illinois, population was analyzed as a single population, as well as the larger fragmented population at Weimer Hill, Missouri. We also used hierarchical *F*-statistics (Wright, 1978) to analyze genetic variation within and among seven subdivided populations sampled at Weimer Hill. This allowed comparison to hierarchical analysis of patch subdivision of *Asclepias verticillata* L. made at a similar landscape scale in southern Ohio (Foré & Guttman, 1996). The PCORD (McCune, 1993) software program was used to analyze population samples by Principal Component Analysis (PCA), using allele frequencies in a variance-covariance matrix, and to calculate allele diversity (H') for each population using the Shannon diversity index where $H' = -\Sigma\, p_i \log p_i$, where p_i = allele frequency at each locus.

Because *Asclepias meadii* has the potential to form more than one aerial shoot (ramet) from its rhizome system, the true number of genets per population could not be determined at the time of sampling. Following analyses of the electrophoretic data, it was determined that for some populations, individual ramets represented the same genet. This was determined by (1) the presence of identical multiple-locus genotypes from the isozyme analyses, (2) identical RAPD patterns on some collections (D. Hayworth and B. Schaal, pers. comm.), and (3) ramet proximity obtained from field maps. Such ramet genotypes were then "collapsed" into a single genotype and, for analysis purposes, assumed to be parts of the same genet. This process results in a conservative estimate of the actual number of genets because different genets could have the same multiple-locus genotype. To assess the relative abundance of ramets and genets within each population, the percentage of all ramets associated with each genotype was determined, and their mean and standard error calculated for each population. The average percent ramets/genet is also calculated as the inverse of the number of genotypes multiplied by 100.

RESULTS

Twelve polymorphic gene loci were identified corresponding to 10 enzyme systems for *Asclepias meadii* (data matrix available upon request). Although no monomorphic loci were found, two of the polymorphic loci (Adh-2 and Me-1) had one allele that was essentially fixed and a second allele that was scored only once. There was an average of 1.5 alleles per locus (Table 2), with 42 alleles occurring

Table 2. Genetic diversity statistics for Mead's milkweed populations: P(%) = percent polymorphic loci; A_p = number of alleles per polymorphic locus; H' = Shannon diversity index; H_o = observed heterozygosity; H_e = expected heterozygosity.

Population	Samples	Genotypes	Mean % ramet/ genet ± s.d.	P(%)	A_p	H'	H_o	H_e
1. Rockefeller	21	15	6.66 ± 2.4	58.3	1.8	2.80	0.194	0.201
2. Dog Leg	7	4	25.00 ± 13.7	41.7	1.5	2.74	0.204	0.175
3. French Creek	9	3	33.33 ± 29.4	33.3	1.3	2.70	0.065	0.074
4. High Prairie	3	2	50.00 ± 23.6	8.3	1.1	2.52	0.028	0.028
5. Colyer	12	9	11.11 ± 4.2	50.0	1.5	2.73	0.181	0.167
6. Jack's	18	5	20.00 ± 26.2	41.7	1.6	2.68	0.175	0.126
7. Osawatomie	3	2	50.00 ± 23.6	33.3	1.6	2.77	0.194	0.206
8. Garnett	21	8	12.50 ± 1.9	50.0	1.8	2.68	0.139	0.140
9. Sunset	10	9	11.11 ± 3.3	75.0	2.1	2.79	0.218	0.232
10. Fowler Hill	4	1	100	16.7	1.2	2.60	0.167	0.095
11. Hinton Creek	15	9	11.11 ± 4.7	58.3	1.7	2.75	0.172	0.179
12. Cook Meadow	16	2	50.00 ± 17.7	25.0	1.3	2.68	0.135	0.135
13. Niawathe	22	8	12.50 ± 10.8	50.0	1.8	2.74	0.141	0.157
14. Wah-kon-ah	8	6	16.67 ± 6.45	58.3	1.8	2.80	0.206	0.213
15. Weimer Hill	48	27	3.70 ± 2.5	75.0	1.8	2.72	0.121	0.147
16. Helton	2	1	100	25.0	1.3	2.66	0.250	0.167
17. Woodside	7	6	16.67 ± 5.8	33.3	1.4	2.70	0.167	0.149
18. Saline	10	5	20.00 ± 10.0	25.0	1.4	2.65	0.092	0.104
19. Ford	1	1	100	16.7	1.2	2.60	0.167	0.167
Mean ± s.d.				40.8 ± 19.2	1.5 ± 0.3	2.70 ± 0.07	0.159 ± 0.054	0.151 ± 0.050

across all 12 loci. Ten alleles at ten different loci were abundant, averaging over 90% frequency among all populations. There were 25 rare alleles (less than 10% frequency), representing all but the Mdh-2 locus. Rare alleles were distributed widely among populations. Only two sites, High Prairie and Fowler Hill, did not have any of the 25 rare alleles but these sites had sample sizes of only three and four, respectively. Eleven populations had one or more of 15 alleles that were unique to single populations. The Saline Co. population had the highest number, representing the Got-2, Pgm-1, and Tpi-1 loci. None of the other three disjunct populations in eastern Illinois, eastern Missouri, or Iowa had unique alleles.

The mean percentage of polymorphic loci across all populations was 40.8%, with 0.159 observed and 0.151 expected mean heterozygosity (Table 2). Percent polymorphic loci was positively correlated with sample size (r^2 = 0.432, P = 0.0022) and reached 75% at Weimer Hill (n = 48) and Sunset haymeadow (n = 10). The lowest values (16.7%) occurred in sites with single plants, but Saline Co. (n = 10) had only 25% polymorphic loci. Observed and expected heterozygosity were not correlated with either sample size (r^2 = 0.026, P = 0.507; r^2 = 0.0046, P = 0.783, respectively) or number of genotypes (r^2 = 0.0002, P = 0.954; r^2 = 0.0664, P = 0.287, respectively). Among all *A. meadii* populations, 123 multiple-locus genotypes were identified among the 237 "collapsed" samples, with 79 (64.2%) restricted to single populations (Table 2). Genotypes and sample size were positively correlated (r^2 = 0.8016, $P < 0.0001$), with the highest numbers at Weimer Hill (27 genotypes) and Rockefeller (15 genotypes). The mean allele diversity (H') was 2.70, and values ranged from 2.52 at High Prairie to 2.80 at the Rockefeller and Wa-kon-tah prairies (Table 2). These values were not correlated with sample size (r^2 = 0.092, P = 0.206). Although the highest H' (2.80) occurred at Rockefeller Prairie, five haymeadows had higher H' values than the fire-managed Weimer Hill (H' = 2.72).

Results of genetic-distance analyses (data not shown) indicated that all populations clustered at a chord distance (Cavalli-Sforza & Edwards, 1967) of 0.32 or less, and that clustering did not conform to expectations based on geographic proximity. The greatest interpopulational distances also involved those populations with the smallest sample sizes, and hence these relationships may be artifactual. There was also no clear geographic pattern among populations with PCA of allozyme frequencies (results not shown). The first PCA axis accounted for 35.18% of the variation and was most highly correlated (i.e., factor loadings > 0.4) with variation in two alleles at the pgm-1 locus. The second axis accounted for 57.6% cumulative variation and was most highly correlated with variation in one allele at the pgi-2 locus. The third axis accounted for 77.9% cumulative variation and was also highly correlated with variation in one allele at the pgi-2 locus. Three additional axes brought cumulative variation to 94.9%, with the strongest correlation in four alleles at the gdh-2 and got-3 loci.

Wright's fixation index provides information on the degree of fixation of individuals relative to their specific population (F_{IS}) and to all populations (F_{IT}), and the differentiation among all populations relative to complete fixation (F_{ST}). An F_{ST} value of 0.0 indicates that all variance resides within populations whereas a value of 1.0 shows that all variance is between populations (i.e., no alleles are shared among populations). The F_{ST} value for *A. meadii* was 0.261, which shows that about 74% of the genetic variation sampled resides within any one population. Hierarchical F-statistical analysis of the subdivided Weimer Hill provided information on the proportion of variance explained by the interactions of subpopulations to the total population. An F_{XY} value of 0.355 for subpopulations to total indicates that about 65% of the variance in the Weimer Hill population of *A. meadii* occurs within its subpopulations.

The type of management regime in effect at each population is shown in Table 1. Fire-managed populations contained more genotypes and a greater proportion of ramets with different genotypes than haymeadows (Tables 1, 2). For example, in thirteen haymeadows, the average percentage of all ramets for each genotype ranged from 11.11% (at three sites) to 100%, with an average of 30.98%. In contrast, the average percentage of ramets per genotype was 6.66% and 3.70% in the fire-managed Rockefeller and Weimer Hill prairies, respectively. Although these average values are positively correlated with sample size (r^2 = 0.3464, P = 0.008), they are meaningful when they represent total population samples. For those populations with ten or more samples, a plot of the ramet/genet ratio and the number of genotypes graphically illustrates the effects of burning versus mowing (Fig. 2). The burned Rockefeller and Weimer Hill sites had high numbers of genotypes and low ramet/genet percentages, whereas the mowed haymeadows had higher mean ramet/genet percentages and lower numbers of genotypes.

DISCUSSION

Given that several other species of *Asclepias* have been examined using allozymes, it is informative to

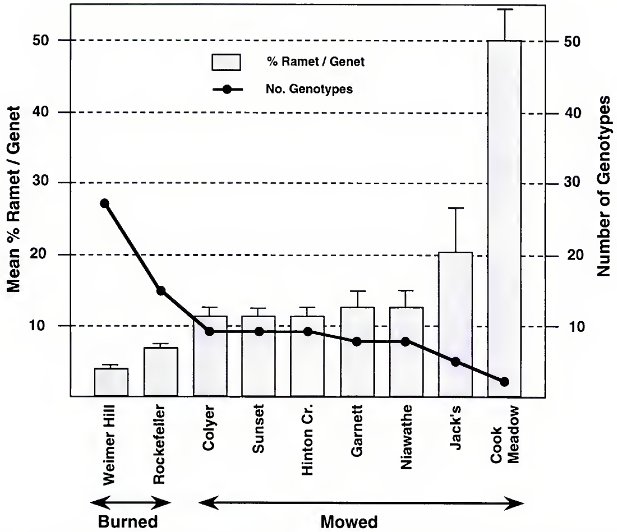

Figure 2. Effect of management methods on genetic structure of Mead's milkweed populations. Only those populations with allozyme sample sizes greater than or equal to 12 are shown. See text and Table 2 for calculations of mean percent ramets per genet and multiple-locus genotypes.

place the *A. meadii* results in context by comparing genetic diversity statistics among these species (Table 3). Although the objectives and methodologies differed somewhat in each study, similar patterns or trends are apparent. The mean number of alleles per locus and percentage of polymorphic loci for *Asclepias texana* Heller, a rare species, and *A. perennis* Walt., a widespread sister species, are remarkably similar to each other and to those of *A. meadii.* Heterozygosity levels in *A. meadii* were not as high as in *A. exaltata* L. or *A. verticillata,* two widespread North American species, but higher than in *A. texana* and *A. perennis.* These data indicate that genetic diversity in milkweeds may be less affected by effective population size and number than in other plants, likely because of their obligate-outcrossing mode of reproduction (see below). Despite severe reductions in population size, *A. meadii* has retained a comparatively high level of genetic diversity, thus making it an excellent candidate for restoration activities. Because levels of heterozygosity and mean allele diversity were not correlated with sample size or number of genotypes, these estimates are likely accurate reflections of the actual genetic diversity in *A. meadii* populations. In contrast, the percentage of polymorphic loci (P) was significantly correlated with sample size, possibly because sample size exceeded 20 plants for only 4 of the 19 populations studied. However, samples for many of the fragmented populations in Iowa, Illinois, and northern Missouri often represented the entire population, and thus these results are meaningful.

The partitioning of genetic variation in *A. meadii,* as measured by *F*-statistical analyses, showed that the greater proportion of genetic variation (74%) is within populations. However, this species partitions more than two to three times as much variation between populations as compared to *A. texana, A. perennis,* or *A. exaltata* (Table 3). Similarly, the hierarchical partitioning of 65% of the genetic diversity within population subdivisions at Weimer Hill was much less than the 97% found within patches of *A. verticillata* (Foré & Guttman, 1996). These comparisons indicate that *A. meadii* maintains more than a moderate amount (26%) of genetic variation

Table 3. Comparison of milkweed genetic-diversity statistics based on allozyme studies: A_p = number of alleles per polymorphic locus; % unique alleles = percentage of alleles restricted to single populations; P(%) = percent polymorphic loci, H_o = observed heterozygosity, H_e = expected heterozygosity, F_{ST} (also reported as G_{ST}) = proportion of genetic variation among populations.

Asclepias species	No. pops.	Total samples	No. loci	A_p	Total alleles	% unique alleles	P(%)	H_o	H_e	F_{ST}	Reference
A. meadii	19	237	12	1.53	42	35.7	40.8	0.159	0.151	0.261	this paper
A. texana	11	357	16	1.51	48	8.3	36.4	0.055	0.061	0.068	Edwards & Wyatt (1994)
A. perennis	18	942	16	1.57	58	24.1	41.3	0.055	0.061	0.082	Edwards & Wyatt (1994)
A. exaltata	18	846	16	2.36	75	14.7	64.5	0.202	0.182	0.093	Broyles & Wyatt (1993a)
A. verticillata	9	459	6	2.17	19	10.5	75.5[a]	0.197	0.214	0.033[b]	Foré & Guttman (1996)

[a] Only polymorphic enzyme systems (of 20 examined) were used in this analysis; P would be lower if loci were considered monomorphic that had the most common allele at a frequency of 0.99 or greater.

[b] Based on F_{YT} (patch-total) hierarchical analysis (Wright, 1978).

within its populations. However, this variation is only slightly higher than the expected level (20%) for widespread, outcrossing species reported by Hamrick and Godt (1990) and follows from the life-history characteristics of milkweeds in general (i.e., wind-dispersed seeds and durable pollinia carried by insects). Thus, any natural *A. meadii* population that meets a minimum size might be expected to comprise much of the genetic diversity occurring across the range of the species, but many genotypes may be distributed among populations. Despite the modern rarity of *A. meadii,* its populations maintain higher levels of genetic variation than naturally rare or endemic colonizing plants such as *Pedicularis furbishiae* S. Wats. (Waller et al., 1987), *Howellia aquatilis* A. Gray (Lesica et al., 1988), and *Trifolium stoloniferum* Eaton (Hickey et al., 1991). The outcrossing breeding system (Schoen & Brown, 1991) and occasional pollen- or seed-mediated gene flow among populations (Wyatt & Broyles, 1994), along with the great longevity (Betz, 1989) and increased survival of heterotic individuals (Schaal & Levin, 1976; Mitton & Pierce, 1980; Ledig, 1986), may contribute to the maintenance of genetic diversity within fragmented populations of *A. meadii.*

Although generally considered neutral, allozyme frequencies may be associated with different soil characteristics (Heywood & Levin, 1985). The lack of (1) large genetic distances among populations and (2) a geographic pattern to genetic variation is somewhat surprising because *A. meadii* is widely distributed over areas where soil conditions range from acid and nutrient-poor in the south to calcareous and nutrient-rich in the north (Bowles et al., 1998). However, our samples did not adequately cover the northeastern part of the former range of this species. *Asclepias meadii* populations in unglaciated Missouri or Kansas could represent points of origin for all *A. meadii* populations. Given their geographic proximity and habitat similarity, glade populations in southern Illinois also might be most closely related to those in Iron Co., Missouri. However, allozymes provide little positive information to address biogeographic hypotheses relating to pre-glaciation refugia, lineages and migration routes, founder events, and current distribution patterns for *A. meadii.*

Burning and mowing management practices appear to have different effects on the genetic structure of *A. meadii* populations, with high numbers of genotypes and low ramet/genet percentages in burned sites, and fewer genotypes with higher ramet/genet percentages in haymeadows. Although these results may correlate with sample size, similar ramet/genet percentages were found with RAPDs (D. Hayworth & B. Schaal, pers. comm.), and higher ramet densities with lower percentages of flowering ramets also occur in haymeadows (Bowles et al., 1998). This evidence suggests that haymowing, which prevents sexual reproduction, promotes clonal spread of certain genotypes but attrition of others. Although sexual reproduction is arrested by the mechanical removal of flowering stems, if such "pruning" does not remove all photosynthetic tissues from ramets, or misses smaller ramets, vegetative growth may continue throughout the growing season. If above-ground tissue is lost, it is also possible that mowing may stimulate lateral buds to form new shoots, thereby increasing rhizome branching. New growth may also be enhanced by reallocation of resources that might have gone toward sexual reproduction (Bowles et al., 1998). The net effect would be an increase in the number of vegetative shoots (ramets) that subsequently arise from the underground root system. Over time, stochastic factors would result in the successive loss of genotypes that do not spread vegetatively, since they are prevented from undergoing sexual reproduction.

The consequences of mowing on the functional dynamics of milkweed populations are apparent. Because of the self-incompatibility of *Asclepias meadii*, its populations may be sensitive to minimum numbers and spatial patterns of genotypes within populations. Even though populations have high levels of heterozygosity, they could still have limited reproductive capacity if they have low numbers of genotypes. A greater percentage of similar genotypes in haymeadows would inflate population numbers, while effective population size (N_e) remained relatively small. Even if large numbers of genotypes are present in haymeadows, the potential for crossing among genetically identical individuals and for consequent reproductive failure is increased in these populations because most local movement of pollinators will be within clones (Pleasants, 1991). Finally, repeated mowing prevents sexual reproduction in haymeadows, regardless of their genetic structure.

The maintenance of most genetic diversity within populations has important implications for restoration and management of *Asclepias meadii*. This structuring of genetic diversity may be selectively advantageous by maximizing the number of different compatibility types, thereby avoiding inbreeding among related individuals. Although plants with different multiple-locus allozyme genotypes are genetically distinct, they may still share identical alleles at a compatibility locus, thus preventing sexual reproduction (Les et al., 1991). Such genetic processes may limit reproduction in extremely small *A. meadii* populations, such as those in Saline Co., Illinois. Demographic factors such as physical isolation of population subdivisions and non-synchronous flowering of compatible plants may prevent pollen transfer among these populations. Although five different genotypes were detected among the four Saline Co. populations (Table 2), such genetic, demographic, and stochastic factors are apparently preventing sexual reproduction, since it has not occurred in this population. Finally, reproduction in small milkweed populations may also be limited by lack of appropriate pollinators, even if sexually compatible plants are present. Such factors may be in operation in the subdivided Weimer Hill population, where hierarchical *F*-statistics found a lower percentage of heterozygosity among population subdivisions (65%) than that found among all milkweed populations (74%). However, the Weimer Hill population regularly produces viable seeds via natural pollination (Bowles et al., 1998).

Without intervention, small, fragmented, clonal populations of *Asclepias meadii*, such as those in the eastern part of the range or possibly those in small haymeadows, appear to have relatively low opportunities for sexual reproduction and therefore high extinction probabilities. Because of the high proportion of rare or unique alleles within populations, a large reservoir of genetic variation would be lost with each extinction. To achieve greater viability and evolutionary potential in small populations, genotype diversity should be maximized through either pollen flow or the introduction of additional, genetically different plants. An argument that local genotypes will be lost through genetic swamping is not relevant, since they would almost certainly be lost otherwise through attrition and lack of sexual reproduction, and once genes are introduced, local habitat selection can act on novel combinations. The same consideration applies to the restoration of new milkweed populations, requiring the establishment of many genetically different individuals to maximize reproduction, evolutionary potential, and high population growth rates. The questions then arise: How many genotypes must be introduced to restore populational viability, and what seed sources should be used? Approximately 30 allozyme genotypes were detected at Weimer Hill, yet it is not presently clear that this represents the minimum number that should be used for restoration purposes. If the primary recovery objective for *A. meadii* is to maximize levels of genetic diversity and numbers of genotypes within populations, then replicating the diversity found in natural viable populations is a logical paradigm. If, as suggested earlier, there has been little selection for genetic change across the range of *A. meadii*, populations in unglaciated Missouri or Kansas would thus be suitable sources of genetic material for population restoration in any part of this species' range. Multiple populations also might be used to collectively maintain higher levels of genetic diversity by management as a metapopulation through periodic transfer of pollen or seed among sites to maintain high levels of diversity and avoid negative effects of inbreeding.

Another concern is that long-distance crossing for population recovery could potentially disrupt locally co-adapted gene complexes and cause outbreeding depression in naturally evolving populations. However, heterosis resulting from such crosses might outweigh any deleterious consequences (Fenster & Dudash, 1994), and such complexes might be regularly broken in outcrossing species with large neighborhoods. Although outbreeding depression may occur in milkweed species (Wyatt, 1976), no evidence has been found for optimal outcrossing because of their usually large neighborhood sizes (Broyles & Wyatt, 1991; Wyatt & Broyles, 1994). No differences were seen in seed germination percentages among natural and geographically distant crosses of *A. meadii* (Bowles et al., 1998). This study also showed that seedlings from distant crosses were competitively superior to seedlings derived from natural crosses, suggesting that heterosis may counteract negative effects of outbreeding. Clearly, these experiments must be extended to the field to ascertain long-term fitness components relevant to restoration efforts.

CONCLUSIONS

Conservation efforts aimed at increasing population size and stability of *Asclepias meadii* can be augmented with genetic data. Most genetic variation in *A. meadii* is contained within populations, and genetic analyses do not provide conclusive evidence for geographic patterning of genetic variation among *A. meadii* populations. Regardless of genetic differences that may occur among populations, the high level of allozyme diversity within extant populations indicates that restoration should attempt to maximize genetic diversity. If different genotypes are correlated with the outcrossing breeding system of milkweeds, then the number of genetically different individuals in restorations must also be maximized. The fragmented eastern populations of *A. meadii* are apparently too small to allow population recovery or restoration from their in situ genotypes, and hence supplemental propagule sources must be identified among the remaining Missouri and Kansas populations for effective restoration. This selection process should balance the maintenance of potential genetic differences across the range of the species against the need for maximizing genetic diversity in restorations. Experimentation is needed to evaluate the genetic consequences of population restoration of *A. meadii*, especially the effects of long-distance crossing among geographically different populations and the long-distance movement of genotypes.

Literature Cited

Alexander, H. M., N. S. Slade & W. D. Kettle. 1997. Application of mark-recapture models to estimation of the population size of plants. Ecology 78: 1230–1237.

Amos, B. & A. R. Hoelzel. 1992. Applications of molecular genetic techniques to the conservation of small populations. Biol. Conservation 61: 133–144.

Asins, M. J. & E. A. Carbonnell. 1987. Concepts involved in measuring genetic variability and its importance in conservation of plant genetic resources. Evol. Trends Pl. 1: 51–61.

Barrett, S. C. H. & J. R. Kohn. 1991. Genetic and evolutionary consequences of small population size in plants: Implications for conservation. Pp. 3–30 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Betz, R. F. 1989. Ecology of Mead's milkweed (*Asclepias meadii* Torrey). Pp. 187–191 *in* T. B. Bragg & J. Stubbendieck (editors), Proceedings of the Eleventh North American Prairie Conference. Univ. Nebraska at Lincoln.

——— & H. F. Lamp. 1992. Flower, pod, and seed production in eighteen species of milkweeds (*Asclepias*). Pp. 25–30 *in* D. D. Smith & C. A. Jacobs (editors), Recapturing a Vanishing Heritage: Proceedings of the Twelfth North American Prairie Conference. Univ. Northern Iowa, Cedar Falls.

———, R. D. Struven, J. E. Wall & F. B. Heitler. 1994. Insect pollinators of 12 milkweed (*Asclepias*) species. Pp. 45–60 *in* R. G. Wickett, P. D. Lewis, A. Woodliffe, & P. Pratt (editors), Proceedings of the Thirteenth North American Prairie Conference. Department of Parks & Recreation, Windsor, Ontario, Canada.

Billington, H. L. 1991. Effect of population size on genetic variation in a dioecious conifer. Conservation Biol. 5: 115–119.

Bowles, M. L., J. L. McBride & R. F. Betz. 1998. Management and restoration ecology of the federal threatened Mead's milkweed, *Asclepias meadii* (Asclepiadaceae). Ann. Missouri Bot. Gard. 85: 110–125.

Broyles, S. B. & R. Wyatt. 1990. Paternity analysis in a natural population of *Asclepias exaltata*: Multiple paternity, functional gender, and the "pollen-donation hypothesis." Evolution 44: 1454–1468.

——— & ———. 1991. Effective pollen dispersal in a natural population of *Asclepias exaltata*: The influence of pollinator behavior, genetic similarity, and mating success. Amer. Naturalist 138: 1239–1249.

——— & ———. 1993a. The consequences of self-pollination in *Asclepias syrica*, a self-incompatible milkweed. Amer. J. Bot. 80: 41–44.

——— & ———. 1993b. Allozyme diversity and genetic structure in southern Appalachian populations of poke milkweed, *Asclepias exaltata*. Syst. Bot. 18: 18–30.

Cavalli-Sforza, L. L. & A. W. F. Edwards. 1967. Phylogenetic analysis: Models and estimation procedures. Evolution 21: 550–570.

DeMauro, M. M. 1993. Relationship of breeding system to rarity in the Lakeside daisy (*Hymenoxys acaulis* var. *glabra*). Conservation Biol. 7: 542–550.

———. 1994. Development and implementation of a recovery program for the federal threatened Lakeside daisy (*Hymenoxys acaulis* var. *glabra*). Pp. 298–321 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Dolan, R. W. 1994. Patterns of isozyme variation in relation to population size, isolation, and phytogeographic history in royal catchfly (*Silene regia*: Caryophyllaceae). Amer. J. Bot. 81: 965–972.

Edwards, A. L. & R. Wyatt. 1994. Population genetics of the rare *Asclepias texana* and its widespread sister species, *A. perennis*. Syst. Bot. 19: 291–307.

Falk, D. A. & K. E. Holsinger. 1991. Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Fenster, C. A. & M. R. Dudash. 1994. Genetic considerations for plant population restoration and conservation. Pp. 34–62 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Amer. Acad. Arts 15: 237–242.

Fitch, H. S. & E. R. Hall. 1978. A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller experimental tract. Museum of Natural History, Univ. Kansas, Lawrence.

——— & W. D. Kettle. 1988. Kansas ecological reserves (Univ. of Kansas natural areas). Trans. Kansas Acad. Sci. 91: 30–36.

Foré, S. A. & S. I. Guttman. 1996. Spatial and temporal genetic structure of *Asclepias verticillata* (whorled milkweed) among prairie patches in a forested landscape. Canad. J. Bot. 74: 1289–1297.

Gilpin, M. E. & M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pp. 19–34 *in* M. E. Soulé (editor), Conservation Biology. Cambridge Univ. Press, Cambridge, Massachusetts.

Gleason, H. A. 1922. The vegetational history of the Middle West. Ann. Assoc. Amer. Geogr. 8: 39–85.

Godt, M. J. W. & J. L. Hamrick. 1996a. Genetic diversity and morphological differentiation in *Liatris helleri* (Asteraceae), a threatened plant species. Biodiversity & Conservation 5: 461–471.

——— & ———. 1996b. Genetic structure of two endangered pitcher plants, *Sarracenia jonesii* and *Sarracenia oreophila* (Sarraceniaceae). Amer. J. Bot. 83: 1016–1023.

Gottlieb, L. D. & N. F. Weeden. 1981. Correlation between subcellular location and phosphoglucose isomerase variability. Evolution 35: 1019–1022.

Guyette, R. & B. E. Cutter. 1991. Tree ring analysis of a post oak savanna in the Missouri Ozarks. Nat. Areas J. 11: 93–99.

——— & E. A. McGinnes. 1982. Fire history of an Ozark Missouri glade in Missouri. Trans. Missouri Acad. Sci. 16: 85–93.

Hamrick, J. L. & M. J. W. Godt. 1990. Allozyme diversity in plant species. Pp. 43–63 *in* A. H. D. Brown, M. T. Clegg, A. L. Kahler & B. S. Weir (editors), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer, Sunderland, Massachusetts.

Harrison, W. F. 1988. Endangered and threatened wildlife and plants; Determination of threatened status for *Asclepias meadii* (Mead's milkweed). Fed. Reg. 53: 33982–33994.

Heywood, J. S. & D. A. Levin. 1985. Associations between allozyme frequencies and soils characterisites in *Gaillardia pulchella* (Compositae). Evolution 39: 1076–1086.

Hickey, R. J., M. A. Vincent & S. I. Guttman. 1991. Genetic variation in running buffalo clover (*Trifolium stoloniferum*, Fabaceae). Conservation Biol. 5: 309–316.

Kahn, A. P. & D. H. Morse. 1991. Pollinium germination and putative ovule penetration in self- and cross-pollinated common milkweed *Asclepias syriaca*. Amer. Midl. Naturalist 126: 61–71.

Karron, J. D. 1991. Patterns of genetic variation and breeding systems in rare plant species. Pp. 87–98 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Ladd, D. 1991. Reexamination of the role of fire in Missouri oak woodlands. Pp. 67–80 *in* G. V. Burger, J. E. Ebinger & G. S. Wilhelm (editors), Proceedings of the Oak Woods Management Workshop. Eastern Illinois Univ., Charleston, Illinois.

Ledig, F. T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. Pp. 77–104 *in* M. E. Soulé (editor), Conservative Biology. Sinauer, Sunderland, Massachusetts.

Les, D. H., J. A. Reinartz & E. J. Esselman. 1991. Genetic consequences of rarity in *Aster furcatus* (Asteraceae), a threatened, self-incompatible plant. Evolution 45: 1641–1650.

Lesica, P., R. F. Leary, F. W. Allendorf & D. E. Bilderback. 1988. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. Conservation Biol. 2: 275–282.

McCune, B. 1993. Multivariate analysis on the PCORD system, August, 1993 Version. Oregon State Univ., Corvallis, Oregon.

McGregor, R. L. 1977. Rare native vascular plants of Kansas. Techn. Publ. State Biol. Surv. Kansas 5: 1–44.

Menges, E. S. 1991. The application of minimum viable population theory to plants. Pp. 45–61 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Mitton, J. B. & B. A. Pierce. 1980. The distribution of individual heterozygosity in natural populations. Genetics 95: 1043–1054.

Nickrent, D. L. & D. Wiens. 1989. Genetic diversity in the rare California shrub *Dedeckera eurekensis* (Polygonaceae). Syst. Bot. 14: 245–253.

Noamesi, G. K. & H. H. Iltis. 1957. Preliminary reports of the flora of Wisconsin. No. 40. Asclepiadaceae—Milkweed family. Trans. Wisconsin Acad. Sci. 46: 107–114.

Olmstead, R. 1989. Phylogeny, phenotypic evolution, and biogeography of the *Scutellaria angustifolia* complex

(Lamiaceae): Inference from morphological and molecular data. Syst. Bot. 14: 320–338.

Pleasants, J. M. 1991. Evidence for short-distance dispersal of pollinia in *Asclepias syriaca* L. Funct. Ecol. 5: 75–82.

Ridgeway, G. J., S. W. Sherburne & R. D. Lewis. 1970. Polymorphisms in the esterases of Atlantic herring. Trans. Amer. Fish. Soc. 99: 147–151.

Rieseberg, L. H. & D. Gerber. 1995. Hybridization in the Catalina Island mountain mahogany (*Cercocarpus traskiae*): RAPD evidence. Conservation Biol. 9: 199–203.

———, S. Zona, L. Aberbom & T. D. Martin. 1989. Hybridization in the island endemic, Catalina mahogany. Conservation Biol. 3: 52–58.

Schaal, B. A. & D. A. Levin. 1976. The demographic genetics of *Liatris cylindracea* Michx. (Compositae). Amer. Naturalist 110: 191–206.

———, W. J. Leverich & S. H. Rogstad. 1991. Comparison of methods for assessing genetic variation in plant conservation biology. Pp. 1123–134 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Schoen, D. J. & A. H. D. Brown. 1991. Intraspecific variation in population gene diversity and effective population size correlates with the mating system in plants. Proc. Natl. Acad. Sci. U.S.A. 88: 4494–4497.

Seavey, S. R. & K. S. Bawa. 1986. Late-acting self-incompatibility in angiosperms. Bot. Rev. (Lancaster) 52: 195–219.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience 31: 131–134.

Shannon, T. R. & R. Wyatt. 1986. Pollen germinability of *Asclepias exaltata*: Effects of flower age, drying time, and pollen source. Syst. Bot. 11: 322–325.

Sipes, S. D. & P. G. Wolf. 1997. Clonal structure and patterns of allozyme diversity in the rare endemic *Cycladenia humilis* var. *jonesii* (Apocynaceae). Amer. J. Bot. 84: 401–409.

Soltis, D. E. & P. S. Soltis. 1989. Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

———, C. H. Haufler, D. C. Darrow & G. J. Gastony. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrophoretic buffers and staining schedules. Amer. Fern J. 73: 9–27.

Swensen, S. M., G. J. Allan, M. Howe, W. J. Elisens, S. A. Junak & L. H. Rieseberg. 1995. Genetic analysis of the endangered island endemic *Malacothamnus fasciculatus* (Nutt.) Greene var. *nesioticus* (Rob.) Kearn. (Malvaceae). Conservation Biol. 9: 404–415.

Swofford, D. L. & R. B. Selander. 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Heredity 72: 281–283.

Waller, D. M., D. M. O'Malley & S. C. Gawler. 1987. Genetic variation in the extreme endemic *Pedicularis furbishiae* (Scrophulariaceae). Conservation Biol. 1: 335–340.

Weeden, N. F. & J. F. Wendel. 1989. Genetics of plant isozymes. Pp. 46–72 *in* D. E. Soltis & P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Weller, S. G. 1994. The relationship of rarity to plant reproductive biology. Pp. 298–321 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Wendel, J. F. & N. M. Weeden. 1989. Visualization and interpretation of plant isozymes. Pp. 5–45 *in* D. E. Soltis & P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Werth, C. R. 1985. Implementing an isozyme laboratory at a field station. Virginia J. Sci. 36: 53–76.

Wilcox, B. A. & D. D. Murphy. 1985. Conservation strategy: The effects of fragmentation on extinction. Amer. Naturalist 125: 879–887.

Woodson, R. E. 1954. The North American species of *Asclepias* L. Ann. Missouri Bot. Gard. 34: 353–432.

Wright, S. 1978. Variability Within and Among Natural Populations. Univ. Chicago Press, Chicago.

Wyatt, R. 1976. Pollination and fruit-set in *Asclepias*: A reappraisal. Amer. J. Bot. 63: 845–851.

——— & S. B. Broyles. 1994. Ecology and evolution of reproduction in milkweeds. Annual Rev. Ecol. Syst. 25: 423–441.

MANAGEMENT AND RESTORATION ECOLOGY OF THE FEDERAL THREATENED MEAD'S MILKWEED, *ASCLEPIAS MEADII* (ASCLEPIADACEAE)[1]

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ABSTRACT

The federal threatened *Asclepias meadii* Torr. (Asclepiadaceae) is a perennial, self-incompatible prairie forb imperiled by habitat destruction and population fragmentation. Many large populations persist in prairie haymeadows in Kansas and Missouri despite removal of seed pods by annual summer mowing. Only a few small populations remain in Illinois, Iowa, and northern Missouri. Recovery of these small populations and restoration of new populations are recovery objectives for this species. This study was conducted to determine habitat differences among populations, to understand how hay mowing and fire management affect the structure of *A. meadii* populations, and to test the effects of different management treatments on restoration of this species. Soils analysis showed a geographic gradient, with southern populations on acid, nutrient-poor soils, and northern populations on calcareous, nutrient-rich soils. Milkweed ramet densities were lower in fire-managed prairies than in haymeadows; but burned sites had 68% flowering ramets while haymeadows had only 19% flowering ramets. This suggests that burning has selected for greater resource allocation toward sexual reproduction, while annual hay mowing has selected for greater resource allocation toward clonal spread. The Morton Arboretum is conducting experimental restoration of *Asclepias meadii* in the eastern part of its range, an objective of Federal Recovery Planning. In greenhouse and garden experiments, competition from oats significantly reduced seedling growth, with greater growth in artificially outcrossed seedlings. At seven restoration sites in Illinois and northern Indiana, significant variation in milkweed germination, survivorship, and growth was caused by weather, differences among sites, and site management. Seedlings were vulnerable to drought, with greater survivorship when rainfall was 200% of normal. Planted juvenile milkweeds had greater survivorship than seedlings, and less sensitivity to drought. Greater growth and survivorship also occurred in burned than in unburned plots at three sites, but not in all life-stages. Propagated plants from Missouri seed sources were larger than Kansas plants in the garden, but not in the field. Continued work is needed to determine if restored populations can become viable, and if there are negative effects of crossing and translocating genotypes.

Managing for viable populations of endangered species requires knowledge of their life-history and habitat requirements, reproductive biology, and the demographic, genetic, and ecological traits that make them vulnerable to extinction processes (Gilpin & Soulé, 1986; Lande, 1988; Menges, 1986, 1991, 1992). Similar information is required to recover and restore new populations of these species, especially how site-management and stochastic environmental processes affect population growth based on their genetic attributes, reproductive characteristics, and survivorship at different life history stages (Fenster & Dudash, 1994; Weller, 1994; Pavlik, 1994, 1996; Guerrant, 1996). This paper examines factors that affect the management and restoration ecology of Mead's milkweed (*Asclepias meadii* Torr., Asclepiadaceae), a federal threatened (Harrison, 1988) plant essentially restricted to the virgin tallgrass prairies of the midwestern United States (Betz, 1989). To better understand how to manage and restore this species, we compare habitat characteristics across its range, examine the effects of management on population structure, and use experimental propagation and

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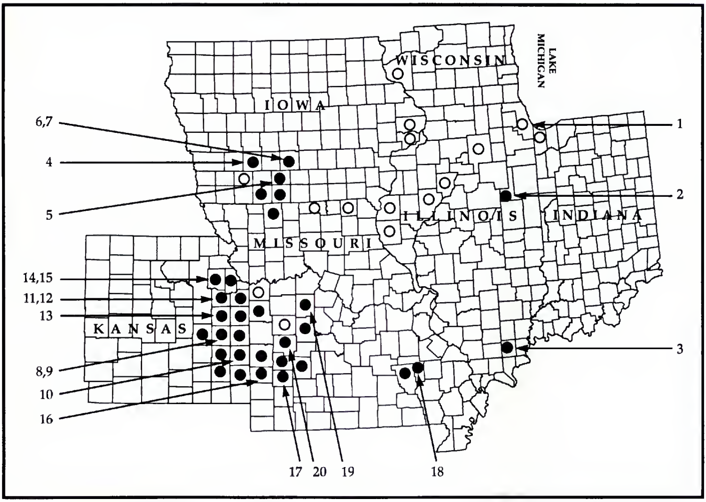


Site Number, Name & State

1	Palatine, IL	6	Cummings, IA	11	Colyer, KS	16	Cook Meadow, MO
2	Ford, IL	7	Martensdale, IA	12	Jack's, KS	17	Niawathe, MO
3	Saline, IL	8	Garnett, KS	13	Flower Hill, KS	18	Weimer Hill, MO
4	Woodside, IA	9	Sunset, KS	14	French Creek, KS	19	Paint Brush, MO
5	Flaherty, IA	10	Hinton Creek, KS	15	Rockefeller, KS	20	Wah-kon-Ta, MO

Figure 1. Distribution by county of *Asclepias meadii*. Closed circles are counties with extant populations; open circles are counties from which populations have been extirpated. Study site locations are numbered corresponding to Table 1.

restoration to understand the effects of environmental variation and site management on population establishment.

DISTRIBUTION AND STATUS

The range of *Asclepias meadii* follows the tallgrass prairie, extending eastward from Kansas through Missouri, Iowa, and Illinois to southwestern Wisconsin and northwestern Indiana (Fig. 1). Because of conversion of tallgrass prairie to agriculture, *A. meadii* has been reduced to about 150 populations, primarily in Kansas and western Missouri native haymeadows. These haymeadows are usually summer-mowed, which removes milkweed pods (follicles), preventing seed dispersal and sexual reproduction (McGregor, 1977; Betz, 1989). Hay mowing has occurred almost annually for a century (Fitch & Hall, 1978), yet many haymeadows contain hundreds of milkweed ramets. One former haymeadow, the Rockefeller Prairie, Jefferson Co., Kansas, has been fire-managed since the 1950s and may contain 200 or more plants (Alexander et al., 1997). Less than 20 former haymeadow populations have been preserved as public prairies in Missouri since the mid 1980s, and only one site contains a large population (Smith, 1997). A metapopulation of *A. meadii* occurs across a complex of non-mowed igneous glades in southeast Iron and Reynolds Cos., Missouri. The largest of these population groups has more than 100 plants and occurs at the

Figure 2. Flowering umbel and follicle of Mead's milkweed (*Asclepias meadii*). Reprinted with permission from *Erigenia* (Journal of the Illinois Native Plant Society); drawing by Nancy Hart Stieber.

fire-managed Weimer Hill site in Iron Co. Eastward, small colonies occur at two sites in northern Missouri, six Iowa sites, and five sites in Illinois; populations are extirpated from Wisconsin and Indiana (Betz, 1989; M. L. Bowles, pers. obs.).

Biology

Asclepias meadii (Fig. 2) is a long-lived rhizomatous perennial herb. As in many prairie plants, dormant season fire appears to stimulate flowering (Betz, 1989; H. M. Alexander, pers. comm.). Mature plants usually have 6–12 paired leaves and a single terminal umbel with about 12 flowers and usually produce a single narrow pod (per plant) with about 60 seeds (Betz, 1989). Flowers within an umbel are open for about 5–6 days, and flowering occurs for about 10–12 days within populations. Plants flower as early as late May in the south through mid to late June in the north, depending upon yearly growing season conditions. Pollinia are most frequently removed by miner bees (*Anthophora* sp.), or by small bumblebees (*Bombus* sp.) (Betz et al., 1994). In a seven-year study, 77% of over 100 *A. meadii* ramets flowered annually, but less than 6.4% matured pods, averaging 61 seeds/pod and 47.6% seed germination (Betz, 1989). This correlates with low levels of pod production reported for most milkweeds (Wyatt, 1976), in which reproduction is regulated by their breeding system and by resource allocation (Willson & Price, 1980). Most milkweed species are self-incompatible, requiring crosses between genetically different individuals to produce viable seeds (Kephart, 1981; Shannon & Wyatt, 1986; Kahn & Morse, 1991; Broyles & Wyatt, 1991, 1993; Wyatt & Broyles, 1994). The apparent longevity of *A. meadii* and its restriction to virgin prairies suggests that it is a late-successional species characterized by poor colonizing but good competitive abilities. As a result, seedling establishment may be infrequent but is probably required for long-term population maintenance and necessary for population establishment. As yet, little experimental information is available about seedling ecology (Betz, 1989).

Asclepias meadii is genetically diverse, with 74% of its allozyme diversity maintained within populations or metapopulations and no geographic genetic pattern among populations (Tecic et al., 1998). Allozyme samples from the Rockefeller and Weimer Hill populations have found 15 or more genotypes per site, with small ramet : genet ratios, while haymeadows and small populations are highly clonal, with fewer genotypes and large ramet : genet ratios (Tecic et al., 1998). Formerly widespread species with outcrossing breeding systems become vulnerable to extinction because of lowered reproductive potential in fragmented populations (Schaal et al., 1991; Weller, 1994; Les et al., 1991; DeMauro, 1993). Such is the case for *A. meadii.* Because of its self-incompatible breeding system, small fragmented populations that are reduced to single clones, such as in Illinois, no longer produce seeds and are vulnerable to stochastic extinction processes. Viable restored populations of self-incompatible species should contain high levels of genetic diversity, which will enhance outcrossing and seed production while lowering inbreeding (DeMauro, 1993). For *A. meadii,* this may require infusion of large numbers of different genotypes from across the range of the species. Such efforts would maximize evolutionary potential and decrease inbreeding, but could alter historic lineages and produce outbreeding depression if co-adapted gene complexes exist and are disrupted (Fenster & Dudash, 1994). This issue is often contentious for restoration ecologists and will only be resolved with case-by-case experimentation among different plant groups (Bowles & Whelan, 1994).

EX-SITU CONSERVATION

To facilitate recovery of *Asclepias meadii,* The Morton Arboretum has assembled a genetically diverse garden population and nursery to provide a propagule source for population restoration and research. The garden environment consists of 1 × 2-m elevated beds filled to 0.3 m with wood chips, in which potted milkweeds are propagated. The pots allow isolation of plants and removal for artificial cross-pollination. Seed sources have included extant populations and herbarium specimens representing western Missouri and Kansas (Bowles et al., 1993a). Important seed sources have included the Rockefeller Prairie and Weimer Hill, which have been supplemented by pollen crosses from fragmented eastern populations in southern (Saline Co.) and central (Ford Co.) Illinois, northern Missouri (Harrison Co.), and southern Iowa (Adair Co.). By 1996, the garden population contained 58 adult plants representing 28 different genotypes.

OBJECTIVES

Our objectives were to analyze ecological factors affecting the distribution, population structure, and restoration of *Asclepias meadii.* In this paper, we first examine the distribution of *A. meadii* in relation to soil characteristics, which, based on the lack of a strong geographic genetic pattern in this species, might be expected to show little variation. We also compare its population structure under regimes of hay mowing and burning, the primary management alternatives for maintaining and restoring prairie. If mowing removes live biomass and prevents sexual reproduction but not vegetative spread, we would expect spatial population structure to correspond to genetic differences found between mowed and burned populations. We then use greenhouse and garden experiments to compare germination and growth among different seed sources and to test seedling growth under different competition and moisture conditions. To further examine factors affecting restoration potential of this species, we compare survivorship and growth of seeds and juvenile milkweeds from different sources planted into native prairie habitats under experimental burning treatments and stochastic climatic variation.

METHODS

STUDY AREAS

Studies were conducted at 1 former and 19 current *Asclepias meadii* stations in Kansas, Missouri, Iowa, and Illinois (Table 1). We collected soil samples during 1992 and 1993 from 18 sites, and population data during the 1992 flowering period from 10 sites. These included the fire-managed Rockefeller Prairie and Weimer Hill, both of which were spring-burned in 1992, five annually mowed private Kansas prairie haymeadows, and three Missouri former haymeadows that were protected in the mid 1980s. Two of the Missouri sites are now managed in hay-burn-rest rotations, while flowering

Table 1. Mead's milkweed (*Asclepias meadii*) study sites sampled for soils (S), and for population structure and plant size (P). Two sites were sampled for soils in Ford and Saline counties. See Figure 1 for site locations.

Site number & name	State & county	Samples	Management history
1) Palatine	Illinois/Cook	S	railroad prairie (population destroyed)
2) Ford	Illinois/Ford	S (2)	railroad prairie (two samples)
3) Saline	Illinois/Saline	S (2)	glade/metapopulation (two samples)
4) Woodside	Iowa/Adair	S	haymeadow (mowed in Sep.)
5) Flaherty	Iowa/Clarke	S	preserve
6) Cummings	Iowa/Warren	S	preserve
7) Martensdale	Iowa/Warren	S	preserve
8) Garnett	Kansas/Anderson	P	haymeadow
9) Sunset	Kansas/Anderson	S, P	haymeadow
10) Hinton Creek	Kansas/Bourbon	S, P	haymeadow
11) Colyer	Kansas/Douglas	S, P	haymeadow
12) Jack's	Kansas/Douglas	S	haymeadow
13) Fowler Hill	Kansas/Franklin	S	haymeadow
14) French Creek	Kansas/Jefferson	S, P	haymeadow
15) Rockefeller	Kansas/Jefferson	S, P	former haymeadow (burned every 1–3 yrs. since 1956)
16) Cook Meadow	Missouri/Barton	S, P	haymeadow (unmowed when milkweeds flower since ~ 1990)
17) Niawathe	Missouri/Dade	S, P	former haymeadow (burn/hay/rest rotation since ~ 1980)
18) Weimer Hill	Missouri/Iron	S, P	glade/metapopulation (burned)
19) Paint Brush	Missouri/Pettis	S	former haymeadow (burn/hay/rest rotation since ~ 1980)
20) Wah-kon-Tah	Missouri/St. Clair	P	former haymeadow (burn/hay/rest rotation since ~ 1980)

milkweeds are left unmowed in the third site. Greenhouse and garden studies were conducted at the Morton Arboretum, Lisle, Illinois. Restoration planting experiments were conducted at seven prairie habitats in northern Illinois and northeastern Indiana (Table 2). None of these sites contain native *A. meadii* populations, but all lie within the former range of the species. All sites are protected and managed by prescribed burning. They provide an among-site drainage gradient from dry-mesic to mesic, and a successional gradient from early- to late-successional vegetation (e.g., Betz, 1989; Betz & Lamp, 1989; Bliss & Cox, 1964).

SOIL SAMPLING AND ANALYSIS

Composite soil collections were made from each site by pooling multiple A-horizon samples from milkweed habitat into a 2-quart plastic bag that was transported to the Morton Arboretum Soils Lab, Lisle, Illinois. Soils were refrigerated until shipped for analysis by the A & L Great Lakes Laboratories, Fort Wayne, Indiana. Samples were tested for pH, milli-equivalents cation exchange capacity (CEC), percent organic matter (% OM), and parts per million (ppm) phosphorous (P), potassium (K), magnesium (Mg), and calcium (CA), following methods of Page et al. (1982). Sample sites were ordinated by their soils data on PCORD software (McCune, 1993) using the Bray-Curtis technique (Beals, 1984) with a variance-regression endpoint selection and Euclidean distance measure. Samples also were clustered by their soils data on PCORD using Ward's method with a Euclidean distance measure (Sneath & Sokal, 1973). Sample means and standard deviations were calculated for geographically similar groups.

SAMPLING AND ANALYSIS OF NATURAL POPULATIONS

With one exception, all *Asclepias meadii* sites were sampled from stratified random transects through milkweed populations during their flowering period, when plants can be most easily located (Alexander et al., 1997). Because random placement of plots along transects rarely encountered milkweeds, flowering plants were randomly selected as centers of non-overlapping 10-m^2 circular plots, in which the numbers of flowering and non-flowering plants were counted. This maximized sampling of flowering plants across sites, and also helped focus plot placement on the clonal ramet clusters of this species. For Rockefeller Prairie, density data were obtained by placing a 10-m^2 grid over a 2-m^2-resolution grid map of milkweed clone locations. At this scale, the comparatively small ramet clusters at Rockefeller (Alexander et al., 1997) were easily quantified within sampling plots. All

Table 2. Location, site characteristics, and number of experimental Mead's milkweed (*Asclepias meadii*) plantings made at Mead's milkweed restoration sites.

Site name	County, state	Size	Drainage/successional stage	Management treatment	Number planted (1994–1996) Seeds	Tubers	Genotypes
Biesecker (Cook)	Lake Co., Indiana	16 ha	dry-mesic/late-succ.	Burned-unburned 1994	201	117	32
Vermont Cemetery	Will Co., Illinois	0.4 ha	mesic/late-succ.	Burned-unburned 1996	196	148	33
Pellville Cemetery	Ford Co., Illinois	0.2 ha	mesic/late-succ.	Burned-unburned 1995	140	93	29
Hickory Creek	Will Co., Illinois	35 ha	dry-mesic/early-succ.	Burned 1994	155	61	28
Schulenberg Prairie	DuPage Co., Illinois	20 ha	dry-mesic/mid-succ.	Burned 1994–1995	201	103	33
Munson Cemetery	Henry Co., Illinois	2 ha	dry-mesic/late-succ.	Burned 1995	243	79	26
W. Chicago Prairie	DuPage Co., Illinois	47 ha	mesic/mid-succ.	Unburned 1995	96	29	24
				Totals:	1232	630	53

ramets sampled were quantified by their reproductive status and size. The extensive vegetative spread of ramets in haymeadows prevented quantifying reproductive status at the genet level. For each flowering ramet, the number of flowers per umbel was recorded. For each plant, the area (length × width) of one randomly chosen leaf from the largest pair of leaves was recorded. This leaf-area was transformed to a plant leaf-area index by multiplying the measured leaf-area for each plant times the number of leaves on the plants.

One-way ANOVA and Duncan's multiple range tests (Steele & Torrie, 1960) were used to compare morphological and population structural differences between fire-managed and mowed populations. The burned Rockefeller and Weimer Hill sites were retained as separate treatments because they occupy ecologically different habitats. To attain similar, but not equal, sample sizes, data were pooled within the Missouri former haymeadows, and within the Kansas current haymeadows. Separate tests were made of the null hypotheses that there were no significant differences between these four groups for mean ramet plot densities, mean percent flowering ramet densities, mean umbel size, mean leaf-area indices of flowering and nonflowering plants, and mean total leaf-area of all *A. meadii* ramets per plot.

GREENHOUSE AND GARDEN EXPERIMENTS

All seeds used in propagation studies were moist-stratified in Petri dishes at 5°C for 4 months before planting in 10-cm-deep flats filled with a mixture of equal parts standard greenhouse soil and prairie loam (Betz, 1989). Seeds were planted in mid May and germinated within 10 days. Flats were retained in the greenhouse until seedlings had developed one pair of leaves, after which they were transferred outside into full sun, which is required for optimum growth (Betz, 1989). Seedling performance was quantified by percent germination for seed pods and seed sources, while performance of older plants was quantified by leaf-area indices after their first year of growth. A one-way ANOVA was used to compare mean percent seed germination of pods from naturally pollinated Rockefeller and Weimer Hill populations against pods derived from garden crosses using geographically distant seed sources.

To assess the effects of grass competition on moisture availability and milkweed seedling growth, we established a drainage gradient among 12 seedling flats (40 seeds/flat), randomly chosen for placement either above ($n = 4$ flats), midway (n

= 4), or below (n = 4) the level of a 30-cm-deep 1 × 2-m sand bed kept moist by watering. Flats placed below the sand level were expected to have the poorest drainage and highest moisture levels because of capillary movement from the sand bed; elevated flats were expected to have greatest drainage. For each drainage position, two flats were planted with seeds (pooled from multiple pods) obtained by long-distance out-crossing of pollen from natural populations to our garden plants, and two were planted with naturally pollinated seeds pooled from Rockefeller and Weimer Hill pods. After seedling germination, half of the flats in each moisture/seed source treatment were randomly selected and sown with annual oats (*Avena sativa* L., Gramineae). This oat species has similar photosynthetic responses to native prairie grasses such as *Sorghastrum nutans* (L.) Nash (Fay & Knapp, 1993), and its annual growth habit can rapidly develop a fibrous root system that can compete with forb seedlings for water and other resources. The flats were watered periodically to sustain seedling growth, allowing surficial drying between watering periods. We measured the moisture gradient during the growing season by inserting an electrical conductivity moisture meter probe into each flat 24 hrs. after watering. Analog readings ranged from 1 (dry) to 8 (wet). After the milkweed seedlings and oats had become dormant, all seedlings were excavated and their tubers weighed. Effects of the drainage and oats on mean moisture level readings were tested with a fixed model two-factorial ANOVA (Sokal & Rohlf, 1981). Effects of the moisture gradient, oats, and seed sources on mean milkweed tuber weight were measured in a mixed model three-level nested ANOVA (Sokal & Rohlf, 1981) comparing the hierarchical effects of oats, moisture gradient, and seed source by flat.

FIELD ESTABLISHMENT EXPERIMENTS

Experimental plantings of seeds and seedlings were conducted at the seven study sites between 1994 and 1996. Our strategy was to maximize numbers of genetically different individuals within sites so as to increase potential for compatible outcrossing and seed production. This resulted in planting of 1232 seeds and 630 juvenile plants representing 53 different genotypes (Table 2). Milkweed seeds and juveniles were planted in early May prior to the breaking of prairie plant dormancy. Clusters of five seeds were planted 1 cm deep in a 1-dm^2 area in which the soil was loosened with a hand trowel. One-year-old dormant milkweed tubers were removed from flats, weighed, and packed with sphagnum in plastic bags for translocation. They were planted upright with buds about 3 cm below the soil surface, in 10-cm-deep incisions made in the prairie with a tile spade. All plantings were watered immediately.

Seeds and tubers were planted within 1-m^2 plots placed along permanently marked stratified random transects. Usually two seedling clusters and four tubers were planted per plot, and were placed within interstitial patches between bunchgrasses. The transects crossed burned and non-burned sections of Biesecker in 1994, Pellville in 1995, and Munson in 1996, allowing comparison of these management treatments on growth and survivorship. Seedlings were monitored for first-year survivorship, while juvenile plants that emerged from tubers were monitored for survivorship and measured for leaf-area indices. Percent survivorship was determined over time for annual cohorts and compared between seed and tuber plantings. Survivorship was compared between burn and nonburn treatments using Chi-square analysis of 2 × 2 contingency tables, and mean leaf-area indices were compared between the same treatments using t-tests. We also compared differences in mean leaf-area indices among planting sites and seed sources using one-way ANOVAs. A two-way ANOVA was used to compare leaf-area indices between garden and field sites planted with Rockefeller and Weimer Hill seed sources using seeds pooled from multiple pods.

RESULTS

SOIL CHARACTERISTICS

Soil samples ordinated and clustered along a chemical- and nutrient-concentration gradient corresponding to their geographic distribution (Fig. 3). Missouri and southern Illinois sites had the lowest scores on the first axis, Kansas sites were intermediate, and Iowa and northern Illinois sites had the highest scores. All soil variables were positively correlated with the first axis, with CEC, and ppm Mg, K, and Ca having correlations greater than 0.5. In general, Missouri and southern Illinois sites are acid and nutrient-poor, Kansas sites are intermediate, and Iowa and northern Illinois sites are calcareous and nutrient-rich (Table 3). Missouri and southern Illinois had comparatively low mean pH, % OM, CEC, and ppm Ca, but comparatively high ppm P. Kansas samples were generally intermediate but variable, with comparatively high mean pH, low mean % OM, intermediate CEC, and extremely low ppm P. Iowa and northern Illinois had the highest mean values for all soil variables.

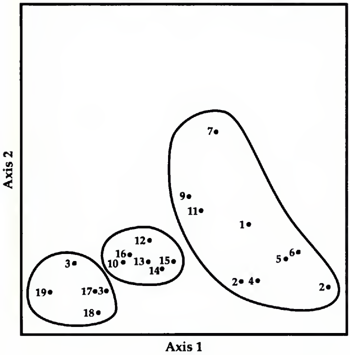


Figure 3. Bray-Curtis ordination of Mead's milkweed (*Asclepias meadii*) habitats by soils characteristics. Axis I represents a geographic gradient with increasing pH, % OM, CEC, and nutrient concentrations (see Table 3). Circles are clusters produced by Ward's method. Number codes: northern Illinois (1–2), southern Illinois (3), Iowa (4–7), Kansas (9–15), Missouri (16–19). See Table 1 for site names and Figure 1 for site locations.

SITE-MANAGEMENT EFFECTS ON POPULATION STRUCTURE

Asclepias meadii ramet densities were significantly higher in Kansas haymeadows than in Rockefeller Prairie, and were intermediate in the former Missouri haymeadows and Weimer Hill (Table 4). At Rockefeller and Weimer Hill, 68% of all ramets were flowering, while only 18.6% of all plants flowered in haymeadows. On a plot basis, the percentage of flowering ramets averaged under 32% in Kansas and former Missouri haymeadows, but more than 60% at Weimer Hill and more than 80% at Rockefeller (Table 4). As a result, the density of flowering plants, but not nonflowering plants, was similar across all study sites and there was no significant difference in mean plot leaf-area across all sites (Table 4). However, flowering ramets were larger than nonflowering ramets across all sites, and Rockefeller plants were larger than haymeadow plants in flowering and nonflowering groups (Table 4). Flowering plant umbels were larger in burned habitats, averaging about 12 flowers, and had about 10 or fewer flowers in Kansas and former Missouri haymeadows (Table 4).

GREENHOUSE AND GARDEN EXPERIMENTS

Between 1993 and 1996, seed production among our garden plants averaged 56 seeds/pod, which

Table 3. Geographic differences in mean (± s.e.) soil chemistry values and nutrient concentrations of habitats supporting extant or former Mead's milkweed (*Asclepias meadii*) populations. See Figure 1 and Table 1 for location and description of sample areas.

Region	Sample size	Community	% OM	CEC	pH	ppmP	ppmK	ppmMg	ppmCa
N. Illinois & Iowa	7	Prairie	11.09 ± 4.00	20.64 ± 3.27	6.67 ± 0.82	6.71 ± 3.27	229 ± 87.88	412.86 ± 108.85	2992.9 ± 921.7
Kansas	7	Prairie/Haymeadow	5.54 ± 0.96	15.27 ± 3.48	6.47 ± 0.77	1.71 ± 1.25	75.43 ± 41.69	255 ± 38.19	2200 ± 754.43
Missouri & S. Illinois	6	Haymeadow/glade	5.05 ± 1.97	6.30 ± 2.24	5.67 ± 0.85	6.67 ± 1.25	73.0 ± 23.43	116.67 ± 54.74	758.33 ± 530.49

Table 4. Site management effects on mean ramet and mean percent flowering ramet density per 10-m² plot, mean umbel size, mean leaf-area index, and average plot leaf-area of Mead's milkweed (*Asclepias meadii*) in burned prairies (Rockefeller and Weimer Hill), former haymeadows (Missouri), and current haymeadows (Kansas). Similar lower case letters indicate similar means across variables with Duncan's multiple range test at $P = 0.05$.

Variable	Rockefeller	Weimer Hill	Missouri prairies	Kansas haymeadows	Test statistic and probability
Mean ramet density ± s.e.	2.525a ± 0.31 $n = 40$	3.625ab ± 0.84 $n = 8$	4.6ab ± 1.3 $n = 15$	6.15b ± 0.91 $n = 34$	$F = 5.16$, $P = 0.0024$
Mean % flowering ramet density ± s.e.	80.07a ± 4.87 $n = 40$	67.26a ± 9.12 $n = 8$	26.05b ± 9.0 $n = 15$	31.29b ± 5.40 $n = 34$	$F = 19.71$, $P < 0.0001$
Mean flowers per umbel ± s.e.	11.89abc ± 0.35 $n = 73$	12.40ab ± 1.15 $n = 15$	9.27cd ± 0.65 $n = 11$	10.09bcd ± 0.52 $n = 45$	$F = 4.68$, $P = 0.0038$
Mean leaf-area index of flowering plants ± s.e.	196.09a ± 8.03 $n = 73$	162.33 ab ± 27.75 $n = 15$	137.52b ± 27.13 $n = 11$	142.89b ± 12.4 $n = 45$	$F = 54.71$, $P < 0.0001$
Mean leaf-area index of nonflowering plants ± s.e.	138.54a ± 10.85 $n = 73$	92.36b ± 17.76 $n = 15$	37.64c ± 4.93 $n = 11$	73.29b ± 4.59 $n = 45$	$F = 15.89$, $P < 0.0001$
Mean plot leaf-area ± s.e.	453.86 ± 78.55 $n = 37$	551.70 ± 106.85 $n = 8$	243.81 ± 56.34 $n = 15$	605.42 ± 118.18 $n = 33$	$F = 1.74$, $P = 0.165$

was similar to the 60 seeds/pod average found by Betz (1989) from 1965 to 1971 for native plants in Missouri and Kansas railroad prairies. Under greenhouse conditions, 74.3% of 1665 seeds germinated. Also with greenhouse propagation, there was no significant difference ($F = 0.78$, $P = 0.4679$) in mean percent germination per pod among our wild-collected seed from Weimer Hill ($n = 11$ pods, $\bar{x} = 60.73 \pm 10.3$), Rockefeller Prairie ($n = 11$ pods, $\bar{x} = 71.12 \pm 8.4$), and pods derived from garden crosses among geographically different seed sources ($n = 17$ pods, $\bar{x} = 74.65 \pm 6.4$). Four life-stage classes could be recognized in garden-propagated plants: first-year seedlings (< 15 cm high, < 5 cm long linear leaves), second-year juveniles (> 15 cm high, 1 × 5 cm lanceolate leaves), and flowering or nonflowering adults (> 30 cm high, > 1 cm broad lanceolate-sagittate leaves with cordate bases). In the field, ramets of adults can revert to juvenile form in successive years (Betz, 1989).

The presence of oats significantly reduced soil moisture levels in milkweed flats, reversing the relationship between moisture level and drainage sequence (Table 5). Overall moisture levels were higher in flats without oats, where the highest drainage position had the lowest mean moisture level. With oats, the moisture gradient was reversed, with a higher mean moisture level at the highest drainage position. Although drainage position did not affect tuber weight ($F = 0.0974$, $P = 0.9095$), the presence of oats significantly reduced the overall mean weight of milkweed tubers, with differences between seed sources (Table 5). Oats reduced the mean weight of tubers from the natural Rockefeller and Weimer Hill seed sources, but not the mean weight of tubers produced by garden outcrosses among geographically distant seed sources.

FIELD ESTABLISHMENT EXPERIMENTS

By the end of 1996, 332 seedlings and 290 juveniles representing 46 genetically different individuals had been established at the seven study sites. Significant variation in the germination, survivorship, and growth of these plants was caused by weather, fire, and differences among seed sources.

Although greenhouse seed propagation rates were stable in 1994–1996, seedling survivorship in the field was 11% or less in 1994 and in 1995, but increased to more than 40% in 1996 (Fig. 4). This difference in survivorship corresponded to below-normal May–July rainfall in 1994–1995 and an above-normal May–July rainfall (200% of normal)

Table 5. Experimental effects of artificial drainage gradient position and presence or absence of oats (*Avena sativa*) on mean moisture levels (conductivity), and effects of presence or absence of oats and seed source (natural within-population crosses vs. artificial long-distance outcrosses) on mean weights of Mead's milkweed (*Asclepias meadii*) tubers. Drainage gradient position: high = greatest elevation and drainage, mid = intermediate elevation and drainage, low = lowest elevation and drainage. Oats' effect on moisture level: $F = 75.58$, $P < 0.0001$; drainage effect on moisture level: $F = 2.39$, $P = 0.0931$; oats × drainage interaction: $F = 9.03$, $P = 0.0001$. Oats' effect on tuber weight: $F = 5.656$, $P = 0.035$; seed source effect on tuber weight: $F = 4.75$, $P = 0.0001$.

	Mean moisture level (conductivity) ± s.e.			Mean tuber weight ± s.e. in grams	
	Gradient position			Seed source	
	high $n = 40$	mid $n = 40$	low $n = 40$	within-population $n = 90$	long-distance $n = 90$
Oats present	3.25 ± 0.19	2.40 ± 0.14	2.54 ± 0.18	0.219 ± 0.010	0.272 ± 0.011
Oats absent	4.62 ± 0.19	5.28 ± 0.22	5.83 ± 0.20	0.338 ± 0.0125	0.326 ± 0.013

in 1996, which enhanced seed germination and seedling survival. Seedling cohort survivorship over time was low, dropping to about 10% after two or three growing seasons; a few seeds delayed germination until the second growing season, causing the upward deflection of the 1994 survivorship curve in 1996 (Fig. 5). Survivorship of planted tubers was higher, with 50% or more of these cohorts alive after two or three growing seasons (Fig. 5). Differences among four planting sites also significantly affected sizes of three-year-old plants, as measured by leaf-area index ($F = 21.53$, $P < 0.0001$). Plants with the largest mean leaf-area occurred in the Vermont Cemetery and averaged twice the size of plants at Biesecker Prairie. Plants at the Schulenberg and Hickory Creek sites were intermediate in size.

Prescribed burning had either positive or neutral effects on seedling and tuber survivorship and leaf-area in all three study sites (Table 6). Two years

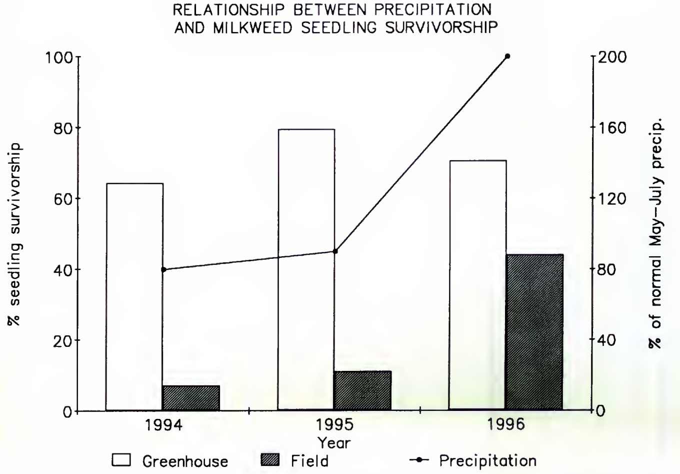
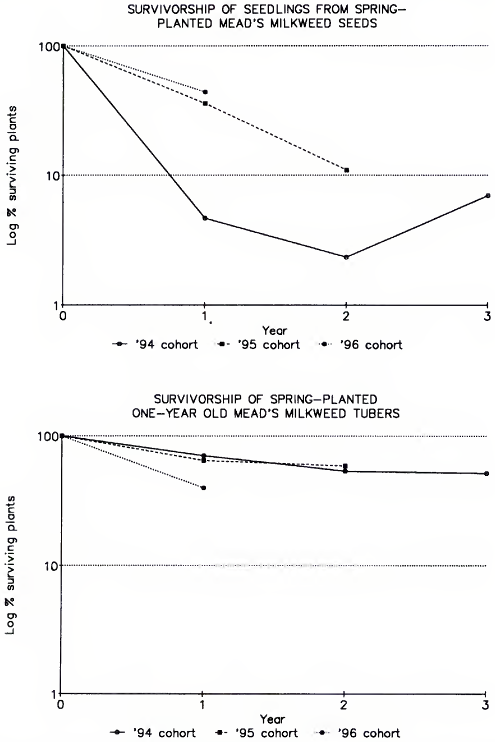


Figure 4. Temporal relationship between percent of normal May–July precipitation and first-year survivorship of greenhouse- and field-germinated Mead's milkweed (*Asclepias meadii*) seedlings. Precipitation levels are northeastern Illinois summaries from the National Oceanic and Atmospheric Administration.



SURVIVORSHIP OF SEEDLINGS FROM SPRING-PLANTED MEAD'S MILKWEED SEEDS

SURVIVORSHIP OF SPRING-PLANTED ONE-YEAR OLD MEAD'S MILKWEED TUBERS

Figure 5. Cohort survivorship curves for spring-planted Mead's milkweed (*Asclepias meadii*) seedlings (upper) and tubers (lower) at seven northeastern Illinois and Indiana restoration sites.

after the burn at Biesecker Prairie, seedling survivorship did not differ significantly between treatments, but tuber survivorship and mean leaf-area index were greater in the burn treatment. One year after the burn at Pellville, seedling survivorship and tuber leaf-area did not differ significantly, but tuber survivorship was greater in the burn treatment. At Munson, only seedling survivorship was significantly greater in the year of the burn. The overall lower survivorship of tubers in 1996 may have been caused by excessive handling and storage. After these plants were excavated from flats and weighed, they had to be held in cold storage for about a month before planting due to a late cold spring.

In the garden versus field comparison of performance between Rockefeller and Weimer Hill seed sources, garden-grown plants had significantly larger mean leaf-area indices than field plants ($F = 363.78$, $P < 0.0001$). After three years, most field plants had reached the size of second-year juvenile garden plants, while garden-grown plants had attained an adult size. Averaged across both planting treatments, Weimer Hill plants were larger than Rockefeller plants ($F = 85.09$, $P < 0.0001$). There was also a significant site × seed source interaction

Table 6. Effects of prescribed burning on Mead's milkweed (*Asclepias meadii*) seedling and tuber survivorship and mean leaf-area indices in three restoration plantings. Survivorship P values are based on Chi-square contingency tables. Leaf-area index P values are based on Student t-tests.

	Site/planting date					
	Biesecker/1994		Pellville/1995		Munson/1996	
Variable	Burned ('94)	Unburned	Burned ('95)	Unburned	Burned ('96)	Unburned
Seedling (N)	18	15	30	25	49	50
survivorship (1996)	17% ($P < 0.825$)	13%	13% ($P = 0.844$)	8%	59% ($P = 0.057$)	38%
Tuber (N)	41	39	14	15	39	40
survivorship (1996)	83% ($P < 0.001$)	51%	86% ($P = 0.013$)	33%	41% ($P = 0.216$)	58%
Leaf-area (N)	41	39	14	15	39	40
index ± s.e. (1996)	25.51 ($P = 0.006$) ± 2.23	14.08 ± 2.09	16.54 ($P = 0.636$) ± 1.74	14.59 ± 2.91	4.42 ($P = 0.467$) ± 0.64	5.14 ± 0.68

($F = 83.28$, $P < 0.0001$); Weimer Hill plants had more than twice the leaf-area of Rockefeller plants in garden, but not in field, habitat. Overall tuber weight also had a significant ($P < 0.0001$) but small ($r^2 = 0.18$) positive correlation with leaf-area index for field-planted milkweeds in 1996. Excessive handling and storage may have reduced this correlation.

DISCUSSION

IMPLICATIONS OF HABITAT DIFFERENCES AND GENETIC VARIATION

Despite the apparent lack of allozyme differentiation across its range (Tecic et al., 1998), *Asclepias meadii* occupies a strong geographic gradient in soil characterisitics, which have been found to affect allozyme frequencies in some species (e.g., Heywood & Levin, 1985). Our initial success in restoring plants from Missouri and Kansas seed sources into the nutrient-rich soils of northern Illinois also suggests that these soil differences may not be critical to *A. meadii.* It is unknown if size differences in garden habitat between plants from these seed sources reflect an important fitness component, or simply phenotypic variation associated with genetically diverse plants under noncompetitive conditions. Certainly, they were not expressed in the field, where competitive stress should make differences that reflect fitness more apparent. In Pitcher's thistle (*Cirsium pitcheri* Torr., Compositae), a monomorphic species with little geographic allozyme variation, plants from Wisconsin and Indiana seed sources differed in seedling morphology in the greenhouse, and in subsequent survivorship and growth when planted in an Illinois restoration (Bowles et al., 1993b; Bowles & McBride, 1996).

When plants from geographically distant seed sources are integrated in restorations and cross-pollinate, the potential exists for disruption of naturally evolved lineages and outbreeding depression caused by breaking up locally co-adapted gene complexes (Fenster & Dudash, 1994). The breeding system, pollen packaging as pollinia, and strong-flying pollinators of milkweeds may contribute to usually large neighborhood sizes (Broyles & Wyatt, 1991; Wyatt & Broyles, 1994), which could select against deleterious effects of outcrossing. This may vary among milkweed species. For example, Wyatt (1976) found greater percent fruit set from within-population crosses of *A. tuberosa* in comparison to between-population crosses across a wide geographic region, suggesting outbreeding depression. However, our failure to find differences in percent seed germination between natural and geographically distant crosses suggests that outbreeding may not be a critical factor for *A. meadii* at this early life-stage. In our garden experiment, seedlings from distant crosses developed larger tubers than seedlings from natural populations when grown in competition with oats, and the larger plants correlated with greater plant size when outplanted the following year. This apparent heterosis effect could outweigh deleterious consequences of long-distance crosses (Fenster & Dudash, 1994). Additional studies are needed to assess the survivorship and growth of seedlings and backcrosses from geographically distant sources to determine if population viability is negatively affected.

In addition to total lack of reproduction, small populations of self-incompatible plants can undergo rapid increases in inbreeding, which could be detrimental to population growth in restorations

(DeMauro, 1993). For *A. meadii*, inbreeding depression could be a serious problem, but we have only circumstantial evidence. For example, our three-year 75% greenhouse germination rate was significantly greater ($X^2 = 280.6$, $P < 0.001$) than the 47.6% germination found by Betz (1989) for 2429 wild-collected seeds. This lower germination may have been caused by inbreeding in the isolated linear railroad prairie populations that Betz studied. In contrast, our seed collections were either from populations known to be genetically diverse or from controlled garden crosses. Although inbreeding may reduce seed production, inbreeding-induced differences in fitness in plant species may be expressed under stressful field conditions and at different life stages depending upon their breeding systems (Dudash, 1990; Fenster & Dudash, 1994; Carr & Dudash, 1996). Further greenhouse and field studies are needed to assess inbreeding effects in *A. meadii*.

HABITAT MANAGEMENT EFFECTS

Prescribed burning and mowing appear to have different effects on population structure of *Asclepias meadii*. The greater leaf-area of flowering milkweeds at Rockefeller and the larger umbel sizes and greater percentage of flowering plants in burned sites suggest that these plants are placing more resources into the potential for sexual reproduction than are plants in haymeadows. For example, although the smaller ramet and flower sizes of haymeadow plants could reflect stress from summer mowing, the greater ramet densities but similar average plot leaf-area in Kansas haymeadows suggest a reallocation of resources into vegetative spread due to lack of sexual reproduction. However, this vegetative spread appears to accompany the loss or attrition of genetically different individuals, which would limit sexual reproduction in this self-incompatible species (Tecic et al., 1998). In comparison, the greater diversity of genotypes in burned areas would facilitate more successful cross-pollination among sexually compatible plants. The Missouri populations on former haymeadows had a comparatively low, although not significantly different, mean plot leaf-area, which does not strongly support our resource reallocation hypotheses. Population structure at these sites could be responding to the novel effect of reduced mowing frequency, which may contribute to loss of genetically similar ramets once annual mowing was stopped.

Fire is a natural factor responsible for maintenance of prairie, with varying effects on individual plant species (Collins & Glenn, 1988; Collins & Gibson, 1990; Evans et al., 1989; Collins & Wallace, 1990). *Asclepias meadii* appears to be fire-adapted. Betz (1989) found 77.1% flowering stems in annually burned prairies in railroad rights-of-ways, and greater flowering occurs in years of prescribed burns at Rockefeller Prairie (H. M. Alexander, pers. comm.). This is reinforced by our finding of increased milkweed juvenile growth and survivorship in burned tracts. Because of the low annual fruit production and seed production in this species (Betz, 1989; Alexander et al., 1997), fire may be critical for long-term population maintenance and could accelerate restored population growth.

POPULATION DEMOGRAPHY

The slow growth of restored milkweeds and lack of sexual reproduction after three years extremely limits demographic interpretations during this period. Seedling survivorship was essentially less than 10% for the first two cohorts, and no seedling plants attained the sizes reached by second-year juveniles in garden plots. The 40% seedling survivorship in 1996 should allow greater second-year survivorship of this cohort, but development into a juvenile or reproductive state may require many years under field conditions. There also have been few transitions from juvenile to reproductive states. For example, 5% of all plants flowered in 1995, but fewer plants flowered in 1996, and only two plants flowered in both years. Also, none of these plants have produced seed pods, either due to lack of pollination or compatible crosses, or to inability to allocate enough resources to produce pods.

Guerrant (1996) suggested that a restoration strategy of using outplanted juveniles rather than seeds would increase survivorship and population growth. Our preliminary data also indicate that initiating a milkweed population with planted juveniles can reduce mortality rates and accelerate development of larger population sizes. However, garden propagation increases chances of recruiting less fit plants that might not survive selective pressures that operate at the seedling stage. Planting of seeds is required to help assess if plants can actually complete their life-cycles, but this necessitates a longer restoration process with higher mortality rates and greater seedling vulnerability.

ENVIRONMENTAL EFFECTS ON DEMOGRAPHY

Demographic monitoring of the trends of restored population growth can be enhanced by resolution of critical factors affecting reproduction, survivorship, and growth (Pavlik, 1994). Three environmental factors—moisture levels, competition, and site variation—appear to have important effects on population establishment and growth of *Asclepias meadii.* DeMauro (1994) found higher seedling recruitment of *Hymenoxys acaulis* (Pursh) K. L. Parker var. *glabra* (A. Gray) K. L. Parker (Compositae) during years without summer drought. We also found that growing season rainfall strongly influenced the fate of field-planted seeds, with survivorship exceeding 40% only in 1996, when rainfall exceeded 200% of normal. This suggests that recruitment into natural populations is uncommon and rainfall-dependent, providing a selective requirement for longevity of adult plants. As a result, lack of growing-season rainfall could negatively impact demographic processes when restoring populations from seed. Competition from grasses, with their fibrous root systems, can negatively affect forb survivorship and growth (Gurevitch, 1986; Louda et al., 1990; Hook et al., 1994). As expected, oats significantly reduced milkweed growth, apparently through competition for moisture. This indicates that competition from existing prairie grasses should slow plant growth and delay transition of cohorts into adult stages. *Asclepias meadii* may be adapted to the bunch-grass structure of late-successional prairie by an ability to establish in patches between grasses, and by using its longevity to persist in this competitive but stable environment. The highly significant difference between garden and field effects on milkweed growth also indicates the high level of competition in field habitats. Greenhouse-propagated plants often flower and may produce pods in three years. But, as indicated, few field-planted milkweeds have flowered, and seedlings from planted seeds still resembled first-year greenhouse seedlings after three years. However, significant differences in growth between different sites indicate that a wide range of conditions affecting plant growth exist in field habitats. For example, the greater size of plants restored at Vermont Cemetery may correlate with its lower landscape position and greater moisture retention compared with other, more well-drained restoration sites.

Our results also suggest that burning should accelerate demographic processes by increasing seedling survivorship and growth of plants. However, weather cycles such as drought may override positive effects of fire, as different precipitation levels clearly affected seedling establishment over time. Although optimum seedling growth for *A. meadii* is in full sun (Betz, 1989; Bowles, pers. obs.), seedling survival requires adequate moisture that could be retained longer in soils under unburned vegetation. These factors also would be affected by site drainage, exposure, and soil water-holding capacity. Burned mesic habitat may have optimum germination but strong late-season grass competition. Dry-mesic habitat may have less competition but stronger moisture requirements for seedling establishment. Because weather is unpredictable, experimental burn and non-burn treatments appear necessary for milkweed establishment when supplemental watering is unavailable. Summer mowing may have some benefit in restoring *A. meadii* if it increases ramet numbers, possibly through decreased competition from warm-season grasses. However, we have no data on the effects of mowing on seedling recruitment, and long-term repeated mowing appears to cause genetic attrition (Tecic et al., 1998).

Summary and Conclusions

Pavlik (1996) identified proximal (completion of life-cycle, cohort replacement, and population increase) and distal (attainment of Minimum Viable Population) restoration objectives for plants. Restoration of *Asclepias meadii* is clearly in the proximal stage, and the time scale for even short-term success of this late-successional species is unknown. These small populations remain vulnerable to impacts from stochastic demographic or environmental events that could eliminate all or a large proportion of their plants (Menges, 1991, 1992), and their effective population size (N_e) is controlled by their outcrossing mating system, which requires crossing with different genotypes. A realistic short-term goal should be establishment of the number of genotypes present in natural populations. Allozyme sampling found 27 genotypes in the Weimer Hill population, and 15 genotypes at Rockefeller (Tecic et al., 1998), and over 200 genetically different plants actually may be present at Rockefeller (Alexander et al., 1997). To restore large numbers of genotypes will require mixing geographically different seed sources. Such crossing has the potential for disrupting locally adapted lineages and causing outbreeding depression, but the unusually large neighborhood sizes of milkweed species may buffer them from these genetic effects. Although our preliminary success with planting of Missouri and Kansas milkweed seedlings into northern Illinois habitats supports this hypothesis, additional work is needed to understand long-term consequences.

Additional constraints on the development of large milkweed populations are related to problems of size or scale (White, 1996). *Asclepias meadii* is so uncommon within natural habitats that it is rarely encountered by random sampling, and its apparent requirement of late-successional vegetation currently limits restoration to small sites, because no large sites exist in the eastern part of its range. Restoration of larger high-quality prairies is also not a short-term process, and has not been attained even after 20 years (Schramm, 1992). As a result, habitat size may regulate population growth by limiting effective population size and reproductive potential, and by enhancing inbreeding effects. Development of an inordinately large or dense population within a small area could result in density-dependent disease or insect infestations that would have disastrous effects on populations. For example, severe damage, and possibly mortality, to *A. meadii* can be caused by milkweed cerambycid beetles (*Tetraopes* sp.) and by milkweed weevils (*Rhyssematus* sp.). The adult *Tetraopes* feed on leaves and flowers, while their larvae feed on roots. *Rhyssematus* grubs feed on milkweed pith, which may weaken the stem, while adults may topple the terminal umbel, thereby preventing seed production (Betz, 1989; R. F. Betz, pers. obs.).

Managing fragmented *A. meadii* restorations as metapopulations may help resolve the population size dilemma. The transferring of genetic material among sites could maintain a high level of genetic variation across restorations (Lacy, 1987, 1994; Tecic et al., 1998). This would help provide demographic stability by enhancing outcrossing potential while avoiding problems otherwise associated with high densities of small populations.

Literature Cited

Alexander, H. M., N. S. Slade & W. D. Kettle. 1997. Application of mark-recapture models to estimation of the population size of plants. Ecology 78: 1230–1237.

Beals, E. W. 1984. Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. Advances Ecol. Res. 14: 1–55.

Betz, R. F. 1989. Ecology of Mead's milkweed (*Asclepias meadii* Torrey). Pp. 187–191 *in* T. B. Bragg & J. Stubbendieck (editors), Proceedings of the Eleventh North American Prairie Conference. Univ. Nebraska at Lincoln.

——— & J. F. Lamp. 1989. Species composition of old settler silt-loam cemetery prairies. Pp. 33–39 *in* T. B. Bragg & J. Stubbendieck (editors), Proceedings of the Eleventh North American Prairie Conference. Univ. Nebraska at Lincoln.

———, R. D. Struven, J. E. Wall & F. B. Heitler. 1994. Insect pollinators of 12 milkweed (*Asclepias*) species. Pp. 45–60 *in* Proceedings of the Thirteenth North American Prairie Conference. R. G. Wickett, P. D. Lewis, A. Woodliffe & P. Pratt (editors), Department of Parks & Recreation, Windsor, Ontario, Canada.

Bliss, L. C. & G. W. Cox. 1964. Plant community structure and soil variation within a northern Indiana prairie. Amer. Midl. Naturalist 72: 115–128.

Bowles, M. L. & J. McBride. 1996. Pitcher's thistle (*Cirsium pitcheri*) reintroduction. Pp. 423–431 *in* D. A. Falk, C. I. Millar & M. Olwell (editors), Restoring Diversity: Strategies for Reintroduction of Endangered Plants. Island Press, Washington, D.C.

——— & C. J. Whelan (editors). 1994. Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

———, R. F. Betz & M. M. DeMauro. 1993a. Propagation of rare plants from historic seed collections: Implications for species restoration and herbarium management. Restoration Ecol. 1: 101–106.

———, R. Flakne, K. McEachern & N. Pavlovic. 1993b. Recovery planning and reintroduction of the federally threatened Pitcher's thistle (*Cirsium pitcheri*) in Illinois. Natural Areas J. 13: 164–176.

Broyles, S. B. & R. Wyatt. 1991. Effective pollen dispersal in a natural population of *Asclepias exaltata*: The influence of pollinator behavior, genetic similarity, and mating success. Amer. Naturalist 138: 1239–1249.

——— & ———. 1993. The consequences of self-pollination in *Asclepias exaltata*, a self-incompatible milkweed. Amer. J. Bot. 80: 41–44.

Carr, D. E. & M. R. Dudash. 1996. Inbreeding depression in two species of *Mimulus* (Scrophulariaceae) with contrasting mating systems. Amer. J. Bot. 83: 586–593.

Collins, S. L. & D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed grass prairie. Pp. 81–98 *in* S. L. Collins & L. L. Wallace (editors), Fire in North American Tallgrass Prairie. Univ. Oklahoma Press, Norman.

——— & S. M. Glenn. 1988. Disturbance and community structure in North American prairies. Pp. 131–143 *in* H. During, M. Werger & J. Willems (editors), Diversity and Pattern in Plant Communities. SPB Academic Publishing, The Hague, The Netherlands.

——— & L. L. Wallace (editors). 1990. Fire in North American Tallgrass Prairie. Univ. Oklahoma Press, Norman.

DeMauro, M. M. 1993. Relationship of breeding system to rarity in the Lakeside daisy (*Hymenoxys acaulis* var. *glabra*). Conservation Biol. 7: 542–550.

———. 1994. Development and implementation of a recovery program for the federal threatened Lakeside daisy (*Hymenoxys acaulis* var. *glabra*). Pp. 298–321 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Dudash, M. R. 1990. Relative fitness of selfed and outcrossed progeny in a self-compatible, protandrous species, *Sabatia angularis* L (Gentianaceae) in three environments. Evolution 44: 1129–1139.

Evans, E. W., J. M. Briggs, E. J. Finck, D. J. Gibson, S. W. James, D. W. Kaufman & T. R. Seastedt. 1989. Is fire a disturbance in grasslands? Pp. 159–160 *in* T. B. Bragg & J. Stubbendieck (editors), Proceedings of the Eleventh North American Prairie Conference. Univ. Nebraska at Lincoln.

Fay, P. A. & A. K. Knapp. 1993. Photosynthetic and stomatal responses of *Avena sativa* (Poaceae) to a variable light environment. Amer. J. Bot. 80: 1369–1373.

Fenster, C. B. & M. R. Dudash. 1994. Genetic considerations for plant population restoration and conservation. Pp. 34–62 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual

Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Fitch, H. S. & E. R. Hall. 1978. A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller Experimental Tract. Publ. Mus. Nat. Hist. Univ. Kansas 4: 1–15.

Gilpin, M. E. & M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pp. 19–34 *in* M. E. Soulé (editor), Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, Massachusetts.

Guerrant, E. O., Jr. 1996. Designing populations: Demographic, genetic, and horticultural dimensions. Pp. 171–207 *in* D. A. Falk, C. I. Millar & M. Olwell (editors), Restoring Diversity: Strategies for Reintroduction of Endangered Plants. Island Press, Washington, D.C.

Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana.* Ecology 67: 46–57.

Harrison, W. F. 1988. Endangered and threatened wildlife and plants; Determination of threatened status for *Asclepias meadii* (Mead's milkweed). Fed. Reg. 53: 33982–33994.

Heywood, J. S. & D. A. Levin. 1985. Associations between allozyme frequencies and soils characteristics in *Gaillardia pulchella* (Compositae). Evolution 39: 1076–1086.

Hook, P. B., W. K. Lauenroth & I. C. Burke. 1994. Spatial patterns of roots in a semiarid grassland: Abundance of canopy openings and regeneration gaps. J. Ecol. 82: 485–494.

Kahn, A. P. & D. H. Morse. 1991. Pollinium germination and putative ovule penetration in self- and cross-pollinated common milkweed *Asclepias syriaca.* Amer. Midl. Naturalist 126: 61–71.

Kephart, S. R. 1981. Breeding systems in *Asclepias incarnata, A. syriaca, & A. verticillata.* Amer. J. Bot. 68: 226–232.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biol. 1: 143–158.

———. 1994. Managing genetic diversity in captive populations of animals. Pp. 63–89 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241: 1455–1460.

Les, D. H., J. A. Reinhartz & E. J. Esselman. 1991. Genetic consequences of rarity in *Aster furcatus* (Asteraceae), a threatened, self-incompatible plant. Evolution 45: 1641–1650.

Louda, S. M., M. A. Potvin & S. K. Collinge. 1990. Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in sand hills prairie. Amer. Midl. Naturalist 124: 105–113.

McCune, B. 1993. Multivariate analysis on the PC-ORD system. Oregon State University, Corvalis.

McGregor, R. L. 1977. Rare native vascular plants of Kansas. Techn. Publ. State Biol. Surv. Kansas 5: 1–44.

Menges, E. S. 1986. Predicting the future of rare plant populations: Demographic monitoring and modelling. Nat. Areas J. 6: 13–25.

———. 1991. The application of minimum viable population theory to plants. Pp. 45–61 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

———. 1992. Stochastic modeling of extinction in plant populations. Pp. 253–275 *in* P. L. Fiedler & S. K. Jain (editors), Conservation Biology: The Theory and Practice of Nature Conservation. Chapman & Hall, New York.

Page, A. L., R. H. Miller & D. R. Keeny (editors). 1982. Methods of Soil Analysis, Part 2: Chemical and Microbial Properties, 2nd ed. American Society of Agronomy & Soil Science Society of America, Madison, Wisconsin.

Pavlik, B. M. 1994. Demographic monitoring and the recovery of endangered plant populations. Pp. 322–350 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

———. 1996. Defining and measuring success. Pp. 127–155 *in* D. A. Falk, C. I. Millar & M. Olwell (editors), Restoring Diversity: Strategies for Reintroduction of Endangered Plants. Island Press, Washington, D.C.

Schaal, B. A., W. J. Leverich & S. H. Rogstad. 1991. A comparison of methods for assessing genetic variation in plant conservation biology. Pp. 123–134 *in* D. A. Falk & K. E. Holsinger (editors), Genetics and Conservation of Rare Plants. Oxford Univ. Press, New York.

Schramm, P. 1992. Prairie restoration: A twenty-five year perspective on establishment and management. Pp. 69–177 *in* D. D. Smith & C. A. Jacobs (editors), Proceedings of the Twelfth North American Prairie Conference. Univ. Northern Iowa, Cedar Falls.

Shannon, T. R. & R. Wyatt. 1986. Pollen germinability of *Asclepias exaltata*: Effects of flower age, drying time, and pollen source. Syst. Bot. 11: 322–325.

Smith, T. 1997. Management Guidelines for Mead's milkweed (*Asclepias meadii* Torrey *ex* A. Gray). Missouri Department of Conservation, Jefferson City, Missouri.

Sneath, P. H. A. & R. R. Sokal. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York.

Steele, R. G. D. & J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, New York.

Tecic, D. L., J. L. McBride, M. L. Bowles & D. L. Nickrent. 1998. Genetic variability in the federal threatened Mead's milkweed, *Asclepias meadii* Torrey (Asclepiadaceae) as determined by allozyme electrophoresis. Ann. Missouri Bot. Gard. 85: 97–109.

Weller, S. 1994. The relationship of rarity to plant reproductive biology. Pp. 90–117 *in* M. L. Bowles & C. J. Whelan (editors), Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation. Cambridge Univ. Press, Cambridge, U.K.

White, P. S. 1996. Spatial and biological scales in reintroduction. Pp. 49–86 *in* D. A. Falk, C. I. Millar & M. Olwell (editors), Restoring Diversity: Strategies for Reintroduction of Endangered Plants. Island Press, Washington, D.C.

Willson, M. F. & P. W. Price. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. Canad. J. Bot. 58: 2229–2233.

Wyatt, R. 1976. Pollination and fruit-set in *Asclepias*: A reappraisal. Amer. J. Bot. 63: 845–851.

——— & S. B. Broyles. 1994. Ecology and evolution of reproduction in milkweeds. Annual Rev. Ecol. Syst. 25: 423–441.

THE POLLINATION ECOLOGY OF FIVE SPECIES OF *PENSTEMON* (SCROPHULARIACEAE) IN THE TALLGRASS PRAIRIE[1]

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ABSTRACT

The floral ecology of *Penstemon cobaea* Nutt. var. *cobaea*, *P. cobaea* var. *purpureus* Pennell, *P. digitalis* Nutt. ex Sims, *P. grandiflorus* Nutt., *P. pallidus* Small, and *P. tubaeflorus* Nutt. was studied by sampling populations at nine prairie sites in Illinois, Kansas, and Missouri. All five species show protandry, but the receptive stigma lies only 2 mm away from the two pairs of fertile stamens. Bagging experiments on three *Penstemon* spp. show that only *P. digitalis* sets seed when insect visitors are excluded. Flowers of all five species exhibit a horizontal presentation of the corolla and emit a slightly discernible scent. However, the presumed pollination systems of *Penstemon* spp. correlate with corolla form and the size of the floral sinus. The tubular, white flowers of *P. tubaeflorus* appear to be pollinated by a combination of diurnal Lepidoptera and some native bees favoring a dorsal deposition of pollen on mouthparts and upper thoraces. The four remaining species have gullet- or bell-shaped corollas ornamented with violet-purple blotches or lines. These species appear to be pollinated primarily by polylectic/polyphagic bees (including six *Bombus* spp.), with *P. digitalis* and *P. cobaea* visited infrequently by the rare *Penstemon* wasp, *Pseudomasaris occidentalis*. Queens of *Bombus pennsylvanicus* subsp. *pennsylvanicus* forage primarily on the large, gullet flowers of *P. grandiflorus* and both varieties of *P. cobaea*. Queens of *Bombus nevadensis* subsp. *auricomus* prefer those *P. digitalis* and *P. pallidus* showing a reduced gullet or bell form. Bee pollination in four *Penstemon* spp. may operate within a two-tiered system. Large-bodied *Bombus* spp., *Megachile brevis*, and anthophorids (*Synhalonia hamata* and *Anthophora terminalis*) carry dorsal depositions of *Penstemon* pollen because they contact anthers and stigmas while they forage exclusively for nectar. In contrast, small-bodied members of the Anthophoridae (*Ceratina*), Colletidae (*Hylaeus* spp.), Halictidae (*Augochlorella*, *Halictus*, *Lasioglossum*), and Megachilidae (*Hoplitis* and *Osmia*) forage actively for *Penstemon* pollen encouraging repeated, ventral contact with the sexual organs of the flowers. *Bombus* queens were more prevalent at large *Penstemon* populations (especially *P. cobaea*). *Bombus* workers were collected primarily on restored sites. The importance of small bees as pollinators appeared to vary indirectly with *Penstemon* population size.

Penstemon (Scrophulariaceae: Cheloneae) is a North American genus of about 270 species (Wolfe et al., 1997) distributed from Alaska to Guatemala. Within the Great Plains, Freeman (1981) recognized 22 species of *Penstemon* in two subgenera and five sections. The Upper Mississippi Valley supports two additional species, *Penstemon arkansanus* Pennell and *P. hirsutus* (L.) Willd., suggesting that 24 *Penstemon* species are native to midwestern American prairies.

Despite the species richness of *Penstemon* in North America, analyses comparing life-histories within this genus lag far behind classical (Pennell, 1935; Keck, 1938) and molecular (Wolfe & Elisens, 1993) taxonomies. We lack significant literature on breeding systems in *Penstemon* compared to other scrophulariaceous genera (e.g., *Pedicularis*; Macior, 1982) distributed through the Northern Hemisphere (Kampny, 1995). References to the pollination biology of *Penstemon* by Pennell (1935) were derived primarily from predictions that were based on floral morphology. In contrast, what literature does exist on *Penstemon* pollination often shows a lack of consensus regarding the efficiency of different bee taxa as true pollen vectors.

Field studies of *Penstemon* pollination began with Robertson (1892, 1929), who noted protandry in "*P. laevigatus*" (= *P. digitalis*) and "*P. pubescens*" (= *P. pallidus*) in Illinois and collected a total of 20 different bee species in their flowers. Rob-

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ANN. MISSOURI BOT. GARD. 85: 126–136. 1998.

ertson was convinced that pollination was effected exclusively by long-tongued bees probing for nectar because small-bodied, short-tongued bees were excluded from the floral throat by the ornamented staminode. Clements and Long (1923) collected floral foragers on *P. gracilis*, in the Colorado foothills, concluding that *Osmia* and *Hoplitis* spp. (Megachilidae) were the most common floral visitors. Straw (1956) insisted that the pseudomasarid wasp-pollinated *Penstemon spectabilis* Thurb. was derived from a stabilized hybrid between bee-pollinated *P. grinnellii* Eastw. and hummingbird-pollinated *P. centranthifolius* (Benth.) Benth. This has since been discredited by Grant (1994; see also Wolfe & Elisens, 1993). Crosswhite and Crosswhite (1966) studied insect-pollination of *P. gracilis* and *P. pallidus* in southern Wisconsin and northern Illinois. Unlike Robertson, they emphasized the role of small, solitary bees, especially *Osmia* and *Hoplitis* spp. Crosswhite (1965) provided the only information on compatibility systems in the genus, concluding that *P. pallidus* was self-compatible. Lawson et al. (1989) analyzed the pollen loads of bees collected on *Penstemon haydenii* S. Wats. in Nebraska, noting an abundance of *Hoplitis* and *Osmia*, but did not comment on which bees regularly contacted the receptive stigmas.

Here we report the results of four years of field studies on six *Penstemon* taxa in five species: *Penstemon cobaea* var. *cobaea*, *P. cobaea* var. *purpureus*, *P. digitalis*, *P. grandiflorus*, *P. pallidus*, and *P. tubaeflorus*. Continued studies of pollination systems of this genus in the American Midwest are needed for two, overlapping reasons. First, further analyses and descriptions of pollination mechanisms in *Penstemon* will make it possible to map pollinator shifts onto a phylogenetic tree (see Armbruster, 1993; Goldblatt et al., 1995). Second, *Penstemon* spp. are native to prairies that are reduced and much endangered habitats through the American Midwest. Basic information on pollen dispersal in prairie *Penstemon* spp. should contribute ultimately to conservation policies and restoration projects.

MATERIALS AND METHODS

The taxonomy of *Penstemon* species follows Yatskievych and Turner (1990). Floral phenologies are based on censuses (as specified below) at each study site for one to four flowering seasons.

POPULATIONS

Penstemon cobaea Nutt. var. *cobaea* (pollinators collected 24 May–22 June 1994–1997, $N = 116$). Sixteen populations of this taxon on or near the Konza Prairie (Kansas) have been studied, most of them small (< 30 blooming stems). The Konza Prairie Research Natural Area is an 8616-acre preserve managed by Kansas State University for the Nature Conservancy. Two large populations (> 500 blooming stems) were studied: (1) in 1995 in White Pasture near the northeastern corner of the Konza in an area considered more floristically rich in tallgrass prairie forbs than much of the rest of the site; and (2) in Wright Prairie, adjacent to the part of Konza known as the Texas Hog Pasture, for which access was provided by Valerie Wright.

Penstemon cobaea var. *purpureus* Pennell (28 May–4 June 1995–1996, $N = 15$). Three populations of approximately 100 flowering shoots each were monitored in roadside glades in Christian, Ozark, and Taney Cos., Missouri. All three sites are listed on the Missouri Department of Conservation Rare Plant Inventory.

Penstemon digitalis Nutt. ex Sims (30 May–5 July 1994–1996, $N = 325$). This species was studied on four sites, two tallgrass prairie restorations in eastern Missouri and two tallgrass prairie relicts in western Missouri: (1) Litzsinger Road Ecology Center of the Missouri Botanical Garden, St. Louis Co., Missouri. This wet mesic prairie restoration was seeded in 1989 and still contains a preponderance of weedy, early successional prairie species. (2) Shaw Arboretum Experimental Prairie of the Missouri Botanical Garden, Franklin Co., Missouri. This site is about 25 years old and is more diverse than Litzsinger, but not so diverse as the natural communities. (3) Paint Brush Prairie, Pettis Co., Missouri. The colony studied is in a relatively impoverished part of the site, but is adjacent to floristically rich prairie. There are notable differences, discussed below, between the floral foragers here as compared to the restorations. (4) Hi-Lonesome Prairie, Benton Co., Missouri. The study area here is a *Penstemon* monoculture embedded in common lenticular sedges (*Carex* spp.).

Penstemon grandiflorus Nutt. (21–30 May 1996–1997, $N = 44$). This species was studied in a population of about 50 blooming plants on and near an ungrazed prairie haymeadow on the Poole Ranch in Geary Co., Kansas, about 2.8 miles south of Interstate 70 on Kansas Hwy. 177. This species is extremely rare on the Konza Prairie proper.

Penstemon pallidus Small (15–24 May 1996–1997, $N = 71$). Two sites were used for this taxon in both 1996 and 1997: (1) Fults Hill Prairie, Monroe Co., Illinois. This area is perched atop the Mississippi River bluffs and is considered the best surviving undisturbed loess hill prairie along the Illinois bluffs. (2) Paint Brush Prairie, Pettis Co.,

Table 1. Pollen loads of foragers collected on *Penstemon* spp.

	Penstemon pollen only	Penstemon + other species	Other species only	No pollen	Total
Large Gullet-Corolla Species					
Penstemon cobaea* var. *cobaea					
Bees					
Augochlorella striata (Provancher) F	2	0	0	0	2
Bombus nevadensis auricomus (Robt.) Q	4	1	0	0	5
Bombus nevadensis auricomus W	2	0	0	0	2
Bombus pennsylvanicus (DeGeer) Q	19	8	2	1	30
Bombus pennsylvanicus W	1	0	0	0	1
Ceratina strenua (Smith) F	0	1	0	0	1
Halictus ligatus Say F	1	0	0	0	1
Hoplitis pilosifrons (Cresson) F	21	21	3	5	50
Hoplitis pilosifrons M	0	0	0	1	1
Lasioglossum (= *Dialictus*) spp. F	6	2	0	1	9
Synhalonia hamata (Bradley) F	1	0	0	0	1
Others					
Bombylius sp.	4	0	0	3	7
Euphoria sepulchralis (Fab.)	0	2	0	4	6
					$\Sigma = 116$
Penstemon cobaea* var. *purpureus					
Bees					
Bombus pennsylvanicus Q	0	0	0	1	1
Hoplitis pilosifrons F	1	2	0	1	4
Lasioglossum imitatum (Smith) F	1	0	0	0	1
Osmia distincta (Cresson) F	1	1	0	0	2
Synhalonia rosae Robertson F	1	0	0	0	1
Xylocopa virginica L. F	0	1	1	1	3
Others					
Bombylius sp.	0	0	0	1	1
Pseudomasaris sp. F	1	0	0	1	2
					$\Sigma = 15$
Penstemon grandiflorus					
Bees					
Augochlorella persimilis (Viereck) F	1	0	0	0	1
Augochlorella striata F	11	2	1	4	18
Bombus griseocollis (DeGeer) Q	0	1	0	0	1
Bombus pennsylvanicus Q	5	3	0	0	8
Hoplitis pilosifrons F	3	0	0	0	3
Lasioglossum (= *Dialictus*) spp. F	6	7	0	1	14
Megachile brevis Say M	1	0	0	0	1
Xylocopa virginica M	1	0	0	0	1
					$\Sigma = 44$
Small Gullet-Corolla Species					
Penstemon digitalis					
Bees					
Anthophora terminalis Cresson F	6	0	0	1	7
Augochlorella striata F	3	1	0	3	7
Bombus bimaculatus Cresson Q	2	0	1	2	5
Bombus bimaculatus W	24	8	6	3	41
Bombus bimaculatus M	5	0	0	0	5
Bombus fraternus (Smith) W	8	1	1	0	10

Table 1. Continued.

	Penstemon pollen only	Penstemon + other species	Other species only	No pollen	Total
Bombus griseocollis Q	0	1	1	2	4
Bombus griseocollis W	3	5	0	1	9
Bombus impatiens Cresson W	9	1	1	0	11
Bombus nevadensis Q	28	2	6	9	45
Bombus nevadensis W	5	5	4	2	16
Bombus pennsylvanicus Q	3	3	1	2	9
Bombus pennsylvanicus W	7	6	1	2	16
Ceratina spp. F	7	5	0	5	17
Hoplitis pilosifrons F	6	2	0	1	9
Hylaeus spp. F	2	0	0	2	4
Lasioglossum (= *Dialictus*) spp. F	36	5	3	12	56
Osmia spp. F	11	0	0	1	12
Synhalonia hamata F	22	13	2	2	39
Synhalonia hamata M	1	0	0	0	1
Others					
Pseudomasaris sp. F	1	0	0	0	1
Pterourus troilus troilus L. F	1	0	0	0	1
					Σ = 325
Penstemon pallidus					
Bees					
Apis mellifera L. W	1	0	0	0	1
Augochlorella striata F	0	0	1	1	2
Bombus bimaculatus Q	2	0	0	1	3
Bombus bimaculatus W	1	1	0	0	2
Bombus nevadensis auricomus Q	0	0	0	2	2
Bombus pennsylvanicus Q	0	0	0	2	2
Ceratina spp. F	2	0	0	5	7
Hoplitis pilosifrons F	13	1	0	6	20
Hoplitis producta (Cresson) F	1	0	0	0	1
Lasioglossum (= Dialictus) sp. F	1	1	0	0	2
Osmia spp. F	15	3	0	6	24
Synhalonia rosae M	3	0	0	2	5
					Σ = 71
		Tubular-Corolla species			
Penstemon tubaeflorus					
Bees					
Anthophora abrupta Say F	0	0	0	2	2
Anthophora abrupta M	1	0	0	2	3
Anthophora ursina Cresson F	1	0	0	0	1
Augochlorella striata F	0	0	0	1	1
Bombus pennsylvanicus Q	3	0	0	0	3
Osmia distincta F	2	0	0	0	2
Others					
Pterourus troilus troilus F	1	0	0	2	3
Pterourus troilus troilus M	0	0	0	1	1
					Σ = 16
					ΣΣ = 587

F = Female, M = male, Q = queen, W = worker.

Missouri. This Osage Plains prairie is particularly rich in late spring forbs which co-flower with penstemons.

Penstemon tubaeflorus Nutt. (4–5 June 1996, *N* = 17). This species was studied at Long Bald, a dolomite glade in Caney Mountain Conservation Area, Ozark Co., Missouri. This is a large and spectacular glade surrounded by dry oak woods, and it contains a wealth of wildflowers, including the Ozark endemic *Echinacea paradoxa* (Norton) Britton.

Taken together, the study areas of this project represent a diversity of *Penstemon* habitats across the tallgrass prairie biome. Although we have pooled the floral forager lists in this paper (Table 1) by *Penstemon* taxa to conserve space, we emphasize the value of repeated samples of the same study areas over several years in evaluating the fidelity of floral foragers to specific penstemons.

The sites themselves are, for the most part, well-known nature preserves in Illinois, Kansas, and Missouri, for which there is a large literature available (e.g., Evers, 1955; Freeman & Hulbert, 1985; Ochs, 1993; Toney, undated; Solecki et al., 1986). These references contain much information on site history, location, ecology, and floristic composition.

Floral fragrance. Whole flowers of each species were placed in clean, glass, stoppered vials for periods up to two hours, following Buchmann et al. (1978). At the end of the two-hour period, the vials were uncorked and smelled.

Bagging experiments. To determine the potential role of self-compatibility and mechanical self-pollination (autogamy) in the absence of insect visitation, inflorescences were bagged during the flowering season. Nylon stockings or wood and mesh exclusion cages were placed over ten flowering shoots, in bud, of *P. cobaea* var. *cobaea*, twelve of *P. cobaea* var. *purpureus*, six of *P. digitalis* and three of *P. grandiflorus* for the length of individual flowering periods. Infructescences were examined for the production of fruit and seed within two months following the withering of the last flower on the shoot.

Pollinator analyses. Field observations recorded foraging behavior of insects on, and within, *Penstemon* flowers. This included noting when foragers collected nectar and/or pollen and whether insects contacted anthers and stigmas while foraging.

The collection and analyses of floral foragers on *Penstemon* flowers represent the harvest of 35–50 insects/site each year. As these *Penstemon* populations represent protected species on nature preserves, overcollection of prospective pollinators may lower seedset. Otherwise, the protocol for netting, killing, and processing specimens followed Bernhardt (1990a, b) and Bernhardt and Weston (1996). Floral foragers were collected on penstemon blossoms and killed in jars poisoned with ethyl acetate.

To verify the presence of *Penstemon* pollen, each euthanized insect was placed on a separate, clean glass slide and bathed in a few drops of absolute ethanol. At this time additional masses of pollen packed onto scopae and corbiculae were teased or scraped off with a dissecting needle. When the ethanol had evaporated, the pollen film left on the glass slide was stained with two to three drops of Calberla's fluid (Ogden et al., 1974). Because insects were sacrificed in a communal killing jar, there is the danger of pollen contamination as bodies of different insects contact each other (see Bernhardt & Weston, 1996). Therefore, we excluded pollen counts of less than 50 grains on insects since the vast majority of floral foragers were extremely hairy and liable to pick up loose grains due to static electricity. Pollen loads were counted on each slide as follows: a total of 200 pollen grains were counted for each insect in increments of five. If there were more than 150 grains of *Penstemon* pollen in the count (> 75%), the load was classified as a " *Penstemon* Pollen Only Load." If more than 150 grains of non-penstemon pollen was present the load was called an "Other Species Only Load." If more than 50 grains of both *Penstemon* and at least one other non-*Penstemon* species were present, this was called a "*Penstemon* + Other Species Load." If less than 200 grains were present on the slide, the load was scored as a "No Pollen Load."

Insect length was recorded by measuring six pinned specimens of each species, gender, and/or caste. The body length of each specimen was measured from the labrum to the apex of the abdomen (Bernhardt & Weston, 1996).

Insect specimens were identified by C. D. Michener, R. Brooks, and colleagues at Snow Entomological Museum, University of Kansas, and by M. Arduser of the Missouri Department of Conservation. Vouchers are deposited at the Snow Museum. Bee genera follow Michener et al. (1994).

RESULTS

Floral phenology. Midwestern *Penstemon* spp. are found in bloom from early May until early July (Fig. 1). Flowering seasons overlap broadly between species. *Penstemon pallidus* is the first species to bloom in spring, while the two varieties of *P. cobaea*

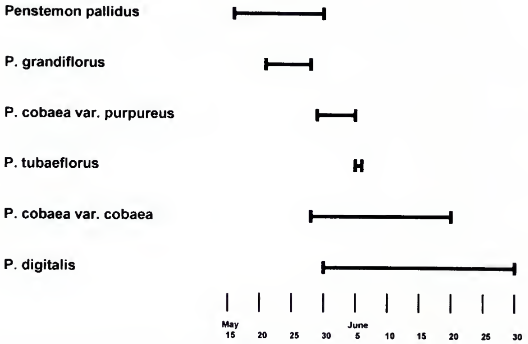

Figure 1. Floral phenology of *Penstemon* spp. (1994–1997).

are usually the last to begin flowering. *Penstemon digitalis* has the longest flowering period.

Bagging experiments. In both varieties of *P. cobaea,* no fruits were produced in the absence of visiting insects. In *P. grandiflorus* approximately 50% of the flowers produced full-sized capsules totally devoid of seed (parthenocarpy). In *P. digitalis,* the vast majority of flowers produced seed-containing capsules.

Floral presentation. All *Penstemon* spp. are protandrous with the stigma located within 2 mm of the two pairs of fertile anthers. All *Penstemon* spp. present their flowers horizontally with respect to the peduncle.

Flowers of all *Penstemon* spp. produce a barely discernible fragrance reminiscent of ripe canteloupe. *Penstemon tubaeflorus* is the only species studied with flowers that are pure, translucent-shiny white to the human eye. Flowers of *P. grandiflorus* appear pink-mauve with faintly discernible nectar guides. *Penstemon digitalis* and *P. pallidus* have white corollas with the floral throat streaked with narrow, light purple lines. *Penstemon cobaea* var. *cobaea* has pink or white corollas, while corollas of variety *purpureus* are deep purple (although we have records of red or white morphs in Taney Co., Missouri). Corollas of both varieties of *P. cobaea* have deep purple blotches and/or broad lines on the throat.

The corollas of *P. tubaeflorus* (sinus 4–6 mm wide) have the most narrow floral tubes. The corollas of both varieties of *P. cobaea* (sinus 18–25 mm wide) and *P. grandiflorus* (15–18 mm wide) form large, bilabiate gullets. In contrast, the corollas of *P. digitalis* (sinus 8–12 mm) and *P. pallidus* (4–7 mm) form small gullets.

Floral foragers. Approximately 600 insects were caught foraging on *Penstemon* flowers. *Penstemon tubaeflorus* was the only species that was visited consistently by the butterfly *Pterourus troilus,* but captures do not reflect the density of field observations (Table 1). The head and proboscis of this butterfly contacts stigmas and dehisced anthers while it probes for nectar, with pollen loads deposited on the proximal portion of the proboscis (Table 2). Bees greater than 10 mm in length cling to the petal lobes while probing for nectar, acquiring dorsal depositions of pollen on their heads (Tables 1, 2).

In all remaining species pollination appeared to be dominated by Hymenoptera, with both varieties of *P. cobaea* also visited by beeflies (*Bombylius* spp.) that carried *Penstemon* pollen while contacting the stigmas (Table 2). Bumblebee flower-beetles (*Euphoria sepulchralis,* Scarabaeideae) collected on *P. cobaea* var. *cobaea* carried loads of *Penstemon* pollen, but they consumed basal floral organs and we were unable to determine whether they contacted stigmas (Table 2).

Penstemon digitalis and *P. cobaea* var. *purpureus* were visited by females of *Pseudomasaris occidentalis* (Vespidae). These wasps contacted the stigmas while swallowing pollen and/or foraging for nectar at the base of the corolla tubes, so pollen deposition was both ventral and dorsal.

The foraging behavior of bees was determined by physical size. Bees greater than 10 mm in length (*Anthophora, Bombus, Megachile,* and *Synhalonia*

Table 2. Size and behavior of floral foragers on *Penstemon* spp.

Floral forager	N = Number caught	$\overline{X}$ = Length of body* (mm)	Observed foraging for pollen	Observed foraging for nectar	Contacted anthers and stigma while foraging
Coleoptera					
Euphoria sepulchralis	6	12.5	−	+	−
Diptera					
Bombylius spp.	8	12.0	−	+	+
Hymenoptera					
Bees					
Anthophora spp. F	9	12.1	−	+	+
Anthophora spp. M	3	13.3	−	+	+
Apis mellifera W	1	13.0	−	+	+
Augochlorella spp. F	31	7.2	+	−	+
Bombus queens	118		−	+	+
B. bimaculatus	8	18.5			
B. griseocollis	5	22.8			
B. nevadensis	52	27.8			
B. pennsylvanicus	53	27.0			
Bombus workers	98		−	+	+
B. bimaculatus	43	15.3			
B. fraternus	10	—			
B. griseocollis	9	19.5			
B. impatiens	11	12.6			
B. nevadensis	9	18.7			
B. pennsylvanicus	16	22.5			
Bombus males					
B. bimaculatus	5	—	−	+	+
Ceratina spp. F	25	6.1	+	−	+
Halictus ligatus F	1	8.5	+	−	+
Hoplitis pilosifrons F	86	7.7	+	−	+
Hoplitis pilosifrons M	1	8.0	?	?	?
Hoplitis producta F	1	8.5	+	−	+
Hylaeus spp. F	4	5.0	+	−	+
Lasioglossum (= *Dialictus*) spp. F	82	6.0	+	−	+
Megachile brevis M	1	11.0	−	+	+
Osmia spp. F	40	8.4	+	−	+
Synhalonia hamata F	40	15.3	−	+	+
Synhalonia hamata M	1	12.5	−	+	+
Synhalonia rosae F	1	14.2	−	+	+
Synhalonia rosae M	5	13.7	−	+	+
Xylocopa virginica F	4	21.4	?	?	?
Xylocopa virginica M	1	22.5	?	?	?
Wasps					
Pseudomasaris sp. F	3	19.0	+	+	+
Lepidoptera					
Pterourus troilus troilus F	4	22.5	−	+	+/?
Pterourus troilus troilus M	1	22.0	−	+	+/?

* Measurement refers to body length measured from the clypeus (excluding the length of the proboscis) to the tip of the abdomen.

F = female, M = male, Q = queen, W = worker.

spp.) entered the floral tube and probed for nectar, receiving dorsal depositions of pollen from dehisced anthers while contacting the stigmas (Table 2). These bees did not collect *Penstemon* pollen by scraping anthers with their legs. Although *Xylocopa virginica* was over 10 mm in length, bees of this species mostly obtained nectar from *Penstemon* flowers by piercing the base of the corolla tube without entering the floral throat. Observations of queen and worker *Bombus* spp. showed that these large bees typically foraged first on the lowest open flower on an inflorescence, and then climbed up the inflorescence following the spiral of open corollas and visiting flowers in both phases of protandry. All the large bee species were observed visiting the flowering shoots of several genets in succession.

In contrast, bees less than 10 mm in length (*Augochlorella, Ceratina, Hoplitis, Hylaeus, Lasioglossum,* and *Osmia* spp.) were not observed to probe for nectar. These bees were observed clinging upside-down and collecting pollen from dehiscent anthers. *Penstemon* pollen was deposited ventrally on these insects, and bees contacted stigmas while foraging for pollen. These small bees did not appear to discriminate between flowers in the young (dehiscent) versus old (empty) anther phases of protandry in *Penstemon* flowers based on corolla features. These bees were observed to enter the floral tube, cling to the old, empty anthers and contact the stigmas for a few seconds, but then they exited the flowers without attempting to scrape old anthers. These small bees were observed visiting several flowering shoots in succession before leaving the site.

Approximately 57% of all bees captured on *Penstemon* spp. carried pure loads of *Penstemon* pollen in their corbiculae or scopae (Table 1). An additional 20% carried *Penstemon* pollen mixed with the pollen of other co-flowering species. Mixed pollen loads included both nectar-producing (*Baptisia* spp., *Delphinium* spp., *Onosmodium* sp., *Pycnanthemum* sp., *Rubus* sp., and *Teucrium* sp.) and nectarless (*Rosa* spp., *Schrankia nuttallii*) species. Pollinaria of several *Asclepias* spp. were found attached exclusively to the first pair of legs.

Some queen bumblebees appeared to restrict their foraging to selected *Penstemon* spp. *Bombus pennsylvanicus* was most abundant on the large-gullet species: *P. cobaea* and *P. grandiflorus. Bombus nevadensis* was found primarily on the small, gullet-bell-shaped corollas: *P. digitalis* and *P. pallidus.* No morphometric difference could be found between *B. pennsylvanicus* and *B. nevadensis* queens. Bumblebees were seldom observed or collected in flowers of populations of *P. cobaea* var. *cobaea* that consisted of < 50 flowering shoots (Konza Prairie sites 1995 and 1997).

The density of bumblebees belonging to the neuter, worker caste was highly skewed in the data set. Ninety percent of all workers of six *Bombus* spp. (Table 1) were restricted to the flowers of *P. digitalis* at the Litzsinger Road Ecology Center, a restored site. The remaining 10% were distributed among all remaining study sites for all *Penstemon* spp. Although the flowering period of *P. digitalis* at the Litzsinger Road site overlapped broadly with *P. digitalis* at the two remaining sites, the presence of worker-caste bumblebees on virgin prairies and on old restored prairies was only a fraction of the total catch of workers of *Bombus* species at a five-year restoration site.

The density and diversity of bees less than 10 mm long differed among the bee-pollinated *Penstemon* spp. (Table 1). Over 50% of all bees collected on *P. cobaea* var. *cobaea* were *Hoplitis pilosifrons* (Megachilidae). In contrast, approximately 45% of bees on *P. grandiflorus* were *Augochlorella striata* (Halictidae). Most of the small-bodied bees collected on *P. digitalis* were *Lasioglossum* spp. (Halictidae). *Osmia* spp. (Megachilidae) and *Hoplitis pilosifrons* were equally represented on *P. pallidus.* Note that most of these bee taxa were collected in smaller proportions on *Penstemon* flowers other than the modal *Penstemon* species (listed above) at each site (Table 1). These smaller bees were observed to visit more than one open flower on an inflorescence, and to visit several flowering shoots in succession. Small bees were rarely observed and collected on flowers of *P. cobaea* var. *cobaea* in populations of > 500 flowering shoots (Konza Prairie sites 1995 and 1997). These results on the foraging preferences of bumblebees versus small, solitary bees on *P. cobaea* populations were highly significant by chi square ($T = 37.33$, $P \ll 0.001$). Statistical procedures follow Conover (1980). Remembering that the square root of the chi square test statistic is approximately the absolute value of the test statistic of the normal distribution, we can estimate that there is an extremely low probability, on the order of one occurrence in a million, that these results are due to chance alone (Stanley Sawyer, pers. comm.). We also emphasize that we do not have a high enough level of sample replication in our data set to use parametric statistics, which would distinguish species effects from site effects, and acknowledge that we thus cannot make definitive comments here on this issue.

DISCUSSION

Pollen dispersal varies among prairie *Penstemon* species in the American Midwest. The putative trend toward butterfly pollination in *Penstemon tubaeflorus* is reflected by the constriction of the floral tube. Otherwise, there appeared to be few floral characters indicative of classic psychophily in this species (Barth, 1985; Proctor et al., 1996). For example, flowers were not held erect and lacked the characteristic pigmentation associated with "butterfly flowers." This suggests that this pollination system is recent and that this species may be derived from a bee-pollinated ancestor.

In the four remaining *Penstemon* spp., bee visitation was dominant, involving a broad diversity of potential pollinators representing four families of Apoideae. Furthermore, bee pollination in midwestern *Penstemon* spp. appeared to be a two-tiered system. Pollination by bees in most angiosperm systems is based on either passive or active contact (sensu Bernhardt, 1996) with the anthers. Pollination by passive contact implies that the bee first contacts dehiscent anthers and receptive stigmas while foraging for nectar, or other rewards, toward the base of the flower. Pollination by active contact suggests that the bee contacted the receptive stigma while foraging specifically for pollen. Both modes of pollination occurred in four *Penstemon* spp., but each pollination mode was performed by two different sets of bees. Large-bodied, long-tongued bees effected passive pollination, while small-bodied bees, with tongues of varying lengths, effected active pollination. Since *Penstemon* flowers were protandrous, this implies that active pollination required automimicry (sensu Dafni, 1993) to encourage cross-pollination. Small bees foraging for pollen were unable to discriminate initially between fresh, dehisced anthers and old, empty anthers, suggesting that pollen collection in *Penstemon* flowers represents a form of partial reinforcement for smaller bees.

We have found no previous citations of pollination of *Penstemon* spp. by bumblebee flower-beetles (*Euphoria sepulchralis*). These greenish scarabs are not hairy, but became dusted with *Penstemon* pollen in the process of feeding on nectar and floral organs while residing inside the base of the corolla tube for long periods of time. It is reasonable to suggest that they played a minor role in the pollination of *Penstemon* spp. on the Konza Prairie Research Natural Area. Likewise, uncommon pseudomasarid wasps probably contributed to the pollination of *P. digitalis* and *P. cobaea* var. *purpureus*. The literature suggests that pseudomasarids are important pollinators of some *Penstemon* spp. native to the west coast of North America (Straw, 1956).

Three patterns of interactions between *Penstemon* flowers and bees were documented. First, the foraging specificity of queens of *Bombus nevadensis* to *P. digitalis* and *P. pallidus* versus that of *B. pennsylvanicus* to *P. cobaea* and *P. grandiflorus* provides an interesting dichotomy. The morphometric differences between the two *Bombus* spp. with respect to glossa length and body parameters are minor, according to taxonomic authorities (Medler, 1962). In both species, the combined length of the glossa and prementum is about 12.5 mm. Based on our collections, it would appear that *B. nevadensis* preferred *Penstemon* corollas with small gullets, while *B. pennsylvanicus* preferred corollas with large gullets and much expanded sinuses. (In contrast, both *B. griseocollis* queens, which rarely visit penstemons, and *B. fraternus* queens, which did not visit penstemons at all in this study, have a combined glossa plus prementum length of about 10 mm.) However, statistical analyses of the foraging preferences of queens of *B. nevadensis* and *B. pennsylvanicus* would require additional data sets from a far greater number of sites. In fact, we acknowledge that the above-mentioned relationship between certain *Bombus* queens and *Penstemon* spp. may actually reflect a combination of overlapping phenologies and biogeographies.

Second, bumblebee queens far outnumbered neuter workers on *Penstemon* flowers. This was to be anticipated considering the well known, annual life-cycle of *Bombus* spp. in the Northern Hemisphere, since *Bombus* queens always forage for pollen in spring until they raise a significant retinue of workers (Heinrich, 1979). What was not expected was the relative abundance of workers on restoration sites ($N = 99$) versus the relative absence of workers ($N = 7$) on both original, tallgrass prairies and true glade sites. We were unable to determine whether *Bombus* workers simply avoided *Penstemon* populations in "virgin" prairies and glades or whether *Bombus* colonies matured more rapidly within, or adjacent to, restored sites. Whatever the case, this pattern, if continuous, may have direct implications for future conservationists who emphasize the restoration of original pollination systems.

Third, collections of small-bodied, solitary bees indicated selective foraging preferences that correlated negatively with the size of *Penstemon* populations. This occurred exclusively in *P. cobaea* var. *cobaea* within sites on the Konza Prairie Research Natural Area. Over four seasons, 59 solitary bees were collected on populations with less than 50 flowering stems, but only four specimens were ever collected on populations with more than 500 flowering stems. These massively flowering populations of *P. cobaea* appeared to be pollinated primarily by *Bombus* queens. Why did solitary bees avoid the greater resources offered by a much higher density of *Penstemon* flowers? Our only explanation is that *Bombus* queens outcompeted solitary bees for access to *Penstemon* corollas in larger populations, even though they did not compete for the same resource. Bernhardt (1993) mentioned older reports that female xylocopines (Anthophoridae) recognized and avoided flowers of *Passiflora* spp. that had been visited and marked with a glandular secretion by another female of the same species. Perhaps solitary bees recognized and avoided *Penstemon* flowers that had been visited and marked by *Bombus* spp. The comparative disinterest that *Bombus* queens showed to smaller populations of *P. cobaea* may have reflected both economic and energetic considerations. As bumblebees are strong fliers and trapline foragers (Heinrich, 1979; Bernhardt & Montalvo, 1979) they may have avoided smaller populations of flowering plants because such populations offered weaker visual/olfactory displays during peak flowering periods. While a traplining forager would seem most appropriate for the pollination of smaller, isolated populations, their visitation contradicts bumblebee economics (Heinrich, 1979). Small flowering populations provide inadequate rewards for both the bees and the larvae provisioned by the foraging queens (Bernhardt, 1990b).

Waser et al. (1996) argued that generalized pollination is the rule, not the exception, in most angiosperm species. Floral generalization becomes selectively advantageous when pollinator populations fluctuate, so that pollinator shifts can occur in angiosperm populations.

We do not accept that bee pollination in all midwestern *Penstemon* spp. must also reflect fluctuations in generalized trends favoring either large or small bees. We interpret bee pollination in four *Penstemon* spp. as two specialized syndromes concurrent within the *same* flowers. A coexisting, two-tiered syndrome has been selected for pollination by both large-bodied, long-tongued, nectar-foraging bees and small-bodied, pollen foragers. Note that all *Bombus* spp. and most of the solitary bees (excluding *Osmia* s. str.) collected in this study are polylectic taxa in grasslands (Bernhardt, 1990a, b). Note also that the same bee species may adopt either active or passive pollen collection on different, coblooming flowers (Bernhardt, 1996).

With two bee-pollination syndromes operating in the same *Penstemon* flower, either syndrome can encourage outcrossing, regardless of demographics, in any *Penstemon* population. It seems naive to presume that dichotomous modes of pollination in the same flower usually represent shifts in generalized patterns. For example, the older literature has long suggested that a two-tiered system has existed in some species pollinated by both birds and bees. Both birds and bees contribute to pollination in one species because two different modes of attractants and rewards overlap within the same flower (Grant & Grant, 1968; Breedlove, 1969; Macior, 1975; Grant, 1976; Schemske, 1978). If bees and homeothermic vertebrates can pollinate the same flower, we should also be able to postulate two different groups of bees pollinating the same flower for different rewards. Frankly, a generalized mode of pollination must always be implied when field studies fail to incorporate basic analyses of pollen loads and observations of foragers contacting receptive stigmas.

Literature Cited

Armbruster, W. S. 1993. Evolution of plant pollination systems: Hypotheses and tests with the neotropical vine *Dalechampia*. Evolution 47: 1480–1505.

Barth, F. G. 1985. Insects and Flowers; The Biology of A Partnership. George Allen & Unwin, Princeton, New Jersey.

Bernhardt, P. 1990a. Pollination ecology of *Oxalis violacea* (Oxalidaceae) following a controlled grass fire. Pl. Syst. Evol. 171: 147–155.

———. 1990b. Anthecology of *Schrankia nuttallii* (Mimosaceae) on the tallgrass prairie. Pl. Syst. Evol. 170: 247–255.

———. 1993. Natural Affairs; A Botanist Looks at the Attachments Between Plants and People. Villard, New York.

———. 1996. Anther adaptations in animal pollination. Pp. 192–220 *in* W. G. D'Arcy & R. C. Keating (editors), The Anther; Form, Function and Phylogeny. Cambridge Univ. Press, Cambridge, U.K.

——— & E. A. Montalvo. 1979. The pollination of *Echeandia macrocarpa* (Liliaceae). Brittonia 31: 64–71.

——— & P. Weston. 1996. The pollination ecology of *Persoonia* (Proteaceae) in eastern Australia. Telopea 6: 775–803.

Breedlove, D. E. 1969. The systematics of *Fuchsia* Section *Encliandra* (Onagraceae). Univ. California Press, Berkeley and Los Angeles.

Buchmann, S. L., C. E. Jones & L. J. Colin. 1978. Vibratile pollination of *Solanum douglasii* and *S. xanti* (Solanaceae) in southern California. Wasmann J. Biol. 35: 1–25.

Clements, F. E. & F. Long. 1923. Experimental pollination. Publ. Carnegie Inst. Wash. 336: 1–274.

Conover, W. J. 1980. Practical Nonparametric Statistics, 2nd ed. John Wiley and Sons, New York.

Crosswhite, F. S. 1965. Revision of *Penstemon* (Sect. *Penstemon*) Series *Graciles* with a Synopsis of the Genus. Unpublished Master's Thesis, University of Wisconsin, Madison.

——— & C. D. Crosswhite. 1966. Insect pollinators of *Penstemon* series *Graciles* (Scrophulariaceae) with notes on *Osmia* and other Megachilidae. Amer. Midl. Naturalist 76: 450–467.

Dafni, A. 1993. Pollination Ecology; A Practical Approach. Oxford Univ. Press, Oxford, U.K.

Evers, R. A. 1955. Hill prairies of Illinois. Bull. Illinois Nat. Hist. Surv. 26: 409–410.

Freeman, C. C. 1981. A Biosystematic Study of the Genus *Penstemon* (Scrophulariaceae) in the Great Plains. Unpublished Master's Thesis, Kansas State University, Manhattan, Kansas.

——— & L. C. Hulbert. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area. Trans. Kansas Acad. Sci. 88: 84–115.

Goldblatt, P., J. C. Manning & P. Bernhardt. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa: Floral divergence and adaptation for long-tongued fly pollination. Ann. Missouri Bot. Gard. 82: 517–534.

Grant, K. A. & V. Grant. 1968. Hummingbirds and Their Flowers. Columbia Univ. Press, New York and London.

Grant, V. 1976. Isolation between *Aquilegia formosa* and *A. pubescens*: A reply and reconsideration. Evolution 30: 625–628.

———. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. Proc. Natl. Acad. Sci. U.S.A. 91: 3–10.

Heinrich, B. 1979. Bumblebee Economics. Harvard Univ. Press, Cambridge and London.

Kampny, C. M. 1995. Pollination and floral diversity in Scrophulariaceae. Bot. Rev. (Lancaster) 61: 350–366.

Keck, D. D. 1938. Studies in *Penstemon* VI. The section *Aurator.* Bull. Torrey Bot. Club 65: 233–255.

Lawson, R. H., V. H. Tepedino & T. L. Griswold. 1989. Pollen collectors and other insect visitors to *Penstemon haydenii* S. Wats. Pp. 233–235 *in* T. B. Bragg & J. Stubbendieck (editors), Proceedings of the Eleventh North American Prairie Conference.

Macior, L. W. 1975. The pollination of *Delphinium tricorne* (Ranunculaceae). Amer. J. Bot. 10: 1009–1016.

———. 1982. Plant community and pollinator dynamics in the evolution of pollination mechanisms in *Pedicularis* (Scrophulariaceae). Pp. 29–45 *in* J. A. Armstrong, J. M. Powell & A. J. Richards (editors), Pollination and Evolution. Royal Botanic Gardens, Sydney, NSW, Australia.

Medler, J. T. 1962. Morphometric studies on bumblebees. Ann. Entomol. Soc. Amer. 55: 212–218.

Michener, C. D., R. J. McGinley & B. N. Danforth. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, D.C., and London.

Ochs, C. 1993. An Ecological Survey of the Litzsinger Road Ecology Center. Education Department, Missouri Botanical Garden, St. Louis.

Ogden, E. C., G. S. Raynor, J. V. Hayes, D. M. Lewis & J. H. Haines. 1974. Manual for Sampling Air-borne Pollen. Hafner Press, New York.

Pennell, F. W. 1935. *Penstemon. In* Scrophulariaceae of eastern temperate North America. Acad. Nat. Sci. Philadelphia, Monogr. 1: 196–273.

Proctor, M., P. Yeo & A. Lack. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon.

Robertson, C. 1892. Flowers and Insects, Asclepiadaceae to Scrophulariaceae. Trans. Acad. Sci. St. Louis. 5: 569–598.

———. 1929. Flowers and Insects. C. Robertson, Carlinville, Illinois.

Schemske, D. W. 1978. Evolution of reproductive characteristics in *Impatiens* (Balsaminiaceae): The significance of cleistogamy and chasmogamy. Ecology 59: 596–613.

Solecki, M. K., J. B. Taft, E. A. Cook & P. S. Haverland. 1986. Vegetational Composition of Three Missouri Tallgrass Prairies with Reference to Past Management. Conservation Commission of the State of Missouri, Jefferson City.

Straw, R. M. 1956. Floral isolation in *Penstemon.* Amer. Naturalist 90: 46–53.

Toney, T. E. [undated]. Public Prairies of Missouri. Missouri Department of Conservation, Jefferson City.

Waser, N. M., L. Chittka, M. V. Price, N. M. Williams & J. Ollerton. 1996. Generalization in pollination systems and why it matters. Ecology 77: 1043–1060.

Wolfe, A. D. & W. J. Elisens. 1993. Diploid hybrid speciation in *Penstemon* revisited. Amer. J. Bot. 80: 1082–1094.

———, W. J. Elisens, L. E. Watson & C. W. dePamphilis. 1997. Using restriction-site variation of PCR-amplified cpDNA genes for phylogenetic analysis of tribe Cheloneae (Scrophulariaceae). Amer. J. Bot. 84: 555–564.

Yatskievych, G. & J. Turner. 1990. Catalogue of the Flora of Missouri. Monogr. Syst. Bot. Missouri Bot. Gard. 37: 1–345.

A COMBINED CLADISTIC ANALYSIS OF ANGIOSPERMS USING *rbc*L AND NON-MOLECULAR DATA SETS[1]

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ABSTRACT

A combined analysis of 162 extant angiosperm taxa for which *rbc*L sequence-data and/or an appreciable amount of non-molecular information is available was calculated. A non-molecular tree, an *rbc*L tree, and a combined tree are presented. Only the *rbc*L and the combined data set show large numbers of groupings with bootstrap percentages greater than 50%, whereas the non-molecular trees show only eleven clades of this kind; this seems due to the number of missing cells in the non-molecular matrix. We tried to identify non-molecular characters (including biochemical) that support groups present in these analyses, especially in cases where clades turned out to be new when compared to one or more "classical" taxonomic systems. New groupings found in the non-molecular analysis that parallel the *rbc*L topologies include a grade containing Illiciales, Austrobaileyaceae, and Amborellaceae (magnoliid II); a clade containing Magnoliales, Laurales, Aristolochianae, and monocots (magnoliid I); a hamamelid group; subgroups of asterids (e.g., a similar asterid III clade containing Scytopetalaceae, Lecythidaceae, Sapotaceae, Ebenaceae, Theaceae, Primulales, Styracaceae, Marcgraviaceae, Actinidiaceae, Clethraceae, and Ericales); an expanded caryophyllid group; a Malvales s.l. clade; a partial Malpighiales grade containing Quiinaceae, Linales s. str., Passiflorales, Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Ochnaceae; and some smaller clades, similar to the corresponding groups found in *rbc*L cladograms (Illiciales–Austrobaileyaceae; Aristolochianae–monocots; Hydrangeaceae–Cornales; Lecythidaceae–Scytopetalaceae; Pittosporaceae–Araliales; Geissolomataceae–Stachyuraceae; Connaraceae–Oxalidaceae). Capparales s.l. and the nitrogen-fixing clade, two novel molecular clades, are only found in the *rbc*L and the combined trees. Cistaceae have been shown to share important characters with Malvales s.l. and are consistently found within this clade. These findings argue against their previous inclusion in Violales. The *rbc*L tree contains 38 terminal taxa that are included for the first time in a published phylogeny. Considerable progress has been made in assembling a morphological/chemical data set that parallels the broad coverage of angiosperms seen in DNA studies.

New opportunities for the study of seed-plant phylogeny have opened due to the continued development of computer hardware and software. In addition, gene sequencing has become reasonably fast, and large nucleotide data matrices have been produced (e.g., Chase et al., 1993; Savolainen et al., 1996; Soltis et al., 1997b). These studies have stimulated even more molecular work on macrosystematics, including the addition of more "critical" taxa to the data matrices, comparison with results from other gene sequences, and the combination of nucleotide with non-molecular data matrices, as has been undertaken in this study. Other examples of broadly sampled combined nucleotide and non-molecular studies are those of Doyle et al. (1994) and Chase et al. (1995).

The non-molecular investigations of this study originated from the question of the position of Cistaceae within eudicots. Cistaceae have been included in Violales (Takhtajan, 1966; Cronquist, 1981) and Malvales (Dahlgren, 1980), yet the most natural (i.e., phylogenetic) position has remained a matter of debate (Thorne, 1983, 1992). Thus, it was a major objective of our non-molecular study to identify the accurate position of Cistaceae and their allies (Bixaceae and Cochlospermaceae) within the eudicots. Most families that have commonly been allied with Malvales or Violales are included in

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ANN. MISSOURI BOT. GARD. 85: 137–212. 1998.

the present study. Many more taxa were added to evaluate the robustness and position of the two orders within eudicots and to compare the trees obtained with other studies (Hufford, 1992; Olmstead et al., 1992; Albert et al., 1992; Chase et al., 1993).

Monophyly of the taxa used has also been evaluated by comparing molecular results with macrosystematic studies (e.g., Urticales: Berg, 1977). This was done to determine which terminal taxa should be used in the non-molecular sampling. In the non-molecular matrix we make use of those clades found in the *rbc*L analysis that are compatible with widely accepted groups. Thus in some cases we have sampled individual families, whereas in others we have used orders (e.g., Gentianales, Annonales, etc.), superorders (e.g., Faganae, Aristolochianae), or larger groups (e.g., monocotyledons) that no recent research (molecular or non-molecular) has indicated are other than monophyletic. Flacourtiaceae s.l. were split into two groups, one with cyanogenic glycosides (e.g., Kiggelariaceae) and one without.

A major caveat for the non-molecular matrix is that we often used single character-states for polymorphic taxa. These assignments are based on assumptions of character polarity, which could result in mistaken interpretations of character evolution. We accept that in some specific cases mistakes may have been made, but we felt that some simplifications were required to deal with such large taxonomic units. However, the character-state assignments were carried out using a consistent approach (see Appendix 5). Because the independent trees are often highly similar, we gain confidence that the historical signal present in the non-molecular data has not been grossly distorted by this method of character-state assignment. We hope that further progress in non-molecular investigations will obviate the need for such a procedure in future studies. We are certain that this approach can be greatly improved upon. Analysis of large, non-molecular matrices is not without precedent in plant systematics (e.g., Donoghue & Doyle, 1989). Working with such large non-molecular matrices could have undesirable effects (i.e., not finding the shortest trees or all islands of trees, cf. Maddison, 1991). These large matrices must nonetheless be much less confounding than matrices using exemplar taxa for groups that are not monophyletic.

We were interested in finding a large set of non-molecular characters that would contain phylogenetic information. We tried to characterize larger taxonomic groupings, especially new ones, by non-molecular synapomorphies, as produced by MacClade 3.04 (cf. Maddison & Maddison, 1992). We wanted to see in which way the non-molecular data set changed or confirmed the topology of the *rbc*L tree, and vice versa, when both data sets are combined (we agree that the inclusion of *rbc*L results in delimiting the terminal taxa and in looking for taxa with more ancestral characters within the larger of these terminal taxa makes it impossible to claim that both data sets are totally independent). We also examined by simple comparison whether the different samplings of taxa in the *rbc*L analysis of Chase et al. (1993) and that of the present study affect the topology of the *rbc*L tree. Finally, we were also interested in the stability of the topologies obtained after applying the parsimony jackknife program (Farris et al., 1997) and bootstrapping (Felsenstein, 1985).

MATERIAL AND METHODS

GENERAL METHODS

The matrices were analyzed using PAUP 3.1.1 (Swofford, 1993). The shortest trees were collected and swapped on to completion, keeping in this case all additional trees found at this shortest branch length. In the Results and Discussion sections, we will mostly use the same terms for the larger angiosperm clades used by Chase et al. (1993: part B of figs. 1–15) to facilitate comparisons.

Ceratophyllum was specified as the outgroup in agreement with the results produced with *rbc*L (Chase et al., 1993). We simply used *Ceratophyllum* as the outgroup to avoid the issue of where in the angiosperms the root should be placed. This topic will be discussed in other papers; we view it as too complex an issue to be dealt with adequately here. The use of non-angiosperm outgroups (Gnetales) for the non-molecular matrix is difficult. Important morphological structures cannot be adequately addressed in terms of their homology at present. Because we used *Ceratophyllum* as the default outgroup, we will not concern ourselves with the evaluation of its position. We were interested only in examining general patterns within the angiosperms for both *rbc*L and non-molecular data. All matrices are available on diskette or by e-mail (m.chase@rbgkew.org.uk) from the second author (please provide a single high-density diskette).

In each case, the products of the initial searches were sets of trees with equally weighted characters.

We intended to use the jackknife procedure of Farris et al. (1997) but found that the number of missing cells in these matrices makes this method unsuitable because it found no support for any groupings in the combined matrices [J. Farris, pers. comm., reports that missing data significantly lower jackknife values; we have also investigated this empirically in another study (Fay et al., 1997)]. We therefore used the bootstrap consistently for an easier comparison. For trees illustrated in this paper, branch lengths are shown above the branches (ACCTRAN optimization, Swofford, 1993), and all branches not present in the strict consensus trees are indicated by an arrow. Bootstrap support for supported groups is indicated below the branches.

NON-MOLECULAR DATA MATRIX (APPENDIX 1)

A selection of 161 angiosperm taxa was scored for 252 characters (Appendix 3); 151 taxa were ultimately included in the non-molecular search (115 families, 32 orders, and 4 supraordinal taxa, mainly in the sense of Takhtajan, 1987; Appendix 2). Data were taken from selected synoptic literature, from primary literature (especially in dilleniids sensu Cronquist, 1981) and from original observations by the first author [leaf venation and dentation (studied in the Herbaria of Zürich, Geneva, and Vienna and in a number of botanical gardens) and observations from anatomical sections or SEM micrographs in Cistaceae, Cochlospermaceae, Bixaceae, Dipterocarpaceae, Sarcolaenaceae, Sphaerosepalaceae, and Berberidopsidaceae]. We had also at hand the extensive anatomical slide collection of the third author. Uncertain cases with regard to the presence or absence of oxalate crystals and to ovule anatomy were resolved by careful observation of selected slides (e.g., oxalate crystals seem to be absent from *Amborella*; see also Metcalfe, 1987).

We used the characters that we considered to contain the most significant phylogenetic information. Floral developmental information could only be scored with two characters (characters 223 and 224 in the matrix) due to the complexity of comparing developmental data. Characters were grouped into the following classes: 1. Serology (16 characters); 2. Chemical compounds (88 characters); 3. Characters at cellular level (22 characters); 4. Embryology (18 characters); 5. Seed anatomy (21 characters); 6. Stem morphology and anatomy (24 characters); 7. Leaf characters (17 characters); 8. Floral and fruiting characters (46 characters). The procedure of assigning character-states to taxa is documented in more detail in Appendix 5, but in general the hypothesized plesiomorphic state was used if more than one state occurred within a terminal taxon. In a few cases, paleobotanical information was also included (e.g., Magnoliaceae, Platanaceae, Buxaceae; Crane, 1989; Crane et al., 1993; Drinnan et al., 1991; Dilcher & Crane, 1984).

Most of the characters are mutually independent. Other characters were chosen as hierarchical sets (e.g., characters 8–10, 80–85, 97–100, 200–202, or 250–251), character pairs (223–224), or character triplets (108–110, 142–144). Compatibility with the molecular data set was reached by only allowing four character-states ("A," "C," "G," "T"). "A" can be equated to "0," "C" to "1," "G" to "2," and "T" to "3". Characters with more than four states were broken up into character sets (233–235), but few characters required such modification.

Of the 252 characters, 207 are binary (in 186 of these simple presence/absence coding is involved) and 45 are multistate characters. The common strategy of character-state assignment described in Appendix 5 was to find a basal pattern for each taxon. With this procedure, we tried to reduce character radiation due to the evolutionary processes within the terminal taxon. In characters with states that have low probability to be evolved, due to their complexity, presence of a state was favored in coding over absence of a state (e.g., presence of phloem stratification; 169; presence of bixoid exotegmen in the chalazal region; 159; presence of salicoid leaf dentation; 201). This implied that the character was coded as being present if at least one representative of the terminal taxon is known to exhibit the character-state. By analogy, for dithetic characters, in which both states are more or less equally likely to have evolved, the character was coded as polymorphic if both character-states occur in a terminal taxon (e.g., successive or simultaneous microsporogenesis; 128). More specific rules, which were rarely applied to cover more complex hypotheses of character evolution, are given in Appendix 5. These exceptions were applied restrictively, since the number of assumptions prior to analysis of data should be low. Appendix 5 also lists characters for which the putative ancestral character-state was searched by scoring the character-state in putatively basal members of the terminal taxon (e.g., Ulmaceae in Urticales, *Ceratonia* in Fabaceae, *Erythrospermum* in Kiggelariaceae).

Biochemical characters were scored as absent, present, or "?" (unknown or uncertain) in certain terminal taxa by considering the extent of knowledge of the biochemical substance classes in question (in the specific taxon). In wood anatomy, the broadly acknowledged evolutionary trends (see e.g., Carlquist, 1988a: chapter 11) from ancestral to derived character-states were used strictly to find character-states of terminal taxa [i.e., uni-or biseriate circular or scalariform vessel side-wall pitting was preferred over opposite, and opposite over alternate (184); vessellessness was preferred over presence of vessels (integrated in 185); scalariform perforation plates were preferred over mixed scalariform and simple plates, and the latter over simple plates (185)].

All characters were scored as unordered. Ambiguous characters for which no priority rule was applied (see Appendix 5) were coded as polymorphic. Assignment of character-states was complicated by the fact that often only the presence (and not the absence) of a character-state is noted in the literature. If one or more thorough published studies of a character class in a certain terminal are available, and a given character-state was not described, it was coded as being absent. This rule was applied to, for example, presence or absence of exotegmic palisades or exotegmic longitudinal fibers in seeds (157). Some extrinsic characters such as hostplant and paleobotanical data were not included in the matrix, but their optimization was evaluated from the trees produced.

Information on taxon circumscription, characters and character-states (including four data errors that were detected after all analyses were completed), character definitions, procedures of character-state assignment, and sources are given in Appendices 2–6. The four errors were examined for effects by initiating searches on the trees found; we found no additional or shorter trees, so we assumed that complete new searches were not warranted.

In Search I, 100 random-addition replicates were run using TBR branch swapping (Swofford, 1993), but keeping only 10 trees per step (TBR = tree bisection-reconnection). The first tree of the shortest tree set obtained was swapped to completion (i.e., MULPARS turned on; Swofford, 1993). The steepest descent option (Swofford, 1993) was not used. This island that was found (sensu Maddison, 1991) contained 136 trees of length 3546, consistency index (CI) = 0.09, and retention index (RI) = 0.41.

In Search II, 1000 random-addition replicates were run using SPR algorithm and keeping only 1 tree per step (SPR = subtree pruning-regrafting; Swofford, 1993). The shortest tree was swapped to completion with MULPARS turned on. The steepest descent option was not used. The resulting island obtained with this method contained 8 trees of length 3545, CI = 0.09, and RI = 0.41.

These two searches were very slow (much slower than the *rbc*L and combined searches), and we suspected that shorter trees could be produced by another strategy, described below.

In Search III, the taxa were divided into three groups. Group I contained taxa 1 to 37 (presumed magnoliids, lower eudicots, and caryophyllids). Group II contained taxa 38 to 106 and taxa 149, 150, 161 (presumed rosids). Group III contained taxa 107 to 148 (presumed asterids). First, group II was processed. One hundred random-addition replicates were done using the TBR algorithm and keeping maximally 10 trees per step. The topology of the strict consensus of the shortest tree set (containing two most-parsimonious trees) was defined as a constraint framework for the following step. The taxa of group I were added. One hundred random-addition replicates were done with TBR swapping and keeping maximally 10 trees per step. After this, the constraints were omitted and all taxa of the first tree of the shortest tree set obtained were allowed to swap freely to completion using the TBR algorithm. The resulting tree set was defined as a constraint for the following step, with the taxa of group III added. One hundred random-addition replicates were done with TBR swapping but keeping maximally 10 trees per step. The constraints were omitted again, and all taxa of the first tree of the shortest tree set obtained were allowed to swap freely to completion using the TBR algorithm. The trees obtained were 3544 steps long. This tree set was reweighted based on the rescaled consistency index with maximal weight of 10. Twenty steps of length reduction were done with this new weight set using the TBR algorithm. After this, all characters were again weighted equally. The trees obtained in the last procedure were swapped to completion. More than 2200 trees of length 3541 were obtained. The search was stopped due to memory constraints. The first 50 trees of the obtained tree set were reweighted based on the rescaled consistency index with maximal weight of 100. Twenty steps of length reduction were done with this new weight set using the TBR algorithm. Afterward all characters were again weighted equally. The trees obtained in the

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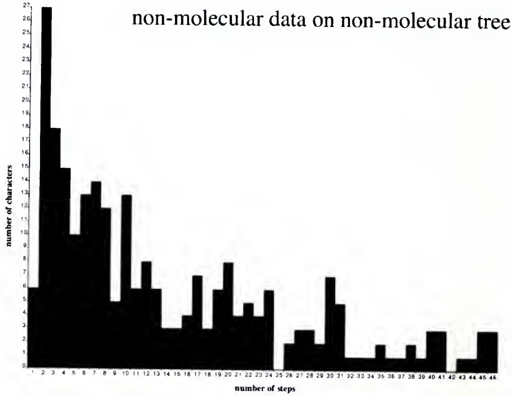
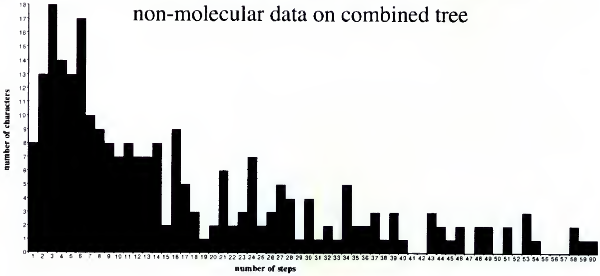
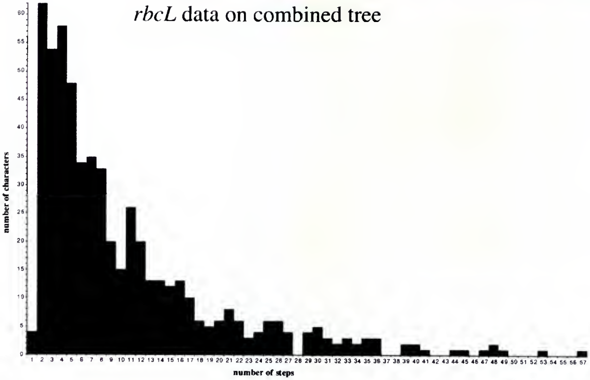
Figure 1. As evidence in support of the use of successive weighting, we used MacClade 3.06 (Maddison & Maddison, 1992) to plot how many steps were contributed by informative characters in each data matrix. In part B, for example, eight characters in the non-molecular matrix were changing one time when these data were optimized on the combined tree, whereas one character was changing 60 times. —A (top). The non-molecular data optimized on one of the shortest trees found with the non-molecular data only. —B (middle). The non-molecular data optimized on a tree from the combined analysis. —C (bottom). Plot of the *rbc*L data mapped onto the combined tree.



non-molecular data on non-molecular tree



non-molecular data on combined tree



rbcL data on combined tree

last procedure were swapped to completion. The steepest descent option was also not used in Search III. An ultimate tree set of 17 trees with a length of 3539, CI = 0.09, and RI = 0.41 was obtained; the first tree of this set is illustrated in Figure 2. Arrows indicate groups not found in all 17 trees. This is obviously only one island of many that exist for this data set, but it is the shortest tree length that we were able to obtain, and in spite of the unorthodoxy of the procedure, it produced far shorter trees than any "standard" method (i.e., with replicates of random taxon-addition). The three taxon-groups in Search III were formed by comparison with *rbc*L topologies. This introduces some bias in the non-molecular trees, but the application of these three groups was responsible for finding the shortest trees.

MATRICES FOR *rbc*L AND COMBINED DATA

The techniques involved in collecting our *rbc*L data have been previously published (Chase et al., 1993; Chase et al., 1995). Because each *rbc*L sequence represents a specific single plant (Appendix 7), which we assume can represent its family or other higher taxon, we used a single *rbc*L sequence to represent each of the terminals scored in the non-molecular matrix. In general, we selected as the *rbc*L representative a species that was not especially sequence-divergent within its group. Many of the sequences included in the present study are previously unpublished. We analyzed this new *rbc*L matrix to be certain that we could obtain results similar to those of other published *rbc*L topologies. Taxa for which we still have no molecular data are marked with "§" in Figure 4 A, B.

Problems in amalgamating nucleotide and non-molecular data sets are discussed in Chase et al. (1995). The main problem is that non-molecular characters were scored for higher taxa whereas each *rbc*L sequence represents a single plant. In our experience, this technique does not appear to produce spurious results (several such studies have been published and more are in progress in the laboratory of M. Chase; Chase et al., 1995; Gadek et al., 1996; Morton et al., 1997). The trees obtained with more taxa, thus spanning the divergence levels present within a family, do not produce wildly different patterns, nor does substitution of one species in a family for another greatly affect the position of the family (provided the family is monophyletic). This fact is obvious when one compares the patterns found for multiple members of a family in the 1993 *rbc*L tree (Chase et al.) with the position of that family in the present analysis, in which only one taxon was included. Furthermore, there should be no expected correspondence between a morphologically plesiomorphic taxon and plesiomorphic molecular characters, so taxon selection based on presumed "basalness" is not an important consideration. However, if faced with a choice between species that are highly divergent and others that are only slightly divergent, then use of one of the latter is helpful in avoiding spurious placements of the family.

We excluded the first 27 base positions at the 5′ end of *rbc*L, leaving a maximum of 1401 basepairs (bp) of data for each species (some were less than this, although none substantially less than 1300 bp). Of these 1401 sites, 785 (56%) were variable and only 562 (40%) were potentially informative.

We used 1000 replicates of random-taxon entries and the TBR-swapping algorithm; only five trees were retained per step, which reduces the amount of time spent swapping on trees from suboptimal tree islands (Maddison, 1991). Although all trees shown were produced by successive weighting, we have shown them with their Fitch branch lengths (Fitch, 1971; i.e., characters with equal weights, character-states unordered) in Figures 3 and 4. In all but the strictly non-molecular matrix, we employed successive weighting to down weight or eliminate the effects of characters that changed excessively (Farris, 1969; Carpenter, 1988, suggested that successive weighting should be used merely to select a subset of the trees found with equal weights). To illustrate the reasons why we favor the use of successive weighting, we plotted the number of steps vs. the number of characters in MacClade 3.06 (Maddison & Maddison, 1992) for both the non-molecular and the *rbc*L matrices (both on the combined tree and on the shortest non-molecular trees). Once excessively homoplasious characters were down weighted, it was logical not to use those characters in estimating internal support. Hence relative weights were employed in the bootstrapping procedure (5000 replicates for each matrix) except for the non-molecular matrix, which was evaluated with equal weights. The rescaled consistency index (RC; Swofford, 1993) was used to calculate the successive weights (with a base weight of 1000) based on the best fit in any tree for each character, and in bootstrapping characters were sampled with equal probability rather than having the frequencies depend on the weights. We used a "fast" bootstrapping procedure in which a minimal amount of NNI swapping was used (the fastest and most superficial of the PAUP swapping algorithms; we permitted only 20 trees to be retained at each step). This procedure obviates the need to swap extensively, significantly shortening the time to carry out bootstrapping. Well supported groups are present in the starting trees (due to the quick distance-based calculations that PAUP and other parsimony programs use to generate a tree upon which swapping is then carried out) and do not need any swapping to be identified. If extensive swapping is required to "find" groups, then they are obviously weakly supported or unsupported; groups with intermediate levels of support necessitate at least some swapping to be effectively evaluated, hence the limited use of NNI swapping. We expect that the use of successive weighting will in many cases, as here, find trees for which the Fitch lengths (equal weighting) are longer than for the shortest trees found with Fitch parsimony. This is due to the fact that when highly homoplasious characters are down weighted, more consistent characters (those with higher relative weights) will be optimized more parsimoniously, thus forcing more changes into already highly homoplasious characters because such actions actually reduce the weighted tree length. Some characters in these matrices do change excessively often (see Results below), and thus it seems logical to us that once we have eliminated the effects of highly variable characters in the tree search procedure, these weights should be employed as well to evaluate internal support. Characters that change as often as 40–60 times should be eliminated from consideration; it seems obvious to us that these characters are not useful at this taxonomic level. In the interests of retaining a reasonable lack of a priori sifting of characters, we kept all characters until the initial patterns obtained indicated a lack of appropriateness of some data (such winnowing is of course not possible with DNA data unless one resorts to whole-category weights, and we do not find any evidence that such weighting schemes are appropriate; Chase et al., 1995, found that third codon positions in *rbc*L were better phylogenetic data than first or second positions).

RESULTS

AMOUNTS OF HOMOPLASY

The numbers of times each character of the non-molecular or of the molecular matrix changed on different trees are illustrated in Figure 1. As estimated on the combined tree found with successive weighting, some characters in the non-molecular matrix were changing up to 60 times (Fig. 1B); in the *rbc*L matrix, fewer sites were changing as frequently, although one site did change 57 times (Fig. 1C). For the non-molecular data, 26.0% of the characters changed five times or less (Fig. 1B; versus 30.3% on the shortest non-molecular tree, Fig. 1A), and 26.4% of the *rbc*L characters fell into this same category. Examples of non-molecular characters that changed frequently are distributed among different character types; pollen: polar pollen diameter (131) changed 45 times, and sexine texture (135) changed 45 times; seed anatomy: ovular or seed vascular bundles (145) changed 45 times, and embryo size (163) changed 45 times; wood anatomy: wood parenchyma (174) changed 46 times; fruits: seed to carpel number (249) changed 45 times. None of the serological or chemical characters changed more than 28 times. Both molecular and non-molecular data had nearly the same percentage of reasonably non-homoplasious characters, but many of the non-molecular characters possessed only two alternate states; therefore when these characters change two or more times homoplasy is involved, whereas base positions in DNA sequences can change up to three times without producing any homoplasy (e.g., from A to C, A to G, and A to T). Thus this comparison of percentages of numbers of steps is not entirely accurate, but the complexity involved in comparing multistate with binary patterns is too high to be discussed here. It should be noted that with successive weighting of nucleotides based on the RC those changing three times uniquely (e.g., from A to C, A to G, and A to T) retain the same weight as those changing only once, whereas binary characters that change three times will be drastically down weight-

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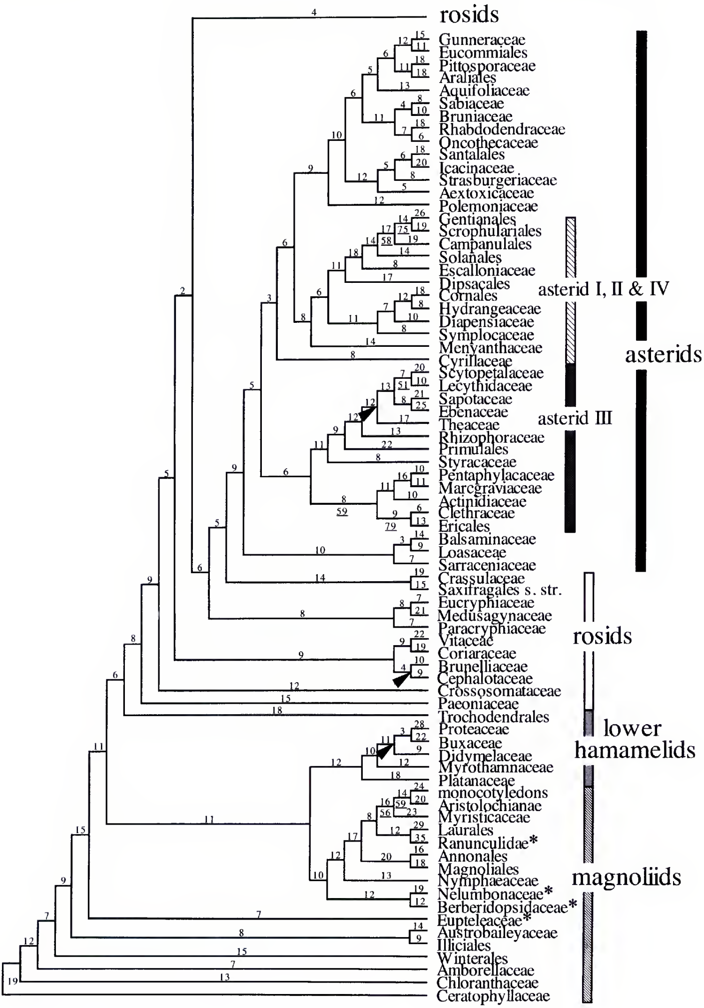
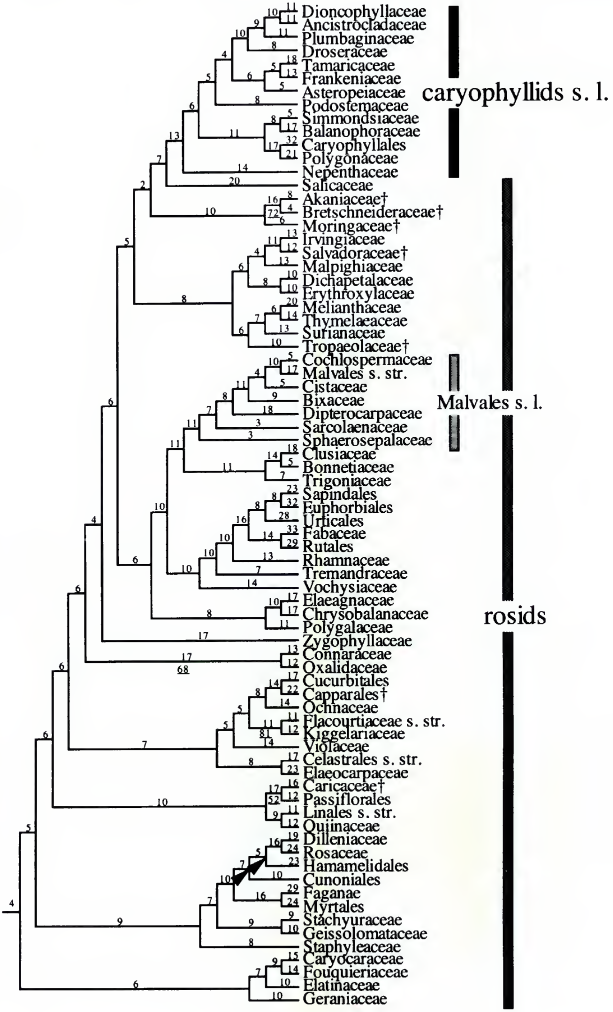
Figure 2. One of seventeen equally most-parsimonious trees derived from the non-molecular matrix in Search III found with equally weighted characters. These trees have 3539 steps with CI = 0.09 and RI = 0.41. Branches not found in all seventeen trees are marked with an arrow. Numbers above the branches are the numbers of estimated substitutions (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids and hamamelids form a grade, out of which most of the eudicots are derived. Within eudicots, rosids form a grade in which the asterids and caryophyllids are embedded. —B (right). Mostly rosid, derived clade. *Triaperturate taxa embedded within uniaperaturate grade. †Glucosinolate-producing taxa.


rosids
Gunneraceae
Eucommiales
Pittosporaceae
Araliales
Aquifoliaceae
Sabiaceae
Bruniaceae
Rhabdodendraceae
Oncothecaceae
Santalales
Icacinaceae
Strasburgeriaceae
Aextoxicaceae
Polemoniaceae
Gentianales
Scrophulariales
Campanulales
Solanales
Escalloniaceae
Dipsacales
Cornales
Hydrangeaceae
Diapensiaceae
Symplocaceae
Menyanthaceae
Cyrillaceae
Scytopetalaceae
Lecythidaceae
Sapotaceae
Ebenaceae
Theaceae
Rhizophoraceae
Primulales
Styracaceae
Pentaphylacaceae
Marcgraviaceae
Actinidiaceae
Clethraceae
Ericales
Balsaminaceae
Loasaceae
Sarraceniaceae
Crassulaceae
Saxifragales s. str.
Eucryphiaceae
Medusagynaceae
Paracryphiaceae
Vitaceae
Coriaraceae
Brunelliaceae
Cephalotaceae
Crossosomataceae
Paeoniaceae
Trochodendrales
Proteaceae
Buxaceae
Didymelaceae
Myrothamnaceae
Platanaceae
monocotyledons
Aristolochianae
Myristicaceae
Laurales
Ranunculidae*
Annonales
Magnoliales
Nymphaeaceae
Nelumbonaceae*
Berberidopsidaceae*
Eupteleaceae*
Austrobaileyaceae
Illiciales
Winterales
Amborellaceae
Chloranthaceae
Ceratophyllaceae
asterid I, II & IV
asterids
asterid III
rosids
lower hamamelids
magnoliids


Dioncophyllaceae
Ancistrocladaceae
Plumbaginaceae
Droseraceae
Tamaricaceae
Frankeniaceae
Asteropeiaceae
Podostemaceae
Simmondsiaceae
Balanophoraceae
Caryophyllales
Polygonaceae
Nepenthaceae
Salicaceae
Akaniaceae†
Bretschneideraceae†
Moringaceae†
Irvingiaceae
Salvadoraceae†
Malpighiaceae
Dichapetalaceae
Erythroxylaceae
Melianthaceae
Thymelaeaceae
Surianaceae
Tropaeolaceae†
Cochlospermaceae
Malvales s. str.
Cistaceae
Bixaceae
Dipterocarpaceae
Sarcolaenaceae
Sphaerosepalaceae
Clusiaceae
Bonnetiaceae
Trigoniaceae
Sapindales
Euphorbiales
Urticales
Fabaceae
Rutales
Rhamnaceae
Tremandraceae
Vochysiaceae
Elaeagnaceae
Chrysobalanaceae
Polygalaceae
Zygophyllaceae
Connaraceae
Oxalidaceae
Cucurbitales
Capparales†
Ochnaceae
Flacourtiaceae s. str.
Kiggelariaceae
Violaceae
Celastrales s. str.
Elaeocarpaceae
Caricaceae†
Passiflorales
Linales s. str.
Quiinaceae
Dilleniaceae
Rosaceae
Hamamelidales
Cunoniales
Faganae
Myrtales
Stachyuraceae
Geissolomataceae
Staphyleaceae
Caryocaraceae
Fouquieriaceae
Elatinaceae
Geraniaceae
caryophyllids s. l.
Malvales s. l.
rosids

ed. The main point here is that successive weighting is based on the rescaled consistency index. This permits the dissection of patterns of change more accurately than merely eliminating base positions that change excessively. Weighting with the RC is also much more appropriate for DNA sequences than simple weighting with CI. Furthermore, merely eliminating all characters that change more than a certain arbitrarily set number of times (e.g., more than ten times) will eliminate some characters with multiple states (e.g., nucleotides) that retain a great deal of signal.

NON-MOLECULAR DATA MATRIX AND TREES

In the construction of the non-molecular matrix, some original observations, mainly in Malvales and Violales, were made. The observations on the placement of Cistaceae applying cladistic methods are convincingly supported by specialized synapomorphies. A seed with a specialized structure in the chalazal region (an exotegmic palisade layer curved inward at the chalaza, and with a hypostase plug fitting into this dome-shaped curvature), was found in the seeds of several taxa (159). We termed this chalaza structure a bixoid chalaza (Nandi, 1998a). The occurrence of this chalaza type was known for Bixaceae, Cochlospermaceae, and Cistaceae. We found it also in Pakaraimaeoideae and Monotoideae (Dipterocarpaceae) and in Sarcolaenaceae (the character-state for Sarcolaenaceae was not included in the data matrix because it was found after the processing of the matrix). In Flacourtiaceae, salicoid leaf dentation (201, definition see Appendix 4) was found in twelve more genera not previously known to exhibit this condition: *Dissomeria, Byrsanthus, Calantica, Carriera, Flacourtia* (only some species), *Homalium, Ludia* (not well developed), *Oncoba, Poliothyrsis, Scolopia, Trimeria,* and *Xylosma.*

One of the 17 most-parsimonious trees (the first one found during the search) from Search III of the non-molecular analysis is shown in Figure 2. It has a length of 3539 steps, CI = 0.09, and RI = 0.41. Branches not found in all 17 trees are indicated by solid arrows. Judging from the bootstrap results, internal support for this topology is weak; only eleven groupings received bootstrap support of 50% or greater: Myristicaceae/Aristolochianae/monocotyledons (56%), Aristolochianae/monocotyledons (59%), Clethraceae/Ericales/Actinidiaceae/Pentaphylacaceae/Marcgraviaceae (59%), Clethraceae/Ericales (79%), Scytopetalaceae/Lecythidaceae (51%), Campanulales/Gentianales/Scrophulariales (58%), Gentianales/Scrophulariales (75%), Caricaceae/Passiflorales (52%), Connaraceae/Oxalidaceae (68%), Flacourtiaceae s. str./Kiggelariaceae (81%), and Akaniaceae/Bretschneideraceae (72%).

Dilleniids sensu Takhtajan (1966) and Cronquist (1981) were not recovered in this analysis, and we thus treat the eudicots as being composed of ranunculids, hamamelids, caryophyllids, rosids, and asterids; we use the narrower categories (i.e., asterid I, rosid II, etc.) as necessary.

New groupings that are similar to those obtained from *rbc*L studies are a grade containing Illiciales, Austrobaileyaceae, and Amborellaceae (magnoliid II), a clade containing Magnoliales, Laurales, Annonales, Aristolochianae, and monocots (magnoliids I), a lower hamamelid group, a number of subgroups of asterids (e.g., a similar asterid III clade containing Scytopetalaceae, Lecythidaceae, Sapotaceae, Ebenaceae, Theaceae, Primulales, Styracaceae, Marcgraviaceae, Actinidiaceae, Clethraceae, and Ericales), an expanded caryophyllid group, a Malvales s.l. group, a partial Malpighiales grade containing Quiinaceae, Linales s. str., Passiflorales, Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Ochnaceae, as well as some smaller clades (Hydrangeaceae–Cornales, Lecythidaceae–Scytopetalaceae; Pittosporaceae–Araliales; Geissolomataceae–Stachyuraceae; Connaraceae–Oxalidaceae). Chloranthaceae appear consistently as an isolated family.

The uniaperturate magnoliids plus the monocots form a grade and not a clade, although a large portion of them do form a monophyletic group. The early-branching taxa include Chloranthaceae, Amborellaceae, Winterales, and Illiciales/Austrobaileyaceae; if the root belongs elsewhere, then Ceratophyllaceae would be a member of a group with these taxa. Certain triaperturate groups (i.e., eudicots) also fall into this grade; these include most of the "lower" hamamelids, plus Ranunculidae, Nelumbonaceae, Berberidopsidaceae, and Eupteleaceae (Fig. 2A). The rosids also form a grade that gives rise on the one hand to the asterids and on the other hand to the expanded caryophyllids (Caryophyllidae s.l.). The composition of Caryophyllidae s.l. is remarkable in the number of groups never associated previously as a whole in any traditional classification with Caryophyllales (Fig. 2B). These include Dioncophyllaceae, Ancistrocladaceae, Droseraceae, Nepenthaceae, Tamaricaceae, Frankeniaceae, Asteropeiaceae, Podostemaceae, Simmondsiaceae, and Balanophoraceae.

An expanded Malvales complex (Malvales s.l.) is present among the rosids (Fig. 2B), but many other groupings within the rosids found in *rbc*L trees are not evident in the non-molecular trees. In particular, the smaller groupings of rosids (rosids I, II, III) are not evident, nor are the clades composed of glucosinolate-producing (Rodman et al., 1993) or nitrogen-fixing families (Soltis et al., 1995b).

The composition of the expanded asterid assemblage contains many of the same groupings seen in the *rbc*L trees, in particular the asterid III grouping composed of Ericales, Ebenales, Primulales, and some Theales. In addition, several other taxa are also present here that would not be expected, either on the basis of molecular studies or previous taxonomies. These include Gunneraceae, Sabiaceae, Santalales, Oncothecaceae, Aextoxicaceae, Bruniaceae, and Rhabdodendraceae.

*rbc*L TREES

The Fitch search of the *rbc*L matrix produced more than 5000 trees of 6057 steps, CI = 0.22, and RI = 0.43 (the search was discontinued at 5000 trees because the memory was becoming too low; all 5000 were swapped on to completion). Several characters changed more than 40 times (Fig. 1C). After down weighting by the use of successive weighting only nine trees were found. These nine had 6091 Fitch steps, CI = 0.22, and RI = 0.42 (weighted length of 531,123 steps, CI = 0.62, RI = 0.65). Branches not found in all nine weighted trees are marked with arrows (Fig. 3A). The first tree found at this length is illustrated in Figure 3 (ACCTRAN optimization). These trees are in general agreement with the results of Chase et al. (1993). The magnoliids form an unsupported monophyletic clade (bootstrap of less than 50%) that is sister to all eudicots, which are strongly supported (97%). Within the magnoliids, Laurales are sister to the monocotyledons; this is different from either of the two searches presented in Chase et al. (1993), but the present study uses different taxa, and in all cases this grouping is unsupported in the present *rbc*L tree (bootstrap of less than 50%). The relationship between Annonales, Magnoliales, and Myristicaceae has some bootstrap support (63%). Weak support (56%) is also shown for the association of the strongly supported pairs Nymphaeaceae/Amborellaceae (92%) and Illiciales/Austrobaileyaceae (98%).

Ranunculidae/Eupteleaceae (supported at 86%) are sister to the rest of the eudicots. The lower hamamelids form a grade between Ranunculidae/Eupteleaceae and asterids/caryophyllids/rosids. Among hamamelids, Buxaceae are strongly supported (82%) as sister to Didymelaceae; Sabiaceae and Proteaceae are weakly supported (53%) as a clade. The clade of Gunneraceae/Myrothamnaceae is also supported to a similar degree (63%). Berberidopsidaceae/Aextoxicaceae form a pair without internal support, which is the sister group to the rest of the asterids.

The only newly added family that falls into the asterid I and II clades is Icacinaceae. Within the asterids, Gentianales/Solanales/Scrophulariales are weakly supported (67%), as is a relationship of Dipsacales (59%) to Pittosporaceae/Araliales, a pair which has high support (95%). In general, this analysis of *rbc*L does not recover exactly the same relationships within the asterid I and II groups as in Chase et al. (1993), but the sampling is much more sparse here. The asterid IV group of Cornales/Hydrangeaceae is also recovered, but is not supported by the bootstrap.

The asterid III grouping is weakly supported (52%), and there are additional families comprising this group that were not covered in Chase et al. (1993). These include Pellicieraceae, Tetrameristaceae, and Marcgraviaceae, which are strongly supported (100%) in a clade including Balsaminaceae; the first two are also strongly supported (87%) as sister families. Lecythidaceae and Scytopetalaceae are also strongly supported (99%) as sister families, but other recent research (Morton et al., 1997) demonstrated that the latter is embedded in the former. Diapensiaceae are weakly supported (65%) as the sister of Sarraceniaceae, and the pairs Ericales/Actinidiaceae and Clethraceae/Cyrillaceae are also weakly supported (58% and 64%, respectively).

The expanded caryophyllid clade first identified in Albert et al. (1992) and further investigated in Williams et al. (1994) received weak internal support in this analysis (69%). Additional newly identified members of this clade include Tamaricaceae/

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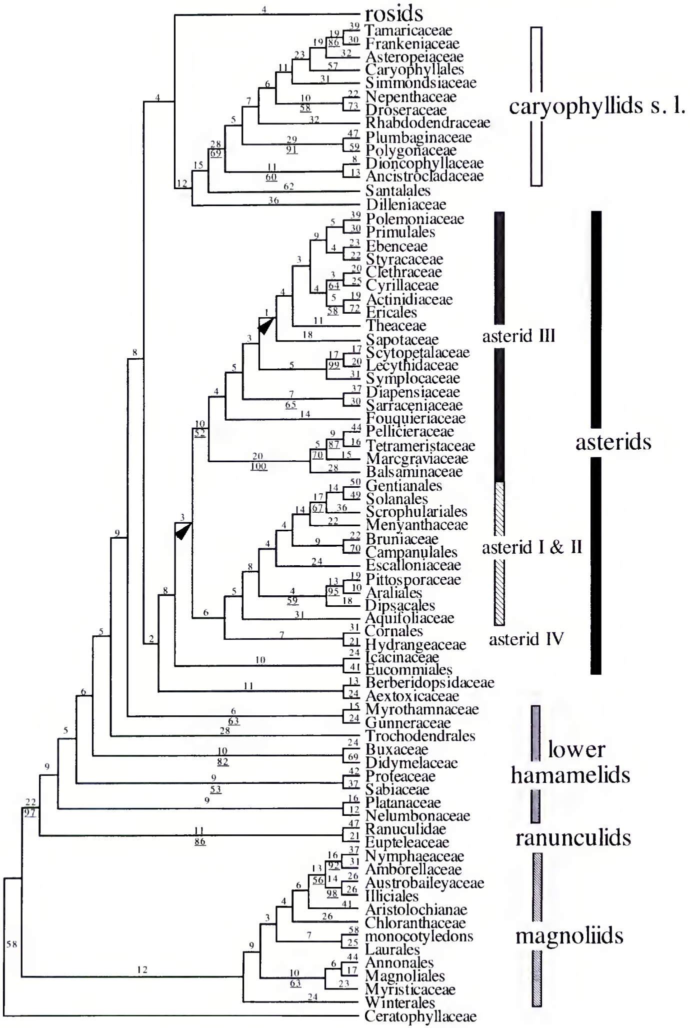
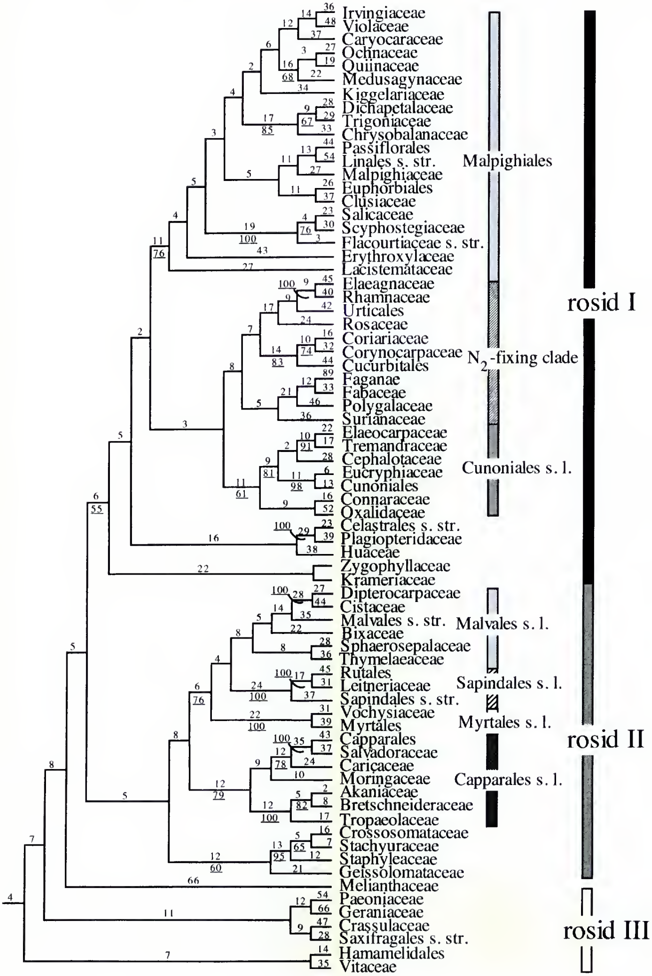
Figure 3. One of nine equally most-parsimonious *rbc*L trees found with successive weighting. Branches not found in all nine trees marked with an arrow. These trees have 6091 steps (Fitch length; i.e., equal weights) with CI = 0.22 and RI = 0.42. Numbers above the branches are the numbers of estimated substitutions (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids form a clade that is sister to the eudicots. Within eudicots, ranunculids and hamamelids form a grade in which the asterids are sister to the caryophyllids/rosids (for rosids, see Fig. 3B). —B (right). Rosid clade. Note that the glucosinolate and nitrogen-fixing families form clades.


rosids
Tamaricaceae
Frankeniaceae
Asteropeiaceae
Caryophyllales
Simmondsiaceae
Nepenthaceae
Droseraceae
Rhabdodendraceae
Plumbaginaceae
Polygonaceae
Dioncophyllaceae
Ancistrocladaceae
Santalales
Dilleniaceae
Polemoniaceae
Primulales
Ebenceae
Styracaceae
Clethraceae
Cyrillaceae
Actinidiaceae
Ericales
Theaceae
Sapotaceae
Scytopetalaceae
Lecythidaceae
Symplocaceae
Diapensiaceae
Sarraceniaceae
Fouquieriaceae
Pellicieraceae
Tetrameristaceae
Marcgraviaceae
Balsaminaceae
Gentianales
Solanales
Scrophulariales
Menyanthaceae
Bruniaceae
Campanulales
Escalloniaceae
Pittosporaceae
Araliales
Dipsacales
Aquifoliaceae
Cornales
Hydrangeaceae
Icacinaceae
Eucommiales
Berberidopsidaceae
Aextoxicaceae
Myrothamnaceae
Gunneraceae
Trochodendrales
Buxaceae
Didymelaceae
Proteaceae
Sabiaceae
Platanaceae
Nelumbonaceae
Ranunculidae
Eupteleaceae
Nymphaeaceae
Amborellaceae
Austrobaileyaceae
Illiciales
Aristolochianae
Chloranthaceae
monocotyledons
Laurales
Annonales
Magnoliales
Myristicaceae
Winterales
Ceratophyllaceae
caryophyllids s. l.
asterid III
asterid I & II
asterid IV
asterids
lower hamamelids
ranunculids
magnoliids


Irvingiaceae
Violaceae
Caryocaraceae
Ochnaceae
Quiinaceae
Medusagynaceae
Kiggelariaceae
Dichapetalaceae
Trigoniaceae
Chrysobalanaceae
Passiflorales
Linales s. str.
Malpighiaceae
Euphorbiales
Clusiaceae
Salicaceae
Scyphostegiaceae
Flacourtiaceae s. str.
Erythroxylaceae
Lacistemataceae
Elaeagnaceae
Rhamnaceae
Urticales
Rosaceae
Coriariaceae
Corynocarpaceae
Cucurbitales
Faganae
Fabaceae
Polygalaceae
Surianaceae
Elaeocarpaceae
Tremandraceae
Cephalotaceae
Eucryphiaceae
Cunoniales
Connaraceae
Oxalidaceae
Celastrales s. str.
Plagiopteridaceae
Huaceae
Zygophyllaceae
Krameriaceae
Dipterocarpaceae
Cistaceae
Malvales s. str.
Bixaceae
Sphaerosepalaceae
Thymelaeaceae
Rutales
Leitneriaceae
Sapindales s. str.
Vochysiaceae
Myrtales
Capparales
Salvadoraceae
Caricaceae
Moringaceae
Akaniaceae
Bretschneideraceae
Tropaeolaceae
Crossosomataceae
Stachyuraceae
Staphyleaceae
Geissolomataceae
Melianthaceae
Paeoniaceae
Geraniaceae
Crassulaceae
Saxifragales s. str.
Hamamelidales
Vitaceae
Malpighiales
N_2-fixing clade
Cunoniales s. l.
Malvales s. l.
Sapindales s. l.
Myrtales s. l.
Capparales s. l.
rosid I
rosid II
rosid III

Frankeniaceae (supported at 86%), Asteropeiaceae, Simmondsiaceae, Rhabdodendraceae, and Dioncophyllaceae/Ancistrocladaceae (supported at 60%). Polygonaceae/Plumbaginaceae are strongly supported (91%).

Within the rosid clade (Fig. 3B), the same three major groups as in Chase et al. (1993) were recovered, but only rosid I (55%) has any bootstrap support, and rosid III is a grade (Hamamelidales pair with Vitaceae). The rosid I group includes several newly sequenced families: Caryocaraceae, Clusiaceae, Corynocarpaceae, Dichapetalaceae, Elaeagnaceae, Flacourtiaceae s. str., Kiggelariaceae (the cyanogenic glycoside-producing genera of Flacourtiaceae s.l.), Lacistemataceae, Medusagynaceae, Plagiopteridaceae, Quiinaceae, Salicaceae, Scyphostegiaceae, and Surianaceae. Within the rosid I clade, Plagiopteridaceae are strongly supported (100%) as the sister family of Celastrales s. str. (with more sampling, the former are embedded within the latter; Savolainen & Chase, unpublished). Elaeagnaceae/Rhamnaceae are strongly supported (100%), and Cucurbitales/Corynocarpaceae/Coriariaceae have a moderate bootstrap (83%). The cunonialean clade (61%) comprises Oxalidaceae, Connaraceae, Eucryphiaceae/Cunoniales (98%), Cephalotaceae, and Tremandraceae/Elaeocarpaceae (91%); all but the first two listed have moderate support as a clade (81%).

Within the moderately supported Malpighiales clade (76%), Salicaceae, Scyphostegiaceae, and Flacourtiaceae s. str. are also strongly supported as a clade (100%; with increased sampling the first two families are embedded within the last; Chase et al., 1996). Chrysobalanaceae/Dichapetalaceae/Trigoniaceae have moderate bootstrap support (85%), and Ochnaceae/Quiinaceae/Medusagynaceae have weak support (68%).

The composition of the rosid II group is more or less like that in Chase et al. (1993), except that it includes Myrtales/Vochysiaceae and leaves out Geraniaceae, which appear in rosid III instead. There is no internal support for this clade, but it is recovered in all most-parsimonious trees. Several new families (since Chase et al., 1993) are represented: Bixaceae, Cistaceae, Geissolomataceae, Salvadoraceae, Sphaerosepalaceae, Staphyleaceae, Stachyuraceae, and Thymelaeaceae.

Crossosomataceae/Stachyuraceae/Staphyleaceae/Geissolomataceae is supported at 60% bootstrap level, and within this clade, a subclade of the last three is strongly supported (95%). The mustard-oil clade has moderate support (79%), and within it Tropaeolaceae/Bretschneideraceae/Akaniaceae is strongly supported (100%; the last two at 82%) and Caricaceae/Salvadoraceae/Capparales has moderate bootstraps (78%; the last two at 100%). Vochysiaceae/Myrtales is strongly supported at 100%, and this pair has moderate support (76%) as the sister of Sapindales/Rutales/Leitneriaceae (100%) plus Malvales s.l., comprised of Dipterocarpaceae/Cistaceae (100%), Malvales s. str., Bixaceae, Sphaerosepalaceae, and Thymelaeaceae.

As mentioned above, the rosid III group forms a grade and contains in addition to those families identified in Chase et al. (1993), Geraniaceae and Vitaceae. With more sampling, Geraniaceae are placed near Crossosomataceae. Dilleniaceae, Melianthaceae, and Santalales are not clearly associated with any other lineage.

COMBINED TREES

Analysis of the combined matrix with equal weights produced only 40 trees of 10,183 steps, CI = 0.16, RI = 0.39. As with *rbc*L alone, many characters changed excessively and so we employed successive weighting, which produced a single tree (Fig. 4) with the length of 10,271 Fitch steps, CI = 0.16, and RI = 0.38 (weighted length 631,329, CI = 0.56, RI = 0.63). In general, this topology is like that for *rbc*L, but there are a number of differences. The differences of the combined tree from the non-molecular trees are more substantial, as are the differences between the *rbc*L and the non-molecular trees. The major differences of the combined from the *rbc*L trees are as follows: the magnoliids form a grade rather than a clade; the ranunculids are sister to one of the clades, Platanaceae/Nelumbonaceae, that make up the hamamelid grade; the caryophyllids are sister to a combined rosid/asterid clade, in which these are monophyletic sister groups; Malvales s. str. are the sister to Bixaceae, Cistaceae, and Dipterocarpaceae in the combined tree, whereas they are placed between Bixaceae and Cistaceae/Dipterocarpaceae in the *rbc*L trees; the Bixales group with the taxa having a bixoid chalaza in their seeds (Nandi, 1998a; 159) thus appears as monophyletic in our combined tree (Sarcolaenaceae, for which no *rbc*L sequence was available, do have a bixoid chalaza; this character was found too late to be included in the matrix; if this character-state could be coded, Sarcolaenaceae would probably appear in the Bixales group as well); Fabaceae are placed outside the nitrogen-fixing clade in the combined tree; Clusiaceae are placed in a clade with Caryocaraceae, Elatinaceae (only non-molecular data), and Bonnetiaceae (only non-molecular data) in the combined tree, whereas they appear as the sister group of Euphorbiales in the *rbc*L trees; Violaceae are found in a group that is sister to a large clade containing, e.g., Flacourtiaceae s. str. and Euphorbiales, whereas they are placed differently in the *rbc*L trees; Kiggelariaceae are sister to Flacourtiaceae s. str., Scyphostegiaceae, and Salicaceae in the combined tree, whereas they are more distant from Flacourtiaceae s. str. in the *rbc*L trees.

The addition of the non-molecular data to the *rbc*L matrix greatly reduced the number of trees obtained; in the case of the Fitch analysis it dropped from more than 5000 (at which point the memory was exhausted) to only 40, and in the weighted analysis from nine to only one. If there were agreement between patterns in the molecular and non-molecular data, then an effect of increased support might be observed in the combined analysis. This is partly the case, but the amount of missing data in the non-molecular analysis makes this assessment difficult; there are many exceptions noticed by comparing Figures 3 and 4. For example, support for an expanded Nymphaeales (including Amborellaceae, Austrobaileyaceae, and Illiciales) decreases slightly (from 56% to 53%), but the support for the two pairs, Nymphaeaceae/Amborellaceae and Illiciales/Austrobaileyaceae, decreases markedly, from 92% and 98% to 86% and 75%, respectively. Citing all such cases is not a worthwhile endeavor at this stage of investigation. At the least, it can be stated that the addition of the non-molecular data does not drastically alter the pattern obtained with *rbc*L alone, nor does it greatly decrease bootstrap support.

TAXA IN THE *rbc*L TREES FOR WHICH INSUFFICIENT NON-MOLECULAR DATA ARE AVAILABLE

A number of small families have been included in the non-molecular matrix, but little information is available for them. The presence of such taxa can destabilize results and produce lower levels of internal support. Most of these taxa received strong support for placement in the *rbc*L trees, and they seem relatively securely placed in the combined tree. We point out these taxa here to draw attention to them: Tetrameristaceae and Pellicieraceae are found near Marcgraviaceae in the *rbc*L and combined trees (Figs. 3A, 4A) and are also sister groups tending to be placed in asterids in the non-molecular trees (Fig. 2A); Corynocarpaceae falls in the clade formed by Coriariaceae and Cucurbitales (including Datiscaceae and Begoniaceae) in the *rbc*L and combined trees; Leitneriaceae have a stable position near Rutales/Sapindales; Huaceae are placed near Celastrales s. str.; and Lacistemataceae and Scyphostegiaceae are found near Flacourtiaceae s. str.

DISCUSSION

Certain caveats must be proffered before further consideration of the results of these analyses. To overcome the disadvantages of high taxon number and large amounts of missing data (which always slows the process of finding shorter trees; pers. obs.), we regrouped the taxa into three subgroups (Search III). These corresponded to what we presumed were magnoliids, lower eudicots, and caryophyllids (group I), rosids (group II), and asterids (group III). This led to the advantage of shorter and more thorough computation and ultimately yielded trees up to six steps shorter than those found with the other two search strategies. This method is somewhat biased in presuming three major groups, but the final unconstrained swapping and reweighting procedures should compensate for the biases thus introduced. With an RI of 0.41, this matrix is highly likely to be subject to islands (Maddison, 1991), and this appeared to cause problems for standard types of search strategies. This is likely true also for the *rbc*L and combined matrices, although these were clearly more consistent in finding reasonably similar tree lengths in each of the random replicates of taxon-entry order.

The methods used for coding of the non-molecular data can be improved. Assessments of character polarity before analysis are assumption-laden. Coding only a single character that is assumed to be the plesiomorphic state for cases in which polymorphisms occur could result in spurious place-

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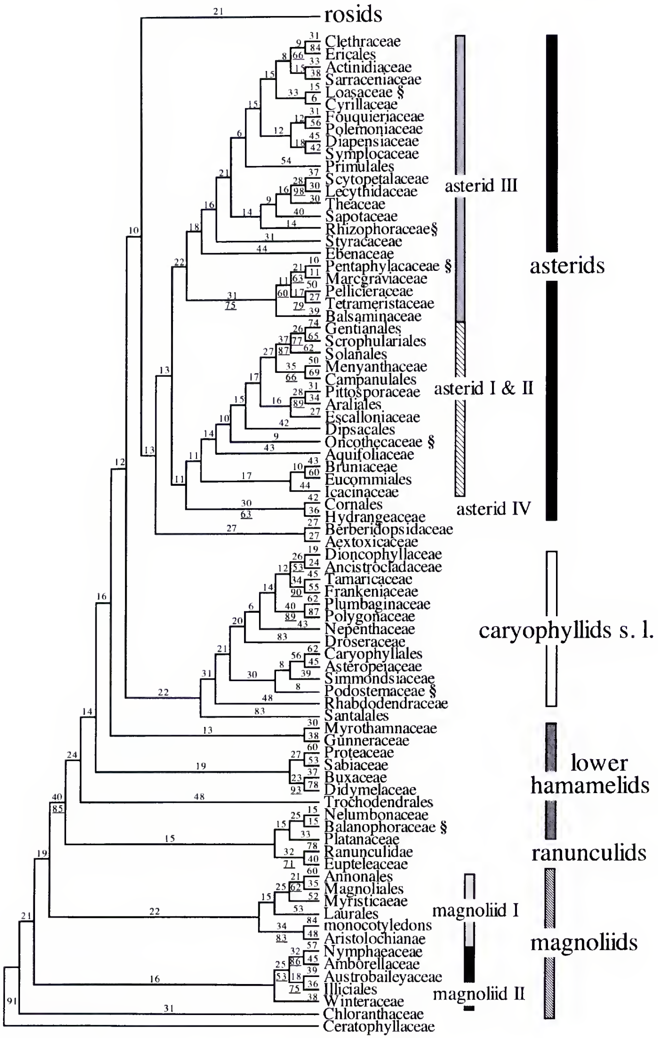
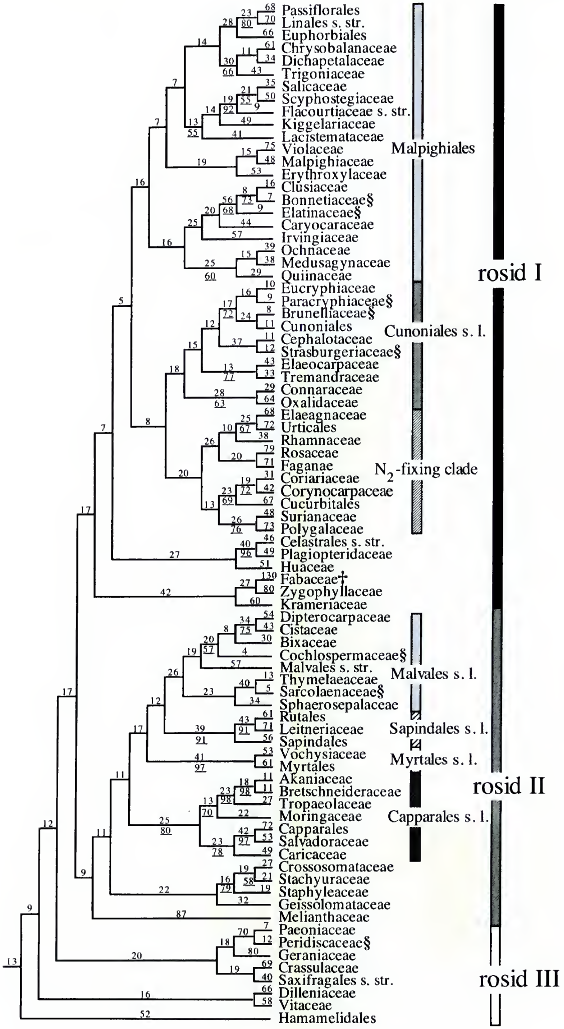
Figure 4. The single most-parsimonious combined tree found with successive weighting. The tree has 10,271 steps (Fitch length; i.e., equal weights) with CI = 0.16 and RI = 0.38. Numbers above the branches are the numbers of estimated changes (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids form a grade composed of two major subclades (magnolid I and II) with the former sister to the eudicots. Within eudicots, ranunculids and hamamelids form a grade. The caryophyllids are sister to the asterids/rosids (for rosids, see Fig. 4B). —B (right). Rosid clade. Note that the glucosinolate and nitrogen-fixing families form clades. §Taxa for which *rbc*L sequences were unavailable. †Nitrogen-fixing family outside the main nitrogen-fixing clade (Fabaceae).


rosids
Clethraceae
Ericales
Actinidiaceae
Sarraceniaceae
Loasaceae §
Cyrillaceae
Fouquieriaceae
Polemoniaceae
Diapensiaceae
Symplocaceae
Primulales
Scytopetalaceae
Lecythidaceae
Theaceae
Sapotaceae
Rhizophoraceae§
Styracaceae
Ebenaceae
Pentaphylacaceae §
Marcgraviaceae
Pellicieraceae
Tetrameristaceae
Balsaminaceae
Gentianales
Scrophulariales
Solanales
Menyanthaceae
Campanulales
Pittosporaceae
Araliales
Escalloniaceae
Dipsacales
Oncothecaceae §
Aquifoliaceae
Bruniaceae
Eucommiales
Icacinaceae
Cornales
Hydrangeaceae
Berberidopsidaceae
Aextoxicaceae
Dioncophyllaceae
Ancistrocladaceae
Tamaricaceae
Frankeniaceae
Plumbaginaceae
Polygonaceae
Nepenthaceae
Droseraceae
Caryophyllales
Asteropeiaceae
Simmondsiaceae
Podostemaceae §
Rhabdodendraceae
Santalales
Myrothamnaceae
Gunneraceae
Proteaceae
Sabiaceae
Buxaceae
Didymelaceae
Trochodendrales
Nelumbonaceae
Balanophoraceae §
Platanaceae
Ranunculidae
Eupteleaceae
Annonales
Magnoliales
Myristicaceae
Laurales
monocotyledons
Aristolochianae
Nymphaeaceae
Amborellaceae
Austrobaileyaceae
Illiciales
Winteraceae
Chloranthaceae
Ceratophyllaceae
asterid III
asterid I & II
asterid IV
asterids
caryophyllids s. l.
lower hamamelids
ranunculids
magnoliid I
magnoliid II
magnoliids


Passiflorales
Linales s. str.
Euphorbiales
Chrysobalanaceae
Dichapetalaceae
Trigoniaceae
Salicaceae
Scyphostegiaceae
Flacourtiaceae s. str.
Kiggelariaceae
Lacistemataceae
Violaceae
Malpighiaceae
Erythroxylaceae
Clusiaceae
Bonnetiaceae§
Elatinaceae§
Caryocaraceae
Irvingiaceae
Ochnaceae
Medusagynaceae
Quiinaceae
Eucryphiaceae
Paracryphiaceae§
Brunelliaceae§
Cunoniales
Cephalotaceae
Strasburgeriaceae§
Elaeocarpaceae
Tremandraceae
Connaraceae
Oxalidaceae
Elaeagnaceae
Urticales
Rhamnaceae
Rosaceae
Faganae
Coriariaceae
Corynocarpaceae
Cucurbitales
Surianaceae
Polygalaceae
Celastrales s. str.
Plagiopteridaceae
Huaceae
Fabaceae†
Zygophyllaceae
Krameriaceae
Dipterocarpaceae
Cistaceae
Bixaceae
Cochlospermaceae§
Malvales s. str.
Thymelaeaceae
Sarcolaenaceae§
Sphaerosepalaceae
Rutales
Leitneriaceae
Sapindales
Vochysiaceae
Myrtales
Akaniaceae
Bretschneideraceae
Tropaeolaceae
Moringaceae
Capparales
Salvadoraceae
Caricaceae
Crossosomataceae
Stachyuraceae
Staphyleaceae
Geissolomataceae
Melianthaceae
Paeoniaceae
Peridiscaceae§
Geraniaceae
Crassulaceae
Saxifragales s. str.
Dilleniaceae
Vitaceae
Hamamelidales
Malpighiales
Cunoniales s. l.
N_2-fixing clade
Malvales s. l.
Sapindales s. l.
Myrtales s. l.
Capparales s. l.
rosid I
rosid II
rosid III

ments of some taxa. An example of an assumed apomorphy can be seen in the results for Lilianae in Chase et al. (1995), in which the combined *rbc*L and morphology trees indicated that an inferior ovary was the plesiomorphic condition. This is the opposite conclusion one would reach based upon generalized character trends in angiosperms, and such conclusions could result in spurious assessments of relationships. Moreover, coding terminals as polymorphic can also produce erroneous topologies (Nixon & Davis, 1991). Adding terminals would be a solution, but it would involve unmanageable matrix dimensions and the need for more specific data on variation within larger clades. For example, if a taxon B is deeply nested within a large taxon A, it would be difficult to detect this relationship with our data. Taxon B would most likely attach to a subgroup of taxon A (which in our matrix may be absent). This would mean that large taxa have to be split up. An example of this problem is our use of Rutales, Sapindales, and Leitneriaceae. With more sampling within the two orders (Gadek et al., 1996), Leitneriaceae is embedded within Simaroubaceae of Sapindales. In our trees, it appears as sister to Sapindales. Despite these caveats, the approach used here is made stronger by the inclusion of many more characters than taxa. As long as most characters are accurately scored, the general results should contain useful and new information, and the "phylogenetic signal" should not be overly distorted.

The non-molecular matrix often deals with large taxonomic units composed of many families. The results are thus meaningful only if these taxa are monophyletic. We used higher-order taxa when the results of Chase et al. (1993) and many published studies (Appendix 6) coincided with the traditonal circumscription of these groups. In the *rbc*L and combined analyses, these groups were represented by only a single sequence of a representative species. The effects of using exemplars is discussed in Sytsma and Baum (1996), but the results do not differ significantly from other *rbc*L studies using more than single representatives.

A different approach would have been to use species as terminals, preferably the same species as covered by the *rbc*L database. This approach, however, would have the disadvantage that not all character fields would be investigated for the species or even the genus in question. Moreover, it seems most likely that the coverage of all angiosperms with exemplar species would require a sample of more terminal taxa than in this study. This again would necessitate more phylogenetically informative characters. This species-terminal approach, at the present time, is impractical and could not be effected; there simply are not enough species studied for all these characters.

We intend this study to be an example of the direction that we think phylogenetic studies should be taking. We will be most gratified if other researchers take our matrices and improve upon them. The literature is voluminous. We have surely missed a number of papers, but these matrices are now there to be completed. The gaps will be obvious to those who are interested. The missing cells need to be filled in, and we can see that if they are, there is hope for improvement. For those taxa on which we have focused most and incorporated more of the relevant literature (e.g., Malvales s.l.), the non-molecular (Fig. 2B), the molecular (Fig. 3B), and combined trees (Fig. 4B) are all highly congruent. The non-molecular results for Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolaenaceae also demonstrate that the search for characters has to consider a wide array of subject areas.

The final caveat concerns the use of successive weighting to "improve" the matrices (Farris, 1969). Some readers will wonder how this procedure has "distorted" the results produced by equal weighting, the results of which we have not shown. All data sets contain characters that are excessively "noisy," and these can be detected by an examination of their consistency on any of the trees (Fig. 1). This is evidence that, although these characters may be useful at some hierarchical level, they are not useful at the broad scale being studied here. A priori one cannot and should not make this sort of decision; it is simply too assumption-laden. When the initial results from an analysis indicate that certain characters are relatively more inconsistent than others, then the effects of the former should be lessened and those of the latter enhanced (i.e., made more consistent). The effect of successive weighting is never vastly different from that of equal weighting; in the great majority of cases, successive weighting merely identifies a subset of the trees found with equal weights as optimal (i.e., those that favor the more consistent characters). This is not the case with any of the trees found here, but both the *rbc*L and combined results have nearly the same Fitch length as the most-parsimonious Fitch tree (the weighted trees are only 0.56% and 0.86% longer than the Fitch trees for *rbc*L alone and the combined matrices, respectively; the CI and RI for the Fitch and weighted trees are nearly identical and only differ at the third decimal point levels, CI = 0.217 versus 0.215 and RI = 0.428 versus 0.424 for *rbc*L, and CI = 0.160 versus 0.159 and RI =

0.390 versus 0.384 for the combined analysis). We attempted to use successive weighting on the non-molecular data, but, like the search protocol itself, this procedure would have occupied many months of computer time and was therefore abandoned.

(A) TREES AND GENERAL PATTERNS

No previous cladistic analysis of the angiosperms has used as many higher-level taxa as this, including Chase et al. (1993) and Soltis et al. (1997b), which both used more species but fewer families. Of course, many of the families are subsumed in these trees by higher-order taxa (i.e., monocotyledons, Faganae, Urticales). This process of selecting terminals did not have a great effect on topology for the *rbc*L-only analysis, which deviates only slightly from that seen in Chase et al. (1993), and our results also do not differ drastically from those produced by 18S rDNA either (Soltis et al., 1997b). Several more divergent families are differently placed, which could be due to the overall sparser sampling permitting branch attractions to occur. These families (relative to Chase et al., 1993) are: Geraniaceae, in rosid II near *Crossosoma* before, here in rosid III (Fig. 3B); Vitaceae, in an isolated position with Dilleniaceae before, here with Hamamelidales; Krameriaceae/Zygophyllaceae, near Rosaceae in rosid I before, here in an isolated position as sister to the rosid I clade; and Fabaceae, which in the *rbc*L trees falls into the nitrogen-fixing clade (Fig. 3B) but in the combined tree is sister to Zygophyllaceae/Krameriaceae.

Several taxa occupy isolated positions in the *rbc*L and combined trees, and these would appear to be critical for understanding the patterns observed in the largest clades (i.e., rosids, asterids, and caryophyllids). These include Aextoxicaceae, Berberidopsidaceae, Dilleniaceae, Gunneraceae, Myrothamnaceae, Vitaceae, and Santalales. These taxa have shifted positions in every published large *rbc*L analysis, but they always come out as the sister taxa of the largest clades of eudicots. Within the asterids, Aquifoliaceae, Eucommiales, and Icacinaceae perform similarly; among rosids the Celastrales s. str./Plagiopteridaceae, Huaceae, Krameriaceae/Zygophyllaceae, Melianthaceae, and Crossosomataceae/Stachyuraceae/Staphyleaceae/Geissolomataceae clades are likewise unstable. Their positions in the non-molecular trees are generally different from their positions in the *rbc*L and combined trees. Aextoxicaceae, Berberidopsidaceae, Dilleniaceae, Gunneraceae, Myrothamnaceae, Vitaceae, and Santalales, those taxa that fall as sister groups of the asterids, caryophyllids, and rosids in Figures 3 and 4, are embedded among the magnoliids or included in the rosid groups that fall apart from the main rosid clade in the non-molecular trees (Fig. 2A). These taxa have a large number of plesiomorphic traits. For example, *Berberidopsis* (Berberidopsidaceae) has an undifferentiated perianth, plesiomorphic wood (presence of mostly solitary vessels with scalariform perforation plates and opposite side-wall pitting, absence of septate fibers), and tricolpate pollen (Miller, 1975; Lemke, 1988).

The *rbc*L data contain significantly greater phylogenetic information than the non-molecular data in this broad study (e.g., they delimit more groups with greater levels of internal support). In part, this must be ascribed to the structure of the non-molecular matrix, containing many empty cells and also a larger number of polymorphisms. Moreover, it has become obvious that all larger clades of angiosperms can only be characterized by few non-molecular traits (see part b of Discussion). This results in a matrix that seems to yield only slightly longer trees using standard methods (i.e., no compartmentalization). In phylogenetics, it has been underestimated that the more "signal" (i.e., the less randomness) is contained in a data matrix, the easier it is to find optimal trees. The 1993 *rbc*L tree was obtained in a relatively short search (Chase et al., 1993); trees only five steps shorter were found by Rice et al. (1995) after many more months of search on more than one computer. The only differences between these minimally shorter trees and the trees found in 1993 concern groupings that are weakly supported regardless of their positions. Nothing more of significance has been obtained except a huge outlay of computing time and personal effort; the 1993 tree contained all of the strongly supported groupings, and represents well the phylogenetic signal present in *rbc*L data. It should be accepted that with large searches for which exact solutions are impossible (such as this and the other large angiosperm matrices) excessive swapping over several months is not reasonable; effort is better spent in finding additional data. When all groups are strongly supported, then finding the optimal solution will be easy and the trees accurate (Soltis et al., in press). Even after many additional months of search on the 1993 *rbc*L matrix, we cannot say that anything new was learned. The most that was achieved was the observation that many groups, especially those with long branches, were unstable. Of course, we performed bootstrap analyses here, and this makes the general weakness of the *rbc*L tree evident. Unpublished analyses of *atp*B for nearly 300 seed plants take even less time than *rbc*L and contain even more groups with strong support. Soltis et al. (1997b) presented 18S rDNA data for 232 seed plants. The authors reported that more time is required for 18S than for *rbc*L alone or *rbc*L-18S combined searches, and again the major problem with large data sets is not just their size, but also the degree of randomness and missing cells that they contain. The large number of question marks and lack of support in the non-molecular matrix are serious obstacles to rapid search. Likewise, they do not permit the use of the jackknife (J. Farris, pers. comm.), which is a fast and accurate method of finding groups with strong internal support, regardless of the size of the matrix (Farris et al., 1997).

Some authors have suggested that hybridization or other forms of horizontal gene transfer could have a major effect on higher level studies within the angiosperms and could be expected to create conflicts between data categories (Syvanen et al., 1989; Syvanen, 1994). Others did not give hybridization a major role at higher levels (Chase et al., 1993). We do not deny that high levels of parallelisms exist among angiosperms, but we find the explanation of widespread horizontal gene transfer as the cause (Syvanen, 1994) unappealing and not conducive to further investigation. Studies of nuclear 18S rDNA (Soltis et al., 1997b) and plastid *atp*B (Savolainen et al., 1996) find results highly congruent with those of *rbc*L. In particular, the congruent topologies found with plastid genome sequences (*rbc*L and *atp*B) as well as with nuclear genome sequences (18s rDNA) argue against hybridization being a major problem in higher level plant systematics. Reticulate evolution, dating to a time when hybridization was still possible between now distant lines, appears to have only minor effects on macrosystematic patterns (for discussion of effects leading to parallelisms, see also Kubitzki et al., 1991).

(B) NON-MOLECULAR CHARACTERS OF TAXON GROUPS DISCUSSED ON THE BASIS OF THE COMBINED DATA TREE (FIG. 4 A, B)

We argue that the trees with the greatest underlying data are the most appropriate to discuss; thus, unless specifically stated, we will discuss only the combined tree from Figure 4. We focus on a series of characters that appear to contribute to the topology obtained in the combined tree. This is not meant to be an exhaustive examination of these topics. We intend instead to illustrate some of the trends in the non-molecular data that agree with the distribution of variation in the *rbc*L matrix. Characters described are synapomorphies as yielded by MacClade 3.04 on the combined tree, unless stated otherwise. Other characters that are widely represented within a clade may represent synapomorphies if the topologies are only slightly rearranged; since many of these branches are weakly supported, discussing these characters as either synapomorphies or plesiomorphies seems premature and potentially misleading. Therefore we discuss many characters as simply being widespread or frequent within clades; many of these will eventually be demonstrated to be synapomorphies. Due to the large number of missing cells and low levels of internal support with present data, it seems most prudent to consider only their relative frequencies or tendencies of occurrence rather than to frame this discussion as an investigation of synapomorphies.

Magnoliidae. The strict dichotomy of the leaf parts in *Ceratophyllum* is unusual in angiosperms, even if compared with other water plants showing the *Hippuris* syndrome of leaf architecture (cf. also Cook, 1978; Rutishauser & Sattler, 1987). The inflorescence is a spike with the flowers frequently arranged in two orthostichies (Raynal-Roques, 1981). This inflorescence type shows some similarities to the decussate spikes in *Chloranthus* and could reflect an old pattern. Also the flowers in *Ceratophyllum* are unisexual (Endress, 1994b), and this could be plesiomorphic for angiosperms or apomorphic as a result of adaptation to an aquatic autecology.

Chloranthaceae occupy an isolated and perhaps early-diverging position (see also Nixon et al., 1994). This is concordant with the fact that the oldest fossils known at present that are clearly attributable to angiosperms are Chloranthaceae-like. Chloranthoid pollen was described from the Valanginian of Israel (Brenner, 1996). *Hedyosmum*-like flowers are known from the Valanginian or Hauterivian of Portugal (Friis et al., 1994; Crane et al., 1995; E. M. Friis, pers. comm.) and are thus even older than the *Ceratophyllum*-like horned fruits found from an Aptian locality (Dilcher, 1989). The fact that distinct Aptian fossil material has been found that appears to combine characters of Chloranthaceae, Piperales, and Circaeasteraceae (Ranunculidae; Crane et al., 1995) indicates that early angiosperms exhibited a suite of traits that are now only known to occur individually within distinct terminal clades of extant angiosperms. The decussate arrangement of the flowers in spicate inflorescences in *Chloranthus* and the Late Cretaceous *Chloranthistemon* (Endress, 1987; Eklund et al., 1997) is paralleled by the decussate inflorescences of *Ephedra* (Hufford, 1996). The comparison of branched male structures in Gnetales and Chloranthaceae is problematical because of unclear homologies (Endress, 1987; Friis & Endress, 1990; Doyle, 1994, 1996). For comparison of Chloranthaceae with Gnetales see also Taylor and Hickey (1996) and critical discussion by Doyle (1996) and Endress and Igersheim (1997). Also the highest diversity of pollen aperture types within an angiosperm family seems to occur in Chloranthaceae (not expressed in the characters used for this analysis; see, e.g., Erdtman, 1952). Sesquiterpenes, as γ-elemene, can serve to indicate relationships of Chloranthaceae to other angiosperm families. At present, γ-elemene is known only from Chloranthaceae, Piperaceae, and Aristolochiaceae (Hegnauer, 1962–1994). The germacrene acoragermacrene occurs only in Chloranthaceae and monocots (Hegnauer, 1962–1994). These two compounds seem to indicate an evolutionary relationship of Chloranthaceae to Aristolochianae–monocots or are a relict of previously more widespread traits.

Amborella also occurs in an isolated position in our non-molecular trees (Fig. 2A). *Amborella* was found as the sister group to the rest of angiosperms in a subset of the 18S rDNA trees (Soltis et al., 1997b), but in a clade supported by the jackknife along with Illiciales, Austrobaileyaceae, and Nymphaeales in the combined analysis of *rbc*L and 18S in Soltis et al. (1997a). Probably ancestral or erratic characters of *Amborella* include the presence of S-type plastids in the sieve-tubes (107), uniaperturate in addition to inaperturate pollen grains (129; Sampson, 1993), minute embryos (163), scanty wood parenchyma (174), no fibers (not coded), tracheids (177), wood rays of Kribs heterogeneous type I (179), circular tracheid side-wall pitting (similar to some Gnetales; 184), no vessels (not coded; probably plesiomorphic), no discontinuous calyx-corolla transgression (210), practically orthotropous ovules (246), and stipitate fruits (239) (Metcalfe & Chalk, 1950; Behnke, 1981; Cronquist, 1981; Takahashi, 1985; Carlquist, 1988a; Endress, 1994c). Brenner (1990, 1996) reported that angiospermous, inaperturate pollen grains, which may have evolved into a *Clavatipollenites* pollen-type, are present in the Valanginian and Hauterivian of Israel. Judging from these paleobotanical finds, one may take into consideration whether the inaperturate pollen grains found in *Ceratophyllum, Ascarina* (Todzia, 1993), *Amborella, Trimenia papuana* (see Sampson & Endress, 1984), and many Laurales (Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae except Atherospermatoideae) are reductions or represent an old, conserved, character-state. Neglect of the presence of inaperturate pollen in the above-mentioned magnoliid taxa based on the assumption that the inaperturate condition does not represent the basal pollen type could result in different topologies at the base of the tree.

All taxa of magnoliids and early-branching eudicots included in this analysis have ovary-to-carpel length ratios greater than 1:2 (i.e., with short or absent styles; 236). The formation of long styles in relation to the whole carpel thus seems to be an apomorphic tendency in basal angiosperms. A mesotesta (middle layer of outer integument in the seed; 154) with sclerified cells is present in many magnoliids: Chloranthaceae (*Chloranthus* spp.), Nymphaeaceae, Austrobaileyaceae, Illiciales, Aristolochianae (*Aristolochia* spp.), Myristicaceae (*Horsfieldia, Myristica*), Annonales, Magnoliales (Corner, 1976; Endress, 1980; Takhtajan, 1988). A mechanical layer in the mesotesta is also found in some early-branching eudicots (Eupteleaceae; Buxaceae: *Sarcococca*; and Hamamelidaceae; Corner, 1976).

The clade formed by Laurales, Aristolochianae, monocots, Myristicaceae, Annonales, and Magnoliales (magnoliid I clade; Fig. 4A) shows a frequent occurrence of the phenylpropane asarone (41). Asarone is known from Lauraceae (*Sassafras*), Piperaceae (Piper), Aristolochiaceae (*Asarum*), Annonaceae, and Magnoliaceae (*Magnolia*) (Gildemeister & Hoffmann, 1956; Hegnauer, 1962–1994; Sethi et al., 1976; Keller, 1982). Outside of this clade Hegnauer (1962–1994) cited only three families of angiosperms that produce asarone. The same clade contains the only plant taxa that Hegnauer (1962–1994) and Harborne and Baxter (1993) found to produce the lignans galbacin (57) and veraguensin (59). The neolignan licarin (58), though described from *Krameria* (Dominguez et al., 1992), is also predominantly found in this magnoliid I clade (Gottlieb et al., 1988, stated that neolignans have their center of diversification in the magnolialean families). Galbacin, a tetrahydrofuranoid lignanoid, occurs in Lauraceae (*Persea*), Aristolochiaceae (*Aristolochia*), Myristicaceae (*Knema, Virola*), and Himantandraceae (*Galbulimima*) (Hegnauer, 1962–1994; Harborne & Baxter, 1993). Veraguensin, also a tetrahydrofuranoid lignanoid, is known to occur in Trimeniaceae (*Trimenia*), Lauraceae (*Ocotea*), Saururaceae (*Saururus*), Myristicaceae (*Virola*), and Magnoliaceae (*Magnolia*) (Harborne & Baxter, 1993). Licarin has been found in Lauraceae (*Licaria*), Aristolochiaceae (*Aristolochia*), Myristicaceae (*Myristica*), and Magnoliaceae (Hegnauer, 1962–1994; Ionescu et al., 1977; Le Quesne et al., 1980; Harborne & Baxter, 1993).

The alkaloid liriodenine (83) is known only in the magnoliid I clade, as well as in Ranunculidae and Nelumbonaceae; the last-mentioned taxa fall into the sister group of the remaining eudicots. As with two of the three lignanoids mentioned above, liriodenine is not known from any families outside of these clades, most significantly not from the magnoliid subclade containing Winterales, Nymphaeaceae, Amborellaceae, Austrobaileyaceae, and Illiciales (Hegnauer, 1962–1994; Harborne & Baxter, 1993), hereafter the magnoliid II clade (Fig. 4A). The magnoliid I clade further has sieve-tube plastids of the P-type (107) in a majority of families (Behnke, 1981), whereas all members of the magnoliid II clade except Canellaceae (here in Winterales) have S-type plastids. Aristolochianae and monocots are further linked by the common presence of crystal sand (in Piperaceae, Metcalfe & Chalk, 1989, and Araceae, but not in *Acorus*, Solereder & Meyer, 1928; Franceschi & Horner, 1980; Seubert, 1993; 115), of a dispersed vascular system (in Piperaceae and monocots, but not in Saururaceae; 167), and of frequent trimery in perianth (212–214), androecium (221), and gynoecium (233–235). Aristolochianae and monocots also cluster on the basis of the widespread occurrence of two stamen whorls (not coded). More similarities, perhaps as the result of common ancestry, are enumerated by Burger (1977) and Dahlgren and Clifford (1982). All magnoliid I families except monocotyledons/Aristolochianae share a stratified phloem (169) and wedge-shaped phloem rays (Metcalfe & Chalk, 1950; Cronquist, 1981; Carlquist, 1988a; 170).

Both the non-molecular and the combined trees show Chloranthaceae as an isolated family apart from the main magnoliid clades. Also equally isolated in all trees are Amborellaceae, Austrobaileyaceae, and Illiciales (magnoliid II clade), separated from the more typical magnoliid I clade, in which the monocots are sister to Piperales/Lactoridaceae/Aristolochianae (Fig. 4A).

Eudicots. Eudicots are held together by their triaperturate pollen grains (129), which most likely evolved in parallel in Illiciales (Erdtman, 1952; Doyle et al., 1990; Qiu et al., 1993).

Many early-branching eudicots have representatives with tricolpate pollen grains; these are cited here, as in Chase et al. (1993), as the ranunculids and lower hamamelids (the latter a grade composed of several small clades). These taxa are nearly all relatively small and could be considered remnants of previously more widespread and numerous archaic lineages. In our scheme, these lineages would include Berberidopsidaceae, Nelumbonaceae, Platanaceae, Ranunculidae, Proteaceae, Gunneraceae, Myrothamnaceae, and Trochodendrales. Vitaceae and Aextoxicaceae appear to be related also to these, but exhibit some more advanced characters, such as tricolporate pollen, which is more predominant in derived eudicot lineages (see, e.g., Erdtman, 1952). In *Nelumbo*, both tricolpate and monosulcate pollen are reported (Kuprianova, 1979; Blackmore et al., 1995; coded only as tricolpate in the matrix because we became aware of the occurrence of monosulcate pollen in *Nelumbo* only after analysis). The sister group of the rest of eudicots consists of Nelumbonaceae, Platanaceae, Eupteleaceae, and Ranunculidae. A number of these families have some members with palmately veined leaves or leaves with no dominant single primary vein (i.e., Menispermaceae, Lardizabalaceae, Circaeasteraceae, Ranunculaceae, Berberidaceae, Nelumbonaceae, and Platanaceae; 198). The leaves of *Kingdonia* and *Circaeaster* are particularly interesting for their dichotomously branching venation, which is rare in angiosperms (for the conditions in *Kingdonia*, see Foster & Arnott, 1960; morphogenetic interpretations by Hagemann, 1970, and Hagemann & Gleissberg, 1996). Foster and Arnott (1960) hypothesized that the dichotomous venation pattern in *Kingdonia* represents an ancestral character-state. Imprint leaf fossils from the Early Cretaceous of Madagascar have been found that show characters similar to extant *Circaeaster* (O. Appert, pers. comm.). Circaeasteraceae and Kingdoniaceae were placed in the ranunculalean clade by Oxelman and Lidén (1995; here including *Trochodendron*) based on an analysis of 28S rRNA. They were also given family rank (as members of a distinct order in the Ranunculidae) by Takhtajan (1997).

Proteaceae and Sabiaceae are linked by the common presence of wedge-shaped phloem rays (Metcalfe & Chalk, 1950; 170) and of a nectary disk (Haber, 1959, 1961, 1966; van Beusekom, 1971; 231), a rare character in the early-branching angiosperms. Buxaceae and Didymelaceae share a simple, bract-like perianth (possibly plesiomorphic; 209) and encyclocytic stomata (195), the latter a rare character-state present in only eleven taxa of our analysis (see also Metcalfe & Chalk, 1950, 1988, 1989). Aextoxicaceae and Berberidopsidaceae are also linked by this same character (Cronquist, 1981; Baas, 1984).

Ellagic acid is not only absent from the magnoliids, with the exception of Nymphaeales (Amborellaceae have not been sampled), but also from the first-branching eudicots, Ranunculidae, Eupteleaceae, Platanaceae, Nelumbonaceae, Proteaceae, Sabiaceae, Buxaceae, and Trochodendrales. Gallic acid (70) shows a similar distribution (Hegnauer, 1962–1994; Gibbs, 1974).

The morphological data set does not establish the sister-group position of Ranunculidae to the remaining eudicots but places them nested in the magnoliid I clade (Fig. 2A). Perhaps a better knowledge of the biochemistry of some basal eudicots (Eupteleaceae, Platanaceae, Sabiaceae, Didymelaceae) would cause a somewhat modified placement of Ranunculidae. The non-molecular trees also do not consistently separate *Nelumbo* from magnoliid I (Fig. 2A). In all trees *Trochodendron, Tetracentron,* Proteaceae, Sabiaceae, Buxaceae, and Didymelaceae are in an isolated position (cf. also Drinnan et al., 1994). *Berberidopsis*, a ditypic Australian–Chilean disjunct genus, shows no close relationships to Flacourtiaceae in either data set. A distinct position of *Berberidopsis* within the core-Flacourtiaceae s.l. was already indicated by Keating (1975) on the basis of pollen morphology and by Miller (1975) on the basis of wood anatomy. The *rbc*L and combined analyses place Berberidopsidaceae and Aextoxicaceae (also from Chile) as sister to the asterids (Figs. 3A, 4A), and the non-molecular analysis places them with the magnoliid I clade (Fig. 2A).

Dilleniaceae and Vitaceae have never been considered closely related, but they share oxalate raphides (Metcalfe & Chalk, 1950; 113), an endotesta containing radially elongate cells (156), and a tracheidal exotegmen (Corner, 1976; 157).

Caryophyllidae s.l. Albert et al. (1992) found an unexpected grouping of Droseraceae and Nepenthaceae with Caryophyllales; the latter have been considered to have no particularly close relatives, other than perhaps Plumbaginaceae and Polygonaceae (Cronquist, 1981). This clade appears in all trees, even non-molecular, with a remarkably similar composition (Figs. 2B, 3A, 4A). Most taxa of the clade formed by Rhabdodendraceae (1), Caryophyllales (2), Tamaricaceae (3), Frankeniaceae (4), Asteropeiaceae (5), Nepenthaceae (6), Droseraceae (7), Dioncophyllaceae (8), Ancistrocladaceae (9), Simmondsiaceae (10), Plumbaginaceae (11), and Polygonaceae (12), here termed as caryophyllids, have some taxa with tricolpate or polycolpate (stephanocolpate) pollen grains (2, 3, 4, 5, 7, 8, 9, 10, 11, 12; Erdtman, 1952; Cronquist, 1981; 129). Many (2, 5, 6, 7, 8, 9, 10, 11, 12) also have spinuliferous or punctitegillate pollen sexine (Erdtman, 1952; 135). The similarity of pollen grains of some Polygonaceae and some Caryophyllales was noted by Erdtman (1952). Likewise the resemblance of pollen of Droseraceae and Nepenthaceae is noteworthy (e.g., Erdtman, 1952; Basak & Subramanyam, 1966; Takahashi & Sohma, 1982). Anomalous secondary growth seems to be particularly well represented in the caryophyllids, occurring in Rhabdodendraceae, Caryophyllales, Frankeniaceae, Dioncophyllaceae, Simmondsiaceae, and Plumbaginaceae (Carlquist, 1988a). Similarly, interxylary phloem occurs in several taxa: Rhabdodendraceae (Record, 1933), Caryophyllales, Simmondsiaceae (Bailey, 1980), Plumbaginaceae, and Polygonaceae. A character-state that was coded as present in only seven taxa outside the extended caryophyllids is the presence of maximally biseriate wood rays, displayed in Frankeniaceae, Asteropeiaceae, Dioncophyllaceae, Ancistrocladaceae, Droseraceae, and Simmondsiaceae (Metcalfe & Chalk, 1950; Carlquist, 1988a; Carlquist & Wilson, 1995).

The caryophyllids, except for Rhabdodendraceae, are further characterized by the presence of only alternate intervessel pitting (secondary xylem present in 2, 3, 4, 5, 7, 8, 9, 10, 11, 12; 184). The exclusive occurrence of the alkaloid ancistrocladine in Amaranthaceae (Arora & Metha, 1981; 85), Dioncophyllaceae, and Ancistrocladaceae (Hegnauer, 1962–1994) also suggests a degree of relatedness. All caryophyllid families for which information was available (3, 4, 6, 7, 9, 11, 12) have an endosperm provided with starch grains (161); only ten other taxa in the matrix share this condition. Tamaricaceae were previously put into the "Nelkengruppe," roughly corresponding to modern concepts of Caryophyllales, by Hallier (e.g., 1914). A tendency linking Tamaricaceae and Frankeniaceae is the presence of exotestal cells with convex surfaces, being represented as papillae in Frankeniaceae or as hairs in Tamaricaceae. Netolitzky (1926) mentioned that the chalazal hair tuft in Tamaricineae is first developed as papillae. Corner (1976) also postulated a link of Frankeniaceae to Tamaricaceae through exotestal morphology. Moreover, Tamaricaceae as well as Frankeniaceae have appendages on the ventral side of their petals. Airy Shaw (1951) suggested a close affinity of Droseraceae, Nepenthaceae, Ancistrocladaceae, and Dioncophyllaceae. Schmid (1964) added new evidence for this grouping. The latter alignment, containing three carnivorous families (Droseraceae, Nepenthaceae, and Dioncophyllaceae) with different trapping systems, has been supported by Hegnauer (1962–1994) on biochemical grounds.

The presence of the naphthoquinones plumbagine (99), droserone (100), and related 1,4-naphthoquinones is another link between Nepenthaceae, Droseraceae, Ancistrocladaceae, Dioncophyllaceae, and Plumbaginaceae (Hegnauer, 1962–1994; Zenk et al., 1969; Durand & Zenk, 1974; Lavault & Bruneton, 1980; Williams et al., 1994); these compounds are otherwise known to be accumulated only by several species of Iridaceae and Ebenaceae (Hegnauer, 1962–1994).

It is mainly the coincidence of these trends in chemistry and pollen morphology that places the families mentioned above into the expanded caryophyllid clade in the non-molecular tree. Thus, it is the coding of the presence of variably exhibited specialized traits that is responsible for the presence of the caryophyllid clade in nearly the same composition as in the *rbc*L trees. Rhabdodendraceae, which fall into the asterids in the non-molecular trees (Fig. 2A), presumably do so because they have unitegmic ovules (see below); with the weak support (69%) present in the *rbc*L data for the expanded caryophyllids, Rhabdodendraceae move into this clade in the combined tree.

One of the remarkable aspects of the caryophyllid clade is the diversity of life history strategies that is found among these taxa. Many of these taxa are adapted to either xeric or saline conditions, and some (i.e., Plumbaginaceae, Frankeniaceae, and Tamaricaceae) have multicellular glands that excrete salt (Hill & Hill, 1976; character not coded), whereas others such as Droseraceae, have similar glands that produce mucilage and enzymes used to trap and digest insects (Juniper et al., 1989).

A similar Caryophyllidae s.l. was also inferred from 18S rDNA data (Soltis et al., 1997b). Comparing the present non-molecular, *rbc*L, and combined trees, the caryophyllids appear in no consistent position with respect to the rosids or asterids. Future combined studies may establish the interrelationships of these clades.

Asteridae s.l. The larger asterid clade found with *rbc*L (Olmstead et al., 1992, 1993; Chase et al., 1993; Savolainen et al., 1994; Soltis et al., 1997b) has been remarkably consistent in composition as well as in the general patterns of relationships. This same grouping is present in the non-molecular trees (Fig. 2A), except that some unexpected taxa have additionally been placed here (i.e., Gunneraceae, Sabiaceae, Rhabdodendraceae, and Santalales), presumably because these are highly autapomorphic (e.g., Gunneraceae) or they have unitegmic ovules like asterids (e.g., Sabiaceae, Rhabdodendraceae). The absence of these groups from the asterids with *rbc*L analysis can be interpreted as meaning that the distribution of unitegmic ovules shows some degree of homoplasy. The presence of unitegmic ovules is a consistent character-state in most asterid clades. In a clade corresponding to asterid I, II, and IV of Chase et al. (1993), most taxa have unitegmic ovules (Hydrangeaceae, Cornales, Oncothecaceae, Sphenostemonaceae–Aquifoliaceae, Icacinaceae, Eucommiales, Dipsacales, Campanulales, Solanales, Gentianales, Scrophulariales, Escalloniaceae, Pittosporaceae, Araliales, Menyanthaceae, and Loasaceae; 137). In addition to characters correlated to some degree with unitegmic and tenuinucellar ovules (137, 139; the correlation including the presence of an integumentary tapetum and endosperm haustoria), the asterids also have a higher percentage of taxa with united sepals (215), and especially with united petals (217), than rosids; this is much more evident than in the more restricted definition of asterids by either Cronquist (1981) or Takhtajan (1987). Caricaceae are the only rosid family in this analysis in which all genera have united petals (best developed in the male flowers). In addition to the tendency for the union of perianth whorls, asterids show a higher degree of haplostemony than rosids, a character that is perhaps functionally linked to the more synorganized perianth/androecium. The core asterids (sensu Cronquist, 1981), Solanales, Campanulales, Gentianales, and Scrophulariales, are held together by alternate vessel side-wall pitting (184), simple vessel perforations (185), and rounded vessel transverse section (Metcalfe & Chalk, 1950; 187).

Loasaceae and Hydrangeaceae both show the presence of deutzioside (Bliss et al., 1968; Uesato et al., 1986), an iridoid compound known only from these two families (Hegnauer, 1962–1994). Other *rbc*L studies (Soltis et al., 1995a) demonstrated that these two families are sister taxa (but an *rbc*L sequence for Loasaceae was unavailable for the present study). Iridoid compounds occur in 19 taxa in our matrix, 16 of which belong to the extended asterids. Light-colored, obdurate, protruding, nonglandular leaf teeth characterize different taxa of Hydrangeaceae (character not coded; O. Nandi, pers. obs.). The investigation of leaf teeth in the sister groups of Hydrangeaceae is potentially interesting. Hydrangeaceae and Cornales share the tendency to form inflorescences with showy, sometimes white leafy organs at their periphery. In Cornales (*Cornus* spp., *Davidia*) these organs are large bracts, differing only slightly from normal foliage leaves. In Hydrangeaceae these organs are the sepals (genera of Hydrangeeae; Engler, 1891). This tendency has not been coded in our matrix (the organs involved are not homologous). The synorganization of flowers into pseudanthia is a recurring phenomenon in asterids IV and II (sensu Chase et al., 1993; character not used in this analysis).

Taxa having iridoid compounds that are not included in asterids s. str. (sensu Cronquist, 1981) are Hydrangeaceae, Cornales, Icacinaceae, Eucommiales, Escalloniaceae, Loasaceae, Fouquieriaceae, Symplocaceae, Ericales, Sarraceniaceae, and Actinidiaceae (Hegnauer, 1962–1994). These are all asterids in the *rbc*L and combined trees (Figs. 3A, 4A), and also, with one exception, in the non-molecular tree (Fig. 2A).

The presence of a theoid exotesta (152), i.e., an exotesta with lignified and often pitted radial and inner walls (cf. Huber, 1991), links some asterid taxa: Sphenostemonaceae–Aquifoliaceae (*Ilex*; Corner, 1976), Solanales (Solanaceae, e.g., *Atropa, Browallia, Cestrum, Lycium, Mandragora, Nicandra, Nicotiana, Petunia, Solanum* p.p. *Withania*; Corner, 1976), Dipsacales (Caprifoliaceae, e.g., *Lonicera*; Corner, 1976), Gentianales (Loganiaceae, e.g., *Strychnos*, Gentianaceae, e.g., *Fagraea*; Corner, 1976), Pentaphylacaceae (*Pentaphylax*; Huber, 1991), Marcgraviaceae (*Souroubea*; Huber, 1991), Symplocaceae (*Symplocos*; Huber, 1991), Diapensiaceae (*Diapensia*; Netolitzky, 1926), Ericales (Empetraceae, e.g., *Corema*; Huber, 1991), Sarraceniaceae (Corner, 1976), Clethraceae (Corner, 1976), Actinidiaceae, slightly differentiated in *Saurauia* (Corner, 1976), and Theaceae (Adinandreae; Corner, 1976).

The occurrence of cantleyoside (48), an ester of the iridoid glucoside loganin with the secoiridoid glucoside secologanic acid, is restricted to a few taxa of the asterids II (sensu Chase et al., 1993). This compound is known only from Icacinaceae, Dipsacales, and Campanulales (Hegnauer, 1962–1994; Sévenet et al., 1971; Jensen et al., 1979; Murai et al., 1985; Harborne & Baxter, 1993). The lignan eucommin A (53) is only known from Eucommiales and Gentianales, a fact that supports the placement of Eucommiales in the asterid I clade (sensu Chase et al., 1993; Hegnauer, 1962–1994; Deyama et al., 1985; Harborne & Baxter, 1993).

Oxalate druses (Metcalfe, 1950) are absent from the clade formed by Balsaminaceae (1), Pentaphylacaceae (2; no *rbc*L data), Marcgraviaceae (3), Pellicieraceae (4), and Tetrameristaceae (5). All but Pentaphylacaceae have the trait of forming oxalate raphides (1, 3, 4, 5), which is unusual for dicots. A subclade of asterid III (sensu Chase et al., 1993) has a persisting free-central column in loculicidal capsules: Ericales (Ericaceae, Epacridaceae; Drude, 1891b, c; Clethraceae; Drude, 1891a); and Theaceae (Cronquist, 1981; 252). Ericales and Sarraceniaceae are linked by the presence of protruding diffuse placentae. Scytopetalaceae and Lecythidaceae share stratified phloem (Metcalfe & Chalk, 1950), cortical vascular bundles (Metcalfe & Chalk, 1950), and a nectary disk in the flowers (Scytopetalaceae, Letouzey, 1961; Lecythidaceae subfam. Planchonioideae, Endress, 1994a).

Rosidae. Relatively minute embryos (compared to seed size) seem more frequent in the first-branching dicots (magnoliids, hamamelids, some of the first-branching asterids) than in the more nested clades such as Caryophyllidae s.l. and Rosidae. Only 4 out of 74 rosid taxa for which the character has been coded exhibit minute embryos (163): Paeoniaceae, Saxifragales s. str. (in our study, Saxifragales s. str. include Grossulariaceae, Haloragaceae, Penthoraceae, Saxifragaceae; without Vahliaceae, Greyiaceae, Francoaceae, Parnassiaceae, and Lepuropetalaceae; cf. Takhtajan, 1987), Peridiscaceae, and Tremandraceae. A possible synapomorphy of Paeoniaceae and Saxifragales s. str. is the presence of an exotestal palisade with thickened outer walls (151) in seeds of *Paeonia* and *Ribes* (Netolitzky, 1926; Corner, 1976). The ridges formed by radial elongation of the exotestal cells in certain Saxifragaceae (similar also in Crassulaceae), according to Corner (1976), "suggest the vestige of a uniformly palisade-like exotesta" in this family. For an extensive study of the Saxifragaceae s.l. and suggestions on their naming see Soltis and Soltis (1997).

Another unexpected grouping in the *rbc*L tree by Chase et al. (1993) is supported in the combined tree. Vochysiaceae/Myrtales (97% bootstrap) have methylated ellagic acids (62), intraxylary phloem (171), vestured pits in vessels (Bailey, 1933; van Vliet & Baas, 1984; Carlquist, 1988a; 183), and unilacunar nodes (Cronquist, 1981; Dahlgren & Thorne, 1984; 190).

Tropaeolaceae, Akaniaceae, and Bretschneideraceae, in addition to their glucosinolate production (36), are linked by tricarpelly (233–235). Caricaceae, Capparales, and Salvadoraceae, three glucosinolate-producing taxa, each contain taxa with a fibrous exotegmen (Corner, 1976). Capparales and Salvadoraceae concur in the presence of intra- or interxylary phloem (Carlquist, 1988a; character partially represented in 171). The presence of a single crystal layer (with one oxalate crystal per cell) in the endotesta in Caricaceae (Corner, 1976) and some Capparales (Resedaceae; Corner, 1976) could be a further argument for their affiliation (155). The glucosinolate clade is also present in the

18S rDNA trees (Soltis et al., 1997b) and *atp*B trees (unpublished).

In Malvales s.l., all families have only simple perforations in the secondary xylem (Metcalfe & Chalk, 1950; 185), and all but two families, Cistaceae and Bixaceae, have representatives with mucilage cells or mucilage cavities (Metcalfe & Chalk, 1950; Cronquist, 1981; 119). All taxa for which the character is known (i.e., all except Sarcolaenaceae and Sphaerosepalaceae) are characterized by the occurrence of centrifugal or rarely (Thymelaeaceae; Heinig, 1951) lateral polyandry (Hirmer, 1918; Gore, 1935; Corner, 1946; Van Heel, 1966; Sattler, 1973; Woon & Keng, 1979; Cronquist, 1981; Ronse Decraene, 1989, 1992; Bayer & Hoppe, 1990; Nandi, 1998b; 224). Another synapomorphic character complex for the extended Malvales can be found in seed anatomy. All families for which information is available have representatives with the exotegmen differentiated as a palisade layer (Thymelaeaceae, Sphaerosepalaceae, Malvales s. str., Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolaenaceae; Corner, 1976; Nandi, 1998a; 157). An exotegmic palisade occurs only rarely outside of this group (e.g., Trochodendrales, Huaceae, and Euphorbioideae). Malvales s.l. are also linked by the presence of wedge-shaped phloem rays in Thymelaeaceae, Sphaerosepalaceae, Malvales s. str., Cochlospermaceae, and Bixaceae (unknown for Sarcolaenaceae; 170). Moreover, most representatives of Malvales s.l. (except Thymelaeaceae) display a stratified phloem (Metcalfe & Chalk, 1950), a character-state known from just 19 other taxa in this analysis.

Sarcolaenaceae (1), Malvales s. str. (2), Cochlospermaceae (3), Cistaceae (4), Dipterocarpaceae (5), and Bixaceae (6) share the presence of stellate hairs (in 2, 4, 5, 6) and peltate scales (in 1, 2, 3, 4, 5, 6; Metcalfe & Chalk, 1988). This group is also characterized by palmate leaf venation (in Tiliaceae, Sterculiaceae, Bombacaceae, Malvaceae, Cochlospermaceae, Bixaceae, and some *Cistus* species; 198) and frequent tricarpelly (233–235). Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolaenaceae show the presence of a bixoid chalazal region in the seed (Nandi, 1998a; definition see Appendix 4; 159) as a nonparalleled apomorphy. Moreover, the group is characterized by the absence of a nectary disk (231), and by parietal placentation (241), and large, curved embryos [Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae (Pakaraimaeoideae, Dipterocarpoideae) have large, curved embryos; Janchen, 1925; Pilger, 1925a, b; Maguire & Ashton, 1980; Cronquist, 1981; Nandi, 1998a)]. Vestured pits are found in many representatives of the group [*Bixa* (Solereder, 1899), *Cistus*, Dipterocarpaceae (Monotoideae: Baas & Werker, 1981; Pakaraimaeoideae, Dipterocarpoideae), Sarcolaenaceae (Morton, 1995), not in *Cochlospermum*; O. Nandi, pers. obs.; 183]. Cistaceae, Dipterocarpaceae, and Bixaceae share the absence of prodelphinidins (60). Bixaceae and Cistaceae share a starchy endosperm (161) with similar structure of larger starch grains (character not coded; Nandi, 1998a). As in the expanded caryophyllids, it is again a set of specialized character-states that establishes the pattern in the non-molecular trees that then parallels the pattern seen in the *rbc*L trees for the same taxa.

Another unexpected clade, identified in the 1993 *rbc*L trees, was an expanded Malpighiales clade that included families such as Euphorbiaceae, Passifloraceae, Ochnaceae, and Violaceae. This clade is also present in our *rbc*L and combined analyses (Figs. 3B, 4B). Many of these taxa have a fibrous exotegmen (157). Together with the three taxa in the mustard-oil group, this assemblage accounts for 19 of 24 taxa exhibiting a fibrous exotegmen: Connaraceae, Oxalidaceae, and Elaeocarpaceae in Cunoniales; Celastrales s. str.; and Irvingiaceae, Euphorbiales (Phyllanthoideae sensu Corner, 1976), Violaceae, probably Kiggelariaceae, Flacourtiaceae s. str., Scyphostegiaceae, Erythroxylaceae, Malpighiaceae, Linales s. str., Ochnaceae (Sauvagesioideae), Medusagynaceae, and Trigoniaceae (Corner, 1976; probable indication of the character for *Medusagyne* by Dickison, 1990). A fibrous exotegmen was also recently described from Rhizophoraceae (*Crossostylis*; Setoguchi et al., 1992), supporting the alliance of this family with rosids having fibrous exotegmen (Malpighiales) and not with Theaceae, as suggested by the non-molecular trees (we became aware of this publication too late to include the character in the matrix). Conti et al. (1996) produced *rbc*L trees that showed Rhizophoraceae in Malpighiales. It is noteworthy that Rhizophoraceae and Erythroxylaceae have tropane alkaloids (character not coded). This alkaloid class is otherwise known only in dicots from Proteaceae, Convolvulaceae, Solanaceae, *Cochlearia* (Brassicaceae), and Elaeocarpaceae. The related hygroline alkaloids are confined to Rhizophoraceae and Erythroxylaceae and are known to occur in only two other families [Solanaceae, Brassicaceae (*Cochleraria*); Hegnauer, 1962–1994].

With present knowledge, hostplants of the butterfly genus *Cymothoë* (Nymphalidae: Limenitinae) include only taxa from a few families near Violaceae (character not used in computation); these families are Clusiaceae, Euphorbiaceae, Dichapetalaceae, Violaceae, Kiggelariaceae, and Flacourtiaceae s. str. (Ackery, 1988). This is one of the rare non-molecular patterns linking Clusiaceae to Euphorbiaceae, and both to Flacourtiaceae.

Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Scyphostegiaceae are linked by the presence of septate fibers (Metcalfe, 1956; Miller, 1975; 176). The clade formed by Salicaceae, Flacourtiaceae s. str., and Kiggelariaceae has thin wood-fiber walls (Appendix 4; Metcalfe & Chalk, 1950; Miller, 1975; 175), lack of calyx-corolla differentiation (210), absence of alignment of the carpels with the median tepals or petals (232), and loculicidal capsules (251). The close alliance of Salicaceae to Flacourtiaceae s. str. is further suggested by the lepidopteran genus *Cupha* (Nymphalidae: Argynninae) feeding exclusively on this group (on *Hydnocarpus*, Kiggelariaceae; *Homalium, Xylosma, Scolopia*, Flacourtiaceae s. str.; and on *Salix*, Salicaceae; Ackery, 1988). Another argynnine genus (*Phalanta*; Ackery, 1988) feeds mainly on *Rinorea, Melicytus, Viola* (Violaceae), *Dovyalis, Flacourtia, Scolopia, Trimeria, Xylosma* (Flacourtiaceae s. str.), *Rawsonia* (Kiggelariaceae), *Populus, Salix* (Salicaceae), and *Maytenus* (Celastraceae). In addition, both Flacourtiaceae s. str. (*Xylosma, Poliothyrsis*) and Salicaceae (*Populus*) have representatives containing the phenolglucoside nigracin, not known from any other family (Hegnauer, 1962–1994; Thieme & Benecke, 1966, 1970; 95). Flacourtiaceae s. str. and Kiggelariaceae, two somewhat preliminary taxa derived from the traditional Flacourtiaceae (e.g., Takhtajan, 1966; Cronquist, 1981), are linked by the presence of finely reticulate pollen ectexine (Keating, 1975; 136), a fibrous exotegmen (in *Casearia, Flacourtia* of Flacourtiaceae s. str.; in *Oncoba*, uncertain position, probably Flacourtiaceae s. str.; probably also in *Hydnocarpus*, Kiggelariaceae; Corner, 1976; 157), a hypostase in the seeds (160), septate fibers in the overwhelming majority of genera (Miller, 1975; 176), opposite in addition to alternate vessel side-wall pitting in the wood of the anatomically most basal representatives (*Erythrospermum, Carpotroche, Mayna, Hydnocarpus*, Kiggelariaceae; *Azara*, Flacourtiaceae s. str.; Miller, 1975; 184), scalariform vessel perforation plates in some representatives (185), and epidermal leaf crystals (196). Within the Flacourtiaceae s. str./Kiggelariaceae assemblage, there seems to be a negative correlation between genera bearing cyanogenic glycosides of the gynocardin type (49) and the genera displaying salicoid teeth (sensu Hickey & Wolfe, 1975; Appendix 4; 201). The two characters seemingly never occur together in the same genus. In addition to the genera described to have salicoid teeth (*Idesia, Populus, Salix* in Hickey & Wolfe, 1975; *Prockia* in Morawetz, 1981), twelve other genera from the tribes Homalieae, Scolopieae, Prockieae, and Flacourtieae (sensu Lemke, 1988) have been found to contain species with salicoid teeth: *Dissomeria, Byrsanthus, Calantica, Carriera, Flacourtia, Homalium, Ludia* (not well developed), *Oncoba* (in Oncobeae in the system of Lemke, 1988), *Poliothyrsis, Scolopia, Trimeria*, and *Xylosma* (O. Nandi, pers. obs.). A broad survey of angiosperm leaves in the herbaria of Zürich (Z and ZT), Geneva (G), and Vienna (WU) indicated that salicoid leaf dentation is a good systematic marker, and that similar tooth types occur only rarely outside of Flacourtiaceae s. str. and Salicaceae (O. Nandi, pers. obs.; e.g., *Tetracentron*). The fact that *Oncoba* lacks both gynocardin-like compounds and has salicoid teeth in addition to glands on the distal end of the petioles (also found in some of the genera with salicoid teeth) indicates that this genus is not well placed among the tribe Oncobeae (the definition of the tribe is based on floral morphology following Warburg, 1894). The tribe Casearieae (sensu Lemke, 1988) lacks both gynocardin-like compounds and salicoid teeth. Moreover, the two closely related butterfly genera *Siderone* and *Zaretis* (Nymphalidae: Charaxinae: Anaeini), are known to feed nearly exclusively on members of this tribe (*Casearia, Laetia, Ryania*, and *Zuelania*; Ackery, 1988). Other genera of the subtribe Anaeini feed mainly on Euphorbiaceae. This pattern could indicate that Casearieae are not immediately connected to other tribes of Flacourtiaceae s.l. Conversely, the genus *Cymothoë*, mentioned previously, feeds on *Casearia* (Casearieae), *Rawsonia* (Erythrospermeae), *Buchnerodendron, Caloncoba* (Oncobeae), *Kiggelaria* (Pangieae), and *Dovyalis* (Flacourtieae), as well as on Clusiaceae, Euphorbiaceae, and Dichapetalaceae (Ackery, 1988). A relationship of Kiggelariaceae to Passiflorales is suggested by the fact that at least three butterfly species of *Acraea* subg. *Acraea* (Nymphalidae: Acraeinae: sensu Pierre, 1984) feed on Kiggelariaceae, and Passifloraceae tribes Paropsieae (no molecular data available) and Passifloreae (an extrinsic character, not in the matrix). The first molecular insights into Flacourtiaceae s.l. using *rbc*L sequence data information were provided in Chase et al. (1996); a great deal more study of this and related families will be required to establish proper family circumscriptions.

A relationship of Violaceae to the flacourtiaceous line is further indicated by the hostplants of *Acraea cerasa*, found to be an early-branching representative of the subgenus *Acraea* in a morphological cladistic study by Pierre (1984). This species is known to feed on both *Rinorea* (Violaceae) and *Rawsonia* (Kiggelariaceae). Other species of subgenus *Acraea* feed exclusively on Violaceae and Passiflorales. *Acraea* subg. *Acraea* thus seems to show loose coevolutionary correlations with representatives of Violaceae, Flacourtiaceae s. str., Kiggelariaceae, Passifloraceae, and Turneraceae.

Linales s. str., Passiflorales, and Euphorbiales also share the exclusive capacity of producing the cyanogenic diglucosides linustatin and neolinustatin (character-states not included in the matrix for Euphorbiales; 29, 30). The two compounds are transport-forms of the widely distributed monoglucosylated cyanogenes linamarin and lotaustralin (Hegnauer, 1962–1994; Smith et al., 1980; Selmar, 1993; Frehner et al., 1990; Mkpong et al., 1990). They are formed during seed development (*Linum*), seed germination (*Hevea*), or tuber formation (*Manihot*).

Quiinaceae, Ochnaceae, and Medusagynaceae have at least some taxa with contorted petal aestivation (*Touroulia*, Quiinaceae, Engler, 1925; Ochnaceae, Gilg, 1925; Medusagynaceae, Engler & Melchior, 1925). Links of Ochnaceae to Medusagynaceae can be seen in the common presence of stratified phloem (known for *Godoya* in Ochnaceae and Medusagynaceae, Metcalfe & Chalk, 1950), cortical vascular bundles in the stem, septicidal capsules, and a persistent free-central column in the fruits (Fay et al., 1997).

Connaraceae and Oxalidaceae (here in Cunoniales; Figs. 3B, 4B) share the absence of ellagic acid and the presence of rapanone, a benzoquinone (Fieser & Chamberlain, 1948; Hegnauer, 1962–1994). Rapanone is only known from a few angiosperm families, including Myrsinaceae, according to Hegnauer (1962–1994). Connaraceae and Oxalidaceae are further linked on the basis of sieve-tube plastids of the PIc-type (Behnke, 1981; 107), the absence of oxalate druses (Metcalfe & Chalk, 1950; 112), a short exotestal palisade [Connaraceae (*Cnestis*, *Connarus* spp., *Jollydora*, *Rourea)*, Oxalidaceae (*Averrhoa*); Corner, 1976; 151], endotestal crystals [Connaraceae (*Jollydora*), Oxalidaceae (*Averrhoa*, *Oxalis*); Corner, 1976; 155], fibrous exotegmen [Connaraceae (*Cnestis*, *Jollydora*, *Rourea*), Oxalidaceae (*Averrhoa*, *Oxalis*); Corner, 1976; 157], and exclusively uniseriate wood rays (181).

Celastrales s. str. and Plagiopteraceae are linked by the common presence of epidermal crystals in the leaves (Baas et al., 1979; 196), the occurrence of weakly crassinucellar ovules in representatives of both taxa (*Celastrus* and *Cassine* (as *Elaeodendron*), Celastrales s. str., Johri et al., 1992; *Plagiopteron*, Tang, 1994; 139), and an integumentary tapetum (Johri et al., 1992; Tang, 1994; 138).

Cephalotaceae, Eucryphiaceae, Brunelliaceae, and Cunoniaceae all have representatives with follicles or ventricidal capsules (Engler, 1930; Bausch, 1938; Cronquist, 1981; 251), and Brunelliaceae and Cunoniaceae have opposite leaves (191) with frequently craspedodromous venation (O. Nandi, pers. obs.; 199). A similar cunonioid clade was found in the 18S rDNA trees (Soltis et al., 1997b).

The taxa with nitrogen-fixing root symbionts in at least some genera [Fabaceae, Cucurbitales (Datiscaceae), Coriariaceae, Faganae (Myricaceae, Betulaceae, Casuarinaceae), Rosaceae, Rhamnaceae, Urticales (Ulmaceae), and Elaeagnaceae; 105], with the exception of Fabaceae, are placed in a monophyletic clade in the combined tree. In the *rbc*L trees (Fig. 3B), Fabaceae are also members of this clade, but they are placed outside the clade in the combined tree (Fig. 4B). Fabaceae, Myricaceae, Betulaceae, Casuarinaceae, Ulmaceae, and Elaeagnaceae are known to contain nodule hemoglobin (Landsmann et al., 1986; this character was not used in the non-molecular matrix). The hostplant taxa of the hyphomycete *Tubercularia ulmea* [Rhamnaceae (*Rhamnus*), Elaeagnaceae (*Elaeagnus*), Urticales (*Ulmus*); Farr et al., 1989] form a monophyletic clade in the trees derived from the combined data set, a fact that could point to a coevolutionary relationship of the fungus and these rosids. In both the 18S (Soltis et al., 1997b) and *atp*B trees (Savolainen et al., 1996), this same nitrogen-fixing clade is present.

There are many other specific characteristics upon which some discussion could be made, but at this point in time, this is not appropriate. We have focused in the previous section on features that are of particular interest to us. The most significant outcome of these comparisons is that chemical and micromorphological (often palynological) data should be included as equally important characters as developmental and floral morphological traits in macrosystematic considerations. These characters seem to correspond most closely to the molecular results. Gross morphological traits, particularly phyllotaxy, presence of stipules, and perianth arrangement, appear especially unreliable for systematic interpretations at this level within angiosperms.

(C) TAXA FOR WHICH *rbc*L SEQUENCES ARE NOT AVAILABLE

Hydnoraceae (not included in our matrices) have been allied to Aristolochiales in some systems (e.g., Takhtajan, 1987). Characters of Hydnoraceae tending to be ancestral are monosulcate, di- or trisulcate as well as trichotomocolpate pollen (x-tomocolpate pollen known in Chloranthaceae, *Cabomba*, Saururaceae, and monocots), psilate exine, thick endexine as compared to the ectexine, unitegmic, orthotropous ovules (as in Ceratophyllaceae, but probably also correlated with the high ovule number and parasitism), a well developed perisperm (a character more widespread in basal than in advanced angiosperms), a minute embryo in the seed, non-arborescent growth form, and a perianth not differentiated into calyx and corolla.

Rafflesiaceae (not included in our matrices) are known to be heterogeneous both in pollen characters and macromorphology (Takhtajan et al., 1985). It is possible that the different families recognized by Takhtajan (1987), i.e., Rafflesiaceae s. str., Apodanthaceae, Mitrastemonaceae, and Cytinaceae, belong to distantly related groups. The occurrence of ellagitannins (characteristic for eudicots) and 2-, 3-, or 4-porate pollen grains in *Cytinus* and the tricolpate pollen grains in *Pilostyles* suggest the absence of a close relationship to *Rafflesia*, *Rhizanthes*, and *Sapria*, which have monosulcate or monoporate pollen (the recent 18S rRNA information on Rafflesiales by Nickrent, 1996, confirms the segregation of *Cytinus* from Rafflesiaceae s. str.). The occurrence of both a lamellate endexine and an atectate ectexine in the pollen of Rafflesiaceae s. str. (Takhtajan et al., 1985) is likely an ancestral character combination for angiosperms.

In the fossil record, epigynous angiosperm flowers from the Early Cretaceous of Portugal have been found (Friis et al., 1994). Partly, these flowers are of unclear systematic affinity; some of them have similarities with Laurales. In extant basal angiosperms epigynous flowers are comparatively rare, although they are present in several families. The fact that Hydnoraceae and Rafflesiaceae s. str. have epigynous flowers and the seemingly ancestral characters found in these two families call for their integration in the research on first-branching angiosperms. It would be especially interesting to include them in molecular systematic studies, because morphological and anatomical characters are difficult to assess (because of reductions due to parasitism). Analysis of 18S rDNA sequences would be the most likely source of useful information to address questions about these parasitic plants, but the high levels of divergence for these plants (Nickrent, 1996) coupled with the low levels of divergence for 18S rDNA found in angiosperms in general (Soltis et al., 1997b) are likely to make sequence evaluations unreliable.

Podostemaceae are another family with unusual biology for angiosperms in general, and are thus difficult to assess. In our non-molecular trees, they generally fall near or in the caryophyllids or less frequently Santalales. Despite rather incomplete data, character-states of systematic importance are the occurrence of silica bodies (111) and secretory cavities in the plant body, tricolpate pollen grains with spinulous exine and colpus membrane (Rutishauser, 1997; 130, 135), tenuinucellar ovules (139), suspensor haustoria (165), absence of calyx-corolla differentiation (210), rare occurrence of centrifugal androecium development (in *Mourera fluviatilis* Aubl., R. Rutishauser, pers. comm.; 224), prolonged stamen connectives (229), generally completely free styles [except for, e.g., "*Synstylis*" (*Polypleurum*); 237], micropyle formation by the outer integument (247), and septicidal capsules (251). Some of these characters may be seen as adaptations to the extreme habitat of Podostemaceae. Ueda et al. (1997), using *rbc*L sequence data, found that Podostemaceae are sister to Crassulaceae in the saxifragoid clade. Les and Philbrick (1996) reported extremely high levels of divergence for several Podostemaceae, but also concluded that they are sister to Crassulaceae.

Balanophoraceae are also highly reduced due to their parasitic ecology. They tend to align in extended caryophyllids. Triangular pollen grains (132) and the occurrence of similar embryo sacs could indicate a link to Santalales (Zweifel, 1939). The 18S rRNA analysis of Nickrent (1996) contradicted a close alliance of Balanophoraceae with Santalales. As with Podostemaceae, our matrix for Balanophoraceae has many gaps.

Strasburgeriaceae tend to be placed in basal asterids in the present non-molecular trees. Oncothecaceae are another small family placed in the asterids near Aquifoliaceae. Preliminary *rbc*L analyses support this position for *Oncotheca* (Savolainen & Chase, unpublished). Paracryphiaceae cluster with basal asterids or Eucryphiaceae.

Rhizophoraceae either fall near to the Stachyuraceae group or often are the sister group to Theaceae. Published and unpublished *rbc*L analyses support a placement of Rhizophoraceae in Malpighiales (Conti et al., 1996) near Erythroxylaceae (Chase et al., unpublished). The fibrous exotegmen in Rhizophoraceae, described by Setoguchi et al. (1992), would be in good agreement with the molecular results (see Discussion, section b).

Sarcolaenaceae align with Malvales s.l.; this is also confirmed with recent *rbc*L analyses (Conti et al., 1996). Cochlospermaceae also clearly align with Malvales s.l. as sister to a branch containing

Bixaceae and Cistaceae. Other analyses of *rbc*L also support this placement (Alverson et al., in press).

Bonnetiaceae, Elatinaceae (non-molecular data), and Clusiaceae (also with *rbc*L) are kept together by an exotegmen with lobate facets in tangential section (158). All three families have representatives with septicidal capsules (251). These three taxa are linked in the non-molecular trees. The close relationship of the three families was emphasized by Stevens (1991). Clusiaceae and Bonnetiaceae, in addition, are united by having representatives with arils (perhaps a vestigial aril in *Ploiarium*; Corner, 1976; 146) and protruding diffuse placentation (242). Preliminary *rbc*L studies of *Ploiarium* place it near Thymelaeaceae in Malvales s.l. (Chase, unpublished), but other Bonnetiaceae may not be related to *Ploiarium* (A. Weitzman, pers. comm.).

(D) CONCLUSIONS

Larger data matrices call for improved computational facilities, both in tree searches and in assessing confidence in the resulting clades (e.g., jackknife program, Farris et al., 1997). It has been recognized in these searches that the stronger the phylogenetic signal in a matrix, the easier it is to obtain reasonably short trees. In a sense, once one has found all the strongly supported clades, then the search is complete. Regardless of the manner in which weakly supported branches are arranged, there can be no confidence in the patterns so produced. In experiments with combining large *rbc*L, *atp*B, and 18S matrices, it has been noted that tree searches have become faster and production of a reasonably short tree length appears relatively easy (Soltis et al., 1997b; Chase & Savolainen, unpublished). We are optimistic that, as we add more data as well as more taxa, searches will in fact become easier rather than more difficult. Hillis's (1996) recent simulations and predictions also support the notion that increased sampling, both of genes and taxa, produces more accurate topologies; increase in accuracy by sampling more genes has been accepted for some time, whereas it has been a hotly disputed topic whether increased sampling of taxa also produces more reliable topologies (see for example Graur et al., 1996).

On the molecular-systematic side, improved topologies will be obtained by integrating and comparing more sequence-information from different genomes; this should allow us to have more confidence in the relationships obtained and to evaluate whether reticulate evolution through ancient hybridization or horizontal gene transfer has macrosystematic effects.

The work on the "classical" side is equally challenging. Cladistic analyses using non-molecular data should rely if possible on original observations of living plants, herbarium material, and anatomical slide collections, but also on primary and synoptic literature. Literature searches ideally should also include the older comparative literature (e.g., works by Baillon, Bentham & Hooker, Eichler, Engler & Prantl, Payer, Troll), which contains much useful and recently overlooked information.

Biochemical work can be refined, and new techniques will doubtless permit more detailed comparison of the different molecule classes. This promises to be a fruitful field, especially for families on which not much biochemical work has been done, such as Ceratophyllaceae, Hydnoraceae, Rafflesiaceae, Amborellaceae, Eupteleaceae, Sabiaceae, Didymelaceae, Aextoxicaceae, Strasburgeriaceae, Sphenostemonaceae, Oncothecaceae, Tetrameristaceae, Pellicieraceae, Pentaphylacaceae, Diapensiaceae, Scytopetalaceae, Dialypetalanthaceae, Bruniaceae, Plagiopteridaceae, Irvingiaceae, Sphaerosepalaceae, Diegodendraceae, and Sarcolaenaceae.

The study of the form and distribution of solid bodies in cells also reveals additional systematic information (e.g., oxalate crystals, starch grains; preliminary works by Czaja, 1969, 1978). The same holds true for investigations of plant hair structure.

Much more information on seed anatomy should also be sampled. Priorities again are small families of restricted distribution, as mentioned above. Seed anatomy has proven to be a good tool for macrosystematics in the present study (see also Corner, 1976; Huber, 1991; Seubert, 1993).

A character-rich field that has not yet received much attention from neobotanists is leaf structure (see Hickey & Wolfe, 1975; Klucking, 1986/1987/1988/1989/1991/1992/1995). Leaf morphology (leaf dentation, leaf venation patterns) is of great potential usefulness, especially in combination with paleobotany.

Rhizome, bulb, and root morphology and anatomy are presently not as well understood as, e.g., floral morphology. Floral ontogeny is a field in which new perspectives have been achieved by the use of SEM (e.g., Endress, 1994a; Tucker & Douglas, 1994; Erbar & Leins, 1996). Because of practical problems in acquiring different ontogenetic stages, there are still many groups that remain poorly known. Inflorescence types have been studied for many families and are likely to be valuable for phylogenetic analyses. Fruit anatomy has not received much attention, probably also due to the large size of many angiosperm fruits. Recent works on Oleales (e.g., Rohwer, 1996) and Cornales (Reidt, 1997) show that comparison of fruit characters is systematically relevant.

As with intrinsic characters of angiosperms, extrinsic ones from fields such as ecology, paleoecology, paleobotany, biogeography, and hostplant and mutualistic relationships should also provide useful data. In the last field, more information should be sampled on hostplants of fungi, Lepidoptera, and other groups of organisms that tend to have taxa with restricted preference for particular angiosperms (perhaps also Orthoptera, Aphididae, and Chrysomelidae). Paleobotany is a promising field for providing insights on early angiosperm radiation and relationships to possible outgroups. It may also add evidence on the position of controversially positioned clades that cannot be assigned clearly to the asterids, rosids, or caryophyllids as described here and in Chase and Cox (in press).

We are optimistic about the prospects for improved analyses of all classes of data. This study provides one example of how this approach can succeed, but a great deal more work on methods of coding characters is needed. In which cases can tendencies be coded as uniform characters for families in which polymorphisms occur? Should a family or order, no matter how clearly supported as monophyletic, be used as a terminal? These results appear to demonstrate that this approach can succeed with both molecular and non-molecular data and that the phylogenetic content of characters so coded is not terribly distorted by this type of summarization. We suspect that, if the patterns are robust, different codings will provide similar results. What is most needed is not a dogmatic approach to character coding and skepticism of the potential for various coding methods to succeed, but an empirical evaluation of real data using consistent methods. Too much emphasis on methodological matters will only serve to impede progress. We maintain that the barriers to creating large matrices and performing analyses on large data sets have less to do with the data collection and analysis than with much skepticism of the process itself.

Literature Cited

Ackery, P. R. 1988. Hostplants and classification: A review of nymphalid butterflies. Biol. J. Linn. Soc. 33: 95–203.

———. 1991. Hostplant utilization by African and Australian butterflies. Biol. J. Linn. Soc. 42: 335–351.

Airy Shaw, H. K. 1951. On the Dioncophyllaceae, a remarkable new family of flowering plants. Kew Bull. 3: 327–347.

Albert, V. A., S. E. Williams & M. W. Chase. 1992. Carnivorous plants: Phylogeny and structural evolution. Science 257: 1491–1495.

Aldrich, J., B. Cherney & E. Merlin. 1986. Sequence of the *rbc*L gene for the large subunit of ribulose bisphosphate carboxylase-oxygenase from alfalfa. Nucl. Acids Res. 14: 9535.

Alverson, W. S., K. Karol, E. Conti & J. Sytsma. 1994. Circumscription of the Malvales and its placement in rosids based on *rbc*L sequence data. Amer. J. Bot. 81 (Suppl., 6): 139. [Abstract.]

———, ———, D. A. Baum, M. W. Chase, S. M. Swensen, R. McCourt & K. J. Sytsma. Circumscription of the Malvales and relationships to other Rosidae: Evidence from *rbc*L sequence data. Amer. J. Bot. (in press).

Arber, A. 1925. Monocotyledons. A Morphological Study. Cambridge Univ. Press, Cambridge.

Arora, O. P. & M. Metha. 1981. Chemical investigations of some Rajasthan desert plants. Indian J. Chem., B 20: 834.

Baas, P. 1969. Comparative anatomy of *Platanus kerrii* Gagnep. Bot. J. Linn. Soc. 62: 413–422.

———. 1972. Anatomical contributions to plant taxonomy II. The affinities of *Hua* Pierre and *Afrostyrax* Perkins et Gilg. Blumea 20: 161–192.

———. 1975. Vegetative anatomy and the affinities of Aquifoliaceae, *Sphenostemon, Phelline* and *Oncotheca.* Blumea 22: 311–407.

———. 1984. Vegetative anatomy and taxonomy of *Berberidopsis* and *Streptothamnus* (Flacourtiaceae). Blumea 30: 39–44.

——— & E. Werker. 1981. A new record of vestured pits in Cistaceae. I.A.W.A. Bull., N. S. 2: 41–42.

———, R. Geesink, W. A. Van Heel & J. Muller. 1979. The affinities of *Plagiopteron suaveolens* Griff. (Plagiopteraceae). Grana 18: 69–89.

Bailey, D. C. 1980. Anomalous growth and vegetative anatomy of *Simmondsia chinensis.* Amer. J. Bot. 67: 147–161.

Bailey, I. W. 1933. The cambium and its derivative tissues. VIII. Structure, distribution and diagnostic significance of vestured pits in dicotyledons. J. Arnold Arbor. 14: 259–273.

———. 1957. Additional notes on the vesselless dicotyledon, *Amborella trichopoda* Baill. J. Arnold Arbor. 38: 374–380.

——— & B. G. L. Swamy. 1948. *Amborella trichopoda* Baill. A new morphological type of vesselless dicotyledon. J. Arnold Arbor. 29: 245–254.

Baillon, H 1873. Histoire des Plantes, Vol. 3. Hachette, Paris.

Baretta-Kuipers, T. 1976. Comparative wood anatomy of Bonnetiaceae, Theaceae and Guttiferae. Leiden Bot. Ser. 3: 76–101.

Barron, D., L. Varin, R. K. Ibrahim, J. B. Harborne & C. A. Williams. 1988. Sulphated flavonoids—An update. Phytochemistry 27: 2375–2395.

Barth, O. P. 1965. Elektronenmikroskopische Beobachtungen am Sporoderm der Caryocaraceen. Grana Palynol. n. s. 6: 7–25.

Basak, R. K. & K. Subramanyam. 1966. Pollen grains of some species of *Nepenthes.* Phytomorphology 16: 334–338.

Batygina, T. B., O. P. Kamelina, A. L. Takhtajan, M. S. Yakovlev & G. Ya. Zhukova. 1985a. Comparative Embryology of the Flowering Plants. Butomaceae–Lemnaceae. Nauka, Leningrad. [In Russian.]

———, ———, ———, ——— & ———. 1985b. Comparative Embryology of the Flowering Plants. Brunelliaceae–Tremandraceae. Nauka, Leningrad. [In Russian.]

———, ———, ———, ——— & ———. 1985c. Comparative Embryology of the Flowering Plants. Davidiaceae–Asteraceae. Nauka, Leningrad. [In Russian.]

Bausch, J. 1938. A revision of the Eucryphiaceae. Bull. Misc. Inform. Kew 1938: 317–349.

Bayer, C. & J. R. Hoppe. 1990. Die Blütenentwicklung von *Theobroma cacao* L. (Sterculiaceae). Beitr. Biol. Pflanzen 65: 301–312.

Bedell, H. G. 1981. Leaf architecture and foliar sclereids in Marcgraviaceae (Theales). Publ. Bot. Soc. Amer., Misc. Ser. 160: 62.

Behnke, H.-D. 1975. The bases of angiosperm phylogeny: Ultrastructure. Ann. Missouri Bot. Gard. 62: 647–663.

———. 1977. Zur Skulptur der Pollen-Exine bei drei Centrospermen (*Gisekia, Limeum, Hectorella*), bei Gyrostemonaceen und Rhabdodendraceen. Pl. Syst. Evol. 128: 227–235.

———. 1981. Sieve-element characters. Nordic J. Bot. 1: 381–400.

———. 1985. Contributions to the knowledge of P-type sieve-element plastids in dicotyledons II: Eucryphiaceae. Taxon 34: 607–610.

Berg, C. C. 1977. Urticales, their differentiation and systematic position. Pl. Syst. Evol., Suppl. 1: 349–374.

Beusekom, C. F. van. 1971. Revision of *Meliosma* (Sabiaceae), section *Lorenzanea* excepted, living and fossil, geography and phylogeny. Blumea 19: 355–529.

Bhandari, N. N. 1971. Embryology of the Magnoliales and comments on their relationships. J. Arnold Arbor. 52: 1–39, 285–304.

Blackmore, S., P. Stafford & V. Persson. 1995. Palynology and systematics of Ranunculiflorae. Pl. Syst. Evol., (Suppl.) 9: 71–82.

Blank, F. 1939. Beitrag zur Morphologie von *Caryocar nuciferum* L. Ber. Schweiz. Bot. Ges. 49: 437–494.

Bliss, C. A., T. J. Danielson & R. A. Abramovitch. 1968. Investigations on the genus *Mentzelia*. I. Mentzeloside, a new iridoid glycoside. Lloydia 31: 424.

Boesewinkel, F. D. 1985. Development of ovule and seed-coat in *Averrhoa* (Oxalidaceae) with notes on some other related genera. Acta Bot. Neerl. 34: 413–424.

———. 1994. Ovule and seed characters of *Balanites aegyptiaca* and the classification of the Linales–Geraniales–Polygalales assembly. Acta Bot. Neerl. 43: 15–25.

——— & F. Bouman. 1980. Development of the ovule and seed-coat of *Dichapetalum mombuttense* Engl. with notes on other species. Acta Bot. Neerl. 29: 103–115.

Bohm, B. A. & J. Chan. 1992. Flavonoids and affinities of Greyiaceae with discussion of the occurrence of B-ring deoxyflavonoids in dicotyledonous families. Syst. Bot. 17: 272–281.

Boureau, E. 1958. Contribution à l'étude des espèces actuelles de Rhopalocarpaceae. Bull. Mus. Hist. Nat. sér. 2, 30: 213–221.

Brenner, G. J. 1990. An evolutionary model of angiosperm pollen evolution based on fossil angiosperm pollen from the Hauterivian of Israel. Amer. J. Bot. 77 (Suppl., 6): 82. [Abstract.]

———. 1996. Evidence for the earliest stage of angiosperm pollen evolution: A paleoequatorial section from Israel. Pp. 91–115 *in* D. W. Taylor & L. J. Hickey (editors), Flowering Plant Origin, Evolution and Phylogeny. Chapman & Hall, New York.

Brizicky, G. K. 1964. The genera of Cistaceae in the southeastern United States. J. Arnold Arbor. 45: 346–357.

Brüning, R. & H. Wagner. 1978. Uebersicht über die Celastraceen-Inhaltsstoffe: Chemie, Chemotaxonomie, Biosynthese, Pharmakologie. Phytochemistry 17: 1821–1858.

Burger, W. C. 1977. The Piperales and the monocots. Alternative hypotheses for the origin of monocotyledonous flowers. Bot. Rev. (Lancaster) 43: 345–393.

Canright, J. E. 1955. Comparative morphology and relationships of the Magnoliaceae—IV. Wood and nodal anatomy. J. Arnold Arbor. 36: 119–140.

Capuron, R. 1974. Une variété nouvelle d'*Asteropeia amblyocarpa* Tul., Théacée de Madagascar. Adansonia n. s. 14: 291–292.

Carlquist, S. 1964. Pollen morphology and evolution of Sarcolaenaceae (Chlaenaceae). Brittonia 16: 231–254.

———. 1976. Wood anatomy of *Myrothamnus flabellifolia* (Myrothamnaceae) and the problem of multiperforate perforation plates. J. Arnold Arbor. 119–126.

———. 1977. Wood anatomy of Tremandraceae: Phylogenetic and ecological implications. Amer. J. Bot. 64: 704–713.

———. 1981. Wood anatomy of Pittosporaceae. Allertonia 2: 355–391.

———. 1984a. Wood anatomy of Loasaceae with relation to systematics, habit and ecology. Aliso 10: 583–602.

———. 1984b. Wood anatomy of Polemoniaceae. Aliso 10: 547–572.

———. 1984c. Wood anatomy and relationships of Pentaphylacaceae: Significance of vessel features. Phytomorphology 34: 84–90.

———. 1984d. Wood and stem anatomy of *Bergia suffruticosa*: Relationships of Elatinaceae and broader significance of vascular tracheids, vasicentric tracheids, and fibriform vessel elements. Ann. Missouri Bot. Gard. 71: 232–242.

———. 1988a. Comparative Wood Anatomy. Springer, Berlin.

———. 1988b. Wood anatomy of Scytopetalaceae. Aliso 12: 63–76.

———. 1990. Wood anatomy and relationships of Lactoridaceae. Amer. J. Bot. 77: 1498–1505.

———. 1993. Wood anatomy of Sabiaceae (s.l.): Ecological and systematic implications. Aliso 13: 521–549.

——— & D. A. Hoekman. 1985. Ecological wood anatomy of the woody southern Californian Flora. I.A.W.A. Bull., N. S. 6: 319–347.

——— & E. J. Wilson. 1995. Wood anatomy of *Drosophyllum* (Droseraceae): Ecological and phylogenetic considerations. Bull. Torrey Bot. Club 122: 185–189.

Carpenter, C. S. & W. C. Dickison. 1976. The morphology and relationships of *Oncotheca balansae*. Bot. Gaz. 137: 141–153.

Carpenter, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.

Chase, M. W. & A. V. Cox. Gene sequences, collaboration, and analysis of large data sets. Austral. Syst. Bot. (in press).

——— & S. M. Swensen. 1995. Relationships of Violales sensu Cronquist from the perspective of cladistic analyses of *rbc*L sequence data. Amer. J. Bot. 82 (Suppl., 6): 119. [Abstract.]

———, M. D. Lledó, M. B. Crespo & S. M. Swensen. 1996. "When in doubt put it in the Flacourtiaceae": Molecular systematics of Flacourtiaceae. Amer. J. Bot. 83 (Suppl., 6): 146. [Abstract.]

———, D. W. Stevenson, P. Wilkin & P. J. Rudall. 1995. Monocot systematics: A combined analysis. Pp. 685–730 *in* P. J. Rudall, P. J. Cribb, D. F. Cutler & C. J. Humphries (editors), Monocotyledons: Systematics and Evolution. Royal Botanic Gardens, Kew.

———, D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Chiarugi, A. 1925. Embriologia delle Cistaceae. Nuovo Giorn. Bot. Ital. n.s. 32: 223–314.

——— & E. Francini. 1930. Apomissia in "*Ochna serratula*" Walp. Nuovo Giorn. Bot. Ital. n.s. 37: 1–250.

Chopra, R. N. & K. Harjinder. 1965. Embryology of *Bixa orellana* L. Phytomorphology 15: 211–214.

Conti, E., A. Fischbach & K. J. Sytsma. 1993. Tribal relationships in Onagraceae: Implications from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 672–685.

———, A. Litt & K. J. Sytsma. 1996. Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbc*L sequence data. Amer. J. Bot. 83: 221–233.

Cook, C. D. K. 1978. The *Hippuris* syndrome. Pp. 163–176 *in* H. E. Street (editor), Essays in Plant Taxonomy. Academic Press, London.

Corner, E. J. H. 1946. Centrifugal stamens. J. Arnold Arbor. 27: 423–437.

———. 1976. The Seeds of Dicotyledons, Vols. 1 and 2. Cambridge Univ. Press, Cambridge.

Crane, P. R. 1989. Paleobotanical evidence of the early radiation of nonmagnoliid dicotyledons. Pl. Syst. Evol. 162: 165–191.

———, E. M. Friis & K. R. Pedersen. 1995. The origin and early diversification of angiosperms. Nature 374: 27–33.

———, K. R. Pedersen, E. M. Friis & A. N. Drinnan. 1993. Early Cretaceous (Early to middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac group of eastern North America. Syst. Bot. 18: 328–344.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1983. Some realignments in the dicotyledons. Nordic J. Bot. 3: 75–83.

Crossley, N. S. & C. Djerassi. 1962. Naturally occurring oxygen heterocyclics. Part XI. Veraguensin. J. Chem. Soc. 1962: 1459–1462.

Cuatrecasas, J. 1985. Brunelliaceae. Fl. Neotrop. Monogr. 2 (Suppl.): 1–189.

Czaja, A. T. 1969. Mikroskopie der Stärkekörner. Parey, Berlin.

———. 1978. Stärke und Stärkekörner bei Gefässpflanzen. Fischer, Stuttgart.

Dahlgren, R. M. T. 1980. A revised system of classification of angiosperms. Bot. J. Linn. Soc. 80: 91–124.

———. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

——— & H. T. Clifford. 1982. The Monocotyledons: A Comparative Study. Academic Press, London.

——— & V. S. Rao. 1969. A study of the family Geissolomataceae. Bot. Not. 122: 207–227.

——— & R. F. Thorne. 1984. The order Myrtales: Circumscription, variation, and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

———, H. T. Clifford & P. F. Yeo. 1985. The Families of the Monocotyledons. Structure, Evolution, and Taxonomy. Springer, Berlin.

Davis, G. L. 1966. Systematic Embryology of the Angiosperms. Wiley & Sons, New York.

Dechamps, R. 1979–1985. Étude anatomique de bois d'Amérique du Sud, Vols. 1–3. Musée Royal de l'Afrique Centrale, Trevuren.

Decker, J. M. 1966. Wood anatomy and phylogeny of Luxemburgieae (Ochnaceae). Phytomorphology 16: 39–55.

Den Outer, R. W. & A. P. Vooren. 1980. Bark anatomy of some Sarcolaenaceae and Rhopalocarpaceae and their systematic position. Meded. Landbouwhoogeschool 80(6): 3–15.

DeVries, P. 1987. The Butterflies of Costa Rica and Their Natural History. Princeton Univ. Press, Princeton.

Deyama, T., T. Ikawa & S. Nishibe. 1985. The constituents of *Eucommia ulmoides* Oliv. II. Isolation and structures of three new lignan glycosides. Chem. Pharm. Bull. 33: 3651–3657.

Dickison, W. C. 1969. Comparative morphological studies in Dilleniaceae. VI. Stamens and young stem. J. Arnold Arbor. 51: 403–418.

———. 1978. Comparative anatomy of Eucryphiaceae. Amer. J. Bot. 65: 722–735.

———. 1979. A survey of pollen morphology of the Connaraceae. Pollen & Spores 21: 31–79.

———. 1981. Contributions to the morphology and anatomy of *Strasburgeria* and a discussion of the taxonomic position of the Strasburgeriaceae. Brittonia 33: 564–580.

———. 1986. Further observations on the floral anatomy and pollen morphology of *Oncotheca* (Oncothecaceae). Brittonia 38: 249–259.

———. 1990. The morphology and relationships of *Medusagyne* (Medusagynaceae). Pl. Syst. Evol. 171: 27–55.

———& P. Baas. 1977. The morphology and relationships of *Paracryphia* (Paracryphiaceae). Blumea 23: 417–438.

———, J. W. Nowicke & J. J. Skvarla. 1982. Pollen morphology of the Dilleniaceae and Actinidiaceae. Amer. J. Bot. 69: 1055–1073.

Dilcher, D. L. 1989. The occurrence of fruits with affinities to Ceratophyllaceae in Lower and Mid-Cretaceous sediments. Amer. J. Bot. 76 (Suppl., 6): 162. [Abstract.]

——— & P. R. Crane. 1984. *Archaeanthus*: An early angiosperm from the Cenomanian of the Western Interior of North America. Ann. Missouri Bot. Gard. 71: 351–383.

Ditsch, F. & W. Barthlott. 1994. Mikromorphologie der

Epikuticularwachse und die Systematik der Dilleniales, Lecythidales, Malvales und Theales. Trop. Subtrop. Pflanzenwelt 88: 1–74.

Domínguez, X. A., B. G. Espinoza, C. Rombold, W. Utz & H. Achenbach. 1992. Neolignans, norneolignans, and other compounds from *Krameria sonorae*. J. Med. Pl. Res. 58: 382–383.

Donoghue, M. J. & J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 17–46 *in* P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae, Vol. 1. Clarendon Press, Oxford.

Downie, S. R. & J. D. Palmer. 1994. A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. Syst. Bot. 19: 236–252.

Doyle, J. A. 1994. Origin of the angiosperm flower: A phylogenetic perspective. Pl. Syst. Evol., Suppl. 8: 7–29.

———. 1996. Seed plant phylogeny and the relationships of Gnetales. Int. J. Pl. Sci. 157 (Suppl., 6): S3–S39.

——— & L. J. Hickey. 1975. Pollen and leaves from the Mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139–206 *in* C. B. Beck (editor), Origin and Early Evolution of the Angiosperms. Columbia Univ. Press, New York.

———, C. L. Hotton & J. V. Ward. 1990. Early Cretaceous tetrads, zonasulcate pollen, and Winteraceae. II. Cladistic analysis and implications. Amer. J. Bot. 77: 1558–1568.

———, J. M. Donoghue & E. A. Zimmer. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. Ann. Missouri Bot. Gard. 81: 419–450.

Drinnan, A. N., P. R. Crane & S. B. Hoot. 1994. Patterns of floral evolution in the early diversification of non-magnoliid dicotyledons (eudicots). Pl. Syst. Evol., Suppl. 8: 93–122.

———, ———, E. M. Friis & K. R. Pedersen. 1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (Mid-Cretaceous) of Eastern North America. Amer. J. Bot. 78: 153–176.

Drude, O. 1891a. Clethraceae. Pp. 1–2 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 1st ed., Vol. IV/1. Engelmann, Leipzig.

———. 1891b. Ericaceae. Pp. 15–65 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 1st ed., Vol. IV/1. Engelmann, Leipzig.

———. 1891c. Epacridaceae. Pp. 66–84 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 1st ed., Vol. IV/1. Engelmann, Leipzig.

Durand, R. & M. H. Zenk. 1974. The homogenisate ring-cleavage pathway in the biosynthesis of acetate-derived naphthoquinones of the Droseraceae. Phytochemistry 13: 1483–1492.

Duvall, M. R., G. H. Learn, L. E. Eguiarte & M. T. Clegg. 1993a. Phylogenetic analysis of *rbc*L sequences identifies *Acorus calamus* as the primal extant monocotyledon. Proc. Natl. Acad. Sci. U.S.A. 90: 4641–4644.

———, M. T. Clegg, M. W. Chase, W. D. Clark, W. J. Kress, H. G. Hills, L. E. Eguiarte, J. F. Smith, B. S. Gaut, E. A. Zimmer & G. H. Learn, Jr. 1993b. Phylogenetic hypotheses for the monocotyledons constructed from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 607–619.

Ehrendorfer, F., W. Morawetz & J. Dawe. 1984. The neotropical angiosperm families Brunelliaceae and Caryocaraceae: First caryosystematical data and affinities. Pl. Syst. Evol. 145: 183–192.

Eklund, H., E. M. Friis & K. R. Pedersen. 1997. Chloranthaceous floral structures from the Late Cretaceous of Sweden. Pl. Syst. Evol. 207: 13–42.

Endress, P. K. 1980. The reproductive structures and systematic position of the Austrobaileyaceae. Bot. Jahrb. Syst. 101: 393–433.

———. 1986. Floral structure, systematics, and phylogeny in Trochodendrales. Ann. Missouri Bot. Gard. 73: 297–324.

———. 1987. The Chloranthaceae: Reproductive structures and phylogenetic position. Bot. Jahrb. Syst. 109: 153–226.

———. 1989. Aspects of evolutionary differentiation of the Hamamelidaceae and the Lower Hamamelididae. Pl. Syst. Evol. 162: 193–211.

———. 1993a. Austrobaileyaceae. Pp. 138–140 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———. 1993b. Cercidiphyllaceae. Pp. 250–252 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———. 1993c. Eupomatiaceae. Pp. 296–298 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———. 1994a. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge Univ. Press, Cambridge.

———. 1994b. Evolutionary aspects of the floral structure in *Ceratophyllum*. Pl. Syst. Evol., Suppl. 8: 175–183.

———. 1994c. Floral structure and evolution of primitive angiosperms: Recent advances. Pl. Syst. Evol. 192: 79–97.

———. 1994d. Shapes, sizes and evolutionary trends in stamens of Magnoliidae. Bot. Jahrb. Syst. 115: 429–460.

——— & A. Igersheim. 1997. Gynoecium diversity and systematics of the Laurales. Bot. J. Linn. Soc. 125: 93–168.

——— & S. Stumpf. 1991. The diversity of stamen structures in "Lower" Rosidae (Rosales, Fabales, Proteales, Sapindales). Bot. J. Linn. Soc. 107: 217–293.

Engler, A. 1891. Saxifragaceae. Pp. 41–93 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed. III., Vol. 2a. Engelmann, Leipzig.

———. 1925. Quiinaceae. Pp. 106–108 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

———. 1930. Cunoniaceae. Pp. 229–262 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 18a. Engelmann, Leipzig.

——— & H. Melchior. 1925. Medusagynaceae. Pp. 50–52 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

——— & K. Prantl (editors). 1887–1914. Die natürlichen Pflanzenfamilien, 1st ed. Engelmann, Leipzig.

——— & ——— (editors). 1924–1995. Die natürlichen Pflanzenfamilien, 2nd ed. Engelmann, Leipzig.

Erbar, C. & P. Leins. 1996. Distribution of the character states "early sympetaly" and "late sympetaly" within the "Sympetalae tetracyclicae" and presumably allied groups. Bot. Acta 109: 427–440.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy. An Introduction to Palynology. I. Angiosperms. Almqvist & Wiksell, Stockholm.

———. 1958. A note on the pollen morphology in the Ancistrocladaceae and Dioncophyllaceae. Veröff. Geobot. Inst. Rübel Zürich 33: 47–49.

Fairbrothers, D. E. 1966. Serological correspondence of the genus *Corokia* with taxa of the Cornaceae, Nyssaceae and Garryaceae. Amer. J. Bot. 53: 637–638.

Farr, D. F., G. F. Bills, G. P. Chamuris & A. Y. Rossman. 1989. Fungi on Plants and Plant Products in the United States. American Phytopathological Society Press, St. Paul.

Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.

———, V. A. Albert, M. Kallersjö, D. Lipscomb & A. G. Kluge. 1997. Parsimony jackknifing outperforms neighbour-joining. Cladistics 12: 99–124.

Fay, M. F., S. M. Swensen & M. W. Chase. 1997. Taxonomic affinities of *Medusagyne oppositifolia* (Medusagynaceae). Kew Bull. 52: 11–120.

Fehrenbach, S. & W. Barthlott. 1988. Mikromorphologie der Epicuticular-Wachse der Rosales s. l. und deren systematische Gliederung. Bot. Jahrb. Syst. 109: 407–428.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

Fernando, E. S., P. A. Gadek & C. J. Quinn. 1995. Simaroubaceae, an artificial construct: Evidence from *rbc*L sequence variation. Amer. J. Bot. 82: 92–103.

Fieser, L. F. & E. M. Chamberlain. 1948. Synthesis of embelin, rapanone and related quinones by peroxide alkylation. J. Amer. Chem. Soc. 70: 71–75.

Filho, W. W., A. I. Da Rocha, M. Yoshida & O. R. Gottlieb. 1985. Ellagic acid derivatives from *Rhabdophyllum macrophyllum*. Phytochemistry 24: 1991–1997.

Fitch, W. M. 1971. Toward defining the course of evolution: Minimal change for a specific tree topology. Syst. Zool. 20: 406–416.

Foster, A. S. & H. J. Arnott. 1960. Morphology and dichotomous vasculature of the leaf of *Kingdonia uniflora*. Amer. J. Bot. 47: 684–698.

Franceschi, V. R. & H. T. Horner, Jr. 1980. Calcium oxalate crystals in plants. Bot. Rev. (Lancaster) 46: 361–428.

Frehner, M., M. Scalet & E. E. Conn. 1990. Pattern of the cyanide-potential in developing fruits. Implications for plants accumulating cyanogenic monoglucosides (*Phaseolus lunatus*) or cyanogenic diglucosides in their seeds (*Linum usitatissimum*, *Prunus amygdalus*). Pl. Physiol. (Lancaster) 94: 28–34.

Friis, E. M. 1984. Preliminary report of Upper Cretaceous angiosperm reproductive organs from Sweden and their level of organization. Ann. Missouri Bot. Gard. 71: 403–418.

——— & P. K. Endress. 1990. Origin and evolution of angiosperm flowers. Advances Bot. Res. 17: 99–162.

———, K. R. Pedersen & P. R. Crane. 1994. Angiosperm floral structures from the Early Cretaceous of Portugal. Pl. Syst. Evol., Suppl. 8: 31–49.

Gadek, P. A., C. J. Quinn, J. E. Rodman, K. G. Karol, E. Conti, R. A. Price & E. S. Fernando. 1992. Affinities of the Australian endemic Akaniaceae: New evidence from *rbc*L sequences. Austral. Syst. Bot. 5: 717–724.

———, E. S. Fernando, C. J. Quinn, S. B. Hoot, T. Terrazas, M. C. Sheahan & M. W. Chase. 1996. Sapindales: Molecular delimitation and infraordinal groups. Amer. J. Bot. 83: 802–811.

Gagnepain, F., H. Humbert & H. Leconte (editors). 1907–1942. Flore générale de l'Indo-Chine. 8 Vols. Masson, Paris.

Garratt, G. A. 1933. Systematic anatomy of the woods of the Myristicaceae. Trop. Woods 35: 6–47.

Gavrilova, O. A. 1993. Types of pollen grain sculpture and their significance for systematics of the family Flacourtiaceae. Bot. Zhurn. (Moscow & Leningrad) 12: 45–52. [In Russian.]

Geetha, K., I. Umadevi & M. Daniel. 1993. Primulales—A reassessment of the taxonomy and phylogeny of the group. Feddes Repert. 104: 67–71.

Giannasi, D. E., G. Zurawski, G. Learn & M. T. Clegg. 1992. Evolutionary relationships of the Caryophyllidae based on comparative *rbc*L sequences. Syst. Bot. 17: 1–15.

Gibbs, R. D. 1974. Chemotaxonomy of Flowering Plants, Vols. 1–4. McGill-Queens, Montreal.

Gildemeister, E. & F. Hoffmann. 1956. Die ätherischen Oele, 4th ed. Akademie Verlag, Berlin.

Gilg, E. 1925. Ochnaceae. Pp. 53–87 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

Goldblatt, P. & L. J. Dorr. 1986. Chromosome number in Sarcolaenaceae. Ann. Missouri Bot. Gard. 73: 828–829.

——— & D. E. Johnson (editors). 1981/1984/1985/1988/1990/1991/1994. Index to Plant Chromosome Numbers. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–533, 8: 1–427, 13: 1–224, 23: 1-264, 30: 1–243, 40: 1–238, 51: 1–267.

Gore, U. R. 1935. Morphogenetic studies on the inflorescence of cotton. Bot. Gaz. 97: 118–138.

Gottlieb, O. R., M. A. C. Kaplan, K. Kubitzki & J. R. Toledo Barros. 1988. Chemical dichotomies in the magnolialean complex. Nordic J. Bot. 8: 437–444.

Gottwald, H. & N. Parameswaran. 1966. Das sekundäre Xylem der Familie Dipterocarpaceae. Anatomische Untersuchungen zur Taxonomie und Phylogenie. Bot. Jahrb. Syst. 85: 410–508.

——— & ———. 1967. Beiträge zur Anatomie und Systematik der Quiinaceae. Bot. Jahrb. Syst. 87: 361–381.

——— & ———. 1968. Das sekundäre Xylem und die systematische Stellung der Ancistrocladaceae und Dioncophyllaceae. Bot. Jahrb. Syst. 88: 49–69.

Graur, D., L. Duret & M. Guoy. 1996. Phylogenetic postition of the order Lagomorpha (rabbit, hares, and allies). Nature 379: 333–335.

Grund, C. & U. Jensen. 1981. Systematic relationships of the Saxifragales revealed by serological characteristics of seed proteins. Pl. Syst. Evol. 137: 1–22.

Gustafsson, M. H. G. & K. Bremer. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Gutzwiller, M. A. 1961. Die phylogenetische Stellung von *Suriana maritima* L. Bot. Jahrb. Syst. 81: 1–49.

Haber, J. M. 1959. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. I. Some Australian taxa. Phytomorphology 9: 325–358.

———. 1961. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. II. Some American taxa. Phytomorphology 11: 1–16, 16: 490–527.

———. 1966. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. III. Some African taxa. Phytomorphology 16: 490–527.

Hagemann, W. 1970. Studien zur Entwicklungsgeschichte der Angiospermenblätter. Ein Beitrag zur Klärung ihres Gestaltungsprinzips. Bot. Jahrb. Syst. 90: 297–413.

——— & S. Gleissberg. 1996. Organogenetic capacity of leaves: The significance of marginal blastozones in angiosperms. Pl. Syst. Evol. 199: 121–152.

Hallier, H. 1914. Der Stammbaum des Pflanzenreichs. 14pp. *in* L. Reinhardt (editor), Vom Nebelfleck zum Menschen, 2nd ed., Vols. 2 and 3. Verlagsbuchhandlung Reinhardt, München.

Harborne, J. B. 1969. Occurrence of flavonol 5-methylethers in higher plants and their systematic significance. Phytochemistry 8: 419–423.

——— & H. Baxter. 1993. Phytochemical Dictionary. A Handbook to Bioactive Compounds from Plants. Taylor & Francis, London.

Hayashi, H., M. Sholichin, T. Sakao, Y. Yamamura & H. Komae. 1980. An approach to chemotaxonomy of the *Asarum* subgenus *Heterotropa*. Biochem. Syst. & Ecol. 8: 109–113.

Heel, W. A. van. 1966. Morphology of the androecium in Malvales. Blumea 13: 177–394.

———. 1967. Anatomical and ontogenetic investigations on the morphology of the flowers and the fruit of *Scyphostegia borneensis* Stapf (Scyphostegiaceae). Blumea 15: 107–125.

———. 1984. Flowers and fruits in Flacourtiaceae. V. The seed anatomy and pollen morphology of *Berberidopsis* and *Streptothamnus*. Blumea 30: 31–37.

Hegnauer, R. 1962–1994. Chemotaxonomie der Pflanzen. 1–11a. Birkhäuser, Basel.

Heimsch, C., Jr. 1942. Comparative anatomy of the secondary xylem in the Gruinales and Terebinthales of Wettstein with reference to taxonomic grouping. Lilloa 8: 83–198.

Heinig, K. H. 1951. Studies in the floral morphology of the Thymelaeaceae. Amer. J. Bot. 38: 113–132.

Hekking, W. H. A. 1988. Violaceae. Part I—*Rinorea* and *Rinoreocarpus*. Fl. Neotrop. Monogr. 46: 1–207.

Hennig, S., W. Barthlott, I. Meusel & I. Theisen. 1994. Mikromorphologie der Epicuticularwachse und die Systematik der Magnoliidae, Ranunculidae und Hamamelididae. Trop. Subtrop. Pflanzenwelt 90: 1–60.

Heo, K. & H. Tobe. 1994. Embryology and relationships of *Suriana maritima* L. (Surianaceae). J. Pl. Res. 107: 29–37.

Heywood, V. H. (editor). 1978. Flowering Plants of the World. Oxford Univ. Press, Oxford.

Hickey, L. J. & J. A. Wolfe. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hideux, M. J. & I. K. Ferguson. 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae s.l. Pp. 327–378 *in* I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Academic Press, New York.

Hill, A. E. & B. S. Hill. 1976. Mineral Ions. Pp. 225–243 *in* U. Lüttge & M. G. Pitman (editors): Encyclopedia of Plant Physiology. New Series. Vol. 2: Transport in Plants II, Part B, Tissues and Organs. Springer, Berlin.

Hillebrand, G. R. & D. E. Fairbrothers. 1966. Phytoserological systematic studies of selected genera of the Rubiales and Umbellales. Amer. J. Bot. 53: 638.

——— & ———. 1970. Serological investigation on the systematic position of the Caprifoliaceae. I. Correspondence with selected Rubiaceae and Cornaceae. Amer. J. Bot. 57: 810–815.

Hillis, D. M. 1996. Inferring complex phylogenies. Nature 383: 130–131.

Hirmer, M. 1918. Beiträge zur Morphologie der polyandrischen Blüten. Flora 110: 140–192.

Huang, T-C. 1972. Pollen Flora of Taiwan. National Taiwan Univ., Botany Department Press.

Huber, H. 1991. Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer. Fischer, Stuttgart.

———. 1993. Aristolochiaceae. Pp. 129–137 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Hufford, L. D. 1992. Rosidae and their relationships to other nonmagnoliid dicotyledons: A phylogenetic analysis using morphological and chemical data. Ann. Missouri Bot. Gard. 79: 218–248.

———. 1996. The morphology and evolution of male reproductive structures of Gnetales. Int. J. Pl. Sci. 157: S95–S112.

——— & P. K. Endress. 1989. The diversity of anther structures and dehiscence patterns among Hamamelididae. Bot. J. Linn. Soc. 99: 301–346.

Humphrey, R. R. 1935. A study of *Idria columnaris* and *Fouquieria splendens*. Amer. J. Bot. 22: 184–207.

Hutchinson, J. 1964/1967. The Genera of Flowering Plants. Dicotyledons. Vols. 1 and 2. Clarendon Press, Oxford.

———. 1973. The Families of Flowering Plants Arranged According to a New System Based on Their Probable Phylogeny, 3rd ed. Clarendon Press, Oxford.

Huynh, K.-L. 1969. Etude du pollen des Oxalidaceae. Bot. Jahrb. Syst. 89: 272–303.

Ilic, J. 1991. CSIRO Atlas of Hardwoods. Springer, Berlin.

Ionescu, F., S. D. Jolad & J. R. Cole. 1977. Dehydrodiisoeugenol: A naturally occurring lignan from *Aristolochia taliscana* (Aristolochiaceae). J. Pharm. Sci. 66: 1489–1490.

Jäger-Zürn, I. 1966. Infloreszenz- und blütenmorphologische, sowie embryologische Untersuchungen an *Myrothamnus* Welw. Beitr. Biol. Pflanzen 42: 241–271.

Janchen, E. 1909. Die Cistaceen Oesterreich-Ungarns. Mitt. Naturwiss. Vereins Univ. Wien 7: 1–124.

———. 1925. Cistaceae. Pp. 289–313 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

Jensen, S. R., S. E. Lyse-Pedersen & B. J. Nielsen. 1979. Novel *bis*-iridoid glucosides from *Dipsacus sylvestris*. Phytochemistry 18: 273–277.

Jensen, U. & B. Greven. 1984. Serological aspects and phylogenetic relationships of the Magnoliidae. Taxon 33: 563–577.

John, J. & K. P. Kolbe. 1980. The systematic position of the "Theales" from the viewpoint of serology. Biochem. Syst. & Ecol. 8: 241–248.

Johri, B. M. 1970. Symposium on comparative embryology of angiosperms. Proc. Indian Natl. Sci. Acad., B 41: 1–385.

——— & D. Kak. 1954. The embryology of *Tamarix* L. Phytomorphology 4: 230–247.

———, K. B. Ambegoakar & P. S. Srivastava. 1992. Comparative Embryology of Angiosperms, Vols. 1 and 2. Springer, Berlin.

———, R. N. Kapil, S. P. Bhatnagar, N. N. Bhandari & M. R. Vijayaraghavan (editors). 1967. Seminar on

Comparative Embryology of Angiosperms. Department of Botany, Univ. Press, Delhi.

Juniper, B. E., R. J. Robins & D. M. Joel. 1989. The Carnivorous Plants. Academic Press, London.

Kamelina, O. P., V. A. Poddubnaya-Arnoldi, A. L. Takhtajan, M. S. Yakovlev & G. Y. Zhukova. 1983. Comparative Embryology of the Flowering Plants. Phytolaccaceae–Thymelaeaceae. Nauka, Leningrad. [In Russian.]

———, ———, I. D. Romanov, A. L. Takhtajan, M. S. Yakovlev & G. Y. Zhukova. 1981. Comparative Embryology of the Flowering Plants. Winteraceae–Juglandaceae. Nauka, Leningrad. [In Russian.]

Kanis, A. 1968. A revision of the Ochnaceae of the Indo-Pacific Area. Blumea 16: 1–82.

Kapil, R. N. & A. K. Bhatnagar. 1991. Embryological evidence in angiosperm classification and phylogeny. Bot. Jahrb. Syst. 113: 309–338.

——— & R. Maheshwari. 1965. Embryology of *Helianthemum vulgare* Gaertn. Phytomorphology 14: 547–557.

Kaur, H. 1969. Embryological investigations on *Bixa orellana* L. Proc. Natl. Inst. Sci. India 35: 487–506.

Keating, R. C. 1972. The comparative morphology of the Cochlospermaceae. III. The flower and pollen. Ann. Missouri Bot. Gard. 59: 282–296.

———. 1975. Trends of specialization in pollen of Flacourtiaceae with comparative observations of Cochlospermaceae and Bixaceae. Grana 15: 29–49.

Keefe, J. M. & M. F. Moseley. 1978. Wood anatomy and phylogeny of *Paeonia* section *Moutan*. J. Arnold Arbor. 59: 274–297.

Keller, K. 1982. Untersuchungen zum ß-Asarongehalt handelsüblicher Kalmusdrogen sowie zu den Inhaltsstoffen des asaronfreien Kalmus. Unpublished Ph.D. Thesis, University of Saarbrücken.

Keng, H. 1962. Comparative morphological studies in Theaceae. Univ. Calif. Publ. Bot. 33: 269–383.

Kessler, P. J. A. 1993. Menispermaceae. Pp. 93–128 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Klucking, E. P. 1986/1987/1988/1989/1991/1992/1995. Leaf Venation Patterns. 1. Annonaceae/ 2. Lauraceae/ 3. Myrtaceae/ 4. Melastomataceae/ 5. Combretaceae/ 6. Flacourtiaceae/ 7. The Classification of Leaf Venation Patterns. Cramer, Stuttgart.

Kobuski, C. E. 1951. Studies in the Theaceae, XXIII. The genus *Pelliciera*. J. Arnold Arbor. 32: 256–262.

Köhler, E. 1994. Parallel evolution of pollen characters in the genus *Buxus* L. (Buxaceae). Acta Bot. Gallica 141: 223–232.

Kolbe, K. P. & J. John. 1979a. Serologische Untersuchungen zur Systematik der Violales. Bot. Jahrb. Syst. 101: 3–15.

——— & ———. 1979b. Serology and systematics of the Ebenales and Theales. Biochem. Syst. & Ecol. 8: 249–256.

Kostermans, A. J. G. H. 1985. Family status for the Monotoideae Gilg and the Pakaraimoideae Ashton, Maguire and de Zeeuw (Dipterocarpaceae). Taxon 34: 426–435.

Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. 96: 547–557.

Kron, K. A. & M. W. Chase. 1993. Systematics of the Ericaceae, Empetraceae, Epacridaceae and related taxa based upon *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 735–741.

Kubitzki, K. 1993a. Calycanthaceae. Pp. 197–200 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———. 1993b. Canellaceae. Pp. 200–203 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———. 1993c. Degeneriaceae. Pp. 290–291 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———, P. von Sengbush & H.-H. Poppendieck. 1991. Parallelism, its evolutionary origin and systematic significance. Aliso 13: 191–206.

Kuprianova, L. A. 1979. On the possibility of the development of tricolpate pollen from monosulcate. Grana 18: 1–4.

Landsmann, J., E. S. Dennis, T. J. V. Higgins, C. A. Appleby, A. A. Kortt & W. J. Peacock. 1986. Common evolutionary origin of legume and non-legume plant haemoglobins. Nature 324: 166–168.

Lavault, M. & J. Bruneton. 1980. Isolement de deux nouveaux alcaloïdes, triphyopeltine et O-méthyl-5'triphyopeltine. J. Med. Pl. Res. 38, Suppl.: 17–21.

Le Quesne, P. W., J. E. Larrahondo & R. F. Raffauf. 1980. Antitumor plants. X. Constituents of *Nectandra rigida*. J. Nat. Prod. (Lloydia) 43: 353–359.

Lebreton, P. & M. P. Bouchez. 1967. Recherches chimiotaxonomiques sur les plantes vasculaires 5. Distribution des composés polyphénoliques chez les Pariétales. Phytochemistry 6: 1601–1608.

Leenhouts, P. W. 1956. Some notes on the genus *Dichapetalum* (Dichapetalaceae) in Asia, Australia, and Melanesia. Reinwardtia 4: 75–87.

Lemke, D. E. 1988. A synopsis of Flacourtiaceae. Aliso 12: 29–43.

Les, D. H. 1988. The origin and affinities of the Ceratophyllaceae. Taxon 37: 326–345.

———. 1993. Ceratophyllaceae. Pp. 246–250 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

———& C. T. Philbrick. 1996. The phylogeny of riverweeds (Podostemaceae): Insights from *rbc*L sequence data. Amer. J. Bot. 83: 174. [Abstract.]

———, D. K. Garvin & C. F. Wimpee. 1991. Molecular evolutionary history of ancient aquatic angiosperms. Proc. Natl. Acad. Sci. U.S.A. 88: 10119–10123.

Letouzey, R. 1961. Notes sur les Scytopetalacées (Révision des Scytopétalacées de l'herbier de Paris). Adansonia n. s., 1: 106–142.

Levin, G. A. 1986. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

Lin, C. M., Z. Q. Liu & S. D. King. 1986. *Nicotiana* chloroplast genome: X. Correlation between the DNA sequences and the isoeletric focusing pattern of the LS of rubisco. Pl. Molec. Biol. 6: 81–87.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40: 315–328.

Maddison, W. P. & D. R. Maddison. 1992. MacClade, Version 3. Analysis of Phylogeny and Character Evolution. Sinauer, Sunderland, Massachusetts.

Maguire, B. & P. S. Ashton. 1980. *Pakaraimaea dipterocarpacea* II. Taxon 29: 225–231.

——— et al. 1972. Botany of the Guyana Highland—Part IX. Tetrameristaceae. Mem. New York Bot. Gard. 23: 165–192.

Martius, C. F. P. von (editor). 1840–1906. Flora Brasiliensis: enumeratio plantarum in Brasilia, Vols. 1–15. Fleischer, München.

Mauritzon, J. 1935. Zur Embryologie der Elaeocarpaceae. Ark. Bot. 26A (10): 1–8.

———. 1936. Zur Embryologie und systematischen Abgrenzung der Reihen Terebinthales und Celastrales. Bot. Not. 1936: 161–211.

Maury, G., J. Muller & B. Lugardon. 1975. Notes on the morphology and fine structure of the exine of some pollen types in Dipterocarpaceae. Rev. Palaeobot. Palynol. 19: 241–289.

Mc Nair, J. B. 1930. The taxonomic and climatic distribution of oil and starch in seeds in relation to the physical and chemical properties of both substances. Amer. J. Bot. 17: 662–668.

McAlpine, J. B., N. V. Riggs & (in part) P. G. Gordon. 1968. Absolute stereochemistry of calopiptin. Austral. J. Chem. 21: 2095–2106.

Melchior, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien. II. Bornträger, Berlin.

Mennega, A. M. W. 1982. Stem structure of the New World Menispermaceae. J. Arnold Arbor. 63: 145–171.

Metcalfe, C. R. 1952. *Medusandra richardsiana* Brenan. Anatomy of the leaf, stem and wood. Kew Bull. 9: 237–246.

———. 1956. *Scyphostegia borneensis* Stapf. Anatomy of stem and leaf in relation to its taxonomic position. Reinwardtia 4: 99–104.

———. 1962. Notes on the systematic anatomy of *Whittonia* and *Peridiscus*. Kew Bull. 15: 472–475.

———. 1987. Anatomy of the Dicotyledons, 2nd ed., Vol. 3. Magnoliales, Illiciales, and Laurales. Clarendon Press, Oxford.

———& L. Chalk. 1950. Anatomy of the Dicotyledons. Leaves, Stem, and Wood in Relation to Taxonomy with Notes on Economic Uses, 1st ed., Vols. 1 and 2. Clarendon Press, Oxford.

——— & L. Chalk. 1988/1989. Anatomy of the Dicotyledons, 2nd ed., Vols. 1 and 2. Oxford Univ. Press, Oxford.

Meylan, B. A. & B. G. Butterfield. 1978. The structure of New Zealand woods. New Zealand Dept. Sci. Industr. Res. Inform. Ser. 222: 1–250.

Miller, R. B. 1975. Systematic anatomy of the xylem and comments on the relationships of Flacourtiaceae. J. Arnold Arbor. 56: 20–102.

Mkpong, O. E., H. Yan, G. Chism & R. T. Sayre. 1990. Purification, characterization and localization of linamarase in Cassava. Pl. Physiol. (Lancaster). 93: 176–181.

Morawetz, W. 1981. Zur systematischen Stellung der Gattung *Prockia*: Karyologie und Epidermisstruktur im Vergleich zu *Flacourtia* (Flacourtiaceae), *Grewia* (Tiliaceae) und verwandten Gattungen. Pl. Syst. Evol. 139: 57–76.

Morgan, D. R. & D. E. Soltis. 1993. Phylogenetic relationships among members of Saxifragaceae sensu lato based on *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 631–660.

———, ——— & K. R. Robertson. 1994. Systematic and evolutionary implications of *rbc*L sequence variation in Rosaceae. Amer. J. Bot. 81: 890–903.

Morton, C. M. 1995. A new genus and species of Dipterocarpaceae from the Neotropics. II. Stem anatomy. Brittonia 47: 237–247.

———, S. A. Mori, G. T. Prance, K. G. Karol & M. W. Chase. 1997. Phylogenetic relationships of Lecythidaceae: A cladistic analysis using *rbc*L sequence and morphological data. Amer. J. Bot. 84: 530–540.

Murai, F., M. Tagawa, S. Matsuda, T. Kikuchi, S. Uesato & H. Inouye. 1985. Abeliosides A and B, secoiridoid glucosides from *Abelia grandiflora*. Phytochemistry 24: 2329–2335.

Nandi, O. I. 1998a. Ovule and seed anatomy of Cistaceae and related Malvanae. Pl. Syst. Evol. (in press).

———. 1998b. Floral development and systematics of Cistaceae. Pl. Syst. Evol. (in press).

Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. Bornträger, Berlin.

Nickrent, D. L. 1996. Phylogenetic relationships of parasitic Santalales and Rafflesiales inferred from 18S rRNA sequences. Amer. J. Bot. 83 (Suppl., 6): 212. [Abstract.]

Nixon, K. C. & J. I. Davis. 1991. Polymorphic taxa, missing values, and cladistic analysis. Cladistics 7: 233–241.

———, W. L. Crepet, D. Stevenson & E. M. Friis. 1994. A reevaluation of seed plant phylogeny. Ann. Missouri Bot. Gard. 81: 484–533.

Olmstead, R. G., B. Bremer, K. M. Scott & J. D. Palmer. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbc*L sequences. Ann. Missouri Bot. Gard. 80: 700–722.

———, H. J. Michaels, K. M. Scott & J. D. Palmer. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Ann. Missouri Bot. Gard. 79: 249–265.

Oxelman, B. & M. Lidén. 1995. The position of *Circaeaster*—Evidence from nuclear ribosomal DNA. Pl. Syst. Evol., Suppl. 9: 189–193.

Payer, J.-B. 1857. Traité d'organogénie comparée de la fleur. Masson, Paris.

Philipson, W. R. 1993. Amborellaceae. Pp. 92–93 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Piccioli, L. 1901. Il legno e la corteccia delle Cistacee. Nuovo Giorn. Bot. Ital. n.s. 8: 473–504.

Pierre, J. 1984. Systématique évolutive cladistique et mimétisme chez les lépidoptères du genre *Acraea*. Unpublished Ph.D. Thesis, University of Paris.

Pilger, R. 1925a. Bixaceae. Pp. 313–315 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

———. 1925b. Cochlospermaceae. Pp. 316–320 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.

Prance, G. T. 1968. The systematic position of *Rhabdodendron* Gilg & Pilg. Bull. Jard. Bot. Belg. 38: 127–146.

———. 1972. Rhabdodendraceae. Fl. Neotrop. Monogr. 11: 1–21.

———& M. F. da Silva. 1973. Caryocaraceae. Fl. Neotrop. Monogr. 12: 1–75.

Price, R. A. & J. D. Palmer. 1993. Phylogenetic relationships of the Geraniaceae and Geraniales from *rbc*L sequence comparisons. Ann. Missouri Bot. Gard. 80: 661–671.

Proctor, M. C. F. 1955. Some chromosome counts in the European Cistaceae. Watsonia 3: 154–159.

Puff, C. & A. Weber. 1976. Contributions to the morphology, anatomy, and karyology of *Rhabdodendron*, and a reconsideration of the systematic position of the Rhabdodendraceae. Pl. Syst. Evol. 125: 195–221.

Qiu, Y.-L., M. W. Chase, D. H. Les & C. R. Parks. 1993.

Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 587–606.

Rao, K. V. & F. M. Alvarez. 1982. Chemistry of *Saururus cernuus*. I. Saucernetin, a new neolignan. J. Nat. Prod. (Lloydia) 45: 393–397.

Rao, T. A. 1991. Compendium of Foliar Sclereids in Angiosperms: Morphology and Taxonomy. Wiley & Sons, New Delhi.

Raynal-Roques, A. 1981. Contribution à l'Étude Biomorphologique des Angiospermes Aquatiques Tropicales—Essai d'Analyse de l'Évolution, Vol. 1. Unpublished Ph.D. Thesis, University of Montpellier. Atélier Duplication, Montpellier.

Record, S. J. 1933. The woods of *Rhabdodendron* and *Duckeodendron*. Trop. Woods 33: 6–10.

Reidt, G. 1997. Fruchtanatomische Studien an den "klassisch" gefassten Cornaceae s.l. *in* E. Smets, L. P. Ronse Decraene & E. Robbrecht (editors), 13th Symposium of Morphology, Anatomy & Systematics, Program & Abstracts. Scripta Bot. Belg. 15: 134.

Rendle, A. B., G. Baker & S. M. Moore. 1921. Systematic account of the plants collected in New Caledonia and the Islands of Pines by Prof. R. H. Compton, M. A., in 1914. J. Linn. Soc., Bot. 45: 246–417.

Ricci, I. 1957. Morphologia e costituzione chimica dei peli nel genere *Cistus* e loro importanza nella sistematica di alcune specie. Ann. Bot. (Rome) 25: 540–566.

Rice, K. A., M. J. Donoghue & R. G. Olmstead. 1995. A reanalysis of the large *rbc*L dataset. Amer. J. Bot. 82 (Suppl., 6): 156–157. [Abstract.]

Rodman, J., R. A. Price, K. Kenneth, E. Conti, K. J. Sytsma & J. D. Palmer. 1993. Nucleotide sequences of the *rbc*L gene indicate monophyly of mustard oil plants. Ann. Missouri Bot. Gard. 80: 686–699.

Rohwer, J. G. 1996. A preliminary survey of the fruits and seeds of the Oleaceae. Bot. Jahrb. Syst. 115: 271–291.

Ronse Decraene, L. P. 1989. The floral development of *Cochlospermum tinctorium* and *Bixa orellana* with special emphasis on the androecium. Amer. J. Bot. 76: 1344–1359.

———. 1992. The Androeceum of the Magnoliophytina: Characterization and Systematic Importance. Unpublished Ph.D. Thesis, University of Leuven, Belgium.

——— & E. F. Smets. 1992. Complex polyandry in the Magnoliatae: Definition, distribution and systematic value. Nordic J. Bot. 12: 621–649.

Rutishauser, R. 1997. Structure and developmental diversity in Podostemaceae (river-weeds). Aquatic Bot. 57: 29–70.

——— & R. Sattler. 1987. Complementary and heuristic value of contrasting models in structural botany. II. Case study on leaf whorls: *Equisetum* and *Ceratophyllum*. Bot. Jahrb. Syst. 109: 227–256.

Sáenz de Rivas, C. 1979. Pollen morphology of Spanish Cistaceae. Grana 18: 91–98.

Sampson, F. B. 1993. Pollen morphology of the Amborellaceae and Hortoniaceae (Hortonioideae: Monimiaceae). Grana 32: 154–162.

——— & P. K. Endress. 1984. Pollen morphology in the Trimeniaceae. Grana 23: 129–137.

Sandwith, N. Y. 1962. Contribution to the flora of tropical America. LXIX. A new genus of Peridiscaceae. Kew Bull. 15: 467–471.

Satabié, B. 1974. Contribution de la palynologie à l'étude des Irvingiacées d'Afrique tropicale. Adansonia n.s. 14: 277–289.

Sattler, R. 1973. Organogenesis of Flowers, a Photographic Text-Atlas. Univ. Toronto Press, Toronto.

Saunders, E. R. 1937. The vascular ground plan as a guide to the floral ground plan: Illustrated from Cistaceae. New Phytol. 35: 47–67.

———. 1937–1939. Floral Morphology. A New Outlook with Special Reference to the Interpretation of the Gynaeceum, Vols. 1 and 2. Heffer, Cambridge.

Savolainen, V., J. F. Amnan, E. Douzery & R. Spichiger. 1994. Molecular phylogeny of families related to Celastrales based on *rbc*L 5′ flanking sequences. Molec. Phylog. & Evol. 3: 27–37.

———, C. M. Morton, S. B. Hoot & M. W. Chase. 1996. An examination of phylogenetic patterns of plastid *atp*B gene sequences among eudicots. Amer. J. Bot. 83 (Suppl., 6): 190. [Abstract.]

Schaeppi, H. 1953. Morphologische Untersuchungen an den Karpellen der Calycanthaceae. Phytomorphology 3: 112–117.

Schmid, R. 1964. Die systematische Stellung der Dioncophyllaceen. Bot. Jahrb. Syst. 83: 1–56.

Schnarf, K. 1931. Vergleichende Embryologie der Angiospermen. Borntraeger, Berlin.

Schweingruber, F. H. 1990. Anatomy of European Woods. Haupt, Bern.

Selmar, D. 1993. Transport of cyanogenic glucosides: Linustatin uptake by *Hevea* cotyledons. Planta 191: 191–199.

Sethi, M. L., G. S. Rao, B. K. Chowdhury, J. F. Morton & G. J. Kapadia. 1976. Identification of volatile constituents of *Sassafras albidum* root oil. Phytochemistry 15: 1773–1775.

Setoguchi, H., H. Tobe & H. Ohba. 1992. Seed coat anatomy of *Crossostylis* Rhizophoraceae: Its evolutionary and systematic implications. Bot. Mag. (Tokyo) 105: 625–638.

Seubert, E. 1993. Die Samen der Araceen. Koeltz, Königstein.

Sévenet, T., C. Thal & P. Potier. 1971. Isolement et structure du cantleyoside, nouveau glucoside terpénique de *Cantleya corniculata* (Becc.) Howard (Icacinacées). Tetrahedron 27: 663–668.

Shiklina, I. A. 1977. The comparative anatomy of the wood of the genus *Oncotheca* (order Theales). Bot. Zhurn. (Moscow & Leningrad) 62: 1273–1275. [In Russian.]

Simon, J. P. 1970. Comparative serology of the order Nymphaeales. I. Preliminary survey on the relationships of *Nelumbo*. Aliso 7: 243–261.

———. 1971. Comparative serology of the order Nymphaeales II: Relationships of Nymphaeaceae and Nelumbonaceae. Aliso 7: 325–350.

Sinnott, E. W. 1914. Investigations on the phylogeny of the angiosperms. 1. The anatomy of the node as an aid in the classification of angiosperms. Amer. J. Bot. 1: 303–322.

Smith, C. R., Jr., D. Weisleder & R. W. Miller. 1980. Linustatin and neolinustatin: Cyanogenic glucosides of lineseed meal that protect animals against selenium toxicity. J. Organic Chem. 45: 507–510.

Solereder, H. 1899/1908. Systematische Anatomie der Dicotyledonen, Vols. 1 and 2. Enke, Stuttgart.

——— & J. F. Meyer. 1928. Systematische Anatomie der Monokotyledonen. Heft III. Principes–Synanthae–Spathiflorae. Bornträger, Berlin.

Soltis, D. E. & P. S. Soltis. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: A comparison of topologies based on 18S rDNA and *rbc*L sequences. Amer. J. Bot. 84: 504–523.

———, Q.-Y. Xiang & L. Hufford. 1995a. Relationships and evolution of Hydrangeaceae based on *rbc*L sequence data. Amer. J. Bot. 82: 504–514.

———, C. Hibsch-Jetter, P. S. Soltis, M. W. Chase & J. S. Farris. 1997a. Molecular phylogenetic relationships among angiosperms: An overview based on *rbc*L and 18S rDNA sequences. Pp. 157–178 *in* K. Iwatsuki & P. H. Raven (editors), Evolution and Diversification of Land Plants. Springer, Tokyo.

———, P. S. Soltis, D. R. Morgan, S. M. Swensen, B. C. Mullin, J. M. Dowd & P. G. Martin. 1995b. Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms. Proc. Natl. Acad. Sci. U.S.A. 92: 2647–2651.

———, P. S. Soltis, M. Mort, M. W. Chase, V. Savolainen, S. B. Hoot & C. M. Morton. Inferring complex phylogenies: An empirical approach using three large DNA sets for angiosperms. Syst. Biol. (in press).

———, P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S.-M. Chaw, L. J. Gillespie, W. J. Kress & K. J. Sytsma. 1997b. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Ann. Missouri Bot. Gard. 84: 1–49.

Souèges, R. 1937. Développement de l'embryon chez l'*Helianthemum guttatum.* Bull. Soc. Bot. France 84: 400.

Sprent, J. I. & D. McKey (editors). 1994. Advances in Legume Systematics. Part 5. The Nitrogen Factor. Royal Botanic Gardens, Kew.

Stearn, F. C. 1946. A Study of the Genus *Paeonia.* The Royal Horticultural Society, London.

Stevens, P. F. 1991. On the phylogeny of the Elatinaceae–Bonnetiaceae–Clusiaceae. Amer. J. Bot. 78 (Suppl., 6): 220. [Abstract.]

Sutter, D. & P. K. Endress. 1995. Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. Bot. Jahrb. Syst. 116: 517–536.

Swensen, S. M., B. C. Mullin & M. W. Chase. 1994. Phylogenetic affinities of Datiscaceae based on an analysis of nucleotide sequences from the plastid *rbc*L gene. Syst. Bot. 19: 157–168.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Sytsma, K. J. & D. A. Baum. 1996. Molecular phylogenies and the diversification of the angiosperms. Pp. 314–340 *in* D. W. Taylor & L. J. Hickey (editors), Flowering Plant Origin, Evolution and Phylogeny. Chapman & Hall, New York.

Syvanen, M. 1994. Horizontal gene transfer: Evidence and possible consequences. Annual Rev. Genet. 28: 237–261.

———, H. Hartmen & P. F. Stevens. 1989. Classical plant taxonomic ambiguities extend to the molecular level. J. Molec. Evol. 28: 536–544.

Takahashi, A. 1985. Wood anatomical studies of Polycarpicae. I. Magnoliales. Sci. Rep. Osaka Univ. 34: 29–83.

Takahashi, K. & K. Sohma. 1982. Pollen morphology of the Droseraceae and its related taxa. Sci. Rep. Tohoku Imp. Univ., Ser. 4, Biology 38: 81–156.

Takhtajan, A. L. 1966. Systema et phylogenia Magnoliophytorum. Nauka, Moscow. [In Russian.]

———. 1987. The System of the Magnoliophytes. Nauka, Leningrad. [In Russian.]

——— (editor). 1985/1988/1991. Comparative Anatomy of Seeds, Vols. 1–3. Nauka, Leningrad. [In Russian.]

———. 1997. Diversity and Classification of Flowering Plants. Columbia Univ. Press, New York.

———, N. R. Meyer & V. N. Kosenko. 1985. The pollen morphology and classification in Rafflesiaceae s.l. Bot. Zhurn. (Moscow & Leningrad) 70: 153–168. [In Russian.]

Tang, Y. 1994. Embryology of *Plagiopteron suaveolens* Griffith (Plagiopteridaceae) and its systematic implications. Bot. J. Linn. Soc. 116: 145–157.

Taylor, D. W. & L. J. Hickey. 1996. Evidence for and implications of an herbaceous origin for angiosperms. Pp. 116–140 *in* D. W. Taylor & L. J. Hickey (edtiors), Flowering Plant Origin, Evolution & Phylogeny. Chapman & Hall, New York.

Taylor, F. H. 1972. The secondary xylem of the Violaceae: A comparative study. Bot. Gaz. 133: 230–242.

Thanikaimoni, G. 1986. Evolution of Menispermaceae. Canad. J. Bot. 64: 3130–3133.

Theisen, I. & W. Barthlott. 1994. Mikromorphologie der Epicutikularwachse und die Systematik der Gentianales, Rubiales, Dipsacales und Calycerales. Trop. Subtrop. Pflanzenwelt 89: 1–62.

Thieme, H. & R. Benecke. 1966. Isolierung eines neuen Phenolglykosides aus *Populus nigra* L. Pharmazie 21: 59–60.

——— & ———. 1970. Ueber die Identität der Glucoside Xylosmosid und Poliothyrsid mit Nigracin. Pharmazie 25: 492.

Thorne, R. F. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85–117.

———. 1992. Classification and geography of the flowering plants. Bot. Rev. (Lancaster) 58: 225–348.

Tobe, H. & C.-I Peng. 1990. The embryology and taxonomic relationships of *Bretschneidera* (Bretschneideraceae). Bot. J. Linn. Soc. 193: 139–152.

——— & P. H. Raven. 1995. Embryology and relationships of *Akania* (Akaniaceae). Bot. J. Linn. Soc. 118: 261–274.

Todzia, C. A. 1993. Chloranthaceae. Pp. 281–287 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Tomlinson, P. B. 1961. Anatomy of the Monocotyledons. II Palmae. Oxford Univ. Press, London.

Tsou, C.-H. 1994. The embryology, reproductive morphology, and systematics of Lecythidaceae. Mem. New York Bot. Gard. 71: 1–110.

Tucker, S. C. & A. Douglas. 1994. Ontogenetic evidence and phylogenetic relationships among basal taxa of legumes. Pp. 11–32 *in* I. K. Ferguson & S. C. Tucker (editors), Advances in Legume Systematics, Vol. 6. Royal Botanic Gardens, Kew.

Ueda, K., T. Hanyuda, A. Nakano, T. Siuchi, A. Seo, H. Okubo & M. Hotta. 1997. Molecular phylogenetic position of Podostemaceae, a marvelous aquatic flowering plant family. J. Pl. Res. 110: 87–92.

Uesato, S., M. Miyauchi, H. Itoh & H. Inouye. 1986. Biosynthesis of iridoid glucosides in *Galium mollugo, G. spurium var. echinospermon* and *Deutzia crenata.* Intermediacy of deoxyloganic acid, loganin and iridodial glucoside. Phytochemistry 25: 2515–2521.

Ukraintseva, V. V. 1993. Pollen morphology of the family Cistaceae in relation to its taxonomy. Grana, Suppl. 2: 33–36.

Veldkamp, J. F. 1984. *Berberidopsis* (Flacourtiaceae) in Australia. Blumea 30: 21–29.

Vestal, P. A. 1937. The significance of comparative anatomy in establishing the relationship of the Hypericaceae to the Guttiferae and their allies. Philipp. J. Sci. 64: 199–252.

Vijayaraghavan, M. R. & U. Dhar. 1976. *Scytopetalum tieghemii*—Embryologically unexplored taxon and affinities of the family Scytopetalaceae. Phytomorphology 26: 16–22.

Vliet, G. J. C. M. van & P. Baas. 1984. Wood anatomy and classification of the Myrtales. Ann. Missouri Bot. Gard. 71: 783–800.

Vogel, C. 1986. Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae; Beiträge zur intrafamiliären Gliederung und zu Beziehungen im extrafamiliären Bereich. Diss. Bot. 98: 1–124.

Walia, K. & R. N. Kapil. 1965. Embryology of *Frankenia* Linn. with some comments on the systematic position of the Frankeniaceae. Bot. Not. 118: 412–429.

Walker, J. W. & A. G. Walker. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Ann. Missouri Bot. Gard. 71: 464–521.

Warburg, O. 1894. Flacourtiaceae. Pp. 1–56 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 1st ed., Vol. 6a. Engelmann, Leipzig.

Whalen, M. A. 1987. Wood anatomy of the American frankenias (Frankeniaceae): Systematic and evolutionary implications. Amer. J. Bot. 74: 1211–1223.

Williams, S. E., V. A. Albert & M. W. Chase. 1994. Relationships of Droseraceae: A cladistic analysis of *rbc*L sequence and morphological data. Amer. J. Bot. 81: 1027–1037.

Williamson, P. S. & E. L. Schneider. 1993. Cabombaceae. Pp. 157–161 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Wilson, C. L. 1965. The floral anatomy of the Dilleniaceae. 1. *Hibbertia* Andr. Phytomorphology 15: 248–274.

Wojciechowska, B. 1969. Seed morphology and anatomy of some *Helianthemum* species. Monogr. Bot. 29: 121–135.

Woon, C. & H. Keng. 1979. Stamens of the Dipterocarpaceae. Gard. Bull. Singapore 32: 1–51.

Wu, C.-Y. & K. Kubitzki. 1993. Circaeasteraceae. Pp. 288–289 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.

Xiang Q.-Y., D. E. Soltis, D. R. Morgan & P. S. Soltis. 1993. Phylogenetic relationships of *Cornus* L. sensu lato and putative relatives inferred from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 723–734.

Yoffe, M. D. 1962. The embryology of *Trochodendron aralioides* Sieb. et Zucc. Trudy Bot. Inst. Komarova Akad. Nauk S.S.S.R., Ser. 7, Morfol. Anat. Rast. 5: 250–259. [In Russian.]

Zenk, M. H., M. Fürbringer & W. Steglich. 1969. Occurrence and distribution of 7-methyljuglone and plumbagin in the Droseraceae. Phytochemistry 8: 2199–2200.

Zhang, Z.-Y. 1987. A study on the pollen morphology of Actinidiaceae and its systematic position. Acta Phytotax. Sin. 25: 9–23. [In Chinese.]

Zurawski, G., B. Perrot, W. Bottomley & P. R. Whitfeld. 1981. The structure of the gene for the large subunit of ribulose-1,5-bisphosphate carboxylase from spinach chloroplast DNA. Nucl. Acids Res. 14: 3251–3270.

Zweifel, R. 1939. Cytologisch-embryologische Untersuchungen an *Balanophora abbreviata* Blume und *Balanophora indica* Wall. Vierteljahrsschr. Naturf. Ges. Zürich 84: 245–306.

Appendix 1. Non-molecular data matrix.

dill.mat5	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
		sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	Al e	amic	dhu	prot	trigl	taxi	proa	hete	card	valin	linar	lotai	linus	neol	tyros	prun	sam	zieri	holo	gluc	dihy	acet	eleo	myri
1	Ceratophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?
2	Chloranthaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
3	Nymphaeaceae	C	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
4	Amborellaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	Austrobaileyaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	A	A	?
6	Illiciales	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
7	Winterales	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
8	Monocotyledons	C	A	C	?	A	A	A	?	?	?	A	?	?	?	?	?	A	C	C	A	C	C	A	C	A	C	C	A	A	A	A	A	A	A	C	A	A	A	A	A
9	Aristolochianae	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C
10	Laurales	C	C	C	?	?	?	?	A	A	A	?	?	?	?	?	?	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
11	Myristicaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	C
12	Annonales	C	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A
13	Magnoliales	C	C	C	?	?	?	?	A	C	C	?	?	?	?	?	?	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
14	Ranunculidae	C	C	C	?	A	A	A	A	A	A	A	A	A	A	?	?	C	A	C	C	C	C	A	A	A	C	C	C	A	A	A	A	A	A	A	A	A	C	A	A
15	Eupteleaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Platanaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
17	Nelumbonaceae	C	C	C	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Trochodendrales	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?
19	Proteaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	C	A	C	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
20	Buxaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	A	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
21	Sabiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?
22	Didymelaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Myrothamnaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Berberidopsidaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A	?	A	A	?
25	Gunneraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Rhabdodendraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?
27	Simmondsiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
28	Caryophyllales	?	A	A	?	A	A	A	?	?	?	A	A	A	A	?	?	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
29	Asteropeiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	Plumbaginaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
31	Polygonaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
32	Dioncophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33	Ancistrocladaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	A	A	?
34	Nepenthaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
35	Droseraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
36	Tamaricaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?
37	Frankeniaceae	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?
38	Hamamelidales	A	A	A	C	?	?	?	A	C	C	?	?	?	?	?	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
39	Dilleniaceae	?	A	A	?	A	A	A	?	?	?	A	A	A	A	A	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	A	A	A
40	Vitaceae	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
41	Eucryphiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Brunelliaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Cunoniales	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?
44	Paeoniaceae	A	A	A	?	A	A	A	A	A	A	A	?	?	?	A	?	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A
45	Cephalotaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Crassulaceae	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A
47	Saxifragales s. str.	?	A	A	C	?	?	?	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A	A	A	A	A
48	Staphyleaceae	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
49	Elaeagnaceae	?	?	?	?	?	?	?	A	C	C	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
50	Rosaceae	?	A	A	C	?	?	?	A	A	A	?	?	?	?	?	A	A	A	C	A	A	A	A	C	C	A	A	A	A	A	C	C	A	A	A	A	A	A	C	A
51	Rhamnaceae	?	?	?	?	?	?	?	A	A	C	?	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
52	Faganae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
53	Cucurbitales	?	?	?	?	A	A	C	A	A	C	A	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?
54	Coriariaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
55	Urticales	?	?	?	?	A	A	C	C	C	?	A	A	A	A	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C

Appendix 1. Continued.

dill.mat5	2	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
		asar	sesc	gern	myo	pinit	quet	deut	cant	cycl	simn	aust	kads	eucc	syri	pino	dihy	galb	licar	vera	prod	ellag	meth	stac	casu	tellin	tellin	pedu	gera	chlo	galli	epig	llavc	afze	davi	bifla	Oura	euxa	nora	mac	benz
1	Ceratophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	Chloranthaceae	?	C	C	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	?
3	Nymphaeaceae	?	?	?	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	C
4	Amborellaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	Austrobaileyaceae	?	?	?	?	?	?	?	?	A	?	C	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	A
6	Illiciales	A	C	C	A	A	A	A	A	A	A	?	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
7	Winterales	?	C	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	A
8	Monocotyledons	C	?	?	C	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	C	A	A	C	A	A	C	A	A	A	A	A
9	Aristolochianae	C	?	?	A	C	A	A	A	A	A	C	C	A	A	A	C	C	C	C	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
10	Laurales	C	C	C	C	A	A	A	A	A	A	C	A	A	C	A	A	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
11	Myristicaceae	?	A	A	C	?	?	?	?	A	?	A	A	A	A	A	C	C	C	C	?	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
12	Annonales	C	C	A	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
13	Magnoliales	C	C	C	A	C	A	A	A	A	A	A	A	A	A	C	A	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
14	Ranunculidae	A	C	A	C	A	A	A	A	A	C	C	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	A	A	A	C
15	Eupteleaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?
16	Platanaceae	?	?	?	?	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	?
17	Nelumbonaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C
18	Trochodendrales	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	?
19	Proteaceae	?	A	A	A	A	C	A	A	A	A	A	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A
20	Buxaceae	?	?	?	?	C	?	?	?	A	C	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	?
21	Sabiaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Didymelaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Myrothamnaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
24	Berberidopsidaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
25	Gunneraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Rhabdodendraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27	Simmondsiaceae	A	?	?	?	C	?	?	?	A	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
28	Caryophyllales	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	C
29	Asteropeiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	Plumbaginaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
31	Polygonaceae	A	C	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A
32	Dioncophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
33	Ancistrocladaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C
34	Nepenthaceae	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A
35	Droseraceae	?	A	A	?	?	?	?	?	A	?	A	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	?
36	Tamaricaceae	?	A	A	A	C	A	A	A	A	A	A	A	A	C	A	A	A	A	A	?	C	C	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A
37	Frankeniaceae	?	?	?	A	C	A	A	A	?	A	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	A	?	C	?	?	?	?	?	?	?	?
38	Hamamelidales	?	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	C	C	C	C	C	A	C	C	A	C	C	?	A	A	A	A	A	A	A	A
39	Dilleniaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	C	?	C	?	?	?	A	?	?	?	A
40	Vitaceae	A	A	A	C	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	C	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	A	A	A
41	Eucryphiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Brunelliaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Cunoniales	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	?	?	C	C	?	?	?	A	?	?	?	?
44	Paeoniaceae	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
45	Cephalotaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	C	?	?	?	?	C	?	?	?	?	A
46	Crassulaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
47	Saxifragales s. str.	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	C	C	A	A	A	C	A	A	C	A	A	A	A	A	A	A
48	Staphyleaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	A
49	Elaeagnaceae	A	A	A	A	A	C	A	A	A	?	?	?	?	?	?	?	?	?	?	C	C	A	A	A	A	A	A	A	A	C	A	?	A	A	A	?	A	A	A	A
50	Rosaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	C	C	C	C	C	C	C	C	C	A	C	A	C	A	A	A	A	A
51	Rhamnaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	?	?	?	?	?	?	?	C	?	?	?	?	C	A	?	?	?	C
52	Faganae	A	A	C	C	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	C	C	C	C	C	C	C	A	A	C	A	?	C	A	C	A	A	A	A	A
53	Cucurbitales	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	?	C	?	A	A	A	A	A	A	A	A	A	A
54	Coriaraceae	?	C	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	C	A	C	?	?	?	?	?	?	?	?	?	A
55	Urticales	A	C	A	C	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	C	C	A	?	A	A	A	A	A	C	C	A

Appendix 1. Continued.

dill.mat5	3	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
		roan	anor	lirioc	prot	anci	cam	indo	irido	secc	corn	olea	arjur	dam	cucu	nigr	arbu	napt	rapa	plum	dros	anth	pher	anth	actir	nitro	chro	siev	stral	rod	epici	SiO2	oxal	elon	solit	crys	spha	myrc	oil c	muci	resir
1	Ceratophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A
2	Chloranthaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	C	A	A	A	C	C	A	C	A	A	A	C	C	A
3	Nymphaeaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	A	C	C	A	A	A	A	C	A	A	A	A	A	A	A	A
4	Amborellaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	A	A	?	A	A	A	A	A	A	A	A	A
5	Austrobaileyacaae	A	A	A	A	A	?	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	A	A	A	C	A	A	A	?	A	A	A	A	A	A	C	C	C
6	Illiciales	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	?	?	?	?	?	?	A	?	A	A	C	C	A	A	A	C	A	A	A	A	A	A	C	C	C
7	Winterales	A	A	A	A	A	?	A	A	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	A	A	A	C	A	C	A	?	C	A	C	A	A	A	C	C	A
8	Monocotyledons	A	A	C	A	A	A	C	A	A	A	C	A	A	A	A	A	C	A	C	A	C	C	C	A	A	C	A	?	?	?	A	C	C	C	C	A	A	C	C	?
9	Aristolochianae	A	A	C	?	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	A	?	A	C	A	C	C	A	C	C	G	C	C	A	A	C	C	C
10	Laurales	C	A	C	C	A	A	C	A	A	A	A	A	A	A	A	C	?	?	?	?	?	C	?	A	A	C	A	C	C	A	C	A	C	C	A	A	A	C	C	C
11	Myristicaceae	A	A	?	C	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	C	A	A	?	A	C	A	C
12	Annonales	C	C	C	C	A	A	C	A	A	A	A	A	C	A	A	A	A	A	A	A	C	A	A	A	A	C	A	C	C	A	C	C	A	C	A	A	A	C	C	C
13	Magnoliales	A	C	C	C	A	A	A	A	A	A	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	C	C	G	C	A	A	A	C	C	C
14	Ranunculidae	C	C	C	C	A	A	C	A	A	A	C	C	A	A	A	C	?	?	?	?	?	C	A	A	A	C	C	C	C	A	C	C	C	C	C	A	A	A	C	C
15	Eupteleaceae	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	?	?	?	?	C	A	A	A	A	A	A	A	A
16	Platanaceae	?	?	?	?	?	?	?	A	A	A	A	A	A	A	?	?	?	?	?	?	?	A	?	?	A	C	C	A	C	A	A	C	G	C	A	A	A	A	A	A
17	Nelumbonaceae	C	C	C	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	C	A	C	A	A	C	A	A	A	A	A	A	A	A
18	Trochodendrales	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	A	A	A	C	A	C	A	A	A	C	A	C
19	Proteaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	A	C	A	?	?	?	C	C	A	C	A	A	A	A	A	A
20	Buxaceae	?	?	?	?	?	A	?	A	A	A	A	A	A	A	?	C	?	?	?	?	?	?	?	?	A	C	A	?	?	?	A	C	A	C	C	A	A	A	A	A
21	Sabiaceae	?	?	?	?	?	A	?	A	A	A	C	A	A	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	C	C	A	A	A	A	A	A	?	C
22	Didymelaceae	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	A	?	A	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A
23	Myrothamnaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	A	C	A	A	A	A	A	C	A	C
24	Berberidopsidaceae	A	A	A	A	?	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	C	C	G	C	A	A	A	A	?	A
25	Gunneraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	A	C	G	C	?	A	A	A	C	A
26	Rhabdodendraceae	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	?	?	?	?	A	?	A	?	?	?	C	?	?	?	?	?	A	C	?	C
27	Simmondsiaceae	?	?	?	A	?	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	C	?	?	?	A	C	G	C	A	A	A	A	A	A
28	Caryophyllales	A	A	A	A	C	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	C	A	A	C	C	C	C	C	A	A	A	A
29	Asteropeiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?	?	?	?	?	A	?	?	?
30	Plumbaginaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	A	C	A	C	C	?	A	?	A	A	C	C	A	A	A	A	C	A	A	A	A	A	A	A	C
31	Polygonaceae	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	C	A	A	A	C	A	C	A	A	C	C	A	A	A	C	C	A	C	C	A	A	A	A	A
32	Dioncophyllaceae	A	A	A	A	C	A	A	A	A	A	A	A	A	?	?	?	C	A	C	A	A	A	A	?	A	A	C	?	?	?	C	A	G	C	A	A	A	A	?	?
33	Ancistrocladaceaa	A	A	A	A	C	A	A	A	A	A	A	A	A	A	?	A	C	A	C	C	A	A	A	A	A	?	?	A	A	A	C	C	A	C	A	A	A	A	A	C
34	Nepenthaceae	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	C	A	C	C	A	A	A	?	A	A	C	A	A	A	A	C	A	A	A	C	A	A	C	A
35	Droseraceae	?	?	?	?	?	?	?	A	A	?	?	?	?	A	?	A	C	A	C	C	A	?	A	?	A	C	C	?	?	?	A	A	A	A	A	A	A	A	A	A
36	Tamaricaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	A	?	?	?	?	?	A	A	A	A	A	C	?	?	?	A	A	A	A	A	A	A	A	A	A
37	Frankeniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	C	A	A	A	A	A	A	A	A
38	Hamamelidales	A	A	A	A	A	A	A	C	A	A	C	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	C	A	C	A	A	C	A	C	A	A	A	A	C	C
39	Dilleniaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	A	A	C	A	C	C	C	A	A	A	C	A
40	Vitaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	?	?	?	A	C	C	C	A	A	A	A	C	A
41	Eucryphiaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	C	G	C	A	A	A	A	A	A
42	Brunelliaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	C	?	C	A	A	A	A	A	A
43	Cunoniales	?	A	A	A	A	A	A	A	A	A	?	?	?	?	A	?	A	A	A	A	A	A	?	A	A	A	C	A	C	C	A	C	A	C	A	A	A	A	C	A
44	Paeoniaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	?	?	?	?	?	A	C	A	A	A	C	A	C	A	A	C	A	C	A	A	A	A	A	A
45	Cephalotaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	A	?	A	?	A	?	A	A	A	A
46	Crassulaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	?	?	A	C	A	A	C	C	A	C	A	A	C	A	C	C	C	A	A	C	C
47	Saxifragales s. str.	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	G	C	A	A	A	A	A	A
48	Staphyleaceae	A	?	?	?	?	A	?	A	A	A	C	A	A	A	A	A	?	?	?	?	?	A	A	?	A	A	C	?	?	?	A	C	A	C	A	A	A	A	C	A
49	Elaeagnaceae	A	A	A	A	A	A	C	A	A	A	A	A	A	A	?	A	?	?	?	?	?	A	A	A	C	C	C	?	?	?	A	C	G	C	C	A	A	A	A	A
50	Rosaceae	A	A	A	A	A	A	C	A	A	A	A	A	C	C	A	C	A	A	A	A	A	A	C	A	?	C	C	A	C	A	A	C	G	C	A	A	A	A	C	A
51	Rhamnaceae	A	A	C	A	A	A	A	A	A	A	C	A	C	A	A	C	C	A	A	A	C	A	A	A	C	A	C	?	?	?	A	C	G	C	A	A	A	A	C	A
52	Faganae	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	C	C	A	A	A	A	A	A	A	C	C	C	A	A	A	A	C	A	C	A	A	A	A	C	A
53	Cucurbitales	A	A	A	A	A	A	A	A	A	A	C	?	?	C	A	A	A	A	A	A	C	A	?	A	A	C	C	?	?	?	A	C	G	C	C	A	A	A	A	A
54	Coriaraceae	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	C	?	?	?	A	C	A	C	A	A	A	A	A	A
55	Urticales	A	A	A	A	A	A	C	A	A	A	A	C	A	A	A	A	C	A	A	A	C	C	A	A	A	C	A	?	?	?	C	C	C	C	A	C	A	A	C	C

Appendix 1. Continued.

dill.mat5	4	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
		latic	fasci	pelta	denc	nonç	glan	anth	micr	polle	type	pola	trian	tnan	angu	sexi	type	intec	intec	nuce	pens	endc	occu	occu	occu	end	aril	pach	sarc	rumi	exot	exot	theo	tann	mes	endc	endc	exot	exot	bixoi	hypc
1	Ceratophyllaceae	A	A	A	A	A	A	A	A/C	A	A	G	A	A	A	A	A	C	A	A	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
2	Chloranthaceae	A	A	A	A	A	A	A	C	C	A	A	A	A	A	G	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	G	A	A	C
3	Nymphaeaceae	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	C	A	A	C	A	C	A	A	A	C	C	A	A	C	A	A	A	A	A	C
4	Amborellaceae	A	A	A	A	A	A	?	?	A	A	C	A	A	A	A	A	A	A	A	A	?	?	?	?	A	A	?	?	?	A	A	A	C	A	A	A	A	A	A	A
5	Austrobaileyaceae	A	A	A	A	A	A	C	C	C	A	G	A	A	A	G	G	A	A	A	A	?	?	?	?	G	A	C	C	C	A	A	A	?	C	A	G	A	A	A	A
6	Illiciales	A	A	A	A	A	A	C	C	G	C	C	A	A	A	G	G	A	A	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	C	?	A	A	A	A	A
7	Winterales	A	A	A	A	A	A	A	C	C	A	C	A	A	A	G	G	A	A	A	C	C	A	A	A	A	A	A	A	C	A	C	A	C	A	C	A	A	A	A	C
8	Monocotyledons	A	A	?	?	A	?	A	A	C	A	A	A	A	A	G	C	A	A	A	C	C/G	C	A	A	A	?	A	C	A	A	A	A	A	A	?	A	G	A	A	C
9	Aristolochianae	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A	A	A	C	C	A	C	A	?	A	A	A	A	A	A	A	A	C	C	A	G	A	A	C
10	Laurales	A	C	C	A	A	A	A/C	A	A/C	A	A	A	A	A	G	G	A	A	A	C	C	A	C	A	C	A	C	A	C	A	A	A	C	A	A	T	A	A	A	C
11	Myristiceceae	A	A	A	C	A	A	C	A	C	A	C	A	A	A	A	A	A	A	A	A	A	?	?	?	G	C	C	A	C	A	A	A	A	C	C	C	G	A	A	A
12	Annonales	A	C	C	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A	C	C	A	A	A	G	C	C	C	C	C	A	A	A	C	A	A	A	A	A	C
13	Magnolielas	A	C	C	A	A	A	C	C	C	A	G	A	A	A	A	A	A	A	A	A	C	A	A	A	G	A	A	C	C	A	A	A	A	C	C	C	A	A	A	C
14	Ranunculidae	C	A	A	A	A	A	A	C	G	C	A	A	A	A	A/T	A	A	A	A	A	A	C	A	A	G	C	A	A	C	A	A	A	A	A	C	C	G	A	A	C
15	Eupteleaceae	A	A	A	A	A	A	C	C	G	C	C	A	A	A	G	C	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	C	A	G	A	A	A	C
16	Platanaceae	A	C	A	C	A	A	C	C	G	C	A	A	A	A	G	G	A	A	A	A	C	?	?	?	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A
17	Nelumbonaceae	A	A	A	A	A	A	C	C	G	C	G	A	A	A	A	A	A	C	A	A	C	?	?	C	A	A	C	A	A	A	A	A	?	A	A	A	A	A	A	A
18	Trochodendrales	A	A	A	A	A	A	C	C	G	C	A	A	C	A	G	G	A	A	A	A	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	G	T	A	A	?
19	Proteaceae	A	A	A	A	C	A	C	C	G	C	A	C	A	C	G	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	G	G	A	A	C
20	Buxaceae	A	A	A	A	A	A	C	C	T	A	A	A	A	A	G	C	A	A	A	A	C	A	A	A	C	C	A	A	A	A	C	A	C	C	A	A	A	A	A	A
21	Sabiaceae	A	A	A	A	A	A	C	?	G	G	C	A	A	A	G	G	C	A	A	?	G	?	?	?	?	?	A	?	?	A	?	?	?	?	?	A	A	A	A	A
22	Didymelaceae	A	A	A	A	A	A	?	?	G	C	C	A	A	A	G	G	A	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Myrothamnaceae	A	A	A	A	A	A	C	C	G	C	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	?	?	A	?	A	?	?	?	?	?	?	?
24	Berberidopsidaceae	A	A	?	A	A	A	?	?	G	C	?	A	A	A	A	A	A	A	A	A	?	?	?	?	A	C	A	A	A	A	A	A	C	A	C	C	A	A	A	C
25	Gunneraceae	A	A	A	A	A	A	C	C	G	C	G	A	A	A	G	C	A	A	A	A	C	?	?	?	A	A	A	?	?	A	A	A	?	A	?	A	A	A	A	A
26	Rhabdodendraceae	A	C	?	?	A	?	?	?	G	G	C	A	A	A	G	C	C	A	A	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?
27	Simmondsiaceee	A	A	A	A	A	A	?	?	G	C	G	A	A	A	C	A	A	A	?	A	C	A	A	A	G	A	A	A	A	C	C	A	C	A	A	A	A	A	A	A
28	Caryophyllales	C	C	A	C	C	A	C	C	G/T	A/C	A	A	C	A	C	A	A	A	A	C	A	C	A	A	G	C	A	A	A	A	A/C	A	C	A	C	A	A	A	A	C
29	Asteropeiaceae	A	A	?	?	A	A	?	?	G	C	G	A	A	A	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	Plumbaginaceae	A	A	A	A	A	A	?	C	G	C	G	A	A	A	C	A	A	?	A	A	A	C	A	A	A	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A
31	Polygonaceae	A	C	C	A	A	C	C	C	G	C	A	A	A	A	C	A	A	A	A	C	A	A	A	A	A	A	C	A	C	A	A	?	C	A	A	A	A	A	A	C
32	Dioncophyllaceae	?	A	C	A	A	A	?	?	G	C	G	A	A	A	C	A	A	A	A	A	A	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A
33	Ancistrocladaceae	A	?	C	A	A	C	?	?	G	C	G	A	A	A	C	A	A	A	?	A	C	?	?	?	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A
34	Nepenthaceae	A	A	A	C	A	A	?	C	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A
35	Droseraceae	A	C	A	A	A	A	C	C	G	C	C	A	A	A	C	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C
36	Tamaricaceae	A	A	A	A	A	A	C	C	G	C	A	A	C	C	A	A	A	A	C	A	A	A	A	A	G	A	A	A	A	C	C	A	A	A	C	A	A	A	A	A
37	Frankeniaceae	A	C	A	A	A	A	C	C	G	C	C	A	A	A	A	A	A	A	C	A	A	A	A	A	G	A	A	A	A	C	A	A	A	A	A	C	A	A	A	A
38	Hamamelidales	A	C	A	A	A	A	A	C	G	C	A	A	C	A	G	C	A	A	A	C	C	C	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	?
39	Dilleniaceae	A	C	C	A	A	A	C	C	G	C	A	A	A	A	G	G	A	A	A	A	A	A	A	A	C	C	A	A	A	C	A	A	C	A	A	C	C	A	A	A
40	Vitaceae	A	A	A	A	C	A	C	C	G	G	C	C	A	C	G	G	A	A	A	A	A	A	A	A	G	A	A	C	A	A	A	A	A	A	C	C	C	A	A	C
41	Eucryphieceae	A	A	A	A	A	A	?	?	G	C	A	A	A	A	G	G	A	A	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Brunelliaceae	A	A	A	A	A	A	?	?	G	G	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	C	A	A	A	A	?	?	?	?	?	?	?	?	?	?
43	Cunoniales	A	C	A	A	A	A	C	C	G	C	A	C	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	A	?	A	?	A	C	A	A	C
44	Paeoniaceae	A	A	A	A	A	A	C	C	G	G	G	A	A	A	G	G	A	A	A	A	A	A	A	A	C	C	A	C	A	A	C	A	A	C	A	A	A	A	A	C
45	Cephalotaceae	A	A	A	A	A	A	?	?	G	G	A	C	A	C	G	G	A	A	A	A	?	?	?	?	A	A	A	?	?	A	A	A	?	A	A	A	A	A	A	C
46	Crassulaceae	A	C	A	A	C	A	C	C	G	G	C	A	A	C	T	A	A	A	A	A	C	C	A	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A
47	Saxifragales s. str.	A	A	A	A	A	C	C	C	G	G	A	A	A	A	A	A	A	A	A	A	C	C	A	A	?	A	A	C	A	A	C	A	?	A	A	A	A	A	A	C
48	Staphyleaceae	A	A	A	A	A	A	C	C	G	G	C	A	A	A	G	G	A	A	A	A	A	?	?	?	C	A	A	A	A	A	C	A	C	C	A	A	A	A	A	A
49	Elaeagnaceae	A	C	C	A	A	A	C	C	G	G	C	A	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	A	C	A	A	A	A	A	C
50	Rosaceae	A	C	A	A	A	A	C	?	G	G	A	A	A	C	T	A	A	A	A	A	A	C	A	A	C	A	C	A	A	A	A	A	A	C	A	A	A	A	A	C
51	Rhamnaceae	A	C	A	A	A	A	C	C	G	G	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	C	C	A	A	A	A	A	C	A	A	A	A	A	A	C
52	Faganae	A	C	C	C	A	C	C	C	G	C	A	A	C	C	C	A	A	A	A	A	A	A	A	A	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
53	Cucurbitales	A	A	C	A	C	C	C	C	G	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	G	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C
54	Coriaraceae	A	A	A	A	A	A	C	C	G	G	C	C	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A
55	Urticales	C	A	C	A	C	C	C	C	G	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	C

Appendix 1. Continued.

dill.mat5	5	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
		endc	endc	emb	emb	susp	grow	disp	anor	phlo	wed	inter	corti	scle	woo	fiber	fiber	tracl	librif	type	hom	rays	stor	vesti	vess	end	vess	vess	vess	denc	leaf	leaf	stipu	glan	leaf	stom	epid	muc	palm	cras	leaf
1	Ceratophyllaceae	T	A	G	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A	?	?	?	A	A	?	A	?	?	A	A	A	A	C	A	A	G	A	A	C	A	A
2	Chloranthaceae	A	A	A	A	A	A	?	A	?	?	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	A	A/C	C	C	A	A	G	A	A	A	A	C
3	Nymphaeaceae	?	A	A	A	A	C	C	A	A	A	A	?	?	?	A	A	C	A	?	?	?	A	A	?	A	A	?	G	A	?	A	C	A	A	G	A	A	C	A	A
4	Amborellaceae	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	A	A	A	A	A	A	A	A	?	A	A	C
5	Austrobaileyaceae	C	A	A	A	A	C	A	A	?	A	A	A	C	A	A	A	C	A	A	A	A	A	A	G	C	A	A	A	A	A	C	A	A	A	A	A	?	A	A	A
6	Illiciales	A	A	A	A	A	C	A	A	?	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	A	A	A	C	A	A	C
7	Winterales	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	A	C	A	A	A	A	A	C	C	A	A	A
8	Monocotyledons	A	A	A	A	C	A/C	C	C	A	A	A	C	C	G	A	A	A	A	T	A	A	A	A	?	C	A	G	C	A	?	A	A	A	A	A	A	A	C	A	A
9	Aristolochianae	A	A	A	A	A	C	C	A	A	A	A	A	C	A	A	A	?	A	A	A	A	C	A	C	G	A	A	A	A	G	A	C	A	A	G	A	A	C	A	A
10	Laurales	A	A	C	A	A	A/C	A	A	A	A	A	C	C	A	A	A	C	A	C	A	A	C	A	C	C	A	G	A	C	A	C	A	A	A	A	A	A	C	A	C
11	Myristicaceae	A	A	A	A	A	A	A	A	C	C	C	A	C	C	A	A	A	C	?	?	?	A	A	C	C	?	G	C	A	C	A	C	A	A	A	A	A	A	A	A
12	Annonales	A	A	A	A	A	A/C	A	A	C	C	A	A	C	A	A	A	A	A	A	A	A	C	A	C	C	A	A	C	C	G	A	A	A	A	A	C	A	A	A	A
13	Magnoliales	A	A	A	A	A	A	A	A	C	C	A	C	C	G	A	A	C	A	A	A	A	A	A	C	C	?	A	A	A	G	A	C	A	A	A	C	A	A	A	A
14	Ranunculidae	A	A	A	A	A	C	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	A	C	C	A	G	A	C	C	A	C	A	A/C	C/G	A	A	C	C	C
15	Eupteleaceae	A	A	A	A	A	A	A	A	A	A	A	A	C	G	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	A	G	A	A	A	A	C
16	Platanaceae	A	A	G	A	A	A	A	A	?	C	A	A	C	A	A	A	C	A	T	C	A	A	A	C	G	A	A	C	A	G	A	C	A	A	G	A	A	C	C	C
17	Nelumbonaceae	G	A	T	A	A	C	?	A	A	A	A	A	A	?	A	A	C	A	?	?	?	A	A	T	C	A	?	A	A	?	G	C	A	A	G	A	A	C	A	A
18	Trochodendrales	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	A	A	A	G	A	G	A	C	A	A	A	A	?	C	C	C
19	Proteaceae	A	A/C	G	A	A	A	A	A	C	C	A	C	C	G	A	A	C	A	C	A	A	A	A	T	G	A	C	A	A	C	A	A	A	A	A	A	A	A/C	C	C
20	Buxaceae	A	A	C	A	A	A	A	A	A	?	A	C	C	C	C	A	C	A	A	A	A	A	A	C	C	A	C	A	A	C	A	A	A	A	C	A	A	C	C	C
21	Sabiaceae	?	A	G	C	A	A/C	A	A	?	C	A	A	C	A	A	A	C	A	C	A	A	A	A	C	C	A	A	A	A	C	A	A	A	A/C	G	A	?	A	C	C
22	Didymelaceae	?	?	C	A	A	A	A	A	?	?	A	?	?	A	A	A	C	A	A	A	A	A	A	G	C	A	?	?	?	?	A	A	A	A	C	?	?	A	?	A
23	Myrothamnaceae	A	A	C	A	A	A	A	A	?	?	A	A	?	A	A	A	C	A	T	A	C	A	A	C	C	A	A	A	A	C	C	C	A	A	G	A	A	C	C	C
24	Berberidopsidaceae	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	G	C	A	A	A	A	?	A	C	A	A	C	A	?	C	A	C
25	Gunneraceae	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	?	?	?	A	?	?	T	?	?	?	?	?	A	C	A	A	G	A	A	C	C	C
26	Rhabdodendraceae	?	?	T	C	A	?	A	C	A	A	C	A	C	A	A	A	?	A	A	A	A	A	?	C	T	C	G	A	A	G	A	C	A	A	G	C	A	A	?	A
27	Simmondsiaceae	?	?	G	A	A	A	A	C	A	A	C	A	C	A	A	A	C	A	T	A	C	A	A	T	T	?	G	A	A	A	C	A	A	A	G	A	A	A	A	A
28	Caryophyllales	A	A	G	C	C	A	A	C	A	A	C	A	C	A	A	A	A	C	G	A	A	C	A	T	G	G	G	C	A	G	A	C	A	A	A/G	C	A	C	A	A
29	Asteropeiaceae	?	?	G	C	A	C	A	?	?	?	?	?	?	G	C	A	A	A	T	A	C	A	A	T	T	C	G	A	A	?	A	A	A	A	G	?	?	A	A	C
30	Plumbaginaceae	C	A	C	A	A	A	A	C	A	A	C	C	C	A	A	C	A	C	G	A	A	A	A	T	T	?	?	C	A	C	A	C	A	A	A/G	A	A	A	A	A
31	Polygonaceae	C	A	C	A	A	A/C	A	A	A	A	C	C	C	A	A	A	A	A	G/T	A	A/C	C	C	T	T	?	G	A	A	?	A	C	A	A	A	A	A	C	A	A
32	Dioncophyllaceae	?	A	C	C	A	C	A	C	A	?	A	C	C	C	A	A	A	A	T	A	C	A	A	T	T	G	G	A	A	?	A	A	A	A	C	?	?	A	A	A
33	Ancistrocladaceae	C	A	C	A	A	C	A	A	A	A	A	A	C	G	A	A	A	A	T	A	C	A	A	T	T	A	G	A	A	C	A	C	A	A	C	A	?	A	A	A
34	Nepenthaceae	C	?	C	A	A	C	A	A	A	A	A	C	C	?	?	A	C	A	?	?	?	A	A	?	T	G	?	?	A	?	A	A	A	A	G	A	?	A	A	A
35	Droseraceae	C	A	C	A	A	A/C	A	A	A	C	A	A	A	G	A	A	C	A	T	A	C	A	A	T	T	C	C	A	A	C	A	C	A	A	G	A	A	A	A	A
36	Tamaricaceae	C	A	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	C	A	T	T	C	G	A	A	?	A	A	A	A	G	A	A	A	A	A
37	Frankeniaceae	C	C	C	A	A	A	A	C	A	A	A	A	A	G	C	A	A	C	T	A	C	A	A	T	T	C	G	C	A	?	C	A	A	A	G	A	A	A	A	A
38	Hamamelidales	A	A	A	A	A	A	A	A	?	A	A	A	C	C	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	C	A	C	A	A	A/G	A	C	C	C	C
39	Dilleniaceae	A	A	A	A	A	A/C	A	A	A	A	C	A	?	C	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	C	A	C	A	A	A	A	?	A	C	C
40	Vitaceae	A	A	A	A	A	C	A	A	C	A	C	A	C	C	A	A	A	C	A	A	A	C	A	C	C	A	C	C	A	C	A	C	A	A	C	A	A	C	C	C
41	Eucryphiaceae	A	?	C	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	G	A	A	A	A	C	C	A	A	C	A	C	C	C	A	A/C	A	A	C	A	?	C
42	Brunelliaceae	?	?	C	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	A	A	A	A	A	C	C	A	?	C	A	C	C	C	A	A	G	A	A	A	C	C
43	Cunoniales	A	A	C	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	G	C	C	A	C	G	A	C	A	C	C
44	Paeoniaceae	A	A/C	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	A	A	A	A	C	C	A	A	C	A	C	A	A	A	A	G	A	?	C	C	C
45	Cephalotaceae	?	?	C	A	A	A	A	A	A	A	A	A	?	?	?	?	C	?	?	?	?	A	?	?	C	A	?	?	?	A	A	A	A	A	?	A	A	A	A	A
46	Crassulaceae	A	C	G	A	C	A	A	A	A	A	A	C	A	?	A	A	A	C	?	?	?	A	A	C	T	A	G	?	?	C	A	A	A	A	G	A	A	A	A	C
47	Saxifragales s. str.	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	?	A	C	C	A	A	A	A	C	C	A	C	A	A	C	A	C	A	A	G	A	A	C	C	C
48	Staphyleaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	G	A	A	C	C	C	A	C	G	A	C	A	A	C
49	Elaeagnaceae	G	C	G	A	A	A	A	A	C	?	A	A	C	A	A	A	C	A	C	A	A	C	A	T	T	C	G	A	A	A	A	A	A	A	G	A	A	A	A	A
50	Rosaceae	?	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	C	A	A	A	A	C	G	A	G	A	C	C	A	C	C	A/C	G	A	C	A	C	C
51	Rhamnaceae	A	A	G	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	A	C	A	C	G	A	C	C	C	C	A	C	A	A	G	A	C	A/C	C	C
52	Faganae	A	A	G	A	A	A	A	A	C	A	A	A	C	C	A	A	A	A	A	A	A	A	A	C	C	A	C	A	C	C	A	C	A	A	G	A	C	A	C	C
53	Cucurbitales	A	A	G	A	A	A	A	A	A	A	C	C	C	G	A	A	A	C	G	A	A	C	A	T	G	C	A	C	A	C	A	C	A	A	G	A	A	C	C	C
54	Coriariaceae	?	A	G	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	A	A	A	C	A	T	T	C	A	A	A	A	C	C	A	A	C	A	A	C	A	C
55	Urticales	A	A	C	A	A	A	A	A	A	C	A	A	C	G	A	A	A	C	C	A	A	C	A	G	G	C	G	A	C	C	A	C	A	A	G	A	A	C	C	C

Appendix 1. Continued.

dlll.mat5	6	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
		salic	chlo	kran	leaf	vein	folia	elon	corti	brac	K-C	peta	num	high	trim	sepa	peta	peta	scak	pena	varia	trim	isom	cent	cent	poly	anth	inve	expa	conr	valva	nect	gync	carp	carp	carp	ovar	carp	degr	stipi	stigr
1	Ceratophyllaceae	A	A	A	A	A	A	A	A	T	A	T	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	T	A	A	A	A	A	A	A	A	A	A	A
2	Chloranthaceae	A	C	A	C	A	A	A	A	C/T	A	T	A	A	A/C	A	A	A	A	C	C	C	A/C	A	A	A	A	A	A/C	T	C	A	A	A	A	A	A	A	A	A	A
3	Nymphaeaceae	A	A	A	C	A	A	A	C	A	A	A	C	A/T	A/C	A	A	A	A	C	A	A	A	C	A	C	A	A	C	C	C	A	A/C	G/T	A/T	A/T	A	A	A	C	C
4	Amborellaceae	A	C	A	A	?	A	A	?	A	A	A	C	C	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	T	A	A	A	T	T	C	A	A	A	C	A
5	Austrobaileyaceae	A	A	A	A	?	?	A	A	A	A	A	C	G	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	T	A	A	A	T	T	G	A	A	A	C	A
6	Illiciales	A	A	A	A	A	A	C	A	A	A	A	C	T	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	T	A	A	A	T	T	T	A	A	A	A	C
7	Winterales	A	A	A	C	A	A	C	A	A	A	A	C	A	C	A	A	A	A	C	A	A	A	C	A	C	A	A	C	T	A	A	A	T	T	C	A	A	A	C	C
8	Monocotyledons	A	A	A	A	A	A	A	C	A	A	A	C	A	C	A	A	A	A	A	G	C	C	A	A	C	A	A	A	T	A	A	C	G	A	A	A	C	A	A	?
9	Aristolochianae	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	G	A/C	C	A	C	C	A	A	A	C	C	A	C	G	A	A	A	C	A	A	?
10	Laurales	A	C	A	C	A	A	A	A	A	A	A	C	T	C	A	A	A	A	A	A	C	A	C	A	C	A	A	A	T	C	A	A	T	T	G	A	A	A	C	A
11	Myristicaceae	A	A	A	?	A	A	A	C	A	A	A	C	A	C	C	A	A	A	A	A	C	A	A	A	C	A	A	A	T	A	A	C	A	A	A	A	A	A	A	A
12	Annonales	A	A	A	C	A	A	C	C	A	A	A	C	A	C	A	A	A	A	C	A	C	A	C	A	C	A	A	C	T	C	A	A	T	T	T	A	A	A	C	C
13	Magnoliales	A	A	A	C	C	C	C	C	A	A	A	C	C	C	A	A	A	A	A	A	A	A	C	A	A	A	A	C	T	C	A	A	T	T	T	A	A	A	C	C
14	Ranunculidae	A	C	C	C	A	A	C	C	A	A	A	C	T	C	A	G	A	A	A	A	C	C	C	A	C	C	A	A	A	C	A	A	G/T	A/T	A/T	A	A	A	C	C
15	Eupteleaceae	A	?	A	A	A	A	A	?	C	A	T	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	T	T	G	A	A	A	C	C
16	Platanaceae	A	A	A	A	A	A	A	?	A	A	A	C	C	A	A	T	A	A	A	C	C	C	A	A	A	A	A	A	T	C	A	A	T	T	C	A	A	A	C	C
17	Nelumbonaceae	A	A	A	A	A	A	C	C	A	A	A	C	T	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	C	A	A	A	T	T	T	A	A	A	A	A
18	Trochodendrales	A	C	A	C	A	A	A	C	T	A	T	A	A	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	A	C	A	A	T	T	G	A	C	A	A	A
19	Proteaceae	A	A	A	C	C	C	A	A	A	A	G	G	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	C	A	C	C	A	A	A	A	A	A	C	A
20	Buxaceae	A	A	A	A	A	A	A	A	G	A	T	A	A	A	A	A	A	A	A	C	A	C	A	A	C	C	A	A	C	A	A	C	G	A	A	A	C	A	A	C
21	Sabiaceae	A	A	A	?	?	?	A	?	A	C	A	T	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	C	A	C	C/G	A/C	A	A	A	C	A	A	A
22	Didymelaceae	A	A	A	C	A	A	A	?	G	A	T	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	?
23	Myrothamnaceae	A	A	A	A	A	A	A	?	G	A	T	A	A	A	A	A	A	A	A	A/C	A	A/C	?	A	A	A	A	A	C	A	A	C	T	C	A	A	C	A	A	C
24	Berberidopsidaceae	A	A	A	A	?	?	A	?	A	A	A	C	G	A	A	A	A	A	A	A	A	A	?	?	A	A	A	A	C	A	C	A	G/T	A/G	A	A	T	C	A	A
25	Gunneraceae	A	A	A	A	A	A	A	A	A	C	?	G	A	A	A	C	A	A	A	C/G	A	A/C	A	?	A	A	A	A	A	A	A	C	C	A	A	A	G	A	A	A
26	Rhabdodendraceae	A	A	?	C	A	A	A	?	A	C	A	T	A	A	C	G	A	A	A	A	A	A	C	?	A	A	A	A	C	A	A	C	A	A	A	A	A	A	A	A
27	Simmondsiaceae	A	A	A	A	A	A	A	?	A	A	A	T	A	A	A	A	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A	C	G	A	A	A	G	A	A	A
28	Caryophyllales	A	A	C	A	C	C	A	C	A	A	C	T	A	A	A	A	A	A	A	C/G	A	C	A	C	C	C	A	A	C	A	C	C	G/T	A/G	A	A	G	A	A	A
29	Asteropeiaceae	?	A	?	C	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	A	A	A	?	?	A	A	A	A	?	A	A	C	G	A	A	A	G	A	A	A
30	Plumbaginaceae	A	A	A	C	C	C	A	A	A	C	C	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	G	A	A	A
31	Polygonaceae	A	A	A	A	A	A	A	?	A	A	A	C	A	C	A	A	A	A	A	G	A	C	C	A	C	C	A	A	A	A	C	C	G	A	A	A	G	A	A	A
32	Dioncophyllaceae	A	A	?	?	?	?	A	?	A	C	C	T	A	A	C	G	A	A	A	G	A	C	?	?	A	A	A	A	C	A	A	C	C/T	G	A	A	G	A	A	A
33	Ancistrocladaceae	A	A	A	A	A	A	A	?	A	C	C	T	A	A	C	G	A	A	A	G	A	C	A	A	A	C	A	A	?	A	A	C	G	A	A	A	T	A	A	A
34	Nepenthaceae	A	A	A	C	A	C	A	?	A	A	A	G	A	A	A	A	A	A	A	A/G	A	A/C	?	?	C	C	A	A	A	A	A	C	T	C	A	A	T	A	A	A
35	Droseraceae	A	A	A	A	A	A	A	A	A	C	C	T	A	A	A	G	A	A	A	A/C	A	A/C	?	?	A	C	A	A	A	A	A	C	T	G	A	A	G	A	A	A
36	Tamaricaceae	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	C	A	G	A	C	A	C	A	C	A	A	A	A	C	C	T	G	A	C	G	A	A	A
37	Frankeniaceae	A	A	A	C	A	A	A	A	A	C	A	C	C	A	C	T	A	C	A	A	A	A	?	?	A	C	A	A	A	A	A	C	G	A	A	G	G	A	A	A
38	Hamamelidales	A	A	A	C	C	A	C	A	T	A	T	T	A	A	A	A	A	A	A	A/C	A	A/C	A/C	A/C	A	A	A	A	C	C	A	A	C	A	A	A	A	A	A	C
39	Dilleniaceae	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	A	C	A	A/C	A	A	C	A	A	C	T	T	G	A	A	A	A	A
40	Vitaceae	A	A	A	?	A	A	A	A	A	C	G	T	A	A	C	G	A	A	A	T	A	A	A	A	A	C	A	A	C	A	C	C	C/T	A/T	A/C	A	T	A	A	A
41	Eucryphiaceae	A	A	A	A	A	A	C	?	A	C	A	G	A	A	A	C	A	A	A	A	A	A	?	?	A	C	A	A	A	A	A	A	T	T	G	C	C	A	A	A
42	Brunelliaceae	A	A	A	A	A	A	A	?	A	A	G	T	A	A	?	A	A	A	A	G	A	C	?	A	A	C	A	A	C	A	C	C	T	G	A	C	A	A	A	A
43	Cunoniales	A	A	A	C	C	A	A	?	A	C	A	T	A	A	A	A/G	A	A	A	G	A	C	C	?	A	C	A	A	C	A	C	C	C/T	A/G	A	A	C	A	A	A
44	Paeoniaceae	A	A	A	?	A	A	A	C	A	A	A	T	A	A	A	G/T	A	A	A	A	A	A	A	C	A	A	A	A	A	A	C	A	T	T	G	A	A	A	A	A
45	Cephalotaceae	A	A	A	A	A	A	A	?	A	A	G	C	C	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	C	C	T	T	C	A	A	A	A	A
46	Crassulaceae	A	A	A	A	A	A	A	A	A	C	G	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	C	A	A	A
47	Saxifragales s. str.	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	A	A	A	A	A	C	C	T	G	A	A	C	A	A	A
48	Staphyleaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	C	A	A	C	G	A	A	A	G	A	A	A
49	Elaeagnaceae	A	A	A	A	A	A	A	A	A	A	G	T	A	A	A	A	A	A	A	G/T	A	C	A	A	A	A	A	A	A	A	C	C	A	A	A	G	A	A	A	A
50	Rosaceae	A	A	A	A	A	C	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	C	A	A	C	A	A	A	A	C	C	T	T	G	A	A	A	A	A
51	Rhamnaceae	A	A	A	C	A	A	A	A	A	C	T	T	A	A	A	G	A	A	A	T	A	C	A	A	A	C	A	A	A	A	C	C	G	A	A	A	G	A	A	A
52	Faganae	A	A	A	?	A	C	A	A	A	A	A	C	C	A	A	A	A	A	A	A/C	A	A/C	A	A	A	A	A	A	A	A	A	A	T	A	A	A	G	A	A	C
53	Cucurbitales	A	A	A	C	A	A	A	A	A	C	A	C	C	A	A	G/T	A	A	A	C	A	C	A	A	A	A	A	A	C	A	C	C	T	T	C	A	G	A	A	A
54	Coriariaceae	A	A	A	A	A	A	A	?	A	C	G	T	A	A	A	G	A	A	A	G	A	C	A	A	A	A	A	A	C	A	A	C	T	G	A	A	A	A	A	A
55	Urticales	A	A	A	A	A	A	A	A	A	A	A	T	A	A	A	A	A	A	A	C/G	A	C	A	A	A	A	A	A	A	A	A	C	C	A	A	A	G	A	A	A

Appendix 1. Continued.

dlll.met5	7	241	242	243	244	245	246	247	248	249	250	251	252
		plac	diffu	stigr	ovar	ovul	ovul	micr	obtu	seec	fruit	type	cent
1	Ceratophyllaceae	A	A	C	A	C	A	G	A	C	C	T	A
2	Chloranthaceae	A	A	A	A	C	A	A/C	A	C	C	T	A
3	Nymphaeaceae	A	C	C	A	T	A/C	C	A	T	A	A	A
4	Amborellaceae	A	A	A	A	C	A	A	A	C	C	T	A
5	Austrobaileyaceae	A	A	C	A	T	C	C	A	T	C	T	A
6	Illiciales	A	A	C	A	T	C	A	A	G	A	A	A
7	Winterales	A	A	C	A	T	C	C	A	T	C	T	A
8	Monocotyledons	A	A	C	A	T	A/C	?	?	T	A	A	A
9	Aristolochianae	A	A	C	A	T	A/C	C	?	T	A	A	A
10	Laurales	A	A	C	A	C/G	C	C	C	C	C	T	A
11	Myristicaceae	A	A	C	A	C	C	C	A	C	A	G	A
12	Annonales	A	A	C	A	T	C	C	C	T	C	T	A
13	Magnoliales	A	A	C	A	T	C	A/C	C	T	A	A	A
14	Ranunculidae	A	A/C	C	A	T	A/C	C	A	T	A	A	A
15	Eupteleaceae	A	A	C	A	T	C	A	A	G	C	T	A
16	Platanaceae	A	A	C	A	C	A	C	A	C	A	A	A
17	Nelumbonaceae	A	A	A	A	C	C	C	C	C	C	T	A
18	Trochodendrales	A	A	C	A	T	C	A	A	T	A	A	A
19	Proteaceae	A	A	A	A	T	A/C	C	C	T	A	A	A
20	Buxaceae	G	A	C	A	G	C	A	C	G	A	C	A
21	Sabiaceae	G	A	A	A	G	?	G	A	A	C	T	A
22	Didymelaceae	A	A	C	A	C	C	A	?	C	C	T	A
23	Myrothamnaceae	G	A	C	A	T	C	C	A	T	A	A	A
24	Berberidopsidaceae	T	A	A	A	T	C	C	A	T	C	T	A
25	Gunneraceae	C	A	A	A	A	C	C	A	A	C	T	A
26	Rhabdodendraceae	A	A	C	?	G	C	G	?	C	C	T	A
27	Simmondsiaceae	G	A	A	A	C	C	?	A	A	A	C	A
28	Caryophyllales	G	A	C	A	T	C	C	C	T	A	C	A
29	Asteropeiaceae	T	A	A	?	T	?	?	?	?	A	C	?
30	Plumbaginaceae	G	A	A	A	A	C	C	C	A	A	C	A
31	Polygonaceae	G	A	C	A	A	A	C	A	A	C	T	A
32	Dioncophyllaceae	T	A	A	A	T	C	C	A	G	A	C	A
33	Ancistrocladaceae	G	A	A	C	A	C	?	A	A	C	T	A
34	Nepenthaceae	G	A	A	A	T	C	C	A	T	A	C	A
35	Droseraceae	G/T	A	C	A	T	C	C	A	T	A	C	A
36	Tamancaceae	T	A	C	A	T	C	C	A	T	A	C	A
37	Frankeniaceae	T	A	C	A	T	C	C	A	T	A	C	A
38	Hamamelidales	A	A	C	A	C/T	C	A	A	C/T	A	A	A
39	Dilleniaceae	A	A	A	A	T	C	A	A	T	A	A	A
40	Vitaceae	T	A	A	A	G	C	C	C	G	C	T	A
41	Eucryphiaceae	G	A	A	A	T	C	A	?	T	A	A	C
42	Brunelliaceae	A	A	A	A	G	C	?	A	G	A	A	A
43	Cunoniales	A	A	A	A	T	C	A	A	T	A	A	A
44	Paeoniaceae	A	A	C	A	T	C	A	A	T	A	A	A
45	Cephalotaceae	A	A	?	A	G	C	C	A	C	A	A	A
46	Crassulaceae	A	A	A	A	T	C	A	A	T	A	A	A
47	Saxifragales s. str.	A	G	A	A	T	C	C	C	T	A	A	A
48	Staphyleaceae	G	A	A	A	T	C	A	A	T	A	C	A
49	Elaeagnaceae	G	A	A	A	C	C	A	C	C	C	A	A
50	Rosaceae	A	A	A	A	T	C	A	C	T	A	A	A
51	Rhamnaceae	G	A	A	A	G	C	C	A	C	A	C	A
52	Faganae	G	A	C	C	G	A/C	A	A	C	C	T	A
53	Cucurbitales	T	A	A	C	T	C	A	C	T	A	C	A
54	Coriaraceae	A	A	A	A	C	C	C	A	C	C	T	A
55	Urticales	C	A	C	A	C	C	A/C	C	A	C	T	A

Appendix 1. Continued.

dill.mat6	8	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
		sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	Al a	amic	dhu	prot	trigl	taxi	proa	hete	card	valin	linar	lota	linus	neol	tyros	prun	sam	zieri	holo	gluc	dihy	acet	eleo	myri
56	Crossosomataceae	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
57	Connaraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
58	Oxalidaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
59	Stachyuraceae	?	?	?	?	A	A	A	?	?	?	A	A	A	A	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
60	Geissolomataceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
61	Geraniaceae	?	?	?	?	?	?	?	A	A	C	?	A	A	A	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
62	Melianthaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
63	Fabaceae	?	A	A	?	?	?	?	A	A	C	?	?	?	?	?	?	A	C	A	A	A	A	C	A	A	C	C	C	A	A	C	C	C	C	C	A	C	A	A	A
64	Surianaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
65	Polygalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
66	Rhizophoraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
67	Zygophyllaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	A
68	Vochysiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
69	Myrtales	?	?	?	?	?	?	?	A	C	C	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A
70	Rutales	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	C	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	C	A	A	C	C	A	C
71	Sapindales	?	?	?	?	?	?	?	A	C	C	?	?	?	?	?	?	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A
72	Celastrales	?	?	?	?	?	?	?	A	A	C	?	A	A	A	A	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A
73	Irvingiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74	Violaceae	?	?	?	?	A	C	C	A	C	C	A	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A
75	Flacourtiaceae	?	?	?	?	A	C	C	C	C	C	A	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
76	Kiggelariaceae	?	?	?	?	C	C	C	?	?	?	A	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
77	Salicaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A
78	Elaeocarpaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	C	A	C	?	?	A	C	A	A	A
79	Moringaceae	?	?	?	?	A	A	A	?	?	?	A	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	?
80	Caricaceae	?	?	?	?	A	A	A	?	?	?	A	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	C	A	A	A	A
81	Passiflorales	?	?	?	?	C	C	C	C	C	C	A	?	?	?	?	?	A	A	A	A	A	A	A	A	A	C	C	C	C	C	C	C	C	C	C	C	A	A	A	A
82	Euphorbiales	?	?	?	?	A	A	C	C	C	?	A	?	?	?	?	?	C	A	C	A	C	C	A	A	A	C	C	C	A	A	A	A	A	A	A	C	C	A	C	A
83	Capparales	?	?	?	?	A	A	C	A	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	?
84	Tropaeolaceae	?	?	?	?	A	A	A	C	C	C	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	?
85	Salvadoraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	?
86	Caryocaraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87	Ochnaceae	?	?	?	?	A	A	A	?	?	?	A	A	A	A	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
88	Medusagynaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
89	Malpighiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
90	Linales s.str.	?	?	?	?	?	?	?	C	C	C	?	A	A	A	?	?	A	A	A	A	A	A	A	A	A	C	C	C	C	C	A	A	C	C	C	A	A	A	A	?
91	Clusiaceae	?	?	?	?	A	A	A	?	?	?	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
92	Bonnetiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93	Elatinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
94	Quiinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
95	Chrysobalanaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	C	?
96	Dichapetalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	A	A	?
97	Trigoniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98	Erythroxylaceae	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
99	Sphaerosepalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100	Thymelaeaceae	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	C
101	Dipterocarpaceae	?	?	?	?	A	A	A	?	?	?	A	A	A	A	A	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	A	?	A	A	A
102	Sarcolaenaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	A	?
103	Bixaceae	?	?	?	?	A	A	A	?	?	?	A	?	?	?	?	?	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A
104	Cochlospermaceae	?	?	?	?	A	A	A	?	?	?	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?
105	Cistaceae	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
106	Malvales s. str.	?	?	?	?	A	A	A	A	A	A	A	?	?	?	?	?	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A
107	Strasburgeriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
108	Podostemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
109	Bruniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
110	Balanophoraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1. Continued.

dill.met5	9	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
		asar	sesc	germ	myo	pinit	quet	deut	cant	cyck	simn	aust	kads	eucc	syrir	pino	dihy	galb	licar	vera	prod	ellac	mett	stac	cast	tellin	tellin	pedi	gera	chlor	gallic	epig	flavc	afze	davi	bifla	Oura	euxa	nora	mac	benz
56	Crossosomataceae	?	?	?	?	?	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
57	Connaraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
58	Oxalidaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
59	Stachyuraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	C	C	C	A	C	C	A	A	?	A	?	A	A	A	?	A	A	A	A
60	Geissolomataceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
61	Geraniaceae	A	A	A	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	C	C	A	A	A	A	A	A	C	A	C	A	?	A	A	A	A	A	A	A	A
62	Melianthaceae	?	?	A	?	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	A	?	A	?	?	?	?	?	?	?	?
63	Fabaceae	A	?	?	?	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	C	A	C	A	A	A	A	A	C	A	?	C	A	C	A	C	A	A	A	A	A
64	Surianaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
65	Polygalaceae	?	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	A
66	Rhizophoraceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	?	A	?	?	C	?	?	A	?	?	?	A
67	Zygophyllaceae	A	A	A	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	A
68	Vochysiaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
69	Myrtales	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	C	C	C	C	C	C	A	C	A	A	C	A	A	A	A	A	A	A
70	Rutales	A	C	A	C	C	A	A	A	A	A	C	A	A	C	A	A	A	A	A	C	C	C	?	?	?	?	?	?	?	C	?	?	?	?	C	A	?	?	?	C
71	Sapindales	A	A	A	?	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	C	A	C	A	?	A	A	A	A	A	A	A	C
72	Celastrales	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	C	A	A	A	C
73	Irvingiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
74	Violaceae	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
75	Flacourtiaceae	A	A	A	C	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
76	Kiggelariaceae	A	A	A	A	A	A	A	A	C	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
77	Salicaceae	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
78	Elaeocarpaceae	A	A	A	?	?	?	?	?	A	?	A	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	C	A	C	A	?	A	A	A	A	A	A	A	A
79	Moringaceae	?	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A
80	Caricaceae	A	A	A	C	A	A	A	A	C	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	A	A	A
81	Passiflorales	A	A	A	A	A	A	A	A	C	A	A	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	A	A	A
82	Euphorbiales	A	C	A	C	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	C	C	A	A	A	A	A	C	A	C	C	?	A	A	A	?	A	A	A	C
83	Capparales	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
84	Tropaeolaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	?
85	Salvadoraceae	?	A	?	A	A	A	A	A	A	?	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	A
86	Caryocaraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
87	Ochnaceae	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	C	C	A	A	A	A
88	Medusagynaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
89	Malpighiaceas	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A
90	Linales s.str.	?	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	?	A	C	A	?	A	A	A	A	A	A	A	A
91	Clusiaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	C	A	C	A	A	C	A	C	C	C	A
92	Bonnetiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?
93	Elatinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
94	Quiinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
95	Chrysobalanaceae	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	?
96	Dichapetalaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
97	Trigoniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98	Erythroxylaceae	A	A	A	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	C	A	A	?	A	A	A	A	A	A	A	A
99	Sphaerosepalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
100	Thymelaeaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	C	A	A	A	A	A
101	Dipterocarpaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	?	C	?	?	C	?	?	?	?	?	?	?
102	Sarcolaenaceae	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
103	Bixaceae	A	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	A	?	C	?	?	?	?	?	?	?	A
104	Cochlospermaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	A	A	A	A	?	C	A	A	?	A	A	A	?
105	Cistaceae	A	?	A	A	C	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	C	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	A
106	Malvales s. str.	A	C	A	A	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	?	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
107	Strasburgeriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
108	Podostemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
109	Bruniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	?
110	Balanophoraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	?	?	?	A	?	A	A	A	?	A	A	A	?

Appendix 1. Continued.

dill.mat5	10	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
		roen	anor	lirioc	prot	anci	cam	indo	indo	secc	corn	olea	arjur	dam	cucu	nigr	arbu	naph	rapa	plum	dros	anth	pher	anth	actir	nitro	chro	sievi	atrat	rod	epici	SiO2	oxal.	elon	solit	crys	spha	myrc	oil c	muci	resir
56	Crossosomataceae	?	?	?	?	?	A	?	A	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	A	A	G	A	A	A	A	A	A	A
57	Connaraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	?	A	C	A	A	A	C	C	A	A	C	A	A	A	A	C	C
58	Oxalidaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	C	A	?	?	?	A	A	A	C	C	A	A	A	A	A
59	Stachyuraceae	A	A	A	A	A	A	A	?	?	?	?	?	?	?	A	A	A	A	A	A	A	?	A	A	A	A	C	A	C	C	A	C	A	A	A	A	A	A	A	A
60	Geissolomataceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	C	A	A	A	A	C	A
61	Geraniaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	C	C	?	?	?	A	C	G	C	A	A	A	A	A	C
62	Melienthaceae	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	C	C	A	C	A	A	A	?	A
63	Fabaceae	A	A	A	A	A	A	C	A	A	A	C	A	C	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	?	C	C	C	G	C	A	C	A	A	C	C
64	Surianaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?	?	?	?	?	A	A	C	A
65	Polygalaceae	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	C	C	?	?	?	A	C	A	C	A	A	A	A	A	A
66	Rhizophoraceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	A	?	?	?	C	C	A	C	A	A	A	A	C	A
67	Zygophyllaceae	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	?	?	?	A	C	C	C	A	A	A	A	C	C
68	Vochysiaceae	?	?	?	?	?	?	?	A	A	A	?	?	?	A	?	A	A	A	A	A	C	A	A	?	A	?	C	?	?	?	C	C	A	C	A	A	A	A	C	A
69	Myrtales	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	C	C	A	A	A	C	C	C	A	A	C	C	?	?	?	A	C	C	C	C	A	A	C	C	C
70	Rutales	A	A	C	C	A	A	C	A	A	A	?	C	C	A	A	C	C	A	A	A	C	A	C	A	A	C	C	?	?	?	C	C	C	C	C	A	A	C	C	C
71	Sapindales	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	?	?	?	C	C	G	C	C	C	A	A	C	C
72	Celastrales	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	?	?	?	C	C	G	C	C	A	A	A	C	A
73	Irvingiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	?	?	?	C	C	A	C	A	A	A	A	?	A
74	Violaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	C	?	?	?	A	C	A	C	A	A	A	A	C	C
75	Flacourtieceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	A	C	G	C	A	A	A	A	C	C
76	Kiggelariaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	C	C	G	C	A	A	A	A	C	A
77	Salicaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	C	A	A	A	C	?	?	?	A	C	A	C	A	A	A	A	C	A
78	Elaeocarpaceae	A	A	A	A	A	A	C	A	A	A	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	C	C	A	C	A	C	C	G	C	A	A	A	A	C	A
79	Moringaceae	A	A	A	A	?	A	?	A	A	A	A	A	A	?	A	?	?	?	?	?	?	?	?	A	A	C	C	?	?	?	A	C	A	A	A	A	C	A	C	A
80	Caricaceee	A	A	A	A	A	A	?	A	A	?	C	A	A	A	?	?	?	?	?	?	?	A	?	A	A	A	C	?	?	?	A	C	A	A	A	A	A	A	A	A
81	Pasaiflorelea	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	C	C	?	?	?	A	C	A	C	A	A	A	A	C	A
82	Euphorbiales	A	A	C	A	A	A	C	A	A	A	C	A	A	C	A	A	C	A	A	A	C	C	A	A	A	A	A/C	?	?	?	C	C	G	C	A	C	A	C	C	C
83	Cappareles	A	A	A	A	A	A	C	A	A	A	A	A	A	C	A	A	?	?	?	?	?	A	A	A	A	C	A	?	?	?	A	C	G	C	A	A	C	A	C	A
84	Tropaeolaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	A	C	C	?	?	?	A	?	?	?	A	?	C	A	C	A
85	Salvadoraceae	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	A	A	C	A	A	A	A	C	A	C	A	A	A	A	A	A
86	Caryocaraceae	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	C	C	C	G	C	A	A	A	A	A	?
87	Ochnaceae	A	A	A	A	A	A	?	A	A	A	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	G	C	A	A	A	A	C	A
88	Medusagynaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	G	C	C	A	A	A	C	A
89	Malpighiaceae	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	C	C	?	?	?	A	C	G	C	A	A	A	A	C	A
90	Linales s.str.	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	C	?	?	?	C	C	A	C	A	A	A	A	C	A
91	Clusiaceae	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	A	C	C	C	G	C	A	A	A	A	A	C
92	Bonnetiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	C	C	C	A	?	A	?	A	A	A	C
93	Elatinaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	C	A	?	?	A	C	A	A	A	A	A	A	A	C
94	Quiinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	C	C	A	A	A	?	A	A	C	C
95	Chrysobalanaceae	?	?	?	?	?	?	?	A	?	?	?	?	?	C	?	?	?	?	?	?	?	A	?	?	A	A	C	A	A	A	C	C	A	A	A	A	A	A	A	A
96	Dichapetalaceae	A	A	A	A	?	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	A	C	A	C	A	A	A	A	C	A
97	Trigoniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	?	?	?	A	C	A	C	A	A	A	A	C	A
98	Erythroxylaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	A	?	?	?	?	A	A	A	A	A	A	A	?	?	?	C	A	A	C	A	A	A	A	C	C
99	Sphaerosepalaceae	?	A	A	?	?	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	A	A	A	?	C	G	?	A	?	A	A	C	C
100	Thymelaeaceae	A	A	A	A	A	A	?	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	A	C	G	C	C	A	A	A	C	C
101	Dipterocarpaceae	?	?	?	?	?	?	?	A	A	A	C	A	C	A	A	?	A	?	A	A	C	A	?	?	A	C	?	A	A	A	C	C	A	C	A	A	A	A	C	C
102	Sarcolaenaceae	A	A	A	A	?	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	A	A	A	?	C	A	?	A	?	A	A	C	C
103	Bixaceae	A	A	A	A	A	A	A	A	A	?	A	C	A	A	A	?	?	?	?	?	?	A	?	A	A	C	C	A	A	A	A	C	A	?	A	?	A	A	C	C
104	Cochlospermaceae	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	A	C	A	A	A	A	A	A	C	C
105	Cistaceae	A	A	A	A	A	A	A	A	A	A	?	?	C	A	A	?	?	?	?	?	?	?	C	A	A	C	C	C	A	A	A	C	A	A	A	A	A	A	C	A
106	Malveles s. str.	A	A	A	A	A	A	C	C	A	A	A	A	C	C	A	A	C	A	A	A	A	A	C	A	A	C	C	A	C	A	C	C	A	C	A	A	A	A	C	C
107	Strasburgeriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	?	C	G	C	?	?	A	A	A	A
108	Podostemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	C	C	A	C	A	A	A	A	A	C
109	Bruniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	A	A	C	C	A	C	?	A	A	A	A	C
110	Balanophoraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	C	A	C	A	A	A	A	A	A

Appendix 1. Continued.

dill.mats	11	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
		latic	fasci	pelta	denc	nonc	glan	anth	micr	polle	type	pola	trian	trian	angu	sexu	type	intec	intec	nuce	peris	endc	occu	occu	occu	end	aril	pach	sarc	rumi	axot	axot	theo	tann	mes	endc	endc	axot	exot	bixoi	hypc
56	Crossosomataceae	A	?	A	A	A	A	C	C	G	G	C	A	A	A	G	G	A	A	A	?	A	A	A	A	?	C	A	A	A	A	?	?	?	?	?	?	A	A	A	C
57	Connaraceae	A	C	A	C	C	A	?	?	G	G	A	A	A	A	G	G	A	A	A	A	A	?	?	?	G	C	A	C	A	A	C	A	A	A	C	C	G	A	A	A
58	Oxalidaceae	A	A	A	A	A	A	C	C	G	C/G	C	A	A	A	G	G	A	A	G	A	A	A	A	A	C	C	A	A	A	A	C	A	A	A	C	A	G	A	A	A
59	Stachyuraceae	A	?	A	A	A	A	?	?	G	G	C	A	A	A	G	C	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	?	C	?	A	A	A	A	A
60	Geissolomataceae	A	?	?	?	A	?	?	?	G	G	C	A	A	A	G	C	A	A	A	?	C	A	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
61	Geraniaceae	A	A	A	A	A	A	C	C	G	C	C	A	A	A	G/T	A/G	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C
62	Melianthaceae	A	C	A	A	C	A	C	A/C	G	G	G	A	A	A	T	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	A	A	A	A	A	A	A	A	C
63	Fabaceae	A	C	C	C	C	C	C	C	G	C	A	A	A	A	T	A	A	A	A	A	A	C	A	A	G	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A
64	Surianaceae	A	A	?	?	A	A	?	?	G	G	C	C	A	C	T	A	C	A	A	C	A	?	?	?	?	A	C	A	A	A	?	?	C	A	?	A	?	A	?	C
65	Polygalaceae	A	A	A	A	A	A	C	C	G	G	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A	C	C	A	A	A	C
66	Rhizophoraceae	A	C	A	A	A	A	?	C	G	G	A	A	A	C	G	C	A	C	A	A	A	?	?	?	C	C	A	A	A	A	C	A	C	A	A	A	A	A	A	A
67	Zygophyllaceae	A	A	A	A	C	A	C	C	G	C	A	A	A	A	G	G	A	A	A	A	A	A	A	A	G	A	A	A	C	A	A	A	A	A	C	A	A	A	A	C
68	Vochysiaceae	A	C	A	A	C	A	?	?	G	G	A	A	A	C	T	A	A	A	A	A	A	?	?	?	?	A	A	A	A	C	A	A	A	?	C	A	A	A	A	C
69	Myrtales	A	C	C	C	C	C	C	C	G	C	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A/C	A	A	A	A	A	C	C	C	C	A	A	A	C
70	Rutales	A	C	C	A	C	C	C	C	G	G	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	A	C	A	A	A	A	C
71	Sapindales	A	C	C	A	C	C	C	C	G	C	A	C	A	C	G/T	A/G	A	A	A	A	A	A	A	A	C	C	C	C	A	A	A	A	A	C	C	A	A	A	A	C
72	Celastrales	C	C	A	A	C	A	C	C	G	G	A	A	A	A	G	G	A	C	A	A	A	C	A	A	G	C	A	A	A	A	A	A	A	A	A	A	G	A	A	C
73	Irvingiaceae	A	A	?	?	A	A	?	?	G	G	A	C	A	C	A	A	A	?	A	A	?	?	?	?	C	A	A	A	A	A	A	A	A	C	?	A	G	A	A	?
74	Violaceae	A	A	A	A	A	A	C	C	G	G	C	A	A	C	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	C	A	G	A	A	C
75	Flacourtiaceae	C	C	A	A	C	A	C	C	G	G	A	A	A	A	G	C	A	A	A	A	A	?	?	?	A	A	A	A	A	A	A	A	?	A	A	C	G	A	A	C
76	Kiggelariaceae	A	A	C	A	A	A	C	C	G	G	A	A	A	A	G	C	A	A	A	A	A	?	?	?	G	A	C	C	A	A	A	A	C	A	A	C	G	A	A	C
77	Salicaceae	A	A	A	A	A	A	C	?	G	G	C	A	A	A	G	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	?	A	A	A	A	A
78	Elaeocarpaceae	A	A	A	A	A	A	C	C	G	G	A	A	A	A	G	C	A	C	A	A	A	A	A	A	G	C	A	A	A	A	A	A	A	A	C	A	G	A	A	C
79	Moringaceae	A	A	A	A	A	A	C	C	G	G	G	A	A	A	A	A	A	A	A	A	A	A	A	A	G	A	A	A	A	A	A	A	A	C	?	A	A	A	A	C
80	Caricaceae	C	A	A	A	A	A	C	C	G	G	G	A	A	A	G	C	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	C	A	G	A	A	C
81	Passiflorales	A	C	A	A	C	A	C	C	G	G	G	A	A	A	G	C/G	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A	A	C	G/T	A	A	A
82	Euphorbiales	A/C	C	C	C	C	C	C	C	G	C	A	A	A	C	C	A	A	A	A	A	A	A	A	A	G	C	C	C	A	A	A	A	A	A	A	C	G/T	A	A	C
83	Capparales	A	C	C	C	C	C	C	C	G	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	A	C	A	C	A	G	A	A	C
84	Tropaeolaceae	A	A	A	A	A	A	C	C	G	G	C	A	A	A	G	G	A	A	G	A	A	?	?	?	A	A	A	A	A	A	A	A	?	A	?	A	A	A	A	C
85	Salvadoraceae	A	A	C	A	A	A	?	C	G	G	A	A	A	A	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	?	A	G	A	A	A
86	Caryocaraceae	A	A	A	A	A	A	?	?	G	G	C	A	A	A	G	G	A	A	?	A	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
87	Ochnaceae	A	A	A	A	A	A	C	C	G	G	A	A	A	A	A	A	A	A	G	A	A	?	?	?	G	A	C	A	A	A	A	A	C	A	C	A	G	A	A	A
88	Medusagynaceae	A	A	A	A	A	A	?	?	G	T	A	A	A	C	G	C	A	A	C	A	?	?	?	?	A	A	A	A	A	A	A	A	?	?	?	A	G	A	A	C
89	Malpighiaceae	A	A	A	A	C	A	C	?	G	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	G	A	A	A
90	Linales s.str.	A	C	A	A	A	A	C	C	G	G	C	C	A	A	G	G	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	G	G	A	A	C
91	Clusiaceae	A	A	A	C	A	A	C	?	G	G	C	A	A	C	A	A	A	C	A	A	A	C	A	A	G	C	A	A	A	A	A	A	C	C	A	A	A	C	A	C
92	Bonnetiaceae	A	A	A	A	A	A	C	C	G	G	G	A	A	A	G	C	A	A	G	A	A	?	?	?	A	C	A	A	A	A	A	A	?	A	A	A	A	C	A	A
93	Elatinaceae	A	C	A	A	A	A	C	C	G	G	C	A	C	A	G	G	A	A	C	A	A	?	?	?	?	?	A	A	A	A	A	A	C	A	A	?	A	C	A	A
94	Quiinaceae	A	A	A	A	A	A	?	?	G	G	C	A	A	A	G	G	?	A	?	A	?	?	?	?	?	?	A	?	?	A	A	?	?	?	?	?	?	?	?	?
95	Chrysobalanaceae	A	C	C	A	A	C	C	C	G	C	C	A	A	A	?	?	A	C	G	A	A	?	?	?	C	A	A	A	A	A	A	?	?	C	?	A	A	A	A	C
96	Dichapetalaceae	A	A	A	A	A	A	?	?	G	G	A	A	A	A	G	G	A	A	G	A	A	?	?	?	C	A	A	?	?	A	A	A	C	A	A	A	A	A	A	A
97	Trigoniaceae	A	A	A	A	A	A	?	?	G	G	G	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	A	A	A	C	A	A	?	A	A	A	G	A	A	A
98	Erythroxylaceae	A	A	A	A	A	A	C	C	G	G	G	A	A	A	G	G	A	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	A	A	A
99	Sphaerosepalaceae	A	A	A	A	A	?	?	?	G	G	?	A	A	A	A	A	A	A	A	A	A	?	?	?	?	A	A	A	C	A	A	?	?	?	?	A	T	A	A	?
100	Thymelaeaceae	A	A	A	A	C	A	C	C	G	C	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	T	A	A	C
101	Dipterocarpaceae	A	C	C	A	A	C	C	?	G	C	C	A	A	A	G	G	A	A	A	A	A	A	A	A	G	C	A	A	A	A	A	A	?	A	A	A	T	A	C	C
102	Sarcolaenaceae	A	C	C	A	C	C	?	?	G	C	G	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	?	?	?	?	?	?	?	?	?
103	Bixaceae	A	C	C	A	A	A	C	C	G	G	G	A	A	?	T	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	?	A	T	A	C	C
104	Cochlospermaceae	A	A	C	A	A	A	?	?	G	G	A	A	A	A	G	C	A	A	A	A	A	?	?	?	A	A	A	A	A	C	A	A	A	A	A	A	T	A	C	C
105	Cistaceae	A	C	C	A	A	C	C	C	G	G	G	A	A	C	G/T	A/C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	T	A	C	C
106	Malvales s. str.	A	C	C	A	C	C	C	C	G	G	A	A	A	C	G	G	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	T	A	A	C
107	Strasburgeriaceae	A	C	?	A	A	A	?	?	G	G	G	C	A	C	A	A	A	?	A	?	A	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	A	A	A	?
108	Podostemaceae	A	A	A	A	A	A	C	A/C	G	C	A	A	A	A	C	A	A	A	G	?	?	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A
109	Bruniaceae	A	A	A	A	A	?	?	?	G	G	A	A	A	A	G	G	C	A	A	?	?	?	?	?	?	C	A	?	?	A	?	?	?	?	?	?	?	?	?	?
110	Balanophoraceae	A	A	A	A	A	A	C	A	G	C	A	C	A	C	A	A	?	A	?	A	C	A	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1. Continued.

dill.mat5	12	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
		endo	endo	emb	emb	susp	grow	disp	anor	phlo	wedg	inter	corti	scler	wood	fiber	fiber	tracl	librif	type	hom	rays	stor	vesti	vess	end	vess	vess	vess	dend	leaf	leaf	stipu	glan	leaf	stom	epid	muci	palm	cras	leaf
56	Crossosomataceae	A	A	C	A	A	A	A	A	A	A	A	A	C	A	C	A	C	A	G	A	A	A	A	T	T	?	A	A	A	C	A	C	A	A	G	A	A	A	A	C
57	Connaraceae	A	A	C	A	A	A/C	A	A	A	A	A	A	C	A	A	A	A	C	T	A	C	A	A	T	T	?	G	A	A	?	A	A	A	C	A	A	C	A	A	A
58	Oxalidaceae	A	A	C	A	A	C	A	A	?	A	A	C	C	A	A	C	A	C	T	A	C	A	A	T	T	?	G	C	A	C	A	C	A	C	A	A	A	A	A	A
59	Stachyuraceae	A	A	C	?	A	A	A	A	A	A	A	A	A	C	?	?	C	A	?	?	?	A	A	?	C	?	?	?	A	C	A	C	A	A	G	A	?	A	A	C
60	Geissolomataceae	?	A	G	A	A	A	A	A	A	A	A	A	C	A	?	A	?	A	A	A	A	?	?	?	?	?	?	A	?	?	C	C	A	A	G	?	C	A	A	A
61	Geraniaceae	A	A	C	A	A	A	A	A	?	A	A	A	C	A	A	A	A	C	?	?	?	A	A	C	G	A	?	C	A	C	A	C	A	A	G	A	A	C	C	C
62	Melianthaceae	A/C	A	C	A	A	A	A	A	A	A	A	A	C	G	A	A	A	A	G	A	A	C	A	C	C	A	C	C	A	G	A	C	A	C	G	A	A	A	C	C
63	Fabaceae	?	C	C	A	A	A	A	A	C	C	A	A	C	G	A	A	A	C	C	A	A	C	C	T	T	C	G	A	C	C	A	C	C	C	A	C	C	A/C	A	A
64	Surianaceae	?	C	C	C	A	A	A	A	?	A	A	A	C	A	C	A	A	A	?	?	?	?	A	?	T	C	C	C	A	?	A	C	A	A	G	A	C	A	?	A
65	Polygalaceae	A	A	C	A	A	C	A	A	A	A	C	A	C	A	A	A	C	A	C	A	A	A	A	T	G	C	C	A	A	A	A	A	A	A	G	A	A	A	A	A
66	Rhizophoraceae	A	A	C	A	A	A	A	A	?	?	A	?	C	A	C	A	C	A	C	A	A	A	A	C	C	A	C	C	A	C	C	C	A	A	A/G	A	A	A	A	A
67	Zygophyllaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	C	A	T	T	C	G	A	A	C	A	C	A	C	G	C	?	A	A	A
68	Vochysiaceae	?	?	C	A	A	A	A	A	A	A	C	A	C	C	A	A	A	C	C	A	A	A	C	T	T	C	G	A	A	A	C	C	A	A	G	A	C	A	A	?
69	Myrtales	?	A	G	A	C	C	A	A	C	A	C	A	C	C	C	A	C	A	A	A	A	A	C	C	C	A	C	A	C	A	A	C	A	A	G	?	A	A	A	C
70	Rutales	A	A	C	A	A	A	A	A	A	A	A	C	C	A	C	A	A	C	A	A	A	C	A	C	G	A	G	C	C	C	A	A	A	C	G	A	C	A	C	A
71	Sapindales	?	A	G	A	A	A/C	A	A	C	A	A	A	C	A	A	A	A	A	C	A	A	C	A	C	G	A	A	A	A	C	A	C	A	C	G	A	C	C	C	C
72	Celastrales	A	A	C	A	A	C	A	A	A	A	A	A	C	A	A	C	C	A	A	A	A	A	A	T	C	A	A	A	A	G	A	C	A	A	G	C	A	A/C	A	C
73	Irvingiaceae	?	?	G	A	A	A	A	A	?	A	A	A	?	G	C	A	A	C	G	A	A	A	A	T	T	?	?	C	A	?	A	C	A	A	A	A	?	A	A	A
74	Violaceae	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	C	C	A	A	A	A	C	A	C	A	A	A/G	A	C	A/C	A	A
75	Flacourtiaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	A	A	A	A	A	G	C	A	A	C	A	C	A	C	C	A	A/G	C	C	C	A	C
76	Kiggelariaceae	A	A	C	A	A	A	A	A	A	C	A	A	C	A	A	C	A	A	A	A	A	A	A	G	C	A	A	A	A	C	A	C	A	A	A/G	C	C	A	A	A
77	Salicaceae	A	A	G	A	A	A	A	A	C	A	A	A	C	A	A	A	A	C	T	A	C	A	A	T	T	C	C	C	A	C	A	C	A	A	A	A	C	C	A	C
78	Elaeocarpaceae	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	C	A	G	G	A	G	A	A	C	A	C	A	A	C	A	A	C	A	C
79	Moringaceae	?	A	G	A	A	A	A	A	A	A	A	A	C	G	A	C	A	A	T	C	A	C	A	T	T	?	G	C	A	?	A	C	?	C	G	A	C	A	A	A
80	Caricaceae	A	A	C	A	A	A	A	A	C	A	A	A	C	G	?	?	A	A	?	?	A	A	?	?	T	G	G	A	A	C/G	A	C	?	A	G	?	A	C	C	C
81	Passiflorales	A	A	C	A	A	A/C	A	A	A	A	A	C	C	A	A	A	A	A	T	A	A	A	A	T	G	A	G	C	A	C	A	C	C	A	G	A	C	C	C	C
82	Euphorbiales	A	A	C	A	A	A	A	A	A	C	C	A	C	A	A	A	A	A	A	A	A	A	A	C	C	A	C	A	A	C	A	C	C	A	A	C	A	A/C	C	C
83	Capparales	?	A	G	A	A	C	A	A	A	A	C	C	C	A	A	A	A	C	T	C	A	C	C	C	T	A	G	C	A	C	A	C	A	A	G	A	C	A	?	C
84	Tropaeolaceae	?	A	T	A	A	C	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	C	A	C	A	A	G	A	C	C	?	A
85	Salvadoraceae	?	A	T	A	A	A	A	?	?	A	C	A	C	A	A	A	A	C	G	A	A	C	A	T	T	?	?	C	A	A	C	C	A	A	A	A	A	C	?	A
86	Caryocaraceae	A	A	G	C	A	A	A	A	A	A	A	A	C	G	C	A	A	C	C	A	A	A	A	T	C	C	C	C	A	G	A	C	A	C	G	A	A	A	A	C
87	Ochnaceae	A	A	C	A	A	A	A	A	C	A	A	C	C	A	C	A	A	A	A	A	A	A	A	T	G	A	A	A	A	C	A	C	A	A	A	A	?	A	A	C
88	Medusagynaceae	A	?	G	A	A	A	A	A	C	?	A	C	C	C	C	A	C	C	A	A	A	A	?	G	T	A	C	A	A	G	C	A	A	A	G	A	?	A	A	C
89	Malpighiaceae	?	C	G	A	A	C	A	A	A	A	A	A	C	G	C	A	A	C	A	A	A	A	C	T	T	?	G	A	A	C	A	C	A	A	A	A	C	A	A	?
90	Linales s.str.	A	A	C	A	A	C	A	A	A	A	A	A	A	G	C	A	C	A	A	A	A	A	A	C	C	A	G	A	A	C	A	C	A	A	A	A	C	A	A	A
91	Clusiaceae	?	A	T	A	A	A	A	A	A	A	A	A	C	C	C	A	C	A	A	A	A	A	A	C	G	C	G	A	A	A	C	A	A	A	A	A	A	A	A	A
92	Bonnetiaceae	?	A	G	A	A	A	A	A	A	A	A	A	C	C	C	A	C	A	C	A	A	A	A	C	T	C	C	A	A	A	A	C	A	A	A	A	?	A	A	A
93	Elatinaceae	?	A	G	C	A	A	A	A	A	A	A	?	?	?	?	?	C	A	?	?	?	?	?	?	C	?	?	?	?	?	C	C	A	A	A	A	A	A	A	C
94	Quiinaceae	?	A	T	A	A	C	A	A	A	A	A	A	C	A	C	A	C	A	A	A	A	A	C	T	C	A	C	A	A	C	C	C	A	A	A	A	?	A	A	C
95	Chrysobalanaceae	?	A	T	A	A	A	A	A	A	A	A	A	C	G	A	A	C	A	T	A	A	A	A	T	T	?	G	A	A	C	A	C	A	A	A	A	A	A	A	A
96	Dichapetalaceae	?	A	T	A	A	C	A	A	A	A	A	A	C	G	C	A	A	A	A	A	A	A	?	C	G	A	G	C	A	?	A	C	A	A	A	A	C	A	A	A
97	Trigoniaceae	A	A	C	A	A	C	A	A	A	A	A	A	?	C	C	A	C	A	C	A	A	A	?	T	G	A	G	A	A	?	A	C	A	A	A	A	C	A	A	A
98	Erythroxylaceae	C	A	C	A	A	A	A	A	C	A	A	C	C	G	C	A	A	A	A	A	A	A	?	T	G	?	G	C	A	C	A	C	A	A	A	A	C	A	A	?
99	Sphaerosepalaceae	A	?	C	A	A	A	A	A	C	C	?	?	?	?	?	?	C	A	?	?	?	?	A	?	T	?	?	?	?	?	A	C	A	A	G	A	?	A	A	A
100	Thymelaeaceae	?	A	C	A	A	A	A	A	A	C	C	A	C	A	A	A	C	A	A	A	A	C	C	T	T	C	C	C	C	A	A	C	A	A	G	A	C	A	A	A
101	Dipterocarpaceae	?	A	C	C	A	A	A	A	C	C	A	C	?	G	C	A	A	A	G	A	A	A	C	T	T	G	G	A	A	C	A	C	A	A	G	A	C	A	A	A
102	Sarcolaenaceae	C	?	?	A	A	A	A	A	C	?	A	?	?	C	?	?	C	A	?	?	?	?	A	?	T	?	?	?	?	C	A	C	A	A	G	A	?	A	A	A
103	Bixaceae	C	A	C	C	A	A	A	A	C	C	A	?	?	A	?	A	A	A	G	A	A	C	C	T	T	C	?	A	A	C	A	C	A	A	G	A	?	C	A	A
104	Cochlospermaceae	A	A	C	C	A	A	A	A	C	C	A	A	C	G	A	A	A	A	G	A	A	C	A	T	T	C	G	C	A	C	A	C	A	A	G	?	C	C	C	C
105	Cistaceae	C	A	C	C	A	A	A	A	C	C	A	A	?	?	?	?	A	?	G	A	A	?	C	T	T	C	G	C	A	C	A	C	A	A	G	A	C	C	A	A
106	Malvales s. str.	A	A	C	C	A	A	A	A	C	C	A	?	?	G	?	?	A	C	G	A	A	C	A	?	T	?	?	?	A	C	A	C	A	A	G	A	C	C	C	?
107	Strasburgeriaceae	A	?	?	A	A	A	A	A	A	A	A	A	?	C	A	?	C	?	A	A	A	A	?	C	C	A	A	A	A	C	A	C	A	A	G	?	?	A	A	C
108	Podostemaceae	?	A	?	A	C	?	A	A	A	A	A	A	A	?	A	A	?	A	?	?	?	A	?	?	?	?	?	?	?	?	A	?	A	A	?	A	A	A	A	?
109	Bruniaceae	?	?	C	A	A	A	A	A	?	C	A	?	C	A	A	A	C	A	A	A	A	A	A	C	C	A	?	A	A	?	A	C	A	A	?	A	A	A	A	A
110	Balanophoraceae	?	?	A	A	A	A	A	A	?	A	?	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	?	A	A	A	A	A

Appendix 1. Continued.

dill.mat5	13	201 salic	202 chlo	203 kran	204 leaf	205 vein	206 folia	207 elon	208 corti	209 brac	210 K-C	211 peta	212 num	213 high	214 trime	215 sepa	216 peta	217 peta	218 scak	219 pena	220 varia	221 trime	222 isom	223 cent	224 cant	225 poly.	226 anth	227 inve	228 expa	229 conr	230 valv.	231 nect	232 gync	233 carp	234 carp	235 carp	236 ovar	237 carp	238 degr	239 stipit	240 stigr
56	Crossosomataceae	A	A	A	?	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	A	A	A	C	?	A	C	A	A	A	A	A	C	T	G	A	A	A	A	C	A
57	Connaraceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	A/T	A/G	A	C	A	A	C	A
58	Oxalidaceae	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	?	A	C	C	T	G	A	?	A	A	A	A
59	Stachyuraceae	A	A	A	A	A	A	A	A	A	C	A	G	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	?	A	A	C	T	C	A	C	T	C	A	A
60	Geissolomataceae	A	A	?	A	A	A	A	?	A	A	A	G	A	A	A	A	A	A	A	G	A	C	A	A	A	C	A	A	C	A	A	C	T	C	A	C	T	C	A	A
61	Geraniaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	G	A	A	A
62	Melianthaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	C	A	G	T	C	A	A
63	Fabaceae	A	A	C	C	A	C	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	A	A	A	A	A	A	C	A
64	Surianaceae	A	A	?	A	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	?	C	T	G	A	G	A	A	C	A
65	Polygalaceae	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	C	A	A	G	T	A	A	A
66	Rhizophoraceae	A	A	A	C	C	C	A	A	A	C	G	C	C	A	A	T	A	A	A	G	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	C	T	A	A	A
67	Zygophyllaceae	A	A	C	C	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	A	A	A	C	A	C	C	T	G	A	A	T	A	A	A
68	Vochysiaceae	A	A	A	C	C	C	A	?	A	C	A	T	A	A	C	G	A	A	A	T	A	C	A	A	A	C	A	A	C	A	A	C	G	A	A	G	T	C	A	A
69	Myrtales	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	A	A	A	C	A	A/C	C	T	G	A	A	G	A	A	A
70	Rutales	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	C/G	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	C	C	A	A	A
71	Sapindales	A	A	C	C	A	A	A	A	A	C	A	C	C	A	A	G	A	A	A	G	A	C	A	A	A	A	A	A	C	A	C	C/G	G/T	A/G	A	A	G	A	A	A
72	Celastrales	A	A	A	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	C/G	A	C	A	A	A	A	A	A	C	A	C	C	T	G	A	A	G	A	A	A
73	Irvingiaceae	A	A	?	C	A	C	A	?	A	C	A	T	A	A	C	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	C	T	C	A	A
74	Violaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	A	A	A	G	A	A	C	G/T	A/G	A	A	T	A	A	A
75	Flacourtiaceae	C	A	A	C	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A/C	A	C	A	C	A	A	A	A	G	A	C	A	G	A	A	A	G	A	A	A
76	Kiggelariaceae	A	A	A	C	A	A	A	A	A	A	A	C	G	A	A	A	A	C	A	A/C	A	C	?	?	A	A	A	A	A	A	A	A	G	A	A	A	G	A	A	A
77	Salicaceae	C	A	A	A	A	A	A	A	?	A	?	?	?	?	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	A	C/G	A	A	A	T	A	A	A
78	Elaeocarpaceae	A	A	A	A	A	A	A	A	A	C	A	C	G	A	A	G	A	A	A	A	A	A	A	C	A	A	A	A	C	A	C	?	T	T	C	A	G	A	A	A
79	Moringaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	G	A	A	C	T	C	A	A
80	Caricaceae	A	A	A	A	A	A	A	?	A	C	C	T	A	A	C	G	C	A	A	G	A	C	A	A	A	C	A	A	C	A	A	C	T	G	A	A	G	A	A	A
81	Passiflorales	A	A	A	C	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	C	A	?	C	G/T	A/G	A	A	G	A	A	A
82	Euphorbiales	A	A	C	C	C	C	A	A	A	C	A	T	A	A	A	G	A	A	A	A/C	A	C	?	C	A	A	A	A	C	A	C	C	G	A	A	A	G	A	A	A
83	Capparales	A	A	A	C	C	C	A	A	A	C	A/C	C/T	A/C	A	A	C/G	A	A	A	A/C	A	A/C	A	C	C	C	A	A	C	A	C	C	T	T	C	A	C	A	A	A
84	Tropaeolaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	G	A	A	G	T	A	A	A
85	Salvadoraceae	A	A	A	A	A	C	A	A	A	C	A	T	A	A	C	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	C	A	A	A	T	C	A	A
86	Caryocaraceae	A	A	?	C	C	A	A	?	A	C	A	T	A	A	C	G	A	A	A	A	A	A	C	?	A	C	A	A	A	A	A	A/C	T	G	A	G	G	A	A	A
87	Ochnaceae	A	A	A	C	A	A	A	A	A	C	C	C	C	A	A	T	A	A	A	A/C/	A	A/C	C	?	A	A	A	A	C	A	C	C	G/T	A/G	A	A	C	A	A	A
88	Medusagynaceae	A	A	A	A	A	A	A	?	A	C	C	T	A	A	A	G	A	A	A	A	A	A	?	?	A	C	A	A	A	A	?	A	T	T	T	A	G	A	A	A
89	Malpighiaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	A	G	G	A	A	A	G	A	A	A
90	Linales s.str	A	A	A	C	A	A	A	A	A	C	C	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	C	G	A	A	A
91	Clusiaceae	A	A	A	C	A	C	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	A	C	A	A	A	A	C	A	A	C	T	T	G	A	G	A	A	A
92	Bonnetiaceae	A	A	A	?	?	?	A	A	A	C	C	T	A	A	A	G	A	A	A	A	A	A	?	?	A	C	A	A	?	A	A	C	T	G	A	C	G	A	A	A
93	Elatinaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	G	A	A	A
94	Quiinaceae	A	A	?	C	A	A	A	?	A	C	C	T	A	A	C	G	A	A	A	A	A	A	?	?	A	C	A	A	?	A	A	C	T	T	G	A	A	A	A	A
95	Chrysobalanaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	A/G	A	A/C	?	?	A	C	A	A	A	A	C	C/G	A	A	A	G	A	A	A	A
96	Dichapetalaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	A	G	A	C	A	C	A	C	A	A	A	C	A	A	A	A	C	C	G	A	A	C	G	A	A	A
97	Trigoniaceae	A	A	A	C	A	A	A	?	A	C	C	T	A	A	A	G	A	A	A	A	A	A	?	?	A	C	A	A	A	A	A	G	G	A	A	C	T	C	A	A
98	Erythroxylaceae	A	A	A	C	A	A	A	A	A	C	A	T	A	A	C	G	A	C	A	G	A	C	A	A	A	C	A	A	A	A	A	C	G	A	A	A	G	A	A	A
99	Sphaerosepalaceae	A	A	?	A	A	A	A	?	A	C	C	T	A	A	A	G	A	A	A	A/G	A	A/C	?	?	A	C	A	A	A	A	C	C	G	A	A	G	T	C	A	A
100	Thymelaeaceae	A	A	A	C	A	A	A	A	A	C	?	T	A	A	C	G	A	A	A	G	A	C	A	C	A	C	A	A	A	A	C	C	T	G	A	G	T	C	A	A
101	Dipterocarpaceae	A	A	A	A	A	A	A	?	A	C	C	T	A	A	A	G	A	A	A	A/G	A	A/C	A	C	A	A	A	A	C	A	A	C	G/T	A/G	A	A	G	A	A	A
102	Sarcolaenaceae	A	A	?	C	A	A	A	?	A	C	C	T	A	A	A	G	A	A	A	A/G	A	A/C	?	?	A	C	A	A	A	A	C	C	G	A	A	?	T	C	A	A
103	Bixaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	A	C	A	C	A	A	A	A	?	C	C	A	A	G	T	C	A	A
104	Cochlospermaceae	A	A	A	A	A	A	A	A	A	C	C	T	A	A	A	G	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	C	T	G	A	G	T	C	A	A
105	Cistaceae	A	A	A	A	A	A	A	A	A	C	C	T	A	A	A	G	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	C	T	G	A	G	T	A	A	A
106	Malvales s. str.	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	C	T	T	C	G	T	C	A	A
107	Strasburgeriaceae	A	A	?	?	?	?	A	?	A	C	C	C	G	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	C	T	C	A	A
108	Podostemaceae	A	A	A	A	A	A	A	?	A	A	A	T	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	C	A	A	C	C/G	A	A	A	G	A	A	A
109	Bruniaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	A/C	G	A	A	A	C	A	C	A	A	A	C	A	A	C	A	C	C	G	A	A	G	G	A	A	A
110	Balanophoraceae	A	A	A	A	?	?	A	?	A	A	G	C	C	A	C	A	A	A	A	A	A	A	?	?	?	A	A	A	A	A	A	A	C/G	A	A	A	G	A	C	A

Appendix 1. Continued.

dill.mat5	14	241	242	243	244	245	246	247	248	249	250	251	252
		plac	diffu	stigr	ovar	ovul	ovul	micr	obtu	seec	fruit	type	cent
56	Crossosomataceae	A	A	C	A	T	C	A	A	T	A	A	A
57	Connaraceae	A	A	A	A	G	A/C	?	A	C	A	A	A
58	Oxalidaceae	G	A	A	A	T	C	?	A	T	A/C	C	C
59	Stachyuraceae	T	A	A	A	T	C	A	C	T	C	T	A
60	Geissolomataceae	G	A	A	A	G	C	A	A	C	A	C	A
61	Geraniaceae	G	A	C	A	T	C	A	C	T	A	C	C
62	Melianthaceae	G	A	A	A	T	C	C	A	C	A	C/G	A
63	Fabaceae	A	A	C	A	T	C	A	C	T	A	A	A
64	Surianaceae	A	A	A	A	G	C	G	?	?	C	T	A
65	Polygalaceae	G	A	A	A	T	C	A	A	C	A	C	A
66	Rhizophoraceae	G	A	A	A	T	C	C	A	C	A	C	A
67	Zygophyllaceae	G	A	A	A	T	C	A/C	C	T	A	C	A
68	Vochysiaceae	G	A	A	A	T	C	A	A	T	A	C	A
69	Myrtales	G/T	A	A	C	T	C	A	C	T	A	C	A
70	Rutales	A	A	C	A	T	C	C	C	T	A	C	A
71	Sapindales	G	A	A	A	G	C	A	C	G	A	C	A
72	Celastrales	G	A	A	A	T	C	A	A	T	A	C	C
73	Irvingiaceae	G	A	A	A	C	C	A	C	C	C	T	A
74	Violaceae	T	A	A	A	T	C	C	A	T	A	C	A
75	Flacourtiaceae	T	A	A	A	T	A/C	A	A	T	A	C	A
76	Kiggelariaceae	T	A	A	A	T	C	A	A	T	A	C	A
77	Salicaceae	T	A	C	A	T	C	A	A	T	A	C	A
78	Elaeocarpaceae	G	A	A	A	T	C	A	A	T	A	C	A
79	Moringaceae	T	A	A	A	T	C	A	A	T	A	C	A
80	Caricaceae	T	G	A	A	T	C	A	A	T	C	T	A
81	Passiflorales	T	G	A	A	T	C	A	A	T	A	C	A
82	Euphorbiales	G	A	C	A	G	A/C	A/C	C	G	A	C	C
83	Capparales	T	A	A	A	T	C	A	A	T	A	C	A
84	Tropaeolaceae	G	A	A	A	C	C	C	A	C	C	T	A
85	Salvadoraceae	G	A	A	A	G	C	C	A	G	C	T	A
86	Caryocaraceae	G	A	A	A	C	C	A	A	A	C	T	?
87	Ochnaceae	G/T	A	A	A	T	C	A	A	T	A	G	C
88	Medusagynaceae	G	A	A	A	G	C	A	?	C	A	G	C
89	Malpighiaceae	G	A	A	A	C	C	A/C	A	C	A	G	A
90	Linales s.str.	G	A	A	A	G	C	C	C	G	A	G	A
91	Clusiaceae	G/T	G	A	A	T	C	A	A	T	A	G	A
92	Bonnetiaceae	G	G	A	A	T	C	A	A	T	A	G	C
93	Elatinaceae	G	A	A	A	T	C	A	A	T	A	G	C
94	Quiinaceae	G	A	A	A	G	C	?	?	T	A	C	A
95	Chrysobalanaceae	?	?	A	A	G	C	A	A	C	C	T	A
96	Dichapetalaceae	G	A	A	A	G	C	C	C	A	C	T	A
97	Trigoniaceae	T	A	A	A	T	C	A	A	T	A	G	C
98	Erythroxylaceae	G	A	A	A	G	C	C	A	A	C	T	A
99	Sphaerosepalaceae	A	A	A	A	T	C	?	?	T	A	C	C
100	Thymelaeaceae	G	A	A	A	C	C	C	C	C	A	C	A
101	Dipterocarpaceae	G/T	A	A	A	T	C	C	A	A	C	T	A
102	Sarcolaenaceae	G	A	A	A	T	C	?	?	T	A	C	A
103	Bixaceae	T	G	A	A	T	C	A	A	T	A	C	A
104	Cochlospermaceae	T	A	A	A	T	C	A	A	T	A	C	A
105	Cistaceae	T	A	A	A	T	A/C	A	A	T	A	C	A
106	Malvales s. str.	G	A	A	A	T	A	A	A	T	A	C	A
107	Strasburgeriaceae	G	A	A	A	C	C	?	C	A	C	T	A
108	Podostemaceae	G	G	A	A	T	C	A	A	T	A	G	A
109	Bruniaceae	G	A	A	C	T	C	G	A	G	A	A	A
110	Balanophoraceae	G	A	A	A	C	A	T	A	A	C	T	A

Appendix 1. Continued.

dill.mat5	15	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
		sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	sero	Al a	amic	dhui	prot	trigl	taxi	proa	hete	card	valin	liner	lotal	linus	neol	tyros	prun	sam	zieri	holo	gluc	dihy	acet	eleo	myr
111	Santalales	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	A	A
112	Aextoxicaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
113	Paracryphiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
114	Pentaphylacaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
115	Oncothecaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
116	Sphenostemonaceae-Aqu	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
117	Icacinaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	A
118	Balsaminaceae	?	?	?	?	?	?	?	A	A	A	?	A	A	A	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?
119	Fouquieriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
120	Polemoniaceae	?	?	?	?	A	A	A	?	?	?	C	?	?	?	C	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?
121	Loasaceae	?	?	?	?	A	A	A	?	?	?	C	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A
122	Cornales	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A
123	Hydrangeaceae	?	A	A	A	?	?	?	?	?	?	?	A	C	?	?	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A	A
124	Diapensiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
125	Scytopetalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
126	Lecythidaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?
127	Sapotaceae	?	?	?	?	?	?	?	?	?	?	?	C	C	C	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	A	?
128	Ebenaceae	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A
129	Styracaceae	?	?	?	?	A	A	A	?	?	?	A	?	C	C	?	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?
130	Primulales	?	?	?	?	A	A	C	A	A	A	C	C	C	C	C	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?
131	Clethraceae	?	?	?	?	?	?	?	?	?	?	?	C	C	C	C	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
132	Actinidiaceae	?	?	?	?	A	A	A	?	?	?	C	C	C	C	C	?	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	A	A	?
133	Sarraceniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A
134	Ericales	?	?	?	A	A	A	C	?	?	?	C	C	C	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
135	Marcgraviaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
136	Cyrillaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?
137	Theaceae	?	?	?	?	A	A	C	?	?	?	A	C	C	C	C	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
138	Pittosporaceae	?	?	?	A	?	?	?	A	A	A	?	?	?	?	?	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	A
139	Araliales	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C
140	Escalloniaceae	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?
141	Dipsacales	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	C	C	A	A	A	C	A
142	Eucommiales	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	?
143	Gentianales	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	C	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	C	A	A	A	A	A
144	Scrophulariales	?	?	?	A	?	?	?	A	A	A	?	?	?	?	?	A	C	C	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	A	A	A	A	A	C	C
145	Solanales	?	?	?	?	A	A	A	A	A	A	A	A	C	?	?	?	A	C	C	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	A
146	Symplocaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	?
147	Menyanthaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
148	Campanulales	?	?	?	?	A	A	A	A	A	A	C	A	A	A	?	?	A	C	A	A	C	A	C	A	A	A	C	C	A	A	C	C	C	C	A	A	A	A	A	A
149	Akaniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?
150	Bretschneideraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?
151	Corynocarpaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
152	Huaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?
153	Krameriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
154	Lacistemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
155	Leitneriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
156	Pelliceraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
157	Peridiscaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
158	Plagiopteraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
159	Scyphostegiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
160	Tetrameristaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
161	Tremandraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1. Continued.

dili.mat5	16	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
		asar	sesc	gern	myo	pinit	quel	deut	cani	cycl	simn	aust	kads	eucc	syrii	pino	dihy	galb	licar	vera	prod	ellag	mett	stac	casu	tellin	tellin	pedu	gera	chlo	galli	epig	flavo	afze	davi	bifla	Oura	euxa	nora	mac	benz
111	Santalales	A	A	A	C	C	C	A	A	A	A	A	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	A	A	A
112	Aextoxicaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
113	Paracryphiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
114	Pentaphylacaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
115	Oncothecaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
116	Sphenostemonaceae-Aqu	?	A	A	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	C	A	A	?	A	A	A	A	A	A	A	A
117	Icacinaceae	A	C	A	A	A	?	A	C	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C
118	Balsaminaceae	?	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	?
119	Fouquieriaceae	A	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	C	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	A
120	Polemoniaceae	?	?	?	?	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	?
121	Loasaceae	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
122	Cornales	A	A	A	C	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	C	C	?	A	A	C	A	C	A	A	C	A	?	A	A	A	A	A	A	A	C
123	Hydrangeaceae	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	A	A	?	A	?	A	A	?	A	?	A	A	A	A	A	A	A	A
124	Diapensiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
125	Scytopetalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
126	Lecythidaceae	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	C	C	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
127	Sapotaceae	?	A	A	C	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	C	A	?	A	A	A	A	A	A	A	A
128	Ebenaceae	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	C	C	C	?	?	?	?	?	?	?	C	?	?	?	?	?	A	?	?	?	A
129	Styracaceae	?	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A
130	Primulales	?	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	C	C	A	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	A
131	Clethraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?
132	Actinidiaceae	?	A	A	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	C	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	?	A	A	A	A
133	Sarraceniaceae	A	?	?	?	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	A	A	A	A	?	?	?	?	?
134	Ericales	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	C	C	C	A	A	A	A	A	A	A	A	A	A
135	Marcgraviaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
136	Cyrillaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
137	Theaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	C	C	A	C	C	C	A	A	A	C	A	A	A	A	A
138	Pittosporaceae	A	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A
139	Araliales	C	C	C	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	C	A	?	?	?	?	?	?	C	A	?	C	?	?	?	A	?	?	?	A
140	Escalloniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
141	Dipsacales	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	C	A	A	A	A	A
142	Eucommiales	?	?	A	A	A	A	A	A	A	?	?	A	C	C	C	A	A	A	A	A	C	A	?	?	?	?	?	?	?	A	?	?	?	?	?	A	?	?	?	A
143	Gentianales	A	C	C	C	C	C	A	A	A	A	A	A	C	C	C	A	A	A	A	C	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	A	A	C	A	C
144	Scrophulariales	C	C	C	C	A	A	A	A	A	C	A	A	A	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	C	A	A	A	A	A	A	A	A
145	Solanales	A	A	A	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A
146	Symplocaceae	?	?	?	A	A	A	A	A	A	?	?	A	A	A	C	A	A	A	A	C	C	A	?	?	?	?	?	?	?	C	?	?	?	C	?	A	A	A	A	C
147	Menyanthaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?
148	Campanulales	C	C	C	C	C	C	A	C	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	C	C	A	C	A	A	A	A	A
149	Akaniaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A	A	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?
150	Bretscheideraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
151	Corynocarpaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A
152	Huaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	A	A	?	A	A	?	?	?	?	?	?	?	?	?
153	Krameriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
154	Lacistemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
155	Leitneriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
156	Pelliceraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
157	Peridiscaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
158	Plagiopteraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
159	Scyphostegiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
160	Tetrameristaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
161	Tremandraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1. Continued.

dili.mat5	17	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
		roen	anor	lirioc	prot	anci	cam	indo	indo	secc	corn	olea	arjur	dam	cucu	nigr	arbu	napl	rapa	plum	dros	anth	pher	anth	actir	nitro	chro	siev	strat	rod	epic	SiO2	oxal	elon	solit	crys	spha	myrc	oil c	muc	resir
111	Santalales	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	C	?	?	?	C	C	A	C	A	C	A	A	C	C
112	Aextoxicaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	C	?	A	A	A	?	A
113	Paracryphiaceae	?	A	A	?	?	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	A	A	A	A	A	G	C	A	A	A	A	A	?
114	Pentaphylacaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	A	A	G	C	A	A	A	A	C	A
115	Oncothecaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	A	A	A	A	C	G	C	?	A	A	A	?	?
116	Sphenostemonaceae-Aqu	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	?	?	?	C	A	A	A	C	A	C	A	A	C	G	C	C	A	A	A	C	C
117	Icacinaceae	A	A	A	A	A	C	A	C	A	A	A	A	A	?	A	?	?	?	?	?	?	A	?	A	A	A	C	A	A	A	A	C	A	C	C	A	A	A	C	A
118	Balsaminaceae	?	?	?	?	?	A	?	A	A	A	?	?	?	A	?	A	C	A	A	A	A	A	A	?	A	C	C	?	?	?	A	A	C	A	A	A	A	A	C	A
119	Fouquieriaceae	A	A	A	A	A	A	C	C	A	A	?	?	C	A	A	A	A	A	A	A	A	A	A	A	A	C	C	?	?	?	A	C	A	C	A	A	A	A	A	C
120	Polemoniaceae	?	?	?	?	?	?	?	?	?	?	C	A	A	C	A	A	A	A	A	A	A	A	A	?	A	A	C	?	?	?	A	C	G	C	A	A	A	A	C	A
121	Loasaceae	?	?	?	?	?	?	?	C	C	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	?	?	?	?	A	C	A	A	A	A	A	A	A	A
122	Cornales	A	A	A	A	A	C	C	C	C	C	C	C	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	C	C	A	A	A	C	A
123	Hydrangeaceae	A	A	A	A	A	?	?	C	?	?	?	?	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	C	A	A	A	A	A	C	A
124	Diapensiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	C	A	C	A	A	A	A	A	A
125	Scytopetalaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	A	A	A	?	A	A	C	A	A	A	A	C	A
126	Lecythidaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	?	?	?	?	?	A	A	A	A	A	C	A	A	A	C	C	A	C	A	A	A	A	C	C
127	Sapotaceae	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	C	?	?	?	C	C	A	C	C	A	A	A	A	C
128	Ebenaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	C	A	C	C	C	A	A	A	A	A	C	?	?	?	A	C	A	C	A	A	A	A	A	A
129	Styracaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	?	A	A	?	?	?	?	A	A	A	A	A	A	C	?	?	?	C	C	A	C	A	A	A	A	A	C
130	Primulales	A	A	A	A	A	A	A	A	A	A	C	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	C	?	?	?	C	C	G	C	A	A	A	A	C	C
131	Clethraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	A	A	A	A	C	A	C	A	C	A	A	A	A
132	Actinidiaceae	A	A	A	A	A	?	A	C	A	A	?	?	?	A	?	?	?	?	?	?	?	?	?	C	A	A	C	C	C	A	A	A	C	A	C	A	A	A	A	A
133	Sarraceniaceae	?	?	?	?	?	?	?	C	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	A	C	C	?	?	?	A	A	A	A	A	A	A	A	A	A
134	Ericales	A	A	A	A	A	A	A	C	A	A	?	A	A	A	A	C	C	A	A	A	A	A	?	A	A	A	C	C	A	C	A	C	A	C	A	C	A	A	A	A
135	Marcgraviaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	C	A	A	A	A	A	C	A	A	?	A	A	C	C
136	Cyrillaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	A	A	A	C	A	C	A	A	A	A	A	A
137	Theaceae	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C	A	C	A	C	C	G	C	A	A	A	A	A	C
138	Pittosporaceae	A	A	A	A	A	A	A	A	?	A	C	A	A	A	?	?	?	?	?	?	?	?	?	A	A	A	C	A	C	A	A	C	G	C	A	A	A	A	A	C
139	Araliales	A	A	A	A	A	A	A	?	A	A	C	A	C	A	A	?	?	?	?	?	?	C	C	A	A	A	C	?	?	?	A	C	G	C	C	A	A	A	C	C
140	Escalloniaceae	A	A	A	A	A	A	A	C	?	?	?	?	?	A	?	?	?	A	A	A	?	?	?	A	A	A	C	?	?	?	A	C	G	C	C	A	A	A	A	C
141	Dipsacales	A	A	A	A	?	?	C	C	C	?	C	A	A	A	A	C	A	A	A	A	A	A	A	C	A	A	C	A	C	A	A	C	A	C	C	A	A	A	A	A
142	Eucommiales	A	A	A	A	A	A	A	C	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	?	?	?	C	C	A	C	C	A	A	A	A	A
143	Gentianales	A	A	A	A	A	C	C	C	C	?	C	C	C	C	A	C	C	A	A	A	C	A	C	C	A	C	C	C	A	A	C	C	C	C	C	C	A	A	C	C
144	Scrophulariales	A	A	A	A	A	A	A	C	A	C	C	A	C	C	A	C	C	A	A	A	C	A	C	C	A	C	C	?	?	?	C	C	G	C	A	C	A	A	C	C
145	Solanales	A	A	A	A	A	A	A	?	A	A	C	A	C	A	A	C	C	C	A	A	A	A	C	A	A	C	C	?	?	?	C	C	G	C	C	A	A	A	A	A
146	Symplocaceae	A	A	A	A	A	A	C	C	?	C	C	C	A	A	?	?	?	?	?	?	?	?	?	A	A	A	C	?	?	?	A	C	A	C	A	A	A	A	A	A
147	Menyanthaceae	?	?	?	?	?	?	?	C	C	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A
148	Campanulales	A	A	A	A	A	A	A	C	C	A	C	A	C	A	A	C	A	A	A	A	C	A	C	A	A	C	C	A	A	A	C	C	G	C	C	C	A	A	C	C
149	Akaniaceae	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C	A	C	A	A	?	A	A	A
150	Bretscheideraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	?	?	?	A	?	?	?	?	?	C	A	A	A
151	Corynocarpaceae	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	C	G	C	A	A	A	A	A	A
152	Huaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	A	A	A	A	C	A	C	A	A	A	A	A	A
153	Krameriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	C	C	?	?	?	?	C	A	A	C	C	A	A	A	A
154	Lacistemaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	A	C	A	C	A	A	A	A	A	C
155	Leitneriaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	C	A	A	A	A	A	A	A	C
156	Pellicieraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	A	A	A	A	A	C	C	A	A	A	A	A	A
157	Peridiscaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	A	C	A	C	A	A	A	A	A	A
158	Plagiopteraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	C	A	C	A	A	A	A	A	A
159	Scyphostegiaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	?	?	?	?	A	C	A	A	A	A	A	A	A	A
160	Tetrameristaceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	A	A	A	A	A	C	A	C	A	A	A	A	A
161	Tremandraceae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	?	A	C	A	C	A	A	A	A	C	A

Appendix 1. Continued.

dIII.mat5	18	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
		latic	fasci	pelta	denc	nonc	glan	anth	micr	polle	type	pola	trian	trian	angu	sexu	type	intec	intec	nuce	peris	endc	occu	occu	occu	end	aril	pach	sarc	rumi	exot	exot	theo	tann	mes	endc	endc	exot	exot	bixoi	hypc
111	Santalales	C	C	A	C	A	A	C	C	G	C	A	C	A	C	A	A	A	A	C	A	C	A	C	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A
112	Aextoxicaceae	A	?	?	?	A	?	?	?	G	G	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	A	?	?	?	A	?	?	?	?	?	?	?	?	?
113	Paracryphiaceae	A	A	A	A	A	A	?	?	G	G	?	A	A	A	G	G	C	A	A	?	C	?	?	?	?	A	A	A	A	A	?	?	?	A	A	A	A	A	A	?
114	Pentaphylacaceae	A	A	?	?	A	?	?	?	G	G	A	A	A	A	A	A	A	A	G	?	?	?	?	?	?	A	A	?	?	A	?	C	?	?	?	?	?	?	?	?
115	Oncothecaceae	A	A	?	?	A	?	?	?	G	G	A	A	A	A	G	C	C	A	A	?	?	?	?	?	?	?	A	?	?	A	?	?	C	?	A	A	A	A	A	A
116	Sphenostemonaceae-Aqu	A	A	A	A	A	A	?	?	G	G	A	A	A	A	A	A	C	A	A	A	C	C	A	A	G	A	A	A	A	A	A	C	A	A	A	A	A	A	A	C
117	Icacinaceae	C	C	C	A	A	A	C	C	G	C	A	C	A	C	C	A	C	A	A	A	A	?	?	?	C	A	C	?	A	A	A	?	?	C	A	A	A	A	A	A
118	Balsaminaceae	A	A	A	A	A	A	C	C	G	C	C	C	A	A	G	G	A	C	G	A	C	A	A	A	?	A	C	A	A	C	A	A	A	A	A	A	A	A	A	A
119	Fouquieriaceae	A	A	A	A	A	A	C	?	G	G	G	A	A	A	G	G	A	A	G	A	C	A	A	A	?	A	A	A	A	C	A	A	A	A	?	A	A	A	A	A
120	Polemoniaceae	A	A	A	C	A	A	C	C	G	G	G	A	A	A	T	A	C	A	G	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A
121	Loasaceae	A	A	A	A	A	A	?	?	G	G	C	A	A	A	G	G	C	C	G	A	C	A	A	A	A	A	A	A	A	A	A/C	A	?	A	A	A	A	A	A	C
122	Cornales	C	C	C	A	C	A	C	C	G	G	A	C	A	C	A	A	C	C	A	A	A/C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
123	Hydrangeaceae	A	C	A	A	A	A	?	?	G	C/G	A	A	A	A	G	G	C	C	C	A	A/C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A
124	Diapensiaceae	A	A	A	A	A	A	C	?	G	G	A	A	A	C	G	C	C	C	G	A	C	A	A	A	A	A	A	?	?	A	A	C	A	A	?	A	A	A	A	A
125	Scytopetalaceae	A	A	A	A	A	A	C	C	G	C	C	C	A	C	A	A	A	C	G	A	?	?	?	?	G	A	A	A	C	C	A	A	?	A	?	A	A	A	A	C
126	Lecythidaceae	A	C	A	A	A	A	C	C	G	C	C	A	A	A	A	A	A	C	G	A	A	?	?	?	G	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A
127	Sapotaceae	A	A	A	A	C	A	C	?	G	G	C	A	A	A	A	A	A	A	C	A	A	C	A	A	C	A	A	A	A	A	A	A	A	A	A	?	A	A	A	C
128	Ebenaceae	A	C	C	A	C	C	?	C	G	G	C	A	A	A	A	A	A	C	C	A	C	A	A	A	G	A	C	A	C	A	A	A	A	C	C	A	A	A	A	C
129	Styracaceae	A	C	C	A	A	A	C	C	G	G	C	A	A	A	A	A	A	C	G	A	C	A	A	A	C	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A
130	Primulales	A	A	C	C	A	C	C	C	G	C	A	A	A	A	G	G	A	C	G	A	A	C	A	A	A	C	A	A	C	C	A	A	C	A	C	A	A	A	A	A
131	Clethraceae	A	C	A	A	A	A	C	C	G	G	A	A	A	C	A	A	C	C	G	A	C	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A
132	Actinidiaceae	A	C	A	C	A	A	C	C	G	G	A	A	A	A	A	A	C	C	G	A	C	A	A	A	G	C	A	A	A	A	A	C	C	A	A	A	A	A	A	C
133	Sarraceniaceae	A	A	A	A	A	A	C	C	G	G	A	A	A	A	A	A	A	C	G	A	C	?	?	?	A	A	A	A	A	C	A	C	?	A	A	A	A	A	A	C
134	Ericales	A	C	C	C	A	C	C	C	G	G	A	A	A	C	A	A	C	C	G	A	C	C	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	?
135	Marcgraviaceae	A	A	A	A	A	A	C	C	G	G	A	A	A	A	A	A	A	A	C	A	C	?	?	?	G	A	A	A	A	A	C	C	C	C	A	A	A	A	A	?
136	Cyrillaceae	A	A	A	A	A	A	C	C	G	G	A	A	A	A	A	A	C	C	G	A	C	?	?	?	?	A	A	A	A	A	A	?	?	A	?	A	A	A	A	A
137	Theaceae	A	C	A	A	A	A	C	C	G	G	A	A	A	A	G	C	A	A	G	A	A	A	A	A	G	C	A	A	A	A	A	C	C	C	A	A	A	A	A	C
138	Pittosporaceae	A	A	A	A	C	A	C	C	G	G	A	A	A	A	G	G	C	C	G	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	?	A	A	A	A	C
139	Araliales	A	C	A	C	C	C	C	C	G	G	A	C	A	A	G	G	C	C	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	?	A	A	A	A	C
140	Escalloniaceae	A	C	C	A	C	C	?	?	G	G	A	A	A	A	C	A	C	?	G	A	C	?	?	?	?	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?
141	Dipsacales	A	C	C	A	A	C	A	C	G	G	C	C	A	C	C	A	C	C	A	A	C	A	C	A	G	A	A	A	C	A	A	C	?	A	?	A	A	A	A	C
142	Eucommiales	C	A	A	A	A	A	C	C	G	G	G	A	C	A	A	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	?	A	?	A	A	A	A	C
143	Gentianales	A	C	C	C	C	A	C	C	G	C	A	C	A	C	A	A	C	C	G	A	C	C	A	A	G	C	C	A	C	A	C	C	C	A	A	A	A	A	A	C
144	Scrophulariales	C	C	C	C	C	C	C	C	G	C	C	C	A	C	G	G	C	C	G	A	C	C	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	C
145	Solanales	A	C	C	C	C	C	C	C	G	C	A	A	A	C	C	A	C	A	A	A	C	C	A	A	C	A	A	A	A	C	A	C	A	A	A	A	A	A	A	C
146	Symplocaceae	A	A	A	A	A	A	C	C	G	G	A	C	A	C	C	A	C	C	G	A	C	A	A	A	G	A	A	A	A	A	A	C	?	A	?	A	A	A	A	A
147	Menyanthaceae	A	A	A	A	A	A	C	C	G	G	A	C	A	A	T	A	C	C	G	A	C	A	A	C	G	A	A	A	A	A	C	A	A	A	A	A	A	A	A	C
148	Campanulales	C	C	C	C	C	C	C	C	G	G	A	C	A	C	C	A	C	C	G	A	C	A	A	A/C	G	A	A	A	A	A	C	A	A	A	A	A	A	A	A	C
149	Akaniaceae	A	A	A	A	A	A	C	?	G	C	G	A	A	A	G	G	A	A	A	A	A	?	?	?	C	A	A	A	A	A	C	A	A	C	A	A	A	A	A	C
150	Bretschneideraceae	A	A	A	A	A	A	C	?	G	C	G	A	A	A	G	G	A	A	A	A	A	?	?	?	G	A	A	A	A	A	C	A	A	A	A	A	A	A	A	C
151	Corynocarpaceae	A	A	A	A	A	A	?	?	G	G	C	A	A	A	A	A	A	A	A	A	A	?	?	?	?	A	A	A	A	A	A	A	?	A	?	A	A	A	A	C
152	Huaceae	A	C	C	A	A	A	?	?	G	T	C	A	A	A	G	G	A	A	?	A	?	?	?	?	G	A	A	A	A	C	A	A	?	A	A	A	T	A	A	?
153	Krameriaceae	A	A	A	A	A	?	?	?	G	G	?	A	A	A	T	A	A	A	A	A	A	?	?	?	C	A	A	A	A	A	A	A	C	A	A	A	A	A	A	C
154	Lacistemaceae	A	A	A	A	A	A	?	?	G	G	A	A	A	A	G	C	A	?	A	A	A	?	?	?	?	A	?	C	A	A	A	?	?	A	?	A	?	?	?	?
155	Leitneriaceae	A	A	A	A	A	A	C	?	G	G	C	A	A	A	G	G	A	A	A	C	A	?	?	?	A	A	A	A	A	A	A	A	A	C	A	G	A	A	A	A
156	Pellicieraceae	A	A	A	A	A	A	?	?	G	G	G	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?
157	Peridiscaceae	A	A	A	A	A	A	?	?	G	G	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
158	Plagiopteraceae	A	C	A	A	A	A	C	C	G	G	C	A	A	A	G	C	A	C	C	A	?	?	?	?	?	?	A	?	?	?	?	?	?	?	?	?	?	?	?	?
159	Scyphostegiaceae	A	A	A	A	A	A	?	C	G	C	?	?	?	?	?	?	A	A	A	A	A	?	?	?	A	C	A	A	A	C	A	A	A	A	A	A	G	A	A	C
160	Tetrameristaceae	A	A	A	A	A	A	?	?	G	G	G	A	A	A	G	G	A	A	?	?	?	?	?	?	?	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?
161	Tremandraceae	A	C	A	A	A	A	?	?	G	G	A	A	A	A	A	A	A	A	A	A	?	?	?	?	A	C	A	A	A	C	A	A	?	?	?	A	?	?	?	C

Appendix 1. Continued.

dill.mets	19	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
		andc	endc	emb	emb	susp	grow	disp	anor	phlo	wedg	inter	corti	scle	woo	fiber	fiber	tracl	librif	type	hom	rays	stor	vesti	vess	end	vess	vess	vess	denc	leaf	leaf	stipu	glan	leaf	stom	epid	muci	palm	cras	leaf
111	Santalales	A	C	A	A	A	A	A	A	A	A	A	A	C	C	C	A	C	A	A	A	A	A	A	C	C	A	G	A	A	C	A	A	A	A	A/G	A	A	A	A	A
112	Aextoxicaceae	?	?	C	A	A	?	A	A	?	A	A	?	?	C	A	A	C	A	A	A	A	A	A	C	C	A	?	?	?	?	A	A	A	A	C	?	?	A	A	A
113	Paracryphiaceae	?	?	C	A	A	?	A	A	?	?	A	A	C	C	A	C	A	A	A	A	A	A	A	C	C	A	C	C	A	C	A	A	A	A	G	A	A	A	A	C
114	Pentaphylacaceae	?	?	G	C	A	A	A	A	A	A	A	A	C	C	C	A	C	A	A	A	A	A	A	C	C	A	A	A	A	A	A	C	A	A	A	A	?	A	A	A
115	Oncothecaceae	?	?	C	A	A	?	A	A	A	A	A	A	C	C	C	A	C	A	A	A	A	A	A	C	C	A	A	A	A	G	A	A	A	A	G	A	?	A	A	C
116	Sphenostemonaceae-Aqu	A	A	A	A	A	A	A	A	A	A	A	A	?	C	A	A	C	A	A	A	A	?	A	C	C	A	A	A	A	C	A	A	A	A	G	A	?	A	A	C
117	Icacinaceae	A	C	C	A	A	C	A	A	?	A	C	A	C	C	A	A	C	A	A	A	A	A	A	C	C	A	C	A	A	C	A	A	A	A	C	A	C	A	A	C
118	Balsaminaceae	?	C	T	A	A	A	A	A	A	A	A	A	A	?	?	?	A	?	?	?	?	?	?	?	T	?	?	?	?	A	A	C	A	A	G	A	A	A	A	C
119	Fouquieriaceae	A	C	G	A	A	A	A	A	A	A	A	A	C	G	C	A	A	A	A	A	A	A	A	C	G	A	C	C	A	A	A	A	A	A	G	A	?	A	A	A
120	Polemoniaceae	A	A	C	A	A	C	A	A	A	A	A	A	C	?	?	A	C	A	T	A	C	?	A	?	G	A	?	?	?	A	A	A	A	A	G	A	A	A	A	C
121	Loasaceae	A	C	C	A	A	C	A	A	?	A	A	A	A	?	A	A	A	A	C	A	A	C	A	C	T	?	?	?	A	?	A	A	A	A	G	A	A	A	A	?
122	Cornales	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	G	A	A	C	A/C	C	A	A	A	A	C	C	A	A
123	Hydrangeaceae	A	?	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	C/G	C	A	A	A	A	A	?	C	C	C
124	Diapensiaceae	?	A	C	A	A	A	A	A	?	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	G	A	C	?	?	A	A	A	A	A	G	A	A	A	A	C
125	Scytopetalaceae	A	A	C	A	A	C	A	A	C	A	A	C	A	G	C	A	A	A	G	A	A	A	A	T	G	?	?	?	?	C	A	A	A	A	G	A	?	A	A	C
126	Lecythidaceae	?	A	C	?	A	A	A	A	C	C	A	C	C	A	C	A	C	A	C	A	A	A	A	C	G	C	G	C	A	G	A	C	A	A	G	A	A	A	A	A
127	Sapotaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	C	C	A	A	A	C	A	A	A	A	T	G	?	G	C	C	C	A	C	A	A	G	A	A	A	A	A
128	Ebenaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	G	C	A	A	A	A	A	A	C	A	C	T	A	A	C	A	A	A	A	A	A	G	A	A	A	A	A
129	Styracaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	G	A	A	A	A	C	A	A	A	A	C	C	A	?	C	A	A	A	A	A	A	G	A	A	A	A	C
130	Primulales	A	A	C	A	A	A	A	A	?	A	A	A	C	A	A	A	A	C	A	A	A	C	A	C	G	A	A	C	?	A	A	A	A	A	G	A	C	A	A	C
131	Clethraceae	A	C	C	A	A	A	A	A	A	A	A	A	A	G	A	A	C	A	A	A	A	A	A	G	C	A	C	A	A	C	A	A	A	A	A	A	A	A	A	C
132	Actinidiaceae	A	A	C	A	A	C	A	A	A	A	A	A	?	C	A	A	C	A	A	A	A	A	?	C	C	A	C	A	A	C	A	A	A	A	G	A	A	A	A	C
133	Sarraceniaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	A	A	A	G	A	A	A	A	A
134	Ericales	A	C	A	A	A	A	A	A	A	A	A	A	C	A	A	C	C	A	A	A	A	A	A	C	C	A	C	A	A	C	A	A	A	A	G	A	A	A	A	A
135	Marcgraviaceae	C	C	G	A	A	C	A	A	A	A	A	A	C	C	A	C	A	C	A	A	A	A	A	G	C	A	G	A	A	A	A	A	A	A	A	A	A	A	A	A
136	Cyrillaceae	?	C	C	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	C	A	A	A	A	C	C	A	G	A	A	?	A	A	A	A	G	A	C	A	A	A
137	Theaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	C	A	A	A	A	A	A	A	C/G	A	A	A	A	A/C
138	Pittosporaceae	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	C	G	C	A	A	A	C	A	A	A	A	A	A	A	C	A	A
139	Araliales	A	A	A	A	A	A/C	A	A	A	A	A	C	C	A	A	A	A	C	C	A	A	A	A	C	C	A	A	C	C	G	A	C	A	A	A	A	A	A/C	C	C
140	Escalloniaceae	?	?	C	A	A	A	A	A	?	A	A	A	C	C	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	C	A	A	A	A	A	A	A	A	A	C
141	Dipsacales	A	A	C	A	A	A	A	A	A	A	A	A	C	A	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	C	C	C	A	A	G	A	A	A	A	C
142	Eucommiales	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	C	A	A	A	A	A	A	G	C	A	C	A	A	C	A	A	A	A	G	A	A	C	A	C
143	Gentianales	A	C	C	A	A	A/C	A	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	?	C	A	C	C	C	C	A	A	A/G	A	C	A	A	C
144	Scrophulariales	A	A/C	G	A	A	A/C	A	A	A	A	C	A	C	C	A	A	A	A	C	A	A	C	C	T	T	?	G	A	C	C	C	C	A	A	G	C	A	A/C	A	C
145	Solanales	A	C	C	A	A	A/C	A	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	A	T	T	?	G	A	C	C	A	A	A	A	A/G	A	A	C	A	C
146	Symplocaceae	A	A	C	A	A	A	A	A	A	A	A	A	C	G	A	A	C	A	A	A	A	A	A	C	C	A	A	A	A	?	A	A	A	A	A	A	A	A	A	C
147	Menyanthaceae	C	A	C	A	A	A	A	A	A	A	A	C	C	?	?	?	?	?	?	?	?	A	A	C	?	?	?	A	A	C	A	A	A	A/C	G	A	A	C	A	A
148	Campanulales	A	A/C	C	A	A	A	A	A	?	A	A	A	C	C	A	A	C	A	T	C	A	C	A	T	T	?	?	A	A	C	A	A	A	A	G	A	A	A	A	C
149	Akaniaceae	?	A	C	A	A	A	A	A	A	A	A	A	C	G	A	C	A	A	A	A	A	A	A	G	G	C	C	C	A	?	A	A	A	C	?	A	A	A	A	C
150	Bretschneideraceae	?	A	G	A	A	A	A	A	?	?	A	?	?	G	A	A	A	A	A	A	A	A	A	C	G	A	A	C	A	?	A	A	A	C	?	?	?	A	A	A
151	Corynocarpaceae	?	A	G	A	A	A	A	A	A	A	A	A	C	G	C	A	A	C	G	A	A	C	A	T	T	?	G	C	A	C	A	C	A	A	A	A	A	A	A	A
152	Huaceae	C	A	C	A	A	A	A	A	A	C	A	A	C	G	C	A	A	C	G	A	A	A	A	T	T	C	G	C	A	C	A	C	A	A	A	A	A	C	A	A
153	Krameriaceae	?	?	T	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	T	A	C	A	A	?	T	?	G	A	A	A	A	A	A	C	A	A	A	A	A	A
154	Lacistemaceae	A	?	C	A	A	A	A	A	?	A	A	A	C	C	C	C	A	C	A	A	A	A	A	G	C	A	G	C	A	C	A	C	A	A	G	A	A	A	A	C
155	Leitneriaceae	C	A	G	A	A	A	A	A	C	C	A	A	C	A	A	A	A	C	T	A	C	A	A	C	T	?	?	C	C	C	A	A	A	A	G	A	A	A	A	A
156	Pellicieraceae	?	?	T	C	A	A	A	A	A	A	A	A	C	?	A	?	?	A	?	?	?	?	?	?	T	A	G	C	?	?	A	A	A	A	C	A	A	A	A	C
157	Pentadiplandraceae	?	?	A	A	A	A	A	A	A	A	A	A	A	C	C	C	A	C	A	A	A	A	A	C	C	A	C	C	A	A	A	C	A	A	G	A	?	C	A	A
158	Plagiopteraceae	?	?	?	?	A	A	A	A	A	C	A	A	A	A	A	C	A	A	A	A	A	A	A	T	T	?	?	A	A	A	C	C	A	A	C	C	A	C	A	A
159	Scyphostegiaceae	A	A	C	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	A	A	A	A	T	T	A	?	C	A	C	A	C	A	A	A	A	A	A	A	C
160	Tetrameristaceae	?	?	C	A	A	A	A	A	A	A	A	A	A	C	C	A	A	?	A	A	A	A	A	T	G	A	C	C	A	C	A	A	A	A	G	A	A	A	A	A
161	Tremandraceae	?	A	A	A	A	A	A	A	A	A	A	A	C	C	A	A	A	C	C	A	A	A	A	C	G	A	G	C	A	A	A	A	A	A	G	A	C	A	C	C

Appendix 1. Continued.

dill.mat5	20	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
		salic	chloi	kran	leaf	vein	folia	elon	corti	brac	K-C	peta	num	high	trim	sepa	peta	peta	scal	pena	varia	trime	isom	cent	cent	poly.	anth	inve	expa	conr	valv	nect	gync	carp	carp	carp	ovar	carp	degr	stipi	stigr
111	Santalales	A	A	A	C	C	C	A	?	A	C	A	G/T	A	A	C	C/G	A/C	A	A	G/T	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	A	G	A	A	A
112	Aextoxicaceae	A	A	?	?	?	?	A	?	A	C	A	T	A	A	A	G	A	A	A	A	A	A	?	A	A	A	A	A	A	A	C	C	C	A	A	A	T	A	A	A
113	Paracryphiaceae	A	A	A	C	A	A	A	?	A	A	A	G	A	A	A	A	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	A	T	T	G	A	C	A	A	A
114	Pentaphylacaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	A	A	A	C	A	A	C	T	G	A	A	T	A	A	A
115	Oncothecaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	C	G	C	A	A	C	A	C	A	A	A	A	A	A	C	A	A	?	T	G	A	A	G	A	A	A
116	Sphenostemonaceae-Aqu	A	A	A	C	A	A	A	A	A	A	A	T	A	A	A/C	G	A	A	A	C	A	C	A	A	A	A	A	C	T	A	A	C	T	C	A	A	G/T	A	A	A
117	Icacinaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	C	G	A	A	A	C	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	A	T	A	A	A
118	Balsaminaceae	A	A	A	A	A	A	A	A	A	A	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	T	A	A	A
119	Fouquieriaceae	A	A	A	A	A	C	A	A	A	C	A	T	A	A	A	G	C	A	A	A	A	A	?	?	A	C	A	A	A	A	A	C	G	A	A	G	G	A	A	A
120	Polemoniaceae	A	A	C	A	A	A	A	A	A	C	C	T	A	A	C	G	C	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	G	A	A	G	T	A	A	A
121	Loasaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	A/G	A	A/C	A/C	A/C	A	A	A	A	C	A	A	C	G/T	A/G	A	A	T	C	A	A
122	Cornales	A	A	A	C	A	C	A	A	A	C	A	G/T	A	A	C	C/G	A	A	A	C/G	A	C	A	A	A	A	A	A	A	A	C	C	T	G/T	A/C	A	G	A	A	A
123	Hydrangeaceae	A	A	A	?	?	?	A	A	A	C	A	C/T	A/C	A	C	G/T	A	A	A	C/G	A	C	A	C	A	C	A	A	A	A	C	C	T	G	A	A	G	A	A	A
124	Diapensiaceae	A	A	A	C	A	A	A	A	A	C	A/C	T	A	A	A	G	C	C	A	C	A	C	A	A	A	C	A	A	A	A	C	C	G	A	A	C	G	A	A	A
125	Scytopetalaceae	A	A	A	C	A	A	A	?	A	C	G	C	C	A	C	T	A	A	A	A	A	A	?	?	A	C	A	A	A	A	C	?	T	T	C	G	T	C	A	A
126	Lecythidaceae	A	A	A	C	A	A	A	A	A	C	A	C	C	A	A	T	A	A	A	A	A	A	A	C	A	C	A	A	A	A	C	C	T	T	C	A	G	A	A	A
127	Sapotaceae	A	A	A	C	C	C	A	?	A	C	A	C	C	A	A	T	C	A	A	G	A	C	A	A	A	C	A	A	C	A	A	C	T	T	C	A	T	C	A	A
128	Ebenaceae	A	A	A	C	A	A	A	?	A	C	A	C	C	A	C	T	C	A	A	G	A	C	A	A	A	A	A	A	C	A	A	A	T	T	C	A	G	A	A	A
129	Styracaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	C	G	C	A	A	G	A	C	A	A	A	C	A	A	C	A	A	C	T	G	A	G	T	C	A	A
130	Primulales	A	A	A	C	C	A	A	A	A	C	A	T	A	A	C	G	A	A	A	C/G	A	C	A	A	A	C	A	A	C	A	A	C	T	G	A	A	T	A	A	A
131	Clethraceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	C	G	A	A	A	G	A	C	A	A	A	C	C	A	A	A	A	C	G	A	A	A	T	A	A	A
132	Actinidiaceae	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	A	A	A	A	C	A	C	C	A	C	A	A	C	T	G	A	G	C	A	A	A
133	Sarraceniaceae	A	A	A	?	?	?	A	?	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	C	A	A	A/C	A	A	A	A	C	T	G	A	A	G	A	A	A
134	Ericales	A	A	A	C	C	A	A	A	A	C	A	T	A	A	C	G	C	A	A	G	A	C	A	A	A	C	C	A	A	A	A	C	T	G	A	A	T	C	A	A
135	Marcgraviaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	A	A	A	?	?	A	A	A	A	A	A	A	C	T	G	A	A	T	C	A	A
136	Cyrillaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	C	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	A	C	A	A	A
137	Theaceae	A	A	A	C	A	C	A	A	A	A	A	C	C	A	A	T	A	A	A	A	A	A	A	C	A	A	A	A	C	A	A	C	T	T	C	A	G	A	A	A
138	Pittosporaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	A	A	A	A	A	C	C	T	G	A	A	G	A	A	A
139	Araliales	A	A	A	A	A	A	A	A	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	A	G	A	A	A
140	Escalloniaceae	A	A	A	A	A	A	A	?	A	C	G	T	A	A	C	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	G	T	C	A	A
141	Dipsacales	A	A	C	C	C	A	A	A	A	C	A	T	A	A	C	G	C	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	G	T	C	A	A
142	Eucommiales	A	A	A	A	A	A	A	?	A	?	?	G	A	A	C	A	A	A	A	G	A	C	A	A	A	A	A	A	C	A	C	C	C	A	A	A	G	A	A	A
143	Gentianales	A	A	A	C	C	C	A	A	A	C	C	T	A	A	C	G	C	A	A	C	A	C	A	A	A	C	A	A	C	A	C	C	G	A	A	A	G	A	A	A
144	Scrophulariales	A	A	C	C	C	C	A	A	A	C	A	T	A	A	C	G	C	A	A	C	A	C	A	A	A	A	A	A	C	A	C	C	C	A	A	A	T	A	A	A
145	Solenales	A	A	C	A	A	A	A	A	A	C	A/C	T	A	A	A	G	C	A	A	C	A	C	A	A	A	C	A	A	C	A	C	C	T	G	A	G	G	A	A	A
146	Symplocaceae	A	A	A	C	A	A	A	?	A	C	A	T	A	A	C	G/T	C	A	A	A	A	A	A	C	A	C	A	A	A	A	C	C	T	G	A	C	T	A	A	A
147	Menyanthaceae	A	A	A	A	A	A	A	?	A	C	G	T	A	A	C	G	C	C	A	C	A	C	A	A	A	C	A	A	A	A	C	C	C	A	A	A	T	A	A	A
148	Campanulales	A	A	C	C	C	C	A	A	A	C	G	T	A	A	C	G	C	A	A	C	A	C	A	A	A	C	A	A	A	A	C	C	T	G	A	G	T	A	A	A
149	Akaniaceae	A	A	?	A	A	A	A	?	A	C	C	T	A	A	?	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	A	C	G	A	A	C	T	A	A	A
150	Bretscheideraceae	A	A	?	?	?	?	A	?	A	C	A	T	A	A	C	G	A	A	A	G	A	C	A	A	A	C	A	A	C	A	C	C	G/T	A/G	A	G	T	C	A	A
151	Corynocarpaceae	A	A	A	A	A	A	A	?	A	C	A	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	C	A	A	C	G	A	A	A
152	Huaceae	A	A	A	A	A	A	A	?	A	C	G	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	A	C	T	G	A	A	T	C	A	A
153	Krameriaceae	A	A	A	C	A	C	A	?	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	A	C	C	A	A	A	T	C	A	A
154	Lacistemaceae	A	A	A	A	A	A	A	?	A	A	T	C	C	A	A	A	A	A	A	A	A	A	A	A	A	C	A	C	A	A	C	C	G	A	A	C	G	A	A	A
155	Leitneriaceae	A	A	A	A	A	A	A	?	T	A	A	C	C	A	A	G	A	A	A	C	A	C	A	A	A	C	A	A	A	A	A	A	A	A	A	A	G	A	A	A
156	Pellicieraceae	A	A	A	C	A	C	A	?	A	C	A	T	A	A	A	G	A	A	A	C	A	C	A	A	A	A	A	A	A	A	A	C	T	G	A	A	T	A	A	A
157	Peridiscaceae	A	A	?	?	?	?	A	?	A	A	A	T	A	A	A	G	A	A	A	A	A	A	?	?	A	C	A	A	A	A	C	A	T	C	A	C	G	A	A	A
158	Plagiopteraceae	A	A	?	A	A	A	A	?	A	A	G	T	A	A	A	G	A	A	A	A	A	A	?	?	A	C	A	A	A	A	C	C	G	A	A	G	T	C	A	A
159	Scyphostegiaceae	?	A	A	A	A	A	A	?	A	A	A	C	A	C	C	A	A	A	A	T	C	C	A	A	A	A	A	A	C	A	A	A	T	T	G	A	T	C	A	A
160	Tetrameristaceae	A	A	A	A	A	A	A	?	A	C	A	G/T	A	A	A	C/G	A	A	A	C	A	C	A	A	A	A	A	A	A	A	A	C	T	C/G	A	C	T	C	A	A
161	Tremandraceae	A	A	A	A	A	A	A	?	A	C	G	T	A	A	A	G	A	A	A	G	A	C	A	A	A	C	A	A	A	A	C	C	C	A	A	A	T	C	A	A

Appendix 1. Continued.

dIII.mat5	21	241	242	243	244	245	246	247	248	249	250	251	252
		plac	diffu	stigr	ovar	ovul	ovul	micr	obtu	seec	fruit	type	cent
111	Santalales	G	A	A	A	C	A/C	C	A	T	C	T	A
112	Aextoxicaceae	T	A	A	A	C	C	C	?	A	C	T	A
113	Paracryphiaceae	G	A	A	A	T	C	G	?	T	A	A	C
114	Pentaphylacaceae	G	A	A	A	G	C	C	?	G	A	C	C
115	Oncothecaceae	G	A	C	A	G	C	G	?	C	C	T	A
116	Sphenostemonaceae-Aqu	G	A	A	A	C	C	G	C	C	C	T	A
117	Icacinaceae	G	A	A	A	G	C	G	C	A	C	T	A
118	Balsaminaceae	G	A	A	A	T	C	C	A	T	A	C	A
119	Fouquieriaceae	G/T	A	A	A	T	C	C	A	T	A	C	C
120	Polemoniaceae	G	A	A	A	T	C	G	C	T	A	C/G	A
121	Loasaceae	G/T	A	A	C	T	C	G	A	T	A	C	A
122	Cornales	G/T	A	C	C	C	C	G	A	A	C	T	A
123	Hydrangeaceae	G	G	C	C	T	C	G	?	T	A	C/G	A
124	Diapensiaceae	G	G	A	A	T	C	G	A	T	A	C	A
125	Scytopetalaceae	G	A	A	A	T	C	C	A	A	A	C	A
126	Lecythidaceae	G	A	A	C	T	C	C	A	T	C	T	A
127	Sapotaceae	G	A	A	A	C	C	?	A	C	C	T	A
128	Ebenaceae	G	A	A	C	G	C	C	A	G	A	C	A
129	Styracaceae	G	A	A	A	T	C	C	A	G	A	G	A
130	Primulales	G	G	A	C	T	C	C	A	T	A	C	A
131	Clethraceae	G	G	A	A	T	C	G	A	T	A	C	C
132	Actinidiaceae	A	A	A	A	T	C	G	A	T	A	C	?
133	Sarraceniaceae	G/T	G	A	A	T	C	?	A	T	A	C	?
134	Ericales	G/T	G	A	A	T	C	G	A	T	A	C	C
135	Marcgraviaceae	T	A	A	A	T	C	C	A	T	A	C	?
136	Cyrillaceae	G	A	A	A	T	C	G	A	C	A	C	?
137	Theaceae	G	A	A	A	T	C	C	A	T	A	C	C
138	Pittosporaceae	T	G	C	C	T	C	G	C	T	A	C	A
139	Araliales	G	A	A	C	G	C	G	C	C	C	T	C
140	Escalloniaceae	T	G	A	?	T	?	A	?	T	A	C	A
141	Dipsacales	G	A	A	C	T	C	G	C	T	A	C	A
142	Eucommiales	C	A	C	A	C	C	G	C	C	C	T	A
143	Gentianales	G	G	A	A	T	C	G	A	T	A	G	A
144	Scrophulariales	G	G	A	A	T	A/C	G	C	T	A	G	A
145	Solanales	G	A/G	A	A	T	C	G	C	T	A	G	A
146	Symplocaceae	G/T	A	A	C	T	C	G	A	T	C	T	A
147	Menyanthaceae	T	A	C	C	T	C	G	A	T	A	C	A
148	Campanulales	G	A/G	A	C	T	C	G	A	T	A	C	A
149	Akaniaceae	G	A	A	A	G	C	A	A	G	A	C	A
150	Bretscheideraceae	G	A	A	A	G	C	A	A	G	A	C	A
151	Corynocarpaceae	C	A	A	A	A	C	C	A	A	C	T	A
152	Huaceae	G	A	A	A	C	C	A	A	A	A	C	A
153	Krameriaceae	G	A	A	A	G	C	C	?	A	C	T	A
154	Lacistemaceae	T	A	A	A	G	C	A	?	T	A	C	A
155	Leitneriaceae	T	A	C	A	C	C	A	?	C	C	T	A
156	Pellicieraceae	G	A	A	A	C	C	?	?	A	C	T	A
157	Peridiscaceae	C	A	A	A	T	?	?	?	A	C	T	A
158	Plagiopteraceae	G	A	A	A	G	C	A	A	T	A	C	A
159	Scyphostegiaceae	G	A	A	A	T	C	A	A	T	A	C	A
160	Tetrameristaceae	G	A	A	A	C	C	?	A	C	C	T	A
161	Tremandraceae	G	A	A	A	G	C	A	C	T	A	C/G	A

Appendix 2. Taxon circumscriptions.

1) Ceratophyllaceae 2) Chloranthaceae 3) Nymphaeaceae 4) Amborellaceae 5) Austrobaileyaceae 6) Illiciales (Schisandraceae, Illiciaceae) 7) Winterales (Canellaceae, Winteraceae) 8) Monocotyledons 9) Aristolochianae (Saururaceae, Piperaceae, Aristolochiaceae, Lactoridaceae) 10) Laurales (Calycanthaceae, Monimiaceae, Hernandiaceae, Gyrostemonaceae, Lauraceae; Trimeniaceae are not included in this study) 11) Myristicaceae 12) Annonales (Eupomaticeae, Annonaceae) 13) Magnoliales (Himantandraceae, Degeneriaceae, Magnoliaceae) 14) Ranunculidae (Menispermaceae, Lardizabalaceae, Circaeasteraceae, Kingdoniaceae, Hydrastidaceae, Ranunculaceae, Berberidaceae, Papaveraceae) 15) Eupteleaceae 16) Platanaceae 17) Nelumbonaceae 18) Trochodendrales (Tetracentraceae, Trochodendraceae) 19) Proteaceae 20) Buxaceae 21) Sabiaceae 22) Didymelaceae 23) Myrothamnaceae 24) Berberidopsidaceae (*Berberidopsis, Streptothamnus*) 25) Gunneraceae 26) Rhabdodendraceae 27) Simmondsiaceae 28) Caryophyllales (Chenopodiaceae, Amaranthaceae, Caryophyllaceae, Nyctaginaceae, Phytolaccaceae, Achatocarpaceae, Aizoaceae, *Giesekia*, Portulacaceae, Basellaceae, Cactaceae, Didiereaceae) 29) Asteropeiaceae 30) Plumbaginaceae 31) Polygonaceae 32) Dioncophyllaceae 33) Ancistrocladaceae 34) Nepenthaceae 35) Droseraceae 36) Tamaricaceae 37) Frankeniaceae 38) Hamamelidales (Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae) 39) Dilleniaceae 40) Vitaceae 41) Eucryphiaceae 42) Brunelliaceae 43) Cunoniales (Cunoniaceae, Davidsoniaceae, Baueraceae) 44) Paeoniaceae 45) Cephalotaceae 46) Crassulaceae 47) Saxifragales s. str. (Grossulariaceae, Haloragaceae, Penthoraceae, Saxifragaceae; without Vahliaceae, Greyiaceae, Francoaceae, Parnassiaceae, and Lepuropetalaceae) 48) Staphyleaceae 49) Elaeagnaceae 50) Rosaceae 51) Rhamnaceae 52) Faganae (Nothofagaceae, Fagaceae, Balanopaceae, Betulaceae, Myricaceae, Casuarinaceae, Rhoipteleaceae, Juglandaceae) 53) Cucurbitales (Datiscaceae, Begoniaceae, Cucurbitaceae) 54) Coriariaceae 55) Urticales (Ulmaceae, Moraceae, Cecropiaceae, Cannabaceae, Urticaceae) 56) Crossosomataceae 57) Connaraceae 58) Oxalidaceae 59) Stachyuraceae 60) Geissolomataceae 61) Geraniaceae 62) Melianthaceae 63) Fabaceae 64) Surianaceae 65) Polygalaceae 66) Rhizophoraceae 67) Zygophyllaceae (incl. Balanitaceae; without Nitrariaceae and Peganaceae) 68) Vochysiaceae 69) Myrtales (Myrtaceae, Combretaceae, Melastomataceae, Punicaceae, Lythraceae, Onagraceae, Trapaceae) 70) Rutales (Anacardiaceae, Simaroubaceae without Picramnioideae and Alvaradooideae, Rutaceae, Meliaceae, Cneoraceae) 71) Sapindales (Aceraceae, Hippocastaneaceae, Sapindaceae) 72) Celastrales (Goupiaceae, Celastraceae, Stackhousiaceae) 73) Irvingiaceae 74) Violaceae 75) Flacourtiaceae (Flacourtieae, *Oncoba*, Homalieae, Scolopieae (without *Banara*), Casearieae; without *Aphloia, Soyauxia*; latter two taxa not included in the study) 76) Kiggelariaceae {Flacourtiaceae with cyclopentenylic cyanogenic compounds (Erythrospermoideae, Pangieae, Kiggelarieae)} 77) Salicaceae 78) Elaeocarpaceae (without *Muntingia*, latter taxon not included in the study) 79) Moringaceae 80) Caricaceae 81) Passiflorales (Passifloraceae incl. Paropsieae) 82) Euphorbiales (Euphorbiaceae s.l., Pandaceae) 83) Capparales (Bataceae, Gyrostemonaceae, Koeberliniaceae, Resedaceae, Tovariaceae, Capparaceae, Brassicaceae) 84) Tropaeolaceae 85) Salvadoraceae 86) Caryocaraceae 87) Ochnaceae 88) Medusagynaceae 89) Malpighiaceae 90) Linales s. str. (Hugoniaceae, Linaceae) 91) Clusiaceae (incl. Hypericaceae) 92) Bonnetiaceae 93) Elatinaceae 94) Quiinaceae 95) Chrysobalanaceae 96) Dichapetalaceae 97) Trigoniaceae 98) Erythroxylaceae 99) Sphaerosepalaceae 100) Thymelaeaceae 101) Dipterocarpaceae 102) Sarcolaenaceae 103) Bixaceae 104) Cochlospermaceae 105) Cistaceae 106) Malvales s. str. (Tiliaceae, Sterculiaceae, Bombacaceae, Malvaceae) 107) Strasburgeriaceae 108) Podostemaceae 109) Bruniaceae 110) Balanophoraceae 111) Santalales (Olacaceae, Opiliaceae, Santalaceae, Loranthaceae, Viscaceae, Eremolepidaceae) 112) Aextoxicaceae 113) Paracryphiaceae 114) Pentaphylacaceae 115) Oncothecaceae 116) Aquifoliaceae (including *Sphenostemon*) 117) Icacinaceae 118) Balsaminaceae 119) Fouquieriaceae 120) Polemoniaceae 121) Loasaceae 122) Cornales (Alangiaceae, Nyssaceae, Davidiaceae, Mastixiaceae, Cornaceae) 123) Hydrangeaceae 124) Diapensiaceae 125) Scytopetalaceae 126) Lecythidaceae 127) Sapotaceae 128) Ebenaceae 129) Styracaceae 130) Primulales (Myrsinaceae, Theophrastaceae, Primulaceae) 131) Clethraceae 132) Actinidiaceae 133) Sarraceniaceae 134) Ericales (Epacridaceae, Ericaceae, Empetraceae, Pyrolaceae) 135) Marcgraviaceae 136) Cyrillaceae 137) Theaceae (incl. Sladeniaceae) 138) Pittosporaceae 139) Araliales (Araliaceae, Apiaceae) 140) Escalloniaceae 141) Dipsacales (Adoxaceae, Sambucaceae, Caprifoliaceae, Viburnaceae, Dipsacaceae, Valerianaceae) 142) Eucommiales (Eucommiaceae, Garryaceae, Aucubaceae) 143) Gentianales (Loganiaceae, Apocynaceae, Asclepiadaceae, Gentianaceae, Rubiaceae) 144) Scrophulariales (Buddlejaceae, Oleaceae, Bignoniaceae, Pedaliaceae, Martyniaceae, Acanthaceae, Scrophulariaceae, Callitrichaceae, Lentibulariaceae, Orobanchaceae, Verbenaceae, Lamiaceae) 145) Solanales (Convolvulaceae, Boraginaceae, Hydrophyllaceae, Solanaceae, Nolanaceae) 146) Symplocaceae 147) Menyanthaceae 148) Campanulales (Goodeniaceae, Brunoniaceae, Calyceraceae, Campanulaceae, Stylidiaceae, Asteraceae) 149) Akaniaceae 150) Bretschneideraceae 151) Corynocarpaceae 152) Huaceae 153) Krameriaceae 154) Lacistemataceae 155) Leitneriaceae 156) Pellicieraceae 157) Peridiscaceae 158) Plagiopteraceae 159) Scyphostegiaceae 160) Tetrameristaceae 161) Tremandraceae

Appendix 3. Characters and character-states.

Serology

1	serological reaction with Nelumbo antiserum (1. group)	A: absent; C: present
2	serological reaction with Nelumbo antiserum (2. group)	A: absent; C: present
3	serological reaction with Victoria antiserum	A: weak or absent; C: present
4	serological reaction with Saxifragaceae antiserum	A: weak or absent; C: present
5	serological reaction with Hydnocarpus antiserum	A: weak or absent; C: present
6	serological reaction with Passiflorales antiserum (1. group)	A: absent; C: present
7	serological reaction with Passiflorales antiserum (2. group)	A: absent; C: present

8	serological reaction with Euphorbiaceae antiserum (1. group)	A: absent; C: present
9	serological reaction with Euphorbiaceae antiserum (2. group)	A: absent; C: present
10	serological reaction with Euphorbiaceae antiserum (3. group)	A: absent; C: present
11	serological reaction with Loasaceae antiserum	A: weak or absent; C: present
12	serological reaction with Sapotaceae antiserum	A: weak or absent; C: present
13	serological reaction with Styracaceae antiserum	A: weak or absent; C: present
14	serological reaction with Primulales antiserum	A: weak or absent; C: present
15	serological reaction with Theaceae antiserum	A: weak or absent; C: present
16	serological reaction with Hydrangeaceae antiserum	A: weak or absent; C: present

Chemical compounds

17	Al accumulation	A: absent; C: present
18	amides	A: absent; C: present
19	dhurrin	A: absent; C: present
20	proteacin	A: absent; C: present
21	triglochinin	A: absent; C: present
22	taxiphyllin	A: absent; C: present
23	proacacipetalin	A: absent; C: present
24	heterodendrin	A: absent; C: present
25	cardiospermin	A: absent; C: present
26	valine- and isoleucine-derived cyanogenic compounds	A: absent; C: present
27	linamarin	A: absent; C: present
28	lotaustralin	A: absent; C: present
29	linustatin	A: absent; C: present
30	neolinustatin	A: absent; C: present
31	tyrosine-derived cyanogenic compounds	A: absent; C: present
32	prunasin	A: absent; C: present
33	sambunigrin	A: absent; C: present
34	zierin	A: absent; C: present
35	holocalin	A: absent; C: present
36	glucosinolates	A: absent; C: present
37	dihydrosterculic acid	A: absent; C: present
38	acetylenes	A: absent; C: present
39	eleostearic acid	A: absent; C: present
40	myristicin	A: absent; C: present
41	asarone	A: absent; C: present
42	sesquiterpene lactones	A: absent; C: present
43	germacrane-like compounds	A: absent; C: present
44	myoinisitol	A: absent; C: present
45	pinitol	A: absent; C: present
46	quebrachitol	A: absent; C: present
47	deutzioside	A: absent; C: present
48	cantleyoside	A: absent; C: present
49	cyclopentenylic cyanogenic glycosids	A: absent; C: present
50	simmondsin-like compounds	A: absent; C: present
51	austrobailignan	A: absent; C: present
52	kadsurin A	A: absent; C: present
53	eucommin A	A: absent; C: present
54	syringaresinol	A: absent; C: present
55	pinoresinol	A: absent; C: present
56	dihydrocubebin	A: absent; C: present
57	galbacin	A: absent; C: present
58	licarin A	A: absent; C: present
59	veraguensin	A: absent; C: present
60	prodelphinidins	A: absent; C: present
61	ellagic acid	A: absent; C: present
62	methylated ellagic acids	A: absent; C: present
63	stachyurins	A: absent; C: present
64	casuaricitin	A: absent; C: present
65	tellimagrandin I	A: absent; C: present
66	tellimagrandin II	A: absent; C: present
67	pedunculagin	A: absent; C: present
68	geraniins	A: absent; C: present
69	chlorogenic acid	A: absent; C: present
70	gallic acid	A: absent; C: present
71	epigallocatechin-3-gallate	A: absent; C: present
72	flavonoid sulphates	A: absent; C: present

73	afzelechin	A: absent; C: present
74	davidigenin	A: absent; C: present
75	biflavonoids or biflavanoids	A: absent; C: present
76	Ouratea catechins	A: absent; C: present
77	euxanthone	A: absent; C: present
78	norathyriol	A: absent; C: present
79	maclura xanthone	A: absent; C: present
80	benzylisoquinoline alkaloids	A: absent; C: present
81	roemerine	A: absent; C: present
82	anonaine	A: absent; C: present
83	liriodenine	A: absent; C: present
84	protoberberine	A: absent; C: present
85	ancistrocladine	A: absent; C: present
86	camptothecine	A: absent; C: present
87	indole alkaloids	A: absent; C: present
88	iridoid compounds	A: absent; C: present
89	secoloiridoid compounds	A: absent; C: present
90	cornin	A: absent; C: present
91	oleanolic acid & derivatives	A: absent; C: present
92	arjunolic acid & derivatives	A: absent; C: present
93	dammaranes	A: absent; C: present
94	cucurbitacins	A: absent; C: present
95	nigracin	A: absent; C: present
96	arbutin	A: absent; C: present
97	naphthoquinones	A: absent; C: present
98	rapanone	A: absent; C: present
99	plumbagin	A: absent; C: present
100	droserone	A: absent; C: present
101	anthraquinones	A: absent; C: present
102	phenanthrenes	A: absent; C: present
103	acetophenones	A: absent; C: present
104	actinidine	A: absent; C: present

Characters at cellular level

105	nitrogen-fixing nodules	A: absent; C: present
106	chromosome number $x = 7$ or $n = 6$ or $n = 8$	A: absent; C: present
107	sieve-tube plastids	A: P-type; C: S-type
108	epicuticular leaf waxes stratified	A: absent; C: present
109	epicuticular leaf waxes rod or tube shaped	A: absent; C: present
110	epicuticular leaf waxes arranged in rosettes	A: absent; C: present
111	SiO2-bodies in wood or leaf	A: absent; C: present
112	oxalate druses	A: absent; C: present
113	elongate oxalate crystals	A: absent; C: raphides; G: prismatic
114	solitary crystals	A: absent; C: present
115	crystal sand	A: absent; C: present
116	sphaerocrystals	A: absent; C: present
117	myrosine cells	A: absent; C: present
118	oil cells	A: absent; C: present
119	mucilage cavities or cells	A: absent; C: present
120	resinous cavities or cells	A: absent; C: present
121	laticiferous cavities	A: absent; C: present
122	fasciculate or stellate hairs	A: absent; C: present
123	peltate scales	A: absent; C: present
124	dendritic hairs	A: absent; C: present
125	nonglandular 2–5 armed hairs	A: absent; C: present
126	glandular scales	A: absent; C: present

Embryology

127	anther tapetum	A: amoeboid; C: secretory
128	microsporogenesis	A: successive; C: simultaneous
129	pollen organization	A: inaperturate; C: monosulcate; G: triaperturate; T: polyforate
130	type of triaperturate pollen	A: not triaperturate; C: tricolpate or polycolpate; G: tri- or polycolporate; T: triporate
131	polar pollen diameter	A: less than 20μ; C: 20–30μ; G: more than 30μ
132	triangular pollen	A: absent; C: present
133	triangular pollen, ora deepened	A: absent; C: present

134	angulaperturate pollen	A: absent; C: present
135	sexine texture	A: psilate or granulate; C: spinulose; G: reticulate; T: striate
136	type of reticulation	A: not reticulate; C: finely reticulate; G: coarsely reticulate
137	integument number	A: bitegmic; C: unitegmic
138	integumentary tapetum	A: absent; C: present
139	nucellus type	A: crassinucellar; C: weakly crassinucellar; G: tenuinucellar
140	perisperm or nucellus-derived surrounding tissue	A: absent; C: present
141	endosperm development	A: nuclear; C: cellular
142	Caryophyllad type of embryogeny	A: absent; C: present
143	Piperad type of embryogeny	A: absent; C: present
144	Asterad type of embryogeny	A: absent; C: present

Seed anatomy

145	end of ovular or seed vascular bundle	A: chalaza; C: beyond chalaza, far from micropyle; G: near micropyle
146	aril	A: absent; C: present
147	pachychalaza	A: absent; C: present
148	sarcotesta	A: absent; C: present
149	ruminate endosperm	A: absent; C: present
150	exotestal hairs or papillae	A: absent; C: present
151	exotestal palisade	A: absent; C: present
152	theoid exotesta thickenings	A: absent; C: present
153	exotesta tanniferous or with brown contents	A: absent; C: present
154	mesotesta	A: unspecialized; C: sclerenchymatous or thickened walls
155	endotestal crystals	A: absent; C: present; G: undefined
156	endotesta	A: unspecialized cells; C: elongate cells; G: lignified, not elongate; T: tracheids
157	exotegmen	A: unspecialized cells or with lobate facets; C: sclerified or tracheidal; G: fibrous or tangentially elongate; T: as palisade layer
158	exotegmen with lobate facets	A: absent; C: present
159	bixoid exotegmen in chalazal region	A: absent; C: present
160	hypostase	A: absent; C: present
161	endosperm storage type	A: oil or proteins; C: starch; G: arabinose; T: undefined
162	endosperm haustoria	A: absent; C: present
163	embryo size	A: less than half seed length; C: bigger than in A, endosperm copious; G: bigger than in A, endosperm scanty; T: no endosperm
164	embryo form	A: straight; C: curved
165	suspensor haustoria	A: absent; C: present

Stem morphology and anatomy

166	growth form	A: no vine; C: vine or creeping axis
167	dispersed vascular bundles	A: absent; C: present
168	anomalous secondary growth	A: absent; C: present
169	phloem stratification	A: absent; C: present
170	wedge-shaped phloem rays	A: absent; C: present
171	internal phloem	A: absent; C: present
172	cortical vascular bundles	A: absent; C: present
173	sclerenchymatous idioblasts in cortex or pericycle	A: absent; C: present
174	wood parenchyma	A: scanty or absent; C: diffuse; G: aggregate
175	fiber wall	A: thin to moderately thick; C: thick to very thick
176	fiber septation	A: absent; C: present
177	tracheids	A: absent; C: present
178	libriform fibers	A: absent; C: present
179	ray-type	A: heterogenous type I; C: heterogenous type IIa; heterogenous type IIb; T: other
180	homogenous multiseriate rays	A: absent; C: present
181	rays maximally biseriate	A: absent; C: present
182	storied wood structure	A: absent; C: present
183	vestured pits in vessel side walls	A: absent; C: present
184	vessel side pitting	A: circular, only one or two rows; C: scalariform or transitional; G: opposite; T: alternate
185	end wall perforation of pit	A: tracheids, no perforation; C: scalariform; G: mixed scalariform and simple; T: simple;
186	vessel end wall angle	A: highly oblique; C: slightly oblique; G: horizontal

187	vessel shape in transverse section	A: angular; C: slightly angular; G: oval
188	vessel aggregation	A: more than 85% solitary; C: less than 85% solitary; G: no vessels
189	dendritic pattern of vessels	A: absent; C: present
Leaf characters		
190	leaf traces	A: one; C: three; G: more than three
191	leaf arrangement	A: alternate; C: opposite; G: whorled
192	stipules	A: absent; C: present
193	glands on distal petiole	A: absent; C: present
194	leaf organization	A: simple; C: pinnate
195	stoma type	A: paracytic or tetracytic; C: encyclocytic; G: other types
196	epidermal crystals	A: absent; C: present
197	mucilaginous epidermis	A: absent; C: present
198	palmate venation	A: absent; C: present
199	craspedodromous venation	A: absent; C: present
200	leaf teeth	A: absent; C: present
201	salicoid teeth	A: absent; C: present
202	chloranthoid teeth	A: absent; C: present
203	kranz structure	A: absent; C: present
204	leaf sclereids	A: absent; C: present
205	vein terminating foliar sclereids	A: absent; C: present
206	foliar tracheoids	A: absent; C: present
Floral and fruiting characters		
207	elongated floral base	A: absent; C: present
208	cortical and axial vascular bundles in floral base	A: absent; C: present
209	bracts instead of perianth or bract-like perianth	A: absent; C: three; G: two or four; T: other numbers
210	K-C differentiation	A: not discontinuous; C: discontinuous
211	petal or tepal aestivation	A: imbricate; C: contorted; G: valvate; T: open or petals/tepals absent
212	number of calyx or tepal organs	A: zero; C: three or more than five; G: four or two; T: five
213	high calyx or tepal number	A: absent; C: six to ten; G: eleven to twenty; T: more than twenty
214	trimery in calyx or tepals	A: absent; C: present
215	sepal union	A: absent; C: present
216	petal number	A: none; C: four or two; G: five; T: six to ten
217	petal union	A: absent; C: present
218	scales on upper side of petal	A: absent; C: present
219	perianth or bract to stamen outline change	A: discontinuous; C: continuous
220	variation of isomerous patterns	A: no isomery; C: haplostemony; G: two or n isomerous or doubled whorls; T: obhaplostemony
221	trimery in androecium	A: absent; C: present
222	isomery in androecium and perianth	A: absent; C: present
223	centripetal polyandry	A: absent; C: present
224	centrifugal polyandry	A: absent; C: present
225	polyandry associated with outer stamen pairs	A: absent; C: present
226	anther to stamen length-ratio	A: more than half; C: less than half
227	inverted anthers	A: absent; C: present
228	expanded stamen	A: absent; C: present
229	connective tip	A: not prolonged; C: prolonged not as in G or T; G: membranaceous; T: expanded or massive
230	valvate anther dehiscence	A: absent; C: present
231	disk	A: absent; C: present
232	gynoecium position	A: not antepetalous (or antetepalous); C: antepetalous or antetepalous, not oblique; G: oblique
233	carpel number I	A: one; C: two; G: three; T: more than three
234	carpel number II	A: three or less; C: four; G: five; T: more than five
235	carpel number III	A: five or less; C: six to ten; G: eleven to twenty; T: more than twenty
236	ovary to carpel length-ratio	A: more than 1:2; C: 1:2 to 1:3; G: less than 1:3
237	carpel union	A: unicarpellate or totally apocarpous; C: ovary partially fused; G: styles free or partially fused; T: styles fully fused
238	degree of syncarpy	A: not totally syncarpous; C: totally syncarpous
239	stipitate free carpels or stipitate unicarpellate fruits	A: absent; C: present
240	stigmatic crest	A: absent; C: present

241	placentation	A: marginal or laminar on apocarpous carpels; C: apical; G: axile, free central or basal; T: parietal
242	diffuse placenta	A: absent; C: laminar diffuse; T: protruding diffuse
243	stigma decurrent	A: absent; C: present
244	ovary position	A: superior; C: inferior
245	ovule to carpel number	A: less than one; C: one; G: two; T: more than two
246	ovule curvature	A: orthotropous; C: anatropous or campylotropous
247	micropyle formation	A: outer or both integuments; C: inner integument; G: by the only integument; T: no integuments
248	obturator	A: absent; C: present
249	seed to carpel number	A: less than one; C: one; G: two; T: more than two
250	fruit type	A: dehiscent fruit; C: indehiscent fruit
251	type of dehiscent fruit	A: follicle, pod or ventricidal capsule; C: capsule types other than in A and T; G: septicidal capsule; T: indehiscent fruit or schizocarp
252	central column in fruit	A: absent; C: present

Data errors in non-molecular matrix that could not be corrected

Amborellaceae: character 129, A/C instead of A (we became aware of Sampson, 1993, too late to include this polymorphism); Myristicaceae: character 251, A instead of G; Fabaceae: character 105, C instead of A; Myrtales: character 87, C instead of A

Appendix 4. Character definitions.

Characters and character-states requiring further explanation are given below.

Characters on cellular level

122	fasciculate or stellate hairs	: definition following Metcalfe & Chalk, 1950
123	peltate scales	: definition following Metcalfe & Chalk, 1950
124	dendritic hairs	: definition following Metcalfe & Chalk, 1950
125	nonglandular 2–5 armed hairs	: definition following Metcalfe & Chalk, 1950
126	glandular scales	: definition following Metcalfe & Chalk, 1950

Seed anatomy

152	theoid exotesta thickenings	: exotesta showing thickenings on radial and inner tangential walls, but not on outer tangential walls (cf. Huber, 1991)
159	bixoid exotegmen in chalazal region	: seeds with exotegmen organized as palisade layer, the latter showing a typical inward curving in the chalazal region associated with a hypostase plug differentiated into core and annulus region (see Nandi, 1998a)

Stem morphology and anatomy

175	fiber wall	: thin to moderately thick means sum of wall-thickness is smaller than fiber lumen diameter

Leaf characters

199	craspedodromous venation	: secondary venation running into leaf teeth
201	salicoid teeth	: leaf teeth showing a proximally rounded hyaline gland with concave gland body in herbarium specimens; see also Doyle & Hickey, 1975
202	chloranthoid teeth	: definition following Doyle & Hickey, 1975
205	vein terminating foliar sclereids	: definition following Rao, 1991
206	foliar tracheoids	: definition following Rao, 1991

Floral and fruiting characters

225	polyandry associated with outer stamen pairs	: definition following Ronse Decraene, 1992
228	expanded stamen	: thecae of anthers widely separated or stamen laminar
230	valvate anther dehiscence	: definition following Endress, 1994d
232	gynoecium position	: defined as antetepalous if one carpel is in line with a median tepal or petal
240	stigmatic crest	: broad, decurrent stigma, deeply furrowed into two parts
242	diffuse placenta	: definition following Endress, 1994a

243	stigma decurrent	: stigmatic surface unilaterally running down more than three times the stigma lobe breadth

Appendix 5. Procedures of character-state assignment.

The procedures for assigning character-states to matrix fields are indicated in the overview given below. In characters that are not listed, presence was favored over absence (monocots: presence only favored if occurring in *Acorus*, Arales, Arecales, or Alismatidae; the restriction to the presumed basal monocot clades reduces parallelisms).

Serology

Characters 1–16: strongest serological reaction > [">" means favored]

Chemical compounds

Characters 17–114: Presence of a chemical compound > absence

Characters at cellular level

107	sieve-tube plastids	Both types equally >, character-state of presumed basal members > in Winterales, Magnoliales, Laurales

Embryology

127	anther tapetum	Both types equally >
128	microsporogenesis	Both types equally >
129	pollen organization	Character-state of presumed basal members >
130	type of triaperturate pollen	Character-state of presumed basal members >
131	polar pollen diameter	least polar pollen diameter >
135	sexine texture	Character-state of presumed basal members >
136	type of reticulation	Character-state of presumed basal members >
137	integument number	A > C
138	integumentary tapetum	Character-state of presumed basal members >
139	nucellus type	A > C > G
141	endosperm development	Both types equally >

Seed anatomy

145	end of ovular or seed vascular bundle	G > C > A
154	mesotesta	C > A
156	endotesta	T, G, and C > A
157	exotegmen	T, G, and C > A
161	endosperm storage type	All types equally >
163	embryo size	A > C > G > T
164	embryo form	A > C

Stem morphology and anatomy

166	growth form	Both types equally >
168	anomalous secondary growth	Character state of presumed basal members >
171	internal phloem	Character state of presumed basal members >
174	wood parenchyma	A > C > G
175	fiber wall	A > C
176	fiber septation	A > C
178	libriform fibers	Absence > presence
179	ray-type	A > C > G > T
180	homogenous multiseriate rays	Character state of presumed basal members >
181	rays maximally biseriate	Character state of presumed basal members >
184	vessel side pitting	A and C > G > T
185	end wall perforation of pit	A > C > G > T
186	vessel end wall angle	A > C > G
187	vessel shape in transverse section	A > C > G
188	vessel aggregation	G > A > C

Leaf characters

190	leaf traces	Character state of presumed basal members >
191	leaf arrangement	Character state of presumed basal members >
194	leaf organization	Both types equally >
195	stoma type	Character state of presumed basal members >
200	leaf teeth	Character state of presumed basal members >

Floral and fruiting characters

209	bracts instead of perianth or bract-like perianth	Character state of presumed basal members >

210	K-C differentiation	A > C
211	petal or tepal aestivation	Character state of presumed basal members >
212	number of calyx or tepal organs	Character state of presumed basal members >
213	high calyx or tepal number	Character state of presumed basal members >
214	trimery in calyx or tepals	Character state of presumed basal members >
215	sepal union	Absence > presence
216	petal number	Character state of presumed basal members >
217	petal union	Absence > presence
219	perianth or bract to stamen outline change	C > A
220	variation of isomerous patterns	Character state of presumed basal members >
221	trimery in androecium	Character state of presumed basal members >
222	isomery in androecium and perianth	Character state of presumed basal members >
223	centripetal polyandry	Character state of presumed basal members >
224	centrifugal polyandry	Character state of presumed basal members >
226	anther to stamen length-ratio	Character state of presumed basal members >
229	connective tip	T > G and C > A
231	disk	Character state of presumed basal members >
232	gynoecium position	A > C and G
233	carpel number I	Character state of presumed basal members >
234	carpel number II	Character state of presumed basal members >
235	carpel number III	Character state of presumed basal members >
236	ovary to carpel length-ratio	A > C > G
237	carpel union	A > C > G > T
238	degree of syncarpy	A > C
241	placentation	Character state of presumed basal members >
242	diffuse placenta	Character state of presumed basal members >
244	ovary position	A > C
245	ovule to carpel number	T > G > C > A
246	ovule curvature	Character state of presumed basal members >
247	micropyle formation	Character state of presumed basal members >
249	seed to carpel number	T > G > C > A
250	fruit type	Character state of presumed basal members >
251	type of dehiscent fruit	A > C and G > T

Appendix 6. Sources.

Literature used for taxon delimitations and for finding character-states.

Taxon delimitations

Albert et al., 1992; Alverson et al., 1994; Baas, 1972, 1975; Carpenter & Dickison, 1976; Chase & Swensen, 1995; Chase et al., 1993, 1995; Conti et al., 1993; Corner, 1976; Cronquist, 1981, 1983; Dahlgren, 1980, 1983; Dahlgren & Clifford, 1982; Dahlgren & Thorne, 1984; Dahlgren et al., 1985; Downie & Palmer, 1994; Duvall et al., 1993b; Engler & Prantl (eds.), 1887–1914, 1924–1995; Fernando et al., 1995; Gadek et al., 1992; Geetha et al., 1993; Gustafsson & Bremer, 1995; Hegnauer, 1962–1994; Huber, 1991; Hutchinson, 1964/1967, 1973; Kolbe & John, 1979a, b; Kron & Chase, 1993; Lemke, 1988; Melchior (ed.), 1964; Miller, 1975; Morgan & Soltis, 1993; Olmstead et al., 1992, 1993; Price & Palmer, 1993; Qiu et al., 1993; Rodman et al., 1993; Savolainen et al., 1994; Soltis et al., 1995b; Sutter & Endress, 1995; Swensen et al., 1994; Takhtajan, 1966, 1987; Thorne, 1983, 1992; van Vliet & Baas, 1984; Xiang et al., 1993

Serology

Fairbrothers, 1966; Grund & Jensen, 1981; Hillebrand & Fairbrothers, 1966, 1970; Jensen & Greven, 1984; John & Kolbe, 1980; Kolbe & John, 1979a, b; Simon, 1970, 1971; Vogel, 1986

Chemical compounds

Arora & Metha, 1981; Barron et al., 1988; Bliss et al., 1968; Bohm & Chan, 1992; Brüning & Wagner, 1978; Crossley & Djerassi, 1962; Deyama et al., 1985; Durant & Zenk, 1974; Filho et al., 1985; Fieser & Chamberlain, 1948; Gibbs, 1974; Gildemeister & Hoffmann, 1956; Harborne, 1969; Harborne & Baxter, 1993; Hayashi et al., 1980; Hegnauer, 1962–1994; Keller, 1982; Lavault & Bruneton, 1980; Le Quesne et al., 1980; Lebreton & Bouchez, 1967; McAlpine et al., 1968; Murai et al., 1985; Rao & Alvarez, 1982; Sethi et al., 1976; Sévenet et al., 1971; Smith et al., 1980; Thieme & Benecke, 1966, 1970; Uesato et al., 1986; Zenk et al., 1969

Characters on cellular level

Baas, 1972, 1975, 1984; Baas et al., 1979; Behnke, 1975, 1977, 1981, 1985; Carpenter & Dickison, 1976; Cronquist, 1981, 1983; Dickison, 1978, 1981, 1990; Dickison & Baas, 1977; Ditsch & Barthlott, 1994; Ehrendorfer et al., 1984; Engler & Prantl (eds.), 1887–1914, 1924–1995; Fehrenbach & Barthlott, 1988; Franceschi & Horner, 1980; Goldblatt & Dorr, 1986; Goldblatt & Johnson (eds.), 1981/1984/1985/1988/1990/1991/1994; Gottwald & Parameswaran, 1966, 1967, 1968; Hennig et al., 1994; Huber, 1991; Hutchinson, 1973; Keng, 1962; Metcalfe, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Miller, 1975; Proctor, 1955; Puff & Weber, 1976; Ricci, 1957; Schmid, 1964; Solereder, 1899/1908; Solereder & Meyer, 1928; Sprent & McKey (eds.), 1994; Theisen & Barthlott, 1994

Embryology

Baas, 1972; Barth, 1965; Batygina et al., 1985a, b, c; Bhandari, 1971; Boesewinkel, 1985, 1994; Boesewinkel

& Bouman, 1980; Carpenter & Dickison, 1976; Chiarugi, 1925; Chiarugi & Francini, 1930; Chopra & Harjinder, 1965; Corner, 1976; Cronquist, 1981; Davis, 1966; Dickison, 1979, 1981, 1986, 1990; Dickison & Baas, 1977; Dickison et al., 1982; Endress, 1993a, b, c; Erdtman, 1952, 1958; Gavrilova, 1993; Gutzwiller, 1961; van Heel, 1967, 1984; Heo & Tobe, 1994; Hideux & Ferguson, 1976; Huang Tseng-Chieng, 1972; Huber, 1991, 1993; Huynh, 1969; Jäger-Zürn, 1966; Johri, 1970; Johri & Kak, 1954; Johri et al., 1967, 1992; Kamelina et al., 1981, 1983; Kapil & Bhatnagar, 1991; Kapil & Maheshwari, 1965; Kaur, 1969; Keating, 1972, 1975; Köhler, 1994; Kubitzki, 1993a, b, c; Les, 1988, 1993; Maguire & Ashton, 1980; Mauritzon, 1935, 1936; Maury et al., 1975; Melchior (ed.), 1964; Netolitzky, 1926; Philipson, 1993; Prance, 1968, 1972; Puff & Weber, 1976; Rutishauser, 1997; Sáenz de Rivas, 1979; Satabié, 1974; Schmid, 1964; Schnarf, 1931; Souèges, 1937; Takhtajan (ed.), 1985/1988/1991; Tang, 1994; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Todzia, 1993; Tsou, 1994; Ukraintseva, 1993; Vijayaraghavan & Dhar, 1976; Walia & Kapil, 1965; Walker & Walker, 1984; Williamson & Schneider, 1993; Wu Cheng-Yih & Kubitzki, 1993; Yoffe, 1962; Zhang Zhi-Yu, 1987

Seed anatomy

Baas, 1972; Blank, 1939; Boesewinkel, 1985, 1994; Boesewinkel & Bouman, 1980; Corner, 1976; Cronquist, 1981; Dickison & Baas, 1977; Endress, 1980, 1987; Engler & Prantl (eds.), 1887–1914, 1924–1995; van Heel, 1967; Huber, 1991; Keng, 1962; Mc Nair, 1930; Netolitzky, 1926; Seubert, 1993; Takhtajan (ed.), 1985/1988/1991; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Wojciechowska, 1969

Stem morphology and anatomy

Baas, 1969, 1972, 1975, 1984; Baas & Werker, 1981; Baas et al., 1979; Bailey, 1980; Bailey, 1933, 1957; Bailey & Swami, 1948; Baretta-Kuipers, 1976; Berg, 1977; Blank, 1939; Canright, 1955; Carlquist, 1964, 1976, 1977, 1981, 1984a, b, c, d, 1988a, b, 1990, 1993; Carlquist & Hoekman, 1985; Carpenter & Dickison, 1976; Cronquist, 1981; Dahlgren & Thorne, 1984; Dechamps, 1979–1985; Decker, 1966; Den Outer & Vooren, 1980; Dickison, 1969, 1978, 1981, 1986, 1990; Dickison & Baas, 1977; Endress, 1993a, b, c; Garratt, 1933; Gottwald & Parameswaran, 1966, 1967, 1968; Gutzwiller, 1961; Heimsch, 1942; Hekking, 1988; Huber, 1993; Humphrey, 1935; Ilic, 1991; Keefe & Moseley, 1978; Keng, 1962; Kessler, 1993; Kribs, 1935; Kubitzki, 1993a, b, c; Les, 1993; Maguire & Ashton, 1980; Maguire et al., 1972; Mennega, 1982; Metcalfe, 1952, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Meylan & Butterfield, 1978; Miller, 1975; Philipson, 1993; Piccioli, 1901; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Record, 1933; Schmid, 1964; Schweingruber, 1990; Shiklina, 1977; Solereder, 1899/1908; Takahashi, 1985; Takhtajan, 1966; Taylor, 1972; Tomlinson, 1961; Vestal, 1937; van Vliet & Baas, 1984; Whalen, 1987; Williamson & Schneider, 1993

Leaf characters

Arber, 1925; Baas, 1969, 1972, 1975, 1984; Baas et al., 1979; Bedell, 1981; Berg, 1977; Blank, 1939; Canright, 1955; Capuron, 1974; Carpenter & Dickison, 1976; Crane, 1989; Crane et al., 1993; Cronquist, 1981; Cuatrecasas, 1985; Dahlgren & Thorne, 1984; Dickison, 1978, 1981, 1990; Dickison & Baas, 1977; Dilcher & Crane, 1984; Engler & Prantl (eds.), 1887–1914, 1924–1995; Heywood (ed.), 1978; Hufford, 1992; Humphrey, 1935; Hutchinson, 1964/1967, 1973; Keng, 1962; Klucking, 1992; Kostermans, 1985; Les, 1993; Levin, 1986; Maguire & Ashton, 1980; Melchior (ed.), 1964; Metcalfe, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Rao, 1991; Schmid, 1964; Sinnott, 1914; Takhtajan, 1966; Thanikaimoni, 1986; Tomlinson, 1961

Floral and fruiting characters

Airy Shaw, 1951; Baas, 1972; Baas et al., 1979; Baillon, 1873; Batygina et al., 1985a, b, c; Bausch, 1938; Bayer & Hoppe, 1990; Berg, 1977; van Beusekom, 1971; Blank, 1939; Boureau, 1958; Brizicky, 1964; Carpenter & Dickison, 1976; Corner, 1946; Crane et al., 1993; Cronquist, 1981, 1983; Cuatrecasas, 1985; Dahlgren & Rao, 1969; Dahlgren et al., 1985; Dickison, 1969, 1978, 1981, 1986, 1990; Dickison & Baas, 1977; Dilcher & Crane, 1984; Drinnan et al., 1991; Drude, 1891a, b; Endress, 1986, 1989, 1993a, b, c, 1994a, b, c, d; Endress & Stumpf, 1991; Engler, 1930; Engler & Prantl (eds.), 1887–1914, 1924–1995; Friis, 1984; Gagnepain et al. (eds.), 1907–1942; Gore, 1935; Gutzwiller, 1961; Haber, 1959, 1961, 1966; van Heel, 1966, 1967, 1984; Heinig, 1951; Hekking, 1988; Heo & Tobe, 1994; Heywood (ed.), 1978; Hirmer, 1918; Huber, 1991, 1993; Hufford, 1992; Hufford & Endress, 1989; Hutchinson, 1964/1967, 1973; Jäger-Zürn, 1966; Janchen, 1909; Johri et al., 1992; Kamelina et al., 1981; Kamelina et al., 1983; Kanis, 1968; Keating, 1972; Keng, 1962; Kessler, 1993; Kobuski, 1951; Kostermans, 1985; Kubitzki, 1993a, b, c; Leenhouts, 1956; Les, 1993; Letouzey, 1961; Maguire & Ashton, 1980; Martius (ed.), 1840–1906; Melchior (ed.), 1964; Metcalfe, 1956; Payer, 1857; Philipson, 1993; Pilger, 1925a, b; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Rendle et al., 1921; Ronse Decraene, 1989, 1992; Ronse Decraene & Smets, 1992; Rutishauser, 1997; Sandwith, 1962; Sattler, 1973; Saunders, 1937; Saunders, 1937–1939; Schaeppi, 1953; Schmid, 1964; Stearn, 1946; Sutter & Endress, 1995; Takhtajan, 1966, 1987; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Todzia, 1993; Veldkamp, 1984; Williamson & Schneider, 1993; Wilson, 1965; Woon & Keng, 1979; Wu Cheng-Yih & Kubitzki, 1993

Hostplants of fungi and butterflies (not included in computation)

Ackery, 1988, 1991; DeVries, 1987; Farr et al., 1989; Pierre, 1984

Appendix 7. Table of *rbc*L taxa.

Table of taxa samples for *rbc*L. These are arranged alphabetically by families (mostly according to Cronquist, 1981).

Species	Family	Voucher/source	Literature citation§	GenBank accession
Actinidia chinensis Planch.	Actinidiaceae	*Kron 2117*, NCU	Albert et al., 1992	L01882
Aextoxicon punctatum Ruiz & Pav.	Aextoxicaceae	*Chase 959*, K	this paper	
Akania bidwillii (Hogg) Mabb.	Akaniaceae	*Fernando & Quinn 21606*, UNSW	Gadek et al., 1992	L12568
Amborella trichopoda Baill.	Amborellaceae	*Thien 500*, NO	Qiu et al., 1993	L12628
Ancistrocladus korupensis D. W. Thomas & Gereau	Ancistrocladaceae	*Gereau et al. 5203*, MO	this paper	
Asimina triloba (L.) Dunal	Annonaceae	*Qiu 15*, NCU	Qiu et al., 1993	L12631
Ilex crenata Thunb.	Aquifoliaceae	*Chase 119*, NCU	Albert et al., 1992	L01928
Acorus calamus L.	Araceae	*French 232*, CH	Duvall et al., 1993a	M91625
Aralia spinosa L.	Araliaceae	*Plunkett 1371*, WS	Chase et al., 1993	L11166
Asarum canadense L.	Aristolochiaceae	none	Chase et al., 1993	L14290
Asteropeia microsteira	Asteropeiaceae	*Civeyrel s.n.*, K	this paper	
Austrobaileya scandens C. T. White	Austrobaileyaceae	*Qiu 90030*, NCU	Qiu et al., 1993	L12632
Impatiens capensis Meerb.	Balsaminaceae	*Chase 114*, NCU	Chase et al., 1993	
Mahonia bealei (Fortune) Carr.	Berberidaceae	*Qiu 74*, NCU	Qiu et al., 1993	L12657
Berberidopsis corallina Hook. f.	Berberidopsidaceae	*Chase 555*, K	this paper	
Bixa orellana L.	Bixaceae	*Alverson s.n.*, WISC	this paper	
Brassica campestris L.	Brassicaceae	unknown	Olmstead et al., 1992	
Bretschneidera sinensis Hemsl.	Bretschneideraceae	*Leu & Lin 726*, WIS	Chase et al., 1993	M95753
Berzelia lanuginosa (L.) Brongn.	Bruniaceae	*Price s.n.*, Ind.	Olmstead et al., 1993	L14391
Pachysandra procumbens Michx.	Buxaceae	*Chase 207*, NCU	Chase et al., 1993	
Chimonanthus praecox (L.) Link	Calycanthaceae	*Qiu 62*, NCU	Qiu et al., 1993	L12639
Lobelia erinus L.	Campanulaceae	*Jansen 989*, MICH	Albert et al., 1992	L01931
Canella winterana (L.) Gaertn.	Canellaceae	*Qiu 90017*, NCU	Qiu et al., 1993	
Viburnum acerifolia L.	Caprifoliaceae	*Jansen 910*, MICH	Olmstead et al., 1992	L01959
Carica papaya L.	Caricaceae	Wisconsin BG	Rodman et al., 1993	M95671
Caryocar glabrum Pers.	Caryocaraceae	*Mori 22997* NY	this paper	
Euonymus alatus (Thunb.) Siebold	Celastraceae	*Chase 137*, NCU	Chase et al., 1993	L13184
Cephalotus follicularis Labill.	Cephalotaceae	*Chase 147*, NCU	Albert et al., 1992	L01894
Ceratophyllum demersum L.	Ceratophyllaceae	*Les s.n.*, CONN	Les et al., 1991	M77030
		Qiu 91027, NCU	Qiu et al., 1993	
Spinacia oleracea L.	Chenopodiaceae	unknown	Zurawski et al., 1981	J01443
Chloranthus japonicus Siebold	Chloranthaceae	*Chase 204*, NCU	Qiu et al., 1993	L12640
Chrysobalanus icaco L.	Chrysobalanaceae	*Fairchild Trop. G 76-311*	Morgan & Soltis, 1993	L11178
Helianthemum grandiflorum (Scop.) DC.	Cistaceae	*Chase 525*, K	this paper	

Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
Clethra alnifolia L.	Clethraceae	*Kron 1884*, NCU	Kron & Chase, 1993	L12609
Clusia gundlachii Stahl	Clusiaceae	*Chase 341*, NCU	Fay et al., 1997	Z75673
Quisqualis indica L.	Combretaceae	*W. R. Anderson s.n.*, MICH	Albert et al., 1992	L01948
Connarus conchocarpus F. Muell.	Connaraceae	*Uhl 601*, BH	Morgan et al., 1994	U06798
Coriaria myrtifolia L.	Coriariaceae	*Chase 245*, NCU	Albert et al., 1992	L01897
Cornus walteri Wangerin	Cornaceae	Arnold Arb. 414-67-A	Xiang et al., 1993	L11220
Corynocarpus laevigata J. R. Forst. & G. Forst.	Corynocarpaceae	no voucher	this paper	
Dudleya viscida (S. Watson) Moran	Crassulaceae	Huntington BG 62801	Morgan & Soltis, 1993	L11182
Crossosoma californicum Nutt.	Crossosomataceae	Rancho Santa Ana BG	Morgan & Soltis, 1993	L11179
Cucurbita pepo L.	Cucurbitaceae	none	Chase et al., 1993	L21938
Ceratopetalum gummiferum Small	Cunoniaceae	*Keller 2135*, CAS	Albert et al., 1992	L01895
Cyrilla racemiflora L.	Cyrillaceae	*Kron s.n.*, NCU	Albert et al., 1992	L01900
Diapensia lapponica L.	Diapensiaceae	*Hills 89018*, NCU	Kron & Chase, 1993	L12612
Dichapetalum macrocarpon Engl.	Dichapetalaceae	*Fison s.n.*, K	this paper	
Didymeles perrieri Leandri	Didymelaceae	*Leandi s. n.*, MO	this paper	
Dillenia indica L.	Dilleniaceae	*Chase 234*, NCU	Albert et al., 1992	L01903
Triphyophyllum peltatum (Hutchison & Dalziel) Airy Shaw	Dionocophyllaceae	*Chase 663*, K	this paper	
Shorea zeylanica (Thwaites) Ashton	Dipterocarpaceae	*Dayanandan D6*, GF	Chase et al., 1993	
Drosera binata Labill.	Droseraceae	*Williams D41*, LVC	Williams et al., 1994	L01911
Diospyros virginiana L.	Ebenaceae	*Kron 3004*, NCU	Kron & Chase, 1993	L12613
Hippophae salicifolia	Elaeagnaceae	*Chase 856*, K	this paper	
Elaeocarpus reticulatus	Elaeocarpaceae	*Quinn s.n.*, UNSW	this paper	
Erica australis L.	Ericaceae	RBG Edinburgh 781912	Chase et al., 1993	L13183
Escallonia coquimbensis Remy	Escalloniaceae	U. Calif. BG 52.1333	Morgan & Soltis, 1993	L11183
Eucommia ulmoides Oliv.	Eucommiaceae	*Qiu 91024*, NCU	Albert et al., 1992	L01917
Eucryphia lucida Druce	Eucryphiaceae	Strybing Arb. 86-0250	Albert et al., 1992	L01918
Jatropha interregima Jacq.	Euphorbiaceae	*Fairchild Trop. G 63169A*	this paper	
Euptelea polyandra Siebold & Zucc.	Eupteleaceae	*Qiu 90026*, NCU	Qiu et al., 1993	L12645
Medicago sativa L.	Fabaceae	unknown	Aldrich et al., 1986	
Nothofagus dombeyi (Mirb.) Oerst.	Fagaceae	U Washington BG	Chase et al., 1993	L13350
Poliothyrsis sinensis Hook. f.	Flacourtiaceae	*K. Wurdack s.n.*, NCU	this paper	
Frankenia pulverulenta L.	Frankeniaceae	*Collenette 6/93*, K	this paper	
Fouquieria columnaris Kellogg	Fouquieriaceae	U of California, Irvine, Arb.	Morton et al., 1997	

Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
Trichadenia zeylanica Thwaites	Kiggelariaceae	*Chase 1289*, K	this paper	
Geissoloma marginatum (L.) A. Juss.	Geissolomataceae	unknown	Savolainen, unpubl.	
Gentiana procera Holm	Gentianaceae	none	Olmstead et al., 1993	L14398
Geranium grandiflorum Gilib.	Geraniaceae	*Price s.n.*, IND	Albert et al., 1992	L01920
Gunnera hamiltonii Kirk ex W. S. Ham.	Gunneraceae	*Chase 562*, K	this paper	
Hamamelis mollis Oliv.	Hamamelidaceae	*Qiu 91035*, NCU	Albert et al., 1992	L01922
Hua gabonii Pierre ex De Wild.	Huaceae	*Wieringa 3177*, WAG	this paper	
Hydrangea macrophylla Torr.	Hydrangeaceae	*Morgan 2150*, WS	Morgan & Soltis, 1993	L11187
Icacina mannii Oliv.	Icacinaceae	*van Setten 460*, WAG	this paper	
Illicium parviflorum Michx. ex Vent.	Illiciaceae	*Qiu 83*, NCU	Qiu et al., 1993	L12652
Irvingia malayana Oliv. ex Benn.	Irvingiaceae	*Simpson 2638*, K	Fernando et al., 1995	
Koeberlinia spinosa Zucc.	Koeberliniaceae	*Al-Shehbaz s.n.*, WIS	Rodman et al., 1993	L14600
Krameria lanceolata Torr.	Krameriaceae	*Simpson 88-05-1-1*, MICH Chase et al., 1993		
Lacistema aggregatum Rusby	Lacistemataceae	*Pennington et al. 583*, K	this paper	
Leitneria floridana Chapm.	Leitneriaceae	*Qiu 91033*, NCU	Chase et al., 1993	
Couroupita guianensis Aublet	Lecythidaceae	RBG Kew 1960-43401	Morton et al., 1997	
Linum perenne L.	Linaceae	*Chase 111*, NCU	Fay et al., 1997	Z75681
Magnolia hypoleuca Siebold & Zucc.	Magnoliaceae	*Qiu 24*, NCU	Qiu et al., 1993	L12655
Byrsonima crassifolia (L.) Kunth	Malpighiaceae	*Fairchild Trop. G 81680*, MICH	Albert et al., 1992	L01892
Gossypium robinsonii F. Muell.	Malvaceae	*Wendel s.n.*, ISC	Chase et al., 1993	L13186
Marcgravia rectiflora Triana & Planch.	Marcgraviaceae	*Chase 331*, NCU	this paper	
Medusagyne oppositifolia Baker	Medusagynaceae	*Chase 670*, K	Fay et al., 1997	Z75670
Bersama lucens Szyszyl.	Melianthaceae	*Chase 1125*, K	this paper	
Menyanthes trifoliata L.	Menyanthaceae	none	Olmstead et al., 1993	L14006
Morus alba L.	Moraceae	none	Albert et al., 1992	L01933
Moringa oleifera Lam.	Moringaceae	*Iltis 30501*, WIS	Rodman et al., 1993	L11359
Knema latericia Elmer	Myristicaceae	*Qiu 91041*, NCU	Qiu et al., 1993	L12653
Maesa myrsinioides Leveille	Myrsinaceae	*Chase 309*, K	this paper	
Myrothamnus sp.	Myrothamnaceae	*Hoot s.n.*, F	this paper	
Nelumbo lutea (Willd.) Pers.	Nelumbonaceae	*Les s.n.*, CONN	Les et al., 1991	M77032
		Qiu 91028, NCU	Qiu et al., 1993	
Nepenthes alata Blanco	Nepenthaceae	*Chase 145*, NCU	Albert et al., 1992	L01936
Nymphaea odorata Aiton	Nymphaeaceae	*Les s.n.*, CONN	Les et al., 1991	M77035
		Qiu 91029, NCU	Qiu et al., 1993	

Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
Ochna multiflora DC.	Ochnaceae	*Chase 229*, NCU	Chase et al., 1993	
Schoepfia schreberi J. F. Gmel.	Olacaceae	*Nickrent 2599*, ILL	Morgan & Soltis, 1993	L11205
Oxalis dillenii Jacq.	Oxalidaceae	*Price s.n.*, IND	Albert et al., 1992	L01938
Paeonia tenuifolia L.	Paeoniaceae	*Kron 2115*, NCU	Chase et al., 1993	L13187
Passiflora quadrangularis L.	Passifloraceae	*Kron 3000*, NCU	Albert et al., 1992	L01940
Pelliciera rhizophora Planchon & Triana	Pellicieraceae	*Pennington et al. 586*, K	this paper	
Pittosporum japonicum Hort. ex C. Presl	Pittosporaceae	*Rieseberg s.n.*, RSA	Morgan & Soltis, 1993	L11202
Plagiopteron suaveolens Griff.	Plagiopteridaceae	*Chase 1335*, K	this paper	
Platanus occidentalis L.	Platanaceae	*Qiu P90005*, NCU	Albert et al., 1992	L01943
Plumbago capensis Thunb.	Plumbaginaceae	unknown	Giannasi et al., 1992	M77701
Gilia aggregata (Pursh) Spreng.	Polemoniaceae	*Chase 970*, K	this paper	
Polygala cruciata L.	Polygalaceae	*Chase 155*, NCU	Albert et al., 1992	L01945
Rheum × *cultorum* Thorsrud & Reisaeter	Polygonaceae	unknown	Giannasi et al., 1992	M77702
Lambertia inermis R. Br.	Proteaceae	Natl. Trop. BG, Hawaii	Morgan & Soltis, 1993	L11190
Quiina pteridophylla (Radlk.) Pires	Quiinaceae	*Pennington 13846*, K	Fay et al., 1997	Z75689
Rhabdodendron amazonicum Huber	Rhabdodendraceae	*Ribéiro 1187*, K	this paper	
Rhamnus carthanticus L.	Rhamnaceae	*Chase 100*, NCU	Chase et al., 1993	L13189
Rosa woodsii Lindl.	Rosaceae	*Soltis & Soltis 2410*, WS	Morgan et al., 1994	U06824
Poncirus trifoliata (L.) Raf.	Rutaceae	*Chase 117*, NCU	Chase et al., 1993	
Sabia sp.	Sabiaceae	*Qiu 91025*, NCU	Chase et al., 1993	L12662
Salix reticulata L.	Salicaceae	*Chase 840*, K	this paper	
Salvadora persica L.	Salvadoraceae	*Verdcourt s.n.*, K	Savolainen, unpubl.	
Koelreuteria paniculata Laxm.	Sapindaceae	*Chase 115*, NCU	this paper	
Manilkara zapota (L.) Royen	Sapotaceae	*Chase 129*, NCU	Albert et al., 1992	L01932
Sarracenia flava L.	Sarraceniaceae	*Chase 144*, NCU	Albert et al., 1992	L01952
Saxifraga integrifolia Hook.	Saxifragaceae	*Soltis & Soltis 2253*, WS	Morgan & Soltis, 1993	L01953
Scyphostegia borneensis Stapf	Scyphostegiaceae	*J. Davis s.n.*, BH	this paper	
Oubanguia alata Baker f.	Scytopetalaceae	*Gereau et al. 5202*, K	this paper	
Digitalis purpurea L.	Scrophulariaceae	none	Albert et al., 1992	L01902
Simmondsia chinensis (Link) C. K. Schneider	Simmondsiaceae	*Hoot s.n.*, F	this paper	
Nicotiana tabacum L.	Solanaceae	unknown	Lin et al., 1986	
Rhopalocarpus sp.	Sphaerosepalaceae	*Chase 906*, K	this paper	
Stachyurus praecox Sieb. & Zucc.	Stachyuraceae	*Chase 800*, K	this paper	
Staphylea trifoliata Payer	Staphyleaceae	*Chase 116*, NCU	this paper	
Styrax americana Lam.	Styraccaeae	*Kron 3002*, NCU	Kron & Chase, 1993	L12623

Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
Symplocus paniculata Miq.	Symplocaceae	*Kron 3005*, NCU	Kron & Chase, 1993	L12624
Suriana maritma L.	Surianaceae	unknown	Fernando et al., 1995	U07680
Tamarix pentandra Bunge	Tamaricaceae	*Chase 252*, NCU	this paper	
Tetacentron sinensis Oliv.	Tetracentraceae	*Qiu 90009*, NCU	Chase et al., 1993	L12668
Tetramerista sp.	Tetrameristaceae	*Coode 7925*, K	Morton et al., 1997	
Aquilaria beccariana Tiegh.	Thymelaeaceae	*Chase 1380*, K	this paper	
Camellia japonica L.	Theaceae	none	Kron & Chase, 1993	L12602
Platytheca verticellata Baill.	Tremandraceae	*Chase 179*, NCU	Chase et al., 1993	L01944
Trigonia nivea Cambess.	Trigoniaceae	*W. R. Anderson 13656*, MICH	Chase et al., 1993	
Tropaeolum majus L.	Tropaeolaceae	*Chase 113*, NCU	Price & Palmer, 1993	L14706
Viola sororia Willd.	Violaceae	none	Olmstead et al., 1992	L11674
Vitis aestivalis Michx.	Vitaceae	*Chase 226*, NCU	Albert et al., 1992	L01960
Qualea sp.	Vochysiaceae	*W. R. Anderson 13660*, MICH	Olmstead et al., 1992	U02730
Drimys winteri J. R. Forst. & G. Forst.	Winteraceae	*Qiu 90016*, NCU	Albert et al., 1992	L01905
Guaiacum sanctum L.	Zygophyllaceae	*W. R. Anderson s.n.*, MICH	Chase et al., 1993	

§ Publication in which an *rbc*L sequence for this taxon was first cited.

Abbreviatons used: Arb., arboretum; BG, botanical garden; G, garden; Natl., national; RBG, Royal Botanic Gardens; Trop., tropical; U, university; herbarium acronyms are the standard ones.

STATISTICAL SUMMARY OF SOME OF THE ACTIVITIES IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 1997

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	20,611	6,523	27,134
Purchase	18,330	3,065	21,395
Exchange	29,942	3,992	33,934
Gifts	11,830	1,169	12,999
Total acquisitions	80,713	14,749	95,462
Mountings			
Newly mounted	49,706	12,095	61,801
Mounted when received	18,234*	0	18,234
Total specimens filed	67,940	12,095	80,035
Repairs			
Specimens repaired	27,241	n/a	27,241
Specimens stamped	1,881	n/a	1,881
Total repairs	29,122	n/a	29,122
Specimens sent			
On exchange	49,071	312	49,383
As gifts	15,560	1,075	16,635
Total	64,631	1,387	66,018
Loans sent			
Total transactions	410	27	437
Total specimens	32,846	4,586	37,432
To U.S. institutions			
Transactions	256	18	274
Specimens	22,374	2,856	25,230
To foreign institutions			
Transactions	154	9	163
Specimens	10,472	1,730	12,202
To student investigators			
Transactions	59	4	63
Specimens	10,160	509	10,669
To professional investigators			
Transactions	326	23	349
Specimens	22,553	4,077	26,630
Loans received			
Transactions	319	20	339
Specimens	33,697	2,204	35,901

* The 18,234 "mounted when received" vascular plants are specimens of Chinese plants purchased directly from China.

	From U.S.A.	From abroad	Total
Visitors	342	107	449

On 31 December 1997 the total number of mounted, accessioned specimens in the herbarium was 4,777,217 (4,482,859 vascular plants and 294,358 bryophytes).

The Garden's herbarium is closely associated with its database management system, TROPICOS. For example, many of the numbers in the preceding chart are taken from TROPICOS, since it is used as a herbarium management tool. Herbarium labels for newly collected specimens are generated through TROPICOS, and the information is retained there for further use. The charts below summarize some of the statistics from TROPICOS both for the calendar year 1997 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about seventeen percent of the bryophytes and twenty-six percent of the vascular plants in the herbarium are now computerized, with an overall total of about twenty-six percent. Distributional records are taken both from herbarium specimens and from literature records, and these are distinguished in TROPICOS. Similarly, information concerning types is taken both from the literature (protologues) and from specimens.

TROPICOS is essentially complete for the names of mosses, except forms, and contains a few thousand records for hepatics, for which no comprehensive effort has yet been undertaken. The 1997 additions to the names for bryophytes, 504, reflects pretty accurately the number of nova published for that group.

TROPICOS records—1997 additions

	Bryophytes	Vascular Plants	Total
Specimens	7,685	92,778	100,463
Names	504	24,545	25,049
Synonyms	944	15,725	16,669
Distributions	1,869	22,545	24,414
Types	123	16,475	16,598
Bibliography	1,348	2,399	3,747

TROPICOS records—Year-End 1997 Totals

	Bryophytes	Vascular Plants	Total
Specimens	50,338	1,179,217	1,229,555
Names	93,121	697,741	790,862
Synonyms	57,614	335,957	393,571
Distributions	36,330	692,513	728,843
Types	6,671	208,981	215,652
Bibliography	18,284	53,178	71,462
Specimens in herbarium	294,358	4,482,859	4,777,217
Percent computerized	17	26	26

—Marshall R. Crosby

Volume 85, Number 1, pp. 1–214 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN
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CONTENTS

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POLLINATION OF PETALOID GEOPHYTES BY MONKEY BEETLES (SCARABAEIDAE: RUTELINAE: HOPLIINI) IN SOUTHERN AFRICA[1]

Peter Goldblatt[2], *Peter Bernhardt*[3], *and John C. Manning*[4]

ABSTRACT

Field observations, floral dissections, and pollen load analyses of insects indicate that pollination by hopliine beetles (Scarabaeidae: Rutelinae: Hopliini) has evolved convergently in many genera of herbaceous perennials in southern Africa. Beetle-pollinated flowers are identified by a suite of characters including a salver- to shallow bowl-shaped perianth and pigmentation emphasizing bright colors (red, orange, cream). Stereotyped "beetle marks" of either pale or dark color are frequently present at the bases of tepals or petals. These flowers are typically odorless and rarely offer nectar. Beetles, however, consume anthers and pollen, which are often a contrasting color from the perianth. Taxa that are pollinated by hopliine beetles include species in genera of the Hyacinthaceae (*Daubenya, Ornithogalum*), Iridaceae (*Aristea, Homeria, Ixia, Moraea, Romulea, Sparaxis, Tritonia*), and Hypoxidaceae (*Spiloxene*) in the monocots and Asteraceae (*Arctotis, Ursinia*), Campanulaceae (*Prismatocarpus, Wahlenbergia*), and Droseraceae (*Drosera*) among the dicots. Hopliine pollinators include both male and female beetles in the genera *Anisonyx, Anisochelus, Heterochelis, Khoina, Lepisia, Lepithrix, Pachycnema,* and *Peritrichia.* These beetles visit flowers to consume pollen and possibly nectar, to compete for mates, and to copulate. Pollen is usually deposited on or between hairs on the exoskeleton. The suite of characters associated with beetle pollination in these herbaceous geophytes is closer to that described in the herbaceous perennials of the eastern Mediterranean Basin and the woody flora of eastern Australia than it is to the classic series of features associated with magnoliid angiosperms.

The consumption of floral rewards (e.g., pollen, nectar, starchy food bodies, epidermal tissue) by Coleoptera has been well documented, and the mechanics of consumption and digestion of pollen, in particular, are extremely variable in beetles. Most beetles studied have either a pollen-cracking "molar" on their mouth parts or swallow pollen grains whole in the presence of hydrating nectar. In a few cases beetles may consume hard trichomes with pollen and use these plant cells as a pollen cracking grit (see review in Bernhardt, 1996). Knowledge of the role of beetles as pollinators of angiosperms has, however, changed radically in the last 15 years. In the classical view of beetle pollination,

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ANN. MISSOURI BOT. GARD. 85: 215–230. 1998.

reviewed by Faegri and van der Pijl (1979), beetles were associated primarily with the pollination of basal angiosperms, especially magnoliids, Araceae, and Cyclanthaceae (Armstrong, 1979; Bernhardt & Thien, 1987). Beetle pollination is traditionally associated with chamber- or urn-like flowers or inflorescences, absence of bright coloration, strong, unpleasant odors, and anthers that often extrude their pollen upon dehiscence. "Beetle flowers" shelter their pollinators, e.g., *Stapfia* (Gottsberger, 1977), but are not usually associated with true nectar secretion. The major pollinators of such flowers are comparatively small nitidulid, curculionid, and staphylinid beetles. Large-bodied dynastine scarab beetles have been associated with the pollination of *Victoria* (Prance & Arias, 1975), *Cyclanthus* (Beach, 1982), and a number of species of Araceae (Gottsberger & Amaral, 1984) and Annonaceae (Gottsberger, 1989a, 1989b).

This view of beetle pollination has expanded radically with ongoing research in temperate-tropical Australia and in the eastern Mediterranean. Work in Australia (Hawkeswood, 1987) showed that large brightly colored buprestids, cerambycids, and scarabs consumed the nectar in bowl-shaped flowers of the Myrtaceae and Burseraceae. Unlike the magnoliids and palms, these plants have flowers with anthers elevated on long stiff filaments, and the beetles often reach the nectar by pushing the filaments aside or crawling between them (Hawkeswood, 1987; photograph by Hawkeswood in Bernhardt, 1993). To the human eye, these flowers are usually white or light pastel shades, and strong fruit-like odors suggesting fermentation are not detectable. In Israel, fieldwork and experimentation (Dafni et al., 1990) have shown that flowers with bowl-shaped, red to orange perianths, blackened tepal bases and/or pollen, and no discernible scent are pollinated almost exclusively by vernal scarabs in the genus *Amphicoma*. These insects are far hairier than the majority of beetles associated with the classic syndrome of cantharophily. Plants with flowers showing this suite of characters comprise a guild of herbaceous perennials dominated by Ranunculaceae and some petaloid monocots (Dafni et al., 1990).

Early work by Scott Elliot (1891) appears to contain the first reference to the importance of hopliine beetles in the pollination of the South African flora. Peringuey (1902) also remarked on the frequency of beetle pollination in southern African plants, noted floral foraging in many genera of native beetles, and suggested that their membranous mouth parts implied a diet emphasizing nectar. Peringuey noted that such beetles departed from flowers covered with pollen, and that "on a bright day in the spring (August–October) no flower is without a tenant." He maintained that few insects were better adapted for flower pollination than such genera of hairy beetles as *Anisonyx*, *Lepithrix*, and *Peritrichia*. Curiously, Vogel (1954) did not cite Peringuey in his mammoth review of pollination systems in southern Africa. Vogel did note that some scarab genera were pollen- and flower-eaters but made few overt references to beetle pollination, and the subject remained virtually dormant for the next 40 years. In their review of insect pollination systems in the Cape Flora (the winter-rainfall climate zone of southern Africa), Whitehead et al. (1987) derived most of their references to scarab pollination from Vogel (1954), although they did note that cetoniids, nitidulids, and staphylinids visited the flowers of some shrubby Proteaceae.

Recent evidence, however, now strongly suggests that scarab beetles in the subtribe Hopliini (tribe Rutelinae) comprise an important pollinator guild in southern Africa and that a suite of floral characters is associated with "monkey-beetle" pollination. Among the few works available to date on the pollination of southern African plants by the Hopliini is that of Picker and Midgley (1996), who listed some 25 species of plants as putatively monkey-beetle pollinated. These included both monocots and dicots representing some 10 families. More importantly, Picker and Midgley recognized three systems of monkey-beetle pollination, based on differences in beetle hairiness, flower color preferences, and whether foraging was restricted to pollen. Goldblatt and Manning (1996) described the foraging behavior of hopliine beetles in the genera *Anisonyx* and *Peritrichia* (as *Lepithrix*), concluding that they were most likely to be the dominant (or sole) pollinators of two species of *Drosera* (Droseraceae), and one species each of *Aristea* and *Moraea* (Iridaceae). These authors also suggested that other species of monkey beetles were likely to be the pollinators of many more species of Iridaceae in genera such as *Aristea*, *Homeria*, *Moraea*, *Romulea*, *Sparaxis*, and *Tritonia*. Studies by Steiner (1998 and pers. comm.) also show the importance of monkey-beetle pollination in the so-called peacock moraeas, *M. villosa* and its close allies, as well as in *Sparaxis* and genera of Asteraceae including *Arctotis*.

Obviously, additional fieldwork on beetle pollination in southern Africa is required. The problem is that while we have a number of observations of monkey beetles visiting flowers, there remains a paucity of data showing that these beetles transport pollen of their host flowers and actually contact stigmatic surfaces. As Hawkeswood (1989) has shown, scarab beetles may pollinate the flowers of some species while destroying those of other co-blooming species. For example, while *Diphucephala affinis* (Scarabaeidae: Melolonthinae) regularly visits flowers of *Hibbertia* (Dilleniaceae) in western Australia, these scarabs fail to transport *Hibbertia* pollen or contact the stigmas. Here, we present our own observations on pollen foraging by beetles on native southern African geophytes and compare beetle pollination in southern Africa to that elsewhere in the world.

MATERIALS AND METHODS

Fieldwork was conducted during August to October 1995, and during the same months in 1996 and 1997 at several sites (Table 1) in the southwestern Cape (Cape Floristic Province) and the western Karoo, South Africa, areas of Mediterranean climate with wet winters and dry summers. Observations of insect foraging involved 4–20 hours per plant species, and included recording of floral attractants (pigment patterns, scent), the behavior of insects on the flower, and the taxonomic identity of floral foragers. Insects were not collected unless they were observed to contact the sexual organs of flowers while foraging or mating. Insects were captured and killed with ethyl acetate fumes for subsequent identification and analysis of pollen loads. To prevent contamination of one insect with pollen carried by another in the same killing jar, individuals were isolated by wrapping in tissue paper.

Removal of pollen from insect bodies involved either gently scraping pollen off the body with a dissecting needle or gently washing the insect bodies in drops of 95% ethanol. The residue from needle probes or washes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). The pollen of a particular plant species was scored as present on the body of an insect if more than 10 individual grains (or polyads) were counted on the slide (Tables 3, 4). Pollen grains were identified by comparison with a reference set of pollen-grain preparations made from plants flowering at our study sites.

Field determinations of nectar (if present) were made by withdrawing nectar from the base of the floral tube with 2 μl capillary tubes after separating the ovary from the perianth. Nectar samples were dried on filter paper and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPLC analysis. The percentage of sugars dissolved in fresh nectar was recorded on a Bellingham & Stanley hand-held refractometer (0–50%) using nectar extracted from flowers in the manner described above. When volumes were too small to measure or to determine sugar concentration, presence of nectar was established by brushing nectariferous areas of flowers against the tongue.

Identifications of beetles were made by M. Picker, University of Cape Town, and H. Dombrow, Worms, Germany. Flies were determined by J. C. Manning and bees by Robert Brooks, Snow Entomological Museum, University of Kansas. Voucher specimens were made of plant species visited by beetles when necessary; these specimens are deposited at MO and NBG (Table 2). Insect vouchers are deposited at the Snow Entomologial Museum and/or the South African Museum.

RESULTS

FLORAL PHENOLOGY AND HABIT

Flowers visited most often by hopliine beetles (monkey beetles) are largely restricted to the winter-rainfall region of southern Africa, namely the southern and western coast of the subcontinent and the near interior. Flowering there is concentrated in the late winter and late spring, August to early November (Table 2). The majority of flowers observed to be visited by beetles belong to herbaceous perennials, especially geophytic petaloid monocots, and subshrubs (Aizoaceae subfam. Mesembryanthemoideae, some Asteraceae).

These species typically form fairly dense populations locally, with over 10 individuals per square meter not uncommon. In some species, e.g., *Gladiolus meliusculus* and *Ixia polystachya*, plants tend to be much more scattered, typically of the order of 1–2 m apart.

FLORAL PRESENTATION AND REWARDS

The majority of flowers visited by monkey beetles have salver- to shallow bowl-shaped, actinomorphic perianths or involucral inflorescences (Asteraceae). Species of Iridaceae subfamily Ixioideae studied (Table 2) have a short, cylindric or more or less funnel-shaped perianth tube, 1.5–10 (rarely to 20) mm long. In species of *Ixia* sect. *Ixia* (*I. curta, I. dubia, I. maculata, I.* cf. *polystachya*), *Romulea, Sparaxis,* and *Tritonia* the tube is filiform below and blocked by the style, and sometimes the mouth of the tube is closed off by the fused or coherent filaments. These nectarless tubes appear to be inaccessible to the mouth parts of the foraging insects described below.

Floral colors are extremely variable (Table 2), but

Table 1. Plant species pollinated or visited by hopliine beetles and study sites. Dates of observation are included in column 3. Parentheses in column 1 indicate species apparently visited casually by hopliine beetles and in column 2 insect species other than hopliine beetles. Their orders and families are as follows: Apoidea: *Andrena* (Andrenidae), *Apis mellifera* (Apidae), halictid bees (Halictidae); Muscoidea: *Philoliche* (Tabanidae); *Musca*, *Orthellia* (Muscidaeidae); *Scathophaga* (Sarcophagidae); *Anthomyia* (Anthomyidae).

Plant species	Hopliine beetles (other insects)	Study site (date of observation)
Homeria ochroleuca	*Anisonyx ursus*, (*Apis mellifera*, *Scathophaga stercoraria*, *Orthellia* sp., *Anthomyia*, Calliphoridae, Syrphidae)	Sir Lowry's Pass Village (Aug. 1995)
Babiana rubrocyanea, *Gladiolus meliusculus*, *Ixia maculata*, *Romulea eximia*, *R. obscura*, *Spiloxene capensis*	*Lepisia rupicola*, *Pachycnema crassipes*, (*Andrena* sp.)	Waylands Reserve, Darling (Sep. 1995, 1996)
Ixia framesii, *Arctotis acaulis*, *Ornithogalum thyrsiflora*	*Lepithrix ornatella*, (*Philoliche atricornis*)	Camphill road, Malmesbury (Sep. 1995)
Ixia maculata, *Ornithogalum thyrsiflora*	*Pachycnema crassipes*, *Lepithrix longitarsis*, *L. fulvipes*	Ysterfontein, Clanwilliam (Sep. 1995)
Ixia maculata, *Ornithogalum thyrsiflora*	*Pachycnema crassipes*, *Heterochelis arthriticus*, *Scelophysa militaris*, *Lepithrix ornatella*	Sandberg, Leipoldtville (Sep. 1995)
Ixia dubia, *Moraea bellendenii*	*Heterochelis arthriticus*, *Pachycnema crassipes*, *Lepithrix ornatella*, *Heterochelis unguicularis*	Darling, renosterveld (Sep. 1996)
Ixia curta, *Ursinia* sp., *Gazania krebsiana*, *Monsonia speciosa*	*Pachycnema crassipes*, *Lepisia rupicola*	Versveld Reserve, Darling (Sep. 1996)
Tritonia crocata, *Ornithogalum dubium*	*Pachycnema tibialis*	Riversdale commonage (Sep. 1995)
Tritonia deusta	*Peritrichia hybrida*	Swellendam (Oct. 1997)
Tritonia squalida, *Agathosma* sp.	*Peritrichia* sp. 1	Blombos road, Riversdale (Oct. 1997)
Homeria elegans, *Aristea teretifolia*, *Hesperantha falcata*	*Peritrichia pseudoplebeia*, (*Apis mellifera*, *Orthellia* sp., *Scathophaga stercoraria*)	Fairfield Estate, Bredasdorp (Aug. 1995, Sep. 1996)
Aristea lugens, *Moraea villosa*, *Agathosma* sp., (*Geissorhiza aspera*)	*Anisonyx longipes*, *A. ursus*, *Lepithrix ornatella*	Malmesbury commonage (Sep. 1995, 1996)
Aristea cantharophila, *Moraea* cf. *lurida*, *Drosera* spp.	*Peritrichia pseudoplebeia*, *Anisonyx ursus*, (*Musca* sp.)	Sir Lowry's Pass (Aug.–Sep. 1995)
Sparaxis elegans, *Arctotis acaulis*, *Ursinia cakilefolia* (*Homeria bifida*)	*Lepisia* sp. 1, (*Philoliche atricornis*)	Bokkeveld Plateau, Glenlyon renosterveld (Sep. 1995, Oct. 1996)
Sparaxis elegans, *Ursinia cakilefolia*	*Anisochelus inornatus*, (*Philoliche atricornis*)	Nieuwoudtville church yard (Sep. 1997)
Hesperantha vaginata, *Romalea monadelpha*, *Sparaxis pillansii*, *Bulbinella elegans*, *Arctotis acaulis*, *Berkheya glabrata*	*Lepisia* sp. 1, (*Philoliche atricornis*)	Bokkeveld Escarpment, Glenlyon dolerite (Sep. 1995, 1966)
Romulea monadelpha, *Arctotis acaulis*	*Lepisia* sp. 1	Near Calvinia (Oct. 1996)
Romulea sabulosa	*Lepithrix stigma*	Bokkeveld Escarpment, Oorlogskloof road (Sep. 1996)
Romulea sabulosa	*Lepithrix stigma*	Bokkeveld Escarpment, Grasberg road (Sep. 1995)
Homeria vallisbelli, *Romulea montana*, *Spiloxene capensis*, (*Oxalis obtusa*)	*Anisochelis inornatus*	Bokkeveld Escarpment, Keyzerfontein road (Sep. 1996)
Daubenya aurea, *Romulea subfistulosa*	*Lepisia* sp. 2, (*Halictid bees*)	Roggeveld Escarpment (Sep. 1995)

Table 1. Continued.

Plant species	Hopliine beetles (other insects)	Study site (date of observation)
Moraea insolens, Ixia flexuosa, Aristea biflora	*Anisonyx lepidotus*	Drayton, Caledon (Oct. 1996)
Aristea biflora, Drosera pauciflora, Spiloxene capensis	*Anisonyx lepidotus*	Near Drayton, Caledon (Sep. 1997)
Thereianthus racemosus	*Khoina bilateralis*	Zuurvlakte, Grootwinterhoek (Nov. 1995)
Ixia cf. *polystachya, Ornithogalum dubium, Prismatocarpus pedunculatus*	*Peritrichia subsquamosa,* (*Pachycnema saga*—only *Prismatocarpus*)	Brandvlei hills, Worcester (Nov. 1996)
Sparaxis grandiflora, Asteraceae spp.	*Peritrichia rufotibialis, Anisochelus inornatus,* (*Philoliche atricornis,* Halictid bees)	Citrusdal—Clanwilliam (Sep. 1997)

intense yellow, bright orange to red, or purple shades predominate at most sites. Contrasting pigmentation may be seen at two different levels. The majority of beetle-visited flowers have dark, or sometimes pale, marks on the tepals or petals (Figs. 1–6), sometimes superimposed on a calloused epidermis (Table 2). In petaloid geophytes, these markings may take the form of a central blotch encompassing the bases of all the tepals and sometimes the filaments (e.g., *Aristea cantharophila, Ixia maculata*), or one or both tepal whorls may have quite discrete marks composed of ovate areas of contrasting pigmentation, sometimes with hazy edges (e.g., *Aristea teretifolia*) or sometimes with a paler or darker central line that resembles the line between the elytra when at rest (Figs. 1, 4, 6). We provisionally call these markings "beetle marks" both for the frequent resemblance to the shape of a beetle and for the presumed function of attracting beetles to flowers. The color of the markings may be black (*Aristea lugens*), light to dark brown (*A. teretifolia, Ixia curta, I. maculata*), or greenish or even yellow on a darker background, and then most often with median dark lines. The markings on the tepals of dark red-flowered *Romulea eximia* and *R. obscura* are light green and closely resemble the beetle *Lepisia rupicola* often seen on their flowers (Goldblatt & Manning, 1996 with color photograph). The floral markings on *Aristea biflora* and *Tritonia crocata* subsp. *hyalina* consist of transparent oval areas at the lower edges of the tepals, which appear dark when viewed from above. The presence of beetle marks on flowers of *Babiana rubrocyanea* is questionable: the deep blue flowers have a uniform, large, bright red center rather than a discrete dark, beetle-like mark. The presence of beetle marks in the flowers of *Ixia dubia* varies from population to population. Flowers observed near Rondeberg have typical dark markings at the tepal bases, whereas these marks are absent in plants from near Darling.

The second level of contrasting pigmentation consists of anthers or pollen of unusual color. The anthers and pollen may be bright orange (Table 2) and thus prominent against dark-colored perianths or filaments, and sometimes the anthers may be black, then presumably forming part of the beetle marks (*I. monadelpha, I.* cf. *polystachya*). The anthers are sometimes unusually large, particularly so in *Homeria elegans* (8–10 mm) and some species of *Aristea* (4.5–7 mm) and *Ixia* (6–10 mm), compared with anthers in other species of these genera.

Floral fragrances were not noted in the majority of species. Flowers of *Homeria elegans* have a sweet odor reminiscent of shredded coconut, whereas those of *H. ochroleuca* have a mild, slightly acrid, musk-like odor reminiscent of flowers of *Rhus* spp. (Anacardiaceae). *Gladiolus meliusculus* has a strong, sweet, honeyed fragrance like that of *Viola odorata* (Goldblatt & Manning, 1998).

The majority of species studied have no discernible nectar glands, and floral nectar does not appear to be secreted. Trace amounts of nectar are present as a wet sheen toward the base of the floral tubes of *Ixia framesii* and species of *Romulea, Sparaxis,* and *Tritonia. Gladiolus meliusculus* secretes nectar at the base of the floral tube [0.8–1.2 μl, 29.2% (SD:1.3) sucrose equivalents, sucrose dominant, n = 5], while *Homeria ochroleuca* secretes nectar on the lower surfaces of the tepals (0.2 μl, concentration not measurable, equal quantities of fructose and glucose and no sucrose). Nectar and/or fragrance were evident only in those species that were visited by a combination of beetles and other insects.

BEETLE DIVERSITY AND PHYSICAL PARAMETERS

Coleoptera captured totaled 26 species in nine genera (Figs. 1–6, 7A–D), all of which belonged to tribe Rutelinae, subtribe Hopliini (Scarabaeidae).

Table 2. Floral characteristics and voucher data for species pollinated by hopliine beetles, including shape, perianth color and marking, presence of nectar, anther color, and flowering time. Abbreviations: b = bowl, f = funnel-shaped, s = salverform, + = presence, − = absence, ± = polymorphic in different populations, tr = trace amount too little to measure volumetrically. Plants collected by P. Goldblatt without voucher are indicated by the abbreviation n/v; voucher numbers are those of P. Goldblatt.

	Flower		Beetle marks	Nectar	Anther/ pollen color	Flowering time	Voucher number
	Shape	Color					
Hyacinthaceae							
Daubenya							
aurea Lindl.	b	red	−	−	yellow	Sep.	n/v
Ornithogalum							
dubium Houtt.	s	white	+	tr	white	Sep.–Nov.	n/v
thyrsiflora Jacq.	s	white	+	tr	white	Sep.–Nov.	n/v
Hypoxidaceae							
Spiloxene							
capensis (L.) Garside	s	cream	+	−	yellow	Aug.–Sep.	n/v
serrata (Thunb.) Garside	s	yellow	−	−	yellow	Aug.–Oct.	n/v
Iridaceae: Iridoideae and Nivenioideae							
Aristea							
biflora Weim.	s	mauve	+	−	orange	Aug.–Sep.	8898
cantharophila Goldblatt & J. C. Manning	s	cream/lilac	+	−	orange	Aug.	10284
teretifolia Goldblatt & J. C. Manning	s	lilac	+	−	orange	Aug.–Sep.	10250
lugens Ker Gawl.	s	white/blue	+	−	orange	Sep.–Oct.	10311
Homeria							
bifida L. Bolus	s	pink	−	tr	yellow	Sep.–Oct.	3969
elegans (Jacq.) Sweet	b	yellow	+	−	yellow	Sep.	10255
ochroleuca Salisb.	b	yellow	−	tr	yellow	Aug.–Oct.	10248
vallisbelli Goldblatt	b	yellow/pink	−	tr	yellow	Sep.–Oct.	4032
Moraea							
bellendenii (Sweet) N. E. Br.	b	yellow	+	−	yellow	Sep.–Oct.	n/v
insolens Goldblatt	s	orange	+	−	orange	Sep.	4880
aff. *M. lurida* Ker Gawl.	b	white	+	−	red	Aug.–Sep	10281
villosa (Ker Gawl.) Ker Gawl.	g	purple	+	−	orange	Sep.	6275
Iridaceae: Ixioideae							
Babiana							
rubrocyanea (Jacq.) Ker Gawl.	b	blue/red	+?	tr	brown	Sep.	n/v
Hesperantha							
falcata (L.f.) Ker Gawl.	s	yellow	−	tr	yellow	Sep.	n/v
vaginata (Sweet) Goldblatt	b	yellow	+	?	yellow	Sep.	4035
Gladiolus							
meliusculus (G. Lewis) Goldblatt & J. C. Manning	g	pink	+	+	yellow	Sep.	10386A
Ixia							
curta Andrews	s	orange	+	−	yellow	Sep.–Oct.	10358
dubia Vent.	s	orange	±	−	yellow	Sep.–Oct.	10338
framesii L. Bolus	s	orange	+	tr	yellow	Sep.	10333
maculata L.	s	orange	+	−	yellow	Sep.–Oct.	10349
cf. *polystachya* L.	s	cream	+	−	blackish	Oct.–Nov.	10568
Romulea							
eximia de Vos	b	red	+	−	yellow	Sep.	10361
monadelpha (Sweet) Bak.	b	red	+	−	yellow	Sep.	4036
montana Schltr. ex Bég.	b	yellow	−	−	yellow	Aug.–Sep.	n/v

Table 2. Continued.

	Flower		Beetle marks	Nectar	Anther/ pollen color	Flowering time	Voucher number
	Shape	Color					
obscura Klatt	b	red	+	–	yellow	Sep.	10317
sabulosa Schltr. ex Bég.	b	red	+	–	yellow	Aug.–Sep.	n/v
subfistulosa de Vos	b	red	+	?	yellow	Sep.	10305
Sparaxis							
elegans (Sweet) Goldblatt	s	salmon	+	tr	brown	Sep.	4286
grandiflora (D. Delaroche) Ker Gawl.	b	yellow	–	tr	yellow	Aug.–Sep.	2438
pillansii L. Bolus	s	red	+	tr	yellow	Oct.	327
Thereianthus							
racemosus (Klatt) G. Lewis	s	blue	–	–	blue	Nov.	10454
Tritonia							
crocata subsp. *hyalina (L.f.) de Vos*	b	orange	+	tr	yellow	Sep.–Oct.	n/v
deusta (Aiton) Ker Gawl.	b	orange	+	–	yellow	Oct.	10782
squalida (Aiton) Ker Gawl.	b	pink	–	tr	white	Oct.	9790
Campanulaceae							
Wahlenbergia							
capensis (L.) A. DC.	s	blue	+	?	blue	Sep.–Oct.	n/v
Prismatocarpus							
pedunculatus (Bergius) A. DC.	s	cream	–	–	cream	Oct.–Nov.	10569
Droseraceae							
Drosera							
cistiflora L.	s	cream/pink	+	–	orange	Aug.–Oct.	10282
pauciflora DC.	s	cream/pink	+	–	orange	Aug.–Oct.	10283

These beetles ranged in length from 6 to 14 mm. Body hairiness varied among genera and species, with *Anisonyx* having the densest and longest hairs (e.g., Figs. 1, 2, 4). The shortest beetles were *Heterochelus arthriticus* (collected on *Ixia dubia*) and *Lepthrix stigma* (collected on *Romulea sabulosa*); the longest were *Anisonyx ursus*, collected on *Drosera cistiflora*. A total of one to five beetle species were captured on 40 species of herbs in four families (Table 3). *Ixia maculata* was the only species recorded with as many as five beetle species on its flowers. Less than half (40%) of the plant species, however, were consistently visited by just one species of beetle (Table 3).

BEETLE FORAGING BEHAVIOR

Monkey beetles are common on warm days in late winter and spring when ambient temperatures are above 18°C. Individual beetles were observed in flight as early as 9.30 hr and as late as 16.00 hr, but peak activity on flowers was between 11.00 and 15.00 hr. Monkey beetles fly slowly and over relatively short distances. Beetle populations appeared to be most dense on inflorescences of Asteraceae and the larger flowers of Aizoaceae subfam. Mesembryanthemoideae. In contrast, beetles captured on the flowers of species listed in Table 2 rarely occurred in groups of more than two or three per flower. In these flowers, beetles were most often seen either foraging on pollen directly on the anthers or pushing their heads into the flower center, leaving the posterior portion of their abdomens prominently displayed. Since the anthers are usually positioned close to the center of the flower and above the beetle marks on the perianth, foraging beetles were usually observed positioned on the beetle marks while they fed.

When more than one beetle of the same species was present on a flower, they often displayed intraspecific agonistic behavior, and one or more of the beetles might be driven off as a result. The beetles also used the flowers as sites to assemble and copulate. Compared to other pollinators, beetle visits to flowers lasted a long time, at least several minutes, or more when mating or evidently at rest. Beetles were often observed moving both to another

Figures 1–6. Hopliine beetles foraging on flowers. —1. *Anisonyx longipes* on *Aristea lugens*. —2. *Anisonyx ursus* on *Drosera cistiflora*. —3. *Anisochelus inornatus* on *Homeria vallisbelli*. —4. *Anisonyx ursus* on *Moraea* cf. *lurida*. —5. *Pachycnema tibialis* on *Tritonia crocata* subsp. *hyalina*. —6. *Lepisia* sp. on *Hesperantha vaginata*. Arrows indicate stigmas of flowers.

flower of the same species and to flowers of different species.

Beetle contact with stigmas occurred in one of two ways depending on the length and position of the style. In *Aristea* spp. and *Drosera cistiflora* and *D. pauciflora* (Figs. 1, 2) the style is twisted to lie parallel to, and above, the perianth surface. The stigmatic areas are thus removed from the center of the flower. In this case, beetles brushed against the stigma or crawled over it when they moved across the flower. In the second, more common, case the style is short and the stigma barely protrudes beyond the short floral tube or cup. The beetle contacted the stigma ventrally while crawling over it or dorsally when climbing into the floral cup, while either foraging or engaging in agonistic or copulatory behavior. As the color of the pollen is often so distinctive and contrasts so sharply with that of the beetles and the stigmas, pollen could easily be seen clinging to the hairs of the beetles and on the stigmas after the beetles departed. The style branches of *Moraea* species are broad and arching, concealing the anthers on their abaxial surfaces (Fig. 4). *Moraea* pollen was deposited on the abaxial stigmatic lobe only when a beetle dusted with pollen crawled under a style branch to lie in the center of the flower. The prominent "nectar guides" and dark tepal claws in some species of *Moraea* may in fact be beetle marks encouraging these insects to move into the center of the flower directly under the gynandrium to contact both pollen and stigmas. As female beetles continued to feed while mating, both males and females sometimes became dusted with pollen and brushed against stigmas.

POLLEN LOAD ANALYSES

A total of 294 monkey beetles were collected on 40 species of flowering herbs (Table 3) representing 14 genera. More than 90% (270) of the beetles carried the pollen of the host flower on which they were collected. However, of these only 28% carried their host plant's pollen exclusively (Table 3). The majority of beetles carried a minimum of two and a maximum of five recognizable pollen taxa on their bodies. The only beetle to carry five pollen taxa was an individual of *Pachycnema crassipes*, 10 mm long, collected on *Gladiolus meliusculus*, which had the pollen of *G. meliusculus*, *Romulea eximia*, *Drosera cistiflora*, *Spiloxene capensis*, and an unidentified member of the Asteraceae clinging to its body surface.

Pollen washes showed that 28 beetles each carried pollen of more than one species of Iridaceae. Of these, four specimens of *Anisonyx longipes*, collected on *Aristea lugens*, each carried pollen of three species of Iridaceae: *A. lugens*, *Geissorhiza ?aspera* Goldblatt, and *Moraea villosa*.

OTHER VISITORS

In *Sparaxis elegans*, *S. grandiflora*, and *S. pillansii*, beetle species (Table 3) appeared to share flowers with the tabanid fly, *Philoliche atricornis*. In contrast to the flower-visiting *Philoliche gulosa* and *P. rostrata* (Goldblatt et al., 1995; Manning & Goldblatt, 1997), which have mouth parts 20–30 mm long, *P. atricornis* has a proboscis only 3–5 mm long. This fly appeared to forage on the flowers of *Sparaxis* species for nectar exclusively, and carried ample quantites of pollen of the host flower, which in *S. elegans* and *S. pillansii* is a distinctive red-brown color, easily visible to the naked eye as the flies foraged or flew from flower to flower (Table 4).

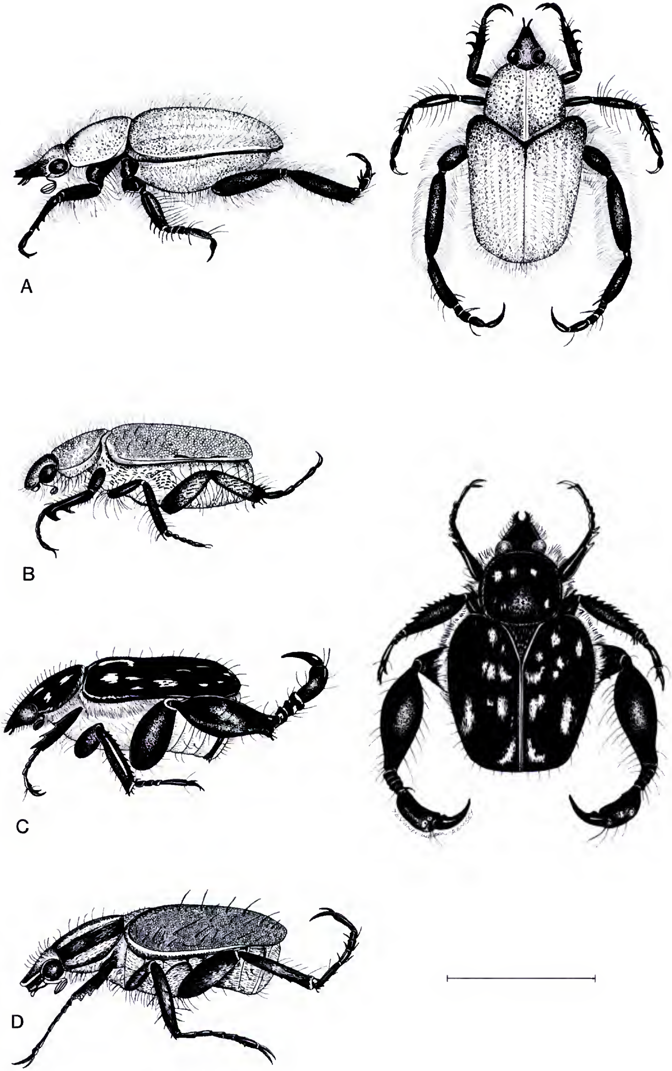
Ixia framesii and *Ornithogalum thyrsiflora* are visited by both the beetle *Lepithrix ornatella* and the tabanid, *Philoliche atricornis*. It also forages for nectar and carries the pollen of both host flowers (Tables 3, 4).

The beetle *Peritrichia pseudoplebia* may share *Homeria elegans* with the muscid fly *Orthellia* sp. and the native honey bee, *Apis mellifera*, all of which may contact the stigmas of *H. elegans* and transport its pollen (Table 4). *Homeria ochroleuca* receives the most diverse assembly of floral foragers. The beetle *Anisonyx ursus* may share the flowers with *Apis mellifera* and as many as six dipteran taxa. However, the particularly large anthers, prominent beetle marks, and depauperate nectar of flowers of *H. elegans* suggest that beetle pollination is more important in that species than in *H. ochroleuca*, with its wider range of visitor species and more ample nectar production.

Gladiolus meliusculus, *Romulea subfistulosa*, and *Daubenya aurea* are visited by a combination of hopliine beetles and solitary bees in the families Andrenidae and Halictidae (Tables 3, 4), and *Aristea biflora* Weim. by hopliine beetles and occasionally by *Apis mellifera*. All three bees, *Andrena* sp. (Andrenidae), *Patellapis* sp. (Halictidae), and *Apis mellifera*, appear to be polylectic foragers, but they do contact the stigmas of their respective flowers.

LOCAL FLORAL GUILDS

At some study sites, there was a tendency for floral pigmentation patterns to converge. This was striking at Sir Lowry's Pass, where *Aristea cantharophila*, *Drosera cistiflora*, *D. pauciflora*, and *Moraea*


A
B
C
D

sp. aff. *lurida* all had cream or lilac flowers with dark centers and orange pollen. At Malmesbury commonage, *Aristea lugens* and *Moraea villosa* flowers were blue to mauve with very dark markings on the outer tepals. Near Caledon, *A. biflora, Drosera pauciflora,* and *Spiloxene capensis* all had whitish to pale mauve, salver-shaped flowers with dark markings near the center. Along the Bokkeveld Escarpment, yellow-flowered species dominated the beetle-pollinated guild that includes *Homeria vallisbelli, Romulea montana,* and *Spiloxene serrata,* as well as other small-flowered dicots including *Ursinia* sp. (Asteraceae) and *Oxalis obtusa* Jacq. At other sites obvious color convergence is not evident, and color patterns are broadly mixed. For example, at sites on the Bokkeveld Plateau, *Romulea monadelpha* and *R. sabulosa* have dark red and black flowers, those of *Hesperantha vaginata* are deep yellow and chocolate, and those of *Sparaxis elegans* and *S. pillansii* are pink to salmon with dark red or purple and yellow markings.

DISCUSSION

Pollination by hopliine monkey beetles obviously conforms to a pattern distinct from classical cantharophily in the magnoliid angiosperms. In particular, flowers and inflorescences in the pollination systems described above do not have urn-like, haplomorphic perianths or overlapping bracts. Pollination by monkey beetles in southern Africa more closely parallels beetle pollination by the large scarabs, buprestids, and cerambycids in Australia and the eastern Mediterranean. Perianths are usually open and shallow, anthers do not extrude or shed pollen, and strong odors are uncommon. In fact, similarities between the red-flower guild of the eastern Mediterranean and the monkey-beetle flowers of southern Africa are particularly marked. Bright orange to red colors, salver-shaped flowers, and absence of floral odor are well distributed in the beetle flowers of southern Africa and the dark, beetle-like marks of the southern African species may be comparable to the blackened stamens or blackened tepal bases in some of the Mediterranean flowers. Few of these flowers, however, appear to secrete nectar as do the Mediterranean species of *Anemone, Ranunculus,* and *Tulipa.*

A primary difference between beetle pollination in the Mediterranean and in southern Africa is the taxonomic diversity of the Coleoptera involved. In the Mediterranean, pollination of the red-flower guild involves only six species of the genus *Amphicoma* (Dafni et al., 1990). The southern African guild of beetle pollinators is far broader, with at least nine genera of floral foragers representing a total of over 20 species.

Our results suggest that plant species visited by Hopliini may be specialized for beetle pollination to varying degrees. Thus, where plants offer nectar in shallow floral bowls, generalist entomophily occurs and beetles are members of a wider pollinator spectrum that includes native Diptera, Hymenoptera, and sometimes Lepidoptera. This would appear to be the most likely scenario in *Homeria elegans, H. ochroleuca, Gladiolus meliusculus, Ixia framesii, Sparaxis elegans, S. grandiflora,* and *S. pillansii.* Pollination by a range of different organisms is known in many flowers; for example, some plant species in the Western Hemisphere and in Australia are pollinated by a combination of birds and bees (Armstrong, 1979). In southern Australia the flowers of a number of woody genera appear to be pollinated by a combination of syrphid flies and small colletid bees (Bernhardt, 1989). Pollination strategies combining beetles and other insects are perhaps less well known, but may be much more common than previously anticipated. For example, Schneider and Buchanan (1980) found that the magnoliid flowers of *Nelumbo lutea* are pollinated by a combination of bees, flower flies, and cantharid beetles. It would appear that monkey beetles are a predictable part of generalist entomophily in the flora of southern Africa, much as syrphid flies and small colletid bees are a dominant part of generalist entomophily in southern Australia (Bernhardt, 1989). In other instances, however, monkey beetles appear to be the sole pollinators and flowers are highly specialized for beetle pollination.

The high incidence of pollination by monkey beetles among the Iridaceae of southern Africa has not been widely appreciated. The literature dealing with pollination ecology of the Iridaceae has emphasized the prominent role of bees, moths, birds (Knuth, 1909; Vogel, 1954), and nectarivorous flies with moderate to long mouth parts (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). However, work by Picker and Midgley (1996), Steiner (1998), and our own

←

Figure 7. Dorsal and/or lateral views of hopliine beetles. —A. *Peritrichia subsquamosa.* —B. *Lepisia rupicola.* —C. *Pachycnema crassipes.* —D. *Lepisia* sp. (Nieuwoudtville). Scale bar = 5 mm. (Drawn by Y. Wilson-Ramsey.)

Table 3. Pollen load analysis of collected beetles.

Plant and beetle taxon	Number of beetles carrying pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
IRIDACEAE				
Aristea				
biflora				
Anisonyx lepidotus	1	2	0	0
cantharophila				
Anisonyx ursus	0	3	0	0
Peritrichia pseudoplebeia	0	9	0	1
lugens				
Anisonyx longipes	1	9	0	0
A. ursus	1	9	0	0
Lepithrix ornatella	2	1	0	0
teretifolia				
Petririchia pseudoplebeia	1	2	0	0
Babiana				
rubrocyanea				
Pachycnema crassipes	0	1	0	3
Gladiolus				
meliusculus				
Lepisia rupicola	2	4	0	1
Pachycnema crassipes	0	6	0	0
hirsutus				
Anisonyx ursus	0	1	0	1
Hesperantha				
falcata				
Peritrichia pseudoplebeia	1	0	0	0
vaginata				
Lepisia sp. 1	7	5	0	0
Homeria				
elegans				
Peritrichia pseudoplebeia	6	0	0	1
ochroleuca				
Anisonyx ursus	2	0	0	0
vallisbelli				
Anisochelus inornatus	3	5	0	1
Ixia				
curta				
Lepisia rupicola	0	3	0	0
Lepithrix fulvipes	0	5	0	0
Pachycnema crassipes	0	1	0	0
dubia				
Heterochelus arthriticus	3	2	0	0
Lepithrix ornatella	0	1	0	0
Pachycnema crassipes	0	2	0	0
framesii				
Lepithrix ornatella	0	5	0	1
maculata				
Heterochelis sexlineatus	0	2	0	0
Lepithrix longitarsis	2	2	0	0
L. ornatella	0	5	0	0
Pachycnema crassipes	0	2	0	0
Scelophysa ornatella	0	1	0	0
monadelpha				
Lepithrix fulvipes	0	1	0	0
polystachya				
Peritrichia subsquamosus	0	3	0	0
Moraea				
bellendenii				
Heterochelus unguiculatus	1	3	0	1
insolens				
Anisonyx lepidotus	1	1	0	0
aff. *lurida*				
A. ursus	3	4	2	1
Peritrichia pseudoplebia	0	6	0	0
villosa				
Anisonyx longipes	1	6	0	0
A. ursus	0	3	1	0
Romulea				
eximia				
Lepisia rupicola	0	4	0	0
Pachycnema crassipes	0	4	0	0
monadelpha				
Lepisia sp. 1	6	8	0	3
sabulosa				
Anisochelus inornatus	3	3	0	0
Lepithrix stigma	0	5	1	0
subfistulosa				
Lepisia sp. 2	0	7	0	0
Sparaxis				
elegans				
Lepisia sp. 1	1	5	0	0
Anisochelus inornatus	0	5	1	0
grandiflora				
Peritrichia rufotibialis	0	2	0	0
Anisochelus inornatus	2	4	0	0
Peritrichia sp. 1	0	2	0	0
pillansii				
Lepisia sp. 1	1	7	1	1
Thereianthus				
racemosus				
Khoina bilateralis	2	1	0	1
Tritonia				
deusta				
Peritrichia hybrida	3	0	0	0
hyalina				
Pachycnema tibialis	0	6	0	0
squalida				
Peritrichia sp. 2	7	2	0	0

Table 3. Continued.

Plant and beetle taxon	Number of beetles carrying pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
HYACINTHACEAE				
Ornithogalum				
dubia				
Peritrichia subsquamosus	1	2	0	0
thyrsoides				
Lepithrix fulvipes	1	0	0	0
L. longitarsis	0	2	0	0
P. crassipes	0	1	0	0
Daubenya				
aurea				
Lepisia sp. 2	0	3	0	0
DROSERACEAE				
Drosera				
cistiflora				
Anisonyx ursus	3	1	0	0
pauciflora				
Anisonyx lepidotus	1	2	0	0
CAMPANULACEAE				
Prismatocarpus				
pedunculatus				
Pachycnema saga	0	3	0	0
Peritrichia subsquamosus	3	1	1	0
Wahlenbergia				
capensis				
Lepisia sp.	3	0	1	0
Total	75	195	8	16

Table 4. Pollen load analysis of insects collected on the same species as beetles. Taxonomic affiliations are as follows: Diptera: *Philoliche* (Tabanidae); *Orthellia* (Muscidae); *Scathophaga* (Sarcophagidae). Hymenoptera–Apoidea: *Andrena* (Andrenidae); *Apis* (Apidae); *Patellapis* (Halictidae).

Plant and insect taxon	Number of insects carrying pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
Gladiolus				
meliusculus				
Andrena sp.	0	2	0	0
Homeria				
elegans				
Apis mellifera	2	0	0	0
Orthellia sp.	0	2	0	1
Scathophaga stercoraria	0	0	0	3
ochroleuca				
Anthomyia	0	0	0	1
Apis mellifera	3	1	0	0
Calliphoridae	0	0	1	0
Orthellia sp.	5	0	0	0
Musca sp.	0	2	0	1
Scathophaga stercoraria	0	2	0	3
Syrphidae	0	1	0	0
Ixia				
framesii				
Philoliche atricornis	3	3	0	0
Moraea				
aff. *lurida*				
?*Musca* sp.	1	0	0	0
Romulea				
subfistulosa				
Patellapis sp.	0	2	0	0
Sparaxis				
elegans				
Philoliche atricornis	0	6	0	0
grandiflora				
Philoliche atricornis	0	3	0	0
Patellapis sp.	0	3	0	0
pillansii				
Philoliche atricornis	0	2	0	0
Total	14	29	1	9

research indicates that beetle pollination must now be accepted as being widespread in the southern African flora. This is especially marked in Iridaceae, which have undergone their greatest adaptive radiation and speciation in western southern Africa, where flower-visiting Hopliini show their greatest diversity.

Modification of the irid flower for pollination primarily by monkey beetles has occurred in several genera with diverse floral morphology. In most, the shift seems to be relatively minor, based more on morphological reduction than enlargement. This applies particularly to genera in which an actinomorphic, bowl-shaped flower is ancestral, including *Hesperantha, Homeria, Ixia, Moraea,* and *Romulea.* In a few genera with primitively zygomorphic flowers, change in symmetry has been necessary; for example, in *Sparaxis* and *Tritonia* the adaptive shift has been more pronounced. The Iridaceae pollinated by monkey beetles are more likely to have prominent, dark nectar guides and produce less nectar than the African Iridaceae pollinated by long-tongued bees, flies, or other insects (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). In Iridaceae subfam. Ixioideae, which is characterized by the presence of a perianth tube, the tube is also reduced in some way in monkey beetle pollinated species, either in length or diameter, resulting in a role change from nectar reservoir to pseudopedicel. Flowers pollinated by long-tongued flies in southern Africa also typically lack a discernible scent, e.g., *Gladiolus*, *Lapeirousia*, *Nivenia* (Goldblatt, 1993; Goldblatt & Manning, 1998; Manning & Goldblatt, 1995, 1996, 1997). The main features that distinguish species of Iridaceae as having beetle-pollinated flowers appear to be the distinctive beetle-like marks often combined with particularly bright flower colors, which have evolved convergently in many other families; a reduction in the amount of nectar produced; and floral actinomorphy. Salver- to shallow bowl-shaped perianths are also a frequent aspect of this syndrome.

Adaptive radiation in response to monkey-beetle pollination is evident in some lineages within several genera of the Iridaceae, most conspicuously in *Ixia* sect. *Ixia.* Nearly all members of that section have spreading tepals, contrasting central marks, a filiform perianth tube, and lack nectar. The tube is blocked by the style and the mouth is closed off by the central filaments that are either coherent or united. Some 20 species are currently included in section *Ixia*, out of a total of 50 species in the genus (Lewis, 1962; de Vos, 1988). Most other species of the genus have campanulate or cylindric perianth tubes that contain nectar in the lower part, which is accessible to nectar-foraging insects (Lewis, 1962; Manning & Goldblatt, 1997, and unpublished data), but at least *I. framesii* (sect. *Morphixia*) is also visited by monkey beetles. In *Sparaxis* and *Tritonia*, floral zygomorphy is most likely ancestral (based on outgroup comparison, Goldblatt & Manning, unpublished), but zygomorphic flowers or at least zygomorphic perianths characterize species pollinated by monkey beetles or a combination of these beetles and *Philoliche atricornis.* In these species, the perianth tube is also filiform and blocked by the style and appears to function only as a stalk for the flower. The actinomorphic, beetle-pollinated flowers of these species appear to be derived in both genera, an unexpected phenomenon.

Pollination in *Moraea* is, as far as recorded, predominantly by bees (Goldblatt et al., 1989), but pollination by monkey beetles has been documented by Steiner (1998) within subgenus *Vieusseuxia*, notably *M. villosa.* Several allied species, loosely called peacock moraeas (for their prominent dark tepal markings often with a central pale eye), also have flowers that do not produce nectar, and in addition often have a sterile flap of tissue at the base of the large outer tepal, the limb of which is broad and outspread. This lineage includes some eight species, of which at least *M. gigandra* L. Bolus, *M. neopavonia* R. Foster, *M. tulbaghensis* L. Bolus, and *M. villosa* have flowers adapted for monkey-beetle pollination. Our observations on *M. villosa* mirror Steiner's conclusions. Other species of this apparently monophyletic group include *M. amissa* Goldblatt, *M. calcicola* Goldblatt, and *M. loubseri* Goldblatt, also likely, on the basis of their floral pigmentation, to be pollinated by beetles. Our own observations show that monkey-beetle pollination in *Moraea* is not confined to this group of species. At least *M. bellendenii*, *M. insolens*, and the new taxon here allied to *M. lurida* also appear to be adapted for monkey-beetle pollination, and according to Scott Elliot (1891), so does *M. tricuspidata* (L. f.) G. J. Lewis. *Moraea lurida* itself has flowers with livid red tepals, sometimes marked with yellow, a fetid odor, and which produce nectar on the tepal claws. The flowers in our study population were whitish with small yellow nectar guides, dark style branches, and produced neither noticeable odor nor nectar. In other respects, the plants appear similar to *M. lurida.*

In *Aristea*, four of the seven species of section *Pseudaristea* currently recognized have flowers adapted in different ways for monkey-beetle pollination. The ancestral condition in the genus is pollination by pollen-collecting female bees (Goldblatt & Manning, 1997), and the species of all other sections have dark blue tepals, small yellow anthers, and yellow pollen, including as well *A. pauciflora* Wolley-Dod of section *Pseudaristea.* Four species of section *Pseudaristea* have whitish, pale blue, or lilac tepals with contrasting markings and elongate anthers with orange pollen, and beetle pollination has now been recorded for all of them (Table 3). Even at sites where beetles were not observed foraging on *Aristea* flowers, pollen washes have shown ample quantities of distinctive *Aristea* pollen, indicating visits to species. For example, the beetle *Anisonyx lepidotus*, collected on *Moraea insolens*, showed the presence of pollen of coblooming *A. biflora*, which grew nearby.

The situation in *Romulea* also suggests that radiation and speciation based on monkey-beetle pollination are fundamental to the genus. Most of the approximately 80 species of *Romulea* in the southern African winter-rainfall zone have bowl-shaped flowers and a perianth tube with a filiform base, and many have beetle-like marks (de Vos, 1972). Pollinators of these species are either monkey beetles exclusively, or a combination of beetles and pollen-collecting bees (Apidae, Halictidae), or in some instances (e.g., *R. flava*, the flowers of which lack markings) possibly only bees (Goldblatt et al., unpublished data).

The floristic diversity of the Cape Floristic Region is greater than that of such Mediterranean regions as the California Floristic Province, Central Chile, and southwestern Australia (Goldblatt, 1997). One reason for this diversity may be that beetle pollinators have acted, and may continue to act, as unusually powerful mechanisms of natural selection as plant populations become isolated due to dispersal and/or vicariance.

Why do monkey beetles, in particular, appear to play such an important role in the radiation of the flora, since they lack the long, specialized mouth parts and rapid flying speeds of large, long-tongued flies and bees (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995)? The answer may be that monkey beetles, for all their apparent limitations, are opportunistic foragers that contact flower stigmas, just like nemestrinid flies and anthophorid bees. Our collections suggest that the majority of beetle-pollinated geophytes may depend on only one or two beetle species to effect pollination. However, no beetle species appears dependent on the flowers of any single geophyte species as a food source or mating site. This is reflected further by the fact that the overwhelming majority of beetles carry mixed loads of pollen. Consequently, while monkey beetles probably find levels of floral diversity adequate, we suggest that the geophytic flora finds the density of beetle pollinators less so. This presumably results in competition between geophytic species for the limited pollinator resource, e.g., fruit set in many species of the Cape Flora is known to be pollinator-limited (Johnson & Bond, 1997). Speciation in the geophytic members of the Cape Flora may thus be driven, in part, by this competition.

Floral morphology in the monkey-beetle pollinated species of the Cape Flora seems conservative, while scent and nectar production are negligible. These floral trends become comprehensible in the light of beetle morphology and behavior. Monkey beetles lack both manipulative forelegs and elongated glossae; they do not appear to respond to floral odors, but require a flat surface to mate. Some flower scarabs may have color vision equal to, or much broader than, for example, that of bumblebees (Dafni et al., 1990). Consequently, the convergent evolution of the guild of monkey-beetle-pollinated flowers in southern Africa emphasizes flattened, radial symmetry combined with complex patterns of pigmentation and perianth colors often contrasting with colors of the anthers and/or pollen.

The pollination of flowers by monkey beetles in southern Africa appears to have shaped the flora in two ways. First, it is another factor that may help explain the unusually brilliant and broad range of floral colors and contrasting patterns in the Cape Flora in general. Second, competition for monkey beetles as pollinators has very likely encouraged both adaptive radiation and convergent floral evolution within several plant families, in particular the Iridaceae.

Literature Cited

Armstrong, 1979. Biotic pollination mechanisms in the Australian flora—A review. New Zealand J. Bot. 17: 467–508.

Beach, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Amer. J. Bot. 72: 346–356.

Bernhardt, P. 1989. The floral ecology of Australian *Acacia*. Pp. 127–135 *in* C. H. Stirton & J. L. Zarucchi (editors), Advances in Legume Biology. Monogr. Syst. Bot. Missouri Bot. Gard. 29.

———. 1993. Natural Affairs: A Botanist Looks at Attachments Between Plants and People. Villard Press, New York.

———. 1996. Anther adaptation in animal pollination. Pp. 192–220 *in* W. G. D'Arcy & R. C. Keating (editors), The Anther: Form, Function, and Phylogeny. Cambridge Univ. Press, Cambridge, England.

———. & L. Thien. 1987. Self-isolation and insect pollination in the primitive angiosperms: New evaluations of older hypotheses. Pl. Syst. Evol. 156: 159–176.

Dafni, A., P. Bernhardt, A. Schmida, Y. Ivri, S. Greenbaum, C. O'Toole & L. Losito. 1990. Red bowl-shaped flowers: Convergence for beetle pollination in the Mediterranean region. Israel J. Bot. 39: 81–92.

Faegri, K. & L. van der Pijl. 1979. The Principles of Pollination Ecology, Ed. 3. Pergamon Press, New York.

Goldblatt, P. 1993. The Woody Iridaceae. Timber Press, Portland, Oregon.

———. 1997. Floristic diversity in the Cape Flora of South Africa. Biodiversity & Conservation 6: 359–377.

——— & P. Bernhardt. 1990. Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. Israel J. Bot. 39: 93–111.

——— & J. C. Manning. 1996. Aristeas and beetle pollination. Veld & Flora 82: 17–19.

——— & ———. 1997. New species of *Aristea* (Iridaceae) from South Africa and notes on the taxonomy and pollination biology of section *Pseudaristea*. Novon 7: 137–144.

——— & ———. 1998. *Gladiolus* in Southern Africa. Fernwood Press, Cape Town.

———, P. Bernhardt & J. C. Manning. 1989. Notes on the pollination mechanisms of *Moraea inclinata* and *M. brevistyla* (Iridaceae). Pl. Syst. Evol. 163: 201–209.

———, J. C. Manning & P. Bernhardt. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa: Floral divergence and adaptation for long-tongued fly pollination. Ann. Missouri Bot. Gard. 82: 517–534.

Gottsberger, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. Pl. Syst. Evol., Suppl. 1: 211–226.

———. 1989a. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae). Pl. Syst. Evol. 167: 165–187.

———. 1989b. Comments on flower evolution and beetle pollination in the genera *Annona* and *Rollinia* (Annonaceae). Pl. Syst. Evol. 167: 189–194.

——— & A. Amaral. 1984. Pollination strategies in Brazilian *Philodendron*. Ber. Deutsch. Bot. Ges. 97: 391–410.

Hawkeswood, T. J. 1987. Pollination of *Leptospermum flavescens* SM. (Myrtaceae) by beetles (Coleoptera) in the Blue Mountains, New South Wales, Australia. Giorn. Ital. Entomol. 3: 261–269.

———. 1989. Notes on *Diphucephala affinis* (Coleoptera, Scarabaeidae) associated with flowers of *Hibbertia* and *Acacia* in Western Australia. Pl. Syst. Evol. 168: 1–5.

Johnson, S. J. & W. Bond. 1997. Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. Oecologia 109: 530–534.

Knuth, P. 1909. Handbook of Flower Pollination. Clarendon Press, Oxford.

Lewis, G. J. 1962. South African Iridaceae. The genus *Ixia*. J. S. African Bot. 28: 45–195.

Manning, J. C. & P. Goldblatt. 1995. Cupid comes in many guises: The not-so-humble fly and a pollination guild in the Overberg. Veld & Flora 81: 50–52.

——— & ———. 1996. The *Prosoeca peringueyi* (Diptera: Nemestrinidae) pollination syndrome in southern Africa: Long-tongued flies and their tubular flowers. Ann. Missouri Bot. Gard. 83: 67–86.

——— & ———. 1997. The *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) pollination guild: Long-tubed flowers and a specialized long-tongued fly-pollination system in southern Africa. Pl. Syst. Evol. 206: 51–69.

Ogden, E. C., G. S. Raynor, J. V. Hayers & D. M. Lewis. 1974. Manual of Sampling Airborne Pollen. Hafner Press, London.

Peringuey, L. 1902. Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae). Trans. S. African Phil. Soc. 12: 1–920.

Picker, M. D. & J. J. Midgley. 1996. Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliinae): Flower and colour preferences. African Entomol. 4: 7–14.

Prance, G. & J. R. Arias. 1975. A study of the floral biology of *Victoria amazonica* (Poepp.) Sowerby (Nymphaeaceae). Acta Amazonica 5: 109–139.

Scott Elliot, G. 1891. Notes on the fertilisation of South African and Madagascan flowering plants. Ann. Bot. 5: 333–405.

Schneider, E. L. & J. D. Buchanan. 1980. Morphological studies of the Nymphaeaceae. XI. The floral biology of *Nelumbo pentapetala*. Amer. J. Bot. 67: 182–193.

Steiner, K. E. 1998. Beetle pollination of peacock moraeas in South Africa. Pl. Syst. Evol. 209: 47–65.

Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. Bot. Stud. 1: 1–338.

Vos, M. P. de. 1972. The genus *Romulea* in South Africa. J. S. African Bot., Suppl. 9.

———. 1988. Three new species of *Ixia* L. (Iridaceae) from the Cape Province. S. African J. Bot. 54: 596–602.

Whitehead, V. B., J. H. Giliomee & A. G. Rebelo. 1987. Insect pollination in the Cape Flora. Pp. 52–82 *in* A. G. Rebelo (editor), A Preliminary Synthesis of Pollination Biology in the Cape Flora. CSIR, Pretoria.

POLLINATION ECOLOGY AND MAINTENANCE OF SPECIES INTEGRITY IN CO-OCCURRING *DISA RACEMOSA* L.f. AND *DISA VENOSA* SW. (ORCHIDACEAE) IN SOUTH AFRICA[1]

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Abstract

The orchid *Disa racemosa* was found to be pollinated by xylocopine and anthophorine bees (*Xylocopa* and *Amegilla* spp.) at several sites in the Cape Floral Region of South Africa. A precise floral mechanism ensures that pollinaria are always attached to the middle pair of legs on the pollinator. Flowers of *D. racemosa* are nonrewarding, but nevertheless attract bees searching for new food sources. Levels of pollination and fruiting success were low, varying from 4 to 48% among the eight study populations. *Disa racemosa* is often sympatric and co-flowering with its very similar, though much rarer, sister species *Disa venosa*. The only character that is consistently different between the taxa is the width of the sepals. Although the two species appear to have the same pollinators, natural hybrids between them have never been found. The results of experimental crosses indicated that a sterility barrier, rather than ethological or mechanical barriers, is responsible for the maintenance of species integrity in mixed populations.

Coexistence of closely related species is possible only if there are effective barriers to hybridization (Levin, 1978). The orchid family is renowned for the apparent ease with which thousands of artificial hybrids have been created by hobbyists (Dressler, 1981). Yet, closely related orchids often occur in sympatry without hybridizing, and an intriguing question is how these species manage to coexist when genetic barriers to hybridization appear to be weakly developed in the family.

It is generally thought that specialized pollinator relationships and elaborate floral mechanisms in orchids prevent, or at least minimize, export of pollen to stigmas of other sympatric species (van der Pijl & Dodson, 1966; Dressler, 1981). Several studies have reported divergent pollination systems in sympatric orchid species that seldom form natural hybrids (Stoutamire, 1974; Smith & Snow, 1976; Chase, 1986; Manning & Linder, 1992; Steiner et al., 1994; Bower, 1996). Isolation of many of these species seems to be based on ethological or mechanical barriers only, since they can be crossed easily by artificial means. However, there is some evidence that sympatric orchid species that share pollinators may occasionally possess sterility barriers, as in the case of the sympatric *Cryptostylis* species studied by Stoutamire (1975).

In this study we focus on a pair of closely related species—*Disa racemosa* L.f. and *Disa venosa* Sw.—which often occur sympatrically in the Cape mountains of South Africa. Most authorities have recognized the two species as being distinct, although Schlechter (1901) reduced *D. venosa* to a variety of *D. racemosa*, a treatment that has not been adopted by any subsequent authors (Linder, 1981).

Disa racemosa is one of the more common orchids in the Cape floral region, growing in marshes and seepage areas. Flowering in *D. racemosa* is strongly stimulated by fire. Hence, populations flower only at intervals of 5–30 years, which corresponds to the frequency of fires in the Cape fynbos vegetation. Flowering occurs during November and December. The inflorescence of *D. racemosa* bears from 1 to 15 pink-magenta flowers, which are

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Ann. Missouri Bot. Gard. 85: 231–241. 1998.

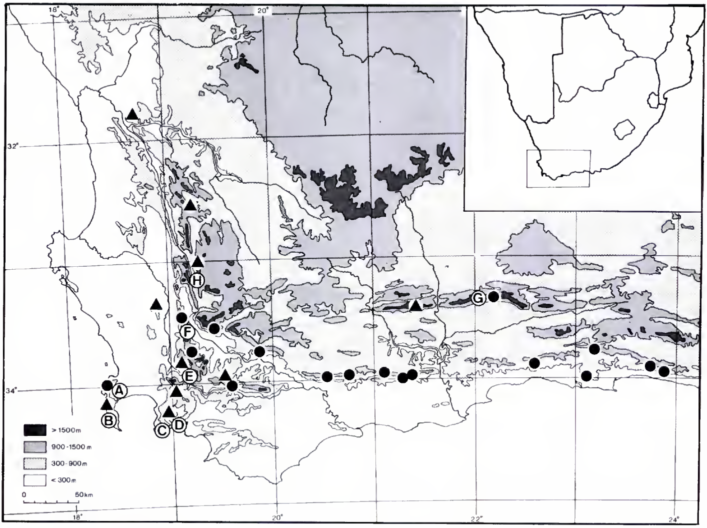

Figure 1. The distribution of *Disa racemosa* (circles) and *D. venosa* (triangles) in the Cape floristic region. The localities of the study sites are indicated by capital letters in open circles. A = Silvermine Nature Reserve, B = Cape Point Nature Reserve, C = Betty's Bay, D = Ysterklip, E = Franschhoek, F = Bains Kloof, G = Swartberg Pass, H = Gydo Pass. Populations of *D. racemosa* occur at all of the study sites, and *D. venosa* is sympatric with *D. racemosa* at sites F and G.

about 40–60 mm in diameter. The flowers do not produce nectar or any other floral reward. Most *Disa* species have a spur formed from the dorsal sepal. However, the spur in *D. racemosa* (and also *D. venosa*) is virtually obsolete, consisting of a mere shallow depression at the back of the dorsal sepal.

Disa venosa is remarkably similar to *D. racemosa*; the only character that consistently separates the two species is the much narrower dorsal and lateral sepals of *D. venosa* (see below). The two species have overlapping distribution ranges and are sometimes found flowering side by side in the same marshes after fire. However, *D. venosa* is much less common than *D. racemosa* and is not as often seen or collected.

Our interest in *Disa racemosa* and *D. venosa* was generated by the observation that the two species are very similar morphologically, yet appear never to hybridize, despite sharing the same habitat and flowering time. As in many other South African orchids, no previous investigation of pollination biology in the species had been undertaken.

This study had the following aims: (1) to confirm whether or not the taxa are readily diagnosable as separate species in the field; (2) to characterize the pollination biology of each species; (3) to determine the levels of pollination and fruiting success in natural populations; (4) to establish the mechanisms that allow coexistence between the species.

MATERIALS AND METHODS

FLORAL CHARACTERISTICS

Floral parts were measured to the nearest 0.5 mm in populations of *Disa racemosa* at Franschhoek and *D. venosa* at the Bains Kloof site during 1993 (see Fig. 1 for localities of study sites). Further measurements were also made of dried specimens in local herbaria (BOL and NBG).

The flowers of *Disa racemosa* and *D. venosa* appear to have a very similar color in the field. To obtain objective measures of floral coloration in the visible spectrum (400–700 nm), we measured the reflectance of sepals of each species with an ACS

550m spectrophotometer. Bee vision is known to extend to wavelengths shorter than 400 nm, but no spectrophotometer capable of measuring ultraviolet reflectance was available. Instead, we took photographs on Tri-X film with and without a Corning 7–60 "black" filter, which only transmits ultraviolet light. The gray scale described in Kevan et al. (1973) was used to standardize exposure of prints. The photographic method has the advantage of being able to reveal floral patterns in the ultraviolet wavelengths, unlike the spectrophotometer, which takes average measurements of reflectance.

POLLINATOR OBSERVATIONS

Observations of pollinator visits to the flowers of *Disa racemosa* were made between 1990 and 1995 at eight sites in the Cape Floral Region (Fig. 1). Populations at these sites varied from ca. 100 plants at Betty's Bay to several thousand plants at Franschhoek. Small populations (ca. 20 plants) of *D. venosa* were found to co-occur with *D. racemosa* at the Bains Kloof and Swartberg sites (Fig. 1). At all of the study sites, the vegetation had been burnt during the previous season, thus triggering a flowering display of the orchids.

Pollinators (defined as insects that remove and deposit pollinaria of the orchids) were captured either directly on the orchids or else while foraging on nearby food plants. A herbarium voucher from the Bains Kloof population (*Steiner 2274*) is deposited in NBG, while the other populations are represented by existing collections in NBG and BOL. Insect vouchers are deposited in the South African Museum, Cape Town.

POLLINATION SUCCESS

Pollination success was measured in most of the populations of *Disa racemosa* by determining the frequency of pollinarium removal and pollen deposition on the stigmas of randomly selected samples of flowers between 1990 and 1995. We also recorded fruiting success where possible.

CROSSING EXPERIMENTS

Since our initial observations indicated that *Disa racemosa* and *D. venosa* may have the same pollinators, we made reciprocal crosses between the two species to determine if they are capable of hybridization. Crosses were performed between *D. racemosa* at the Franschhoek site and *D. venosa* at the Bains Kloof site. Although the two species occur sympatrically at the Bains Kloof site, no plants of *D. racemosa* flowered there in 1994, making it necessary to use plants from another site.

At each site, we covered inflorescences with pollinator-exclusion bags while flowers were still in bud. Following anthesis, flowers were randomly assigned to one of the following treatments: (1) unmanipulated to test for autogamy, (2) hand-pollinated with pollinaria from conspecific plants, and (3) hand-pollinated with pollinaria from the sister species. To make the latter crosses, we transported freshly cut inflorescences between the sites, a distance of ca. 30 km, and withdrew pollinaria from the anthers immediately before the hand-pollinations. This method ensured that all pollinaria used in the experiment were in optimal condition. All the crosses were made on 29 November 1994, and the fruits were harvested on 31 December 1994 before dehiscence had taken place.

To test seed viability, we used standard tissue culture procedures that have been found to work well for germinating seeds of *Disa* species. Before opening each fruit, we sterilized the outside with 10% sodium hypochlorite to minimize the chances of fungal and bacterial infection. The fruits were then opened in a laminar flow cabinet and the seeds from each fruit placed in separate 50-ml tissue culture flasks containing a sterile agar-based nutrient medium. The medium consisted of ¼-strength MS solution (George & Sherrington, 1984) fortified with 20g banana per litre and 2g peptone per litre. The flasks were placed in a dark cabinet for three months, followed by a 12 hr light/12 hr dark cycle at 20–25°C. Germination and development of protocorms were noted in some flasks 3–5 months after the commencement of the experiment. Seeds that had not germinated after 12 months were considered to be unviable.

RESULTS

MORPHOLOGY

Disa racemosa and *D. venosa* can be distinguished by the narrower sepals of *D. venosa*. Analysis of existing herbarium specimens of the two taxa showed a bimodal distribution of the dorsal sepal width/length ratio (Fig. 2). More detailed measurements of floral dimensions in populations of *D. racemosa* and *D. venosa* confirmed that the absolute width of the sepals differs markedly between the species (Table 1). The flowers of *D. venosa* at Bains Kloof were slightly smaller than those of *D. racemosa* at Franschhoek, resulting in statistically significant differences in the means of several characters (Table 1). However, sepal width was the only character that showed no overlap in the range of measurements from individuals of the two species (Table 1).

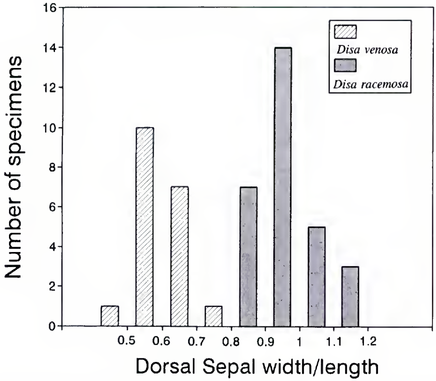

Figure 2. Frequency distribution of dorsal sepal width/length in a sample of herbarium specimens of *Disa racemosa* and *D. venosa*. Dorsal sepal width/length is the main diagnostic character separating the two species.

SPECTRAL REFLECTANCE

The reflectance spectra of flowers of *Disa racemosa* and *D. venosa* are remarkably similar, supporting the impressions gained in the field. The magenta-pink color results from strong reflectance of blue and red wavelengths (Fig. 3). The magenta-pink coloration is due to anthocyanin pigments in *D. racemosa* and *D. venosa* (Vogelpoel et al., 1985) and is a common color among bee-pollinated flowers in the Cape and elsewhere (e.g., Thien & Marks, 1972; Nilsson, 1983).

Photographs of the flowers with ultraviolet light showed that the petals, labellum, and rostellum in both species are UV-absorptive, forming a contrast with the relatively UV-reflective sepals (Fig. 4C, D).

POLLINATOR OBSERVATIONS

Our observations indicated that *Disa racemosa* and *D. venosa* are both pollinated by medium-sized anthophorid bees and large xylocopine bees. Carpenter bees (*Xylocopa rufitarsus* Lepeletier and *X. caffra* L.) were observed to visit *D. racemosa* at five of the sites (Silvermine, Theewaterskloof, Betty's Bay, Bains Kloof, and Swartberg Pass). Smaller anthophorid bees (*Amegilla niveata* and *Amegilla spilostoma*) visited *D. racemosa* at the Swartberg and

Table 1. Measurements of floral characters in *Disa racemosa* (Franschhoek population) and *D. venosa* (Bains Kloof). All units are millimeters. NS. = not significant.

Character	*Disa racemosa* (n = 10 plants) x ± S.D. (range)	*Disa venosa* (n = 8 plants) x ± S.D. (range)	t	P
Dorsal sepal length	20.4 ± 1.9 (17–24)	19.4 ± 1.4 (18–22)	1.35	NS.
Dorsal sepal width	19.7 ± 1.8 (15–21)	9.3 ± 0.7 (9–10)	17.39	***
Lateral sepal length	22.1 ± 2.2 (18–26)	20.0 ± 1.0 (19–21)	2.70	*
Lateral sepal width	14.2 ± 2.3 (10–18)	9.0 ± 0.0 (8–10)	6.65	***
Lip length	11.8 ± 1.4 (10–14)	9.5 ± 0.7 (8–10)	4.54	***
Petal length	12.1 ± 1.5 (10–15)	10.3 ± 0.7 (9–11)	3.69	**
Distance between viscidia	4.4 ± 0.4 (4.5–5)	4.3 ± 0.4 (4–5)	0.73	NS.
Distance from rostellum to top of stigma	8.8 ± 0.8 (7–10)	8.1 ± 0.6 (7–9)	2.24	NS.
Length of pollinaria	10.0 ± 0.0	10.0 ± 0.0	0.00	NS.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

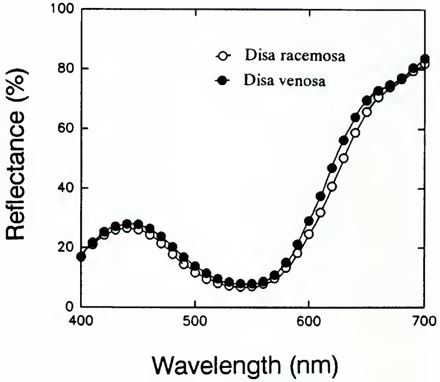

Figure 3. Reflectance spectra for *Disa racemosa* and *D. venosa.*

Bains Kloof sites. All of these bees except *X. caffra* (which may be too large to act as a pollinator) carried pollinaria attached to their middle legs. The rarity of *D. venosa* made it difficult to observe pollination in this species. A single carpenter bee (probably *X. rufitarsus*) was seen to visit flowers of *D. venosa* and *D. racemosa* in succession at the Swartberg Pass site. The behavior of the bee was identical on flowers of *D. venosa* and *D. racemosa.*

Since the orchids in this study have no floral rewards, the bees obviously need to rely on other plants in the community for pollen and nectar requirements. The observation that most floral visitors to *D. racemosa* are female bees (Table 2) suggests that the orchid primarily exploits pollen-seeking insects. Pollen-rewarding flowers that occurred at the same sites as *D. racemosa* included pink-flowered *Chironia jasminoides* L. (Gentianaceae) and *Drosera regia* Stephens (Droseraceae). Flowers of *C. jasminoides* are buzz-pollinated by female *Xylocopa* bees (S. Johnson; unpublished). At Swartberg, however, the primary food source for the smaller *Amegilla* bees was *Moraea ramosissima* (L.f.) Druce (Iridaceae), a nectar-producing species with yellow flowers.

FUNCTIONAL MORPHOLOGY

Pollinaria of *Disa racemosa* were consistently attached to the middle pair of legs on the bees, implying a precise interaction between the morphology of the bees and the flower. Unlike other *Disa* species, where the dorsal sepal forms a galeate chamber, and a spur in some species, the dorsal sepal of *D. racemosa* is almost flattened and apparently serves no function other than visual attraction. The flowers of *D. racemosa* and *D. venosa* differ from those of most other *Disa* species in having a floral chamber formed by the petals, rather than the dorsal sepal.

When alighting on a flower of *Disa racemosa,* bees grasp the petals and insert their heads forcibly into the floral chamber (Fig. 5A, B). The bees are presumably attracted to this part of the flower by the contrast between the strongly UV-absorptive petals and the relatively UV-reflective sepals (Fig. 4). In addition, the inner surface of the petals has an alternating pattern of dark and light stripes that may function as "nectar guides." While settled on the flower, the bees clasp the petals with their front legs, while the middle legs rest across the rostellum and the back legs are placed on the lateral sepals. Pollinaria become attached to the basal segment of the middle legs by means of a large sticky viscidium. It was interesting that pollinaria were always attached to the middle legs, regardless of the great variation in bee size. There appears to be space for just one pollinarium on the first segment of each middle leg, as none of the captured bees carried more than two pollinaria (one per leg), despite being observed to visit several flowers in a sequence. After withdrawal from the anther, the pollinaria are positioned so that the tip is correctly angled to strike the stigma, which is tucked underneath the projecting rostellum. The sectile pollinaria remain

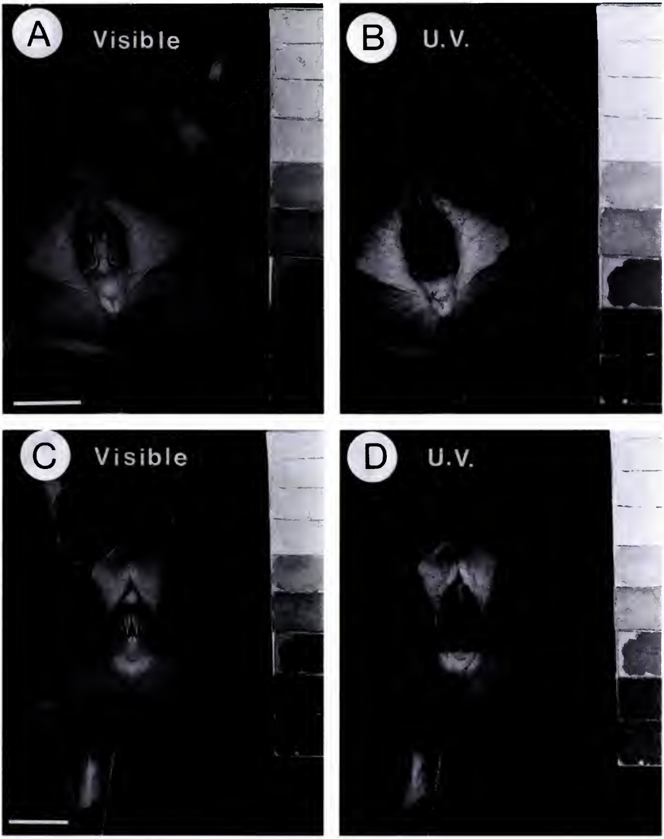

Figure 4. Comparison of reflectance of flowers of *Disa racemosa* and *D. venosa* in both visible and ultraviolet light. The gray scale is used to ensure a comparable range of contrast in each photograph. A, B *Disa racemosa*, C, D *Disa venosa*. Scale bar = 10 mm.

attached to the bees and gradually become worn as massulae are torn away from the tip after each contact with a stigma (Fig. 5D, E).

POLLINATION SUCCESS

Bees were relatively uncommon at most of the sites, except Swartberg Pass where seven bees were caught in two days. The paucity of pollinator visits was reflected in the low levels of pollination and fruiting success, which varied between 4% and 48% (Table 3). The median level of pollination success in seven populations was only 13.6%, while the median level of fruit set in a smaller sample of four populations was 30.3% (Table 3). Since orchid

Table 2. Bee species that visited flowers of *Disa racemosa* at the study sites.

Study site	Observation time (hrs.)	Floral visitors to *D. racemosa*	Sex and pollinarium load	Food plants for the bees (P = pollen source, N = nectar source)
Swartberg	ca. 15	*Xylocopa rufitarsus* Lepeletier	♂(1)	—
		Amegilla niveata (Friese)	♀(2), ♀(2)	*Moraea ramosissima* (N)
		Amegilla spilostoma (Cameron)	♀(0), ♀(2), ♀(1), ♀(1), ♀(2)	*M. ramosissima* (N)
Bains Kloof	ca. 15	*X. rufitarsus*	♀(2), ♂(0)	*Drosera regia* (P) *Chironia jasminoides* (P)
		Xylocopa caffra L.	♀(0)	—
Silvermine	ca. 10	*X. rufitarsus*	♀(2), ♀(0)	—
Franschoek	ca. 10	*X. rufitarsus*	♀(0)	—
Betty's Bay	ca. 5	*X. caffra*	♀(0)	*M. ramosissima* (N)
Gydo Pass	ca. 5	*A. spilostoma*	♀(2)	—

flowers are long-lived (ca. 7–14 days in *D. racemosa*), "snapshot" measures of pollination success may lead to an underestimate of the final levels of fruit set.

HYBRIDIZATION EXPERIMENTS

Flowers that were bagged and left unmanipulated did not form fruits, indicating that both species are incapable of autogamy. Both intra- and interspecific crosses resulted in the formation of well-developed fruits with seeds. While seeds resulting from intraspecific crosses germinated and formed vigorous seedlings after five months, seeds resulting from crosses between *D. racemosa* and *D. venosa* showed no signs of germination after twelve months (Table 4).

DISCUSSION

POLLINATION BY DECEPTION

The observations reported in this study show that *Disa racemosa* is pollinated by xylocopine and anthophorine bees that visit the flowers even though they do not contain a floral reward. The large pink floral display seems to be sufficient to attract bees that enter the general vicinity of the population. These bees are probably sampling potential new food sources and after probing a few empty flowers they usually fly off again. There is no compelling evidence that *D. racemosa* is a mimic of other rewarding species, although the flowers do bear a general resemblance to pink buzz-pollinated flowers, such as *Chironia jasminoides*, which was sympatric with the orchid at two of the sites. The pollination system of *D. racemosa* and *D. venosa* can best be characterized as generalized food-source deception (Ackerman, 1981, 1983; Boyden, 1982; Dafni, 1984; Nilsson, 1992).

The *Disa racemosa–D. venosa* pair have interesting similarities to many of the bumblebee-pollinated northern hemisphere orchids. The most striking similarity is the possession of large pink-magenta flowers (Thien & Marks, 1972; Nilsson, 1980, 1983; Fritz, 1990). A characteristic that appears to be shared by all deceptive orchid species is a very low level of pollination success (Nilsson, 1980; Boyden, 1982; Nilsson, 1983; Ackerman, 1986; Gill, 1989; Fritz, 1990). This may be a consequence of insects learning to avoid the unrewarding flowers (Nilsson, 1992). The low levels of fruit set in *D. racemosa* are clearly due to pollen-limitation, as supplemental hand-pollinations in two populations led to significant increases in fruit set at a whole plant level (Johnson & Bond, 1997). This was most pronounced in the Franschhoek population, where hand-pollination led to an increase in fruit set from 4% of the flowers in control plants to 63% of the flowers in hand-pollinated plants (Johnson & Bond, 1997).

MECHANISMS OF COEXISTENCE IN *DISA*

A plethora of artificial hybrids has been made between the species of *Disa* sect. *Disa,* to which *D. racemosa* and *D. venosa* belong (Vogelpoel, 1992 and references therein; Linder, 1990). *Disa racemosa* has been successfully crossed with several other *Disa* species, including *Disa uniflora* Berg, *D. cardinalis* Linder, *D. atricapilla* (Harv. ex Lindl.) H. Bolus and *D. bivalvata* (L.f.) Durieu & Schinz (Vogelpoel et al., 1985; Wodrich, 1995). *Disa venosa* has been successfully crossed with *D. cardinalis* and *D. tripetaloides* (L.f) N. E. Br. (Vogelpoel, 1992).

Geographical, seasonal, and ethological barriers probably explain why genetically compatible *Disa* species seldom hybridize in nature. *Disa racemosa*

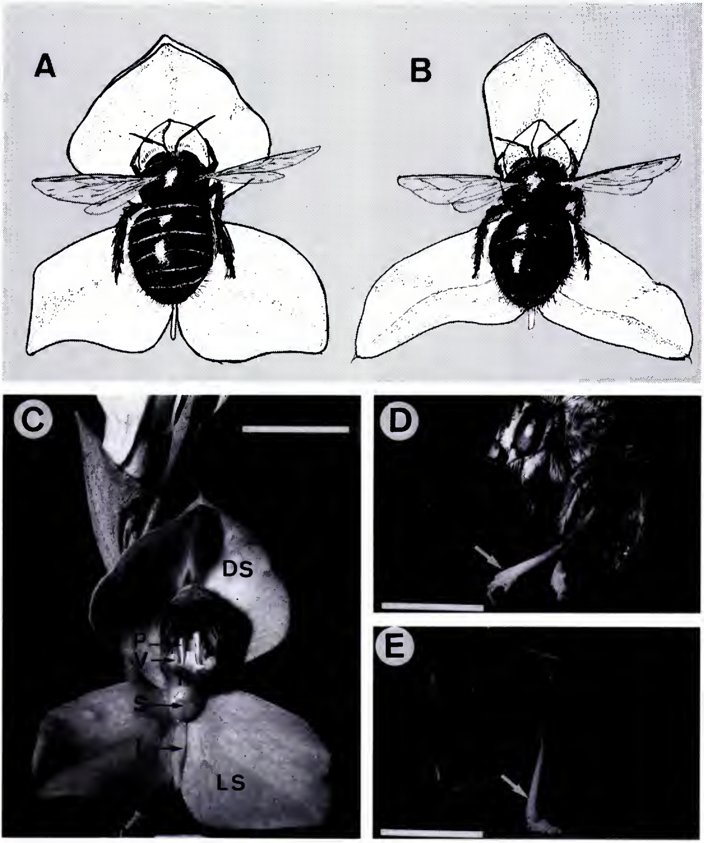

Figure 5.—A. Carpenter bee (*Xylocopa rufitarsus*) settled on a flower of *Disa racemosa.* The front legs are used to grasp the petals, the middle legs are placed over the rostellum, and the back legs are resting on the lateral sepals. The bee's head is inserted into the chamber formed by the petals. —B. Carpenter bee settled on a flower of *D. venosa.* —C. Floral morphology of *D. racemosa.* Abbreviations: DS = dorsal sepal, PT = petal, P = pollinarium, V = viscidium, R = rostellum, S = stigma, L = lip, LS = lateral sepal. Scale = 10 mm. —D. *Amegilla niveata* (Anthophorinae) with two pollinaria of *D. racemosa* attached to its middle legs. Scale = 5 mm. —E. *Xylocopa rufitarsus* (Xylocopinae) with a single attached pollinarium of *D. racemosa.* Scale = 5 mm.

and *D. uniflora,* for example, are highly interfertile, but have different habitats and pollinators; *D. uniflora* is pollinated exclusively by butterflies (Johnson & Bond, 1994), while *D. racemosa* is pollinated by anthophorine and xylocopine bees (this study). A possible natural hybrid between *D. racemosa* and *D. atricapilla* (a wasp-pollinated species, see below) was discovered recently (Wodrich, 1995).

Table 3. Pollination and fruiting success in populations of *Disa racemosa* and *D. venosa*. Median values are given in bold type.

Study site	Date	Number of flowering individuals	Flowers with pollinaria removed % (*n*)	Flowers with pollen on the stigma % (*n*)	Flowers that set fruit % (*n*)
Disa racemosa					
Franschhoek	Dec. 1994	ca. 2000	4.9 (41)	7.3 (41)	4.1 (48)
Bains Kloof	Jan. 1991	ca. 250	—	33.9 (115)	45.3 (589)
Cape Point	Dec. 1991	ca. 100	22.2 (81)	4.9 (81)	—
Silvermine	Nov. 1992	ca. 100	33.8 (59)	10.1 (59)	38.6 (210)
Swartberg	Dec. 1992	ca. 400	63.6 (44)	47.7 (44)	—
Ysterklip	Jan. 1992	ca. 50	—	—	21.9 (160)
Betty's Bay	Dec. 1993	ca. 40	4.8 (42)	9.5 (42)	—
Gydo Pass	Jan. 1995	ca. 150	23.8 (88)	17.0 (88)	—
			23.0	**13.6**	**30.3**
Disa venosa					
Bains Kloof	Nov. 1993	ca. 30	49.1 (57)	19.2 (57)	—

Steiner et al. (1994) showed that the rarity of natural hybrids between *Disa bivalvata* and its sympatric sister species *D. atricapilla* can be attributed to ethological factors. Although these sexually deceptive orchids are interfertile, they are pollinated by different wasp species, thus preventing the formation of hybrids. The formation of occasional hybrids was attributed to beetles that visit the two species indiscriminately.

By contrast, no ethological barriers appear to exist between *Disa racemosa* and *D. venosa*. These species have very similar flowers with closely matched reflectance spectra. They appear to share pollinators and, importantly, their column and pollinarium morphology is identical, thus ruling out the possibility of mechanical barriers to hybridization. In the absence of ethological or mechanical barriers between these species, the only plausible explanation for the lack of natural hybrids is a sterility barrier. This hypothesis was supported by the crossing experiments. Crosses between *D. racemosa* and *D. venosa* resulted in seeds that failed to germinate, while seeds resulting from intraspecific crosses in the same populations germinated readily to form healthy seedlings (Table 4).

There is little other evidence for sterility barriers among closely related orchids. Stoutamire (1975) found that several sympatric *Cryptostylis* species in Australia share the same wasp pollinators without forming natural hybrids. Crossing experiments suggested that a sterility barrier may prevent hybrid formation. Genetic barriers are known to occur among less closely related orchids. Nilsson (1980), for example, showed that natural hybridization between bumblebee-pollinated *Dactylorhiza sambucina* (L.) Soó and co-flowering *Orchis* species is prevented by a sterility barrier. Dressler (1981) pointed out that it is difficult to estimate the extent of sterility barriers in the Orchidaceae, since unsuccessful attempts to hybridize species are seldom reported.

The basis for the apparent sterility barrier between *Disa racemosa* and *D. venosa* is not known. Differences in cytology can be ruled out as the two species share a diploid chromosome number of $2n = 38$ (Pienaar et al., 1989). It is curious that while

Table 4. Results of reciprocal crosses to determine the compatibility of *Disa racemosa* and *D. venosa*. Floral measurements taken in the parent populations are given in Table 1.

Pollen recipient	Pollen donor	Number of crosses	Number of swollen fruits	Number of fruits flasked	Number of flasks with seedlings	Number of seedlings per flask
D. racemosa	*D. venosa*	8	8	5	0	0
D. venosa	*D. racemosa*	6	6	3	0	0
D. racemosa	*D. racemosa*	3	3	3	3	>100
D. venosa	*D. venosa*	7	7	3	2	>100

less closely related *Disa* species hybridize easily, these two sister species should be inter-sterile. Because of the rarity of *D. venosa,* we were not able to replicate the crossing experiments on a large scale, but it would be useful to attempt further crosses to determine if the sterility barrier between the two species is absolute or not. Since crosses between *D. racemosa* and *D. venosa* resulted in apparently normal fruits and seeds with embryos, we assume that the isolating barrier is postzygotic.

DIVERGENCE OF *DISA RACEMOSA* AND *D. VENOSA*

It is difficult to determine if the evolutionary divergence between *Disa racemosa* and *D. venosa* has an ecological basis. The only consistent external difference between the species is the width of the dorsal sepals. There seems to be no difference in the habitat, pollination biology, or flowering time of the two species. This situation is quite unlike that in the rest of the genus *Disa* where speciation has been clearly associated with shifts between pollinators (Johnson et al., 1998). We can only guess at the factors that promoted speciation in the *D. racemosa–D. venosa* pair. The width of the sepals in *D. racemosa* and *D. venosa* does not have any obvious adaptive significance for bee-pollination. Presumably this character diverged through non-adaptive processes, such as genetic drift in small isolated populations, while the overall divergence in the genomes of the two daughter species was profound enough to cause a sterility barrier. We doubt that a sterility barrier between *D. racemosa* and *D. venosa* could have arisen through natural selection, as it is difficult to imagine why a hybrid between species that share near-identical floral morphology and habitat would suffer reduced fitness in terms of pollinator attraction or seedling establishment.

Ultimately, it is difficult to determine with certainty whether a sterility barrier between congeners arose through natural selection (reinforcement), as a single mutation that preceded divergence in sympatric populations, or as a pleiotropic consequence of character divergence in allopatric populations (Grant, 1994). The present-day distribution of closely related species offers few clues about the mode of speciation. For example, although *D. racemosa* and *D. venosa* are often found sympatrically, this does not exclude the possibility that they diverged in allopatry and later expanded their ranges to become sympatric at some sites.

The findings of this paper contradict much of the current dogma about isolating mechanisms in orchids. The *Disa racemosa–D. venosa* pair is one of the few known cases where sterility barriers, rather than divergent pollination systems or floral mechanisms, are responsible for species integrity of sympatric orchid species.

Literature Cited

Ackerman, J. D. 1981. Pollination biology of *Calypso bulbosa* var. *occidentalis* (Orchidaceae): A food deception system. Madroño 28: 101–110.

———. 1983. Euglossine bee pollination of the orchid *Cochleanthes lipscombiae*: A food source mimic. Amer. J. Bot. 70: 830–834.

———. 1986. Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1: 108–113.

Bower, C. C. 1996. Demonstration of pollinator-mediated reproductive isolation in sexually deceptive species of *Chiloglottis* (Orchidaceae: Caladeniinae). Austral. J. Bot. 44: 15–33.

Boyden, T. C. 1982. The pollination biology of *Calypso bulbosa* var. *americana* (Orchidaceae): Initial deception of bumblebee visitors. Oecologia 55: 178–184.

Chase, M. W. 1986. Pollination ecology of two sympatric, synchronously flowering species of *Leochilus* in Costa Rica. Lindleyana 1: 141–147.

Dafni, A. 1984. Mimicry and deception in pollination. Annual Rev. Ecol. Syst. 15: 259–278.

Dressler, R. L. 1981. The Orchids: Natural History and Classification. Harvard Univ. Press, Cambridge, Massachusetts.

Fritz, A. L. 1990. Deceit pollination of *Orchis spitzelii* (Orchidaceae) on the island of Gotland in the Baltic: A suboptimal system. Nordic J. Bot. 9: 577–587.

George, E. F. & P. D. Sherrington. 1984. Plant Propagation by Tissue Culture. Egegetics, Wiltshire.

Gill, D. E. 1989. Fruiting failure, pollinator efficiency and speciation in orchids. Pp. 456–481 *in* D. Otte & J. A. Endler (editors), Speciation and its Consequences. Sinauer, Sunderland, Massachusetts.

Grant, V. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. Proc. Natl. Acad. Sci. U.S.A. 90: 7729–7733.

Johnson, S. D. & W. J. Bond. 1994. Red flowers and butterfly pollination in the fynbos of South Africa. Pp. 137–148 *in* M. Arianoutsou & R. H. Groves (editors), Plant-animal Interaction in Mediterranean Ecosystems. Kluwer Academic Press, Dordrecht.

——— & ———. 1997. Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. Oecologia 109: 530–534.

———, H. P. Linder & K. E. Steiner. 1998. Phylogeny and adaptive radiation of pollination systems in *Disa* (Orchidaceae). Amer. J. Bot. 85: 402–411.

Kevan, P. G., N. D. Grainger, G. A. Mulligan & A. R. Robertson. 1973. A gray-scale for measuring reflectance and color in the insect and human visual spectra. Ecology 54: 924–926.

Levin, D. A. 1978. The origin of isolating mechanisms in flowering plants. Evol. Biol.11: 185–317.

Linder, H. P. 1981. Taxonomic studies on the Disinae III. A revision of *Disa* Berg, excluding sect. *Micranthae.* Contr. Bolus Herb. 9: 1–370.

———. 1990. Hybrids in *Disa* (Diseae–Orchidoideae). Lindleyana 5: 226–230.

Manning, J. C. & H. P. Linder. 1992. Pollinators and evolution in *Disperis*, or why are there so many species. S. African J. Sci. 88: 38–49.

Nilsson, L. A. 1980. The pollination ecology of *Dactylorhiza sambucina* (Orchidaceae). Bot. Not. 133: 367–385.

———. 1983. Anthecology of *Orchis mascula* (Orchidaceae). Nordic J. Bot. 3: 157–179.

———. 1992. Orchid pollination biology. Trends Ecol. Evol. 7: 255–259.

Pienaar, R. V., G. M. Littlejohn, M. S. Hill, C. du Plessis & S. Cywes. 1989. Chromosome numbers of various *Disa* hybrids and their interspecific and complex hybrids. S. African J. Bot. 55: 394–399.

Pijl, L. van der & C. H. Dodson. 1966. Orchid Flowers: Their Pollination and Evolution. Univ. Miami Press, Coral Gables.

Schlechter, R. 1901. Monographie der Diseae. Bot. Jahrb. Syst. 31: 134–313.

Smith, G. R. & G. E. Snow. 1976. Pollination ecology of *Platanthera (Habenaria) ciliaris* and *P. blephariglottis* (Orchidaceae). Bot. Gaz. 137: 133–140.

Steiner, K. E., V. B. Whitehead & S. D. Johnson. 1994. Floral and pollinator divergence in two sexually deceptive South African orchids. Amer. J. Bot. 81: 185–194.

Stoutamire, W. P. 1974. Relationships of the purple-fringed orchids *Platanthera psycodes* and *P. grandiflora*. Brittonia 26: 42–58.

———. 1975. Pseudocopulation in Australian orchids. Amer. Orchid Soc. Bull. 44: 226–233.

Thien, L. B. & B. G. Marks. 1972. The floral biology of *Arethusa bulbosa*, *Calopogon tuberosus* & *Pogonia ophioglossiodes* (Orchidaceae). Canad. J. Bot. 50: 2319–2325.

Vogelpoel, L. 1992. *Disa* hybridization in the western Cape—Current status and future prospects. Part 5. The hybridization potential of *Disa venosa* and *Disa caulescens*, and future trends. S. African Orchid J. 23: 82–87.

———, D. W. Van Der Merwe & B. D. Anderson. 1985. A white form of *Disa racemosa*—A rare mutant with a great future. Amer. Orchid Soc. Bull. 54: 47–50.

Wodrich, K. 1995. A new natural hybrid from the western Cape? S. African Orchid J. 26: 63–64.

TRIBAL PHYLOGENY OF THE ASTERACEAE BASED ON TWO NON-CODING CHLOROPLAST SEQUENCES, THE *trn*L INTRON AND *trn*L/*trn*F INTERGENIC SPACER[1]

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ABSTRACT

Asteraceae are the largest family of dicotyledonous plants and have long been known for their taxonomic complexity. The ubiquitous parallelisms in morphology within the family have made phylogenetic reconstruction and tribal circumscription an area of long debate. In this study we explored the utility of using two relatively short non-coding chloroplast DNA sequences, the *trn*L intron and *trn*L/*trn*F intergenic spacer, to resolve phylogenetic relationships among the tribes. The results of the phylogenetic analysis produced trees that are topologically congruent with prior phylogenetic hypotheses based on both morphological and molecular data sets. The Asteroideae are a monophyletic group, but the Cichorioideae are paraphyletic. The primary clades of the Cichorioideae are the Mutisieae–Cardueae, Liabeae–Vernonieae, and of the Asteroideae, the Inuleae–Plucheeae, Astereae–Anthemideae, Senecioneae–Gnaphalieae, and the helianthoid clade (Helenieae, Heliantheae s. str., and Eupatorieae). The Inuleae–Plucheeae clade is sister to the remainder of the Asteroideae, and the paraphyly of the Inuleae s.l. (Gnaphalieae, Inuleae s. str., and Plucheeae) is firmly supported by our analysis. Our study illustrates the utility of the *trn*L intron and *trn*L/F intergenic spacer for resolving relationships among tribes of the Asteraceae. Using approximately 874 bp, we were able to produce a phylogeny of comparable resolution to phylogenies based on well-known coding regions such as *rbc*L and *ndh*F. For phylogenetic inference at the family level the *trn*L intron and *trn*L/F spacer provide similar levels of resolution to longer coding sequences (e.g., *rbc*L, *ndh*F), while having the advantage of being much easier to amplify and sequence due to their short lengths and universal primers. The numerous insertions and deletions commonly found in this region are easily aligned and are phylogenetically informative, thus adding considerably to the information content per base pair sequenced.

Asteraceae are the largest family of dicotyledonous plants (ca. 23,000 spp.) and have long been recognized for their taxonomic complexity. Ubiquitous parallelisms in morphology within the family have made it difficult to find conservative (non-homoplasious) characters that can be used reliably in phylogenetic reconstruction (Carlquist, 1976). Cassini (1826) was the first to divide the Asteraceae into tribes (19 tribes), and the first to suggest their natural relationships. Significant early contributions were also made by Bentham (1873), who reduced the number of tribes to 13, and Cronquist (1955), who placed Heliantheae at the base of his 12 recircumscribed tribes. Hoffmann (1894) recognized two distinct lineages within the Asteraceae: the Liguliflorae, in which he placed the single tribe Lactuceae; and the Tubuliflorae (= Asteroideae of modern authors), in which he placed all the remaining tribes. Subsequent authors have continued to recognize two lineages within the family, but their circumscriptions have differed dramatically. Among these major revisions, Carlquist (1976) was perhaps the first to recognize an expanded Cichorioideae (= Liguliflorae) by placing 6 tribes within each of his subfamilies Cichorioideae and Asteroideae. Beginning in the late 1980s, the discovery and subsequent analysis of a phylogenetically informative inversion in the cpDNA of Asteraceae

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(Jansen & Palmer, 1987), in addition to the morphological work by Bremer (1987) and others, demonstrated that the former Barnadesiinae (in Mutisieae) was monophyletic. This work also indicated that this subtribe was the basal group in the Asteraceae and worthy of being recognized as the archaic subfamily, the Barnadesioideae. As a result of these and other morphological and molecular studies (Bremer, 1987; Michaels et al., 1993; Gustafsson & Bremer, 1995; Kim & Jansen, 1995), it is becoming clear that the Asteraceae arose in South America (Bremer, 1992) and are probably sister to the South American endemic family Calyceraceae.

Phylogenetic relationships within the Asteraceae have long been an area of debate, beginning with Cassini (1826) and continuing to the present day. Although much has been accomplished over the past 15 years to resolve phylogenetic relationships among the tribes, the taxonomic limits and relationships of many tribes are still unclear. In particular, the question of the monophyly of the Cichorioideae and the "old" Inuleae are important relationships that have not been resolved. In addition, the tribal circumscriptions of tribes such as the Helenieae and Eupatorieae are still very much in doubt.

Since the advent of molecular systematics, protein-encoding gene sequences have been very useful for resolving higher-order questions (e.g., Chase et al., 1993). However, in groups such as the Asteraceae that have undergone a rapid radiation (Carlquist, 1976), coding regions may not always provide sufficient information to resolve relationships. In this study we explored the utility of using two relatively short, non-coding chloroplast DNA sequences, the *trn*L intron and *trn*L/*trn*F intergenic spacer, to resolve phylogenetic relationships among tribes of the Asteraceae. The availability of *rbc*L- (Kim et al., 1992) and *ndh*F- (Kim & Jansen, 1995) derived phylogenetic trees allows for a direct comparison of the phylogenetic utility of the *trn*L intron and *trn*L/*trn*F intergenic spacer relative to these widely used sequences.

MATERIALS AND METHODS

OUTGROUP SELECTION

Outgroup taxa were selected on the basis of the *ndh*F analysis of Kim and Jansen (1995), the restriction fragment length polymorphism (RFLP) studies by Jansen and Palmer (1987, 1988), the *rbc*L analysis by Kim et al. (1992), and the morphological works of Bremer (1987, 1994). Although attempts were made to use groups from outside the Asteraceae to polarize trees, alignments were ambiguous and could not be used for phylogenetic reconstruction. Two members of the Barnadesioideae (i.e., *Chuquiraga* and *Doniophyton*) were thus chosen as a functional outgroup (Watrous & Wheeler, 1981). The basal position of this subfamily is confirmed in all the above-mentioned studies, and its use as an outgroup for the remainder of the Asteraceae is not without precedent (Jansen et al., 1990, 1991; Keeley & Jansen, 1991).

INGROUP SAMPLING

Tribal circumscriptions and nomenclature are based on the treatment of the Asteraceae by Bremer (1994). One or two members from each of the recognized tribes were sequenced. For the 26 taxa used in this study, all sequences were generated by us (Table 1) from fresh leaf material, except for representatives of *Artemisia, Chuquiraga, Doniophyton, Liabum,* and *Osteospermum,* which were obtained from dried material. Material was collected in the field for some genera, whereas other samples were obtained from commercial sources; herbarium vouchers are cited in Table 1.

DNA ISOLATION, AMPLIFICATION, AND SEQUENCING

Total DNA was isolated as outlined in Bayer et al. (1996). The *trn*L/F region was amplified via the polymerase chain reaction (PCR) using *Taq* DNA polymerase on a GeneE® thermal cycler (Techne Incorporated, Princeton, NJ). The PCR reaction mixture consisted of 5 μl of 20× reaction buffer, 6 μl of 25 mM magnesium chloride solution, 16 μl of a 1.25 mM dNTP solution in equimolar ratio, 25 pmol of each primer, 10–50 ng of template DNA, and 1.0 unit of polymerase in a total volume of 100 μl. The PCR samples were heated to 94°C for three minutes prior to the addition of DNA polymerase to denature unwanted proteases and nucleases. The double-stranded PCR products were produced via 30 cycles of denaturation (94°C for 1.0 min), primer annealing (48°C for 1 min), and extension (72°C for 2 min). A 7-min final extension cycle at 72°C followed the 30th cycle to ensure the completion of all novel stands.

The *trn*L intron and *trn*L/*trn*F spacer, hereafter referred to as *trn*L5′/F (Fig. 1), was amplified as a single piece using primers "c" and "f" of Taberlet et al. (1991). Primers "a" and "b" (Fig. 1) were used to estimate the approximate size of the *trn*T/L intergenic spacer in the Asteraceae, but these were not sequenced. Double-stranded PCR products were cleaned by differential filtration using Millipore Ultra-free®-MC tubes (30,000 NMWL filters) prior to sequencing.

The double-stranded PCR products were then

Table 1. Collections of Asteraceae used in the *trnL/trnF* sequencing study. Presented are species, origin (location of voucher), and accession numbers. All voucher numbers beginning with two letters (signifying a state, province, or from cultivation (GH)) followed by 5 digits are collections of Bayer or Bayer et al. GenBank accession numbers for the sequences (intron, spacer) are given.

Species	Accession numbers and (voucher location)	Source	GenBank (intron, spacer)
1) *Ageratum houstonianum* Mill.	GH-95011 (CANB)	Commercially grown plants	U82012, U82013
2) *Antennaria luzuloides* Torr. & A. Gray	OR-91002 (ALTA)	U.S.A.: Oregon	U82014, U82015
3) *Artemisia tridentata* Nutt.	CO-90072 (ALTA)	U.S.A.: Colorado	U82016, U82017
4) *Aster novae-angliae* L.	AB-95003 (CANB)	Commercially grown plants	U82018, U82019
5) *Calendula officinalis* L.	GH-95009 (CANB)	Commercially grown plants	U82020, U82021
6) *Chuquiraga aurea* Skottsb.	*Stuessy et al. 12911* (OS)	Argentina	U82022, U82023
7) *Cirsium subniveum* Rydb.	WY-90044A (CANB)	U.S.A.: Wyoming	U82024, U82025
8) *Crepis tectorum* L.	AB-95002 (CANB)	Canada: Alberta	U82026, U82027
9) *Doniophyton anomalum* (D. Don) Wedd.	*Stuessy et al. 12857* (OS)	Argentina	U82028, U82029
10) *Echinops exaltatus* Schrad.	AB-95005 (CANB)	Commercially grown plants	U82030, U82031
11) *Gaillardia aristata* Pursh	GH-95006 (CANB)	Commercially grown plants	U82032, U82033
12) *Gazania rigens* R. Br.	GH-95012 (CANB)	Commercially grown plants	U82034, U82035
13) *Gerbera jamesonii* Bolus ex Hook.	GH-95004 (CANB)	Commercially grown plants	U82036, U82037
14) *Helianthus annuus* L.	GH-95007 (CANB)	Commercially grown plants	U82038, U82039
15) *Inula helenium* L.	GH-95013 (CANB)	Commercially grown plants	U82040, U82041
16) *Lactuca sativa* L.	AB-95007 (CANB)	Commercially grown plants	U82042, U82043
17) *Liabum solidagineum* (Kunth) Less.	*Dillon & Sánchez 6253* (F)	Peru: Prov. Huancabamba	U82044, U82045
18) *Matricaria matricarioides* (Less.) Port.	AB-95005 (CANB)	Canada: Alberta	U82046, U82047
19) *Osteospermum clandestinum* (Less.) Norl.	WA-94070 (CANB)	Australia: Western Australia	U82048, U82049
20) *Petasites frigidus* (L.) Fr.	*Starr 96001* (WIN)	Canada: Manitoba	U82050, U82051
21) *Senecio vulgaris* L.	AB-95006 (CANB)	Canada: Alberta	U82052, U82053
22) *Stokesia laevis* Greene	GH-95014 (CANB)	Commercially grown plants	U82054, U82055
23) *Streptoglossa cylindriceps* (J. M. Black) Dunlop	WA-94049 (ALTA)	Australia: Western Australia	U82056, U82057
24) *Stuartina muelleri* Sond.	*Burrows s.n.* (CANB)	Australia: New South Wales	U82058, U82059
25) *Tagetes patula* L.	*Bayer s.n.* (CANB)	Commercially grown plants	U82060, U82061
26) *Townsendia exscapa* (Richardson) Porter	CO-93037 (CANB)	U.S.A.: Colorado	U82062, U82063

used as templates in cycle sequencing reactions, which employed three primers (Taberlet et al., 1991) to sequence the two regions, including the terminal primers "c" and "f" and an internal primer "d" (Fig. 1). Sequencing primers were 5' end-labeled in a preliminary reaction involving T4 polynucleotide kinase and [γ^{32}P] - dATP (Amersham). The double-stranded DNAs were then cycle-sequenced using the dideoxy chain termination method (Sanger et al., 1977) with use of Promega's *fmol*®*1 Sequencing System (Promega Corporation, Madison, Wisconsin). An annealing temperature of 57°C was used for primer "f," while temperatures ranging from 60 to 62°C were employed for primers "c" and "d." The cycle-sequencing protocol followed the manufacturer's instructions. Termination products were separated in 6.0% polyacrylamide gels (0.4 mm thickness; 1× TBE buffer); the gels were fixed in 10% acetic acid for 20 minutes, washed in distilled water, and allowed to air-dry. They were then used to expose Kodak BIOMAX®-MR film for 8–48 hr depending on the intensity of the radioactive signal from the gel.

SEQUENCE ANALYSIS AND PHYLOGENETIC RECONSTRUCTION

Sequences were aligned initially using CLUSTAL V (Higgins et al., 1992), then adjusted man-

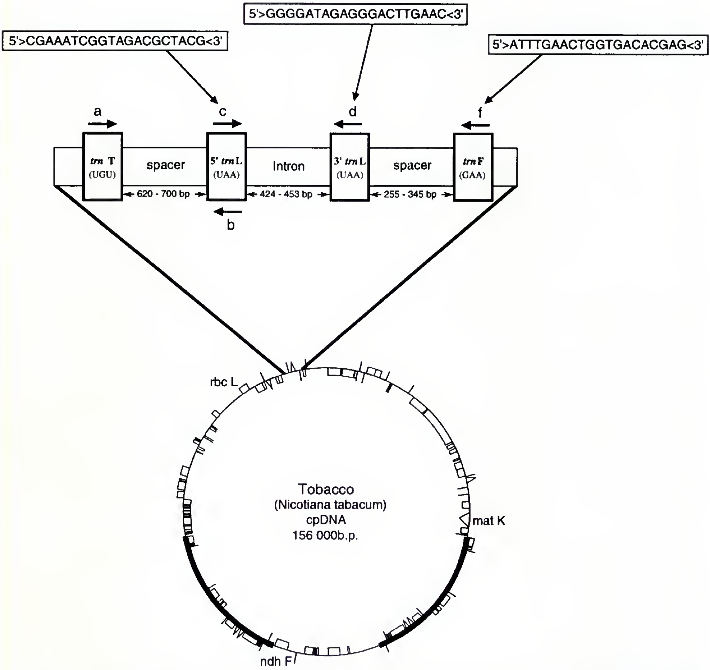


Figure 1. Structure of chloroplast DNA in *Nicotiana tabacum* L. (Solanaceae). Presented are positions of the *trnT* exon (UGU), the *trn*L/T intergenic spacer, the *trn*L intron, the *trn*L 3′ and 5′ exons (UAA), the *trn*L/F intergenic spacer, and the *trn*F exon (GAA), relative to the commonly sequenced genes *rbc*L, *mat*K, and *ndh*F, the large and small single-copy regions, and the inverted repeats (two bold semicircular regions). Relative positions of the Taberlet et al. (1991) primers (c, d, and f) used in PCR and sequencing are indicated, along with their base sequences.

ually (Swofford & Olsen, 1990) to minimize gap number using SeqApp vers. 1.8A (Gilbert, 1992). Several divergence weights [20%, 40%, 60% (the default), and 80%] were explored during sequence alignment (Delay Divergence Option of Clustal V), including several combinations of the gap-opening penalty (GOP) and gap-extension penalty (GEP) options of CLUSAL V (Higgins et al., 1992). GOPs of 10 (the default) and 100 were explored in all permutations with GEPs of 5 (the default) and 10. The different permutations resulted in very similar alignments, and one was chosen as a starting point to continue with manual adjustment of the alignment. The alignment of the sequences necessitated inference of many insertions and deletions (Table 2).

Small portions of the *trn*L and *trn*F genes were also sequenced along with the intron and spacer sequences. No variation was observed among the taxa for any of these gene regions with the exception of a single point mutation (C→T) at the 3^{rd} position of the 5′ segment of *trn*F. *Artemisia, Aster, Lactuca, Matricaria, Petasites, Senecio,* and *Townsendia* have "T" at this position, whereas all other taxa have a "C." This character was included in all analyses.

The proportion of nucleotide differences between taxa was calculated using the "Show Distance Matrix" option of PAUP. A total of 101 phylogenetically informative base pairs and 32 indels from the *trn*L5′/F region was available for use in the analysis

Table 2. Insertions and deletions in the chloroplast *trn*L intron and the *trn*L/F intergenic spacer in the Asteraceae. Presented are type and size of the indel, start point of the indel based on the first bp of the intron sequence (*trn*L intron is 1–533; *trn*L/F spacer is 534–913), and the species in which the mutation occurs (numbers of the species refer to those given in Table 1). Also given are the repeat sequences for those insertions that are repeats of adjacent sequences, as well as the locus of the start point from which the repeat is derived. * = potentially phylogenetically informative indels.

Indel number	Type of mutation	Size in (bp)	Direct repeat sequence	Fragment from base	Repeated from base	Mutated species
1*	del	1		144		2, 24, 26
2*	del	1		205		4, 26
3*	del	1		264		5, 19
4*	del	1		273		4, 6, 7
5*	del	1		293		1, 11, 14, 25
6	del	1		316		9
7*	del	1		388		3, 18
8*	del	1		402		1, 11, 14, 15, 23, 25
9	del	1		591		1
10*	del	1		755		2, 24
11*	del	1		844		1, 11, 14, 25
12	del	1		887		15
13	del	2		303		9
14	del	2		309		9
15*	del	2		606		8, 17, 22
16	del	2		670		2
17*	del	2		672		3, 18, 20, 21, 24, 26
18	del	2		679		20
19	del	2		763		20
20	del	3		602		17
21	del	4		189		25
22*	del	4		283		1, 11, 14, 25
23	del	4		295		19
24	del	4		332		26
25	del	4		592		6
26*	del	4		621		4, 26
27	del	4		660		20
28	del	5		432		21
29	del	5		598		9
30	del	5		743		22
31	del	5		875		13
32	del	6		666		13
33*	del	7		635		9, 16
34	del	8		115		17
35	del	8		598		19
36*	del	8		682		15, 17, 22
37	del	8		806		17, 22
38	del	9		420		13
39	del	9		617		19
40*	del	9		654		1, 11, 14
41*	del	9		747		20, 21
42	del	9		798		5
43*	del	10		115		5, 19
44	del	10		602		6
45	del	10		690		9
46*	del	10		754		15, 23
47*	del	10		835		5, 19
48*	del	11		123		6, 7
49*	del	11		761		5, 6, 7, 19
50*	del	15		777		3, 18

Table 2. Continued.

Indel number	Type of mutation	Size in (bp)	Direct repeat sequence	Fragment from base	Repeated from base	Mutated species
51*	del	18		295		3, 18
52	del	19		652		16
53	del	82		730		25
54	ins	1		141		13
55	ins	1		143		3
56*	ins	1		613		3, 5, 9, 18, 19
57	ins	1		626		18
58*	ins	1		683		1, 18, 19, 20, 21
59	ins	1		691		4
60*	ins	1		841		1, 11, 14, 21, 25
61	ins	2		666		11
62	ins	4		704		4
63*	ins	6		288		2, 12, 24
64	ins	7		233		11
65	repeat	4	AAAA	149	145	18
66	repeat	4 (8)	AATC[AATC]	337	345	18 (3)
67	repeat	5	AATAC	278	284	4
68*	repeat	5	TTGAA	327	322	2, 3, 18
69	repeat	6	TTCACC	389	396	12
70*	repeat?	6	C(A/G)TT(C/T)(A/T)	606	612	3, 5, 8, 9, 17, 18, 19, 22
71	repeat	6	AACTTA	782	776	9
72	repeat	7	GATCAAA	360	380	1
73*	repeat?	7	(C/T)TA(C/T)-(T/A)C(T/G/A)	619	612	All (except 5, 9)
74*	repeat?	7	GT(GCA)A(CT)-A(CT)	673	682	All (except 5, 6, 7, 8, 10, 12, 13)
75	repeat	20	GATCAAATCATTCACTCCAT	360	380	6

of the 26 taxa. Invariant sites and autapomorphic base changes were removed from the analysis using the "Ignore Uninformative Characters" option. *trn*L5′/F sequences for all taxa are available from GenBank (see Table 1 for accession numbers) or can be obtained from the authors upon request. Insertion/deletion events (indels) were scored as binary characters (Table 2), following the recommendations of Wojciechowski et al. (1993), with gaps treated as missing. Primary sequence lengths and G/C contents were determined in Amplify 1.2 (Engels, 1993). These values were manually recalculated for those sequences with ambiguous nucleotide characters (e.g., N, Y, R), which are unacceptable to the program.

Sequence data were analyzed using PAUP version 3.1.1 (Swofford, 1993). Phylogenetic reconstruction was performed on unweighted characters by heuristic searches with "simple," "closest," and "furthest" addition of taxa. Heuristic searches employing a random-addition sequence of 1000 replicates were also conducted to search for other islands of most parsimonious trees (Maddison, 1991).

Three separate data sets were analyzed. The first excluded all potentially phylogenetically informative indels, and the second included all indels. The third data set included only those potentially phylogenetically informative indels greater than 2 bp in length. This follows the recommendations of van Ham et al. (1994) and Lloyd and Calder (1991), who suggested that most of the homoplasy in insertion/deletion events is accounted for by smaller indels. Strict and 50% majority rule consensus trees (Margush & McMorris, 1981) were constructed for the set of equally most-parsimonious cladograms. The distribution of phylogenetically informative characters (point mutations and indels) on tree topologies was examined using MacClade version 3.0 (Maddison & Maddison, 1992).

Bootstrap (Felsenstein, 1985) and decay (Bremer, 1988; Donoghue et al., 1992) analyses were used to estimate the robustness of clades. Bootstrap

Table 3. Sequence characteristics of the *trn*L intron, *trn*L/F spacer, and combined *trn*L–*trn*L/F non-coding region sequenced in this study.

	*trn*L intron	*trn*L/F spacer	Combined (*trn*L intron + *trn*L/F spacer)
Length range (bp)	424–453	(255)308–345	(685)733–793
Length mean (bp)	437.50	329.54	767.65
Aligned length (bp)	505	369	874
G + C content range (%)	33.6–36.2	33.8–38.1	33.4–36.3
G + C content mean	34.9	35.5	35.1
Sequence divergence (%)	1.1–6.4	1.2–11.7	1.0–7.7
Number of variable sites	96 (19.0%)	123 (33.3%)	219
Number of potentially informative sites	43 (8.5%)	58 (15.7%)	101
Number of constant sites	409 (81.0%)	246 (66.7%)	655
Number of autapomorphic sites	53 (10.5%)	65 (12.9%)	118
Number of indels	31	44	75
Indel size range (bp)	1–29	1–20 (82)	1–82
Ratio of indels to potentially informative sites	1:1.39	1:1.32	1:1.57

analyses employed 100 replicates of heuristic (SIMPLE addition sequence) searching. Decay analyses were performed using a converse constraint (ENFORCE CONVERSE command) method (Baum et al., 1994). The amount of phylogenetic information in the parsimony analysis was assessed by use of the consistency index (C.I.; Kluge & Farris, 1969) and the retention index (R.I.; Farris, 1989).

RESULTS

Length variation for the entire *trnL* intron ranged from a low of 424 bp in *Matricaria* to a high of 453 bp in *Gazania* (Table 3). The proportion of nucleotide differences ranged from 1.1 to 6.4% between all species of Asteraceae, and from 2.7 to 6.4% between species of the Barnadesioideae and the rest of the Asteraceae (Table 3). The *trn*L intron had an average G/C content of 34.9% (33.6 to 36.2%) (Table 3).

The complete *trn*L/F intergenic spacer (corresponding to positions 49876–50231 in the *Nicotiana* genome; Fig. 1) was sequenced for all taxa in this study, and ranged in length from 255 bp in *Tagetes* to 345 bp in *Aster* (Table 3). The great range in length is somewhat misleading, because *Tagetes* has a unique 82 bp deletion; the next shortest sequence was that of *Osteospermum* (308 bp) (Table 3). The proportion of nucleotide differences in the spacer is greater than that found in the *trn*L intron and ranges from 1.2 to 11.7% between all species of Asteraceae, and from 2.2 to 10.0% between the Barnadesioideae and the ingroup (Table 3). Like the intron, the spacer has an average G/C content of 35.5% (33.8 to 38.1%) (Table 3).

Within Asteraceae, the proportion of nucleotide differences in the combined spacer and intron sequences ranged from 1.0 to 7.7% (Table 3). Total average A/T content was 64.9%, whereas G/C content was 35.1% on average (Table 3). A total of 101 sites (11.3% of the sequence length) provided potential phylogenetic information; all other sites (87.2%) were either invariant or autapomorphic (Table 3).

Seventy-five indels (Tables 2, 3), ranging in length from 1 to 82 bp, were needed to align sequences. Deletions relative to the outgroup taxa accounted for 71% (53/75) of the indels, unique sequence insertions 14.5% (11/75), and insertions that are repeats of adjacent sequence also accounted for 14.5% of the indels (Table 2). Thirty-two of the indels (Table 2) are phylogenetically informative and support relationships based on nucleotide substitutions alone (Figs. 2–4). Many more of the 1 and 2 bp (hereafter referred to as "small") indels (64%) were homoplasious (Table 2, Fig. 3), when compared with those 3 bp and greater (35%; hereafter called "large"indels; Table 2, Fig. 4).

PHYLOGENETIC RECONSTRUCTIONS

All three analyses (Figs. 2–4) show similar phylogenetic relationships within Asteraceae. In the 50% majority-rule trees (Figs. 2–4), branches not appearing in the strict consensus are indicated by dotted lines. The phylogenetic analysis of the sequence data excluding all indels yielded 180 equally parsimonious trees of 234 steps (C.I. = 0.61; R.I. = 0.63; Fig. 2). The data set including all indels produced 244 trees, 293 steps in length (C.I. = 0.61; R.I. = 0.64; Fig. 3),

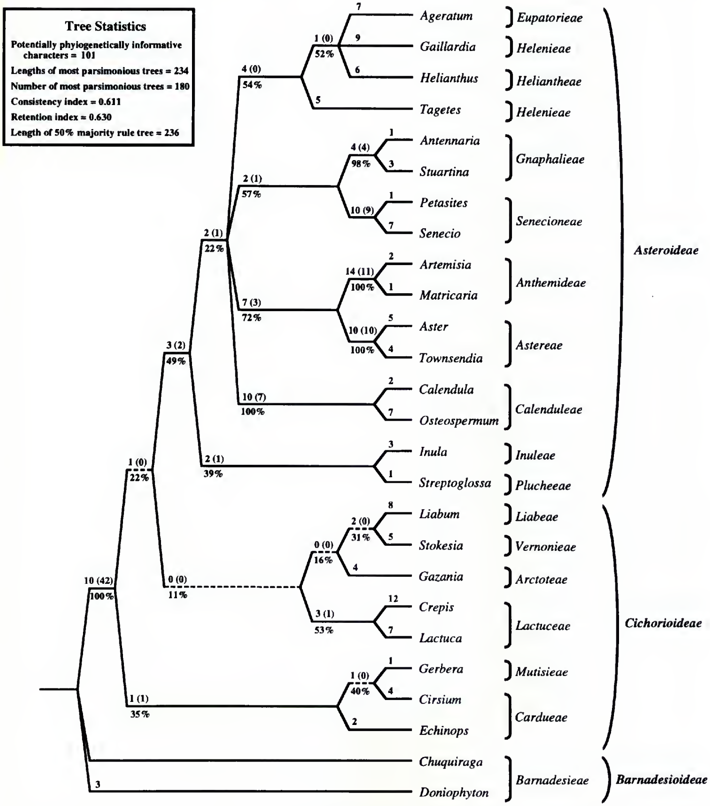


Figure 2. The 50% majority rule consensus tree of 180 equally parsimonious trees resulting from phylogenetic analysis of sequence data of the *trn*L intron and the *trn*L/F intergenic spacer using all informative base pairs, but excluding all indels. Branches that did not appear in the strict consensus tree are indicated by dashed lines. The tree gives the number of apomorphies above the branches, decay index values (in parentheses) also above the branches, and bootstrap values given as percentages below each branch. Taxon labels are from left to right: genera, tribes, and subfamilies.

whereas the data set including only large indels yielded 258 trees, 267 steps long. The latter trees have the highest consistency and retention indices of all three analyses (C.I. = 0.62; R.I. = 0.65; Fig. 4). Island searches (Maddison, 1991) on the data sets did not reveal any islands of shorter length trees.

TOPOLOGY OF MAJOR CLADES

All trees (Figs. 2–4) indicate that Asteroideae are monophyletic and place a clade or clades containing part of Cichorioideae, including members of tribes Liabeae, Vernonieae, Arctoteae, and Lactuceae, as sister(s) to the Asteroideae clade. Decay index values

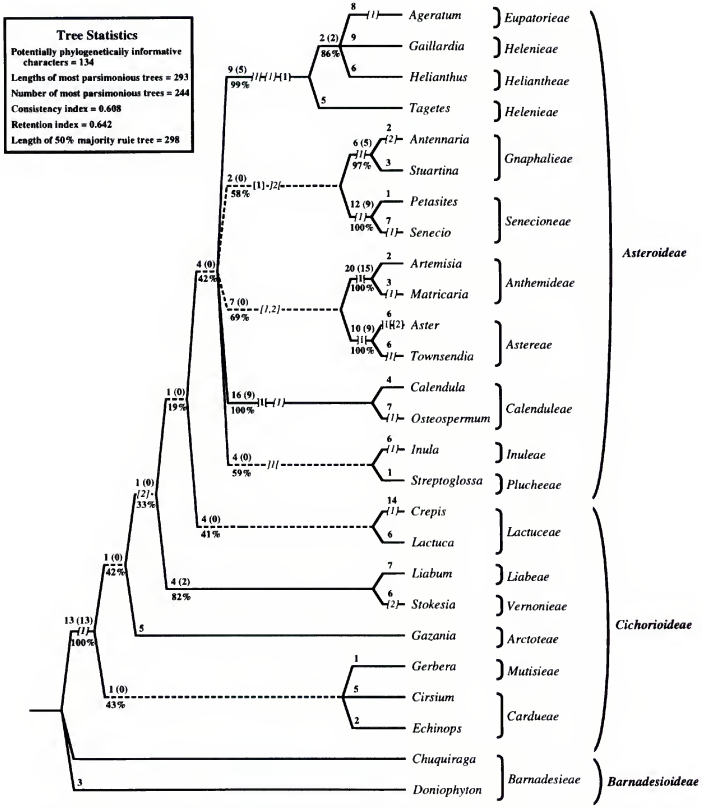
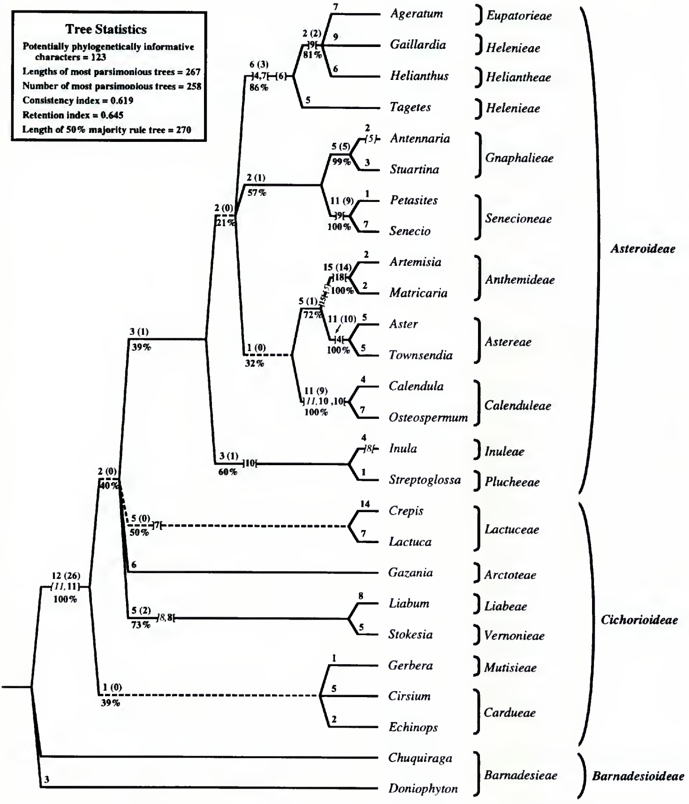


Figure 3. The 50% majority rule consensus tree of 244 equally parsimonious trees resulting from phylogenetic analysis of sequence data of the *trn*L intron and the *trn*L/F intergenic spacer using all informative base pairs and both large and small indels. Branches that did not appear in the strict consensus tree are indicated by dashed lines. The tree gives the number of apomorphies (including indels) above the branches, decay index values (in parentheses) also above the branches, and bootstrap values given as percentages below each branch. Small (1 and 2 bp) phylogenetically informative insertions are shown with bp length enclosed in [ ], deletions are] [, **boldface** type indels are those with C.I. of 1.00, and *italic* type are the homoplasious indels. Taxon labels are from left to right: genera, tribes, and subfamilies.

(D.I.) of 0–2, synapomorphies (SYN) of 3–4, and bootstrap values (B.V.) of 39% to 49%, provide only weak support for this relationship. A clade containing members of the Mutisieae and Cardueae is seen at the base of these trees (Figs. 2–4). In most cases, tribes represented by more than one genus (i.e., the Anthemideae, Astereae, Calenduleae, Cardueae, Gnaphalieae, Helenieae, Lactuceae, Senecioneae) are monophyletic. Exceptions to this are Helenieae, which is paraphyletic in all trees (Figs. 2–4), and Cardueae, which proved to be unnatural in the analysis that excluded indels (Fig. 2).



Tree Statistics

Potentially phylogenetically informative characters = 123
Lengths of most parsimonious trees = 267
Number of most parsimonious trees = 258
Consistency index = 0.619
Retention index = 0.645
Length of 50% majority rule tree = 270

Figure 4. The 50% majority rule consensus tree of 258 equally parsimonious trees resulting from phylogenetic analysis of sequence data of the *trn*L intron and the *trn*L/F intergenic spacer using all informative base pairs, but excluding all small (1 and 2 bp) indels. Branches that did not appear in the strict consensus tree are indicated by dashed lines. The tree gives the number of apomorphies (including indels) above the branches, decay index values (in parentheses) also above the branches, and bootstrap values given as percentages below each branch. Large phylogenetically informative insertions are shown with bp length enclosed in [ ], deletions are] [, **boldface** type indels are those with C.I. of 1.00, and *italic* type are the homoplasious indels. Taxon labels are from left to right: genera, tribes, and subfamilies.

TOPOLOGY OF MINOR CLADES

Clades containing members of the tribes Eupatorieae, Helenieae, and Heliantheae (the helianthoid clade) are common to all most parsimonious trees, but are most strongly supported (SYN = 6–9; B.V. = 86–99%) in the analyses that included indels (Figs. 3 and 4). There is low support for two additional clades within the Asteroideae, one containing members of the Gnaphalieae and Senecioneae (SYN = 2; D.I. = 0–1; B.V. = 57–58%) and another containing members of the Anthemideae and Astereae (SYN = 5–7; D.I. = 0–3; B.V. = 69–72%). These clades are found in all the most parsimonious trees from the data sets containing no indels and large indels only (Figs. 2, 4). In two of the analyses (Figs. 2, 3), both of the genera in the Calenduleae are part of the main Asteroideae clade, whereas in the analysis containing only large indels (Fig. 4), they are part of a weakly supported (D.I. = 0; SYN = 1; B.V. = 32%) group that is sister to the Anthemideae–Astereae clade. In both groups of trees derived from data sets containing no indels and large indels only (Figs. 2, 4), the Inuleae–Plucheeae clade is sister to the rest of the Asteroideae, whereas in the third analysis containing all indels this clade is part of a basal polytomy of a less resolved Asteroideae (Fig. 3).

Cichorioideae are a paraphyletic group in all analyses (Figs. 2, 4). The Cardueae–Mutisieae clade mentioned above received weak support in all our trees (SYN = 1; D.I. = 0–1; B.V. = 35–43%). In all the analyses (Figs. 2–4), a clade or clades representing the tribes Liabeae, Vernonieae, Arctoteae, and Lactuceae are patristically closer to the Asteroideae clade than are Cardueae and Mutisieae. All of the trees (Figs. 2–4) show Vernonieae and Liabeae as sister taxa (SYN = 2–5; D.I. = 0–2; B.V. = 31–82%). One of the trees (all indels excluded; Fig. 2) provides weak support for a relationship in which the Arctoteae is the sister group to the Vernonieae–Liabeae clade (SYN = 0–1; B.V. = 16–42%). The Lactuceae clade has weakly supported relationships in the three trees, as sister to the Arctoteae–Liabeae–Vernonieae clade (Fig. 2; B.V. = 11%), as sister to the Asteroideae (Fig. 3; SYN = 1; B.V. = 19%), and as part of a polytomy (Fig. 4).

DISCUSSION

This study represents one of the few to use the *trn*L intron and/or *trn*L/F intergenic spacer for phylogenetic reconstruction. The initial study of Taberlet et al. (1991) introduced PCR primers for these regions and showed that they could be amplified across a broad taxonomic range from algae to bryophytes, vascular cryptogams, gymnosperms, and angiosperms. This was followed by a phylogenetic reconstruction of some Crassulaceae genera using the *trn*L/F spacer by van Ham et al. (1994), who demonstrated the utility of the sequence to reconstruct phylogeny at the family level. Gielly and Taberlet (1996) and Gielly et al. (1996) used the *trn*L intron to produce a phylogeny for *Gentiana* (Gentianaceae), comparing it to phylogenies for the same group based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA. They concluded that ITS was more informative than the chloroplast sequence for resolving phylogenies at this level, and that the *trn*L intron sequences would probably be more useful at the intergeneric level (Gielly et al., 1996). Most recently Böhle et al. (1996) employed both of the regions used in this study, along with the *trn*L/T intergenic spacer and ITS sequences, to reconstruct the phylogeny of *Echium* (Boraginaceae) in the island groups off the northwest coast of Africa and the adjacent mainland. They obtained good resolution of the major clades (especially island versus mainland clades) within the genus, and showed the utility of combining ITS and chloroplast spacers in phylogenetic reconstruction at the generic level.

In resolving relationships in the Asteraceae, we found that the combined use of base substitutions and large indels produced trees that were better supported and less homoplasious than trees produced using only base substitutions or base substitutions and all indels. Our results agree with those of other studies (van Ham et al., 1994; Lloyd & Calder, 1991) in showing that smaller indels tend to be more homoplasious.

The averages of G/C vs. A/T content we found for the *trn*L intron and *trn*L/F spacer are nearly identical [combined average = 35.1% (Table 3) and 64.9%, respectively]; this compares favorably to the relatively narrow range in G/C content (36–39%) reported in angiosperm cpDNA (Palmer, 1991).

The topologies of our trees (Figs. 2–4) largely agree with those from other studies (Bremer, 1987; Jansen et al., 1990; Jansen et al., 1991; Karis et al., 1992; Kim et al., 1992; Karis, 1993; Kim & Jansen, 1995) of tribal relationships in the Asteraceae. Our Asteroideae, consisting of the Anthemideae, Astereae, Calenduleae, Eupatorieae, Gnaphalieae, Helenieae, Heliantheae, Inuleae, Plucheeae, and Senecioneae (Figs. 2–4), is the same monophyletic group found by Bremer (1987) based on morphology, and by Jansen et al. (1991), Kim et al. (1992), and Kim and Jansen (1995) based on molecular studies. We have also found that the Cichorioideae is paraphyletic, as reported in most other studies (Bremer, 1987; Karis et al., 1992; Kim & Jansen, 1995). The exceptions to a paraphyletic Cichorioideae are seen in the *rbc*L (Kim et al., 1992) and RFLP studies (Jansen et al., 1990; Jansen et al., 1991). The *rbc*L study, however, lacked representation from critical taxa like the Inuleae s. str., Plucheeae, and Gnaphalieae, taxa that cause notable topological differences within the Cichorioideae when excluded in our analysis (results not shown). The *rbc*L study (Kim et al., 1992) portrayed relationships within the Cichorioideae largely incongruent with those suggested by ours and the above-mentioned studies. A recent reanalysis (Mishler et al., 1996) of the RFLP studies has found a paraphyletic Cichorioideae and has called into question the original methods of analysis (Jansen et al., 1990; Jansen et al., 1991) of those data.

The Mutisieae and Cardueae form a monophyletic group (Figs. 2–4) that is sister to a clade consisting of the remainder of the Cichorioideae and Asteroideae. Similar basal positions for the Mutisieae and Cardueae are found in morphological (Bremer, 1987; Karis et al., 1992) and most molecular-based (Jansen et al., 1990; Jansen et al., 1991; Kim & Jansen, 1995) phylogenetic reconstructions. There is some weak evidence (Fig. 2) that the Cardueae may be paraphyletic, as suggested by Dittrich (1977). He split the Cardueae into three separate tribes, of which two, the Echinopeae and Cardueae s. str., were represented in our study (by *Echinops* and *Cirsium*, respectively).

As in many other studies (Bremer, 1987; Jansen et al., 1991; Karis et al., 1992; Kim et al., 1992), the relationships of the Lactuceae, Arctoteae, Liabeae, and Vernonieae (LALV), which form the remainder of the Cichorioideae, were largely unresolved in our investigation. We have only weak evidence for a monophyletic LALV group (Fig. 2), and Kim and Jansen (1995) also found only modest support (SYN = 3; deletion = 1) for the monophyly of this group. Most studies (Bremer, 1987; Jansen et al., 1990; Jansen et al., 1991; Kim & Jansen, 1995), including ours (Figs. 2–4), show Liabeae and Vernonieae as sisters, except for the *rbc*L study by Kim et al. (1992). Although Liabeae were once placed in Senecioneae (Robinson, 1983; Bremer, 1987), it is now clear that they are quite distinct from that tribe and are indeed most closely related to Vernonieae. It has been suggested that Vernonieae and Liabeae should be united (Jansen & Stuessy, 1980), although it appears that there are morphological synapomorphies that warrant their recognition as distinct lineages (Bremer, 1987).

We now turn our attention to the Asteroideae clade. The recent work of Anderberg (1989, 1991a, 1991b, 1991c) and Karis (1993) has shown that the Inuleae sensu Merxmüller et al. (1977) should be considered as three separate tribal lineages: the Inuleae s. str., Gnaphalieae, and Plucheeae. Although Anderberg presented strong cases for separation of the tribes, some studies (Kim et al., 1992; Jansen et al., 1991; Bremer et al., 1992) have chosen not to address the "Inuleae problem." Our current long-term research into the molecular phylogenetics of the Gnaphalieae necessitates that we first resolve the sister-group relationships of the Gnaphalieae. We have thus included members of all three of Anderberg's tribes, and our results corroborate the morphological (Anderberg, 1989, 1991a, 1991b, 1991c; Karis, 1993) and single-molecular analysis (Kim & Jansen, 1995) in indicating that the "old" Inuleae are not a monophyletic lineage. In all of our analyses, the Inuleae s. str. and the Plucheeae are sister taxa, and these in turn are sister to the remainder of the Asteroideae in two analyses (Figs. 2, 4). Kim and Jansen (1995), using *ndh*F, showed a strong sister relationship between the Plucheeae and Inuleae, but the base of their Asteroideae was not resolved finely enough to show the sister relationships of that clade. Our topological relationships on the other hand were nearly identical to those of Karis (1993). Only the RFLP-based study of Keeley and Jansen (1991), which included members of all three tribes, showed the "old" Inuleae to be monophyletic. Therefore, based on the available evidence, the segregation of the Gnaphalieae from the "old" Inuleae seems warranted, although the circumscription of the Plucheeae is still unresolved. The sister relationships of the Gnaphalieae remain controversial. In our analysis (Figs. 2–4), the Gnaphalieae are sister to the Senecioneae. Karis (1993) showed them as sister to a clade containing the Astereae and Anthemideae, Jansen et al. (1991) as sister to the Inuleae (represented by *Inula*), Keeley and Jansen (1991) as sister to a clade consisting of the Inuleae and Plucheeae, and Kim and Jansen (1995) in an unresolved clade containing the Calenduleae, Astereae, and Anthemideae. The sister relationships of the Gnaphalieae remain unresolved due to the discordance among studies.

The sister relationships of the Astereae seem less controversial (Zhang & Bremer, 1993). We have shown them to be a well-supported sister group to the Anthemideae (Figs. 2–4), as also seen in the morphological study of Karis (1993) and the molecular studies of Jansen et al. (1991), Keeley and Jansen (1991), Kim et al. (1992), and Kim and Jansen (1995). Only Bremer (1987) portrayed them in a different relationship, as sister to the Eupatorieae. The relationships of the Calenduleae are controversial, and in only one of our analyses (Fig. 4) are their affinities to other tribes resolved, i.e., as sister to the Astereae–Anthemideae clade. Most morphological analyses do not show this relationship (Bremer, 1987; Karis, 1993), while other molecular analyses (Kim et al., 1992; Kim & Jansen, 1995) support our findings. Interestingly, RFLP's in cpDNA (Jansen et al., 1991; Keeley & Jansen, 1991) show the Calenduleae as sister to the Senecioneae, which has been the traditionally recognized relationship since the time of Bentham (1873).

The helianthoid clade, including the Eupatorieae, Helenieae (Tageteae, pro parte of some authors), and Heliantheae, is a strong monophyletic group in all our analyses (Figs. 2–4). Problems arise when trying to resolve relationships and circumscribe tribes within the helianthoid clade because it appears to contain a badly understood series of phylogenetically basal branches forming successive sister groups to the rest. The combined evidence suggests that some of the tribes in the helianthoid clade are paraphyletic and need to be re-examined.

Tagetes was treated as part of the Helenieae by Bremer (1994), as a member of subtribe Pectidinae (in Heliantheae) by Robinson (1981), and as the type genus of the tribe Tageteae by many authors from Cassini (1826) to Karis (1993). Our results have part of the Helenieae (*Tagetes*) as sister to a group consisting of the Eupatorieae, Helenieae (*Gaillardia*), and the Heliantheae, a disposition common to other molecular studies (Jansen et al., 1990; Jansen et al., 1991; Keeley & Jansen, 1991; Kim et al., 1992). Phylogenetic analyses using morphology (Bremer, 1987; Karis, 1993) and *ndh*F (Kim & Jansen, 1995) did not provide enough resolution to reveal relationships among most of the genera in the helianthoid clade.

The remainder of the helianthoid clade forms an unresolved polytomy containing the Heliantheae, the Eupatorieae, and the Helenieae (sensu Bremer, 1994). The Helenieae are represented by *Gaillardia*, which some authors (Robinson, 1981; Karis, 1993) have included in the Heliantheae (as the type genus of subtribe Gaillardiinae). Our analysis does indicate that the Heliantheae in the sense of Bremer (1994), Robinson (1981), and Karis (1993), are closely related to the Eupatorieae. This is a relationship that is also reflected by a number of additional molecular analyses including those of Keeley and Jansen (1991), Jansen et al. (1991), Kim et al. (1992), and Kim and Jansen (1995). Bremer's (1987) morphological analysis showed that Astereae and Eupatorieae were sister taxa, whereas Karis (1993) portrayed a close relationship between helianthoid elements and the Eupatorieae.

In conclusion, our phylogenetic analysis of the tribes of the Asteraceae produced trees largely congruent with other hypotheses based on both morphological and molecular data sets. Asteroideae are a monophyletic group, but Cichorioideae are paraphyletic. The primary clades of Cichorioideae are Mutisieae–Cardueae, Liabeae–Vernonieae; those of Asteroideae are Inuleae–Plucheeae, Astereae–Anthemideae, Senecioneae–Gnaphalieae, and the helianthoid clade (Helenieae, Heliantheae s. str., and Eupatorieae). The Inuleae–Plucheeae clade is sister to the remainder of the Asteroideae. The paraphyly of the "old" Inuleae (sensu Merxmüller et al., 1977) has been confirmed by our analysis. Calenduleae are sister to the Astereae–Anthemideae clade in some trees. A clade consisting of Lactuceae, Arctoteae, Verononieae, and Liabeae was also present in some most-parsimonious trees.

Our study illustrates the utility of the *trn*L intron and *trn*L/F intergenic spacer for resolving the relationships among tribes in the largest dicot family, Asteraceae. Using approximately 874 bp (Table 3), we were able to produce a phylogeny that shows a similar level of resolution to that produced by Kim and Jansen (1995) using 2200–2300 bp of *ndh*F. Comparison of the divergence values in the 17 taxa shared by our study and that of Kim and Jansen (1995) revealed that the combined *trn*L intron and *trn*L/F spacer evolves at a rate that is 1 to 1.28 times faster than *ndh*F. Further resolution could also be expected if additional taxa and the ca. 620–700 bp of *trn*L/T intergenic spacer were added to our analyses. Another chloroplast sequence, *rbc*L, which is 1428 to 1458 bp long in the Asteraceae and is often used in phylogeny reconstruction at the family level and above, did not provide as much resolution of the tribal relations in Asteraceae (Kim et al., 1992) as did *ndh*F (Kim & Jansen, 1995). RFLPs of chloroplast DNA, although providing fairly good resolution of relationships in the Asteraceae, resulted in several equally parsimonious trees that had moderately large amounts of homoplasy (C.I. = 0.54) (Jansen et al., 1990; Jansen et al., 1991). Additionally, that study was labor-intensive, requiring eleven restriction enzymes to produce 328 phylogenetically informative sites, and the methods of cladistic analysis of the RFLP data (Jansen et al., 1990; Jansen et al., 1991) have recently been criticized by Mishler et al. (1996). The sequences used in the present study have three advantages over the other commonly used gene regions: (1) they are easy to amplify across a wide taxonomic range because the universal primers designed by Taberlet et al. (1991) are placed in highly conserved tRNA genes; (2) the primers used to amplify the region can also be used to sequence it entirely using manual methods; and (3) the numerous large indels provide additional phylogenetic information. For phylogenetic reconstruction at the family level the *trn*L intron, *trn*L/F intergenic spacer, and the *trn*L/T intergenic spacers may represent an ideal sequence, providing levels of resolution similar to those of longer gene sequences (*rbc*L and *ndh*F), but requiring much less labor to generate data.

Literature Cited

Anderberg, A. A. 1989. Phylogeny and reclassification of the tribe Inuleae (Asteraceae). Canad. J. Bot. 67: 2277–2296.

———. 1991a. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). Opera Bot. 104: 1–195.

———. 1991b. Taxonomy and phylogeny of the tribe Inuleae (Asteraceae). Pl. Syst. Evol. 176: 75–123.

———. 1991c. Taxonomy and phylogeny of the tribe Plucheeae (Asteraceae). Pl. Syst. Evol. 176: 145–177.

Baum, D. A., K. J. Sytsma & P. C. Hoch. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. Syst. Bot. 19: 363–388.

Bayer, R. J., L. Hufford & D. E. Soltis. 1996. Phylogenetic relationships in Sarraceniaceae based on *rbc*L and ITS sequences. Syst. Bot. 21: 121–134.

Bentham, G. 1873. Notes on the classification, history, and geographical distribution of the Compositae. J. Linn. Soc. Bot. 13: 335–577.

Böhle, U.-R., H. H. Hilger & W. F. Martin. 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). Proc. Natl. Acad. Sci. U.S.A. 93: 11740–11745.

Bremer, K. 1987. Tribal interrelationships of the Asteraceae. Cladistics 3: 210–253.

———. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———. 1992. Ancestral areas—A cladistic reinterpretation of the center of origin concept. Syst. Biol. 41: 436–445.

———. 1994. Asteraceae: Cladistics and Classification. Timber Press, Portland, Oregon.

———, Jansen, R. K., P. O. Karis, M. Källersjö, S. C. Keeley, K. Kim, H. J. Michaels, J. D. Palmer & R. S. Wallace. 1992. A review of the phylogeny and classification of the Asteraceae. Nordic J. Bot. 12: 141–148.

Carlquist, S. 1976. Tribal interrelationships and phylogeny of the Asteraceae. Aliso 8: 465–492.

Cassini, H. 1826. Opuscules Phytologiques. Vols. I and II. Strasbourg, Paris.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedren, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences form the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. Amer. Midl. Naturalist 53: 478–511.

Dittrich, M. 1977. Cynareae—Systematic review. Pp. 999–1015 *in* V. H. Heywood, J. B. Harbourne & B. L. Turner (editors), The Biology and Chemistry of the Compositae. Academic Press, London.

Donoghue, M. J., R. G. Olmstead, J. F. Smith & J. D. Palmer. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79: 333–345.

Engels, B. 1993. Amplify 1.2, Software for designing, analyzing, and simulating experiments involving the polymerase chain reaction (PCR). Available free on the Internet at http://iubio.bio.indiana.edu:80.

Farris, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

Gielly, L. & P. Taberlet. 1996. A phylogeny of the European gentians inferred from chloroplast *trn*L (UAA) intron sequences. Bot. J. Linn. Soc. 120: 57–75.

—, Y.-M. Yuan, P. Küpfer & P. Taberlet. 1996. Phylogenetic use of noncoding regions in the genus *Gentiana* L.: Chloroplast *trn*L (UAA) intron versus nuclear ribosomal internal transcribed spacer sequences. Molec. Phylogenet. Evol. 5: 460–466.

Gilbert, D. 1992. Seqapp version 1.8a, a multiple sequence editor for Macintosh computers. Published electronically on the Internet (ftp.bio.indiana.edu).

Gustafsson, M. H. G. & K. Bremer. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Ham, R. C. H. J. van, H. Hart, T. 't. Mes & J. M. Sandbrink. 1994. Molecular evolution of noncoding regions of the chloroplast genome in the Crassulaceae and related species. Curr. Genet. 25: 558–566.

Higgins, D. G., A. J. Bleasby & R. Fuchs. 1992. CLUSTAL V: Improved software for multiple sequence alignment. Computer Applic. Biosci. 8: 189–191.

Hoffmann, O. 1894. Compositae. *In:* A. Engler & K. Prantl, Die natürlichen Pflanzenfamilien 4(5): 87–391. Wilhelm Engelmann, Leipzig.

Jansen, R. K. & J. D. Palmer. 1987. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (Asteraceae). Proc. Natl. Acad. Sci. U.S.A. 84: 1–5.

——— & ———. 1988. Phylogenetic implications of chloroplast DNA restriction site variation in the Mutisieae (Asteraceae). Amer. J. Bot. 75: 753–766.

——— & T. F. Stuessy. 1980. Chromosome counts of Compositae from Latin America. Amer. J. Bot. 67: 585–594.

———, H. J. Michaels & J. D. Palmer. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Syst. Bot. 16: 98–115.

———, K. E. Holsinger, H. J. Michaels & J. D. Palmer. 1990. Phylogenetic analysis of chloroplast DNA restriction site data at higher taxonomic levels—An example from the Asteraceae. Evolution 44: 2089–2105.

Karis, P. O. 1993. Morphological phylogenetics of the Asteraceae–Asteroideae, with notes on character evolution. Pl. Syst. Evol. 186: 69–93.

———, M. Källersjö & K. Bremer. 1992. Phylogenetic analysis of the Cichorioideae (Asteraceae), with emphasis on the Mutisieae. Ann. Missouri Bot. Gard. 79: 416–427.

Keeley, S. C. & R. K. Jansen. 1991. Evidence from chloroplast DNA for the recognition of a new tribe, the Tarchonantheae, and the tribal placement of *Pluchea* (Asteraceae). Syst. Bot. 16: 173–181.

Kim, K.-J. & R. K. Jansen. 1995. *ndh*F sequence evolution and the major clades in the sunflower family. Proc. Natl. Acad. Sci. U.S.A. 92: 10379–10383.

———, ———, R. S. Wallace, H. J. Michaels & J. D. Palmer. 1992. Phylogenetic implications of *rbc*L sequence variation in the Asteraceae. Ann. Missouri Bot. Gard. 79: 428–445.

Kluge, A. G. & J. S. Farris. 1969. Quantitative phyletics and the evolution of Anurans. Syst. Zool. 18: 1–32.

Lloyd, D. G. & V. L. Calder. 1991. Multi-residue gaps, a class of molecular characters with exceptional reliability for phylogenetic analysis. J. Evol. Biol. 4: 9–21.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most parsimonious trees. Syst. Zool. 40: 315–328.

Maddison, W. P. & D. R. Maddison. 1992. MacClade, Analysis of Phylogeny and Character Evolution, Version 3.0. Sinauer, Sunderland, Massachusetts.

Margush, T. & F. R. McMorris. 1981. Consensus n-trees. Bull. Math. Biol. 43: 239–244.

Merxmüller, H., P. Leins & H. Roessler. 1977. Inuleae—Systematic review. Pp. 577–601 *in* V. H. Heywood, J. B. Harbourne & B. L. Turner (editors), The Biology and Chemistry of the Compositae. Academic Press, London.

Michaels, H. J., K. M. Scott, R. G. Olmstead, T. Szaro, R. K. Jansen & J. D. Palmer. 1993. Interfamilial relationships of the Asteraceae—Insights from *rbc*L sequence variation. Ann. Missouri Bot. Gard. 80: 742–751.

Mishler, B. D., V. A. Albert, M. W. Chase, P. O. Karis & K. Bremer. 1996. Character state weighting for DNA restriction site data: Asymmetry, ancestors, and the Asteraceae. Cladistics 12: 11–19.

Palmer, J. D. 1991. Plastid chromosomes: Structure and evolution. Pp. 5–53 *in* L. Bogorad & I. K. Vasil (editors), Cell Culture and Somatic Cell Genetics in Plants, vol. 7A: The Molecular Biology of Plastids. Academic Press, Orlando.

Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithsonian Contr. Bot. 51: 1–102.

———. 1983. A generic review of the tribe Liabeae (Asteraceae). Smithsonian Contr. Bot. 54: 1–69.

Sanger, F., S. Nicklen & A. R. Coulson. 1977. DNA sequencing with chain-terminating inhibitors. Proc. Natl. Acad. Sci. U.S.A. 74: 5463–5467.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Illinois Natural History Survey, Champaign.

——— & G. J. Olsen. 1990. Phylogeny reconstruction. Pp. 411–501 *in* D. M. Hillis & C. Moritz (editors), Molecular Systematics. Sinauer, Sunderland, Massachusetts.

Taberlet, P., L. Gielly, G. Pautou & J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Pl. Molec. Biol. 17: 1105–1109.

Watrous, L. E. & Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Syst. Zool. 34: 364–366.

Wojciechowski, M. F., M. J. Sanderson, B. G. Baldwin & M. Donoghue. 1993. Monophyly of the aneuploid *Astragalus* (Fabaceae): Evidence from the nuclear ribosomal DNA internal transcribed spacer sequences. Amer. J. Bot. 80: 711–722.

Zhang, X. P. & K. Bremer. 1993. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. Pl. Syst. Evol. 84: 259–283.

A SYNOPSIS OF THE GENUS *ECHINOPEPON* (CUCURBITACEAE: SICYEAE), INCLUDING THREE NEW TAXA[1]

Alex K. Monro[2] *and Peter J. Stafford*[2]

ABSTRACT

Following a palynological and general morphological survey, the genus *Echinopepon* (Cucurbitaceae) has been divided into three species groups on the basis of stamen and pollen morphology. Three new species of *Echinopepon* are described and illustrated: *E. tultitlanapaensis* A. K. Monro & Staff., *E. belizensis* A. K. Monro & Staff., and *E. micropaniculatus* A. K. Monro & Staff.; three new combinations are proposed: *E. arachoides* (Dieterle) A. K. Monro & Staff., *E. gemellus* (DC.) A. K. Monro & Staff., and *E. glutinosus* (Cogn.) A. K. Monro & Staff.; and *E. floribundus* (Cogn.) Rose is reduced to synonymy of *E. pubescens* (Benth.) Rose. A nomenclatural review is presented, and the 18 species of the genus *Echinopepon* are listed, together with the specimens examined.

Echinopepon (Cucurbitaceae) is a genus of 18 New World taxa whose center of diversity is the Pacific coast of Mexico at middle to high elevations (above 1000 m) in the Sierra Madre Occidental and the Sierra Madre del Sur. While preparing accounts of *Echinopepon* for *Flora Mesoamericana*, it became clear that this genus was in great need of nomenclatural and systematic revision. Previous palynological work on the genus (Stafford & Sutton, 1994) and systematic treatments of the family (Jeffrey, 1964; Rangaswami Ayyangar, 1976) indicated that a synoptic revision of the genus based on macromorphological and palynological observations would be appropriate.

Echinopepon is one of four genera to have been separated from the genus *Sicyos* L. as originally proposed in *Hortus Cliffortianus* in 1737 (Stocking, 1955). In 1840, Torrey and Gray formed a separate genus of the New World taxa in the Linnaean *Sicyos*, which they named *Echinocystis*. Over the next decade *Echinocystis* was divided into three sections, *Echinocystis* ("*Euechinocystis*"), *Echinopepon*, and *Marah* (Cogniaux, 1877; Cogniaux, 1881), which were later recognized at generic rank by Watson (1887, in which he referred to *Marah* Kellogg under the synonym: *Megarrhiza* Torr.).

Despite further papers on the nomenclature and taxonomic status of *Echinopepon* (Watson, 1889; Rose, 1897; Stocking, 1955), the genus has not been comprehensively reviewed since 1881, when Cogniaux treated it as a section of *Echinocystis*.

GENERAL MORPHOLOGY

The principal characters used to classify subfamilies, tribes, and subtribes in the family Cucurbitaceae relate to the pistil, stamens, tendrils, and pollen (Cogniaux, 1877; Jeffrey, 1990). Within the tribe Sicyeae, anther arrangement, the disposition of the ovules within the ovary, fruit and seed morphology, and the branching of tendrils have been used to define the genera (Jeffrey, 1990). Naudin (1866) defined *Echinopepon* as monoecious, with 5–6-merous flowers, having three fused stamens (one unilocular and two bilocular), a unilocular ovary bearing 8–10 ovules, a 2-chambered, coriaceous, cylindrical fruit possessing a dehiscent, apical operculum, and seeds that are ovoid-compressed and corrugate.

Within the genus *Echinopepon* itself, inflorescence disposition, flower size, the disposition of the anther thecae, the relative length of the corolla lobes to the hypanthium, and fruit size, shape, and spine-length have all been used to distinguish taxa (Naudin, 1866; Cogniaux, 1877; Rose, 1897; Watson, 1889).

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[1] We thank Helen Greenop for the botanical drawings, Lourdes Rico (K) for help with Mexican localities, Carol Furness (K) for pollen samples of *Echinopepon jaliscanus*, Philipe Morat for a warm reception at P, Charlie Jarvis (BM) for help with nomenclature, Norman Robson (BM) for help with the Latin diagnoses, Bob Press (BM), Sandra Knapp (BM), and Mary Gibby (BM) for help with the manuscript, and the following herbaria for the loan of reference material: B, BR, F, GH, GOET, MA, MO, NY, P, and US.

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ANN. MISSOURI BOT. GARD. 85: 257–272. 1998.

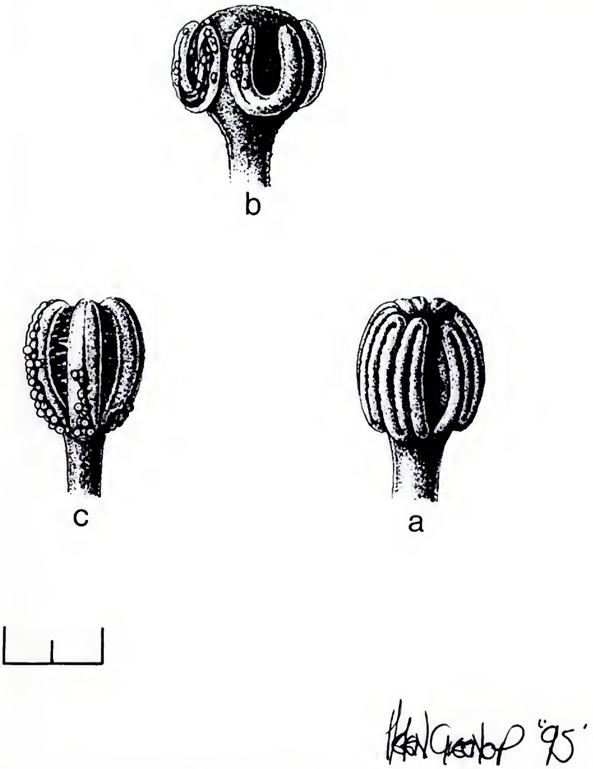

Figure 1. —a. Anther of the *Echinopepon racemosus* species group.—b. Anther of the *E. torquatus* species group.—c. Anther of the *E. paniculatus* species group. Scale bar = 1 mm.

POLLEN MORPHOLOGY

Pollen characters in the family Cucurbitaceae show a high degree of diversity and have long been perceived as indicators of relationships at all taxonomic levels. In an overview of pollen morphology in the Cucurbitaceae, Jeffrey (1964) found that his earlier conventional classifications of the family (Jeffrey, 1961, 1963) corresponded to a high degree with the natural order of taxa as indicated by pollen morphology, "much more so than any previous classification scheme." Rangaswami Ayyangar (1976)

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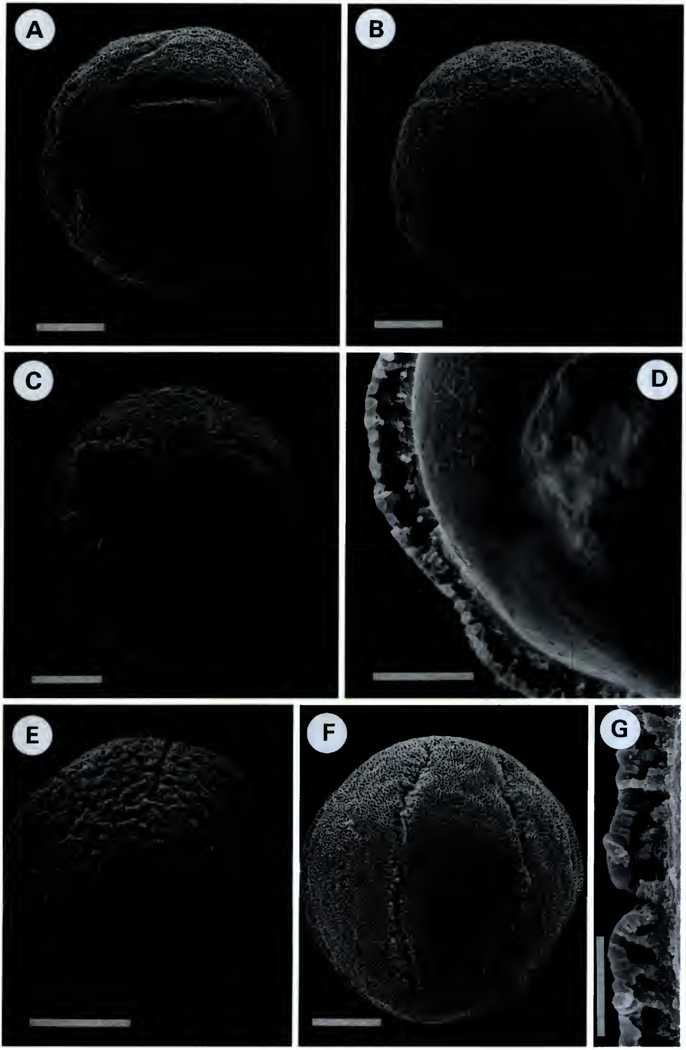
Figure 2. Polypantocolpate to irregularly syncolporate pollen type (SEM micrographs).—A. *Echinopepon racemosus* (scale bar = 25 μm).—B. *E. tultitlanapaensis* (scale bar = 25 μm).—C. *E. jaliscanus.* Note branching colpi (scale bar = 25 μm).—D. *E. racemosus.* Section showing exine stratification (scale bar = 8 μm). 6–8-zonocolpate pollen type.—E. *E. coulteri.* Polar view (scale bar = 20 μm).—F. *E. coulteri.* Equatorial view (scale bar = 25 μm).—G. *E. coulteri.* Section showing exine structure (scale bar = 5 μm).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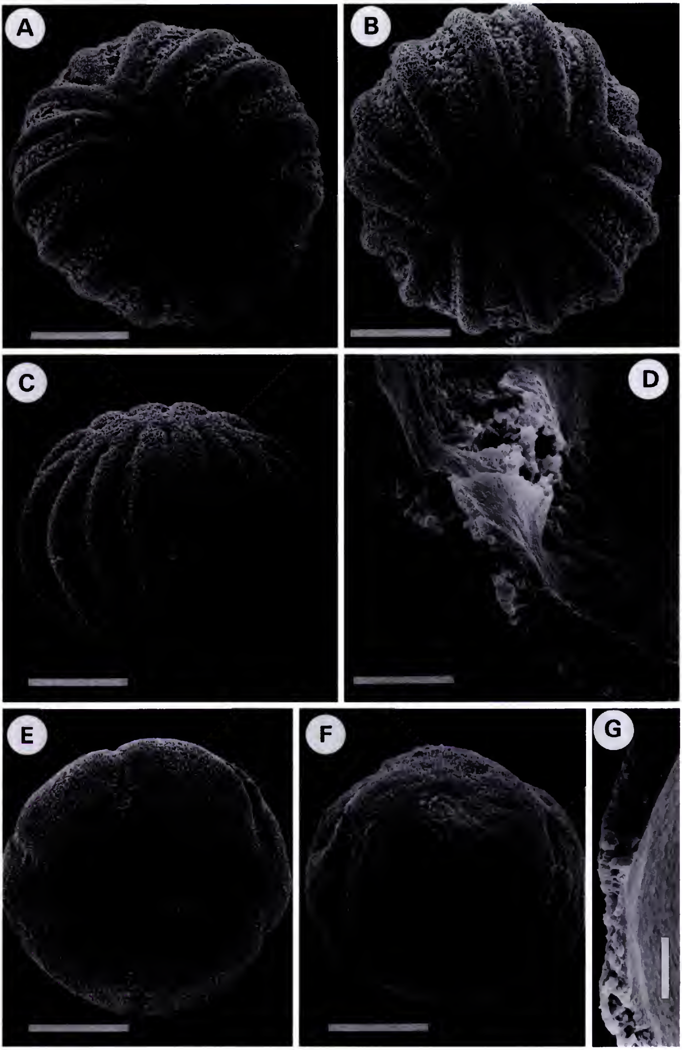
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also found that dividing the family into seven tribes on a palynological basis agreed with his own previous classification (Rangaswami Ayyangar, 1967) based on karyological characters (although it was not highly congruent with Jeffrey's classification).

Except in the case of *Echinopepon,* pollen morphological divisions within the subtribe Cyclantherinae otherwise correspond almost perfectly with present generic boundaries (Stafford & Sutton, 1994). In a general account of pollen morphology in the Cyclantherinae, Stafford and Sutton (1994) grouped the pollen of a selection of species representing each of the genera into seven main types, within which taxa can be further identified to generic and, in some cases, to specific level.

Pollen of the genus *Echinopepon* is particularly variable. Stafford and Sutton (1994) indicated that three or more conspicuous pollen types could be identified within *Echinopepon,* which conform to the groupings of Jeffrey (1980).

In the light of these distinct infrageneric groupings, an analysis of pollen characters in *Echinopepon* and related genera has been undertaken which extends preliminary work conducted by Stafford and Sutton (1994).

MATERIALS AND METHODS

All the taxa in the genus *Echinopepon* and representative taxa from the related genera *Echinocystis, Marah, Brandegea,* and *Vaseyanthus* were studied. For *Echinopepon* the extant type material was examined, although it was not always possible to include these in the palynological review. In addition, all of the specimens at K, BM, and P were seen, as were selected specimens from BR, F, GH, GOET, MA, MO, NY, and US. Specimens were examined by eye and at a magnification of ×64 to ×400 under a Leitz Wild M3C microscope.

The following characters were found to be of particular value: indument of the leaf, petiole, stem, and fruit; staminate and pistillate inflorescence type; staminate and pistillate perianth morphology; fruit spine length; seed ornamentation; and pollen morphology.

Pollen samples from each of the specimens studied were prepared by acetolysis (Erdtman, 1969). Due to the thin nature of the exine, acetolysis time was restricted in some cases to two or three minutes to minimize pollen collapse. A small portion of the acetolyzed residue was mounted on aluminum stubs for scanning electron microscopy (SEM), and the remaining material was used to prepare microscope slides for light microscopy. Observations were made using a Zeiss Axioplan light microscope and a Hitachi S800 field emission scanning electron microscope, using secondary electron detection and an accelerating voltage of 8 kV. Material for observation in the SEM was first sputter coated with gold palladium for one and a half minutes at 20 mA. The following parameters were measured: polar axis (P), equatorial axis (E), grain symmetry, number and character of colpi, exine thickness at center of mesocolpium, and ornamentation characteristics. Measurements were made from light microscope preparations in glycerine jelly, and are based on an examination of ten pollen grains from each specimen.

RESULTS

Anther morphology falls into three groups: obovoid anthers with the thecae appearing 2–3-sigmoid (Fig. 1a); subglobose anthers with the thecae appearing "horse-shoe"-shaped (Fig. 1b); and ovoid anthers with the thecae appearing "banana"-shaped (Fig. 1c).

The pollen of the genus *Echinopepon* is remarkably variable and may be grouped into four distinct pollen types:

Pollen type 1 (Fig. 2A–D). Grains polypantocolpate to irregularly syncolporate; colpi short, sometimes branched and fused, dividing the exine into angular plates; endoaperture a weak, circular thinning of the nexine, distinguishable in the scanning electron microscope but indistinct in light microscopy; exine thin and of three layers: nexine thin with covering of coarse granules, sexine 1 of sparsely distributed columellae, sexine 2 a relatively thin perforated tectum; ornamentation punctitegillate. Size range: longest axis 85–164 μm. Species: *Echinopepon racemosus, E. pringlei, E. tultitlanapaensis, E. jaliscanus.*

Pollen type 2 (Fig. 3A–D). Grains 10–16-zonocolpate, radially asymmetrical with sunken colpi; colpus long, broad and conspicuous, usually with

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Figure 3. Polyzonocolpate pollen type (SEM micrographs).—A. *Echinopepon torquatus.* Polar view (scale bar = 25 μm).—B. *E. arachoides.* Polar view (scale bar = 20 μm).—C. *E. cirrhopedunculatus.* Equatorial view (scale bar = 25 μm).—D. *E. torquatus.* Section of colpus showing exine stratification (scale bar = 5 μm). 6–9-zonocolpate to zonocolporate pollen type.—E. *E. micropaniculatus.* Polar view (scale bar = 20 μm).—F. *E. belizensis.* Equatorial view (scale bar = 20 μm).—G. *E. pubescens.* Section showing exine stratification (scale bar = 12 μm).

elaborate, distinctly granular margins and a margo (see Fig. 3A–C); exine of three layers, thickest at center of mesocolpium with corresponding thinning of nexine and sexine toward colpi: nexine thin, without covering of granules, sexine 1 of densely spaced columellae, sexine 2 a perforated tectum; ornamentation punctitegillate. Size range: P60–148 μm, E60–135 μm. Species: *Echinopepon torquatus, E. milleflorus, E. gemellus, E. cirrhopedunculatus, E. arachoides, E. minimus.* This pollen type also embraces *Apatzingania* Dieterle (herein synonymized with *Echinopepon*).

Pollen type 3 (Fig. 2E–G). Grains 6–8-zonocolpate, radially symmetrical, colpi not or only slightly sunken; colpus long and narrow without any marginal differentiation of the exine; exine thin and of three layers: nexine very thin, with covering of fine granules, sexine 1 of broadly spaced columellae, sexine 2 a relatively thin, perforated tectum; ornamentation punctitegillate to weakly verrucate. Size range: P85–135 μm, E95–110 μm. Species: *Echinopepon coulteri.*

Pollen type 4 (Fig. 3E–G). Grains 6–9-zonocolpate to -zonocolporate; colpus long, broad, and conspicuous, with granular surface, sunken; endoaperture when present a poorly defined circular pore, arranged alternately above and below the equator and rarely on the equatorial plane itself, sometimes characterized by a raised annulus; exine of three layers: nexine thin, without covering of granules, sexine 1 of densely spaced columellae, sexine 2 a perforated tectum; ornamentation punctitegillate. Size range: P74–104 μm, E70–94 μm. Species: *Echinopepon paniculatus, E. glutinosus, E. wrightii, E. pubescens, E. longispinus, E. belizensis, E. micropaniculatus.*

Discussion

On the basis of the above characters we suggest that the genus *Echinopepon* be divided into three clearly defined species groups, as outlined below. We feel that one of these, the *racemosus* group, may well represent a distinct genus. In view of the fact that this tribe (Sicyae) and subtribe (Cyclantherinae) are among the least well known in the Cucurbitaceae (Jeffrey, 1964), the related genera in this tribe require further investigation before such a taxonomic decision can be made.

The monospecific genus *Apatzingania* Dieterle shows many similarities to *Echinopepon* in both palynology and macromorphology (Dieterle, 1974). *Apatzingania* is distinguished from *Echinopepon* by the presence of a unilocular, single-seeded, indehiscent fruit. We interpret these characters as adaptational consequences of geocarpy. The pollen most closely resembles that of *E. cirrhopedunculatus,* a taxon whose fruit, although not geocarpous, is also borne on an exceptionally long peduncle and whose seeds are very similar in their ornamentation. Although the habit of geocarpy is extremely rare in the Cucurbitaceae (the only other species is the South African *Cucumis humifructus* Stent), geocarpy by itself may not be sufficient reason for distinguishing *Apatzingania* as a separate genus. In consideration of this and the morphological similarities outlined above, we include *Apatzingania arachoidea* Dieterle in the genus *Echinopepon.*

CONSPECTUS OF THE GENUS *ECHINOPEPON*

I. *E. racemosus* species group

Flowers campanulate; anther obovoid; thecae appearing tubular prior to dehiscence after which ribbon-like, folded into 2- and 3-sigmoid curves (Fig. 1a); pollen polypantocolpate to irregularly syncolporate (Fig. 2A–D).

1. *Echinopepon racemosus* (Steud.) C. Jeffrey
2. *E. pringlei* Rose
3. *E. tultitlanapaensis* A. K. Monro & Staff.
4. *E. jaliscanus* Rose

II. *E. torquatus* species group

Flowers campanulate to infundibuliform; anther subglobose; thecae "horse-shoe"-shaped, appearing tubular prior to dehiscence after which ribbon-like (Fig. 1b); pollen 10–16-zonocolpate and radially asymmetrical, the colpus margins distinctly differentiated and granular (Fig. 3A–D); or 7–9 symmetrically zonocolpate, the colpus margins undifferentiated (*E. coulteri,* Fig. 3E–G).

5. *Echinopepon torquatus* (DC.) Rose
6. *E. milleflorus* Naudin
7. *E. gemellus* (DC.) A. K. Monro & Staff.
8. *E. coulteri* (A. Gray) Rose
9. *E. cirrhopedunculatus* Rose
10. *E. arachoides* (Dieterle) A. K. Monro & Staff.
11. *E. minimus* (Kellogg) S. Watson

III. *E. paniculatus* species group

Flowers campanulate to infundibuliform; anther subglobose; thecae "banana"-shaped, appearing tubular prior to dehiscence after which ribbon-like (Fig. 1c); pollen 6–8-zonocolporate and radially asymmetrical with indistinct endoapertures, the colpus margins undifferentiated and not granular (Fig. 3E–G).

12. *Echinopepon paniculatus* (Cogn.) Dieterle
13. *E. glutinosus* (Cogn.) A. K. Monro & Staff.
14. *E. wrightii* (A. Gray) S. Watson
15. *Echinopepon pubescens* (Benth.) Rose
16. *E. longispinus* (Cogn.) Rose
17. *E. belizensis* A. K. Monro & Staff.
18. *E. micropaniculatus* A. K. Monro & Staff.

TAXONOMIC SYNOPSIS

This synopsis presents a key to all of the species of *Echinopepon* discussed above. Full descriptions are only given for previously undescribed taxa. However, full nomenclature, including synonymy and literature citations, is given for each taxon together with a list of all specimens examined.

KEY TO THE SPECIES OF *ECHINOPEPON*

All inflorescence and floral characters refer to those of staminate flowers only.

1a. Peduncle of mature fruit thread-like, 60–80 mm in length at maturity.
  2a. Fruit geocarpous, lacking an apical operculum .... *E. arachoides*
  2b. Fruit not geocarpous, with an apical operculum .... *E. cirrhopedunculatus*
1b. Peduncle of mature fruit not thread-like, more robust, 3–45 mm in length at maturity.
  3a. Peduncle of mature fruit glabrous.
    4a. Leaves weakly lobed to entire; inflorescences with fewer than 25 flowers .... *E. milleflorus*
    4b. Leaves profoundly lobed; inflorescences with more than 25 flowers .... *E. torquatus*
  3b. Peduncle of mature fruit pubescent, occasionally only sparsely so.
    5a. Hypanthium glabrous; anther thecae never folded into 2- to 3-sigmoid curves.
      6a. Corolla lobes 6–10 mm in length .... *E. paniculatus*
      6b. Corolla lobes 2–4.5 mm in length.
        7a. Petiole glabrous, although occasionally with small, white plate-like structures; anther thecae "horse-shoe"-shaped.
          8a. Unbranched portion of tendrils 4–10 mm long; pedicel 3–5 mm long .... *E. gemellus*
          8b. Unbranched portion of tendrils 10–65 mm long; pedicel 10–20 mm long .... *E. minimus*
        7b. Petiole densely pubescent; anther thecae "banana"-shaped.
          9a. Pedicel 3–5 mm long; anthers fused to form an ovoid or obovoid head .... *E. micropaniculatus*
          9b. Pedicel 8–10 mm long; anthers fused to form a subglobose head .... *E. wrightii*
    5b. Hypanthium pubescent; anther thecae "horse-shoe"-shaped, "banana"-shaped, or folded into 2- to 3-sigmoid curves.
      10a. Corolla less than 5 mm in length; anther thecae "banana"-shaped.
        11a. Pedicel 4–6 mm long; fused filaments subsessile, less than 0.2 mm long .... *E. glutinosus*
        11b. Pedicel 8–10 mm long; fused filaments ca. 1 mm long .... *E. wrightii*
      10b. Corolla 5 mm or more in length; anther thecae folded into 2–3-sigmoid curves or, "horse-shoe"-shaped.
        12a. Inflorescence branched.
          13a. Inflorescences with 12–20 flowers; fruit more than 50 mm in length .... *E. belizensis*
          13b. Inflorescences with 90–120 flowers; fruit less than 50 mm in length .... *E. longispinus*
        12b. Inflorescence unbranched.
          14a. Thecae not folded into 2- to 3-sigmoid curves.
            15a. Corolla 5–8 mm long; anther thecae "horse-shoe"-shaped .... *E. coulteri*
            15b. Corolla 12–18 mm long; anther thecae "banana"-shaped .... *E. pubescens*
          14b. Thecae folded into 2- to 3-sigmoid curves.
            16a. Corolla divided to less than half its length; peduncle of mature fruit less than 8 mm in length.
              17a. Inflorescences 80–340 mm long; corolla (12)16–22 mm diam.; anthers fused to form an obovoid head 3–3.5 mm long .... *E. jaliscanus*
              17b. Inflorescences 45–95 mm long; corolla 7–10 mm diam.; anthers fused to form an ovoid or obovoid head 2 mm long .... *E. tultitlanapaensis*
            16b. Corolla divided to more than half its length; peduncle of mature fruit greater than 10 mm in length.
              18a. Calyx lobes ca. 1 mm long .... *E. pringlei*
              18b. Calyx lobes 2–4.5(–9) mm long .... *E. racemosus*

1. Echinopepon racemosus (Steud.) C. Jeffrey, Kew Bull. 33: 357. 1979. *Momordica muricata* Vell., Fl. flumin. 10: t. 94. 1831, non Willd. (1805). *Momordica racemosa* Steud., Nomencl. bot. Ed. 2, 2: 155. 1841. *Echinocystis racemosa* (Steud.) Mart. Crov., Notul. Syst. (Paris) 9: 56. 1955. TYPE: t. 94 in Vell., Fl. flumin. 10. 1831 (holotype).

Echinopepon horridus Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 19. 1866. TYPE: material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866 (holotype, P; isotype, GH n.v.).

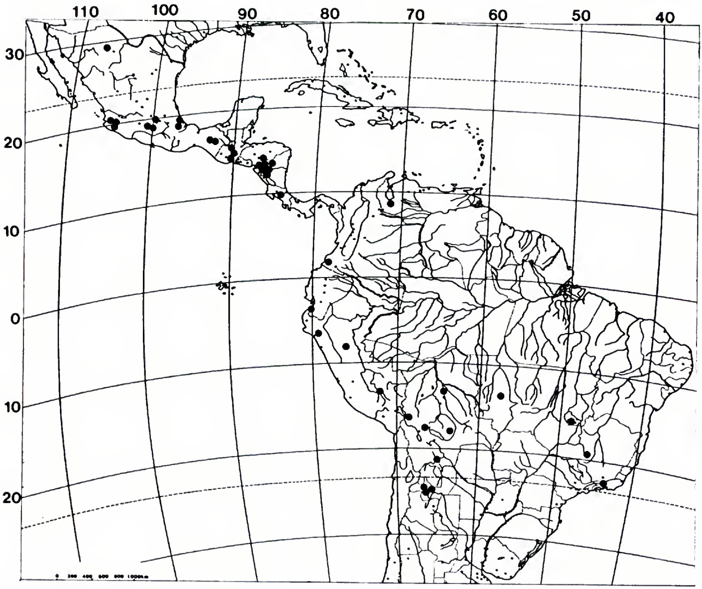

Figure 4. Distribution of *Echinopepon racemosus.*

Echinocystis polycarpa Cogn., Diagn. Cucurb. Nouv. 2: 90. 1877. TYPE: Venezuela. *Ernst 940* (syntype, BM); Venezuela. Colonia Tovar, *Fendler 503* (syntype, K); Colombia. *Triana 3017* (syntype, P).

Echinocystis lanata Cogn., Diagn. Cucurb. Nouv. 2: 92. 1877. TYPE: Mexico. *Galeotti s.n.* (syntype, BR); Mexico. *Liebmann 49* (syntype, C).

Echinocystis araneosa Griseb., Symb. fl. argent. 135. 1890. TYPE: Argentina, *Lorentz & Hieronymus 551* (holotype, BR; isotypes, GOET, K).

Distribution. From northern Mexico (Baja California Sur, Chihuahua) to northern Argentina (Salta Province) at elevations of 300–3500 m (Fig. 4).

Additional specimens examined. MEXICO. **Chiapas:** *Breedlove 13896*[3] (F*, K), *Breedlove & Raven 13157* (K, NY), *Laughlin 2166* (K), *Lira 957* (BM*). **Chihuahua:** *Gentry 2645* (K). **Jalisco:** *Lott 1315* (K), *Botter 573* (K), *Lott 609* (K), *Bullock 1267* (K). **México:** *Hinton 14694* (K), *Hinton 2524* (K), *Hinton 4963* (K), *Hinton 8619* (K). **Oaxaca:** *Carlson 4150* (F). **Veracruz:** *Nee 23573* (K), *Bourgeau 1478* (P), *Bourgeau 3266* (K). GUATEMALA. **Alta Verapaz:** *von Tuerckheim 1099* (K), *Wilson 40897* (F), *Williams 40316* (F), *Williams et al. 40361* (MO, NY, F). **Baja Verapaz:** *Hawkes 1939* (K); Jutiapa, *Steyermark 30378* (F), *Heyde & Lux 4188* (K). HONDURAS. **El Paraíso:** *Hawkes et al. 2055* (F, K), *Molina 23380* (F, MO, NY), *Molina 8688* (F), *Rodríguez 1893* (F). **Francisco Morazán:** *Chorley 374* (BM*), *Escobar 126** (MO), *Lezama 88* (MO), *Molina 24563* (NY*, MO), *Molina 730* (MO). NICARAGUA. **Estelí:** *Moreno 22570* (K), *Moreno 18406* (K), *Moreno 22352* (K), *Stevens & Krukoff 16221* (K, NY). **Jinotega:** *Molina 27288* (F), *Molina 22947* (F, NY), *Stevens 22580* (BM, K), *Williams et al. 24750* (NY), *Williams & Molina 42753* (F*). COSTA RICA. Locality unknown: *Echeverría 877* (F), *Lankester 130* (K), *León 259* (F). **Cartago:** *James 79* (F), *Cooper 5775* (K), *Echeverría 203* (F), *Torres 79* (F).

VENEZUELA. Locality unknown: *André 2809* (K), *Fendler 609* (K). BRAZIL. Locality unknown: *Pohl 1996* (K), *Burchell 6122* (K). **Distrito Federal:** *de Paula & Conçeicao 1537* (K). **Mato Grosso:** *Hatschbach 34110* (K). **Minas Gerais:** *Glaziou 19380* (K). **Rio de Janeiro:** *Glaziou 12739* (K). BOLIVIA. Locality unknown: *Buchtien s.n.* (K), *Lectrae 533* (K). **Cochabamba:** *Eyerdam 25318* (K). **La Paz:** *Fiebrig 2750* (K*), *Solomon 8921* (K). **Santa Cruz:** *Beck 6487* (K). **Tarija:** *Solomon 10073* (K). PERU. Locality unknown: **Cajamarca:** *Sagástegui 12980* (K), *Sagástegui 11419* (K). **Cuzco:** *Stork 10500* (K). **Tumbes:** *Weberbauer 7726* (K). **San Martín:** *Young 241* (K). AR-

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[3] An asterisk (*) denotes source of pollen for this study.

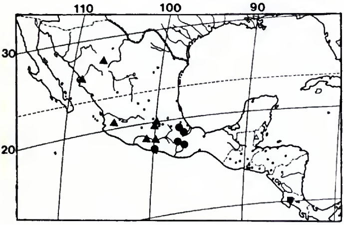

Figure 5. Distribution of *Echinopepon pringlei* (●), *E. cirrhopedunculatus* (▲), *E. micropaniculatus* (■), and *E. belizensis* (△).

GENTINA. Locality unknown: *Lorentz & Hieronymus 552* (K), *Lorentz & Hieronymus 551* (K). **Salta:** *Krapovickas 28245* (K), *Pedersen 12846* (K), *Pedersen 12842* (K).

2. Echinopepon pringlei Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Morelos: *Pringle 6183* (holotype, GH; isotypes, BM*, P).

Distribution. Southern Mexico (Veracruz to Oaxaca) at elevations of ca. 1500–2500 m (Fig. 5).

Additional specimens examined. MEXICO. **Oaxaca:** *Galeotti 1880* (K), *Barnes & Lord 474* (K), *Pringle 4958* (BM*). **Veracruz:** *Galeotti 1899* (K).

3. Echinopepon tultitlanapaensis A. K. Monro & Staff., sp. nov. TYPE: Mexico. Puebla: San Luis Tultitlanapa, *Purpus 3548* (holotype, BM*; isotypes, F, GH, MO, NY, US). Figure 6a, b.

E. pringlei Rose affinis, sed corolla profundiore incisa, antheris maioribus, staminorum longiori columna, fructu parvo, bene differt.

Leaves ca. 5.0–6.5 × 4–7 cm, lobate, chartaceous, upper and lower surface strigose to hispid, the trichomes with broad multicellular bases; lobes 3, 5, or 7, the base subsagittate, the margins remotely denticulate, the apex acuminate; petiole ca. 12–27 × 1 mm, densely villous; tendrils bifid, ca. 5–6 cm long before branching. Staminate flowers ca. 9–12, borne in a raceme ca. 4.5–9.5 cm long bearing flowers for ⅓ of its length; pedicel ca. 4–5 × 0.3 mm, pilose to villous; hypanthium ca. 3–4 × 2–3 mm, campanulate, villous; calyx lobes ca. 2 mm long, spiciform to filiform; corolla ca. 7–10 mm long, broadly campanulate, fused for ⅓ of its length, inner surface glabrous, outer surface sparsely pilose to villous, lobes ovate, the apices acute; filaments ca. 2 mm in length, fused; anthers ca. 2 mm in length, fused to form an obovoid head 1.2 mm diam.; unilocular and bilocular thecae 3-sigmoid, glabrous; pollen pantocolporate to syncolporate, colpi 18–24, branched. Pistillate flowers solitary; pedicel ca. 5 × 0.5 mm, villous; hypanthium ca. 2 × 3 mm, broadly campanulate, sparsely puberulous, constricted at base, constriction ca. 4–5 × 0.5 mm, puberulous; calyx lobes ca. 2–3 mm long; corolla ca. 10 × 7 mm, infundibuliform, fused for ⅓ of its length, inner surface glabrous, outer surface sparsely puberulous, lobes ovate, the apices acute; ovary ca. 6–7 mm, ovoid, pilose to villous, spines ca. 3–5 mm; style ca. 2–2.5 mm, glabrous; stigma ca. 1 × 1.5 mm. Fruiting peduncle ca. 4–6 mm, puberulous; fruit ca. 22–37 × 10–12 mm; spines ca. 10–17 mm, pilose; seeds 5 per locule, ca. 5 × 3.5 × 2 mm, obovoid.

Distribution. Known only from the type collection at an elevation of ca. 2000–3000 m (Fig. 7).

This species most closely resembles *Echinopepon pringlei* in that it has a broadly campanulate hypanthium, 2- and 3-sigmoid anther thecae, and pantocolpate pollen. It differs, however, with respect to the perianth and stamens. The perianth of *E. tultitlanapaensis* is larger and the corolla lobes are fused for only ⅓ of their length (compared to ⅔ in *E. pringlei*), causing them to spread to a much greater extent. In addition, the anthers of *E. tultitlanapaensis* are significantly larger, glabrous, and attached to longer filaments. The name is derived from the locality of the type collection, San Luis Tultiltanapa.

4. Echinopepon jaliscanus Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Jalisco: *Pringle 4563* (holotype, US n.v.; isotype, K).

Distribution. Pacific side of central Mexico (México to Guerrero) at elevations of ca. 1750 m (Fig. 8).

Additional specimens examined. MEXICO. **México:** *Hinton 1968* (K*), *Hinton 5004* (K), *Hinton 5211* (K), *Hinton 8257* (K). **Guerrero:** *Hinton 10978* (K*), *Hinton 11621* (K).

5. Echinopeon torquatus (DC.) Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. *Elaterium torquatum* DC., Prodr. 3: 310. 1828. *Echinocystis torquata* (DC.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: tab. 38, fig. C in Moç. & Sessé, Icones Fl. Mexic. ined. (holotype, G[4] n.v.).

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[4] A reproduction of the plates in *Icones Fl. Mexic. ined.* can be found in A. DC., Calques Fl. Mexique. 1874 (BM!).

Figure 6. Photograph of the holotype of *Echinopepon tultitlanapaensis* (*Purpus 3548*, BM).—a. Habit.—b. Staminate flower. All scale bars in mm.

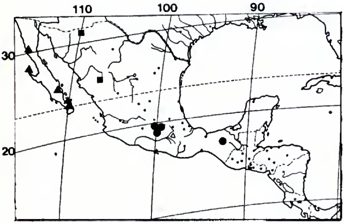

Figure 7. Distribution of *Echinopepon milleflorus* (●), *E. minimus* (▲), *E. wrightii* (■), and *E. tultitlanapaensis* (△).

Echinopepon quinquelobatus Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 18. 1866. TYPE: *Bourgeau s.n.* (material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866) (holotype, P).

Distribution. The Pacific side of Mexico at elevations of 2000–2600 m (Fig. 9).

Additional specimens examined. MEXICO. Locality unknown: *Sessé et al. 4656* (MA n.v., photograph K), *Hahn 290* (P). **Baja California Sur:** *Barclay 3107* (BM). **Chiapas:** *Ortiz 1207* (F), *Breedlove 6769* (F*), *Breedlove 12431* (F*). **Distrito Federal:** *Bourgeau 1060* (K, P). **México:** *Hinton 7648* (K).

6. **Echinopepon milleflorus** Naudin, Ann. Sci. Nat., Bot. sér. 5, 6: 18. 1866. *Echinocystis milleflora* (Naudin) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: Mexico. *Bourgeau s.n.* (material cultivated in Paris from seed sent from Mexico by Bourgeau in 1865–1866) (holotype, P).

Distribution. Pacific side of central and southern Mexico at elevations of 1500–2640 m (Fig. 7).

Additional specimens examined. MEXICO. **Chiapas:** *Laughlin 963* (K), *Laughlin 1169* (K). **Distrito Federal:** *Pringle 6516* (BM*, K, P), *Pringle 6457* (BM*, K, P), *Roe 1516* (K), *Roe 1632* (K), *Rose & Painter 7121* (BM). **México:** *Hinton 8561* (K), *Hinton 7366* (K).

7. **Echinopepon gemellus** (DC.) A. K. Monro & Staff., comb. nov. Basionym: *Elaterium gemellum* DC., Prodr. 3: 310. 1828. *Echinocystis gemella* (DC.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: tab. 38, fig. B in Moç. & Sessé, *Icones Fl. Mexic. ined.* (holotype, G n.v.).

Sicyos eremocarpus Peyr., Linnaea 30: 56. 1859–1860. TYPE: Mexico. *Heller 393* (lectotype, here designated, P); *Aschenborn s.n.* (syntype, not traced).

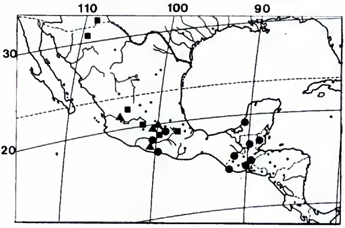

Figure 8. Distribution of *Echinopepon paniculatus* (●), *E. coulteri* (■), and *E. jaliscanus* (▲).

Distribution. Pacific side of central Mexico at elevations of ca. 2700 m (Fig. 9).

Additional specimens examined. MEXICO. **Distrito Federal:** *Schmitz 87* (BM). **Morelos:** *Schmitz 997* (BM), *Berlandier 1115** (BM).

This species was placed in the *Echinocystis* sect. *Echinopepon* by Cogniaux (1881). Rose did not incorporate this into the genus *Echinopepon* when this was resurrected by him (Rose, 1897) since he was unable to obtain herbarium material of this taxon.

8. **Echinopepon coulteri** (A. Gray) Rose, Contr. U.S. Natl. Herb. 5: 116. 1897. *Elaterium coulteri* A. Gray, Pl. wright. 2: 61. 1853. TYPE: Mexico. Zacatecas: *Coulter 51* (holotype, GH; isotype, K).

Echinopepon confusus Rose, Contr. U.S. Natl. Herb. 5: 115. 1897. TYPE: U.S.A. New Mexico: *Thurber 1122* (holotype, GH).

Echinopepon nelsoni Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. TYPE: Mexico. Oaxaca: *Nelson 1878* (holotype, US).

Echinopepon parvifolius Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. TYPE: Mexico. Oaxaca: *Conzatti 139* (holotype, US).

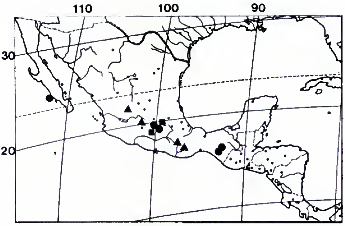

Figure 9. Distribution of *Echinopepon torquatus* (●), *E. pubescens* (▲), and *E. gemellus* (■).

Distribution. Southwestern United States (New Mexico) to southern Mexico (Veracruz) at elevations of ca. 2000–2350 m (Fig. 8).

Additional specimens examined. U.S.A. **New Mexico:** *Metcalfe 1348* (BM*). MEXICO. **Distrito Federal:** *Bourgeau 789* (K, P), *Hahn 162* (P*). **Guanajuato:** *Haag & Schmidt 598* (K). **Morelos:** *Bourgeau 1388* (P), *Greene 17011* (K). **Veracruz:** *Nee & Soulé 33055* (K*). **Zacatecas:** *Wright s.n.* (K), *Rose 2699* (K).

Balls & Gourlay 530 (BM), collected in Puebla, Mexico, at 2600 m elevation, differs from all other specimens examined in having significantly larger flowers and relatively longer stamens.

9. Echinopepon cirrhopedunculatus Rose, Contr. U.S. Natl. Herb. 5: 115. 1897. TYPE: Mexico. Sonora: *Palmer 634* (holotype, US; isotype, K).

Distribution. Northern to central Mexico at elevations of ca. 500–1000 m (Fig. 5).

Specimens examined. MEXICO. **Chihuahua:** *Gentry 2355* (K). **Guerrero:** *Hinton et al. 10496* (K, P). **Jalisco:** *Pringle 4562* (BM*). **México:** *Hinton 1364* (K*), *Hinton 9257* (K), *Hinton 6438* (K), *Hinton 8483* (K).

10. Echinopepon arachoides (Dieterle) A. K. Monro & Staff., comb. nov. Basionym: *Apatzingania arachoidea* Dieterle, Brittonia 26: 131. 1974. TYPE: Mexico. Michoacán: *Dieterle 4379* (holotype, MICH n.v.; isotype, K).

Distribution. Pacific Coast of Mexico (Michoacán to Guerrero) at an elevation of ca. 300 m.

Additional specimen examined. MEXICO. **Guerrero:** *Hinton 6424* (K*).

11. Echinopepon minimus (Kellogg) S. Watson, Proc. Amer. Acad. Arts 24: 52. 1889. *Marah minima* Kellogg, Proc. Calif. Acad. Sci. 2: 18. 1863. *Elaterium minimum* (Kellogg) S. Watson, Proc. Amer. Acad. Arts 12: 252. 1877. TYPE: Mexico. Baja California Sur: Cedros Island, *Streets s.n.* (lectotype, designated by Stocking (1955), US n.v.; isolectotypes, GH n.v., NO photograph).

Distribution. Limited to Baja California Sur at elevations of ca. 200–1000 m (Fig. 7).

Additional specimens examined. MEXICO. **Baja California Sur:** *Brandegee s.n.* (K photo, US), *Palmer 719* (K), *Anthony 299* (K), *Gentry 4125* (K), *Palmer 65* (K), *Wiggins 14436* (K*), Aug. 1859–Jan. 1860, *Xantus de Vesey* (GH).

12. Echinopepon paniculatus (Cogn.) Dieterle, Fieldiana, Bot. 24(11): 342. 1976. *Echinocystis paniculata* Cogn., Diagn. Cucurb. Nouv. 2: 90. 1877. TYPE: Mexico. Guerrero: *Galeotti s.n.* (holotype, BR).

Distribution. Central Mexico (Guerrero) to southern Guatemala (Chiquimula) at elevations of 50–1360 m (Fig. 8).

Additional specimens examined. MEXICO. **Campeche:** *Andres & Nee 157* (K). **Chiapas:** *Lira et al. 930* (BM), *Lira et al. 942* (BM), *Soto 13269* (BM). **Guerrero:** *Mexía 8703* (K), *Hinton 6623* (K), *Hinton 8509* (K). BELIZE. *Bartlett 12882* (F), *Lundell 2190* (F), *Liesner & Dwyer 1626* (K, MO). GUATEMALA. Locality unknown: *Bernoulli & Cario 2838* (K). **Chiquimula:** *Standley 73737* (F). **Huehuetenango:** *Molina 21325* (F), *Molina & Molina 30171* (F, MO), *Williams 41113* (F*), *Williams 41364* (F*). **Jalapa:** *Standley 77384* (F), *Standley 76495* (F*). **Petén:** *Ortiz 547* (MO*).

13. Echinopepon glutinosus (Cogn.) A. K. Monro & Staff., comb. nov. Basionym: *Echinocystis glutinosa* Cogn., Diagn. Cucurb. Nouv. 2: 93. 1877. TYPE: *Bourgeau s.n.* 1866 (material cultivated in Paris in 1867 from seed sent from Mexico by Bourgeau in 1866) (holotype, P*).

Distribution unknown. Mexico; known only from the type collection.

This species was placed in *Echinocystis* sect. *Echinopepon* by Cogniaux (1881). Rose did not incorporate this into the genus *Echinopepon* when this was resurrected by him (Rose, 1897), since he had been unable to obtain herbarium material of this taxon.

14. Echinopepon wrightii (A. Gray) S. Watson, Bull. Torrey Bot. Club 14: 158. 1887. *Elaterium wrightii* A. Gray, Pl. wright. 2: 61. 1853. TYPE: Mexico. Sin. loc., *Wright 1090* (holotype, US; isotypes, GH-257*, -259* & -260).

Distribution. Central Mexico at elevations of ca. 1000–2000 m (Fig. 7).

Additional specimen examined. MEXICO. **Zacatecas:** *Emory 397* (K).

The GH isotype contains two different types of pollen: sheet 260 has zonocolpate, spinulose pollen of a type found in the Sicyinae, whereas sheets 257 and 259 have 7–9-zonocolpate, non-spinulose pollen similar to that of the holotype. It is not, however, possible to say with any certainty whether this is the result of a mixed collection or whether this species has dimorphic pollen, since sheet 260 does not have any additional, sufficiently mature flowers from which to draw a conclusion.

15. Echinopepon pubescens (Benth.) Rose, Contr. U.S. Natl. Herb. 5: 118. 1897. *Elaterium pubescens* Benth., Pl. hartw. 6. 1839. *Echinocystis pubescens* (Benth.) Cogn., Diagn. Cucurb. Nouv. 2: 88. 1877. TYPE: Mexico. Aguascalientes: *Hartweg 15* (holotype, K; isotype, BM*).

Echinocystis floribunda Cogn., Diagn. Cucurb. Nouv. 2: 89. 1877. *Echinopepon floribundus* (Cogn.) Rose, Contr. U.S. Natl. Herb. 1: 116. 1897. TYPE: Mexico. Oaxaca: *Liebmann 53* (syntype, B missing and probably destroyed); *Liebmann 28* (syntype, B missing and probably destroyed); *Galeotti 1890* (lectotype, here designated, P; isolectotypes, G, K, W).

Distribution. Central to southern Mexico (Aguascalientes to Oaxaca) at elevations of ca. 1500–1800 m (Fig. 9).

Additional specimens examined. MEXICO. Locality unknown: *Hartweg s.n.* (K). **Michoacán:** *Pringle 4346* (BM*, K). **Oaxaca:** *Galeotti 1890* (K, P), *Pringle 4957* (BM*, K), *Purpus 4204* (BM*, K), *Rose 11313* (K).

16. Echinopepon longispinus (Cogn.) Rose, Contr. U.S. Natl. Herb. 5: 117. 1897. *Echinocystis longispina* Cogn., Diagn. Cucurb. Nouv. 2: 91. 1877. TYPE: Mexico. Veracruz: *Schiede 1080* (lectotype, here designated, GH; isolectotype, B missing and probably destroyed).

Distribution. Central Pacific side of Mexico at elevations of ca. 1200 m.

Additional specimens examined. MEXICO. **Morelos:** *Pringle 11301* (K), *Ravias 541* (P), *Hahn s.n.* (K, P).

17. Echinopepon belizensis A. K. Monro & Staff., sp. nov. TYPE: Belize. Cayo: El Cayo, *Bartlett 11989* (holotype, NY*; isotypes, GH, US). Figure 10a, b.

E. pubescenti (Benth.) Rose affinis, sed hypanthio latissimo brevissimoque, corollae lobis brevibus latisque, corollae glandis pedicellatis, antheris subsessilibus, bene differt.

Leaves ca. 5.0–7.5 × 4.5–7.0 cm, lobate, membranous, upper surface puberulous and minutely pustulate, lower surface puberulous, lobes 3, 5, or 7, the base cordate, the margins remotely denticulate, the apex acuminate; petiole ca. 30–50 × 1 mm, densely puberulous; tendrils bifid, ca. 4.5 cm long before branching. Staminate flowers ca. 12–20, borne in a panicle ca. 60 mm long, bearing flowers for ⅔ of its length; pedicels ca. 11 × 0.2 mm, puberulous; hypanthium ca. 1 × 2 mm, patelliform, glabrous; calyx lobes dentate, ca. 0.5 mm long, glabrous; corolla ca. 5–6 × 10–12 mm, patelliform, fused for ⅓ of its length, inner surface stalked glandular, outer surface farinaceous, lobes ovate, the apices acuminate; filaments ca. 0.1 mm in length, fused; anthers ca. 1–1.5 mm in length, fused to form an ovoid to obovoid head 0.5–0.8 mm diam., subsessile; unilocular and bilocular thecae semi-sigmoid or "J"-shaped, microechinate; pollen ca. 7-zonocolporate, radially asymmetrical (there may be a raised annulus-like structure encircling the pore, as present in the related genus *Rytidostylis*, clearly seen in SEM but indistinct in LM). Pistillate flowers 1-2, solitary or borne in a fascicle; pedicel ca. 4–15 × 0.5 mm, glabrous, sparsely puberulous; hypanthium ca. 2.5 × 4 mm, campanulate, sparsely puberulous, constricted at base, constriction ca. 3.5–4.5 × 0.5 mm, densely puberulous; calyx lobes ca. 0.5 mm long; corolla ca. 7 × 9 mm, narrowly patelliform, fused for ⅓ of its length, inner surface stalked glandular, outer surface glabrous, lobes ovate, the apices acuminate; ovary ca. 3–4 mm, ovoid, puberulous, spines ca. 1.5–3 mm; style ca. 0.5 mm, glabrous; stigma ca. 0.8 × 1 mm. Fruit not seen.

Distribution. Known only from the type collection made at 200 m (Fig. 5).

This species most closely resembles *Echinopepon pubescens* in having ovoid anthers and zonocolporate pollen. It differs, however, in hypanthium shape, corolla shape, corolla indument, and anther disposition. The staminate and pistillate perianths in *E. pubescens* are composed of a relatively long, narrow campanulate hypanthium from which spread out the deeply divided, long, narrow and recurving corolla lobes; in *E. belizensis*, however, the hypanthium is very broad, and plate-like, the corolla lobes less divided, shorter, broader and not recurved. The glands covering the inner surface of the corolla lobes are stalked in *E. belizensis* and sessile to subsessile in *E. pubescens*. The anthers of *E. belizensis* are subsessile, while those of *E. pubescens* are supported by a filament 1–1.5 mm long. The two species also differ greatly in their altitudinal ranges, *E. pubescens* not having been collected below 1500 m while *E. belizensis* was collected at ca. 200 m.

18. Echinopeon micropaniculatus A. K. Monro & Staff., sp. nov. TYPE: Costa Rica. Guanacaste: 2 km E of Hacienda Palo Verde, Comelco property, *Keeler 192* (holotype, MO*). Figure 11a, b.

E. paniculato (Cogn.) Dieterle affinis, sed floribus minoribus, antheris ovoideis, bene differt.

Leaves ca. 6–10 × 5–9.5 cm, lobate, subchar-

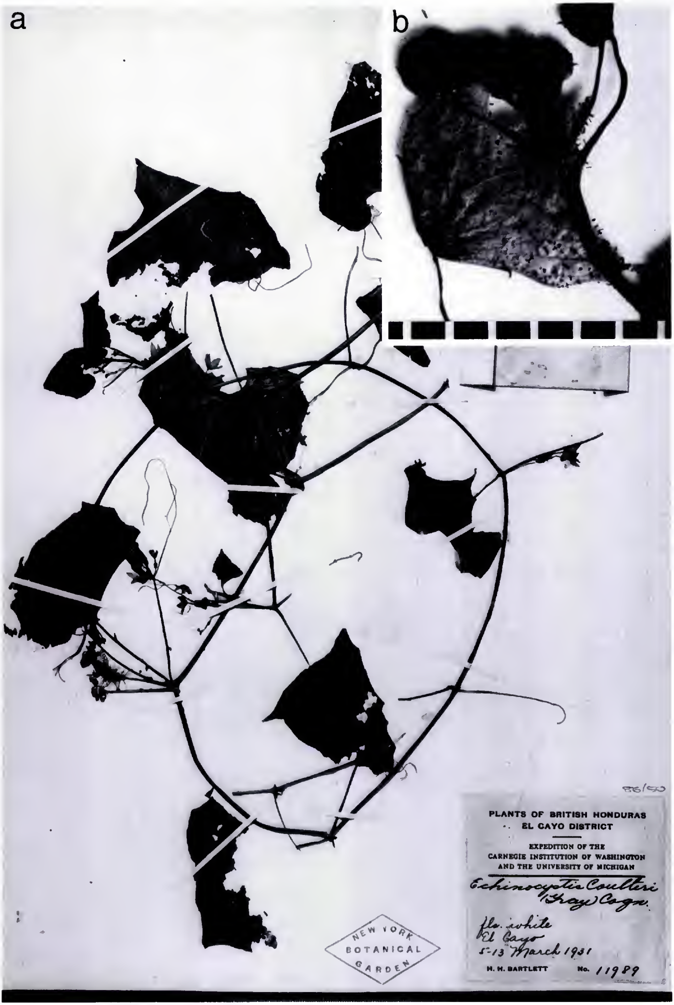

Figure 10. Photograph of the holotype specimen of *Echinopepon belizensis* (*Bartlett 11989*, NY).—a. Habit.—b. Staminate flower. All scale bars in mm.

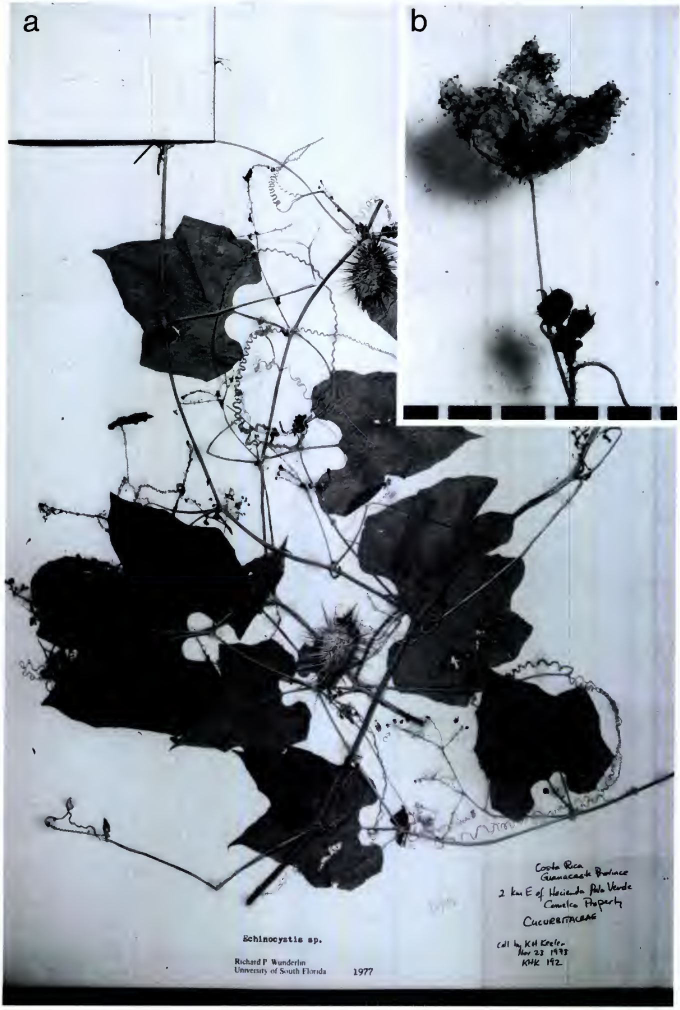

Figure 11. Photograph of the holotype specimen of *Echinopepon micropaniculatus* (*Keeler 192*, MO).—a. Habit.—b. Staminate flower. All scale bars in mm.

taceous to chartaceous, upper and lower surface villous, lobes 3, 5, or 7, the base sagittate to cordate, the margins remotely denticulate, the apex acuminate; petiole ca. 25–40 × 1.5–2 mm, densely villous; tendrils trifid, ca. 2.5–9.0 cm long before branching. Staminate flowers ca. 50–60, borne in a panicle ca. 80–100 mm long bearing flowers for ⅓–½ of its length; pedicels ca. 3–5 × 0.3 mm, pilose; hypanthium ca. 1.5 × 2 mm, broad campanulate to patelliform, glabrous; calyx lobes deltate, ca. 0.3 mm long; corolla ca. 2 × 3 mm, patelliform to broadly campanulate, fused for ½ of its length, inner surface subsessile, outer surface glabrous, lobes elliptic to ovate, the apices acute to obtuse; filaments ca. 1.5 mm in length, fused; anthers ca. 1 mm in length, fused to form an ovoid to obovoid head 0.4 mm diam.; unilocular and bilocular thecae semi-sigmoid or "J"-shaped, glabrous; pollen ca. 6-zonocolporate, radially asymmetrical. Pistillate flowers not seen. Fruiting peduncle ca. 5 mm, pilose; fruit ca. 30 × 14 mm; spines ca. 15–16 mm, sparsely pilose; seeds 2 per locule, ca. 6 × 3.5 × 1–1.5 mm, rectangular, armored.

Distribution. This species is known only from the type collection (Fig. 5).

Echinopeon micropaniculatus most closely resembles *E. paniculatus* in the morphology of the perianth and pollen. It differs significantly, however, in flower size and anther structure. The flowers of *E. micropaniculatus* are ca. 3 mm in diameter, while those of *E. paniculatus* are 7–14 mm in diameter.

Literature Cited

Cogniaux, A. 1877. Diagnoses de Cucurbitacées nouvelles et observations sur les espèces critiques. Deuxième fascicule. F. Hayez, Brussels.

———. 1881. Cucurbitaceae. Pp. 798–820 *in* A. De Candolle A., Monographiae Phanerogamarum 3. G. Masson, Paris.

Dieterle, J. V. A. 1974. A new geocarpic genus from Mexico: *Apatzingania* (Cucurbitaceae). Brittonia 26: 129–132.

Erdtman, G. 1969. Handbook of Palynology. Munksgaard, Copenhagen.

Jeffrey, C. 1961. Notes on Cucurbitaceae including a proposed new classification of the family. Kew Bull. 15: 337–371.

———. 1963. Notes on Cucurbitaceae including a proposed new classification of the family. Kew Bull. 16: 483.

———. 1964. A note on pollen morphology in Cucurbitaceae. Kew Bull. 17: 473–477.

———. 1980. A review of the Cucurbitaceae. Bot. J. Linn. Soc. 81: 233–247.

———. 1990. Appendix: An Outline Classification of the Cucurbitaceae. Pp. 449–463 *in* D. M. Bates, R. W. Robinson & C. Jeffrey (editors), Biology and Utilization of the Cucurbitaceae. Comstock Publishing, Cornell Univ. Press, Ithaca.

Naudin, C. H. 1866. Cucurbitacées nouvelles cultivées au Muséum d'Histoire Naturelle en 1863, 1864, et 1865. Ann. Sci. Nat., Bot., sér. 5, 6: 17–19.

Rangaswami Ayyangar, K. 1967. Taxonomy of Cucurbitaceae. Bull. Natl. Inst. Sci. India 34: 380–396.

———. 1976. Palynological highlights of Cucurbitaceae. Advances Pollen-Spore Res. 2: 54–59.

Rose, J. N. 1897. Studies of Mexican and Central American plants. Contr. U.S. Natl. Herb. 5: 109–144.

Stafford, P. J. & D. A. Sutton. 1994. Pollen morphology of the Cyclantherinae C. Jeffr. (Tribe Sicyeae Schrad., Cucurbitaceae) and its taxonomic significance. Acta Bot. Gallica 141: 171–182.

Stocking, K. M. 1955. Some considerations of the genera *Echinocystis* and *Echinopepon* in the United States and northern Mexico. Madroño 13: 84–100.

Torrey, J. & A. Gray. 1840. A flora of North America 1: 542. Wiley & Putnam, New York.

Vellozo, J. M. da C. 1831 ["1827"]. Florae Fluminensis Icones. A. Senefelder, Paris.

Watson, S. 1887. The genera *Echinocystis*, *Megarrhiza* and *Echinopepon*. Bull. Torrey Bot. Club 14: 155–158.

———. 1889. Contributions to American botany. Proc. Amer. Acad. Arts 24: 51–52.

THE GENERA *CESTRUM* AND *SESSEA* (SOLANACEAE: CESTREAE) IN VENEZUELA[1]

Carmen Benítez de Rojas[2] *and William G. D'Arcy*[3]

ABSTRACT

Solanaceae, tribe Cestreae, is represented in Venezuela by the two genera *Cestrum* (31 species) and *Sessea* (1 species). This treatment distinguishes the genera and their species by dichotomous keys. All species are provided with descriptions, illustrations, distribution maps, and notes on their appearances, phenology, and geographical ranges. A list of specimens seen that were made in Venezuela is also provided.

Tribe Cestreae of the Solanaceae is represented in Venezuela by two genera, *Cestrum* L. and *Sessea* Ruiz & Pav. Plants of the tribe are shrubs, trees, and vines with entire leaves, and the flowers have tubular corollas that are long-exserted from small calyces. The flowers of *Cestrum* and *Sessea* are so similar that the genera usually cannot be distinguished without fruit. *Cestrum* has a juicy berry and more or less prismatic seeds, while *Sessea* has a dehiscent capsule with winged seeds.

This paper, based on field, herbarium, and greenhouse studies, revises the Venezuelan species in the two genera. A summary of the work with statistics on ranges, ecology, and other relationships is being published elsewhere (Benítez & D'Arcy, in press). Photographs of representative species (Figs. 1, 2) and line drawings and distribution maps for all species (Figs. 3–62) are provided. Data for specimens cited in this paper and that support statements about distribution outside of Venezuela have been entered into TROPICOS, the Missouri Botanical Garden computer database of scientific information, where they may be accessed via the Internet at http://mobot.org/pick/search/pick.html.

SYSTEMATICS

Tribe Cestreae embraces plants with near-actinomorphic flowers, small, persistent calyces, long, narrowly tubular corollas, small, longitudinally dehiscent anthers held near the corolla mouth, and superior ovaries.The tribe includes three closely related genera, *Cestrum* (150 species), *Sessea* (25 species), and *Vestia* Willd. (1 species), and two more distant monospecific genera, *Metternichia* Mikan (eastern coastal Brazil), and *Tsoala* Bosser & D'Arcy (Madagascar). *Cestrum* ranges from northern Mexico and southern Florida to southern Chile. *Sessea* is restricted to tropical South America except for a dubious record from Hispaniola, and its diversity is centered in Andean regions, especially Ecuador. *Vestia* is restricted to south–central Chile. It has flowers similar to those of *Cestrum* and *Sessea* but much larger and a capsular fruit with more or less prismatic seeds. The tribe is a member of subfamily Cestroideae, which in recent phylogenetic schemes (Olmstead & Palmer, 1992; Olmstead et al., in press) is basal to the other subfamily, Solanoideae. *Cestrum* was revised for Venezuela by Pittier in 1932 and in its entirety by Francey in 1935–1936, who recognized 257 species. Within *Cestrum*, a section *Habrothamnus* has been recognized, which encompasses a small suite of showy species ranging from Mexico to Nicaragua, but the remainder of the genus (sect. *Cestrum*) is still undivided. *Sessea* was revised by Bitter (1922), who divided the genus into series. It was revised again by Francey (1934), who ignored the series of Bitter and recognized 23 species. D'Arcy (1979) suggested that *Sessea* may not have nearly as many as 23 species.

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Figure 1. Selected *Cestrum* species.—A. *Cestrum petiolare.* Inflorescence on branch (after *D'Arcy 18235*).—B. *Cestrum bigibbosum.* Fruits on an arching branch (after *Benítez 5083*).

DESCRIPTIVE NOTES

Most Venezuelan species of Cestreae are shrubs or small trees, but some *(Cestrum humboldtii, C. lindenii, C. microcalyx, C. racemosum)* become large trees, and three (*C. scandens, S. strigilatum, C. reflexum)* are scrambling or twining vines. Most species coppice readily and root at the nodes when the stems are cut off, thus altering the growth form from a tree with a single trunk to a many-stemmed shrub.

The leaves of Solanaceae are estipulate, but those of Cestreae are often paired, a normal "major" leaf accompanied by a much smaller, often sessile "minor" leaf, a condition sometimes suggestive of stipules (Fig. 57, *Cestrum tomentosum*). An interpretation of the minor leaves of Cestreae as homologous with those in subfamily Solanoideae (see Eichler, 1875; Danert, 1958) seems reasonable, but morphological study to verify such homology is desirable. Minor leaves are more commonly present on seedlings and turions and are caducous in many species. They are a conspicuous and useful taxonomic character in some species (*C. mariquitense, C. petiolare, C. tomentosum, C. humboldtii*). Leaves are often malodorous, even when not bruised.

The inflorescences of Cestreae are mostly several- to many-flowered clusters among the foliage of ascending branches, but in a few species such as *C. megalophyllum,* they are more or less cauliflorous in the axils of shoots on the main stem or trunk. Bracts are commonly present, often in a series grading from normal leaves to small structures subtending branches of the inflorescence or individual flowers. In addition, a small, linear, and often caducous bract termed a bracteole subtends each pedicel. Pedicels, which usually appear to be basal contractions of the calyx, sometimes extend several millimeters down to the subtending bracteole, but in many species they are obsolete, so that the calyx is sessile in the axil of the bracteole, and sometimes on the peduncle or inflorescence branch: in many cases, where there is no peduncle or stalk below the bracteole, flowers are termed sessile, even when a short pedicel is present above the bracteole. [In this sense, the term sessile means lacking a stalk below the bracteole.]

The flowers of *Cestrum* and *Sessea* all have tubular corollas exserted from small calyces. The flowers of most Venezuelan Cestreae species open in the evening or at night and are closed during the day. When open, the corolla lobes spread widely or are reflexed (Fig. 2A, B), and a sweet fra-

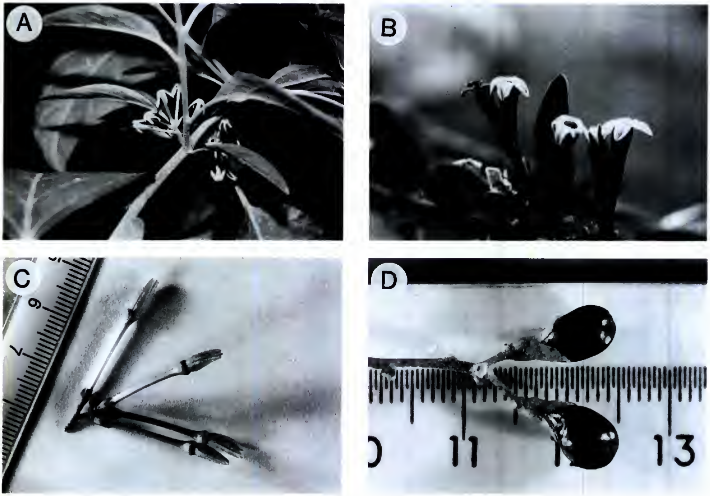

Figure 2. Selected *Cestrum* species.—A. *Cestrum latifolium.* Night view of inflorescence (*Benítez 5079*).—B. *Cestrum buxifolium.* Flowers, midday view, greenhouse plant (*D'Arcy 18236*).—C. *Cestrum alternifolium.* Flowers, daytime view, greenhouse plant (*D'Arcy 18206*). Note expansion at top of corolla tube.—D. *Cestrum tomentosum.* Fruits, greenhouse plant (*D'Arcy 17838*).

grance is emitted. In these species, thin, mostly pubescent, marginal tissue between the corolla lobes folds out of sight during the day (Fig. 2C).

The calyces of Venezuelan Cestreae are usually apically pubescent with the margins ciliate and the tips "tufted." They may have other pubescence as well. Corollas are mostly inconspicuous greenish, yellowish, or whitish, and nocturnal or crepuscular in opening, but in some species they are showy with bright red, orange, or other colors and open during the day. In Venezuela, only *C. lindenii* and *C. diurnum* have showy corollas, the first of these bright yellow and purple, and the second bright white. Red, blue, purple, and pink flowers, found in species of *Cestrum* in other areas, are absent from the suite of species occurring in Venezuela, although some species have violet or purplish markings on otherwise whitish or yellowish corollas.

The corollas of Cestreae are inserted about halfway up the height of the ovary, but the distance between the point of corolla insertion and the base of the calyx, either the cupular portion or the narrowed, pedicel-like portion, varies between species. In this treatment, corolla length refers to the distance between the point of corolla insertion and the tip of the corolla lobes, a measurement that requires dissection of the flower. Flower length refers to the distance from the bracteole (base of the pedicel) to the tip of the corolla lobes, a measurement that can be made without dissection.

The stamens are of similar but usually slightly unequal lengths, and anthers are clustered just inside the corolla mouth. Pubescence, size, and shape of the filaments are of taxonomic utility. Filaments are adnate to the corolla tube for different distances from the corolla insertion and are often evident as raised areas along the corolla interior. The 0.5–1.5-mm-long tumid region where the filament is inserted in the corolla tube is termed the insertion. In some species, the insertion is not adnate to the corolla tube for its entire length, but is free in its distal part. In some species the insertion is associated with umbos or teeth, and when the filament departs abruptly from the corolla wall, it is termed geniculate. Above the insertion, the filament is glabrous, slender, and of roughly uniform diameter except at the apex, where it narrows into a neck that supports the versatile anther.

In Venezuelan members of Cestreae, the stigma is usually situated within the corolla mouth and above the anthers, but in *Cestrum diurnum* and *Sessea corymbiflora* it is exserted from the corolla. In *Sessea,* the stigmas of the species examined are positioned laterally or obliquely on the style (Fig. 61H), while in *Cestrum* and *Vestia* the stigmatic surface is apical. If this oblique stigma is constant in other species of *Sessea,* it may serve in addition to characters of the fruit to separate *Sessea* from the other two genera. Most species of *Cestrum* have fewer than 16 ovules and many have 8 or fewer, but *C. petiolare* is unusual in the genus in having as many as 32 ovules. Seed number varies with species and in individual fruits, and the size and shape of seeds appear to depend on seed number, 1- and 2-seeded fruits bearing larger seeds. Seed shape is variable, seemingly depending on the position of neighboring seeds in the berry. In some species, such as *C. diurnum,* the placental area remains juicy long after the mesocarp is dry, providing a moisture reward to dispersers over an extended period. Fruits of most native Venezuelan species have dark and juicy or fleshy mesocarp, but *C. diurnum* and a number of species in Central America have white fruits with spongy mesocarp.

POLLINATION AND DISPERSAL

The factors selecting for morphological diversity in *Cestrum* are largely unknown. In Mexico, red- and yellow-flowered and red-fruited species appear to be associated with hummingbird pollination (D'Arcy, in press), and this syndrome may also be represented in the bright yellow-flowered *C. petiolare* in Venezuela. Flowers of most other species open at dawn or dusk or at night, and are sweet-scented. Many species bloom sporadically, producing few or many blossoms over a short period and then, after weeks or months, producing another flush of blooms. In some species, such as *C. latifolium* and *C. alternifolium,* plants are "mass-bloomers," producing a display of hundreds of flowers lasting only one or two days. In greenhouse plants we found that flowers of *C. alternifolium, C. latifolium, C. mariquitense, C. megalophyllum, C. racemosum,* and *C. strigilatum* had undetectable amounts of nectar. Nectars produced by other species vary greatly in sugar concentration and composition. Nectar content was reported by Percival (1965) and Bernardello et al. (1994), and we studied eight different greenhouse-grown species. Nectars in our eight species had concentrations ranging from 11% to 40%. Nectars in most species were sucrose-dominant, but some had more fructose than sucrose. In nectar of the yellow-flowered *C. corymbosum* Schltdl., which was characterized as hummingbird pollinated, Gottsberger et al. (1984) reported a content of amino acids. Bernardello et al. (1994) recorded phenols, lipids, and amino acids in nectar from *Cestrum* cf. *bracteatum* Link & Otto. Thus, while some data have been reported about Cestreae nectar, the picture is still poorly sketched.

Overland (1960) studied the temporal opening and closing of flowers of *Cestrum nocturnum* and found that these movements are independent of light but are affected by temperature. She reported that scent emanates from the tips of the corolla lobes.

Actual pollinator observations have been published for only one species, *Cestrum alternifolium.* In Costa Rica, Haber and Frankie (1989) and White et al. (1994) examined pollination of *C. alternifolium* by hawkmoths (Sphingidae), which are night-flying insects commonly attracted to white flowers with strong fragrance. Similarities of many other species of *Cestrum* suggest that they, too, are sphingid pollinated. Hummingbirds and sphingids are characterized as being drawn to plants with sucrose-dominant nectars (Procter et al., 1996) such as those in *Cestrum,* which might facilitate shifts between or sharing by these pollinators in flowers such as those of *C. petiolare* and *C. aurantiacum,* where the corolla mouth is large enough to permit access by hummingbirds.

Fruits of *Cestrum* are mostly juicy berries presumably dispersed by birds, but bat dispersal cannot be ruled out. Bat dispersal of fruits and seeds reported for several species with strongly foetid foliage, e.g., *Solanum* sect. *Brevantherum* (Fleming, 1988) and *Cleome* (Ruiz Zapata, 1993), may be enhanced by the odor of the leaves. Thus, species of *Cestrum* with foetid foliage and more or less leathery fruits (*C. glabrescens*?) may be suspected of attracting bats to disperse their fruits.

USES AND TOXICITY

A few species of *Cestrum,* none native to Venezuela, are cultivated for ornament. *Cestrum nocturnum* is grown for the evening fragrance of its flowers, and *C. aurantiacum* for its showy orange-yellow flowers. *Cestrum racemosum* is sometimes cultivated as a city park tree. The fruit pulp of *Cestrum buxifolium* is used as writing ink.

The Solanaceae are well known for having a wide array of alkaloids (Romeike, 1978), and species of *Cestrum* have been implicated in more than one toxicity system. One system mimics vitamin D attributes and influences calcium uptake (Prema & Raghuramulu, 1994), leading to a condition referred to as calcinosis (Wasserman, 1978). Thus, *C. diurnum*, occasionally cultivated in Venezuela, has been implicated in fatal poisoning of horses in Florida (Krook et al., 1975). This toxicity is also found in *Solanum glaucophyllum* Desv. (*S. malacoxylon* Sendtn.) in Brazil, producing an illness called "enteque seco" (Wasserman, 1974). Another system involving liver poisoning has killed cattle in other countries (Atkinson & James, 1979; McLennan & Kelly, 1984) and must be suspected in *Cestrum* species growing in Venezuela. Most reports of hepatic toxins involve *Cestrum parqui* L'Her., an Argentine species now naturalized in South Africa and Australia, but herbarium labels and at least one published report (Atkinson & James, 1979) indicate similar properties in red-flowered species in Central America. These hepatotoxic species have relatively large showy flowers like those of *C. lindenii* or *C. petiolare* in Venezuela, suggesting the possibility that these too may have toxic properties. *Cestrum acuminatissimum* is used in Venezuela for stunning fish.

Much of what is known about the toxicity and biology of *Cestrum* may apply also to *Sessea*. One relevant investigation was carried out by Andrade (1960).

CYTOLOGY

Cytological reports (cited below under species descriptions) for a number of species of *Cestrum* indicate that a chromosome number of $n = 8$ is general in the genus. Numbers other than $n = 8$ or $2n = 16$ have been reported for some cultivated species. A chromosome number of $n = 8$ has also been reported for *Vestia*, but no chromosome data are known for *Sessea*. The numbers $n = 8$, $2n = 16$ in Cestreae contrast with the prevailing number in subfamily Solanoideae of $n = 12$, $2n = 24$, suggesting a significant taxonomic gap.

Berg and Greilhuber (1992, 1993a, 1993b) noted that chromosomes of *Cestrum* are unusual in flowering plants in having cold-sensitive regions. The functional or adaptive roles of these regions are not understood, but variation was found in the five species they studied.

MATERIALS AND METHODS

Fieldwork comprised three extended trips with students and other helpers covering most parts of Venezuela, and many shorter, less directed trips to various parts of the country. Specimens were studied from herbaria in Venezuela: CAR, CORO, GUYN, IRBR, MER, MERC, MERF, MY, MYF, PORT, TFAV, UCOB, VEN, and VZU; and in other countries: BM, BR, CM, CORD, F, G, GH, HBG, K, LINN, MA, MO, NY, P, US, W, and WIS. Many species were grown in the St. Louis greenhouse over several years for day and night examination of flowering behavior and as a source of plant parts to examine in the laboratory. Specimens were examined under stereoscopic microscopes in Maracay, St. Louis, and other places. Nectar sugar ratios were obtained by C. E. Freeman (pers. comm.) using the protocol outlined in Freeman et al. (1984).

TAXONOMIC TREATMENT

Cestreae ("Cestrineae") G. Don, Gen. Hist. 4(2): 400. 1838. TYPE: *Cestrum* L.

Unarmed shrubs, trees, or vines; pubescence of simple, branched, or stellate, sometimes glandular hairs. Leaves simple, entire, minor leaves sometimes present. Inflorescences variously branched panicles or racemes, often with bracts, the flowers mostly subtended by a small bracteole. Flowers mostly 5-merous, calyx cupular or tubular, lobed less than halfway; corolla tubular or funnelform with 5 short, usually spreading lobes; stamens inserted in the corolla tube, anthers opening lengthwise; ovary superior, often basally differentiated into a nectariferous disk and sometimes short-stipitate; locules 2, stigma positioned near the anthers, ovules 4–20(–37). Fruit a juicy berry or an apically dehiscent capsule. Seeds of various shape, sometimes winged; embryo straight. In Venezuela 2 genera: *Cestrum* and *Sessea*.

KEY TO GENERA (*CESTRUM AND SESSEA* OF TRIBE CESTREAE IN VENEZUELA

1a. Fruit a berry; seeds unwinged .... *Cestrum*
1b. Fruit a capsule; seeds winged .... *Sessea*

Cestrum L., Sp. Pl. 191. 1753; Gen. Pl., ed. 5. 88. 1754. TYPE: *Cestrum nocturnum* L.

Parqui Adans., Fam. Pl. 2: 219. 1763. *Parquis* Raf., Sylva Tellur. 56. 1838. TYPE: *Alkekengi* Feuillée (= *Cestrum hediundum* Lam.).

Meyenia Schltdl., Linnaea 8: 251. 1833, nol *Meyenia* Nees, in Wall. (1832), Acanthaceae. *Habrothamnus* Endl., Gen. Pl. 667. 1839. TYPE: *Meyenia fasciculata* Schltdl. (= *Cestrum fasciculatum* (Schltdl.) Miers).

Lomeria Raf., Sylva Tellur. 56. 1838. TYPE: *Lomeria purpurea* Raf. (= *Cestrum longiflorum* Ruiz & Pav.).

Wadea Raf., Sylva Tellur. 56. 1838. TYPE: *Wadea latifolia* Raf. (= *Cestrum latifolium* Lam.).

Unarmed shrubs, trees, or rarely vines; pubescence of simple, branched, or stellate hairs, sometimes glandular. Leaves simple, entire, pinnately nerved, mostly glabrate above; mostly short-petiolate; minor leaves present or not. Inflorescences axillary and pseudoterminal, few- or many-flowered racemes, spikes or cymes, often large and appearing paniculate; bracts often present. Flowers diurnal or nocturnal, mostly fragrant, mostly 5-merous, pedicellate, bracteolate; calyx small, cupular or tubular, mostly shallowly lobed; corolla narrowly tubular, much exceeding the calyx, lobed, the lobes narrow, shorter than the tube, spreading or reflexed when open; stamens inserted in the corolla tube at similar levels, the insertion levels varying greatly in different species, the adnate portion mostly evident from the corolla base, the insertion variously pubescent, tumid, or denticulate, anthers small, mostly situated together at the corolla mouth; ovary mostly shorter than the calyx, 2-locular, ovules (1–) 4–16(–32), style slender, mostly puberulent or papillose near the apex, style capitate or variously lobed, small, sometimes exserted beyond the anthers or corolla mouth. Fruit blackish, purplish, red, or white, an ovoid, ellipsoidal or obovoid, juicy or fleshy berry; fruiting calyx sometimes accrescent and splitting; seeds varying in number, variable in shape, even in the same berry, embryo straight.

References to the last revision of the entire genus by Francey (1935–1936) are found in brackets at the end of descriptions in the following accounts of the Venezuelan species.

Key to Species of *Cestrum* and *Sessea* in Venezuela

1a. Mature leaves pubescent beneath.

2a. Leaf undersides sparingly pubescent or glabrate with minute simple hairs; calyx mostly glabrous outside.

3a. Leaves subcoriaceous and rigid; corolla tube stout, > 1 mm wide from near the calyx; flowers apparently open during the day ..... *Cestrum tubulosum*

3b. Leaves membranous, flexuous; corolla slender, < 1 mm wide to more than halfway up; flowers closed during most of the day.

4a. Flowers subumbellate on leafy (bracteate) shoots, few per inflorescence, > 20 mm long; calyx ≥ 2.5 mm long; corolla > 25 mm long; fruit mostly ≥ 10 mm long ..... *Cestrum alternifolium*

4b. Flowers in short, leafless racemes or spikes, ≤ 20 mm long; calyx < 2.5 mm long; corolla < 22 mm long; fruit mostly ≤ 10 mm long ..... *Cestrum latifolium*

2b. Leaf undersides copiously pubescent with simple or branched hairs; calyx pubescent outside.

5a. Flowers ≥ 25 mm long; corolla pubescent outside; calyx > 6 mm long; minor leaves wanting.

6a. Calyx teeth cuspidate/apiculate, > 3 mm long; corolla 2.5 mm across at the mouth; filaments unexpanded and straight at insertion area ..... *Cestrum strigilatum*

6b. Calyx teeth blunt, < 2 mm long; corolla 3–3.5 mm across at the mouth; filaments tumid and geniculate at insertion area ..... *Cestrum olivaceum*

5b. Flowers ≤ 25 mm long; corolla glabrous outside; calyx < 6 mm long; minor leaves present.

7a. Leaves drying dark with floccose to evenly distributed whitish pubescence; leaves mostly with > 12 veins on each side; calyx lobes < 1.5 mm long ..... *Cestrum humboldtii*

7b. Leaves drying green or brown with evenly distributed yellowish or brownish pubescence; leaves mostly with < 12 veins on each side; calyx lobes > 1.5 mm long ..... *Cestrum tomentosum*

1b. Mature leaves glabrate beneath.

8a. Leaves with ≥ 10 pairs of lateral nerves.

9a. Calyx > 7 mm long; minor leaves conspicuous ..... *Cestrum petiolare*

9b. Calyx < 7 mm long; minor leaves wanting.

10a. Leaves with the veins drying salient beneath, half or more as wide as long; petioles of mature leaves mostly > 12 mm long; inflorescences held erect or nodding; trees.

11a. Inflorescences terminal; peduncles sturdy; calyx > 4 mm long; corolla mouth > 2 mm wide; fruit a dehiscent capsule; plants found above 2100 m ..... *Sessea corymbiflora*

11b. Inflorescences mostly axillary along leafy stems; peduncles slender; calyx < 3.5 mm long, corolla mouth < 2 mm wide; fruit a juicy berry; plants found below 2100 m.

12a. Inflorescences spicate; filament insertion geniculate and tumid; leaf bases mostly cuneate ..... *Cestrum cuneifolium*

12b. Inflorescences racemose; filaments straight and unthickened; leaf bases mostly rounded.

13a. Corolla 13–18 mm long; fruit globose; petioles often drying dark, especially at the base ..... *Cestrum racemosum*

13b. Corolla 28–31 mm long; fruit ellipsoidal; petiole bases mostly drying light-colored.

14a. Leaves with veins ascending at < 70°; stamens pubescent just below the insertion; corolla mouth 2.5 mm across ..... *Cestrum acuminatissimum*

14b. Leaves with veins strongly ascending at > 70°; stamens glabrous near the insertion; corolla mouth 3.5 mm across ..... *Cestrum schulzianum*

10b. Leaves with veins drying ± plane beneath; leaves broad or narrow, diminishing in size toward the terminal inflorescences, often much narrower than half their length; petioles mostly < 12 mm long; inflorescences arching and dangling; slender, willowy treelets.

15a. Flowers pedicellate (bracteole along the length of flower stalk); peduncle 1-flowered; leaves narrow with > 15 lateral veins on each side .... *Cestrum salicifolium*

15b. Flowers sessile (bracteole immediately beneath calyx); peduncle 2–3-flowered; leaves narrow or broad with < 15 lateral veins on each side .... *Cestrum bigibbosum*

8b. Leaves with ≤ 10 pairs of lateral nerves.

16a. Flowering calyx ≤ 3.5 mm long; free portion of filaments ≤ 5 mm.

17a. Corolla > 20 mm long.

18a. Minor leaves persistent, often conspicuous; leaves < 4 cm wide ... *Cestrum mariquitense*

18b. Minor leaves wanting on mature growth; leaves wide or narrow.

19a. Flowers subtended by bracts or bracteoles > 6 mm long (> 3 mm wide).

20a. Bracts not folded, not enclosing flowers; inflorescences stalked clusters on a terminal, elongate central axis; climbing shrub .... *Cestrum reflexum*

20b. A bract or bracteole longitudinally folded and half enclosing the basal part of the flower; inflorescences stalked clusters, terminal or axillary without a central axis; erect shrubs.

21a. Enveloping bract half enclosing the corolla tube and the fruit, persistent; leaf bases rounded or truncate .... *Cestrum jaramillanum*

21b. Enveloping bract hardly extending along the corolla tube, caducous; leaf bases cuneate .... *Cestrum pariense*

19b. Flowers lacking conspicuous bracts (mostly with caducous bracteoles < 6 mm long).

22a. Leaves < 2 cm wide, much longer than wide; inflorescences few-flowered fascicles .... *Cestrum neblinense*

22b. Leaves mostly > 2 cm wide, if narrower, then < 3 times longer than wide; inflorescences few- or many-flowered racemes.

23a. Climbing vines; flowers > 28 mm long .... *Cestrum scandens*

23b. Erect or sprawling shrubs or trees; flowers < 27 mm long.

24a. Leaves mostly < 4.5 cm wide, membranous; free portion of filaments > 2.5 mm, the insertion toothed; fruit white; corolla lobes < 3 mm long; widespread and cultivated species . *Cestrum nocturnum*

24b. Leaves mostly > 5 cm wide, often coriaceous; free portion of filaments < 2 mm, the insertion smooth (untoothed); fruit purple or green?; corolla lobes > 3 mm long; local endemic species.

25a. Filaments 1–2 mm free, glabrate; calyx lobes < 1 mm long; corolla mostly > 23 m long; Amazonas endemic *Cestrum glabrescens*

25b. Filaments 4–5 mm free, pubescent; calyx lobes 1–2 mm long; corolla mostly < 23 m long; Cordillera de la Costa endemic .... *Cestrum potaliifolium*

17b. Corolla < 20 mm long.

26a. Corolla not closing, mouth 3–3.5 mm across, the lobes recurved, rounded, bright white, < 1.5 mm long .... *Cestrum diurnum*

26b. Corolla mostly closed during the day, mouth < 1.5 mm across, the lobes spreading or reflexed at night, straight when expanded, pointed, greenish white or purple, > 1.5 mm long.

27a. Peduncles > 1 cm long; leaves membranous, mostly drying plane, the minor venation unobtrusive, drying similar colored to other venation beneath; petioles drying as the stems (sometimes darker only at the base) .... *Cestrum microcalyx*

27b. Peduncles < 1 cm long; leaves coriaceous, often drying wrinkled, the costa and main veins conspicuous and salient beneath, minor venation drying whitish beneath; petioles drying dark .... *Cestrum megalophyllum*

16b. Flowering calyx ≥ 3.5 mm long; free portion of filaments mostly > 5 mm.

28a. Corolla < 25 mm long, the lobes < 5 mm long.

29a. Leaves < 3 cm wide; corolla lobes ≤ 3 mm long.

30a. Leaves mostly < 1 cm wide; petioles ≤ 3 mm long; calyx tube glabrous; free portion of filaments 5–9 mm .... *Cestrum buxifolium*

30b. Leaves mostly > 1 cm wide; petioles ≥ 3 mm long; calyx tube puberulent; free portion of filaments 4–5 mm .... *Cestrum tillettii*

29b. Leaves mostly > 3 cm wide; corolla lobes mostly > 3 mm long.

31a. Calyx > 5 mm long; inflorescences terminal panicles.

32a. Corolla > 22 mm long, the mouth > 3.5 mm across; filaments glabrous, the insertion geniculate-tumid, lacking teeth; leaves mostly < 6 mm long and < 3 cm wide *Cestrum ruizteranianum*

32b. Corolla < 22 mm long, the mouth < 3 mm across; filaments pubescent, the insertion hardly bent or expanded, denticulate; leaves mostly > 6 mm long and > 3 cm wide *Cestrum lindenii*

31b. Calyx < 5 mm long; inflorescences mostly arranged along the stems, subumbellate, racemose, or spicate.

33a. Inflorescences at or near the end of elongate, slender, wandlike, often declining branches that bear diminishing leaves or terminal, few-flowered pedunculate or subsessile clusters; filaments pubescent *Cestrum bigibbosum*

33b. Inflorescences mostly distributed along branches with leaves not conspicuously diminishing upward and terminal on stiff branches; filaments glabrous.

34a. Leaves membranous, large, often > 4 cm wide; free portion of filaments 1–2 mm; flowers < 23 mm long *Cestrum glabrescens*

34b. Leaves coriaceous, mostly < 3 cm wide; free portion of filaments 5–9 mm; flowers > 22 mm long.

35a. Leaves ascending, mostly widest at or below the middle; free portion of filaments glabrous, 6–8 mm; calyx often drying darker near the apex, the nerves not darker, the teeth ca. 0.5 mm long *Cestrum imbricatum*

35b. Leaves spreading, mostly widest at or above the middle; free portion of filaments pilose, ca. 5.5 mm; calyx drying evenly from base to apex, the teeth ca. 1 mm long *Cestrum cuneifolium*

28b. Corolla > 25 mm long, the lobes ≥ 4 mm long.

36a. Vines or scramblers; free portion of filaments 0.5–1 mm, glabrous.

37a. Flowers lacking pedicels (the subtending bracteole sessile on the axis); corolla lobes < 6 mm long; plants drying dark brown or gray; twigs and inflorescences puberulent; petioles tomentose *Cestrum reflexum*

37b. Flowers on short, distinct pedicels (below the subtending bracteole); corolla lobes > 6 mm long; plants drying greenish or yellowish; twigs and inflorescences mostly glabrous; petioles glabrate *Cestrum scandens*

36b. Erect shrubs or trees; filaments free for various distances, glabrous or pubescent.

38a. Corolla showy, yellow or orange, the mouth > 5 mm across; calyx > 5 mm long; fruit white; petioles > 2 cm long; sparingly cultivated exotic species *Cestrum aurantiacum*

38b. Corolla inconspicuous, green, yellow, or whitish purple, the mouth < 5 mm across; calyx > 5 mm long; fruit purple-black; petioles < 1 cm long; native species.

39a. Minor leaves abundant, often conspicuous; stamens barbate at insertion *Cestrum mariquitense*

39b. Minor leaves wanting; stamens glabrous or pubescent but not at insertion.

40a. Calyx > 5 mm long; flowers and fruits half-enfolded lengthwise in a persistent leafy bract; filaments glabrous; leaves mostly < 3 mm wide *Cestrum jaramillanum*

40b. Calyx < 5 mm long; lacking persistent bracts; filaments mostly pubescent.

41a. Calyx glabrous; leaves mostly > 3 mm wide.

42a. Corolla < 26 mm long; Andean species > 2500 m *Cestrum ruizteranianum*

42b. Corolla > 26 mm long; Guayanan species < 500 m.

43a. Inflorescence axes slender, glabrate *Cestrum acuminatissimum*

43b. Inflorescence axes stout, tomentose *Cestrum tubulosum*

41b. Calyx puberulent.

44a. Corolla > 29 mm long; corolla lobes > 5 mm long; Guayanan species < 500 m *Cestrum schulzianum*

44b. Corolla < 26 mm long; corolla lobes < 5 mm long; central Venezuela, > 1000 m *Cestrum glabrescens*

1. **Cestrum acuminatissimum** Dunal, in A. DC., Prodr. 13(1): 627. 1852. TYPE: French Guiana "circa Cayennam," *Leprieur s.n.* (holotype, G-DC not seen, = IDC microfiche, = F photo 6907).

Cestrum loretense Francey, Candollea 6: 225. 1935. TYPE: Peru. Loreto: La Victoria on the Amazon river, *Williams 3129* (holotype, F).

Shrub 1.5–3 m tall, sometimes sprawling, branches terete, striate, nodes of leaves and inflorescences thickened; pubescence of simple, moniliform ascending and crumpled hairs. *Leaves* narrowly ovate or elliptical, 8–16(–18) × 4–7 cm, apically short-acuminate, acute or obtuse and then forming a narrow apicule, the base narrowly cuneate, truncate or subtruncate, the margins slightly revolute, papery-coriaceous, dark green above, light green beneath, glabrous on both sides but sometimes with minute trichomes on the veins beneath, the veins impressed above, prominent beneath, ascending, 6–12 on each side; petiole 3–5(–10) mm long, the base somewhat thickened; minor leaves wanting. *Inflorescences* short axillary racemes, axes 5–10 mm long, 1.5–2 mm thick, tomentose with ascending, curved hairs; bracts 1–2.5 mm long, foliaceous, subulate, yellowish or reddish pubescent. *Flowers* apparently nocturnal, 28–32 mm long; pedicels 0.5 mm or obsolete; bracteoles narrow, tomentose; calyx tubular, 3.5–5.5 × 1.5–3 mm, the tube 3.5–5 mm long, glabrous, the teeth triangular-acute, 0.5 mm long, ciliate and tufted, the costas and lateral veins salient, the 5 costas thickened upward; corolla pale greenish yellow, 28–31 mm long, the tube narrow, very gradually expanded upward, slightly contracted at the throat, mouth 2–2.5 mm wide, the lobes narrowly acuminate, 4–7.5 m long, sometimes sparingly pubescent, ciliolate; stamens 20.5–24.5 mm long, filaments adnate for 18–22 mm, pilose to 1 mm or 8–15 mm above the base, insertion straight, smooth, free 0.5–3 mm, anthers orbicular, 0.5–0.8 mm across; ovary ellipsoidal, 1–1.5 × 1 mm, glabrous, disk conspicuous, ovules 8–10, style 20–24.5 mm long, filiform, puberulent just below the stigma, the stigma capitate, included. *Fruit* dark purple, ellipsoidal, 10–13(–16) × 6–9 mm, with a thin pericarp; fruiting calyx hardly accrescent; seeds 3–5, dark brown, 4–7 mm long. [Francey 6: 314.] Figure 3.

Cestrum acuminatissimum is distinguished by a number of features that tend to overlap with other species, notably *C. megalophyllum.* The longer flowers, pubescent stamen insertion, and matte appearance of the upper sides of the revolute leaves are good recognition features. The corolla is quite variable in length but is usually more than 28 mm long with the lobes 4–7.5 mm long. The inflorescence axes are notably slender.

Distribution (Fig. 4). Amazonas, Apure, Barinas, and Táchira. Gallery forests along riverbanks; 100 to 300 m. Also in French Guiana, Colombia, Peru, and Brazil.

Phenology. Collected in flower between November and March, and in fruit mostly in March and May.

Common names and uses. Beecotó (Pumé language), *Derello*, *Mecla.* Mixed with other herbs, plants are used for stunning fish (*Gragson & Gragson 48*, MY).

Representative specimens seen. VENEZUELA. **Amazonas:** Maroa–Yavita road, 5.5 km from Maroa port, *Clark 6948* (MO, NY); 20 km S of confluence of Río Negro and Brazo Casiquiare, *Liesner 6877* (MO, VEN); 4 km S de Solano, *Morillo & Hasegawa 5026* (MY, VEN). **Apure:** Distrito Pedro Camejo, main road S of Paso de San Pablo to Río Cinaruco, *Davidse & González 15984* (MO, VEN); Reserva Forestal San Camilo, quebrada de El Dique, SW de San Camilo (El Nula), *Steyermark et al. 101530* (US, VEN). **Barinas:** 5 km SW of dam site on Río Caparo, 31 km ESE of Santa Bárbara, *Liesner & González 9311* (MO, VEN), *9322* (MO, VEN). **Táchira:** E of La Fundación around Represa Dorada, *Liesner & González 10412* (MO, VEN); Montaña Guafitas, NW of El Piñal, *Steyermark et al. 119545* (MO, VEN).

2. **Cestrum alternifolium** (Jacq.) O. E. Schulz, in Urb., Symb. Antill. 6: 270. 1909. *Ixora alternifolia* Jacq., Enum. Syst. Pl. 12. 1760. TYPE: Cultivated Europe, seed from Martinique, *Jacquin s.n.* (lectotype, here designated, W not seen, = F photo 33021).

Chiococca alternifolia L., Syst. Nat. ed. 12, 2: 165. 1767. Based on *Chiococca scandens sarmentis tenuissimis & fere indivisis* P. Browne, Civ. Nat. Hist. Jamaica 164. 1756. TYPE: not located.

Cestrum confertum Miller, Gard. Dict. ed. 8, *Cestrum* no. 5. 1768. TYPE: not indicated.

Cestrum vespertinum L., Mant. Pl. 2: 206. 1771. TYPE: Hort. Upsala (holotype, LINN 258.2 not seen, = IDC microfiche).

Cestrum pendulinum Jacq., Pl. Hort. Schoenbr. 3: 42, pl. 327. 1798. *Cestrum alternifolium* var. *pendulinum* (Jacq.) O. E. Schulz, in Urb., Symb. Antill. 6: 272. 1909. TYPE: Venezuela. Caracas, plate 327 in Jacquin, 1798 (lectotype, here designated).

Cestrum amelanchier Dunal, in A. DC., Prodr. 13(1): 662. 1852. TYPE: Cultivated hort. Rothomagensi (holotype, G-DC not seen, = IDC microfiche, = F photo 6896).

Cestrum depauperatum Dunal, in A. DC., Prodr. 13(1): 660. 1852. TYPE: Guadeloupe, *Bertero s.n.* (holotype, G-DC not seen, = IDC microfiche, = F photo 33966).

Cestrum alternifolium var. *mithanthum* O. E. Schulz, in Urb., Symb. Antill. 6: 273. 1909. TYPE: Venezuela. Nueva Esparta: Margarita ad El Valle, *J. R. Johnston 285* (holotype, GH).

Shrub 3–4 m tall, much branched, the branching irregular, often wand-like or pendulous, twigs green, minutely pubescent, glabrescent, the tips often sharp, mature stems often whitish or yellowish, lenticellate; pubescence of simple hairs. *Leaves* malodorous, ovate, sometimes elliptical or narrowly elliptical, (1.5–)3.7–12.5 × 1.5–4.5 cm, attenuate toward the apex, the apex itself obtuse, rounded

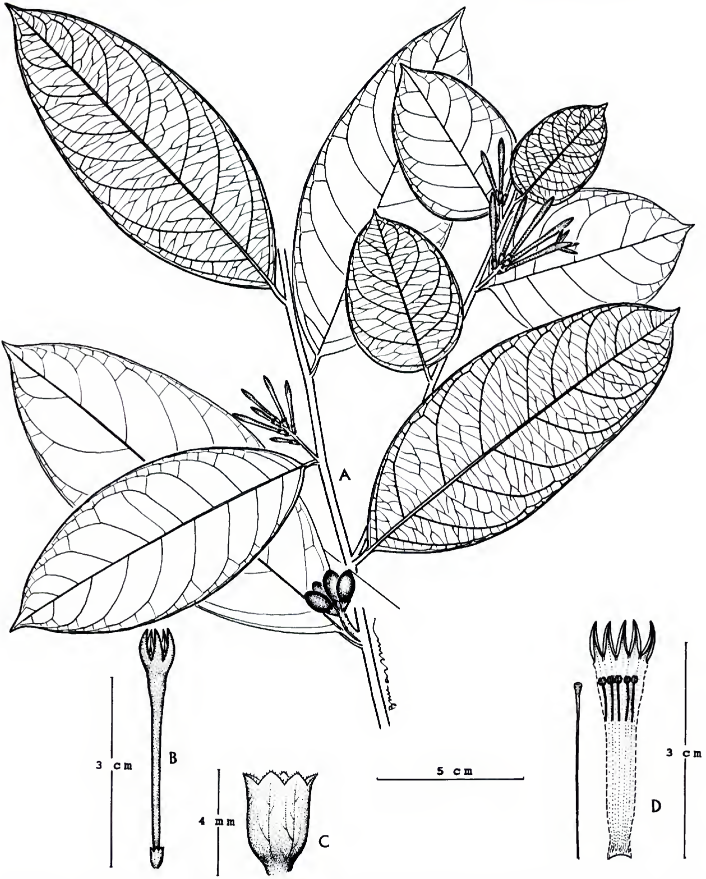

Figure 3. *Cestrum acuminatissimum.*—A. Flowering and fruiting branches.—B. Flower.—C. Calyx.—D. Corolla opened to show stamens and style. A, upper section, B, C after *Davidse & González 21967* (VEN). A, lower section after *Steyermark 101530* (VEN).

toward the base, often narrowly cuneate, not revolute, membranous or firmly papery, both sides pale green, lamina and veins puberulent on both sides, sometimes glabrescent, veins 5–10 on each side, ascending; petiole 5–11 mm long, pilose; minor leaves sometimes present, 14–17 × 5–10 mm, their petioles 3.5 mm long. *Inflorescences* mass-blooming, terminal and axillary, few(7–10)-flowered, congested fascicles or umbels mostly near the ends of leafy branches, axes 5–10 cm long, slender, tomentose; peduncles 1–2 mm, thickened, unbranched. *Flowers* crepuscular and nocturnal, fragrant, 26–33 mm

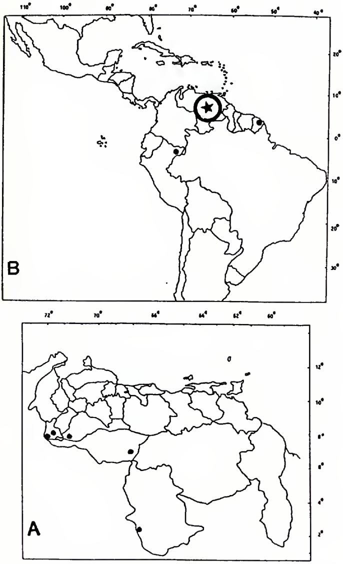

Figure 4. *Cestrum acuminatissimum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

long, pedicels obsolete; bracteoles linear, 1.5–3 mm long, glabrate; calyx cupular, 2.5–3 mm long, basally narrowed and stipe-like, pilose or glabrous outside, the tube 2–4 mm long, teeth 0.5–1 mm long, costate, ciliolate and tufted; corolla white or yellowish green, sometimes with slight purplish coloration on the tube, the tube contracted just above the ovary, then slightly and gradually expanded upward, abruptly expanded just below the apex and around the anthers, slightly contracted at the mouth, 24–32 mm long, glabrous, mouth 3–4 mm wide, lobes narrowly triangular, 4–6 mm long, ciliolate, the folds puberulent; stamens equal, 20–22 mm long, filaments adnate for 18–23 mm, insertion straight, smooth, glabrous, free part 0.5–2 mm, anthers orbicular, 0.5 mm across, included; ovary 1–1.5 mm across, glabrous, disk conspicuous, ovules 6–10, style 18–22 mm long, the apical 2 mm puberulent, stigma capitate, included in the corolla. *Fruit* maturing through violet to purple-black, shiny, ellipsoidal, 10–12 × 5–8 mm, the pulp 1.5 mm thick, spongy, whitish; fruiting calyx hardly accrescent; seeds 4–8, dark brown, 4.5–5.5 mm long. [Francey 6: 211.] Figures 2C, 5.

Cestrum alternifolium may be recognized by its umbel-like inflorescences with sessile flowers and the slender corollas that are expanded into a small bulb around the anthers. This species resembles *C. mariquitense,* which tends to be a larger, leafier tree of more mesic regions. The absence of pubescence on the filaments distinguishes it from *C. mariquitense.*

Although Jacquin cited Plumier (Pl. Amer. 7: 150, plate 157, fig. 1, 17. 1758), suggesting that the name *Ixora alternifolia* was based on the plate of Plumier, neither the plate nor one-line description with it provide the details found in Jacquin's own description. Hence we select as lectotype the specimen at W from the garden at Schoenbrunn where Jacquin worked. We think that this specimen was grown from Jacquin's own collections in Martinique, where he said the plant was found, and was probably the material from which the plate was made. *Cestrum confertum* Miller was placed in synonymy by Francey (1935: 211).

Plants of this species are often associated with ants. The flowers often begin to open and emit fragrance from about an hour before sunset to an hour after sunrise. Nectar is scant or absent in this species. Pollination by hawkmoths (Sphingidae) was reported by Haber and Frankie (1989) and White et al. (1994).

Distribution (Fig. 6). Aragua, Bolívar, Falcón, Guárico, Lara, Mérida, Miranda, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Zulia, and the Distrito Federal, as well as on the Island of Testigo Grande. Dry coastal scrub, savannas, riverbanks, deciduous and semideciduous forests below 1300 m and in cloud forests around 2000 m. Also occurring from Mexico to northern South America and in the Antilles.

Phenology. The flowering season seems to depend on the climatic patterns of the particular vegetation formations where the species occurs, thus varying from place to place.

Common names. *Clavito, Dama de Noche, Fruto de Culebra, Puta de Noche, Putica de Noche, Tapacamino, Tinte, Uvito Gallinero.*

Representative specimens seen. VENEZUELA. **Aragua:** Colonia Tovar, *Allart 475* (NY, US, VEN). **Bolívar:** escarpment E of Miamo leading to Hato Nuria, Altiplanicie de Nuria, *Steyermark 88525* (NY, VEN). **Falcón:** Cerro Santa Ana, *van der Werff & Wingfield 3107* (MY). **Guárico:** Estación Biológica de Los Llanos, *Ramirez 234* (MY, NY), *2148* (MY, NY). **Lara:** Barquisimeto, *Saer 15* (US, VEN). **Mérida:** Carretera Ejido–Las González, *Ruiz-*

Figure 5. *Cestrum alternifolium.*—A. Branch with flowers and fruit.—B. Flower.—C. Style and stigma.—D. Corolla opened to show stamens. After *Benítez 1809* (MY).

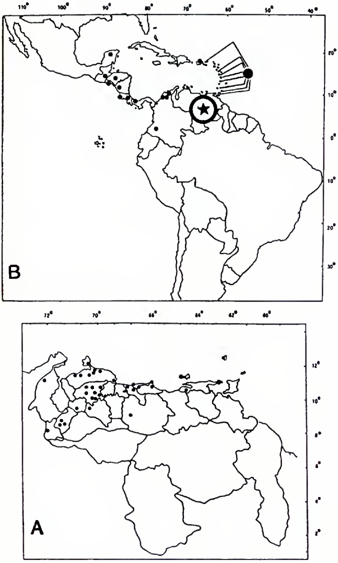

Figure 6. *Cestrum alternifolium*.—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Terán & R. Gallardo 12641 (MERF, MY). **Miranda:** hills between Carenero and Chirimena, *Steyermark & Bunting 102318* (VEN). **Nueva Esparta:** El Espinal–La Guardia, NW de Margarita, *Benítez 1609* (MY). **Portuguesa:** El Rodeo de Santa Lucía, *Benítez et al. 4281* (MY). **Sucre:** Cerro Turimiquire, N slopes above La Trinidad, *Steyermark 62525* (F, VEN). **Táchira:** entre Colón y San Pedro del Río, *Ruiz-Terán 3579* (MER). **Trujillo:** Carretera a Jajó, Distrito Urdaneta, *Benítez 1944* (MY). **Zulia:** Río Guasare, Campamento Carichuano, *Steyermark et al. 123025* (MO, VEN, VZU); Perijá, *Tejera 133* (US). **Distrito Federal:** Jardín Botánico, Caracas, *Nee 17563* (F, VEN, WIS). **Archipiélago Los Testigos:** Testigo Grande, *Fernández et al. 200* (CAR, MY, PORT).

3. Cestrum aurantiacum Lindl., Edward's Bot. Reg. 30: Misc. 71. 1844. TYPE: Cultivated, seed from G. U. Skinner, Chimalapa, Guatemala, not located.

Cestrum pedunculare Dunal, in A. DC., Prodr. 13(1): 618. 1852. TYPE: Mexico. *Pavón s.n.* (holotype, G, = F photo 34132).

Cestrum chaculanum Loes., Verh. Bot. Vereins Prov. Brandenburg 65: 97. 1923. *Cestrum aurantiacum* var. *chaculanum* (Loes.) Francey, Candollea 6: 104. 1935. TYPE: Guatemala. *Seler 2836* (holotype, B destroyed, = F photo 2972).

Cestrum paucinervium Francey, Candollea 6: 101. 1935. TYPE: Guatemala. Quiché: San Miguel Uspantán, *Heyde & Lux 3135* (holotype, B destroyed).

Shrub or *tree* 1–3 m tall, branched, older trunks gnarled, conspicuously lenticellate, stems terete, flexible, soon glabrate, pubescence of reduced, glandular, perhaps branched, crumpled hairs. *Leaves* sometimes malodorous, narrowly ovate, 7.5–10 × 4.5–6.8 cm, apically acuminate, basally attenuate, margins undulating, sometimes appearing ciliolate, subcoriaceous to membranous, matte bright green, glabrous, veins 7–9 on each side, strongly ascending, slightly sunken above, main veins elevated beneath, minor veins plane, reticulate, drying conspicuous; petiole canaliculate, 2.3–3 cm long, glabrous; minor leaves wanting. *Inflorescences* showy, axillary and terminal, mostly emergent from the leaves near the branch ends, lax racemes 1.5–3 cm long, axes 2.5–6 cm long; bracts occasional, foliaceous, 5–10 × 15 mm, pubescent; peduncles mostly short, occasionally to 3 cm long, slightly longer in fruit, tomentose, clusters of 2–6 sessile or subsessile flowers separated by a 2–6-mm-long rachis. *Flowers* diurnal, unscented, 25–29 mm long, buds with calyx teeth bent out, sessile in groups of 2–3; bracteoles linear, 5–8 mm long, glabrate; calyx tubular, 5.5–7 × 2–3 mm, glabrous outside, the veins conspicuous, pilose inside, tube ca. 5 mm long, teeth narrowly deltoid or subulate, 0.5–1 mm long, the tips subulate, often as long as the tube; corolla bright yellow to orange, 26–28 mm long, glabrous, tube 21–23 mm long, expanding gradually upward, mouth (2–)3–4.5(–5.5) mm wide, lobes 5 mm long, narrowly ovate, apically mucronulate; stamens 17–19 mm long, filaments adnate for 13–15 mm, pubescent to 10–12.5 mm from the base, insertion straight, smooth, tumid, geniculate, slightly denticulate, glabrous or sparingly pilose, free part 4–5 mm; ovary globose 1–1.5 mm across, glabrous, disk inconspicuous, ovules 12–13, style 18–19 mm long, glabrous, stigma capitate, slightly exserted. *Fruits* numerous per inflorescence, white, ovoid, 8.5–10 × 5–7.5 mm, juicy; fruiting calyx often accrescent, 6–9 mm long, sometimes splitting at the sinuses; seeds 5–9 per fruit, bright dark brown, 3.5–6 mm long. [Francey 6: 102.] Figure 7.

This species of *Cestrum* is easily recognized in Venezuela by its showy orange or yellow flowers and white fruits. This is the only species of section *Habrothamnus* recorded from Venezuela.

The flowers of *Cestrum aurantiacum* are unscent-

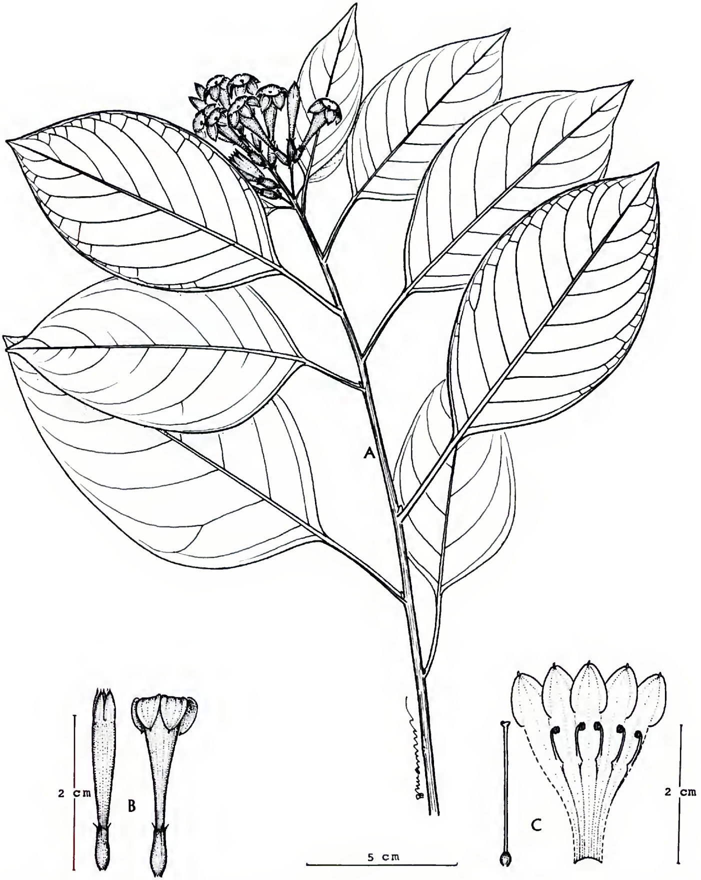

Figure 7. *Cestrum aurantiacum.*—A. Flowering branch.—B. Corollas with lobes open and closed.—C. Corolla opened to show stamens and style. After *Ernst s.n.* (HBG).

ed and open night and day. The corolla lobes are strongly reflexed or recurved when open.

Chromosome numbers for this species have been reported as $n = 8$, $2n = 16$ (Dyer, 1963; Sharma & Sharma, 1958; Madhavadian, 1968; Berg & Greilhuber, 1993b).

Steudel (1840) listed the name *Cestrum aurantiacum* but did not provide a description.

Distribution. Occasionally cultivated in tropical gardens for its showy flowers, this species is native to Nicaragua and Guatemala. Although not stated on the label, the sole Venezuelan collection was undoubtedly from a cultivated plant.

Specimen seen. VENEZUELA. **Lara:** Barquisimeto, montium Coro, *Ernst s.n.* (HBG).

4. **Cestrum bigibbosum** Pittier, J. Wash. Acad. Sci. 22: 35. 1932. TYPE: Venezuela. Between El Aguacatal and Alto del Cogollal, 1500 m, *Pittier 9245* (holotype, VEN; isotype, US).

Cestrum laetum Francey, Candollea 6: 378. 1935. TYPE: Venezuela. Aragua: Colonia Tovar, 1854, *Fendler 955* (holotype, NY; isotypes, GH, MO).
Cestrum pumilum Francey, Candollea 6: 373. 1935. TYPE: Colombia. Santander: Eastern Cordillera, vicinity of Las Vegas, 2600–3000 m, *Killip & Smith 15962* (holotype, NY).
Cestrum umbrosum Francey, Candollea 6: 375. 1935. TYPE: Venezuela. *Moritz 348* (holotype, W not seen, = F photo 33043).
Cestrum venezuelense Francey, Candollea 6: 377. 1935. TYPE: Venezuela. Mérida: *Moritz 212b* (neotype, here designated, BM).

Weak, sparingly branched *shrub* or small *tree* 2–6 m tall, sometimes a solitary unbranched wand-like stem, 1–3 cm DBH, branches arching or erect, striate, young branches pubescent, young parts and inflorescences with a faint dark purple color; pubescence of simple, moniliform ascending and crumpled hairs. *Leaves* elliptical or ovate, sometimes narrow, (7–)13–26 × (2–)5–10 cm, apex acute or acuminate, base rounded or attenuate, sometimes unequal or slightly arching downward, margin revolute, membranous to subcoriaceous, dark green and shiny, lighter beneath, glabrous, veins 5–14 on each side, ascending at an angle of 50°–65°, somewhat irregular, major veins slightly impressed above, elevated beneath; petiole canaliculate, 1–3 cm long, glabrous, often curving and twisting depending on orientation of the branch; minor leaves wanting. *Inflorescences* large, pendulous, terminal or axillary panicles, sometimes short axillary racemes; axes dark purple, 10–25 cm long with 1–10 branches, peduncles 8–25 mm long, 0.3–0.7 mm thick, bracts foliaceous, ovate, becoming narrower upward, glabrous, 6–40 × 5–30 mm wide. *Flowers* nocturnal?, 25–30 mm long; pedicels 0.5–1 mm; bracteoles linear, 1.5–3 mm long, glandular pilose; calyx cupular, basally narrowed into an indistinct stipe, 3.5–7 × 2 mm, firmly membranous, often 5-costate, glabrous, tube 2.5–6 mm long, teeth 1 mm long, ciliate, tufted; corolla greenish white, yellowish, or dark olive-green, the lobes pale yellow, 23–29 mm long, narrowly funnelform, the tube gradually expanded upward, mouth 2.5–3 × 1–2 mm, 5 lobes narrowly triangular or oblong, 4–8.5 mm long, apically acute or obtuse; stamens 17–23 mm long, filaments adnate for 13–20 mm, bigibbous, insertion 2 mm long and free, sometimes tumid and sparingly pilose, free part 3–3.6 mm, anthers orbicular, 0.5–0.8 mm across, the surface conspicuously rameniferous; ovary ellipsoidal, 1 × 0.8 mm, with minute papillae near the top, stipitate, the disk yellow, conspicuous, style 15–22 mm long, pilose for 3 mm below the stigma, exserted 1.5 mm, stigma subcapitate. *Fruit* often in dense, pendulous or sometimes arcuate-ascending racemes, dark purple and shiny, subglobose or ovoid; fruiting calyx hardly accrescent, wrinkled, broadly cupular, inside with 2–4 glandular bands that extend to the base of the teeth, the teeth with thickened margins; seeds 4–11 per fruit, yellow, 4.5–6.5 mm long. [Francey 6: 376.] Figures 1B, 8.

This species typically occurs as a slender treelet with reclining branch ends and leaves that diminish in size near the branch apices. However, many examples, perhaps damaged plants, are short shrubs with one or two stiff, inflorescence-bearing branches and larger than normal leaves. In this species, the flowers are inconspicuous and the fruits usually few. The staminal insertion usually bears one or two tooth-like emergences but is sometimes smooth. Some plants greatly resemble *C. salicifolium*, having narrow leaves and dangling inflorescences, but the flowers are sessile on an often caducous subtending bract and not pedicellate as in *C. salicifolium*.

The collection here designated as the neotype of *C. venezuelense*, *Moritz 212b* (BM), was not seen by Francey, and we have not seen another collection of this number among material from G-DC, W, HAL, or HBG, where Francey borrowed material for his revision. However, this specimen agrees with Francey's description and is a close match for specimens of *Moritz 212* (HBG), one of which was annotated by Francey as *C. venezuelense* but was not cited in his protologue. *Moritz 212* (B = F photo 2985) was a different species *(C. scandens* Vahl (as *C. laxiflorum* Dunal)), and is different in HBG (*C. venezuelense*) and G-DC (*C. scandens* Vahl (as *C. laxiflorum* Dunal)). Until an example of *Moritz 212b* that was annotated by Francey is located, we consider the specimen at BM to be acceptable as a neotype. Francey also cited a specimen of Karsten from Colonia Tovar, which we have not located.

Distribution (Fig. 9). Aragua, Barinas, Carabobo, Cojedes, Falcón, Lara, Mérida, Miranda, Monagas, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, and the Distrito Federal. Evergreen cloud forests of low stature (9–11 m) in shade or in natural woodlands; 1200–2200 m. Also in Colombia.

Figure 8. *Cestrum bigibbosum.*—A. Flowering branch.—B. Closed flower.—C. Flower opened to show stamens and style.—D. Stamen. After *Badillo 6629* (MY).

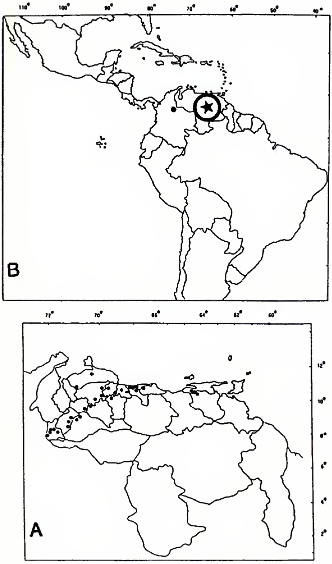

Figure 9. *Cestrum bigibbosum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Phenology. Maximum flowering is in January, diminishing to May. Fruiting is mainly from March to August.

Common names. *Mata Perro, Uvito.*

Representative specimens seen. VENEZUELA. **Aragua:** Carretera Maracay–Choroní, después de las Morochas, *Benítez & Rojas 4998* (MY). **Barinas:** road from Altamira to Santo Domingo, *van der Werff & Ortiz 5859* (MO, VEN). **Carabobo:** without other locality, *Funck & Schlim 627* (G). **Cojedes:** Cerro Azul, fila La Blanquera, *Delascio 4118* (CAR). **Falcón:** El Chorro entre La Chapa y Uría, *Benítez et al. 5149* (MY). **Lara:** Arriba de Sanare, *Badillo 6693* (MY). **Mérida:** Carretera El Celoso–Las Mesas, *Benítez & Rojas 4811* (MY). **Miranda:** Los Guayabitos, Baruta, *Aristeguieta 2291* (VEN). **Monagas:** slopes of Cerro Negro above La Sabana de Las Piedras, NW of Caripe, *Steyermark 61844* (F, VEN). **Portuguesa:** 21 km S de Biscucuy, El Rodeo de Santa Lucía, *Benítez et al. 4287* (MY). **Sucre:** foothills of Cerro Turumiquire, SW of Cumanacoa, *Knapp & Mallet 6754* (VEN). **Táchira:** Parque Cazadero, 16 km NW of San Cristóbal, *Liesner & Guariglia 11658* (VEN). **Trujillo:** between La Playa, SW of Carache and Potreritos de Cendé, *Dorr et al. 5099* (VEN). **Yaracuy:** Carretera Nirgua–La Chapa, *Benítez et al. 5097* (MY). **Distrito Federal:** Carretera Caracas–Colonia Tovar, *Meier 1211* (MY, VEN).

5. **Cestrum buxifolium** Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 57. 1818. TYPE: Regni Novo–Granatensis, near sanctuary of Montserrat, 1650 hex, *Humboldt & Bonpland s.n.* (holotype, P-Bonpl., = IDC microfiche).

Cestrum parvifolium Willd., in Roem. & Schult., Syst. Veg. 4: 808. 1819. TYPE: Colombia. Collector unknown (holotype, B-W 4460 not seen, = IDC microfiche).
Cestrum melanochloranthum Dunal, in A. DC., Prodr. 13(1): 622. 1852. SYNTYPES: Colombia. Santander: *Killip & Smith 15691* (NY), *Killip & Smith 18215* (NY), *Holton 571* (G? not seen).Venezuela. Mérida: around Portachuelo, *Funck & Schlim 1264* (G-DC not seen, = IDC microfiche, = F photo 6911; MO, P).
Cestrum parvifolium var. *venezuelense* Francey, Candollea 6: 330. 1935. TYPE: Venezuela. Mérida: Chachopito, near San Rafael, *Pittier 13210* (holotype, VEN; isotypes, B destroyed, F, MO, US).
Cestrum cuneatum Francey, Candollea 6: 326. 1935. SYNTYPES: Colombia. *Linden (Funck & Schlim) 1645* (B not seen, G not seen, = photo F 28356, BR not seen, MO, P); Bogotá, *Troll 3587* (G? not seen); Norte de Santander, *Killip & Smith 19890* (NY). Venezuela. Mérida: Chachopo, *Linden 363* (G not seen). Ecuador. Quetame, *André 897* (NY).

Shrub to 3 m tall, often dwarfed and 40–60 cm tall or prostate, irregularly branched, the branches often ascending, young branches pubescent, young shoots terete, often dark purple, mature branches dark yellowish and tomentose; pubescence of branched trichomes. *Leaves* ascending, imbricate and facing the stems, elliptical, 2–3(–5) × 0.6–1.1(–1.6) cm, apex obtuse, base attenuate or cuneate, margin slightly revolute, coriaceous to chartaceous, both sides bright green and shiny, glabrous, veins 4–10 on each side, above deeply furrowed, only the principal veins impressed beneath; petiole dark purple, 1.5–3 mm long, sparingly puberulent; minor leaves 4–5 × 1.5–4 mm, sessile. *Inflorescences* dense, axillary and terminal, axes and pedicels dark purple, axes 3.5 cm long, peduncles 1 cm long, bracts foliaceous, 1.5–5 × 0.5–1.5 mm, pilose. *Flowers* not closing, fragrance crepuscular and nocturnal, 16–25 mm long; sessile, calyx cupular, 3.5–6.5 × 2 mm, coriaceous, 5-costate, glabrous, the tube 3–5 mm long, the 5 teeth triangular, 0.5–1.5 mm long, ciliolate, the sutures pilose; corolla 15–24 mm long, tube dark purple to greenish yellow, ampliate, slightly contracted above the ovary, nearly cylindrical to about halfway up, then expanded and again cylindrical, glabrous, mouth 3–4 (2.5–3) mm across, the lobes triangular, dark purple, 2–5 mm long, the folds yellowish green, pilose, reflexed at anthesis; stamens 11–19 mm long, filaments green, adnate for 4.5–7.5 mm, insertion geniculate-tumid, glabrous or sparingly pubescent, free part 5–9 mm, anthers dark brown, orbicular, 0.5 mm across; ovary lobed, 1–1.5 mm long, disk inconspicuous, ovules 7–13, style purplish, 13.5–19.5 mm long, slightly sunken in the ovary apex, puberulent 1.5 mm below the stigma, stigma capitate, bright green 0.5–1 mm across, exserted 0.5–1 mm from the anthers. *Fruit* in umbellate clusters, dark purple to black, narrowly ovoid, 0.9–1.2 × 0.9–1.1 cm, smooth, the mesocarp dark purple, pulpy, staining fingers and paper deep purple; seeds 2–8 per fruit, light brown, 5–8 mm long. Figures 2B, 10.

Cestrum buxifolium often occurs on paramos as a dwarf shrub, flowering and fruiting when less than 60 cm tall with irregular branching and small leaves. In more sheltered places, it may be a shrub to 3 m tall, and such specimens are separated by the characters noted in the key.

Distribution (Fig. 11). Andean regions of Lara, Mérida, Táchira, and Trujillo. Rocky exposed slopes, dry pastures, and around watercourses in dwarf cloud forests and paramos; 2650–4000 m. Also in Colombia and Venezuela.

Phenology. Flowering is throughout the year, more plentiful from October to May. The fruiting maximum is in April and May.

Common names and uses. *Chupa Sol, Chongalé, Chungagué, Chungalé, Fruta Negra, ñungagué, Uvito.* The pulp of the fruit is used as writing ink (*Benítez de Rojas et al. 4674*, MY; *M. López del Pozo 477, 848, 868*, MYF).

Representative specimens seen. VENEZUELA. **Lara:** Without other locality, *Burandt & Garófalo V0596* (MY). **Mérida:** Laguna Negra, SE of Laguna de Mucubají, *Barclay & Juajibioy 9754* (MO); La Culata, Río Mucujún, to 15 km NE of Mérida, *D'Arcy et al. 18236* (MO, MY); Sierra de La Culata, *Ruiz-Terán 6911* (MERF). **Táchira:** Páramo de Tamá, frontera Colombo–Venezolana, *Steyermark et al. 98775* (MY, US, VEN). **Trujillo:** Páramos de El Jabón–El Turmal, 15 km al E de Carache, *Ruiz-Terán & López-Figueiras 949* (MERF).

6. **Cestrum cuneifolium** Francey, Candollea 7: 60. 1936. TYPE: Colombia. Santander: Eastern Cordillera, eastern slope of Páramo del Hatico, from Toledo to Pamplona, 2900 m, *Killip & Smith 20590* (lectotype, here designated, NY).

Shrub or *tree* 2.5–7 m tall, 3.5 cm DBH, branched in the upper half, branches terete; pubescence of reduced simple, sometimes gland-tipped and perhaps branched hairs. *Leaves* solitary, narrowly obovate, 6–12 × 2–4 cm, apically short-acuminate or obtuse, basally cuneate and fine-decurrent on the petiole, margins revolute, coriaceous, mostly drying reddish brown, glabrous, veins 7–9 on each side, parallel, arcuate, branching and anastomosing to form a looping, partial submarginal vein, veins elevated beneath; petiole 5–10 mm long, glabrous; minor leaves wanting. *Inflorescences* short, axillary racemes of 5–8 flowers; peduncles 5 mm long. *Flowers* nocturnal?, 18–22 mm long, pedicels to 1.5 mm long, bracteoles foliaceous, 1.5–2.5 mm long, puberulent, caducous; calyx tubular, 4–5 × 2–2.5 mm, the veins inconspicuous, tube 3–5 mm long, glabrous outside, with minute hairs on the upper half within, teeth ca. 1 mm long, minutely ciliolate and tufted; corolla purplish and yellowish, often drying yellowish with darker tips, 16–19 mm long, tube 13–16 mm long, slightly contracted above the ovary, expanding abruptly on emerging from the calyx, expanding gradually upward and appearing sub-cylindrical or clavate, mouth 3–4 (2.5–3) mm wide, lobes narrowly triangular, 2.5–5 mm long, ciliate, the folds tomentose; stamens 10.5–14.5 mm long, filaments adnate for 5.5–8 mm, pilose to 2–2.5 mm from the base, insertion geniculate, tumid, slightly pilose, free part 6–8 mm; ovary 1–2 mm across, glabrous, disk conspicuous, 0.5 mm long, ovules 3–5, style 13–14 mm long, papillose 2.5 mm below the stigma, stigma 0.5 mm long, bilobed, exserted 1 mm. *Fruits* subglobose, 6–8.5 × 6.7 mm wide; fruiting calyx almost unchanged; seeds 1 per fruit, 6–6.5 × 4.5–6.5 mm wide. [Francey 7: 28.] Figure 12.

This species is similar to *Cestrum imbricatum* Rusby, differing conspicuously in its smaller, crowded leaves. The calyx and corolla in *C. imbricatum* are often purple rather than green as in *C. cuneifolium.*

Distribution (Fig. 13). Western Venezuela in the Andean states of Mérida and Táchira. In cloud forest; 2200–2900 m. Also in eastern Colombia.

Phenology. Collected in flower in March and November.

Representative specimens seen. VENEZUELA. **Mérida:** La Carbonera, *Bernardi et al. 13056* (NY), *17200* (MO, NY); San Eusebio, *Meier et al. 531* (MY, VEN). **Táchira:** Pico de Vela and Buena Vista *Charpin & Jacquemoud 13146* (MO, NY); Delicias–Villa Paez, *Morillo & García 11385* (MERF, MY).

7. **Cestrum diurnum** L., Sp. Pl. 191. 1753. TYPE: Cuba. Hortus Cliffortianus (lectotype, here designated, LINN 258.4).

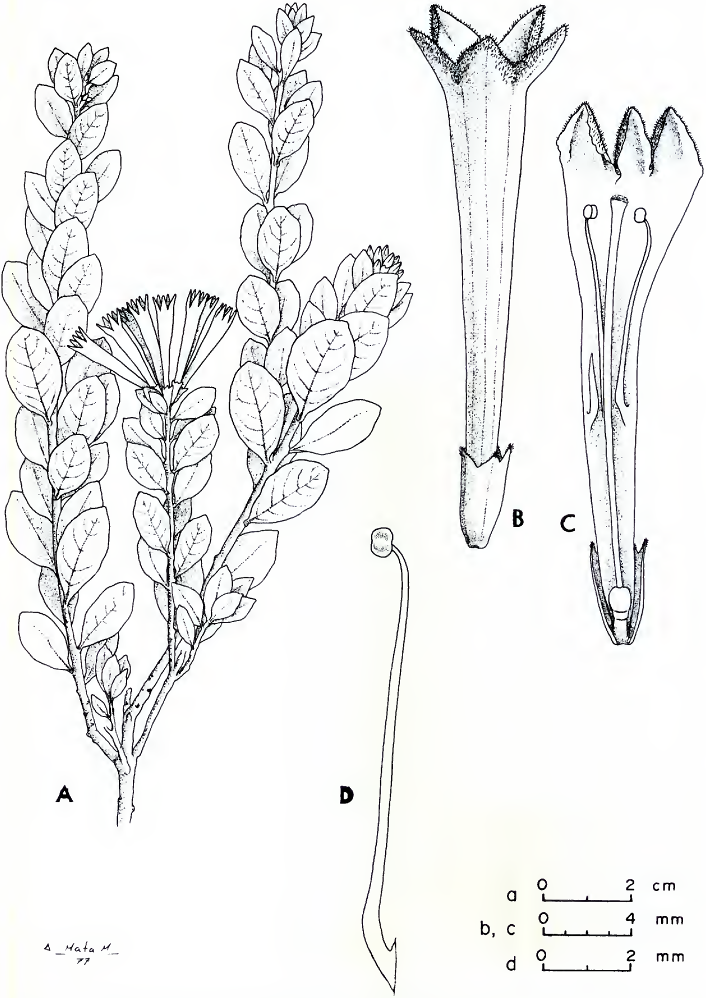

Figure 10. *Cestrum buxifolium.*—A. Flowering branch.—B. Flower.—C. Flower opened to show stamens and pistil.—D. Stamen. After *Tamayo 4367* (VEN).

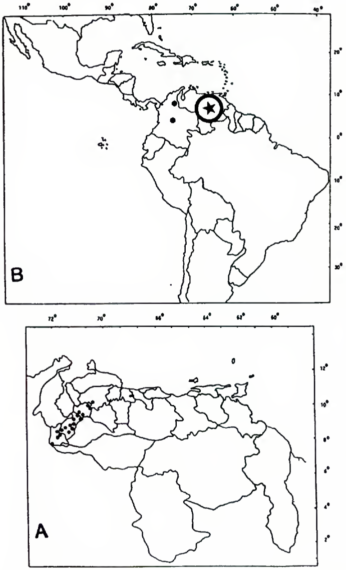

Figure 11. *Cestrum buxifolium*.—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Cestrum fastigiatum Jacq., Pl. Hort. Schoenbr. 3: 44, pl. 330. 1798. *Cestrum diurnum* var. *fastigiatum* (Jacq.) Stehlé, in Fournet, Fl. Illustr. Guad. Mart. 1281. 1978. TYPE: provenance unknown, plate 330 in Jacquin, 1798 (lectotype, here designated).

Cestrum odontospermum Jacq., Pl. Hort. Schoenbr. 3: 44, pl. 331. 1798. *Cestrum diurnum* var. *odontospermum* (Jacq.) O. E. Schulz, in Urb., Symb. Antill. 6: 264. 1909. TYPE: provenance unknown, plate 331 in Jacquin, 1798 (lectotype, here designated).

Cestrum tinctorium Jacq., Pl. Hort. Schoenbr. 3: 45 pl. 332. 1798. *Cestrum diurnum* var. γ *tinctorium* (Jacq.) M. Gómez, Anales Hist. Nat. 23: 269. 1894. TYPE: from Caracas, plate 332 in Jacquin, 1798 (lectotype, here designated).

Cestrum venenatum Mill., Gard. Dict. ed. 8, *Cestrum* no. 6. 16 Apr. 1768, non *C. venenatum* Burm. f. (1 Mar.–6 Apr. 1768). *Cestrum diurnum* var. *venenatum* (Mill.) O. E. Schulz, in Urb., Symb. Antill. 6: 263. 1909. TYPE: Jamaica. *Houston s.n.* (BM? not seen).

Cestrum vespertinum Lunan, Hort. Jamaic. 2: 78. 1814, non L. (1771).

Cestrum laurifolium Fawc., Jamaic. Bull. 11: 7. 1889, non *Cestrum laurifolium* L'Herit. (1788). TYPE: Jamaica. *Fawcett 660* (not seen).

Shrub or *tree* 2–6 m high, crown conical, trunk erect, branches light green, terete; pubescence of erect and crinkly, white, simple hairs, glabrate except on calyces and corolla apices. *Leaves* ovate or elliptical, 4.5–7.5 × 1.5–4.5 cm, apically obtuse or acute, basally narrowly acute to rounded, slightly asymmetrical, gradually attenuate above the middle, firmly membranous or subcoriaceous, bright shiny green above, lighter beneath, glabrous on both sides, veins 6–7 on each side, main veins elevated above, evident and whitish beneath; petiole terete, 5–10 mm long; minor leaves mostly rotund, 10–12 × 4–7 mm, sessile, caducous. *Inflorescences* axillary and terminal, pedunculate congested spicate cymes, racemes, or umbels, peduncles green or tan, elongate, to 9 cm long, bracts foliaceous, 3 × 1.5 mm, pubescent with branched or simple hairs. *Flowers* open and fragrant day and night, 12–17 mm long, often 6-merous, pedicels obsolete; calyx light green, cupular, 2.5–3.5 × 1.5–2 mm, costate, the tube 2–3 mm long, glabrous, teeth less than 0.5 mm long, ciliolate; corolla funnelform, obconical, 11–16 mm long, the tube evenly expanded toward the top, mouth 3–3.5 mm wide, the 5–6 lobes rounded, 1.5 mm long, recurved at anthesis, the folds puberulent; stamens 8–11 mm long, filaments adnate for 7.5–10 mm, pilose 2.5–3 mm from the base, insertion straight, smooth, 0.5–1 mm free, anthers cordiform, 0.5–0.8 mm long; ovary oblong, 1 mm long, seated in a conspicuous disk, style white, 8.5–10 mm long, pilose 2 mm below the stigma, stigma dark green, capitate, slightly exserted. *Fruits* purple-black, subglobose, 11–12 × 8 mm; seeds 13–14, dark brown, 2.5–3.5 mm long. [Francey 6: 284.] Figure 14.

Cestrum diurnum is distinctive in its bright white flowers with 5–7 strongly recurved corolla lobes, and in its often slightly bluish foliage.

The plate (332 in Jacquin, 1798) that typifies *Cestrum tinctorium* Jacq. was prepared from a plant cultivated from seeds from Caracas, Venezuela. See D'Arcy (1970) for a discussion of Jacquin's career and typification of his names. *Cestrum vespertinum* Lunan is based on *Jasminum laurinis foliis...*, Sloane Voy. Jamaica 2: 96, pl. 204, f. 2. 1725, and on *Fruticosum, follis oblongo-ovatis...*, Browne Civ. Hist. Nat. Jamaica 178. 1756. This name was placed in the synonymy of this species by Francey (1935: 284). *Cestrum laurifolium* Fawc. was placed in synonymy by Francey (1935: 284). *Cestrum diurnum* var. *venenatum* (Mill.) O. E. Schulz was placed in synonymy by Francey (1935: 288).

Chromosome numbers of this species have been reported as $n = 8$ (Gill, 1972), the normal comple-

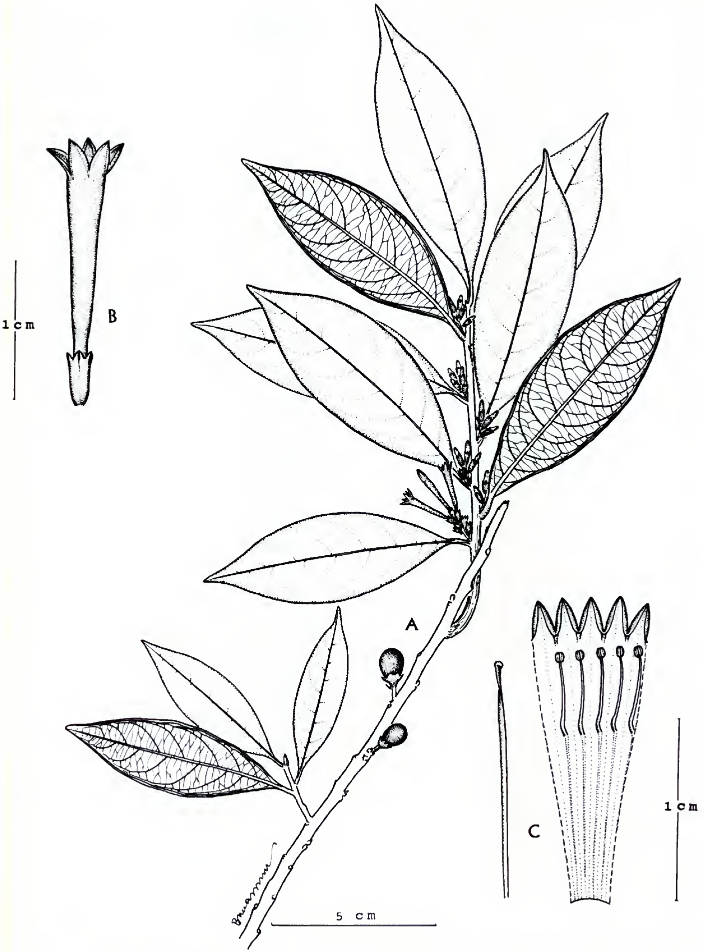

Figure 12. *Cestrum cuneifolium*.—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens and style. After *Morillo & Garcia 11385* (MY).

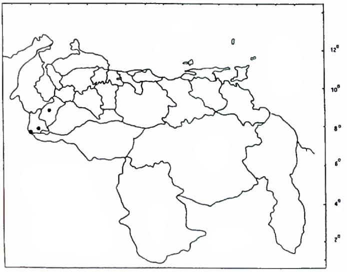

Figure 13. *Cestrum cuneifolium.* Distribution in Venezuela.

ment in the genus. There is also a curious, older report of n = 15, 16 (Sharma & Sharma, 1957, 1958).

Distribution (Fig. 15). Cultivated for ornament and sparingly naturalized in Venezuela. Aragua, Carabobo, Falcón, Mérida, Miranda, Sucre, Táchira, and the Distrito Federal. In sun and shade; to 1500 m. Also in Florida and the Antilles and infrequent on Caribbean coasts of Mexico. Perhaps native to the Greater Antilles.

Phenology. Flowering in irregular spurts 3–5 times a year. Flowers stay open night and day.

Common names and toxicity. *Miel.* Other common names referring to night-blooming probably refer to *Cestrum nocturnum.* The species has been implicated in deaths of horses (Krook et al., 1975).

Representative specimens seen. VENEZUELA. **Aragua:** Maracay, Universidad Central de Venezuela, *Benítez 1556* (MY). **Carabobo:** Canoabo, cerca de la Universidad Francisco de Miranda, *Benítez et al. 5162* (MY). **Falcón:** Coro, Plaza Manaure, *Wingfield 5116* (CORO, MY). **Mérida:** Plaza Bolívar de Ejido, *Ruíz-Terán & S. López-Palacios 6113* (MERF, MY). **Miranda:** Petare, *Elías 239* (CAR). **Sucre:** Cultivated, Eulogio Mago, Valley of Cocollar, *Steyermark 62434* (MY, VEN). **Táchira:** Plaza de Lobatera, *Ruíz-Terán 3606* (MER). **Distrito Federal:** Jardines de Caracas, *Lasser 3533* (MY, VEN).

8. Cestrum glabrescens (C. V. Morton) Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 463. 1967. *Cestrum tenuiflorum* var. *glabrescens* C. V. Morton, Bull. Torrey Bot. Club 58: 466. 1931. TYPE: Venezuela. Amazonas: Agüita, Mount Duida, *Tate 885* (holotype, US).

Shrubs 1.5–4 m tall, adult stems glabrous, young branches puberulent; pubescence of simple and perhaps branched, moniliform ascending and crumpled hairs, most parts soon glabrescent. *Leaves* elliptical or ovate, sometimes narrow, (7–)9–16(–21) × 3–6(–8) cm, apex acute, acuminate or abruptly acuminate, base rounded or short-cuneate, margins plane or slightly revolute, firmly membranous, papery or subcoriaceous, dark green above, lighter beneath, glabrous, veins 6–13 on each side, ascending, arcuate or bending toward the tips, impressed above, salient beneath; petiole 0.5–1.8 cm long, glabrous; minor leaves wanting; bracts wanting or caducous. *Inflorescences* axillary spikes or racemes, sometimes forming paniculate masses, 2.5–3 cm long, axes glabrescent. *Flowers* nocturnal?, 23–28 mm long, pedicels 0.5–2.5 mm long, tomentose; bracteoles linear, 3–6 mm long, tomentose; calyx cupular, 3–5 × 1–1.5 mm, costate, pubescent outside, glabrous within, the tube 2.5–4 mm long, the 5–6 teeth unequal, deltoid, 0.5–1 mm long, ciliolate; corolla yellowish green with purplish marks on the tube and lobes, 22–27 mm long, the tube gradually expanded upward, mouth 2 mm wide, lobes narrowly ovate, 3–4.5 mm long; stamens 14–19.5 mm long, filaments glabrate, adnate for 13–18 mm, insertion straight, smooth, free part 1–2 mm, the anthers orbicular, 0.3–0.5 mm across; ovary lobed, 1.5–1.8 mm across, glabrous, ovules 10–13, style 15–20 mm long, glabrous, papillose below the stigma, the stigma bilobed. *Fruit* purple, subglobose, 8–11 × 5–8 mm, the pericarp thick; seeds 3–4, olive-colored, 6–8 mm long (*Steyermark 93274*). Figure 16.

This species resembles *Cestrum latifolium,* but the leaves are glabrous and the flowers are longer. When dry, the membranous leaves of *C. glabrescens* are often shiny with yellowish veins. The inflorescences are usually reduced on relatively thick stems, but sometimes they are enlarged into racemose or spicate subterminal clusters.

Distribution (Fig. 17). Tepuis (inselbergs) of Amazonas and Bolívar. Associated with low-growing plants along riverine woods and hills in cloud-forest (?); 870–1900 m. Apparently endemic.

Phenology. Collected in flower from October to June, and in fruit in May and June.

Representative specimens seen. VENEZUELA. **Amazonas:** Dept. Atabapo, slope of cerro Marahuaca, *Liesner 17789* (MO); Cerro Marahuaca, *Steyermark 129677* (MO, MY, VEN). **Bolívar:** above Camp 3, *Maguire et al. 42032* (NY); Caño Mojado, Chimantá–Massif, Torono–tepui, *Wurdack & Steyermark 1083* (F, NY, VEN).

9. Cestrum humboldtii Francey, Candollea 6: 393. 1935. TYPE: Peru. Pampayacu, hacienda at mouth of Chincao Río, 1050 m, *Macbride 5129* (holotype, F).

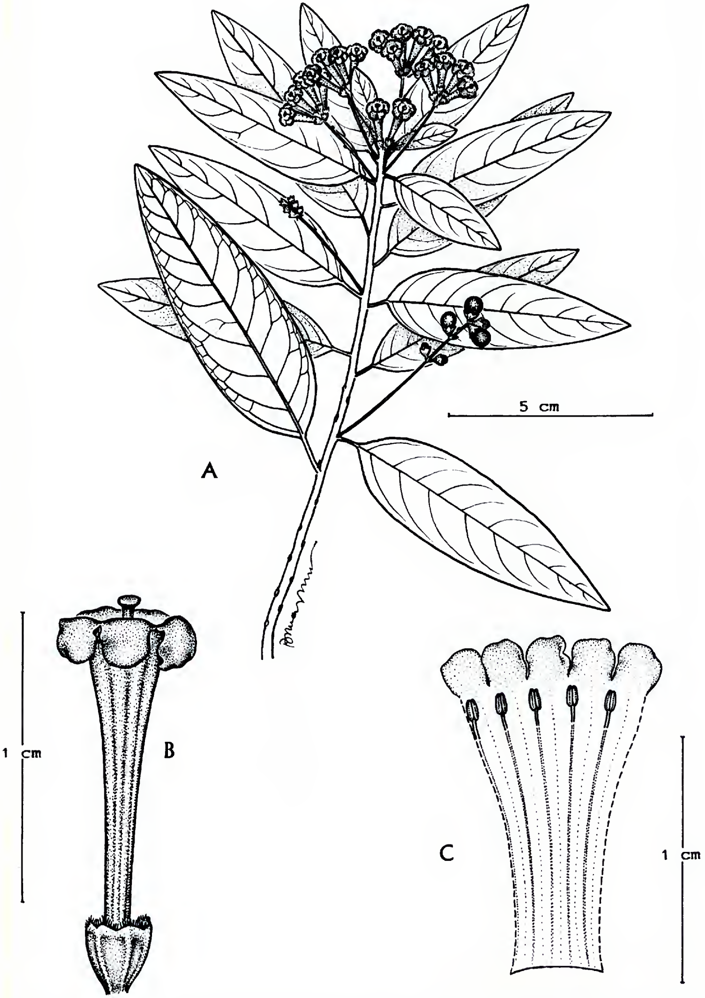

Figure 14. *Cestrum diurnum.*—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens and style. After *Cawz 12* (MY).

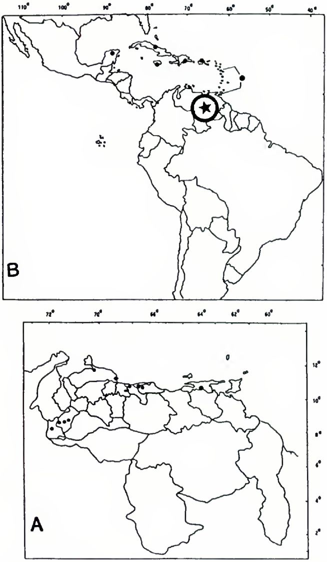

Figure 15. *Cestrum diurnum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Cestrum humboldtii var. *calycinum* Francey, Candollea 6: 394. 1935. TYPE: Peru. Muna, trail to Tambo de Vaca, 8000 ft., *Macbride 4332* (holotype, F).

Cestrum humboldtii var. *tenuiflorum* Francey, Candollea 6: 394. 1935. TYPE: Colombia. Bogotá, Monte de Fusagasugá, *Triana s.n.* (holotype, G-DC, = IDC microfiche, = F photo 28363).

Shrub or *tree* 4–13(–20) m tall, branches terete, densely gray pubescent, the dark color of the stems visible beneath them; pubescence of branched, stellate and simple hairs. *Leaves* ovate or elliptical, 9–27(–45) × 4.5–11 cm, apically attenuate, base cuneate, occasionally long-cuneate, sometimes somewhat oblique, firmly membranous to coriaceous, sometimes rugose, above drying dark brown, beneath dark green, veins 9–16 on each side, mostly parallel, ascending, and moderately arcuate, the major veins impressed and all veins pubescent, the major veins black, reticulate veined beneath; petiole canaliculate, purple, 1.5–5.5 cm long, puberulent; minor leaves present on young branches, 3 × 1.5 cm, subsessile. *Inflorescences* axillary panicles, axes basally branched, 2.5–5(–7) cm long, sometimes lax and arching out from the stems, peduncles 2–4 mm long, bracts foliaceous, 18 × 5 mm; bracteoles linear, 6–8 mm long. *Flowers* fragrant, 16–21 mm long; pedicels 0.5–1.5 mm long; calyx mostly tubular, 3.5–6 × 2–2.5 mm, costate, subcoriaceous, sometimes densely tomentose outside, especially near the base, lanose-pubescent within, the tube 2.5–4.5 mm long, the teeth 1–1.5 mm long, ciliate, the tips pilose; corolla whitish, yellowish, or light purple, 14–20 mm long, the tube contracted above the ovary, slightly expanded upward, contracted below the limb and appearing clavate, glabrous outside, mouth 2–2.5 (2.5–3.5) mm wide, the lobes 2–4 mm long, ciliolate, the folds puberulent; stamens 11–14 mm long, filaments adnate for 6–10 mm, the insertion 1–2 mm long, geniculate-tumid, pilose with dispersed hairs, free part 3.5–5 mm, anthers rounded, 0.5 mm across, dark brown; ovary ellipsoid, 0.5–0.7 mm across, glabrous, disk conspicuous, style 10.5–14.5 mm long, puberulent 2 mm below the stigma, stigma capitate, exserted 1 mm. *Fruit* dark purple to almost black, globose or elliptical, 4–6 mm across, slightly stipitate, pericarp slightly thickened, the calyx slightly accrescent and glabrescent; seeds 4–6, dark brown to almost black, 2–5 mm long, embryo white, epicotyl 0.5 × 0.5 mm, hypocotyl 1 × 0.5 mm. [Francey 6: 393.] Figure 18.

This species is recognizable by its large stature, large leaves, and uneven, often floccose whitish pubescence. Except for the pubescence, the leaves mostly dry dark. Most of the collections from Venezuela have glabrate calyces. *Cestrum humboldtii* is apparently related to *C. tomentosum.* While plants of the two species seem amply distinct in Venezuela, some collections from Ecuador suggest a close relationship and are easily confused.

Distribution (Fig. 19). Mérida, Táchira, and Trujillo. Cloud forests; 1000–2500 m. Also in the Andes of Colombia, Ecuador, and Peru.

Phenology. The species has been collected in flower from January to August and in fruit from August to December.

Common name. *Uvito.*

Representative specimens seen. VENEZUELA. **Mérida:** Puente de la Quebrada del Plan hasta Los Magos, Municipio Aricagua, *Bernardi 6194* (MY, NY, P). **Táchira:** Parque Tamá, zona de Buena Vista, *Morillo & García 11475* (MERF, MY). **Trujillo:** Vía La Morita, *Benítez et al. 3783* (MY).

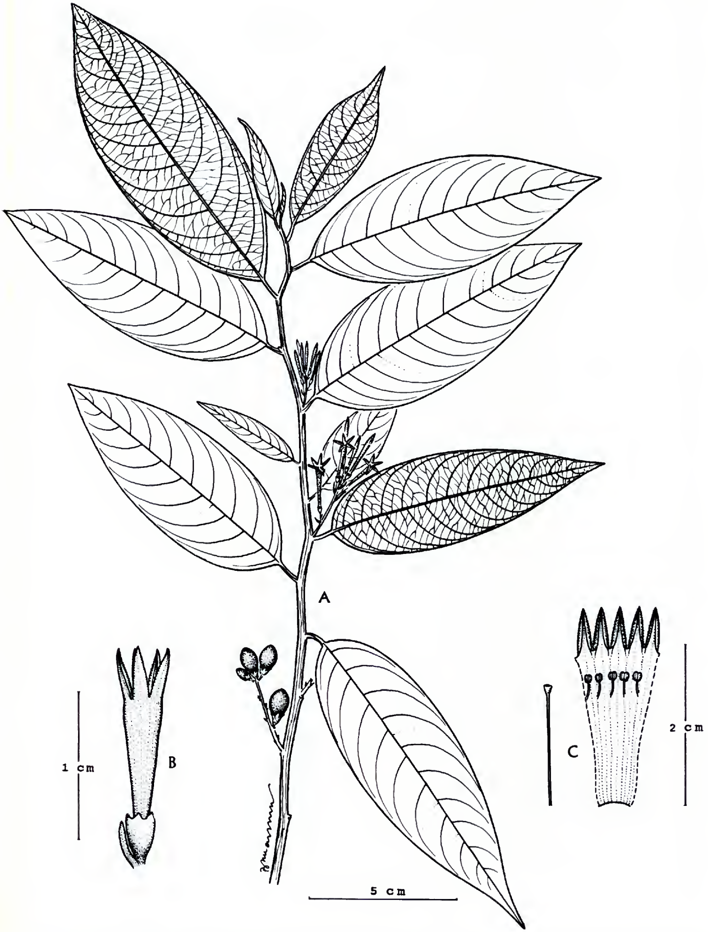

Figure 16. *Cestrum glabrescens*.—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens and style. After *Nee 30689* (VEN).

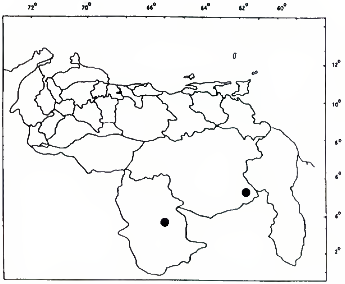

Figure 17. *Cestrum glabrescens.* Distribution in Venezuela.

10. Cestrum imbricatum Rusby, Descr. S. Amer. Pl. 119. 1920. SYNTYPES: Colombia. Santa Marta: rare on the extreme top of the San Lorenzo ridge, 7000 ft., *H. H. Smith 1896* (CM, NY).

Shrub 2–3 m tall, branches terete, densely leafy, glabrous; pubescence of reduced simple hairs. *Leaves* narrowly ovate, 5–8 × 2–2.5 cm, apically short-acuminate, basally narrowed and decurrent on the pedicel, margin subrevolute, coriaceous and rigid, dark green above, dull green beneath, glabrous, lateral veins 6–8 on each side, main veins elevated beneath, petiole drying dark brown, 5–10 mm long; minor leaves wanting. *Inflorescences* axillary racemes 1–2 cm long, 8–10-flowered, peduncles 4–5 mm long, glabrate. *Flowers* 12–21 mm long, sessile, bracteoles drying almost black, linear, 3.5 mm long, sparingly pilose; calyx tubular, 3–4.5 × 1.5–2.5 mm, glabrous, tube 2.5–4 mm long, teeth deltoid, 0.5 mm long, ciliolate and tufted; corolla purple, 10–19 mm long, tube 13 mm long, slightly compressed at the ovary, expanding gradually, mouth 2.5–3.5 mm wide, lobes 2.5 mm long, folds pilose; stamens 13–14 mm long, filaments glabrous, adnate for 7.5 mm, insertion geniculate, tumid, slightly granular, free part 5.5 mm; ovary lobed, 1 mm across, disk conspicuous, ovules 8, style 11–15 mm long, stigma lobed, 1 mm long. *Fruit* not seen. [Francey 6: 381.] Figure 20.

This species is similar to and may include *Cestrum cuneifolium* Francey, from which it differs mainly in its conspicuously smaller and more uniform leaves. Because specimens from Venezuela lack fully developed flowers, much of the above description was made from the type collection, which is from Colombia.

Distribution (Fig. 21). Táchira. 2350–2500 m. Also in Colombia at 2100 m

Phenology. Collected in flower in May (Colombia) and November.

Additional specimens seen. VENEZUELA. **Táchira:** Tierra Negra, cabeceras del Río Quinimarí, *Steyermark 101047* (MO, US, VEN).

11. Cestrum jaramillanum Benítez & D'Arcy, Novon 5: 311. 1995; Phytologia 81: 382. 1996. TYPE: Ecuador. Pichincha: Centenela, Montañas de Ila, 12 km E of Patricia Pilar, virgin rain forest, 550–650 m, 79°19'W, 0°34'S, *Løjtnant & Molau 15835* (holotype, AAU; isotype, GB).

Shrub or small *tree* 2–3 m tall, branched, the branches slender, at first compressed, sometimes drying grooved, later terete, tomentulose, the internodes 3–4.5 cm long; pubescence of reduced, simple, crinkled, ascending hairs. *Leaves* ovate, 10–14 × 4–7.5 cm, apically short-acuminate, basally rounded, truncate, or subcordate, the margin plane, membranous or chartaceous, glabrous above on emerging, the basal half beneath tomentulose on emerging, glabrescent, veins 7–8 on each side, ascending, distally arcuate or looping and forming a submarginal vein 0.5–1 cm from the margin, veins inconspicuous above, the costa and major veins slightly reddish, somewhat elevated and finely puberulent beneath; petiole 5–10 mm long, finely pubescent; minor leaves ovate, 7 × 1.5 mm, sessile, glabrate. *Inflorescences* axillary; peduncle dark, 1–15 mm long; bracts foliaceous, 30 × 10 mm wide. *Flowers* nocturnal?, 25–34 mm long, sessile; bracteoles foliaceous, narrowly lanceolate, 10 × 3.5 mm, acuminate, glabrate or pubescent on both sides, persistent; calyx tubular, 4 × 2.5 mm, drying stramineous, basally rugulose, glabrate, tube 3–3.5 mm long, the teeth deltoid to broadly acuminate, 1.5 mm long, faintly 5-costate; corolla pale green, 29–30 mm, the tube 26 mm long, gradually expanded upward, the mouth not contracted, 2.5–3 mm wide, 5-lobed, the lobes 6–6.5 × 1 mm, oblong, the apex acute, the pleated margin short-pilose; stamens 22–23 mm long, the filaments adnate for 21 mm, insertion straight, smooth, glabrous, free part 1 mm, anthers orbicular, 1 mm across; ovary 0.7 mm across, slightly rugose, glabrous, ovules 5–6, style 23 mm long, stigma slightly bilobed, included. *Fruit* ovoid, 8–10 × 6–7 mm, the pericarp thin, about equaling and loosely enclosed in the bract; fruiting peduncle 15 mm long; fruiting bracteole partially enveloping the fruit laterally; seeds 3–4, dark brown, 5–6.5 mm long. Figure 22.

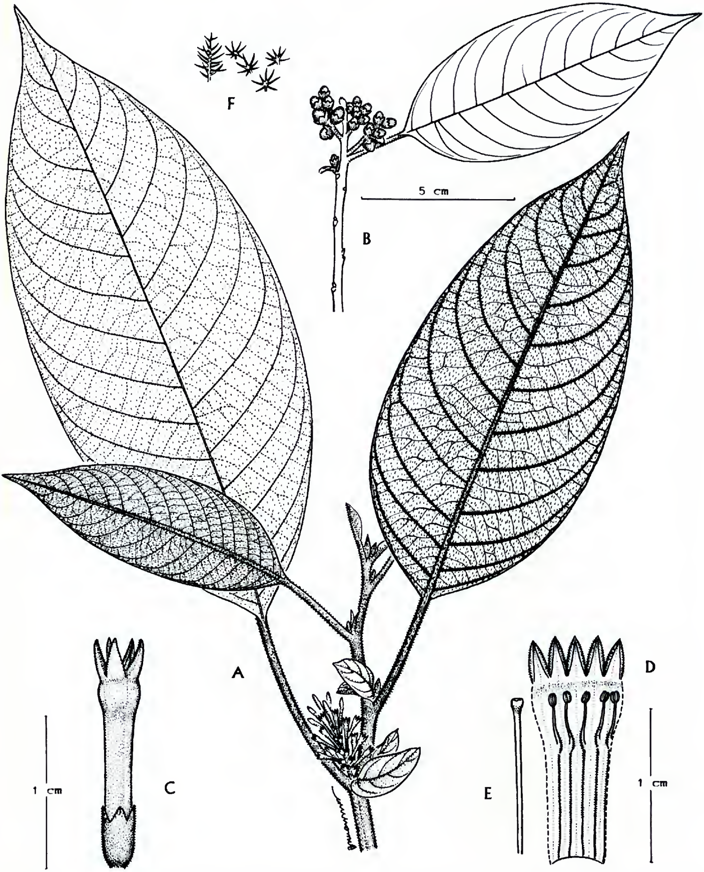

Figure 18. *Cestrum humboldtii*.—A. Flowering branch.—B. Fruiting branch.—C. Flower.—D. Corolla opened to show stamens.—E. Style.—F. Trichomes. After *Benítez 4870* (MY).

This species is distinct in its folded bracts, which half envelop the flower and fruit. The inflorescences are congested at the ends of peduncles that appear to elongate in age, leaving one or two fruits at the apex. These mature peduncles are usually shorter than the neighboring leaves. The specimen on which the Venezuelan report is based is in fruit and is identified with this species with some hesitation.

Distribution (Fig. 23). Distrito Federal; 1000–1300 m. Also in Ecuador.

Phenology. Flowering and fruiting in November.

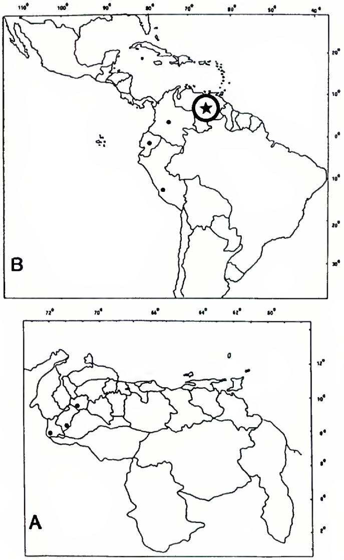

Figure 19. *Cestrum humboldtii.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Specimens seen. VENEZUELA. **Distrito Federal:** Cerro Naiguatá, *Steyermark 92147* (MY, NY, P, US, VEN); Fila Las Delicias, arriba de Naiguatá, 1000 m (fr), *Bunting & Manara 2092* (MY).

12. **Cestrum latifolium** Lam., Tabl. Encycl. 2: 5. 1794. TYPE: [Trinidad?] (holotype, P-LA).

Cestrum tenuiflorum Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 61. 1818. *Cestrum latifolium* var. *tenuiflorum* (Kunth) O. E. Schulz, in Urb., Symb. Antill. 6: 270. 1909. TYPE: Venezuela. Amazonas: Monte Duidae, near district of Esmeraldas of the Orinoco, *Humboldt & Bonpland 1017* (P, = F photo 39047).

Cestrum floribundum Willd. ex Roem. & Schult., Syst. Veg. 4: 807. 1819. TYPE: Brazil. *Hoffmannsegg s.n.* (holotype, B-W 4443 not seen, = IDC microfiche, = F photo 3019).

Cestrum ovatum Willd. ex Roem. & Schult., Syst. Veg. 4: 807. 1819. TYPE: Venezuela. Near Esmeraldas, *Humboldt* (holotype, B-W 4439 not seen, = IDC microfiche).

Cestrum hirtum Sieber ex Sendt., in Mart., Fl. Bras. 10: 210. 1846, non *C. hirtum* Sw. (1788). TYPE: Martinique. *Sieber 81* (MO).

Cestrum poeppigii Sendtn., in Mart., Fl. Bras. 10: 210. 1846. TYPE: Brazil. *Poeppig 2979* (lectotype, here designated, HAL, isolectotypes, G not seen, = F photo 6905, G-DC not seen, = IDC microfiche, W not seen, = F photo 33037).

Cestrum albopunctatum [*albo-punctatum*] Dunal, in A. DC., Prodr. 13(1): 635. 1852. TYPE: Brazil (erroneously attributed to Peru). *Poeppig 2979* (holotype, G-DC not seen, = IDC microfiche; isotypes, HAL, G not seen, = F photo 6905, W not seen, = F photo 33037).

Cestrum chloranthum Dunal, in A. DC., Prodr. 13(1): 636. 1852. TYPE: Trinidad. *Sieber 143* (holotype, G-DC not seen, = IDC microfiche; isotype, MO).

Cestrum oliganthum Dunal, in A. DC., Prodr. 13(1): 634. 1852. TYPE: French Guiana. *Leprieur 250* (holotype, G-DC not seen, = IDC microfiche, = F photo 6906).

Cestrum oliganthum var. *latifolium* Dunal, in A. DC., Prodr. 13(1): 634. 1852. TYPE: French Guiana, collector not indicated [annotated by Francey] (holotype, G-DC not seen, = IDC microfiche, = F photo 23176).

Cestrum prieurei Dunal, in A. DC., Prodr. 13(1): 635. 1852. TYPE: Guyana. *Leprieur s.n.* (holotype, G-DC not seen, = IDC microfiche, = F photo 6904).

Cestrum billbergianum Beurl., Kongl. Vetensk. Acad. Handl. 40: 140. 1854. TYPE: Panama. Portobelo, *Billberg s.n.* (holotype, S, = MO photo).

Cestrum vespertinum Griseb., Fl. Brit. W.I. 5: 443. 1862.

Shrub or *tree* 1.5–7 m tall, 10–12 cm DBH, bark grayish, smooth, branches terete, elongate, sometimes decumbent or lianoid, sprawling, young parts densely pubescent, glabrescent; pubescence of simple hairs. *Leaves* malodorous, ovate or elliptical, sometimes oblique, 5–11 × 2.5–6.5 cm, apically acuminate, the very tip acute or acuminate, rounded at the base, membranous to firmly membranous, dark green above, light green beneath, both sides pubescent, more so beneath and on the major veins, lateral veins 5–7 on each side, mostly strongly ascending; petiole 0.8–1.5 cm long, pilose; minor leaves wanting. *Inflorescence* mass-blooming, axillary or terminal, of short racemes or short-branched panicles, many-flowered, peduncles 0.7–1.5 cm long, branched, pubescent. *Flowers* crepuscular or nocturnal, fragrant, nectar scant or wanting, 15–20 mm long, pedicels 0.5–0.8 mm long, pubescent, bracteoles arcuate, 1.5–2 mm long, puberulent; calyx membranous, 2–2.5 × 1 mm, 5-costate, sparingly pilose outside, glabrous inside, the tube 1.5–2 mm long, the teeth short, 0.5 mm long; corolla greenish white, 15.5–18 mm long, tube narrow, slightly contracted above the ovary then gradually expanded upward, mouth 1.5 mm wide, the lobes sometimes light purple, narrowly deltoid, 2–4 mm long, ciliate and the folds pilose; stamens equal, 11–14 mm long, filaments adnate for 9.5–12 mm, insertion straight, smooth, adnate, free part 2–2.5 mm, pilose 2–2.5 mm below the insertion and at

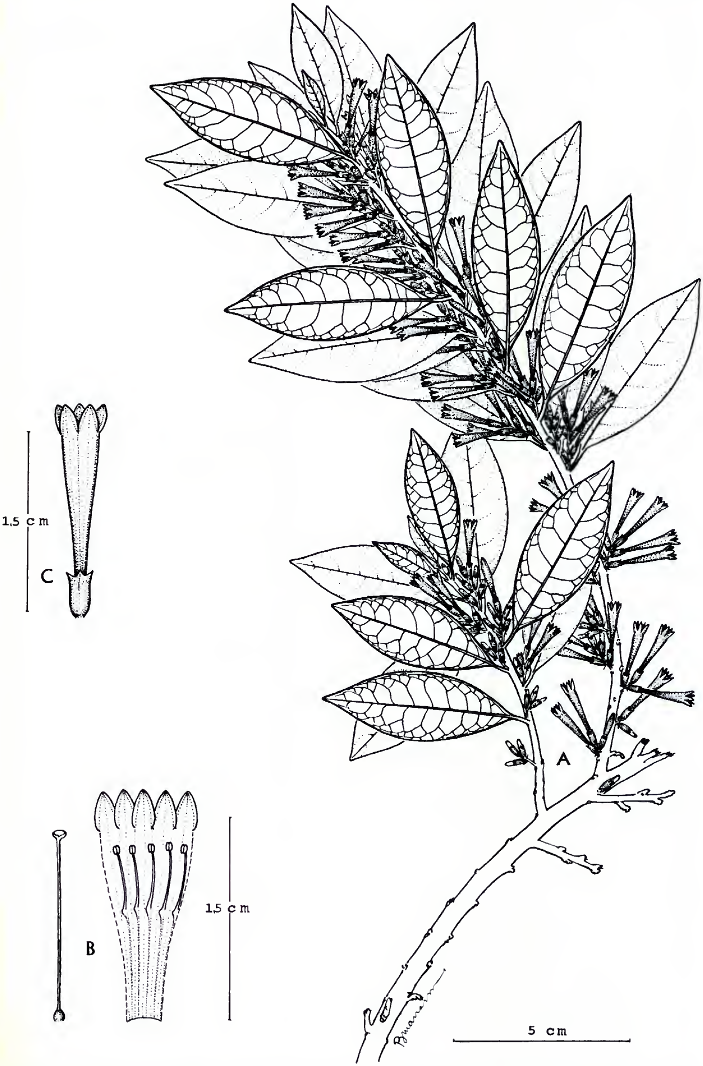

Figure 20. *Cestrum imbricatum.*—A. Flowering branch.—B. Corolla opened to show stamens and style.—C. Flower. After *Steyermark & Dunsterville 101047* (MY).

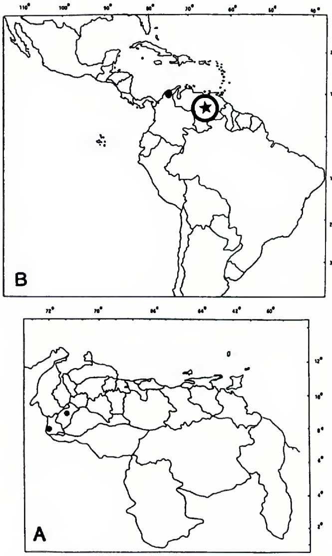

Figure 21. *Cestrum imbricatum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

the base, anthers suborbicular, 0.5 mm across; ovary 0.7–1 × 0.5–1 mm, glabrous, disk inconspicuous, ovules 5–7, style 13–13.5 mm long, about equaling the stamens, stigma subcapitate, included. *Fruit* several per inflorescence, obovoid, 6–10 × 4–8 mm, bluish purple to almost black, shiny, mesocarp white; fruiting calyx slightly accrescent, the limb and lobes spreading; seeds 2–6 per fruit, dark brown, 3–4.5 mm long (*Aristeguieta et al. 7260*); embryo white. [Francey 6: 289.] Figures 2A, 24.

This species may be recognized by its sparingly pubescent leaf undersides and filament pubescence found well below the point of insertion.

The unpublished name "*Cestrum latifolium* var. *genuinum* Stehlé" was applied by Fournet (1978: 1282) in a sense of including C. *chloranthum*, *C. hirtum*, *C. vespertinum*, *C. nocturnum*, and perhaps *C. latifolium* in a single taxon. This may have been Stehlé's way of indicating a typical variety, or it may be a form taxon which has little meaning, as its name was not validly published in conformity with the ICBN (which has required clear designation of a type since 1958). Fournet employed this varietal concept for plants from the French Antilles. *Cestrum vespertinum* Griseb. was placed in synonymy by Francey (1935: 289).

Distribution (Fig. 25). All states except Lara, Miranda, and Nueva Esparta. Widely distributed in deciduous, semideciduous, riverine, and gallery forests, on savannas and secondary vegetation; 50–1200 m. Also in Nicaragua, Costa Rica, Panama, the Antilles, Colombia, Guyana, Surinam, French Guiana, and Brazil.

Phenology. Flowering and fruiting sporadically throughout the year, mainly from January to May, and most heavily in April. The species blooms nocturnally in very fragrant masses for 1–3 days at a time.

Common names and uses. Barriga de Sapo, Bello de Noche, Bonita de Noche, Cazabe, Ciruelilla, Ciruelo de Monte, Clavito, Coral Blanco, Hoja privada, Huele de Noche, Ke Tipen (Panare language), *Mortiño, Palo hediondo, Quasimillo, Rabo Pelado, Tepuru, Uvito.* Used in popular medicine against mange (*Ruiz-Terán 2878,* MER, MERF).

Representative specimens seen. VENEZUELA. **Amacuro:** between Tucupita and Las Mulas, *Steyermark et al. 114590* (MO, NY, VEN). **Amazonas:** Río Siapa, *Gutiérrez 225* (TFAV). **Anzoátegui:** between San Durrial and Mata Redonda, *Davidse & González 19999* (MO, VEN). **Apure:** P. Nacional Santos Luzardo, *Ruiz et al. 4501* (MY). **Aragua:** entre La Victoria y Colonia Tovar, *Benítez 563* (MY). **Barinas:** Río Zulia, Santa Bárbara de Barinas, *Valverde & Peña 1061* (MER, MY). **Bolívar:** entre Villa Lola y Río Grande, *Fernández 2671* (MY). **Carabobo:** Hacienda La Cumaca, Municipio Valencia, *Benítez et al. 5159* (MY). **Cojedes:** entre Manrique y Tierra Caliente, *Benítez 2169* (MY). **Falcón:** Avaria and cerro Montero, *Agostini & Agostini 1171* (MY, VEN). **Guárico:** Estación Biológica de Calabozo, *Aristeguieta 5041* (VEN). **Mérida:** La Florida, SE de Santa María de Caparo, *Aymard et al. 4496* (MY). **Monagas:** Río Guarapiche, 2 km SSW of Jusepín, *Pursell et al. 8432* (VEN). **Portuguesa:** Fundo El Chaparral, Río Portuguesa, *Aymard & Cuello 5591* (MO, MY, PORT). **Sucre:** P. Nacional Península de Paria, Río Grande Arriba, *Benítez et al. 5120* (MY). **Táchira:** Granja Naren, cerca de La Fría, *Benítez de Rojas & Rojas 4756* (MY). **Trujillo:** Cerro Gordo, *Steyermark & Espinoza 111662* (F, NY, US, VEN). **Yaracuy:** Río Yurubí, Labernabó, *Delascio & López 2555* (CAR, VEN). **Zulia:** Casigua, sector Las Cruces, *Bunting & Alfonzo 7294* (MO, VEN). **Distrito Federal:** Cuenca del Río Macarao, *Montes 61* (VEN).

13. Cestrum lindenii Dunal, in A. DC., Prodr. 13(1): 611. 1852. TYPE: Venezuela. Trujillo: 6000 hex, *Linden* (*Funck & Schlim*) *784* (holotype, G-DC not seen, = IDC microfiche, = F photo 6912; isotype, BM).

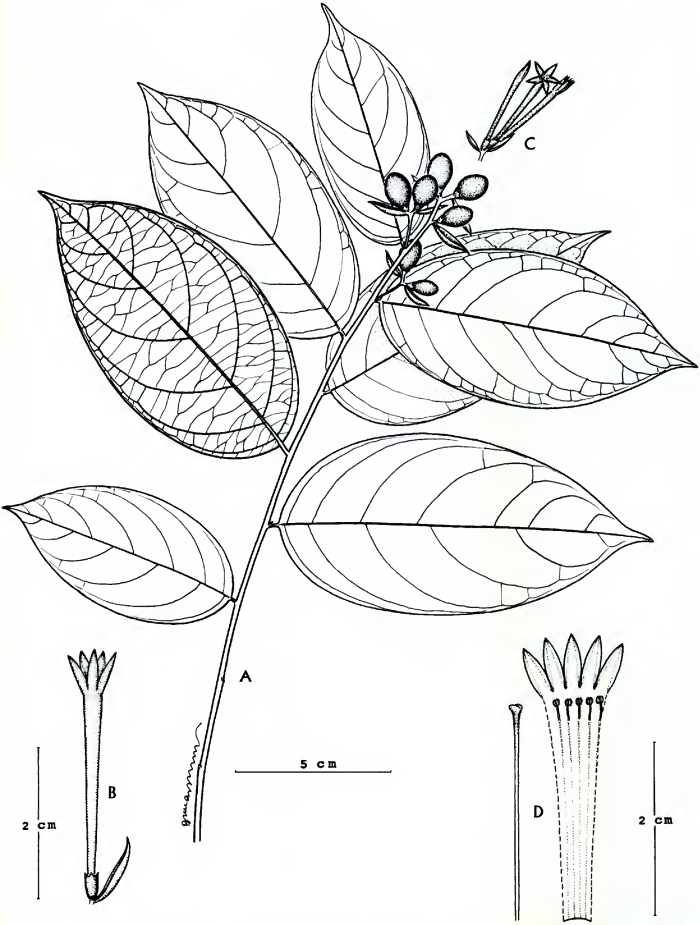

Figure 22. *Cestrum jaramillanum.*—A. Fruiting branch.—B, C. Flowers.—D. Corolla opened to show stamens and style. After *Løjtnant & Molau 1585* (AAU).

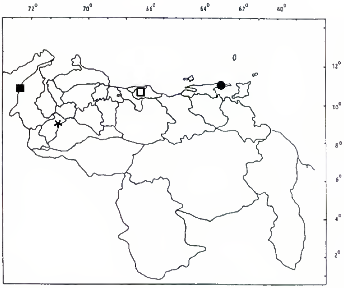

Figure 23. Distribution of *Cestrum* species. Distribution in Venezuela of four species with restricted occurrence. Solid square = *Cestrum tillettii*. Open square = *Cestrum jaramillanum*. Circle = *Cestrum pariense*. Star = *Cestrum ruizteranianum*.

Cestrum amplum Pittier, J. Wash. Acad. Sci. 22: 35. 1932. TYPE: Venezuela. Mérida: *A. Jahn 1075* (holotype, VEN; isotype, US).

Cestrum dubium Pittier, J. Wash. Acad. Sci. 22: 30. 1932, non Steud. (1843). *Cestrum costanensis* Steyerm., Acta Bot. Venez. 3: 212. 1968. TYPE: Venezuela. Distrito Federal: Los Venados de Galipán, 1500–1800 m, *E. Pittier 166* (holotype, VEN).

Cestrum amplum var. *grandifolium* Francey, Candollea 6: 381. 1935. TYPE: Venezuela. Aragua: Colonia Tovar, *Fendler 954* (holotype, NY).

Shrub or *tree* 4–15 m tall, 12–14(–30) cm DBH, the crown little branched, the bark dark and nearly smooth, the branches terete-furrowed, glabrous twigs sometimes stout, often drying blackish; pubescence of simple hairs. *Leaves* strongly malodorous, narrowly elliptical, 6–13(– 16) × 2.7–6 cm, apically acute, obtuse or short-cuspidate, the base cuneate or acute, sometimes slightly decurrent on the petiole, articulated at the base, the margin slightly revolute and slightly folded, plane or undulate, thick-coriaceous or subcoriaceous, dark green and shiny above, light green beneath, glabrous, veins 7–13 on each side, somewhat ascending and parallel, elevated, major veins impressed above, elevated beneath; petiole dark purple, drying black, canaliculate, 4–12(–15) mm long; minor leaves glabrous, 5–14 × 3–3.5 mm, subsessile. *Inflorescences* lax terminal panicles, axes trigonal, dark purple, 5–8 mm long, glabrous. *Flowers* closed but fragrant at midday, 18–23 mm long, sessile; calyx dark purple, 4.5–7.5 × 2–3.5 mm, thick, costate, tubular, the tube 3.5–6 mm long, 5-toothed, glabrous outside, the teeth 1–1.5 mm long, pilose within, ciliolate and the folds puberulent; corolla dark purple with bright yellow lobes, 17–22 mm long, tube contracted around the ovary then gradually expanded to the top, glabrous, mouth (2.5–)3–4 mm wide, the lobes inflexed, triangular, 3.5–5 mm long, apex acute; stamens 12–17 mm long, filament adnate for 5–10.5 mm, adnate portion pilose, the insertion geniculate-tumid and denticulate, pilose, free part 5–7.5 mm, anthers orbicular, 0.5–1 mm across; ovary dark purple, obovoid or subglobose, 0.6–2.5 × 0.5–2 mm, glabrous, style green, 9.5–14.5 mm long, apically pilose, stigma bright green, capitate, 0.5 mm long. *Fruit* purple-black, ovoid or globose, 8–12 × 6–9 mm, the pulp purple; fruiting calyx cupular, dark purple; seeds 5–6 per fruit, dark brown, 6.5–7.5 mm long, drop-like. [Francey 7: 14.] Figure 26.

This upland species has clavate corollas with mouths mostly 3–4 mm wide, wider than most species in Venezuela and suggestive of pollination by birds. The combination of broad corollas and numerous veins on the leaves is diagnostic among the Venezuelan species of *Cestrum.*

"Cestrum glabrum Klotzsch & Karsten" is an unpublished manuscript name that identifies a Colombian specimen *(Karsten 58)* represented by the photo F 2979. The specimen represented is *C. lindenii.*

Distribution (Fig. 27). Aragua, Mérida, Miranda, Táchira, and Trujillo. Dense cloud forests and in dwarf forests, 1600–3000 m. Also in Colombia.

Phenology. Collected in flower and fruit from March to January, but not collected in February.

Common names. Borrachero negro, Cafecito, Laurel, Tábano, Verdecito.

Representative specimens examined. VENEZUELA. **Aragua:** Colonia Tovar, *Tamayo et al. 2504* (VEN). **Mérida:** La Culata, *D'Arcy & Benítez 18258* (MO, MY). **Miranda:** La pica Sabas Nieves–La Silla, *Meier 3180* (MY, VEN). **Táchira:** P. Nacional Los Páramos, *Benítez & Rojas 4740* (MY). **Trujillo:** Arriba de La Puerta, hacia el páramo Los Laureles, *Bono 5891* (MY, VEN). **Distrito Federal:** Junquito, *Aristeguieta 792* (VEN).

14. Cestrum mariquitense Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 57. 1818. TYPE: Colombia: near Santa Ana and Mariquita, 550 hex., *Humboldt* (holotype, P-Bonpl., = IDC microfiche).

Cestrum bogotense Willd. ex Roem. & Schult., Syst. Veg. 4: 807. 1819. TYPE: Colombia. Bogotá, *Humboldt* (holotype, B-W 4454 not seen, = IDC microfiche).

Cestrum bogotense var. *latifolium* Francey, Candollea 6: 211. 1935. *Cestrum mariquitense* var. *latifolium* (Francey) Standl. & C. V. Morton, Field Mus. Nat. Hist. Bot., Ser. 18: 1049. 1938. TYPE: Costa Rica.

Figure 24. *Cestrum latifolium.*—A. Flowering branch.—B. Flowers and fruits.—C. Flower.— D. Corolla opened to show stamens and style. After *Benítez 92* (MY).

San José: El General, 600 m, *Pittier 10509* (holotype, BR not seen; isotype, US).

Shrub 2–4 m tall, leafy, much branched, nodes many-branched, stems striate, pilose; pubescence of simple, moniliform, sometimes collapsing, sometimes gland-tipped, ascending hairs. *Leaves* often crowded, membranous, elliptical or ovate, 3.5–9 × 1.5–4 cm, apically acute or acuminate, basally

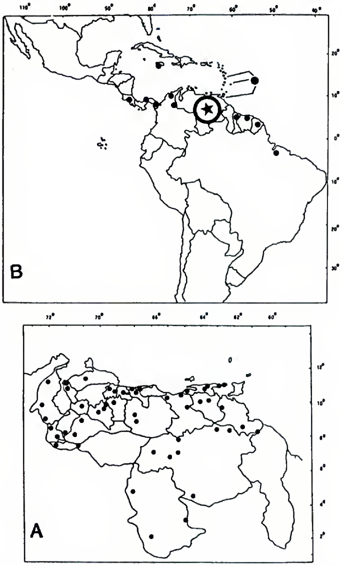

Figure 25. *Cestrum latifolium.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

acute, obtuse or acuminate, light green, glabrous, lateral veins 5–8, ascending, the main veins sparingly pilose beneath; petioles 3–7 mm long, pilose; minor leaves 10–20 × 5–6 mm. *Inflorescences* terminal or axillary, few-flowered, peduncles unbranched, 10 mm long, pilose, hairs sometimes gland-tipped, bracteoles foliaceous, 3–5 mm long, puberulent. *Flowers* crepuscular or nocturnal, fragrant, 29–35 mm long, sessile; calyx cupular, 3.3–5.5 × 1.5–3 mm, inconspicuously costate, tube 3–4 mm long, glabrous outside and in, the teeth 0.3–1.5 mm long, triangular or slightly acuminate, ciliolate, apically pubescent; corolla creamy white or yellow green, 28–35 mm long, tube narrow, gradually expanded upward, obconic-cylindrical, mouth 1.5–2.5 mm, the 5 lobes 4–7 mm long, ciliolate, the folds puberulent; stamens 25–28 mm long, filaments adnate for 20–26 mm, pilose basally and just below the insertion, insertion pilose-barbate, straight, slightly denticulate, free part 1.5–4 mm, glabrous, anthers orbicular, 1 mm across; ovary globose, 0.5–1 mm across, glabrous, disk inconspicuous, style 20–28 mm long, puberulent 1.5–3 mm below the stigma, stigma capitate, 0.5 mm across, exserted 0.5 mm. *Fruit* shiny dark purple, inside purplish white, ovoid, 10–14 mm long, 6–8 mm wide with a small apical protuberance, the pulp 2 mm thick, not juicy; seeds 5–9, dark brown to almost black, 4–6 mm long. Figure 28.

Cestrum mariquitense is distinguished by its abundant, congested minor leaves and by the barbate stamen insertions. Additionally, herbarium specimens of this species may be recognized by the blackish leaves with whitish, irregular pubescence.

Distribution (Fig. 29). Barinas, Lara, Mérida, Portuguesa, and Táchira. At edges of semideciduous, riverine, and cloud forests; 400–1800 m. Also in Costa Rica and Colombia.

Phenology. Flowering is from March to September with a peak in June.

Common names. *Jazmin de Monte, Rudo, Cafecillo.*

Representative specimens seen. VENEZUELA. **Barinas:** Altamira, *Quintero & Ricardi 1524* (MER). **Lara:** 2 km de Villa Nueva, finca de FUDECO, *Casadiego & Campos 378* (MY). **Mérida:** between Mucuchachí and Canaguá, *Steyermark 56322* (F, MY, VEN). **Portuguesa:** NE of Biscucuy, *Nee & Mori 4107* (US). **Táchira:** entre Río Negro y Puente Salom, *Badillo et al. 7848* (MY).

15. **Cestrum megalophyllum** Dunal, in A. DC., Prodr. 13(1): 638. 1852. TYPE: Trinidad. *Sieber 176* (lectotype, here designated, G-DC, = IDC microfiche, = F photo 33963; isolectotype, MO).

Cestrum clausseni Dunal, in A. DC., Prodr. 13(1): 637. 1852. TYPE: Brazil. Minas Gerais: *Claussen 446* (lectotype, designated by D'Arcy (1974: 606), MPU; isolectotypes, G, P).
Cestrum faucheri Dunal, in A. DC., Prodr. 13(1): 640. 1852. TYPE: Cultivated in Spain, *Faucher s.n.* (holotype, G not seen).
Cestrum baenitzii Lingelsh., Repert. Spec. Nov. Regni Veg. 7: 248. 1909. TYPE: Bolivia. *Bang 1634* (lectotype, designated by D'Arcy (1974: 606), MO).

Shrub or *tree* 1.5–8 m tall, 6–8 cm DBH, the trunk erect or somewhat arching, bark smooth and gray-green, young branches and emerging growth puberulent; pubescence of scruffy, simple, sometimes glandular, and sometimes branched hairs. *Leaves* obovate to ellipitical, ± upfolded from the median vein, 10.5–27(–34) × 3.6–8(–12) cm, apically acute or attenuate, the base cuneate and somewhat decurrent on the petiole, margin slightly revolute, coriaceous or subcoriaceous, thick, dark green and opaque above, paler and silvery beneath,

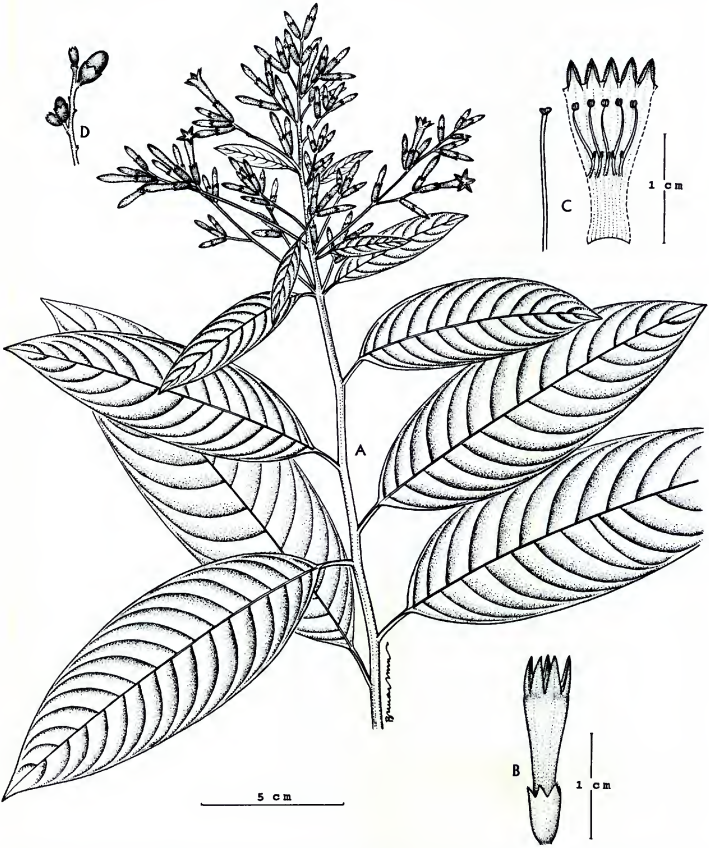

Figure 26. *Cestrum lindenii.*—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens and style.—D. Fruits. After *Benítez 4740* (MY).

often drying dark, laminas glabrous on both sides, veins 7–12 on each side, sometimes variably spaced, strongly ascending, the main veins and lateral veins impressed above, elevated beneath and sometimes with a few hairs, minor venation plane beneath and drying light-colored; petiole dark purple, 1.2–2(–3) cm long, canaliculate, slightly flexible, swollen at the base, glabrous; minor leaves wanting. *Inflorescences* axillary, groups of small fascicles or short pedunculate clusters, axes 3–5 mm long, generally unbranched, puberulent. *Flowers* nocturnal, faintly fragrant, 18–22 mm long, buds white with a purplish tinge, sessile or subsessile; bracteoles linear, slightly arcuate, 1 mm long, puberulent; calyx purple, 2.8–3.6 × 1–1.5 mm, firmly membranous, 5-costate, the tube 2–2.8 mm long,

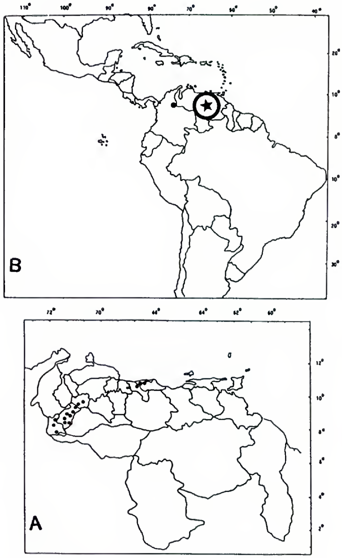

Figure 27. *Cestrum lindenii.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

sparingly pilose outside, irregularly 5-dentate, teeth 0.8 mm long, ciliolate and tufted; corolla greenish white or pale green, 14–20 mm long, tube narrow, expanding gradually upward, slightly contracted around the ovary and again at the mouth, mouth 1–1.5 mm wide, 5-lobate, the lobes white or purplish, narrowly ovate, apically acute, the folds pilose outside, 2.5–3.5 mm long, reflexed or spreading; stamens equal, 11–14 mm long, filaments adnate for 7–11 mm, basally pubescent, insertion mostly straight, sometimes geniculate, tumid, pubescent, free part 2–4 mm, anthers 0.2–0.4 mm across; ovary 0.5–1 × 8 mm, glabrous, ovules 2–3, style 10–14 mm long, sparingly pilose below the stigma, stigma capitate, 0.5 mm across. *Fruit* borne on older woody branches, purple-black, ellipsoidal and obovoid, juicy; seeds 1–3 per fruit, dark brown, 3–4.5 mm long. [Francey 6: 312.] Figure 30.

This species typically has large firm leaves that often dry dark, especially the costa of the leaf undersides and the petioles. Some specimens of *Cestrum lindenii* have similar-appearing dark petioles and major veins, but the minor venation beneath is not light-colored as in *C. megalophyllum.*

The name *Cestrum schwenckiiflorum* Dammer was used by Ule (1908: 401) for a specimen labeled "Peru. Iquitos, July 1902, *Ule 6240*" deposited at HBG and perhaps other places. *Cestrum faucheri* Dunal was placed in synonymy by Francey (1935: 312).

Distribution (Fig. 31). Amazonas, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Falcón, Lara, Mérida, Miranda, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia, and the Distrito Federal. Shady, gallery forests; 30–600 m and in primary and secondary cloud forests, especially in very moist and shady sites; 1200–1500 m. Also in Mexico, Central America, the Antilles, Colombia, Ecuador, Peru, Bolivia, and Brazil.

Phenology. Flowering is mainly from November to April, with the maximum in January. Fruiting is during the dry season, from January to May, with the maximum in March and April. While sometimes seen full of flowers, plants often produce only a few flowers at a time.

Common name. *Bella de Noche.*

Representative specimens seen. VENEZUELA. **Amazonas:** Río Negro, Caño Baría, *Liesner 16999* (MO, MY, VEN). **Aragua:** Carretera hacia Ocumare de La Costa, *Benítez & Aguilera 4692* (MY). **Barinas:** Río Caparo, *Liesner & González 9478* (MO, NY, VEN). **Bolívar:** between Río Mawarinuma at base of Neblina and Río Baría, *Thomas et al. 3392* (NY, MY). **Carabobo:** Río San Gián, arriba de la Toma, S Borburata, *Steyermark & Steyermark 95366* (NY, US, VEN). **Cojedes:** Cerro Azul, fila La Blanquera, NE de La Sierra, *Delascio 7579* (VEN). **Falcón:** Sierra de San Luis, arriba de Santa María, *van der Werff et al. 3209* (WIS). **Lara:** Laguna Negra, loma de Los Naranjos, S de Río Claro, *Steyermark et al. 111522* (US, VEN). **Mérida:** La Isla, Jají, *López-Palacios 1886* (MO, US, VEN). **Miranda:** El Guapo, *Aristeguieta 4009* (MO, VEN). **Nueva Esparta:** Cerro Copey, *Hoyos & Delascio 4285* (CAR, VEN). **Portuguesa:** Quebrada Cuchilla Alta, *Stergios et al. 6626* (MO, MY, NY, PORT). **Sucre:** Río Grande Arriba hasta La Pava, *Benítez et al. 5124* (MY). **Táchira:** Quebrada La Buenañita, Las Coloradas, *Benítez & Rojas 5046* (MY). **Trujillo:** 1 km W of Guaranecal, *Liesner et al. 12836* (MO, VEN). **Yaracuy:** Cerro Negro, Río Cocorotico, *Steyermark & Wessels Boer 100397* (MO, US, VEN). **Zulia:** Río Guasare, Serranía de Perijá, *Gentry 41165* (MO, NY). **Distrito Federal:** between Colonia Tovar and Carayaca, 2.3 km below the junction with Colonia Tovar–Caracas road, *Croat 54467* (MO, NY, VEN).

16. Cestrum microcalyx Francey, Candollea 6: 301. 1935. TYPE: Colombia. Prov. Túquenes, 3000 m, *Triana 2295* (holotype, G-DC, = IDC microfiche; isotype, P).

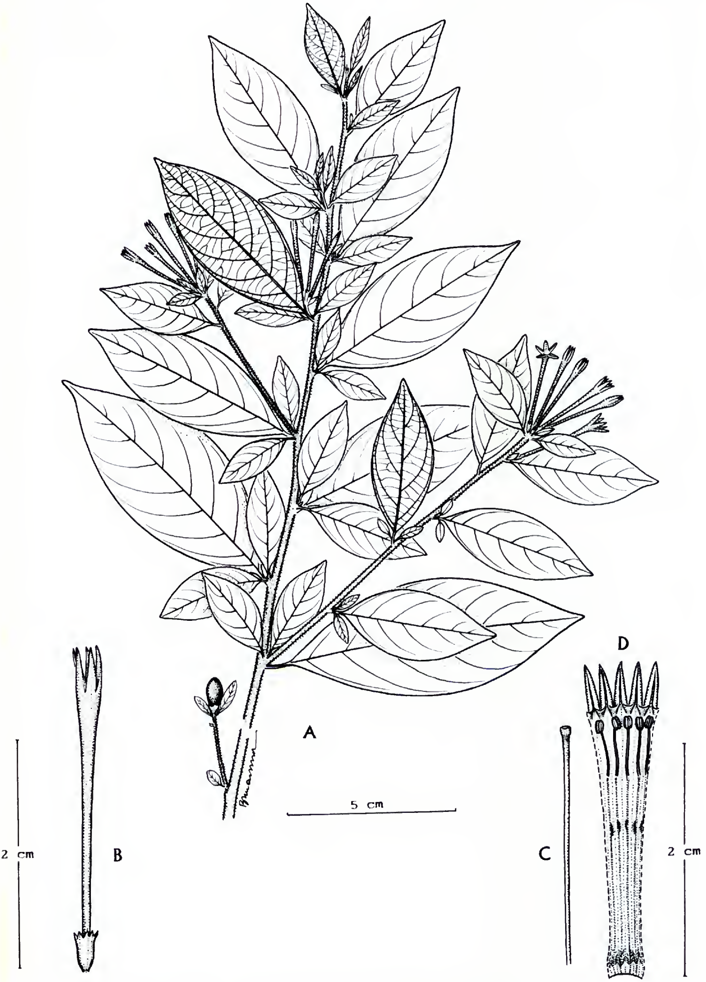

Figure 28. *Cestrum mariquitense.*—A. Branch with flowers and fruit.—B. Flower.—C. Style.—D. Corolla opened to show stamens. After *Benítez 4901* (MY).

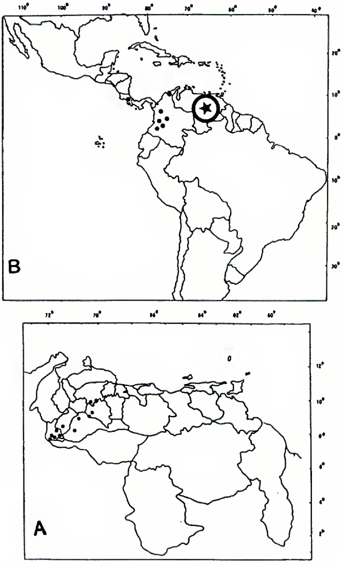

Figure 29. *Cestrum mariquitense.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

Cestrum silvaticum Francey, Candollea 6: 316. 1935, non *C. sylvaticum* Dunal (1852). TYPE: Peru. Junín: Pichis trail, Yapas, 1300–1600 m, *Killip & Smith 25483* (lectotype, here designated, F; isolectotypes, NY, US).

Cestrum standleyi Francey, Candollea 6: 249. 1935. TYPE: Costa Rica. San José: Zurquí, 2000–2500 m, *Standley & Valerio 48082* (holotype, F).

Cestrum tenuissimum Francey, Candollea 6: 248. 1935. SYNTYPES: Bolivia. Mapiri, 700 m, *Troll 2752* (B destroyed, G not seen, F); *Buchtien 32* (B, G, LAU, none seen, B = F photo 28375, MO).

Shrub or *tree* to 6 m tall, much branched from 1.5 mm above the base, 5–15 cm DBH, branches bright grayish green, young branches puberulent; pubescence scant, of reduced, simple, mostly gland-tipped hairs. *Leaves* narrowly elliptical, 8–17 × 2–5.5 cm, apically acuminate, the tips sometimes arching, basally obtuse, or acute, sometimes slightly oblique, margin mostly plane, firmly membranous, dark green and lustrous above, lighter beneath, glabrous, veins 6–11 on each side, often ill-spaced, ascending, major veins not impressed, elevated beneath, minor venation inconspicuous on both sides; petioles 7–12 mm long; minor leaves generally wanting. *Inflorescences* axillary, short, lax, few(–7)-flowered racemes, axes 2–12 mm long. *Flowers* nocturnal, 18–23 mm long; sessile, inserted along the rachis leaving a cicatrice when fallen; bracteoles to 1 mm long, filiform, caducous; calyx tubular-urceolate, 2–3 mm long, inconspicuously costate, tube 1.5–2.5 mm long, glabrous, the teeth 0.5 mm long, unequal, narrowly triangular, curving outward, mostly glabrate, ciliate; corolla light yellowish green, 19–22 mm long, cylindrical, the tube slender, slightly contracted at the ovary, then hardly expanded upward, expanded apically around the anthers and contracted at the mouth, the mouth 1.5–2 mm across, the lobes narrowly triangular, 3–4.5 mm long, ciliate and puberulent on the folds, otherwise glabrous; stamens 15.5–17.5 mm long, filaments adnate for 12–15 mm, pilose 1–2 mm below the insertion, insertion straight, smooth, free part 2–3.5 mm, anthers orbicular, 0.5 mm across; ovary globose, 0.5–0.8 mm across, disk inconspicuous, ovules 7–8, style 16–17 mm long, laxly puberulent near the apex, exceeding the stamens by 0.5 mm. *Fruit* dark purple, globose, 4–10 mm across, with little pulp or juice; seeds black, 2–3, 9 mm long. Figure 32.

This species may be confused with *Cestrum racemosum* or *C. megalophyllum*, but it has fewer, more membranous leaves with fewer veins than the former and smaller leaves than the latter.

Distribution (Fig. 33). Aragua, Táchira, and the Distrito Federal. Restricted to cloud forests; 800–1700 m. Also in Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, and Bolivia.

Phenology. Collected in flower in May and June, especially the latter, and in fruit in October.

Common names. *Tapa Camino.*

Representative specimens seen. VENEZUELA. **Aragua:** Río Hondo, carretera Maracay–Choroní, *Benítez & Rojas 3994* (MY). **Táchira:** Cerro de Cuite, quebrada La Colorada, *Steyermark et al. 119733* (MO, NY). **Distrito Federal:** Carretera Colonia Tovar–Puerto Cruz, *Trujillo 15831* (MY).

17. Cestrum neblinense D'Arcy & Benítez, Ann. Missouri Bot. Gard. 77: 206. 1990. TYPE: Venezuela. Amazonas: Dept. Río Negro, cerro de La Neblina, 0°51′N, 65°57′W, 700 m, *Liesner 16661* (holotype, MO; isotypes, MY, VEN).

Shrub 1–2 m tall, branches reddish, tomentose, hairs curved, ascending, glabrescent, the base of the internodes and inflorescences thickened; pubes-

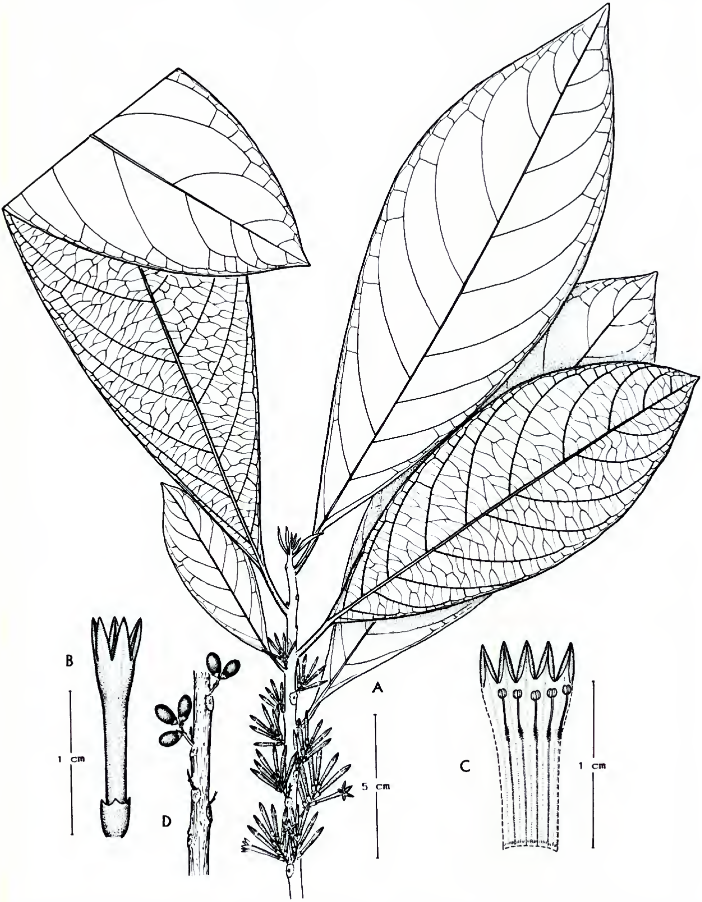

Figure 30. *Cestrum megalophyllum.*—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens.—D. Twig with fruits. After *Benítez 3617* (MY).

cence of small, simple, coarse, multicellular yellowish hairs, often reduced. *Leaves* linear or narrowly ovate, sometimes slightly oblique, 5–10 × 0.5–2.5 cm, attenuate above the middle, apically obtuse, basal third attenuate, margin slightly revolute, subcoriaceous or papery, bright green above, lighter beneath, veins 4–6 on each side, strongly ascending, the major veins sunken, venation elevated beneath; petioles 2–4 mm long, slender; minor leaves wanting. *Inflorescences* of 1–3 flowers grouped in the leaf

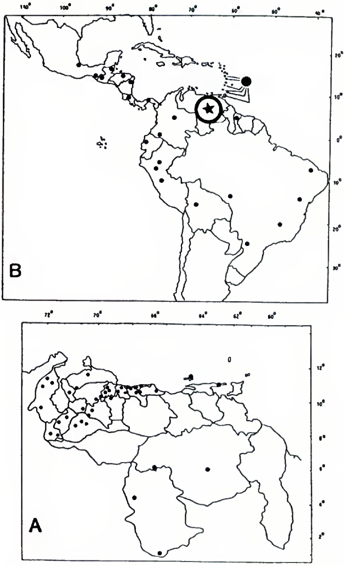

Figure 31. *Cestrum megalophyllum*.—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

axils or terminal, peduncles tomentose, 2–5 mm long, bracts 4–5 mm long; bracteoles 2 mm long. *Flowers* 27–30 mm long, sessile or on pedicels 1.5 mm long, bracteoles linear, ca 3 mm long, pubescent; calyx cupular, 2.5–3.5 × 2.5 mm, 5-costate, glabrate, tube 2.2–3 mm long, 5-toothed, the teeth undulate, ciliolate, 0.3–0.5 mm long; corolla white, 25–27 mm long, tube narrow, slightly expanded upward and at the throat, mouth 3.5 mm wide, the lobes narrowly elliptic, ciliolate, 2.5–3.5 mm long; stamens subequal, 17–19 mm long, filaments adnate for 16–17.5 mm, pilose at the base, insertion straight, smooth, free part 1.5–2 mm, anthers suborbicular, 0.8 mm across; ovary globose, 1 mm across, style 19 mm long, moderately pilose for 10 mm below the stigma, stigma capitate. *Fruit* ellipsoidal or obovoid, 9 mm long, 6.5–7 mm wide; fruiting calyx ca. 6 mm long; seeds 7, 5–7 mm long. Figure 34.

This species is distinctive in its coriaceous, narrow leaves and abbreviated inflorescences. The colors of the fruit and seeds are unknown.

Distribution (Fig. 35). Amazonas. Evergreen cloud forests in the Cerro La Neblina, partly flooded forests along the River Yatúa in sandy soil; 780–2200 m. Apparently endemic.

Phenology. Collected in flower and fruit in March.

Additional specimens seen. VENEZUELA. **Amazonas:** rocky beaches, Cañon Grande, SSW Cumbre Camp, Río Yatúa, cerro La Neblina, *Maguire et al. 42500* (MO, NY, US).

18. Cestrum nocturnum L., Sp. Pl. 1: 191. 1753. TYPE: Jamaica. Pl. Hortus Cliffortianus (LINN 258.1), fide Howard, Fl. Lesser Antilles 6: 276. 1989.

Cestrum suberosum Jacq., Pl. Hort. Schoenbr. 4: 26, pl. 452. 1798. TYPE: from Caracas, pl. 452 in Jacquin, 1798 (lectotype, here designated).

Shrub 2–3 mm tall, branches angular, sprawling, leafy, olive or bluish green, lenticellulate, emerging growth puberulent; pubescence of simple hairs. *Leaves* narrowly ovate to ovate, 8–13 × 2–4.5 cm, evenly attenuate from the middle, the tip acute, basally obtuse or narrowly cuneate, membranous to coriaceous, dark shiny green above, lighter beneath, veins 7–8 on each side, ascending, elevated beneath; petioles 1–2 cm long, slender, glabrous; minor leaves wanting. *Inflorescences* axillary and terminal, many-flowered racemes or panicles, axes glabrous, 3–8 cm long; peduncle 5–10 mm long, glabrous. *Flowers* nocturnal, heavily fragrant, yellowish or greenish white, 21–27 mm long, buds sometimes with a slight violet tint, pedicels 0.5 mm long; bracteoles 2, one foliaceous, 3.5 mm long and puberulent, the other linear, pilose 2.5 mm long; calyx cupular, 2.5–3.5 × 1–1.5 mm, glabrous outside, costate, tube 2–4.5 mm long, 5–6-toothed, teeth 0.5–1 mm long, ciliolate and minutely tufted; corolla 20–30 mm long, the tube gradually expanded upward, slightly contracted beneath the ovary, 5-lobed, mouth 2.5 mm wide, lobes 2–5 mm long, puberulent, apically obtuse or slightly apiculate; stamens inserted equally, 13–15.5 mm long, filaments adnate 10–12 mm, mostly pilose from the base to the middle of the adnate portion, the insertion straight or geniculate, bidentate, glabrous, free part 2.5–3 mm; anthers included; ovary 0.5–1 mm long, the disk yellow, about as long as the ovary, clearly delimited, ovules 7–9, style exserted 1 mm, puberulent 2 mm below the stigma, stigma bilobed. *Fruit* white, sublustrous, globose, 5–9 mm across, mesocarp white, spongy-granular, the placenta green, juicy; fruiting calyx slightly accrescent; seeds 1–3 per fruit, black, ovoid, 2.5–6 mm

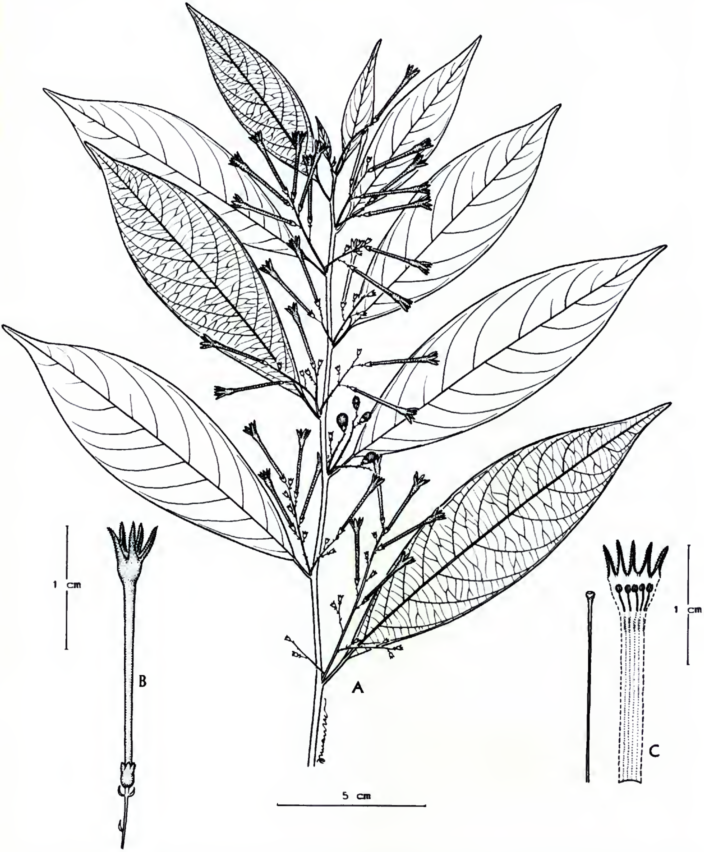

Figure 32. *Cestrum microcalyx.*—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens and style. After *Benítez 3093* (MY).

long, abortive ovules dull yellow-orange. Figure 36; Nee, 1986: 55.

Cestrum nocturnum is cultivated as an ornamental for the nocturnal fragrance of its flowers. The greenish flowers have small, glabrous calyces, and the axes are slender, although the inflorescence structure varies greatly. Herbarium specimens are superficially much like other species, but the two small teeth at the stamen insertion are a good recognition character.

Chromosome numbers of this species have been reported as $n = 8$, $2n = 16$, the normal complement for the genus (Darlington & Wylie, 1955).

Distribution (Fig. 37). Aragua, Mérida, Miran-

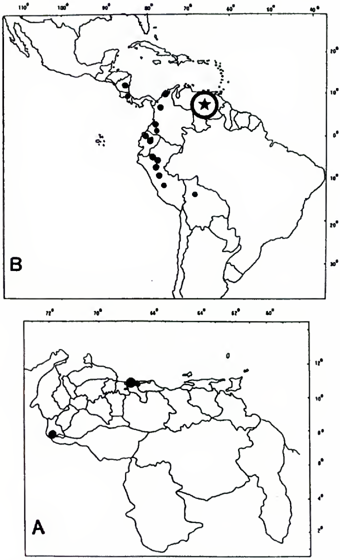

Figure 33. *Cestrum microcalyx*.—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

da, Monagas, Sucre, Táchira, and the Distrito Federal. Widely spontaneous and naturalized; sea level to 1300 m. Also in Mexico, the Antilles, and Central America. Perhaps native to Central America.

Phenology. Flowering occurs in short or long spurts or almost continuously throughout the year but is heaviest in June. Flowering periodicity was also reported by Sachs (1985). Fruiting is sporadic, especially in the second half of the year.

Common names. Bella de Noche, Dama de Noche.

Representative specimens seen. VENEZUELA. **Aragua:** Maracay, *Benítez 1033* (MY). **Mérida:** Municipio San Juan, *Quintero 29* (MER). **Miranda:** cultivated, Carrizal, Distrito Guaicaipuro, *Tillett 746-454* (MY). **Monagas:** San Antonio de Maturín, *Barrios 14* (MY). **Sucre:** Chamariapo, 6 km de Cariaco, *Ruíz-Terán & López-Palacios 9975* (MY). **Táchira:** Distrito Cárdenas, Río Torbes, *Bono 5043* (MY). **Distrito Federal:** Caracas, *Lasser 3469* (VEN).

19. Cestrum olivaceum Francey, Candollea 6: 129. 1935. TYPE: Colombia. Santander: eastern cordillera, vicinity of Charta, 2000–2600 m, *Killip & Smith 18917* (lectotype, here designated, NY).

Shrub 3–4 m tall, branches climbing, terete, tomentose; pubescence of stellate hairs. *Leaves* descending or disposed vertically, ovate, 5–11 × 3.5–6.5 cm, attenuate from the lower third upward, apically acute, basally rounded, margins mostly drying slightly revolute, densely rugose above and beneath, subcoriaceous, dark olive green above, lighter beneath, pubescent, more so beneath, veins 6–8 on each side, elevated beneath; petiole 0.5–1 cm long, tomentose; minor leaves wanting. *Inflorescences* short, axillary, condensed racemes, axes 1.5–2.5 cm long; bracts filiform, 5.5 mm long, pubescent. *Flowers* nocturnal?, 25–26.5 mm long, sessile; calyx green, 5–7 × 3.5–4 mm long, tubular, stellate pubescent outside, glabrous inside, tube 5.5 mm long, 4–5-dentate, teeth 1.5 mm long, obtuse or acute; corolla lilac, apically with whitish and purplish markings, funnelform, 24–26 mm long, pubescent outside, especially above the middle, tube contracted below and above the ovary, mouth 4 mm wide, lobes 4–6.5 mm long, deltoid; stamens 17–19.5 mm long, filaments glabrous, adnate for 10–12 mm, insertion geniculate-tumid, free part 7–8.5 mm, anthers 0.7 mm long, orbicular; ovary subglobose, 1.5 mm across, glabrous, ovules 9–12 mm, style 19–20 mm long, filiform, papillose below the stigma, stigma capitate, included. *Fruit* ovoid, 8–9 × 6–7 mm wide; seeds 5, 4–5 mm long. Figure 38.

Cestrum olivaceum is distinctive in its dense overall brownish yellow pubescence and lilac flowers.

Distribution (Fig. 39). Táchira. Cloud forests along ravines and disturbed forest margins; 2150 to 2450 m. Also in the Department of Santander, Colombia.

Phenology. Of the two collections seen, one was in flower in April and the other in fruit in July.

Additional specimens seen. VENEZUELA. **Táchira:** Parque Tamá, zona de Buena Vista, 5–6 km arriba de San Vicente de La Revancha, *Morillo & García 11478* (MERF, MY); Quebrada Azul, S of El Reposo, 14 km SE of Delicias, *Steyermark & Liesner 118501* (MO, VEN).

20. Cestrum pariense Steyerm., Acta Bot. Venez. 1(2): 62. 1966. TYPE: Venezuela. Sucre: Cerro Patao, N de Puerto de Hierro, NE de Güiria, 850 m, *Steyermark & Agostini 91026* (holotype, VEN; isotype, US).

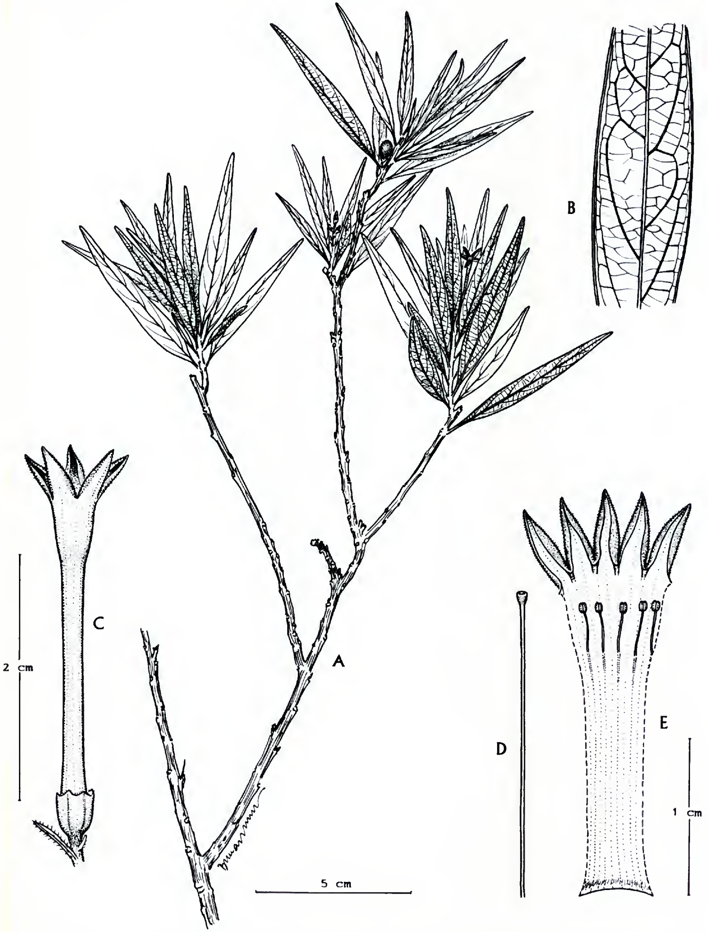

Figure 34. *Cestrum neblinense*.—A. Branch with fruit.—B. Detail of leaf venation.—C. Flower.—D. Style and stigma.—E. Corolla opened to show stamens. After *Liesner 1661* (MY).

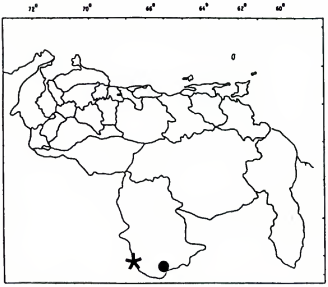

Figure 35. Distribution of two localized species of *Cestrum*. Circle = *Cestrum neblinense*. Star = *Cestrum schulzianum*.

Shrub or *subshrub* 0.6–2.5 m tall, stems fleshy, young parts pilose, glabrescent; pubescence of reduced, crinkled, simple and branched hairs. *Leaves* elliptical, 10–25 × 6–10 cm, apically acute or short-acuminate, basally cuneate, firmly membranous, sometimes fleshy or coriaceous, dark green above, pale beneath, glabrous, veins 6–9 on each side, salient beneath; petiole purple, 1–3.5 cm long, puberulous; minor leaves wanting. *Inflorescences* axillary, peduncles solitary, 2.5–4 cm long, 1–4-flowered, pendulous or erect, elongated in fruit, puberulent; bracts foliaceous, folded upward along the costa and covering the sides of the calyx, pilose, especially along the costa beneath, 7–10.5 mm long, 5–6(–10.5) mm wide. *Flowers* nocturnal, 29–31 mm long, sessile; calyx cupular, 3–3.5 × 2 mm, sparingly pilose, inconspicuously 5-costate, tube 2.5–3 mm long, 5-toothed, the teeth 0.5 mm long, narrowly triangular, ciliate, tufted; corolla greenish white, 28–31 mm long, glabrous, subfunnelform, tube contracted around the ovary, abruptly expanded toward the apex, 5-lobed, mouth 2.5 mm wide, lobes 6.5–8 × 1.5–2.5 mm, ciliolate, folds puberulent; stamens 16–17 mm long, filaments glabrous, adnate for 13.5–14 mm, 1–1.5 mm free, insertion straight, smooth, anthers suborbicular, 0.8 mm across; ovary subglobose, 1–1.5 mm across, glabrous, ovules 6–8, style 15.5–16.5 mm long, exserted 0.5 mm, papillose 1 mm below the stigma then short-pilose 2 mm further down, stigma bilobed, 1 mm long. *Fruit* dark purple, compressed-globose, 14–15 × 10–13 mm wide; seeds 7, 6.5 mm long. Figure 40.

This species is similar to *Cestrum bigibbosum* in its habitat and in the length of its corolla lobes. Small (to 1 m) plants are similar in aspect. However, flowers of *C. pariense* are elevated on slender peduncles and have much smaller calyces.

Distribution (Fig. 23). Sucre. Evergreen forests and river banks; 600–1400 m. Apparently endemic to the Paria Peninsula.

Phenology. Collected in flower in July and in fruit in February and March.

Additional specimens seen. VENEZULEA. **Sucre:** P. Nacional Península de Paria, La Pava, Municipio Mariño, *Benítez et al. 5130* (MY); Cerro de Humo o Terrón de Azúcar, NE de Irapa, *Fernández 3154* (MY); Cerro de Humo, NE de Irapa, *Steyermark 95075* (VEN), *95076* (US); Río Tacarigua and headwaters of Río Tacarigua, E of Cerro Humo, N of Río Grande Arriba, *Steyermark et al. 121595* (MO, VEN).

21. Cestrum petiolare Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 58. 1818. *Sessea petiolaris* (Kunth) Spreng., Syst. Veg. 1: 584. 1825. SYNTYPES: Peru. Between Ayavaca and Yanta, 800 hex, *Humboldt 1409* (P-Bonpl. not seen, = microfiche 63-1-4, = F photo 39046, B destroyed, = F photo 3020).

Cestrum venosum Willd. ex Roem. & Schult., Syst. Veg. 4: 807. 1819. TYPE: Amer. Merid. *Humboldt s.n.* (holotype, B-W 4438 not seen, = IDC microfiche).

Cestrum caloneurum Pittier, J. Wash. Acad. Sci. 22: 31. 1932. TYPE: Venezuela. Aragua: Colonia Tovar, 1800–1900 m, *Pittier 10045* (holotype, VEN; isotypes, G-DC, US).

Cestrum calycosum Pittier, J. Wash. Acad. Sci. 22: 31. 1932. TYPE: Venezuela. Aragua: Colonia Tovar, 1800–2000 m, *Allart 480* (holotype, VEN).

Shrub or small *tree* 4–5(–8) m tall, 5 cm DBH, bark smooth, dark green to gray with prominent lenticels, branches flexuous, young parts often puberulent; pubescence of dendritic white or yellow hairs. *Leaves* malodorous, conspicuously revolute, narrowly elliptical or narrowly ovate, sometimes oblique, (7–)16–22(–29) × (3.5–)5–8(–11) cm, apically acute, often shortly and narrowly prolonged, basally obtuse or narrowly cuneate, sometimes almost truncate, firmly papery to subcoriaceous, above yellowish green, matte, beneath paler, somewhat shiny, veins 14–21(–26) on each side, parallel and ascending near the margins, sunken above, some pustular, purplish beneath, and the minor venation mostly elevated, often appearing pulverulent; petiole purplish on young leaves, green when mature, flexuous, canaliculate, 2–4.5 cm × 1.2–1.5 mm; minor leaves 7–15 × 5–8 mm, sessile, amplexicaulous, sometimes falcate, pointed, glabrous, often caducous, sometimes wanting on mature branches. *Inflorescences* axillary and terminal, form-

Figure 36. *Cestrum nocturnum.*—A. Flowering branch.—B. Twig with fruits.—C. Flower.—D. Stamen.—E. Corolla opened to show stamens. After *Benítez 1034* (MY).

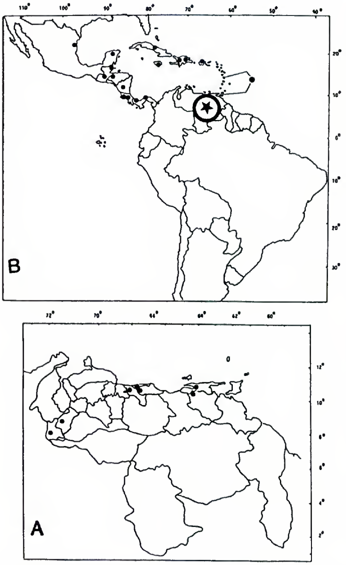

Figure 37. *Cestrum nocturnum*.—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

ing lax, paniculate clusters between the branches, sometimes enlarged panicles 5–8(–13) cm long, flexuous, axes angular and pulverulent. *Flowers* diurnal, fragrant, 20–24 mm long, sessile, bracteoles linear-subulate, deciduous, 5 mm long; calyx bright green, tubular, 7–10.5 × 3.5–4 mm, inconspicuously 5-costate, coriaceous, thick, glabrate outside and puberulent inside, especially on the veins within, tube 6–9 mm long, 3–5-toothed, teeth unequal, 1–1.5 mm long, ciliolate and apically pubescent; corolla yellow, yellowish green, or greenish white, 18–23 mm long, clavate, tube obconical, gradually expanded upward, barely contracted below the ovary and lobes, glabrous, mouth 3.5–4.5 mm wide, the lobes narrowly ovate, ciliolate, apically mucronate, 2.5–4.5 mm long; stamens 12–16 mm long, filaments adnate for 5.5–9.5 mm, pilose 2–5 mm from the base or to the insertion, insertion geniculate-tumid, pilose, 1.5–2.5 mm long, free part 4.5–9.5 mm, anthers orbicular, 0.5 mm across; ovary ovoid or subglobose, 1–2 × 1.5–2 mm, glabrous, disk conspicuous, ovules 8–32, style 14–18 mm long, bright dark green, glabrous, stigma bright green, capitate, 0.5 mm long, slightly exserted. *Fruit* narrowly ellipsoidal, dark purple, 13–25 × 5–12 mm, pulp whitish, 1.7 mm thick; fruiting calyx enclosing about half of the fruit; seeds (6–)18–31 per fruit, brownish yellow, 2.5–3 mm long (*Croat 54936*), embryo white, straight. Figures 1A, 41.

Cestrum petiolare, with its broad corollas and numerous veins on the leaves, resembles *C. lindenii*, but it differs in its pubescence of dendritic rather than simple hairs on twigs and leaf undersides, and in usually having much larger calyces. This species commonly has many more ovules than any other species in the genus.

Francey (1935: 390) referred the unpublished name "*Cestrum moritzianum* Klotzsch & Karsten," used on a manuscript in Berlin, to this species.

Distribution (Fig. 42). Aragua, Mérida, Miranda, Táchira, Trujillo, and the Distrito Federal. Transitional cloud forests, dwarf cloud forests, and near ravines on paramo; 1120–3200 m. Also in Colombia and Peru.

Phenology. Flowering year-round except in July, mainly from January to April and in August. Fruiting is year-round.

Common names. *Borrachero, Tabacón, Titiera, Uvito de árbol.*

Representative specimens seen. VENEZUELA. **Aragua:** entre El Lagunazo y Colonia Tovar, *Fernández 856* (MY). **Mérida:** Río Los Granates, páramo de Los Granates, *López-Figueiras 8754* (MERF, MY). **Miranda:** Pico de Naiguatá, el fondo de la quebrada Rancho Grande, *Meier 3330* (MY, VEN). **Táchira:** Carretera Seboruco–El Suspiro, *Benítez & Rojas 4746* (MY). **Trujillo:** Carretera Tuñame–Jajó, *Aristeguieta & Medina 3689* (NY, US, VEN). **Distrito Federal:** entre La Rosita y El Portachuelo, *Benítez 1438* (VEN).

22. **Cestrum potaliifolium** Dunal, in A. DC., Prodr. 13(1): 638. 1852 [*potalaefolium*]. TYPE: Venezuela. Aragua: Colonia Tovar, *Moritz 824* (holotype, G-DC, = IDC microfiche; isotypes, B destroyed, = F photo 2991, BM).

Cestrum tovarense Francey, Candollea 6: 388. 1935. TYPE: Venezuela. Aragua: Colonia Tovar, *Fendler 962* (holotype, NY; isotype, GH).

Shrub or *tree* to 5 m tall, 6 cm DBH, stems straight, slightly branched, ridged and grooved, with dispersed glands, young growth pulverulent or puberulent with a purplish hue; pubescence of simple reduced hairs. *Leaves* inodorous, ovate or elliptical, rarely obovate, 10–28 × 5–12 cm, apically acute, basally unequal or rounded, rarely narrowly

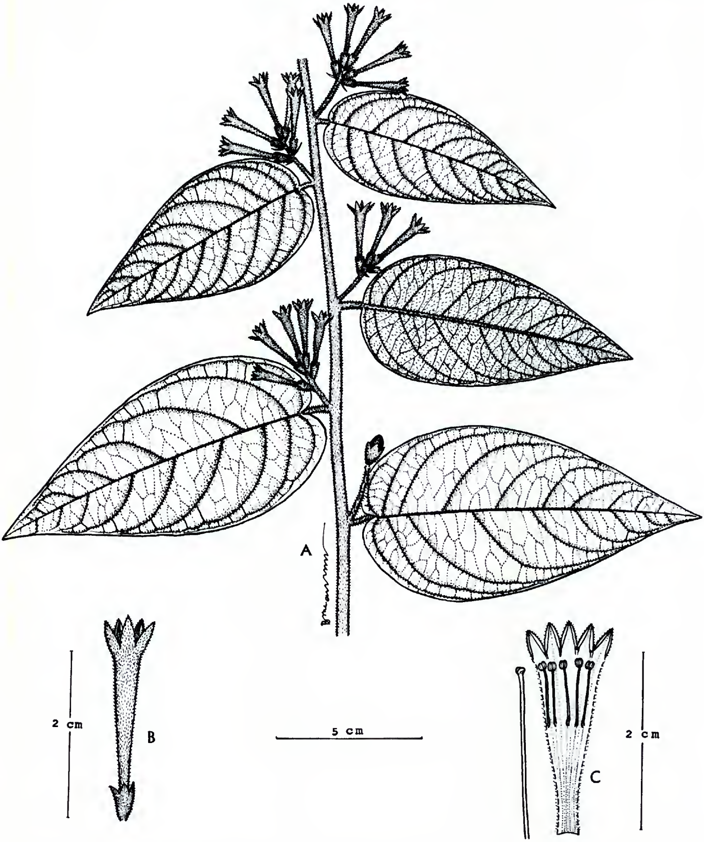

Figure 38. *Cestrum olivaceum.*—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens and style. After *Morillo & Garcia 11478* (MY).

cuneate, the margin sometimes retracted between the main lateral veins and appearing dentate or erose, slightly revolute, lamina coriaceous or subcoriaceous (papery when living), bright dark green above, pale yellowish green beneath, drying yellow, glabrate, sometimes with scarce minute glands beneath, veins 6–10 on each side, ascending, slightly prominent above, elevated beneath, and the minor venation reticulate, inconspicuous when alive; petioles flat-topped, distally canaliculate, flexible in mature leaves, 1.2–2.5 cm long, glabrous, the insertion at the stem often expanded into a rounded pillow-like form; minor leaves wanting. *Inflorescences* axillary, clustered. *Flowers* 20–24 mm long, sessile or with pedicels 0.5 mm long, bracteoles linear, arching, 2–4.5 × 0.5–1 mm, puberulent; ca-

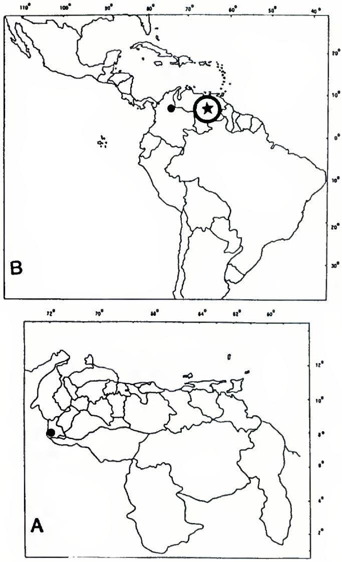

Figure 39. *Cestrum olivaceum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

lyx cupular, 4–5.5 × 2 mm, slightly coriaceous, rugose, glabrous or sparingly puberulent, tube 3–4.5 mm long, 5-dentate, teeth narrowly ovate, 1–2 mm long, apically cuspidate, pilose and with sparse dispersed glands; corolla greenish white or pale yellow, 18–23 mm long, narrowly funnelform, tube gradually expanded upward, slightly contracted at the ovary, mouth 2–2.5 mm wide, lobes 3.5–4.5 mm long, narrowly ovate, apically obtuse; stamens 13.5–15.8 mm long, filaments adnate for 9–11 mm, sparingly pilose from the base to the insertion, straight, barbate, free part 4–5 mm, anthers suborbicular, 0.5 mm across; ovary globose or elliptical, 0.8–1 mm across, glabrous, disk conspicuous, style 12–15 mm long, exserted 0.5 mm, stigma capitate. *Fruit* purple, obovoid to ellipsoid, 8–12 × 7–9 mm wide; seeds 6–8, dark brown, 7–7.5 mm long. [Francey 7: 65.] Figure 43.

Cestrum potaliifolium is similar to *C. megalophyllum* but is distinct in its often yellowish leaves and in the expansion of the stem around many of the petiole bases into a conspicuous, often pillow-like ridge.

In the original publication, Dunal erroneously cited the type collection as being from Colombia.

Distribution (Fig. 44). Aragua and the Distrito Federal. Endemic to Venezuela. Found in evergreen cloud forests; 1000 to 2000 m.

Phenology. Collected in flower from June to October, mainly in June. Fruiting collections have been made from September to January, mainly in January.

Representative specimens seen. VENEZUELA. **Aragua:** entre Las Marochas y Choroní, *Benítez et al. 4912* (MO, MY); Portachuelo forest, *Wood 322* (VEN). **Distrito Federal:** E of Junquito, *Steyermark 57006* (MY, VEN).

23. Cestrum racemosum Ruiz & Pav., Fl. Peruv. 2: 29, pl. 154. 1799. TYPE: Peru. Chinchao and Macora, *Ruiz s.n.* (holotype, F).

Cestrum mathewsii Dunal, in A. DC., Prodr. 13(1): 637. 1852. SYNTYPES: Peru. Chachapoyas: *Mathews s.n.* (MPU, G, neither seen, US).

Cestrum panamense Standl., J. Wash. Acad. Sci. 15: 460. 1925. *Cestrum racemosum* var. *panamense* (Standl.) Francey, Candollea 6: 274. 1935. TYPE: Panama. Río Tapía, *Standley 28042* (holotype, US).

Cestrum grande Pittier, J. Wash. Acad. Sci. 22: 32. 1932. *Cestrum racemosum* var. *grande* (Pittier) Francey, Candollea 6: 275. 1935. TYPE: Venezuela. Distrito Federal: Curucutí, 400 m, on old road from Caracas to La Guaira, *Pittier 10393* (holotype, VEN; isotypes, GH, NY, US).

Cestrum racemosum var. bolivianum Francey, Candollea 6: 274. 1935. SYNTYPES: Bolivia. Santa Cruz: Bosques del Fraile, Buenavista, 450 m, *Steinbach 7259* (B not seen, MO, S not seen).

Trees 6–20(–25) m tall, trunk 12(–60) cm DBH, grayish green, straight, branching with a narrow crown, wood soft and whitish, stems lenticellular, young growth sparingly puberulent; pubescence of simple, white, moniliform ascending and crumpled hairs. *Leaves* malodorous, spreading, ovate 11–19 (–22) × 2.5–7(–9) cm, apically acute or acuminate, base rounded, membranous, slightly sticky to touch, matte dark green above, pale yellowish green beneath, glabrate with a few scattered hairs above, when mature glabrous and often lenticellulate beneath, veins (10–)15–22(–27) on each side, equally spaced and arcuate-ascending at (62°–)70°(– 75°), prominent beneath; petioles canaliculate, 0.7–2 cm long; minor leaves absent. *Inflorescences* mostly axillary clusters of short racemes, peduncles 1.5–2.5 cm long, sparingly pilose. *Flowers* greenish white or yellowish green, the apex sometimes slightly purple, 14–20 mm long; pedicels 1–2 mm long, pubescent; bracteoles 1–2.7 mm long, linear, pubes-

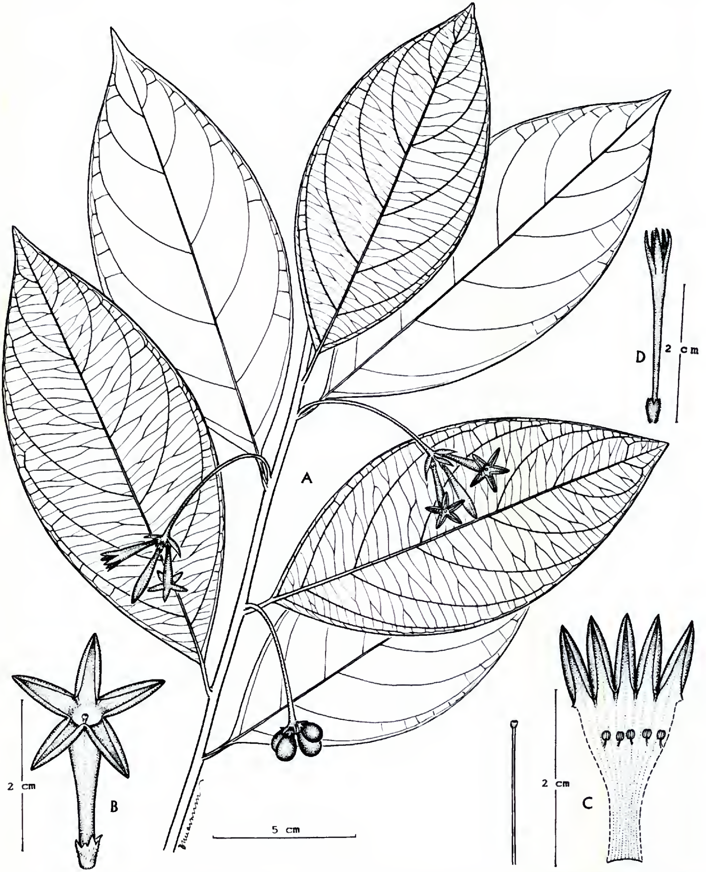

Figure 40. *Cestrum pariense.*—A. Branch with flowers and fruit.—B. Fully opened (night) flower.—C. Corolla opened to show stamens and style.—D. Closed (day) flower. After *Benítez 5130* (MY).

cent; calyx cupular, 1.7–3.6 × 1–1.5 mm, basally narrowed into a stipe, 5–6-costate, membranous, pilose outside, tube 1.5–2.8 mm long, 5-dentate, teeth 0.2–0.8 mm long, pilose outside on the veins and the tips; corolla narrowly funnelform, 13–18 mm long, tube gradually expanded upward, slightly contracted below the ovary, mouth 1.5 mm wide, lobes triangular, ± acute apically, folds pilose, 2–3.5 mm long; stamens 10.5–12.5 mm long, filaments adnate for 8–12 mm, with sparse hairs from the base to 1.5–2.5 mm below the insertion, the base glabrous or pubescent, insertion straight, smooth, free part 1.5–2.5 mm, anthers spherical, 0.2–0.5 mm across; ovary 1–1.5 × 0.5–0.8 mm,

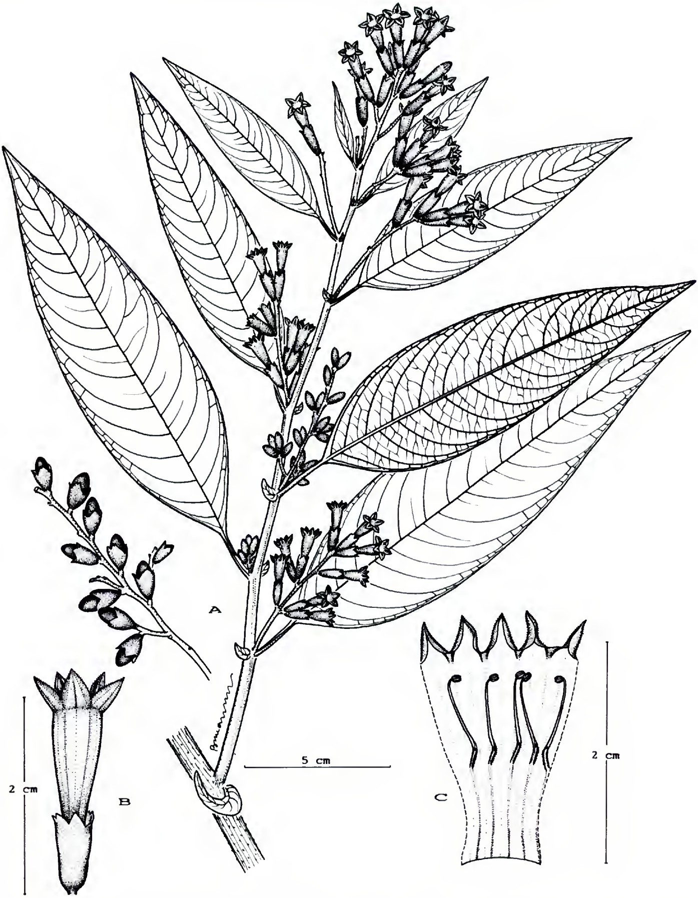

Figure 41. *Cestrum petiolare.*—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens. After *Benítez 4739* (MY).

glabrous, disk inconspicuous, ovules 4–7, style 9–12.5 mm long, papillose below the stigma, stigma capitate, included. *Fruit* purple, globose, 5–6 mm long, 3–5 mm wide; fruiting calyx accrescent and cupulate; seeds 3–7 per fruit, brown, 3 mm long (after *Greenman 5218*), embryo white, 1.5 mm long. Figure 45; D'Arcy, 1974: 609, figure 5.

Cestrum racemosum may be recognized by its usually arborescent stature and usually narrow

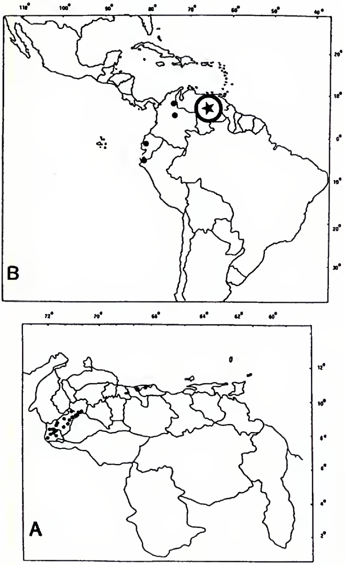

Figure 42. *Cestrum petiolare.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

leaves with numerous, evenly spaced veins, which are salient on the leaf undersides.

Distribution (Fig. 46). Amazonas, Anzoátegui, Aragua, Barinas, Falcón, Lara, Mérida, Miranda, Portuguesa, Táchira, Yaracuy, Zulia, and the Distrito Federal. Evergreen forests, secondary forests, and gallery forests; 400–2200 m. Also occurring from Mexico to Bolivia.

Phenology. Flowering and fruiting year-round with maxima in the first half of the year.

Common names and uses. Used to shade coffee plants, sometimes cultivated in parks and gardens.

Representative specimens seen. VENEZUELA. **Amazonas:** Cerro de la Neblina, *Ewel 195* (MY). **Anzoátegui:** Río Maravilla, E of Bergantín, *Steyermark 61711* (MY, VEN). **Aragua:** Carretera Maracay–Choroní, *Benítez & Rojas 4996* (MY). **Barinas:** Barrancas, *Marcano-Berti & Torres-Lozana 207* (MER, VEN). **Falcón:** La Chapa, Sierra de San Luis, *van der Werff 241* (MO, WIS). **Lara:** Paso de Angostura, represa de Yacambú, confluencia de la Quebrada Honda con el Río Yacambú, *Steyermark & Carreño Espinoza 108771* (VEN). **Mérida:** entre San Jacinto y Tienditas del Chama, *Quintero 526* (MER); La Punta, *Ricardi & Salcedo 5744* (MER), *5756* (MER). **Miranda:** Hacienda de café Turgua, *Aristeguieta 2769* (NY, US, VEN). **Portuguesa:** Pueblo de Anzuátegui, *Smith 7153* (VEN). **Táchira:** La Petrolea, carretera Rubio–San Vicente de la Revancha, *Benítez et al. 4864* (MY). **Yaracuy:** El Chorro, entre La Chapa y Uría, en la vía hacia Curimagua, *Benítez et al. 5151* (MY). **Zulia:** Cerro Sasa, *Steyermark 99894* (MO, US, VEN). **Distrito Federal:** between Caracas and La Guaira, *Fendler 961* (GH).

24. Cestrum reflexum Sendtn., in Mart., Fl. Bras. 10: 218. 1846. TYPE: Bolivia [Brazil]. Chiquitos, *Orbigny 659* (lectotype, here designated, P).

Cestrum floribundum Britton, Mem. Torrey Bot. Club. 6: 92. 1896. TYPE: Bolivia. La Paz: Guanai–Tipuani, Apr.–June 1892, *Bang 1470* (MO, NY not seen).
Cestrum reflexum var. *densiflorum* Francey, Candollea 6: 267. 1935. SYNTYPES: Bolivia. Santa Cruz: bosque de Buenavista, 450 m, *Steinbach 1480* (B destroyed), *3216* (B destroyed), *6172* (MO, B destroyed, S not seen), *7162* (MO, B destroyed, S not seen).

Climbing *shrub* 2–3 mm tall, branches flexuous, puberulent; pubescence of simple and sparingly branched, often cobwebby hairs. *Leaves* often drying grayish, ovate or narrowly ovate, 4.5–11 × 2–6 cm, apically acuminate, the tip acute or obtuse, basally rounded, sometimes short-decurrent on the petiole, membranous, shiny green and puberulent on both sides, 7–8 veins on each side, minor veins impressed above; petiole 1–1.3 cm long, at insertion slightly bent and hooked, slightly thickened and densely tomentose; minor leaves not seen. *Inflorescences* leafy axillary or terminal racemes and panicles, axes 3–5 cm long, pubescent; bracts foliaceous, reduced upward. *Flowers* whitish or yellowish, 25–29 mm long, pedicels obsolete, bracteoles 3 mm long, pilose; calyx cupular, 2.5–4.5 × 1.5 mm, inconspicuously costate, pilose at the level of the teeth, tube 1.5–3.5 mm long, the teeth 1 mm long, narrowly triangular, ± reflexed, pilose inside and out, ciliolate, tufted; corolla 24–27 mm long, glabrous, tube contracted below the ovary, cylindrical, suddenly expanded apically, mouth 1.5–2 mm wide, lobes 4–6 mm long, narrowly ovate, folds and margin puberulent; stamens 19–19.5 mm long, filaments adnate for 18.5 mm, glabrous, insertion straight, smooth, free part 0.5–1 mm, glabrous, anthers rotund, 0.5 mm across; ovary 0.5–1 mm long, glabrous, disk conspicuous, 0.5 mm long, ovules 10–14, style 19–19.5 mm long, stigma bilobate, exserted 1 mm. *Fruit* dark purple, ellipsoidal, 6.5–7(–10) × 5 mm wide; fruiting calyx often drying dark, sometimes flaring; seeds 6–14, light brown,

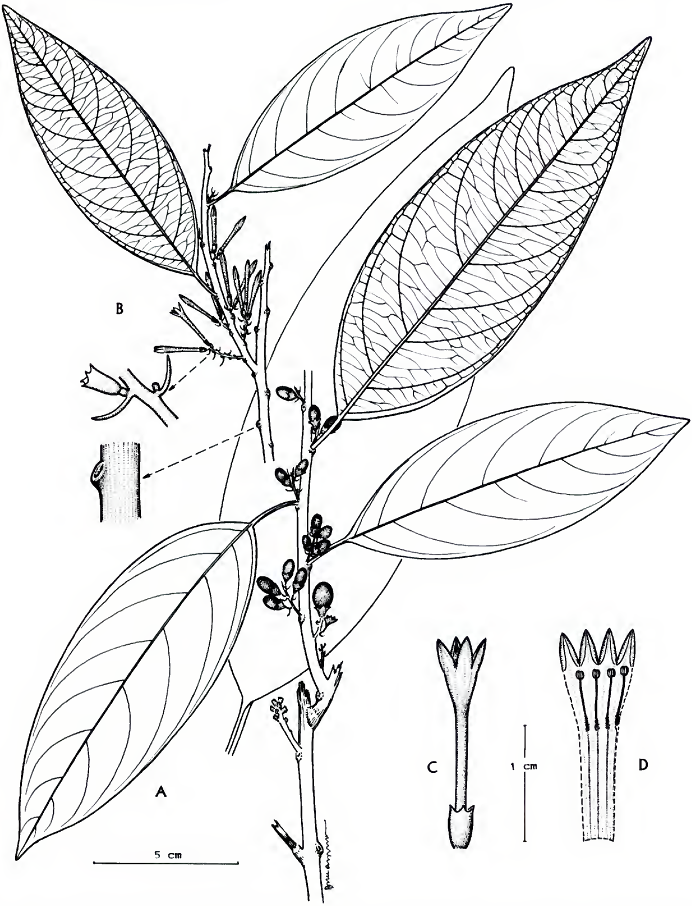

Figure 43. *Cestrum potaliifolium.*—A. Fruiting branch.—B. Flowering branch.—C. Flower.—D. Corolla opened to show stamens. After *Steyermark 57006* (VEN).

4–4.5 mm long. [Francey 6: 265.] Figure 47; D'Arcy, 1974: 611, figure 6.

Herbarium specimens of *Cestrum reflexum* are often best recognized by their grayish color and small but persistent, foliaceous bracts. The plant is a scrambler.

Distribution (Fig. 44). Bolívar; 290 m. Also in

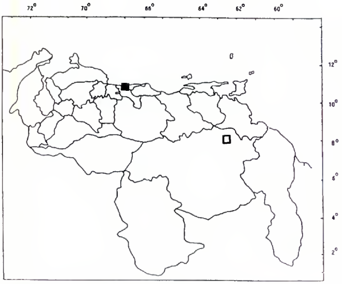

Figure 44. Distribution of two localized species of *Cestrum*. Solid square = *Cestrum potaliifolium*. Open square = *Cestrum reflexum*.

Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Brazil. The species may be native to Brazil.

Phenology. The sole collection from Venezuela was flowering in February.

Outside of Venezuela, *Cestrum reflexum* is an uncommon species found from 50 to 300 m in gallery forest, rainforests, and disturbed areas.

Specimens seen. VENEZUELA. **Bolívar:** Camino a la estación Magdalena, El Palmar, NE, *Bernardi 7127* (MER, VEN).

25. Cestrum ruizteranianum Benítez & D'Arcy, Novon 5: 313. 1995. TYPE: Venezuela. Mérida: Distrito Rangel, trail from La Negrita downstream towards Puente de La Escalera, montane cloud forest, 2550–2950 m, *Luteyn et al. 6171* (holotype, NY; isotypes, MY, VEN).

Shrub 1–4 m tall, erect, branched, young stems angular, terete when mature, scurfy pubescent; pubescence of dark, crinkled, perhaps branched hairs. *Leaves* narrowly elliptical to elliptical, 4–6 × 1.5–3 cm, apically acute or obtuse, basally obtuse, margins slightly revolute, firmly membranous, glabrous on both sides except for some scurfy hairs on minor veins, the major veins impressed above, elevated beneath, 8–10 on each side, ascending, looping and uniting near the margins; petioles 6–8 mm long, slender, inrolled, tomentulose above; minor leaves sometimes present, ovate, 10–13 × 5–7 mm, with petioles 0.5–1 mm long. *Inflorescences* axillary racemes, sometimes appearing as terminal panicles, 2.5–6 cm long; peduncles 0.7–5 cm long; bracts 1.5–2.5 mm, linear. *Flowers* 22–26 mm long, pedicels obsolete; bracteoles linear, 3 mm long, sparingly pubescent, caducous; calyx drying dark brown, tubular, 6–8 × 3–3.5 mm, faintly striate, thick, glandular and with sparse hairs outside, pubescent within and with glandular hairs halfway down, 5-toothed, the teeth 2 × 2 mm; corolla pale green, purplish outside, pale yellowish green inside, 20–26 mm long, exserted ca. 19 mm from the calyx, the tube 17–20 mm long, 3–3.5 mm at its widest, contracted around the ovary and then gradually expanded upward, the throat not constricted, mouth 3.5–4 mm wide, lobes 3–5 × 1.5–2 mm, narrowly triangular-acuminate, sometimes sparingly pubescent, the folds tomentose; stamens 15.5–19 mm long, adnate for 7–9 mm, the adnate portion pubescent for the basal 3–4 mm, insertion geniculate-tumid, 1.5–2.5 mm long, free part 7.5–9.5 mm, anthers orbicular, 1 mm across; ovary lobed, 0.7 mm across, glabrous, ovules 16–18, papillose 4–5 mm below the stigma, exceeding the stamens by 1.5 mm, style 15–19 mm, stigma subcapitate, slightly bilobed, included. *Fruit* unknown. Figure 48.

Cestrum ruizteranianum is very like *Cestrum lindenii* but differs in its uniformly smaller leaves, larger flowers, and glandular calyces.

Distribution (Fig. 23). Mérida. Montane cloud forest; 2950–2550 m. Endemic.

Phenology. Collected in flower in November.

Additional specimens seen. VENEZUELA. **Mérida:** Gavidia, Dist. Rangel, *Ruiz-Terán et al. 16171* (MERF, MY), *16154* (MY).

26. Cestrum salicifolium Jacq., Pl. Hort. Schoenbr. 3: 42, pl. 326. 1798. TYPE: from "Caracas," pl. 326 in Jacquin, 1798 (lectotype, here designated).

Cestrum salicifolium var. *angustifolium* Dunal, in A. DC., Prodr. 13(1): 670. 1852. TYPE: cultivated in Europe as *C. salicifolium* in herb. Requien (MPU not seen).

Shrub or *tree* 1.5–5 m tall, trunk very slender, sometimes arching, 5–8 cm DBH, branching high on the trunk, branches narrow, often hanging, purple when young, twigs slender, purplish, the epidermis longitudinally striate; pubescence of simple, multicellular hairs, evident only on bracts and perhaps emerging growth, plants otherwise glabrous. *Leaves* narrowly elliptical, 7–15 × 0.8–3 cm, narrowing upward, base obtuse or acute and ± decurrent on the petiole, margin slightly revolute, membranous to subcoriaceous, glabrous, veins 16–18 (–30), arising nearly perpendicular to the costa, appearing straight and evenly spaced, furcating near the margin and forming a partial, undulating submarginal vein, reticulate venation plane above,

Figure 45. *Cestrum racemosum.*—A. Branch with flowers and fruits.—B. Flower.—C. Corolla opened to show stamens. After *Morillo & Manara 2135* (VEN).

mostly not evident, the costa and sometimes major lateral veins elevated beneath; petiole flat-topped, distally canaliculate, 0.4–1 cm long, often curving and twisting depending on orientation of the stem, leaf scars discoid; minor leaves wanting. *Inflorescences* axillary and terminal, lax panicles of racemes, 10–12 (5.5–9) cm long, not leafy; peduncles purple, 1–2 cm long, 0.5–1 mm thick, glabrous, unbranched or 2–3-branched, ultimate segments resembling the pedicels, 1–7 mm long, the distal

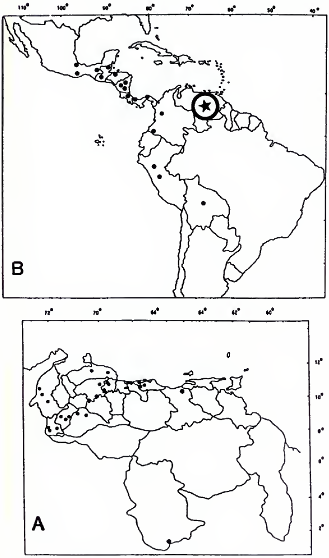

Figure 46. *Cestrum racemosum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

ones usually shortest; bracts linear, 2–6 mm long, inserted at base of the rachis, the branches, and along the peduncle and rachis branches. *Flowers* 25–32 mm long, buds purple, pedicels 0.5–5 mm long, articulated, bracteoles filiform, 1–5 mm long, puberulent with weak caducous simple hairs that dry appearing moniliform; calyx tubular, 3.5–5 × 2 mm, subcoriaceous, wrinkled, venation obscure or evident on the lobes, tube 3–4 mm long, 5-dentate, pilose, teeth deltoid, 0.5–0.8 mm long, minutely ciliate and tufted; corolla greenish white, 26–31 mm long, funnelform, tube slender, slightly contracted above the ovary, then gradually expanded toward the apex, (10–)13–15 mm long, mouth 1.5–2 mm wide, teeth narrowly acute, 4–6(–8) mm long, ciliate, folds pubescent; stamens inserted 0.5 mm apart, 18–21 mm long, filaments adnate for 14–20 mm, glabrous, insertion free 0.5 mm, straight, pilose, gibbose (with a tooth 1 mm long), free part 3–5 mm, anthers globose, 0.5 mm across; ovary 0.6–1 mm across, papillose, ovules 8–10, style 18–21 mm long, papillose below the stigma, stigma subcapitate, exserted 0.5 mm. *Fruit* dark purple, ellipsoidal, (8–)10–15 × 6.5–10 mm, stalked, pulp fleshy; fruiting calyx flaring, conspicuously wrinkled, not splitting; seeds 6–9, dark brown, 3.5–5 m long. [Francey 6: 359.] Figure 49.

Cestrum salicifolium is a slender treelet with arching crown and branches and narrow, membranous leaves. The inflorescences are open and pendent. Specimens are often very like narrow-leaved examples of *C. bigibbosum,* but the bracteole (or articulation) along the flower stalk is distinctive.

With its saliciform leaves and aspect, this species appears to be a rheophyte, adapted to inundation in periodic torrents that flood narrow watercourses.

A specimen of *Cestrum salicifolium,* labeled as having been collected by Sintenis in November 1886 in open woods at Bayamon, Puerto Rico, is deposited at Hamburg (HBG). That the species is otherwise known only from Venezuela, where it is confined to narrow ravines, casts doubt on the provenance of this specimen. Although Sintenis is not known to have visited Venezuela, the specimen is labeled "ex Herbario Reineck," a possible setting for a mix-up in label data.

Cestrum salicifolium var. *angustifolium* Dunal was placed in synonymy of Francey (1935: 359).

Distribution (Fig. 50). Carabobo, Miranda, and the Distrito Federal. Cloud forests and ravines; 1300–1800 m. Probably endemic to the Caribbean region of Venezuela.

Phenology. Flowering takes place mainly in November and December and fruiting in December and April, but some flowering takes place in other months. Flowers are open at night, with the corolla lobes spreading, and are closed during the day. They are strongly scented when open. Nectar was not detectable.

Representative specimens seen. VENEZUELA. **Aragua:** Carretera Maracay–Choroní, *Benítez et al. 4907* (MY). **Carabobo:** Cuenca hidrográfica del Río Morón, carretera hacia La Justa, *Díaz 526* (MO). **Miranda:** Quebrada de las Comadres cerca de Las Mostazas, *Allart 254* (NY, US, VEN). **Distrito Federal:** Cordillera del Avila above Caracas, *Steyermark 55008* (MY, VEN).

27. Cestrum scandens Vahl, Eclog. Amer. 1: 24. 1797. TYPE: Colombia. Santa Marta: *von Rohr s.n.* (holotype, C not seen, = IDC microfiche, = F photo 22927).

Cestrum paniculatum Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 62. 1818. TYPE: Venezuela. Distrito Federal: banks of river Guayre near Caracas,

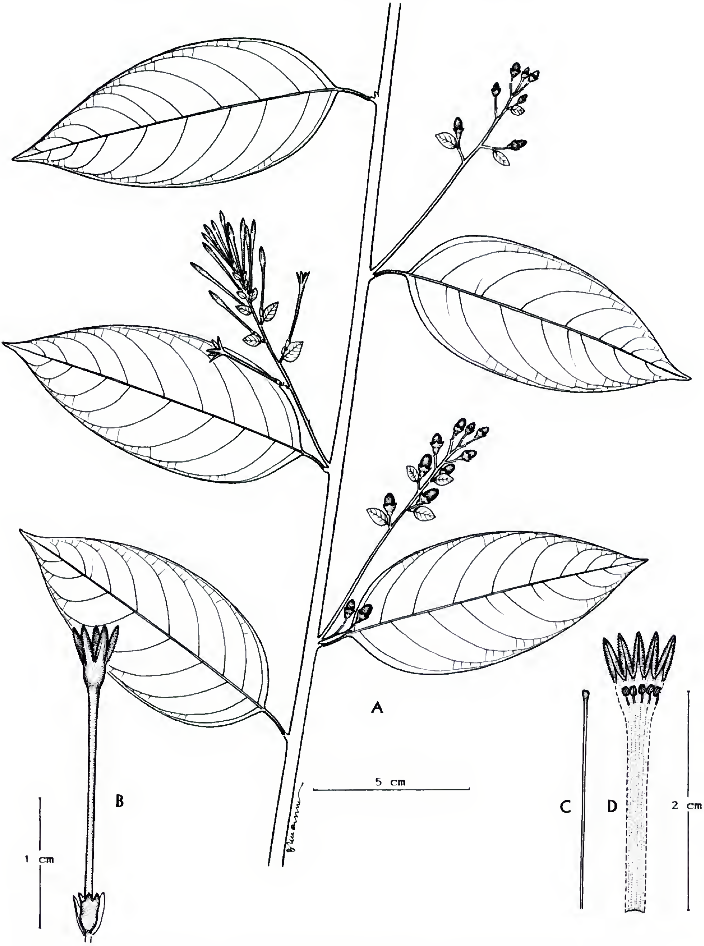

Figure 47. *Cestrum reflexum.*—A. Branch with flowers and fruits.—B. Flower.—C. Style.—D. Corolla opened to show stamens. After *Bernardi 7127* (MER).

Figure 48. *Cestrum ruizteranianum.*—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens and style. After *Luteyn 6171* (NY).

alt. 420 hex, *Humboldt s.n.* (holotype, B-W 4453, = IDC microfiche, = F photo 2989).

Cestrum laxiflorum Dunal, in A. DC., Prodr. 13(1): 655. 1852. TYPE: Venezuela. *Moritz 212* (holotype, G-DC, = IDC microfiche; isotypes, B destroyed, = F photo 2985, BM).

Cestrum scandens var. *terminale* Dunal, in A. DC., Prodr. 13(1): 665. 1852. *Cestrum terminale* (Dunal) Pittier, J. Wash. Acad. Sci. 22: 33. 1932. TYPE: Colombia. Santa Marta: *Bertero s.n.* (holotype, G-DC, = IDC microfiche).

Cestrum perilambanon Loes., Verh. Bot. Vereins Prov. Brandenburg 65: 98. 1923. TYPE: Guatemala. *Seler 3381* (B? destroyed; F, fragment).

Climbing *shrub* 2.5–4 m tall, main stem erect,

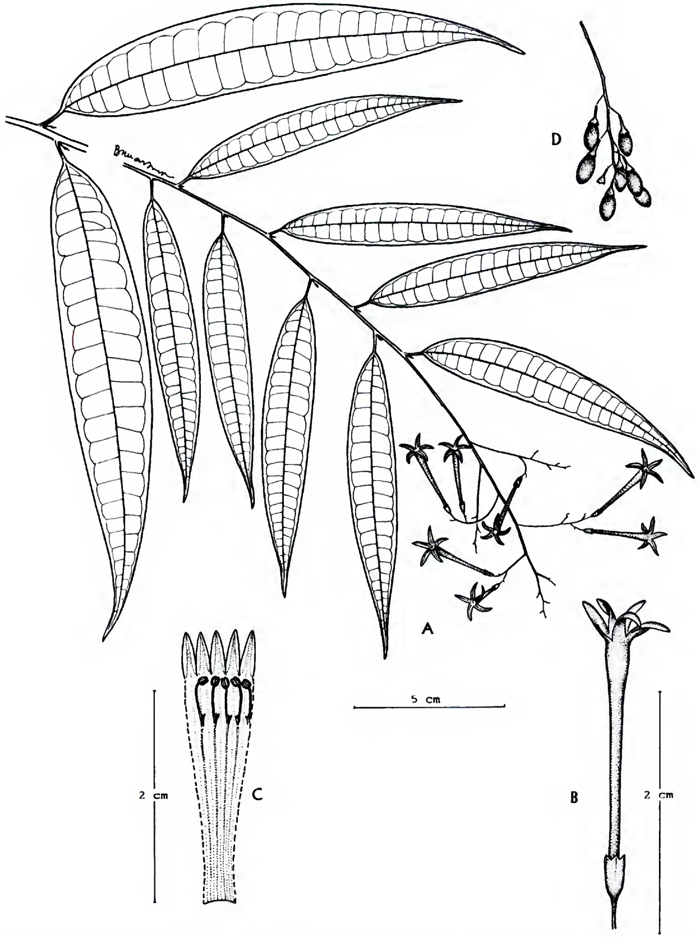

Figure 49. *Cestrum salicifolium.*—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens.—D. Fruits. After *Manara 65436* (MY).

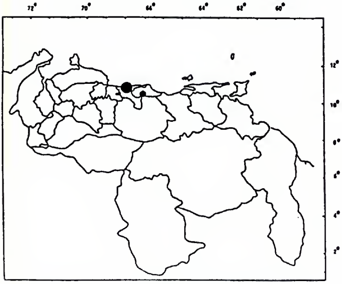

Figure 50. *Cestrum salicifolium*. Distribution in Venezuela.

branches high-climbing or decumbent, terete, mostly glabrous; pubescence of reduced simple hairs. *Leaves* ovate, 5.5–13 × 2.4–8 cm, apically acute or acuminate, basally rounded, margin plane or slightly revolute, membranous or subcoriaceous, shiny on both sides, glabrate, veins 6–9 on each side, sometimes puberulent; petioles canaliculate, 7–17 mm long, glabrate; minor leaves wanting. *Inflorescences* axillary or terminal, many-flowered, lax, scandent compound racemes, often dangling, axes 8–15 cm long; peduncles ca. 1 mm long, bracts foliaceous, 1.5 cm long. *Flowers* nocturnal, fragrant, 25–35 mm long, pedicels 1.5–3 mm long, glabrous; bracteoles linear, 0.5–3 mm long; calyx 3.5–5.3 × 2–3.5 mm, costate and rugose, glabrous outside, pilose within, tube 3–3.5 mm long, teeth 0.5–1.8 mm long, erect, ciliate, especially within; corolla yellowish white or pale green, sometimes with purple areas outside, 23–34 mm long, narrowly funnelform, tube narrow, mouth 2–3.5 mm wide, lobes pilose, 6–8 mm long; stamens 17–20 mm long, filaments adnate for 15–19 mm, sparingly pilose 1–3 mm above the base, insertion straight, smooth, free part 0.5–1.2 mm, anthers rotund, 0.5–1 mm across; ovary 1–1.2 × 0.5 mm, glabrous, disk inconspicuous, ovules 8–9, style 16–21 mm long, pilose toward the apex, stigma dilated or subcapitate. *Fruit* color unknown, obovoid, 11–12 × 7.5–8 mm wide; seeds 6–8, brown, 5–5.5 mm long (after *Nee 3627*). [Francey 6: 268.] Figure 51.

In this species and in *Cestrum reflexum*, the peduncle and pedicels appear as a single continuous stalk, their identities delimited by an articulation and bracteole. In *Cestrum scandens*, the basal, peduncular portion is only about 1 mm long, and the pedicel base continues about 1 mm further, while in *C. reflexum* the peduncle forms the whole stalk with the bracteole at the top.

Duplicates of *Moritz 212* at herbaria not noted above are other species. See note pertaining to *Cestrum venezuelense* under *C. bigibbosum* (above).

Distribution (Fig. 52). Aragua, Barinas, Carabobo, Falcón, Lara, Miranda, Yaracuy, Zulia, and the Distrito Federal. Gallery forests, and deciduous, semideciduous, and low evergreen forests; 60–1200 m. Also in Mexico, all Central American countries, and Colombia.

Phenology. Flowering is from November to April and fruiting from January to April, with maxima in March.

Common names. Iguanito Blanco.

Representative specimens seen. VENEZUELA. **Aragua:** El Limón, *Ferrari 221* (MY). **Barinas:** Isla Mapora, Reserva Forestal de Caparo, *Hernández 1189* (MER). **Carabobo:** Canoabo, *Trujillo 6147* (MY). **Falcón:** 1 km W of bridge over Río Tocuyo at El Alto, *Nee & Mori 3961* (US, VEN, WIS). **Lara:** N de Sanare, *Ferrari 991* (MY). **Miranda:** Dos Caminos and Los Chorros, *Pittier 5925* (P, US, VEN). **Yaracuy:** Quebrada Berracón, 3 km de Albarico, la carretera hacia Aroa, *Manara & Vera s.n.* (MY-28669). **Zulia:** Vía entre El Pensado y Las Tres Marías, *Bunting & Arboleda 8726* (MO, VZU). **Distrito Federal:** El Valle, *Arteaga 251* (CAR).

28. Cestrum schulzianum Francey, Candollea 6: 272. 1935. TYPE: Venezuela. Amazonas: near San Carlos de Río Negro, *Spruce 2974* (syntypes, BR not seen, G not seen, = F photo 28372, NY, W not seen).

Shrub 1.5–3 m tall, young stems pubescent, branches ridged, leaf scars slightly enlarged; pubescence of simple, moniliform ascending and crumpled hairs. *Leaves* narrowly ovate or narrowly elliptical, sometimes slightly asymmetric, 12–16 × 2.5–4 cm, apically long attenuate, basally acute or slightly cuneate, margin slightly revolute, subcoriaceous, undulate, glabrate, sometimes with fine pubescence on the main veins, veins 6–15 on each side, arising at (60°–)70°(–75°); minor leaves not evident. *Inflorescences* short axillary or terminal racemes, peduncles 3–5 mm long, pubescent with very small ascending hairs; bracts 1–3 mm long, foliaceous, pubescent. *Flowers* nocturnal, fragrant, 28–32 mm long, pedicels 1 mm long or obsolete; calyx tubular, 4–5.5 × 3–3.5 mm, puberulent when young, glabrescent, slightly zygomorphic, costate, the veins salient, tube 3–4 mm long, teeth 1–1.5 mm long, ciliate; corolla pale yellow-green, 27–31 mm long, narrowly funnelform, tube gradually expanded toward the apex, contracted below the limb

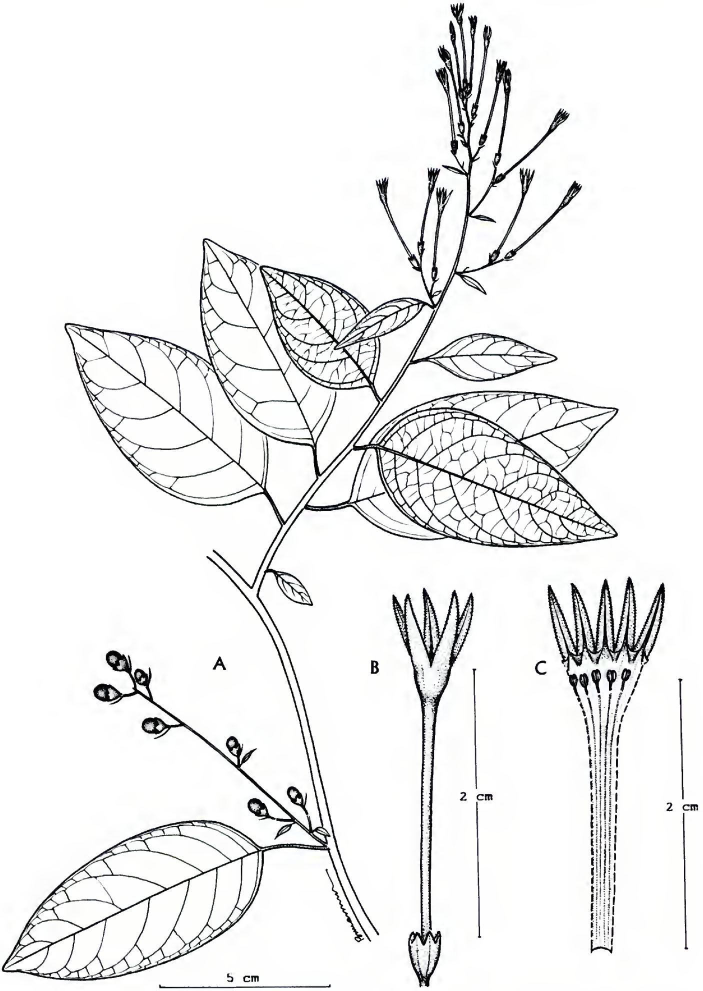

Figure 51. *Cestrum scandens.*—A. Branch with flowers and fruit.—B. Flower.—C. Corolla opened to show stamens. After *Trujillo 6147* (MY).

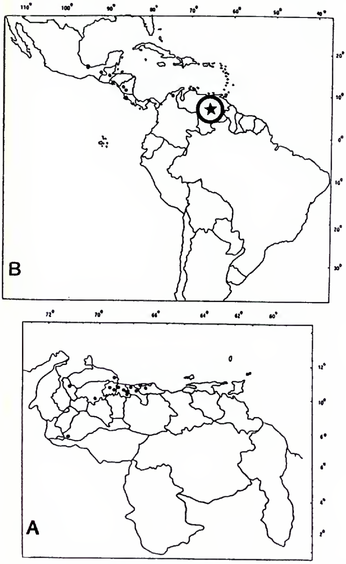

Figure 52. *Cestrum scandens.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

and then expanded, mouth 1–2 mm wide, lobes 5–7.5 mm long, very narrowly ovate, acuminate, pubescent outside; stamens 18.5–21 mm long, filaments adnate for 17–19 mm, base pilose to 13–15 mm up, insertion straight, smooth, free part 0.5–3 mm, anthers globose, 0.5 mm across; ovary 1–1.5 mm across, disk inconspicuous, glabrous, ovules 7–8, style 18–22 mm long, filiform, papillose below the stigma, stigma subcapitate, exserted 0.5 mm. *Fruit* dark purple, subglobose, contracted at the base, 11–12 × 8–9 mm, pericarp thin; seeds 5–7, brown, 5–6 mm long. [Francey 6: 272.] Figure 53.

This species is recognizable by its lanceolate, often narrow, firm leaves with even venation nearly perpendicular to the midvein, and its large corolla lobes. The flowers tend to be aggregated in dense, several-flowered clusters.

Distribution (Fig. 35). Amazonas. Evergreen rainforests and "morichales" (successional palm groves occurring on sandy substrates with high water table); 100 to 400 m elevation. Apparently endemic.

Phenology. Flowering specimens have been seen from April and May. Fruiting data are lacking.

Common names. Cafecillo hoja fina.

All additional specimens seen. VENEZUELA. **Amazonas:** San Carlos de Río Negro, *Liesner 7134* (MO, VEN); Río Casiquiare entre Chapazón y Guirape, W de Solano, *Morillo et al. 4004* (MY, VEN); Río Negro entre la desembocadura del Río Casiquiare y San Carlos de Río Negro, *Morillo et al. 4040* (VEN); Río Negro, entre isla Paleta y El Caño de la División, W y S de Santa Lucía, *Morillo et al. 4105* (MY, VEN); San Carlos de Río Negro, *Stergios & Aymard 7311* (PORT); Río Casiquiare, entre la boca y la piedra Guachapita, *Stergios & Aymard 7358* (MO); Bajo Casiquiare, entre la boca del Pasimoni y Porvenir, *Stergios & Aymard 7606* (PORT).

29. Cestrum strigilatum Ruiz & Pav., Fl. Peruv. 2: 29, pl. 156. 1799. SYNTYPES: Peru. Pozuzo, Chinchao and Cuchero, *Ruiz & Pavon s.n.* (B not seen, = F photo 18394, HAL).

Cestrum calycinum Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 58. 1815–1816. *Cestrum strigilatum* var. β *calycinum* (Kunth) Kuntze, Revis. Gen. Pl. 3(2): 220. 189. TYPE: Peru. Near Gonzanama, 1180 hex, *Bonpland s.n.* (holotype, B-W 4461 not seen, = IDC microfiche, = F photo 2998).

Cestrum viridiflorum Hook., Bot. Mag. pl. 4022. 1843. TYPE: Brazil. Porto Alegre, *Tweedie s.n.* (holotype, K).

Cestrum cancellatum Dunal, in A. DC., Prodr. 13 (1): 657. 1852. TYPE: Peru. *Poeppig 3080* (holotype, G-DC, = IDC microfiche; isotypes, B destroyed, = F photo 2969, F).

Cestrum unibracteatum var. β *brachystachys* Dunal, in A. DC., Prodr. 13(1): 657. 1852. TYPE: Brazil. Circa Cujaba ubique, *da Silva Manso 34* (holotype, G-DC, = IDC microfiche, = F photo 23178).

Cestrum unibracteatum Dunal, in A. DC., Prodr. 13(1): 656. 1852. SYNTYPES: Peru. Cochero, *Dombey s.n.* (G-DC not seen, = IDC microfiche, = F photo 6899; MPU not seen); *Poeppig 96* (G-DC as "*C. longifolium* Ruiz & Pav. 1246" not seen).

Cestrum lundianum Dunal, in A. DC., Prodr. 13 (1): 658. 1852. TYPE: Brazil. Sancti Pauli, *Lund 34* (holotype, G-DC, = IDC microfiche, = F photo 6898).

Cestrum strigilatum var. *laxiflorum* Kuntze, Revis. Gen. Pl. 3 (2): 220. 1898. SYNTYPES: Argentina. Oran, *Lorentz & Hieronymus s.n.* (NY); Bolivia. Jungas [Juntas] collector unknown.

Cestrum impressum Rusby, Bull. New York Bot. Gard. 4: 425. 1905. TYPE: Bolivia. *Bang 2516* (holotype, NY not seen).

Sessea rugosa Rusby, Bull. New York Bot. Gard. 8 (28): 119. 1912. TYPE: Bolivia. Apolo, 4800 ft., *Williams 2449* (NY not seen).

Cestrum calycinum var. *tenuiflorum* Francey, Candollea 6: 142. 1935. SYNTYPES: Paraguay. Villa Encarnación, *Bettfreund 131* (place of deposit not indicated); Argentina. Yaguara–Zapa, *Niederlein 2686* (G not seen, = F photo 2998).

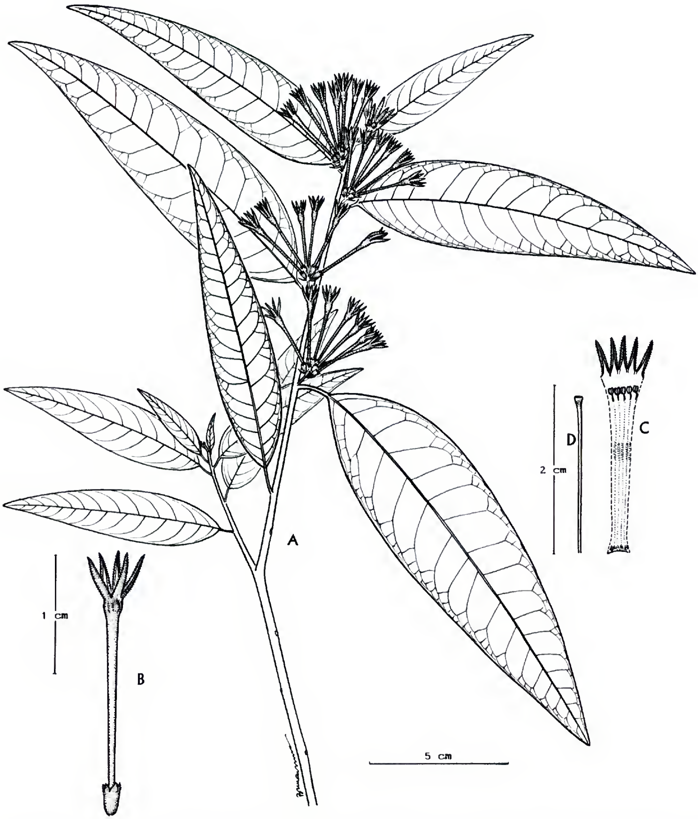

Figure 53. *Cestrum schulzianum*.—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens.—D. Style and stigma. After *Morillo et al. 4004* (VEN).

Cestrum strigilatum var. *tenuiflorum* Francey, Candollea 6: 144. 1935. TYPE: Ecuador. Balao, *Eggers 14274* (lectotype, here designated, W; isolectotype, US fragment).

Cestrum aristeguietae Steyerm., Acta Bot. Venez. 6: 86. 1971. TYPE: Venezuela. Carabobo: along Río San Gean, 2 km below planta eléctrica, S of Borburata, 350 m, *Steyermark & Steyermark 95463* (holotype, VEN; isotypes, NY, P, US).

Sprawling or climbing *shrub* or *tree*, 2–4 m tall, 10 cm DBH, much branched, branches elongate, tomentose; pubescence of dendritic and stellate hairs. *Leaves* usually not malodorous, ovate to narrowly ovate, 11–24.5 × 5.5–11 cm, apically attenuate, short-acuminate, base rounded or truncate, margin revolute in firmer leaves, membranous to subcoriaceous, above bright green, gray-green beneath, pubescent, especially on the main veins, lamina glabrescent, sometimes appearing pustular, tomentose beneath, veins 5–8, prominent on each side, veins sunken above; petiole terete, 0.9–1.5 cm long, tomentose; minor leaves wanting. *Inflorescences* simple axillary or terminal racemes, sometimes short, lateral racemes, peduncles 1.5–4 cm long, pubescence dendritic or stellate, bracts linear, 6–7 mm long, stellate pubescent. *Flowers* diurnal, fragrant?, 30–36 mm long, sessile; calyx firmly tubular, 8–13.5 × 3–3.5 mm, 5-costate, the costas salient, membranous, densely stellate pubescent outside, glabrous within, tube 5–7 mm long, 5-toothed, teeth cuspidate, unequal, 3–6.5 mm long; corolla pale green to white, 29–35 mm long, narrowly funnelform, tube slightly curved, slightly contracted below the ovary, gradually expanded upward, tomentose, especially in the upper half, mouth 2.5–3 mm wide, the lobes narrowly elliptical, 5–8 mm long, apically subacute, folds stellate pubescent; stamens equal, 20–25.8 mm long, filaments glabrous, adnate for 18.5–24.5 mm, insertion straight, smooth, free part 1–1.2 mm, anthers spherical; ovary 1 × 0.8 mm, glabrous, disk inconspicuous, ovules 4–6, style green, 24–25 mm long, hirsute below the stigma, stigma green, capitate. *Fruit* maturing from white to purple, ellipsoidal, 6–10 × 3–5 mm wide; fruiting calyx accrescent, 14–20 mm long, often splitting along one side; seeds 3–7, light brown, 5–5.5 mm long. [Francey 6: 137, 142.] Figure 54; Benítez de Rojas, 1974: 89, figure 22, as *C. aristeguietae.*

Cestrum strigilatum is distinct in its uniform pubescence, large, almost spathaceous fruiting calyces, and slender, pubescent corollas.

The unpublished name *"Cestrum longifolium"* was used by Ruiz and Pavón on a specimen of *C. strigilatum* from Peru that was later seen by Dunal (1852: 657). *Cestrum impressum* Rusby was placed in synonymy by Francey (1935: 137). *Sessea rugosa* Rusby was placed in synonymy by Francey (1935: 142).

The chromosome number for this species was reported as $2n = 16$ by Berg and Greilhuber (1993a).

Distribution (Fig. 55). Amazonas, Aragua, Carabobo, and Táchira. Evergreen moist riverine and gallery forests; 300–1600 m. Also in Costa Rica, Panama, Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, and northern Argentina.

Phenology. Collected in flower from January to April and in fruit in March and April.

Representative specimens seen. VENEZUELA. **Amazonas:** Raudal Montserrat, Alto Orinoco, *Croizat 666* (NY). **Aragua:** P. Nacional Henri Pittier, *Benítez & Aguilera 4691* (MY). **Carabobo:** Borburata, *Aristeguieta 4465* (MO, NY, VEN). **Táchira:** Palo Grande, Distrito Lobatera, *Benítez de Rojas 1269* (GH, MY).

30. Cestrum tillettii Benítez & D'Arcy, Novon 5: 315. 1995. TYPE: Venezuela. Zulia: headwaters of Río Guasare, Distrito Perijá, Sierra de Perijá, Serranía de Valledupar, environs of Campamento Frontera V, along international boundary, 2700–3300 m, 10°23′07.8″N, 72°52′42.5″W, *Tillett 747-1021* (holotype, MY; isotypes, AAU, MO, MYF, VEN).

Tree 2–3 m tall; stems brown, glabrous, striate and scarred; pubescence of reduced, simple, glandular hairs. *Leaves* narrowly elliptical, 4–6 × 1–1.7 cm, slightly acute apically, the tip obtuse, basally narrowly cuneate, margin conspicuously revolute, firm, subcoriaceous, dark green, shiny above, dull beneath, glabrous, veins 6–8 on each side, the major veins sunken above, salient beneath, minor veins impressed beneath; petiole canaliculate, 3–7 mm long, glabrous; minor leaves wanting. *Inflorescences* axillary, congested, the main axes tomentose, bright matte green, 1.5–3 cm long, the peduncles 5–7 mm long, pubescent, thickened, with circular scars from fallen flowers, flowers few per node. *Flowers* nocturnal?, 15–19 mm long, sessile (pedicels obsolete) with faint, sweet fragrance during the day; calyx yellow-green, flushed distally with dark purple, tubular, thick, costate, the costas especially conspicuous distally, slightly pubescent outside with hairs slightly thickened near the base, 4.5–5.5 × 2–2.5 mm, 5-toothed, the teeth 1.5–2.5 mm long, narrowly triangular, the apex pubescent; corolla yellow-green and purplish, drying light with darker lobes, clavate, 15–19 mm long, tube 13–16 mm long, slightly expanded toward the apex, the throat not noticeably contracted, mouth ca. 1.5–2 mm wide, lobes 2–2.5 mm long, the folded margins puberulent; stamens 10–13 mm long; filaments white, adnate for 6–9 mm, the insertion geniculate-tumid, slightly pilose, 1 mm long, free part 4.5 mm, anthers brown, spherical, 0.5 mm across; ovary ovoid, glabrous, smooth, 1 mm across, ovules 5, style 12–13.5 mm long, papillose 1–2 mm below the stigma, exceeding the stamens by 1.5 mm, stigma green. *Fruit* shiny blue-black, ovoid, 9 × 6 mm, pericarp thick, opaque; seeds 6–7 per fruit, brown, 3–3.5 mm long. Figure 56.

Cestrum tillettii has more or less congested small leaves of uniform appearance on relatively thick, rough branches. The congested flowers are situated among the leaves and close to the stems.

Distribution (Fig. 23). Zulia. Slopes on lime-

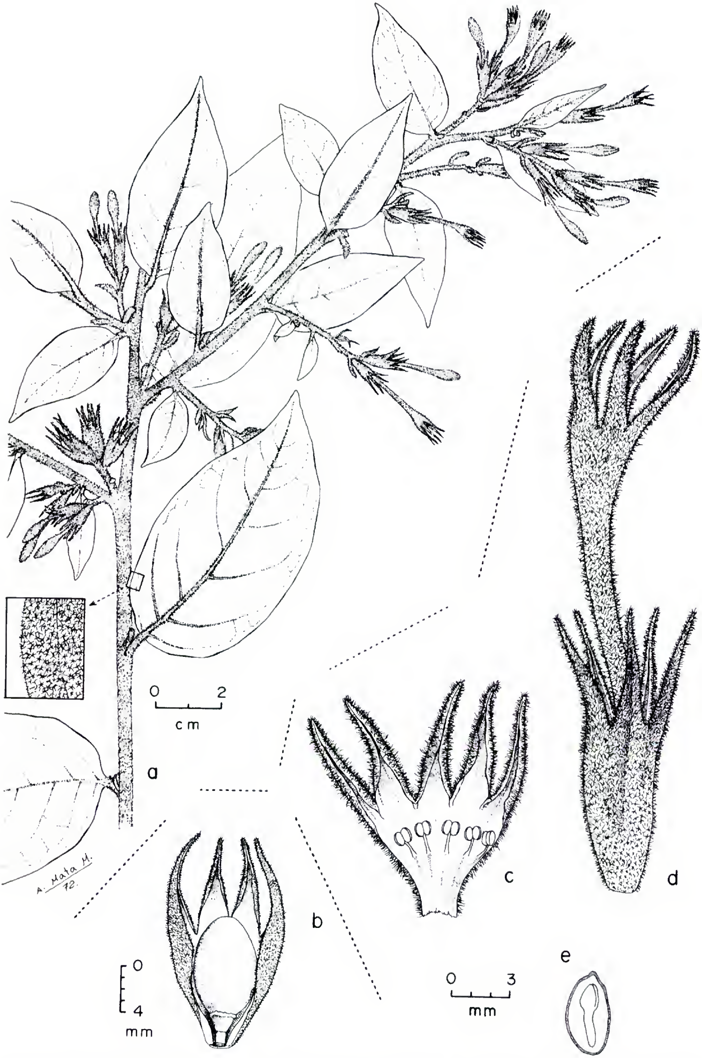

Figure 54. *Cestrum strigilatum.*—a. Flowering branch.—b. Fruit enclosed in persistent calyx.—c. Corolla opened to show stamens.—d. Flower.—e. Seed opened to show embryo. After *Benítez 1269* (NY).

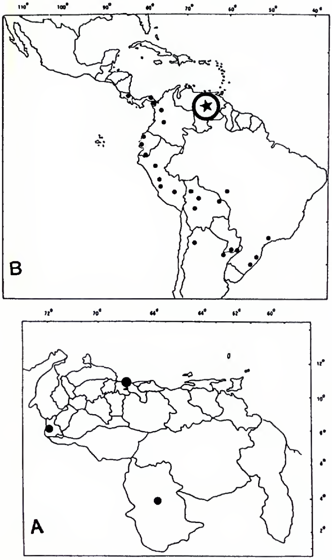

Figure 55. *Cestrum strigilatum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

stone; 2700–3620 m. Restricted to the western border between Venezuela and Colombia.

Phenology. Specimens seen were collected in July and were in flower.

All other collections seen. VENEZUELA. **Zulia:** Sierra de Perijá, *Tillett & König 747-929* (MY, VEN); headwaters of Río Guasare, *Wood & Berry* 88 (MO, VEN).

31. Cestrum tomentosum L. f., Suppl. Pl. 150. 1782. SYNTYPES: Colombia. *Mutis 94* (LINN. 258.6, = IDC microfiche), *95* (LINN. 258.7, = IDC microfiche).

Cestrum hirsutum Jacq., Pl. Hort. Shoenbr. 3: 41, pl. 324. 1798. TYPE: West Indies. Cultivated hortus Schoenbrunensis (holotype, W; isotype, B-W 4449, = IDC microfiche, = F photo 33032).

Cestrum lanuginosum Ruiz & Pav., Fl. Peruv. 2: 30, pl. 157. 1799. TYPE: Peru. Arequipa: Camana, collibus arenosis, *Ruiz s.n.* (lectotype, here designated, G not seen, = F photo 2984; isolectotype, F).

Cestrum lanatum M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12: 146. 1845. TYPE: Mexico. Colonie de Mirador, 3000 pieds, *Galeotti 1208* (holotype, BR not seen; isotypes, G, K, NY, US, W).

Cestrum moritzii Dunal, in A. DC., Prodr. 13(1): 619. 1852. TYPE: Venezuela. Caracas, *Moritz 309* (holotype, G-DC, = IDC microfiche, = F photo 2988; isotypes, B destroyed, BM, HBG, MO).

Cestrum miersianum Wedd., Chlor. Andina 2: 97. 1859. TYPE: Colombia. Sierra Nevada de Santa Marta, 3300 m, *Linden 1615* (holotype, G-DC, = IDC microfiche).

Cestrum diasae Pittier, J. Wash. Acad. Sci. 22: 29. 1932. TYPE: Venezuela. Mérida: Misintá, arriba de Mucuchíes, 3500 m, *Pittier 12919* (holotype, VEN; isotype, US).

Cestrum meridanum Pittier, J. Wash. Acad. Sci. 22: 36. 1932. TYPE: Venezuela. Vecinidades de Mérida, 1700 m, *Pittier 12858* (holotype, VEN; isotype, US).

Cestrum miersianum Pittier, J. Wash. Acad. Sci. 22: 37. 1932, non Wedd. (1857). *Cestrum neomiersianum* Benítez, Revista Fac. Agron. (Maracay) 7: 90. 1974. TYPE: Venezuela. Mérida: San Rafael de Mucuchíes, 3150 m, *A. Jahn 767* (holotype, VEN; isotypes, MO, ?NY not seen, US).

Cestrum ambatense Francey, Candollea 6: 169. 1935. TYPE: Ecuador. Tungurahua: vicinity of Ambato, *Pachano 75* (holotype, NY; isotype, US fragment).

Cestrum densiflorum Francey, Candollea 6: 195. 1935. TYPE: Venezuela. Mérida: between Chachopo and Timotes, *Pittier 13294* (lectotype, designated by Benítez & D'Arcy (1995: 317), NY; isolectotypes, F, MO, US, VEN).

Cestrum densiflorum var. *puberulum* Francey, Candollea 6: 196. 1935. TYPE: Venezuela. Trujillo: San Pablo de Mendoza, *Pittier 13323* (syntypes, F, MO, US, VEN).

Cestrum sesseoides Francey, Candollea 6: 395. 1935. TYPE: Colombia. Santander: eastern cordillera between El Robel and Tona, 1500–1900 m, *Killip & Smith 19423* (NY).

Cestrum verbascifolium Zucc. ex Francey, Candollea 6: 191. 1935. SYNTYPES: cultivated Berlin and Munich (B not seen, BR not seen).

Shrub or *tree* 1–8 m tall, much branched, stems terete, flexible, tomentose, lenticellate, sometimes subscandent or sprawling, branches often arching or horizontal, brownish tomentose with a yellowish cream hue; pubescence of mostly sessile, branched and some stellate hairs. *Leaves* malodorous, ovate to elliptical, 4–17 × 2–7.5 cm, apically obtuse, acute or acuminate, basally truncate, rounded or obtuse, narrowly cuneate, margins slightly revolute, sometimes appearing ciliolate, subcoriaceous to membranous, dark green, glabrescent above and then shiny, yellow green, softly tomentose beneath, veins (4–)7–8(–12) on each side, evenly spaced, slightly elevated beneath; petiole canaliculate, 5–12 mm long, tomentose; minor leaves sometimes present, rotund, to 2 cm long, subsessile, sometimes persistent. *Inflorescences* axillary and terminal, mostly among the leaves near the branch ends, many- or few-flowered, congested fascicles, racemes or spikes, much shorter than the leaves, to 6 cm long, sometimes appearing paniculate; bracts

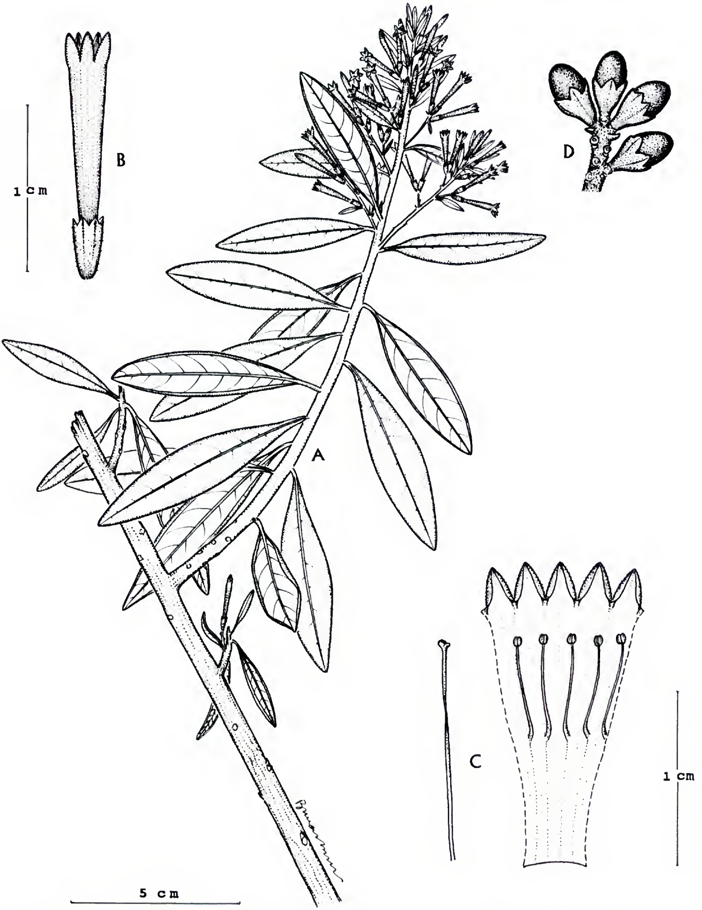

Figure 56. *Cestrum tillettii.*—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens and style.—D. Fruits. Based on *Tillett & König 747-929* (VEN).

ovate or lanceolate, foliaceous, 5–20 × 3–8 mm, pubescent; peduncles mostly short, occasionally to 3 cm long, slightly longer in fruit, tomentose, clusters of 2–6 sessile flowers separated by a 2–6-mm-long rachis. *Flowers* nocturnal; 12–21 mm long, buds with dark purple lobes; sessile; bracteoles linear, rarely narrowly ovate, to 12 mm long, mostly tomentose, caducous; calyx cupular, campanulate, or tubular, 3–6.5 × 1–3 mm, outside tomentose except sometimes near the base, the veins sometimes inconspicuous beneath the pubescence, glabrescent, inside glabrous, tube 3–5 mm long, teeth narrowly deltoid or obtuse, 0.5–2.5 mm long, narrowly triangular, ciliolate, minutely tufted; corolla greenish, whitish, or yellowish, dark purple outside, often drying dark and with 15 fine nerves evident, yellow-green within, 10–19 mm long, glabrate outside, glabrous within, tube 7–9(–15) mm long, basally slender, expanding gradually or about 2/3 way up, mouth 2.5–4.5 mm wide, lobes greenish white inside, dark brown or dark purple outside, often colored differently from the tube, 1.5–3.5 mm long, acute, ovate, often ciliolate; stamens inserted equally or 1.5 mm apart, 9–15 mm long, filaments adnate for 4.5–11 mm, mostly pubescent, insertion free 1–3 mm, geniculate, tumid, slightly denticulate, glabrous or sparingly pilose, free part (2.5–) 4.5–5 mm; ovary bright green, lobed, 0.5–1 mm across, glabrous, disk 0.5 mm long, ovules 4–8, style 8–15 mm long, bright green 1 mm below the stigma, puberulent, stigma capitulate, included. *Fruits* 16–40 per inflorescence, violet, then purple-black, shiny, ovoid, 6–8 × 3–4 mm, juicy; fruiting calyx slightly accrescent, 5–6 mm, basally multinervate, slightly splitting irregularly at the sinuses, often glabrescent; seeds 2–4 per fruit, yellowish brown, 2.5–3.5 mm long. [Francey 6: 171.] Figures 2D, 57.

In Venezuela, *Cestrum tomentosum* is usually amply distinct in its overall pubescence and small, dense flower and fruit clusters. Some collections of *C. humboldtii* from Colombia and eastern Venezuela have similar leaves, but these can be separated by their larger leaves and glabrate calyces. The name *Cestrum verbascifolium* Francey is placed in synonymy based on Francey's (1935–1936) description and key.

Chromosome numbers for this species have been reported as $2n = 16$ (Sharma & Sharma, 1958, as *C. hirsutum*; Nanda, 1962, as *C. lanatum*).

Distribution (Fig. 58). Aragua, Lara, Mérida, Miranda, Monagas, Sucre, Táchira, Trujillo, and the Distrito Federal. Dwarf evergreen forests, ravine banks, dense thickets, roadsides, abandoned coffee plantations; 700 to 2800 m. Also occurring from northwest Sonora, Mexico, through all countries of Central America, and in Colombia, Ecuador, and Peru.

Phenology. Flowering occasionally year-round but mostly from January to April. Fruiting is mainly April to May.

Common names. *Hedionda, Hediondo, Quesillo, Puta Vieja, Trompillo, Uvito.*

Representative specimens seen. VENEZUELA. **Aragua:** P. Nacional Henri Pittier, between Ocumare de la Costa and El Mirador, *Benítez et al. 4876* (MY). **Lara:** Sanare, Montecarlo arriba, *Badillo 6763* (MY). **Mérida:** 8 km E of Jají, *D'Arcy et al. 18260* (MO, MY). **Miranda:** El Paraíso, vertiente sur, en antiguos cafetales, 1465 m, *Meier 3603* (MY, VEN). **Monagas:** Praderas between Sabana de Las Piedras and las selvas de Cerro Negro, NW of Caripe, *Steyermark 61816* (F, MY, VEN). **Sucre:** humid trail to Carapas, *Tate 24* (US), *25* (US). **Táchira:** entre Cordero y páramo El Zumbador, *Romero 750* (MY). **Trujillo:** La Puerta, entre La Lagunita y la quebrada El Portachuelo, *Ruiz-Terán & Dugarte 11999* (MERF, MY). **Distrito Federal:** Antímano, near Caracas, *Archer 2991* (US).

32. Cestrum tubulosum Sendtn., in Mart., Fl. Bras. 10: 207. 1846. SYNTYPES: Brazil. São Paulo: near city of Ytu, *da Silva Manso 336* (BR); Campinas, *Severin 168* (S not seen).

Cestrum rojasianum Hassl., Repert. Spec. Nov. Regni Veg. 9: 120. 1910. TYPE: Paraguay. Río Aquidaban, *Rojas 10033* (holotype, G not seen, = F photo 28371).

Shrub or small *tree* to 2 m tall, branches terete, pubescent, especially toward the tips, internodes 10–15 mm long; pubescence of small, simple or sparingly branched, stout yellowish or reddish, ascending, usually dense, curved, sometimes gland-tipped hairs. *Leaves* ovate or elliptical, strongly upfolded from the costa, 5–9 × 3–4.8 cm, attenuate upward from the middle, basally obtuse, rounded, slightly cordate, margins revolute, subcoriaceous, rigid, matte dark green above, lighter beneath, glabrous above, beneath with few ascending, gland-tipped hairs, veins 5–9 on each side, elevated beneath, minor (5th order) venation forming well-developed areoles, less visible beneath; petioles 2–6 mm long, margined above by leaf base; minor leaves wanting. *Inflorescences* few-flowered in the leaf axils; axes stout, short, densely pubescent with long, branched hairs. *Flowers* diurnal, strongly fragrant, 25–32 mm long, sessile, bracteoles linear to narrowly ovate and foliaceous, 3–5 mm long, pubescent; bracts ascending, resembling the leaves, caducous; calyx cupular, 3.5–6 × 2 mm, costate, glabrous outside, tube 3–4 mm long, 2.5 mm, teeth 0.5–2 mm long, slightly unequal, sutures rounded, ciliate, apically mucronate; corolla light green, 24–31 mm long, tubular, tube cylindrical and expanded upward, slightly contracted below the limb, mouth 3.5–5 mm wide, lobes narrowly ovate, apically tufted, sinuses basally ciliate, 4–6 mm long; stamens equal, 19.5–21.5 mm long, filaments adnate for 15–20 mm, basally pilose, insertion straight, smooth, free part 1.5–2 mm, anthers spherical, 0.5 mm across; ovary globose, 1.2 mm across, glabrous, disk conspicuous, ovules 9–11,

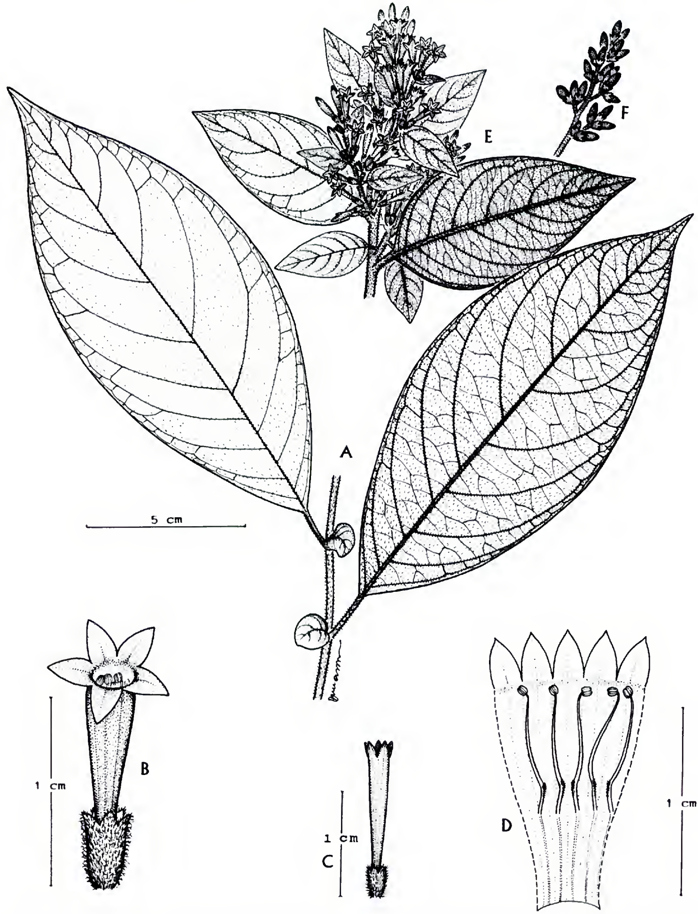

Figure 57. *Cestrum tomentosum.*—A. Vegetative branch showing minor leaves.—B. Flower.—C. Flower beginning to open.—D. Corolla opened to show stamens.—E. Flowering branch.—F. Fruits. A, B, D, E, F after *Morillo 3017* (VEN). C after *Benítez 4667* (MY).

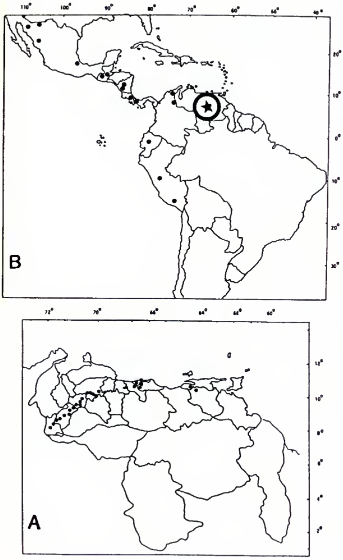

Figure 58. *Cestrum tomentosum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

style filiform, 16–20 mm long, papillose below the stigma, stigma peltate, inconspicuously 4-lobed. *Fruit* green?, ovoid, 8–11 × 5–6 mm, pericarp thin; seeds 3–4, olive brown, 6–7.5 mm long. [Francey 6: 208.] Figure 59.

Hairs on *Cestrum tubulosum* are much like those of *C. neblinense,* but denser, and the leaves are broader, mostly more than 2 cm wide.

Our use of this name is based on a photo of the type of *Cestrum rojasianum* and Francey's (1935–1936) placement of *C. rojasianum* in synonymy under *C. tubulosum.*

Distribution (Fig. 60). Amazonas and Bolívar. Gallery forests; 100 to 300 m, and riverine woods associated with tepui vegetation; 1100 to 1400 m. Also in Paraguay and Brazil.

Phenology. The collections seen were flowering in January and March and fruiting in March.

All remaining specimens seen. VENEZUELA. **Amazonas:** Dept. Atures, Río Corocoro, W of Serranía de Yutajé, *Holst & Liesner 3173A* (MO); Dept. Atabapo, Marahuaca, *Liesner 18464* (MO); Serranía Yutajé, Río Manapiare, Camp Yutajé, *Maguire & Maguire 35094* (MO, NY, US). **Bolívar:** Distrito Cedeño, Serranía de Guanay, Río Parguaza, *Huber 11033* (MY, MYF).

Sessea Ruiz & Pav., Fl. Peruv. Prodr. 21. 1794. TYPE: *Sessea stipulata* Ruiz & Pav.

Unarmed trees; pubescence of simple or branched hairs. Leaves simple, entire, pinnately nerved, mostly glabrate above; mostly short petiolate; minor leaves present or not. Inflorescences axillary and pseudoterminal, few- or many-flowered racemes, spikes, or cymes, often large and appearing paniculate; bracts often present. Flowers mostly 5-merous, pedicellate, bracteolate; calyx small, cupular or tubular, mostly shallowly lobed; corolla narrowly tubular, much exceeding the calyx, lobed, the lobes narrow, shorter than the tube, spreading or reflexed when open; stamens inserted in the corolla tube at similar levels, the insertion levels varying greatly in different species, the adnate portion mostly evident from the corolla base, the insertion variously pubescent or tumid, anthers small, situated together at the corolla mouth; ovary mostly shorter than the calyx, 2-locular, ovules 4–16, style slender, style capitate or variously lobed, small, in at least some species oblique on the style apex. Fruit a narrowly ellipsoid or ovoid, terminally dehiscent capsule; seeds varying in number, ovoid, surrounded by a hyaline wing; embryo straight.

The name *Sessaea* Endlicher (1838: 668) is an orthographic variant of *Sessea* Ruiz & Pav.

1. **Sessea corymbiflora** Goudot ex Rich. Taylor & R. Phillips, Philos. Mag. Ann. Chem. 3: 132. 1828. TYPE: near Bogotá, *Goudot 1* (lectotype, designated by Benítez & D'Arcy (1993: 324), P; isolectotypes, K, G-DC not seen, = IDC microfiche, G).

Sessea corymbosa Miers, Hooker's J. Bot. Kew Gard. Misc. 5: 156. 1846. TYPE: Bogotá ad Barro Blanco, *Goudot 1* (holotype, K not seen; isotypes, G-DC not seen, = IDC microfiche, P, G).

Cestrum atrovirens Dunal, in A. DC., Prodr. 13(1): 648. 1852. *Sessea atrovirens* (Dunal) B. D. Jacks., Index. Kew. 2: 892. 1895. TYPE: Ecuador [Peru]. Quito, *Hartweg 1309* (holotype, G = F photo 8573; isotypes, B not seen, K not seen, P).

Shrubs or *trees* to 6 m tall; unarmed, pubescence of reduced moniliform simple hairs to 0.5 mm long, glabrous on most parts; twigs angled from the petiole bases and often striate-furrowed. *Leaves* 11–15 per twig, not odorous, perennial, elliptical, occasionally ovate or obovate, mostly 9–13(–20) × 3–

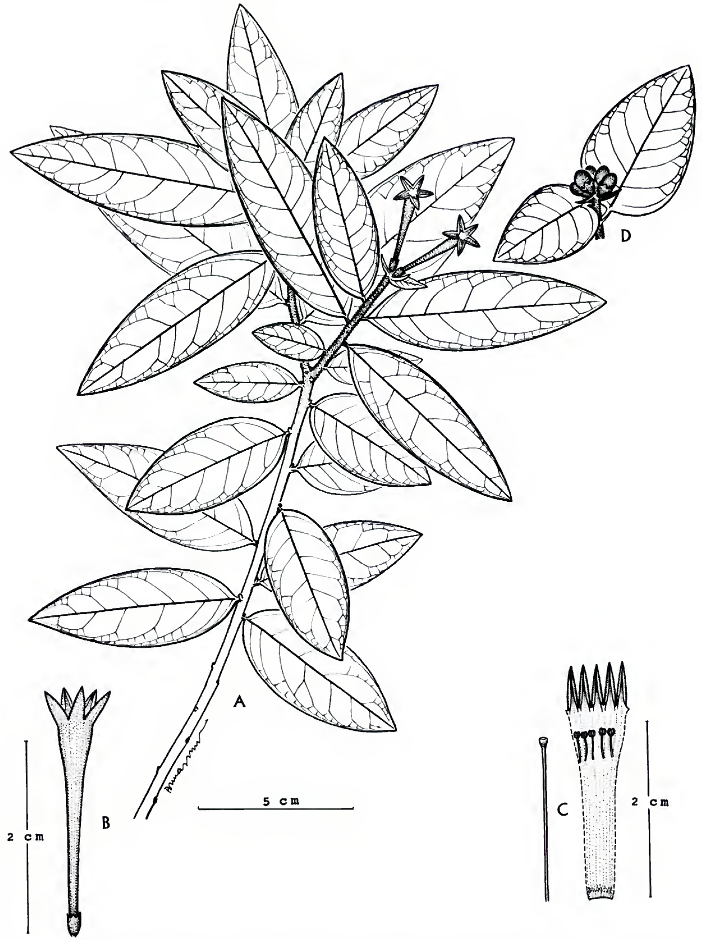

Figure 59. *Cestrum tubulosum*.—A. Flowering branch.—B. Flower.—C. Corolla opened to show stamens and style.—D. Fruiting branch. After *Huber 3245* (VEN).

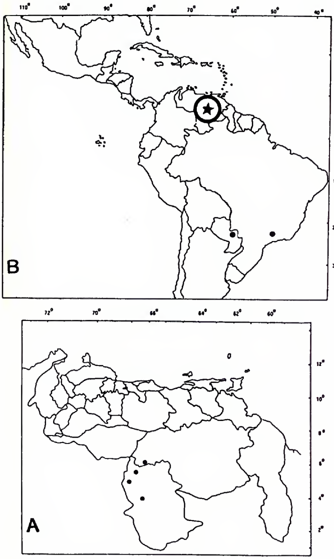

Figure 60. *Cestrum tubulosum.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

5(–6) cm, apically obtuse or acute, sometimes slightly short-acuminate, basally obtuse, margins sometimes slightly revolute, coriaceous or firmly membranous, costa drying dark above, elevated and excurrent beneath, glabrous or with occasional reduced trichomes near the base, major veins 17–20, mostly evenly spaced 3–6 mm apart, arcuate at 30°–40° to the costa, plane above, finely reticulate beneath, drying reddish or slate gray; minor leaves mostly wanting, when present oblong, to 6 cm long and resembling the major leaves; petioles mostly slender, 5–25 mm long, slightly scurfy with reduced trichomes, drying darker than the leaf, especially at the base. *Inflorescences* lax, crowded, terminal corymbs to 6 cm long; peduncles and pedicels drying dark, pedicels wanting, bracts few, scattered among the inflorescence and resembling reduced leaves; pedicels obsolete; bracteoles 1.5 mm long, narrowly ovate or linear, glabrate with sparse, reduced, glandular-appearing trichomes, soon caducous. *Flowers* numerous (ca. 83), crowded, malodorous, 20–22 mm long, sessile; calyx dark green, tubular-obconical, 5–6 × 4 mm, glabrous outside, the costas sometimes conspicuous, the teeth sinuate-deltoid 0.5 mm long, minutely ciliate, but not tufted apically, pubescent within; corolla green with purple areas, 14–21 mm long, exserted 9–13 mm from the calyx, tube 13–21 mm long, basally slender, 1 mm wide, expanding about ⅓ way up to 4–5 mm wide, glabrous outside, the fine nerves inconspicuous, glabrous within, mouth 2.5–3.5 mm wide, lobes 1–3 mm long, obtuse or rounded, glabrous outside; stamen insertion levels subequal, filaments adnate for 6–7 mm, 6 mm free, the free insertion 1.5–2 mm, distal free portion 5 mm long, insertion tumid, a few minute hairs present just below the insertion, distal portion glabrous; style 12–13 mm, glabrous, stigma unequally bilobate, the two lobes forming a mouth flanking the stigmatic surface; ovary glabrous, disk inconspicuous, ovules 6–8. *Fruit* a woody, apically dehiscent capsule, 6–7 mm long, the valves 4, linear, 2.5 mm wide at the base; fruiting calyx slightly accrescent, 6–7 mm, enclosing the base of the capsule, splitting irregularly; seeds 5–12, appearing flat and 14–15 mm long overall, the seed body ellipsoidal, 3–4 × 1 mm, chestnut-brown, surrounded by a light green, membranous, minutely reticulate, oblong wing extending 3–4 mm beyond each end of the seed and 0.25 mm on each side, the ends pointed or rounded, sometimes with one or more narrow wings in another plane; embryo white, 2.5–3 mm long, the hypocotyl straight, terete, the epicotyl laminar, broadly elliptical, forming ¼ the length of the embryo. Figure 61.

In the absence of fruit, *Sessea corymbiflora* is similar to *Cestrum lindenii*, with its large leaves with many veins and in the general appearance of its flowers. However, the flowers of *S. corymbiflora* are shorter, and the stigma is placed obliquely on the style. The spent capsules are persistent for several months, and from a distance the trees resemble arborescent Asteraceae.

Distribution (Fig. 62). Mérida, Táchira, and Trujillo. Subparamos; 2200–2900 m. Also in Colombia and Ecuador.

Phenology. Flowering collections have been seen from February, July, and September.

All specimens seen. VENEZUELA. **Mérida:** Páramo Las Nieves, 48 km al sur de Estanquez, *Benítez et al. 4839* (CAR, MA, MO, MY, P, VEN). **Táchira:** P. Nacional Los Páramos, carretera Pregonero–El Portachuelo, *Benítez et al. 4741* (F, MER, MERF, MO, MY, NY, PORT, US, VEN). **Trujillo:** entre El Alto de Tuñame y Quebrada El Pajarito, *Ruíz-Terán & López-Palacios 7552* (MERF, MY).

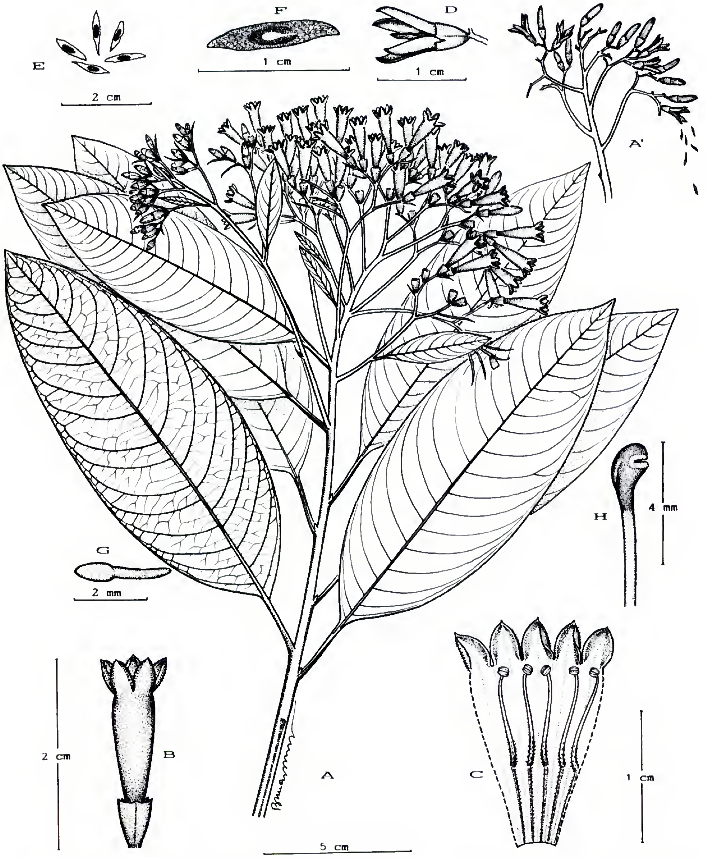

Figure 61. *Sessea corymbiflora.*—A. Flowering branch.—A′. Infructescence.—B. Flower.—C. Corolla opened to show stamens.—D. Fruiting capsule.—E. Seeds.—F. Seed showing body and wing.—G. Embryo.—H. Style. A–H after *Ruiz-Terán 7552* (MERF). A′ after *Benítez 4741* (MY).

Literature Cited

Andrade, S. O. 1960. Estudios sobre a toxicidade de *Sessea brasiliensis.* Arq. Inst. Biol. (S. Paulo) 27: 191–196.

Atkinson, G. C. & T. K. James. 1979. Preliminary study on the control of Red Cestrum. Pp. 289–291 *in* Proceedings of the 32nd New Zealand Weed & Pest Control Conference. New Zealand Weed and Pest Control Society, Palmerston North, New Zealand.

Benítez de Rojas, C. E. 1974. Los géneros de las Solanaceae de Venezuela. Revista Fac. Agron. (Maracay) 7(3): 25–108.

——— & W. G. D'Arcy. 1993. Nomenclature of *Sessea*

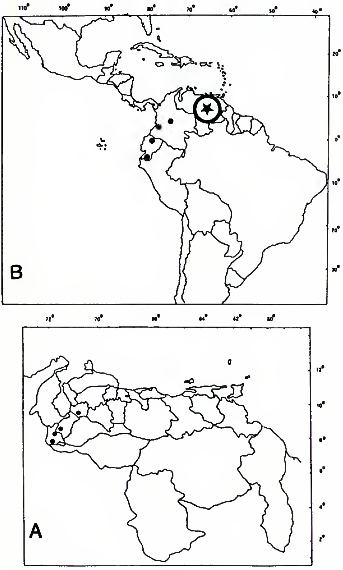

Figure 62. *Sessea corymbiflora.*—A. Distribution in Venezuela.—B. Representative occurrences outside of Venezuela.

corymbiflora (Solanaceae) and its occurrence in Venezuela. Novon 3: 324–327.

——— & ———. 1995. New species of *Cestrum* (Solanaceae) and synonymy under two widespread species. Novon 5: 311–317.

——— & ———. 1998. Cestreae in Venezuela. *In* M. Nee, D. Symon, J. Jessup & J. G. Hawkes (editors), Solanaceae IV: Advances in Biology and Utilization. Royal Botanic Gardens, Kew (in press).

Bernardello, L. M., L. Galetto, J. Jaramillo & E. Grijalba. 1994. Floral nectar chemical composition of some species from Reserva Río Guajalito, Ecuador. Biotropica 26: 113–116.

Berg, C. & J. Greilhuber. 1992. Cold-sensitive chromosome regions and their relation to constitutive heterochromatin in *Cestrum parqui* (Solanaceae). Geome 35: 921–930.

——— & ———. 1993a. Cold-sensitive chromosome regions and heterochromatin in *Cestrum* (Solanaceae): *C. strigilatum*, *C. fasciculatum*, and *C. elegans*. Pl. Syst. Evol. 185: 133–151.

——— & ———. 1993b. Cold-sensitive chromosome regions and heterochromatin in *Cestrum aurantiacum* (Solanaceae). Pl. Syst. Evol. 185: 259–273.

Bitter, G. 1922. Zur Gattung *Sessea*. Repert. Spec. Nov. Regni Veg. 18: 199–215.

Danert, S. 1958. Die Verzweigung der Solanaceen im reproductiven Bereich. Abh. Deutsch. Akad. Wiss. Berlin, Kl. Chem. 6: 1–292.

D'Arcy, W. G. 1970. Jacquin names, some notes on their typification. Taxon 19: 554–560.

———. 1974. Solanaceae. *In* R. E. Woodson et al., Flora of Panama. Ann. Missouri Bot. Gard. 60: 573–870.

———. 1979. The classification of the Solanaceae. Pp. 3–48 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (editors), The Biology and Taxonomy of the Solanaceae. Academic Press, London.

———. 1997. Red-flowered cestrums and red-loving hummingbirds. *In* M. Nee, D. Symon, J. Jessup & J. G. Hawkes (editors), Solanaceae IV: Advances in Biology and Utilization. The Royal Botanic Gardens, Kew (in press).

Darlington, C. D. & A. P. Wylie. 1955. Chromosome Atlas of Flowering Plants, 2nd ed. Allen & Unwin, London.

Dunal, F. 1852. Solanaceae. *In* A. De Candolle, Prodromus systematis naturalis regni vegetabilis 13(1): 1–741. Paris, France.

Dyer, A. F. 1963. Allocyclic segments of chromosomes and the structural heterozygosity that they reveal. Chromosoma 13: 547–576.

Eichler, A. 1875. Blüthendiagramme Construirt und Erläutert. W. Engelmann, Leipzig.

Endlicher, S. L. 1838. Genera Plantarum 668.

Fleming, T. H. 1988. The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions. Univ. Chicago Press, Chicago.

Fournet, J. 1978. Flore Illustrée des Phanérogames de Guadeloupe et de Martinique. Inst. Nat. Recherche Agronomique, Paris.

Francey, P. 1934. Übersicht über die Gattung *Sessea*. Notizbl. Bot. Gart. Berlin-Dahlem 11: 978–990.

———. 1935–1936. Monographie du genre *Cestrum* L. Candollea 6: 46–398; 7: 1932.

Freeman, C., W. H. Reid, J. E. Becvar & R. Scogin. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. 145: 132–135.

Gill, L. S. 1972. Chromosome numbers in West-Himalayan bicarpellate species II. Bull. Torrey Bot. Club 99: 36–38.

Gottsberger, G., J. Schrauwen & H. F. Linskens. 1984. Amino acids and sugars in nectar, and their putative evolutionary significance. Pl. Syst. Evol. 145: 55–77.

Haber, W. A. & G. W. Frankie. 1989. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. Biotropica 21: 156–172.

Jacquin, N. J. 1798. Volume 3. Plantarum rariorum horti caesarei schoenbrunnensis. Vienna.

Krook, L., R. H. Wasserman, J. N. Shively, A. H. Tashjian, T. D. Brokken & J. F. Morton. 1975. Hypercalcemia and calcinosis in Florida horses: Implication of the shrub, *Cestrum diurnum*, as the causative agent. Cornell Veterin. 65: 26.

Madhavadian, P. 1968. Chromosome numbers in South Indian Solanaceae. Caryologia 21: 343–347.

McLennan, M. W. & W. R. Kelly. 1984. *Cestrum parqui* (green cestrum) poisoning in cattle. Austral. Veterin. J. 61: 289–291.

Mehra, P. N. & K. S. Bawa. 1969. Chromosomal evolution in tropical hardwoods. Evolution 23: 466–481.

Nanda, P. C. 1962. Chromosome numbers of some trees and shrubs. J. Indian Bot. Soc. 41: 271–277.

Nee, M. 1986. Solanaceae I. *In* Flora de Veracruz. Fasc. 49: 1–191. Inst. Nac. Inv. Recurs. Biot., Xalapa.

Olmstead, R. G. & J. D. Palmer. 1992. A chloroplast DNA phylogeny of the Solanaceae: Subfamilial relationships and character evolution. Ann. Missouri Bot. Gard. 79: 346–360.

———, J. A. Sweere, R. E. Spangler, L. Bohs & J. D. Palmer. 1997. Phylogeny and provisional classification of the Solanaceae based on chloroplast DNA. *In* M. Nee, D. Symon, J. Jessup & J. G. Hawkes (editors), Solanaceae IV: Advances in Biology and Utilization. The Royal Botanic Gardens, Kew (in press).

Overland, L. 1960. Endogenous rhythm in opening and odor of flowers of *Cestrum nocturnum.* Amer. J. Bot. 47: 378–382.

Percival, M. 1965. Floral Biology. Pergamon Press, Oxford.

Pittier, H. 1932. Studies in Solanaceae. I. The species of *Cestrum* collected in Venezuela up to 1930. J. Wash. Acad. Sci. 22: 25–37.

Prema, T. P. & N. Raghuramulu. 1994. Free vitamin D_3 metabolites in *Cestrum diurnum* leaves. Phytochemistry 37: 677–681.

Procter, M., P. Yeo & A. Lack. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon.

Romeike, A. 1978. Tropane alkaloids—Occurrence and systematic importance in angiosperms. Bot. Not. 131: 85–96.

Ruiz Zapata, T. 1993. La morfología del polen de *Cleome* L. en relación con su taxonomía y síndromes de polinización. Pittieria 21, ed. especial 297. [Abstract.]

Sachs, R. M. 1985. *Cestrum.* Pp. 176–184 *in* A. H. Halevy (editor), CRC Handbook of Flowering, Vol. 2. CRC Press, Boca Raton, Florida.

Sharma, A. K. & A. Sharma. 1958. Karyotype studies in *Cestrum* as an aid to taxonomy. Genetica 29: 83–100.

Ule, E. 1908. Die Pflanzenformationen des Amazonas-Gebietes II. Pflanzengeographische Ergebnisse meiner in der Jahren 1900–1903 in Brasilien und Peru unternommenen Reisen. Bot. Jahrb. Syst. 40: 398–443.

Wasserman, R. H. 1974. Calcium absorption and calcium-binding protein synthesis: *Solanum malacoxylon* reverses strontium inhibition. Science 183: 1092–1194.

———. 1978. The nature and mechanism of action of the calcinogenic principle of *Solanum malacoxylon* and *Cestrum diurnum,* and a comment on *Trisetum flavescens.* Pp. 545–553 *in* R. F. Keeler, K. R. van Kampen & L. F. James, Effects of Poisonous Plants on Livestock. Academic Press, New York.

White, R. H., R. D. Stevenson, R. R. Bennett, D. E. Cutler & W. A. Haber. 1994. Wavelength discrimination and the role of ultraviolet vision in the feeding behavior of hawkmoths. Biotropica 26: 427–435.

List of Species

1. *Cestrum acuminatissimum* Dunal
2. *Cestrum alternifolium* (Jacq.) O. E. Schulz
3. *Cestrum aurantiacum* Lindl.
4. *Cestrum bigibbosum* Pittier
5. *Cestrum buxifolium* Kunth
6. *Cestrum cuneifolium* Francey
7. *Cestrum diurnum* L.
8. *Cestrum glabrescens* (C. V. Morton) Steyerm. & Maguire
9. *Cestrum humboldtii* Francey
10. *Cestrum imbricatum* Rusby
11. *Cestrum jaramillanum* Benítez & D'Arcy
12. *Cestrum latifolium* Lam.
13. *Cestrum lindenii* Dunal
14. *Cestrum mariquitense* Kunth
15. *Cestrum megalophyllum* Dunal
16. *Cestrum microcalyx* Francey
17. *Cestrum neblinense* D'Arcy & Benítez
18. *Cestrum nocturnum* L.
19. *Cestrum olivaceum* Francey
20. *Cestrum pariense* Steyerm.
21. *Cestrum petiolare* Kunth
22. *Cestrum potaliifolium* Dunal
23. *Cestrum racemosum* Ruiz & Pav.
24. *Cestrum reflexum* Sendtn.
25. *Cestrum ruizteraninnum* Benítez & D'Arcy
26. *Cestrum salicifolium* Jacq.
27. *Cestrum scandens* Vahl
28. *Cestrum schulzianum* Francey
29. *Cestrum strigilatum* Ruiz & Pav.
30. *Cestrum tillettii* Benítez & D'Arcy
31. *Cestrum tomentosum* L. f.
32. *Cestrum tubulosum* Sendtn.
33. *Sessea corymbiflora* Taylor & Phillips

Index to Exsiccatae

Specimens are listed alphabetically by collector, followed by collector number and herbarium of deposit; the species is indicated by a number in parentheses corresponding to the number in the List of Species above.

Agostini (MY-56467) (16); 76 (VEN) (2). Agostini & de Agostini 1171 (MY, VEN) (12). Agostini & Fariñas 90 (MY, US, VEN) (4). Agostini et al. 1187 (VEN) (31). Aguiar 8 (VEN) (7). Allart 254 (NY, US, VEN) (26); 475 (US, VEN) (2); 480 (VEN) (21). Alston 6619 (MO, US) (5); 7098 (BM, US) (29); 7099 (US) (31). Archer 2986 (US) (27); 2987 (US) (27); 3090 (US) (12). Aristeguieta 792 (VEN) (13); 1667 (VEN) (15); 2291 (VEN (4); 2514 (VEN) (5); 2525 (F, MER, VEN) (21); 2765 (VEN) (26); 2769 (US, VEN) (23); 2869 (US, VEN) (15); 3689 (VEN) (21); 3691 (MO, US, VEN) (31); 3703 (F, MO, US, VEN) (26); 4009 (MO, VEN) (15); 4179 (VEN) (12); 4465 (MO, VEN) (29); 5041 (VEN) (12); 5434 (VEN) (26); 5463 (MO, VEN) (27); 5962 (VEN) (31); 6464 (VEN) (12); 6649 (VEN) (7); 747 (VEN) (31); 748 (VEN) (21); 7757 (VEN) (31); 7812 (VEN) (31); 12460 (VZU) (2). Aristegnieta & Foldats 1504b (VEN) (4). Aristeguieta & Huber 302 (VEN) (31). Aristeguieta & Medina 3651 (VEN) (5). Aristeguieta et al. 7260 (F, MER, MY, US, VEN) (12). Arroyo 75-105 (VEN) (4); 75-123 (VEN) (15). Arroyo & Aristeguieta 75-100 (VEN) (15). Arteaga 107 (CAR) (31); 251 (CAR) (27). Ayala 697 (MER, MY) (12). Aymard 2 (MER) (7); 524 (MY, PORT) (12); 1020 (VEN) (12); 1951 (MY, PORT) (12); 4496 (MY) (12); 5536 (MO, MY, PORT, VEN) (12). Aymard & Cuello 3567 (MY, PORT) (12); 5591 (MY, MO, PORT) (12). Aymard & Ortega 1343 (MY) (5); 2541 (MY, PORT) (12). Aymard et al. 2222 (MER, MY) (14); 1922 (MY, PORT) (31); 2747 (MY, PORT) (12); 3741 (MY, PORT) (4).

Badillo 1726 (MY) (31); 218 (VEN) (31); 5255 (MY) (21); 6629 (MY) (4); 6693 (MY) (4); 6763 (MY) (31); 6818 (MY) (5); 6836 (MY) (5); 6909 (MY) (21); 691 (VEN) (21); 6942 (MY) (21); 7058 (MY) (21); 7078 (MY) (13); 7085 (MY) (21); 720 (VEN) (2); 8004 (MY) (21). Badillo & Badillo 6782 (MY) (5); 7297 (MY) (31). Badillo et al. 7848 (MY) (14). Barclay & Juagibioy 9754 (MO) (5). Barcos (MY-67838) (15). Barrios 14 (MY) (18). Bascopé 34 (MY) (31). Belandria 191 (MER) (14); 204 (MER) (14); 9

(MER) (14). Benítez 87 (MY) (18); 91 (MY) (12); 95 (MY) (12); 550 (MY) (12); 563 (MY) (12); 1033 (MY) (18); 1034 (MY) (18); 1211 (MY) (27); 1212 (MY) (12); 1213 (MY) (12); 1218 (MY) (12); 1269 (MY) (29); 1294 (MY) (31); 1303 (MY) (21); 1307 (MY) (12); 1309 (MY) (12); 1438 (MY) (21); 1448 (MY) (16); 1556 (MY) (7); 1564 (MY) (16); 1609 (MY) (2); 1809 (MY) (2); 1825 (MY) (4); 1895 (MY) (13); 1937 (MY) (12); 1944 (MY) (2); 1960 (MY) (12); 1979 (MY) (31); 2034 (MY) (21); 2111 (MY) (23); 2130 (MO, MY, NY) (29); 2144 (MY) (31); 2164 (MY) (12); 2168 (MY) (23); 2169 (MY) (12); 2606 (MY) (2); 2750 (MY) (4); 2828 (MY) (12); 2883 (MY) (12); 2913 (MY) (12); 2929 (MY) (12); 3093 (MY) (16); 3140 (MY) (16); 3212 (MY) (4); 3560 (MY) (26); 3577 (MY) (15); 3616 (MY) (15); 3783 (MY) (9); 3850 (MY) (26); 3857 (MY) (26); 3902 (MY) (12); 3920 (MY) (12); 3955 (MY) (21); 3994 (MY) (16); 4159 (MY) (15); 4230 (MY) (15); 4239 (MY) (12); 4281 (MY) (2); 4287 (MY) (4); 4522 (MY) (21); 4551 (MY) (26); 4668 (MY) (31); 4674 (MY) (5); 4675 (MY) (5); 4681 (MY) (2); 4692 (MY) (15); 4739 (MY) (21); 4740 (MY) (13); 4746 (MY) (21); 4756 (MY) (12); 4782 (MY) (31); 4784 (MY) (31); 4795 (MY) (31); 4799 (MY) (5); 4802 (MY) (21); 4803 (MY) (5); 4811 (MY) (4); 4828 (MY) (31); 4844 (MY) (31); 4846 (MY) (13); 4849 (MY) (31); 4851 (MY) (5); 4854 (MY) (13); 4860 (MY) (21); 4864 (MY) (23); 4870 (MY) (9); 4876 (MY) (31); 4877 (MY) (23); 4885 (MY) (15); 4895 (MY) (12); 4896 (MY) (12); 4897 (MY) (14); 4900 (MY) (23); 4901 (MY) (14); 4907 (MY) (26); 4909 (MY) (4); 4912 (MO, MY) (22); 4913 (MY) (4); 4915 (MY) (15); 4916 (MY) (2); 4997 (MY) (26); 4998 (MY) (4); 4999 (MY) (22); 5036 (MY) (14); 5037 (MY) (12); 5040 (MY) (14); 5046 (MY) (15); 5049 (MY) (14); 5051 (MY) (21); 5056 (MY) (13). Benítez & Aguilera 4691 (MY) (29). Benítez & Baldizán 4945 (MY) (23). Benítez & Gimenez 4157 (MY) (15). Benítez & Otero 4604 (MY) (13); 4716 (MY) (31). Benítez & Rojas 3083 (MY) (12); 4719 (MY) (23); 4996 (MY) (23). Benítez et al. 3576 (MY) (4); 4110 (MY) (4); 4223 (MY) (15); 4667 (MY) (31); 4814 (MY) (5); 4741 (F, MER, MERF, MO, MY, NY, PORT, US, VEN) (33); (CAR, MA, MO, MY, P, VEN) (33). Bernardi 313 (P) (13); 484 (MER, NY) (2); 2045 (MER) (4); 2079 (VEN) (5); 3329 (MER, MY) (12); 6097 (MER) (31); 6183 (MER) (21); 6235 (MER) (4); 7127 (MER, VEN) (24); 7439 (MER) (23); 7626 (VEN) (15); 7760 (VEN) (5). Bernardi et al. 13056 (NY) (6); 17200 (G, MO, NY) (6). Berry 3492 (MY) (2); 3663 (MO) (2); 379 (VEN) (2); 439 (VEN) (12); 4807 (MO, MYF) (12); 49 (MO, VEN) (2); 501 (VEN) (2). Bevilacqua 163 (VEN) (2); 414 (VEN) (2). Birschel s.n. (GH) (18). Blanco 24 (VEN) (31). Bond et al. 101 (US) (12). Bono 4022 (MY) (4); 5043 (MY) (18); 5082 (MY) (4); 5891 (MY, VEN) (13); 5956 (CAR, MY) (13). Boon & Grillo 6559 (MO, MYF, NY) (12). Breteler 3352 (MER, P, U, US, VEN) (5); 3384 (VEN) (21); 3568 (MER, P, VEN) (31); 3614 (MER, MO, US, VEN) (31); 3721 (MER, US, VEN) (14); 3732 (F, MER, US, VEN) (12); 3898 (F, MO, US, VEN) (12); 4029 (F, MER, MO, P, US, VEN) (12); 4072 (MER) (4); 4305 (MER, MO, US, VEN) (2); 4652 (F, MO, VEN) (5). Briceño 40 (VEN) (18). Briceño & Adamo 717 (MY) (5). Broadway 316 (US) (12); 707 (US) (12). Bruijn 1183 (MER, MO, US, VEN) (23). Bunting 5598 (MO, VZU) (12); 7747 (MO) (12); 8042 (MO, VEN, VZU) (12); 9418 (MO, VZU) (12). Bunting & Alfonso 13278 (MY, VZU) (12); 7294 (MO, VEN) (12). Bunting & Arboleda 8726 (MO, VZU) (27); 8759 (VZU) (12). Bunting & Fucci 6049 (MO, VZU) (15); 7577 (MO, VEN) (12). Bunting & Stoddart 8907 (MO, VZU) (12); 9055 (VZU) (27). Bunting et al. 11120 (MY, VEN) (15). Bunting et al. 12023 (MO) (12). Bunting et al. 12481 (MO, MY, VZU) (12). Bunting et al. 12800 (MY) (15). Bunting et al. 7345 (MO, VZU) (12). Burandt V0049 (MY, UCOB) (4). Burandt & Garófalo V0596 (MY) (5). Burkart Arturo 16396 (VEN) (27).

Calvo 0003 (MY) (23). Camero (MY-85034) (27). Cárdenas de Guevara, L. 1707 (MY) (2). Cardona 31 (US, VEN) (12). Cardozo 1137 (MY) (4); 1225 (MY) (4); 1364 (MY) (4); 1515 (MY) (22); 1709 (MY) (4). Carnevali et al. 535 (VEN) (27). Caro 3 (MY) (12). Casadiego & Campos 378 (MY) (14). Castillo 1961 (MY) (16); 1962 (VEN) (15); 478 (VEN) (12). Castroviejo et al. 411 (MA) (12). Cawz 12 (MY) (7). Chaffanjon s.n. (P) (12). Chardon 33 (VEN) (12); 271 (US, VEN) (4). Chardon et al. 3204 (VIA) (12); 3222 (VIA) (29). Charpin & Jacquemoud (HAC-13440 G, MO) (21). Charpin et al. 13146 (MO, NY) (6). Clark 6948 (MO, NY) (1). Colella & Morales 563 (MY) (15). Colma et al. 103 (CORO, MY, VEN) (2); 244 (CORO, MY, VEN) (2); 247 (VEN) (2); 248 (CORO, MY, VEN) (2); 351 (CORO, MY) (2). Croat 21406 (MO, VEN) (15); 54467 (MO, VEN) (15); 54936 (MO) (21); 60795 (MO, VEN) (4). Croizat 392A (F) (12). Cumana 1274 (IRBR, MY) (12); 1574 (IRBR, MY) (12). Curran & Haman 988 (MO, US) (23).

D'Arcy & Benítez 18236 (MO) (5); 18258 (MO) (13); 18261 (MO) (21). Davidse & González 15984 (MO, VEN) (1); 16721 (MO) (15); 19999 (MO, VEN) (12); 21967 (MO, VEN) (1). De Martino et al. SPB 1120 (MYF) (12). Delascio 4087 (CAR, VEN) (4); 4118 (CAR) (4); 7579 (VEN) (15); 7673 (CAR) (12); 9724 (VEN) (4). Delascio & Benkowski 3145 (CAR) (12); 3125 (CAR) (12). Delascio & Delascio 5042 (CAR, VEN) (5). Delascio & López 2555 (CAR, VEN) (12). Delascio & Velasquez 692 (CAR) (22); 693 (CAR) (22). Delascio et al. 13401 (VEN) (12); 15026 (VEN) (12); 5006 (CAR, VEN) (5). Delgado 236 (VEN) (21). Díaz 526 (MO) (4). Diederichs 172 (VEN) (4); 303 (VEN) (4). Dorr & Barnett 5163 (VEN) (5). Dorr et al. 4858 (VEN) (23); 7900 (MY, NY, PORT) (13).

Edwards & Roe 28 (MY) (4). Edwards et al. 99 (MY) (22); 107 (K, MY) (4); 360 (K, MER, MERF, MO, MY, NY, PORT, US, VEN) (29); 467 (K, MY) (29). Elias 239 (CAR) (7). Ernst s.n. (HBG) (3). Ewell 195 (MY) (23).

Fendler 9 (MY) (27); 547 (MY) (31); 746 (MY) (21); 2090 (MO) (26); 2091 (GH) (29); 935 (GH, MO) (31); 954 (MO, P) (13); 955 (GH, MO, NY) (4); 956 (MO) (21); 958 (GH) (27); 959 (GH, MO, NY) (2); 961 (GH) (23); 962 (GH, NY) (22); 963 (GH) (31); 966 (GH, MO, NY) (12). Fernández 1266 (MY) (12); 2480 (MY) (4); 2671 (MY) (12); 3154 (MY) (20); 3888 (MY) (12); 4017 (MY) (12); 4018 (MY) (12). Fernández et al. 10 (MER) (2); 200 (CAR, MY, PORT) (2); 5239 (MY, PORT) (12); 84 (MER) (2). Ferrari 141 (MY) (27); 142 (MY) (27); 221 (MY) (27); 272 (MY) (12); 991 (MY) (27). Ferrari & Bunting 1672 (MY) (31). Field 282a (K, MY) (15); 313 (K, MY) (15); 441 (K, MY) (15); 497 (MY) (16). Figuera (MY-68080) (27). Funck & Schlim 429 (BM, P) (31); 627 (G) (31); 784 (G, P) (13).

García 142 (VEN) (22); 153 (VEN) (4); 172 (VEN) (31). Gebriger 255 (F, P, VEN) (31); 299 (F, MO, VEN) (21); 40 (F, MO, VEN) (5). Gentry 41165 (MO) (15). Gentry et al. 10439 (MO, VEN) (12). Gines & Rudd 1599 (CAR) (31). Gentry & Stein 47262 (MO, MY, VEN) (15). Gines 1763 (CAR, US) (5); 2003 (MY) (12); 4665 (US) (31). González 160 (MER) (2); 3 (VEN) (2). González & Ortega 1310 (MO, MY, VEN) (15). Gragson & Gragson 48 (MY) (1). Grosourdy 13 (P) (2). Guánchez & Mercado 1921

(TFAV) (12). Guevara (MY-68083) (12). Gutiérrez 225 (TFAV) (12)

Hernandez 1189 (MER) (27). Holst 3733 (MO) (8). Holst & Liesner 2724 (VEN) (15). Holst et al. 2024 (VEN) (12). Holt 19 (VEN) (2). Horner 419 (MO, MYF) (12). Horner et al. 404 (MO, MYF) (12). Hoyos 2091 (CAR) (7). Hoyos & Delascio 4285 (CAR, VEN) (15); 4292 (CAR, VEN) (2). Hoyos & Foldats 3091 (CAR) (2). Huber 207 (VEN) (4); 6250 (MY, MYF) (23); 11033 (MY, MYF) (32). Huber & Roth 1732 (VEN) (15). Humbert 26521 (P) (2). Hurtado (MY-68082) (27).

Ijjasz 305 (MY, VEN) (21).

Jahn 767 (MO, US, VEN) (31); 811 (US, VEN) (5); 923 (US, VEN) (5); 1075 (US, VEN) (13). Jeffrey & Trujillo 2457 (MY) (5). Jimenez Saa 1320 (MER) (12). Johnston 385 (GH) (2).

Killip 37251 (F, GH, US, VEN) (12).

Laskowski & Ramirez 70 (VEN) (12). Lasser 70 (VEN) (2); 1091 (VEN) (13); 1114 (US, VEN) (22); 189 (US, VEN) (2); 2037 (VEN) (22); 2279 (VEN) (26); 2281 (VEN) (2); 2334 (VEN) (15); 2339 (VEN) (23); 3469 (VEN) (18); 3533 (MY, VEN) (7); (VIA-3275) (26). Lasser & Aristeguieta 3376 (F, VEN) (2). Lasser & Foldats 3150 (VEN) (2). Lasser & Vareschi 6052 (VEN) (5). Lasser et al. 2904 (VEN) (23). Liesner 3611 (MO, MY, VEN) (1); 5373 (MO, VEN) (2); 6877 (VEN) (1); 7083 (MO, VEN) (1); 7134 (MO, VEN) (28); 7557 (VEN) (1); 8210 (MO, VEN) (15); 10024 (MO, VEN) (15); 11803 (MO) (15); 13384 (MO) (2); 16661 (MO, MY, VEN) (17); 16999 (VEN, MY) (15); 17789 (MO) (8); 18484 (MO) (8). Liesner & González 5822 (MO, VEN) (12); 9311 (MO, VEN) (1); 9322 (MO, VEN) (1); 9478 (MO, VEN) (15); 9844 (VEN) (4); 9930 (MO, VEN) (15); 10179 (MO, VEN) (4); 10412 (MO, VEN) (1); 10471 (MO, VEN) (14); 11265 (MO, VEN) (12); 13238 (MO, MY, VEN, VZU) (15). Liesner & Guariglia 11658 (MO, VEN) (4). Liesner & Medina 13524 (MY, VEN) (26); 13559 (MO, MY) (21); 13578 (MY, VEN) (4). Liesner & Steyermark 12330 (MA, MO, VEN) (12); 12347 (MO, VEN) (4). Liesner et al. 12617 (MY, VEN) (14); 12836 (MO, VEN) (15); 7755 (MO, VEN) (4). Little 15360 (MER, VEN) (23); 15522 (VEN) (13); 15745 (VEN) (13). Løjnant & Molau 15835 (AAU, GB) (11). López & Sandoval 495 (CAR, MY, VEN) (12). López-Figueiras 8754 (MERF, MY) (21). López-Palacios 86 (MER, MO) (7); 340 (MER, MO) (2); 1255 (MERF, MY) (12); 1373 (MERF) (5); 1505 (MO) (31); 1507 (MO) (31); 1886 (MO, VEN) (15); 1988 (MERF, MO, MY, VEN) (12); 2145 (MERF, MY) (2); 2150 (MER, MO, VEN) (23); 2637 (MO) (21); 2732 (MERF) (4). López-Palacios & Bautista 3193 (MER) (12). Lozada (MY-67062) (23). Luteyn 5250 (F, MO, NY, US, VEN) (5); 6191 (NY) (25). Luteyn & Lebrón-Luteyn 6240 (MO, VEN) (21); 9834 (MO) (21). Luteyn et al. 5370 (F, MO, VEN) (13); 6076 (F, VEN) (5); 6171 (MY, NY, VEN) (25); 6196 (F, MO, VEN) (21); 8208 (MY, NY, VEN) (15); 9802 (MO) (5). Madriz 50 (MY) (23).

Maguire & Maguire 35219 (NY) (1). Maguire et al. 42500 (MO, US) (17). Manara 113381 (MO) (15); s.n. (F-1805024) (2); s.n. (MO-2671613) (31); s.n. (MY-65436 (26); s.n. (VEN-113158) (31); s.n. (VEN-113165) (2); s.n. (VEN-115002) (21); s.n. (VEN-1805023) (21); s.n. (VEN-115003) (2); s.n. (VEN-172746) (2); s.n. (VEN-174788) (29); s.n. (VEN-174796) (15); s.n. (VEN-175090) (15); s.n. (VEN-176654) (22). Manara & Vera (MY-28669) (27); Marcano-Berti 1519 (MER) (12). Marcano-Berti & Torres-Lezama 207 (MER, VEN) (23). Marcano-Berti et al. 457-979 (MER, MY) (23). Matos 120 (CAR) (12); 1122 (CAR, VEN) (13). Medina 520 (VEN) (4); 531 (VEN) (22); 533 (VEN) (15). Meier & Silva 1565 (MY, VEN) (21); 61 (MY, VEN) (31); 768 (MY) (13); 901 (MY, VEN) (13); 1205 (MY, VEN) (22); 1312 (MY, VEN) (13); 1329 (MY, VEN) (13); 1723 (MY, VEN) (13); 1816 (MY, VEN) (13); 1909 (MY, VEN) (31); 3174 (MY, VEN) (13); 3180 (MY, VEN) (13); 3284 (MY, VEN) (4); 3330 (MY, VEN) (21); 3603 (MY, VEN) (31). Meier & Silva 1565 (MY, VEN) (21). Meier et al. 2642 (MY, VEN) (15). Mocqueris 1092 (MY, P, US, VEN) (31). Montes 61 (VEN) (12). Morales 215 (MY) (31); 249 (MY) (21). Moreno 23 (MY) (27). Mori et al. 14667 (VEN) (4). Morillo 1777 (MY, VEN) (2); 8346 (MY, VEN) (2); 11105 (MERF) (5). Morillo & García 11385 (MY) (6); 11475 (MERF, MY) (9); 11478 (MERF, MY) (19). Morillo & Hasegawa 5026 (MY, VEN) (1). Morillo & Liesner 9130 (MO, VEN) (12). Morillo & Manara 2135 (MER, MO, MY, VEN) (23); 667 (MY) (31). Morillo & Medina 8730 (VEN) (4). Morillo & Morillo 2966 (VEN) (15); 7112 (MY, VEN) (12). Morillo & Ramirez 8135 (MY, VEN) (12). Morillo & Seres 8627 (VEN) (26). Morillo & Smith 5856 (MY, VEN) (4); 6018 (MY, VEN) (31). Morillo et al. 9572 (VEN) (12); 4004 (MY, VEN) (28); 4040 (VEN) (28); 4105 (MY, VEN) (28); 4257 (F, MO, US) (12); 7149 (VEN) (12); 8452 (VEN) (27). Moritz 212 (B, HBG, G-DC) (27); 212b (BM) (4); 309 (BM, G-DC, MO) (31); 348 (W) (4); 824 (BM, G-DC) (22); 1641 (BM) (26); 1931 (P) (12). Moritz s.n. (BM) (21).

Nee 17450 (F, VEN) (12); 17563 (F, VEN, WIS) (2); 30689 (MY, VEN) (8); 31259 (MY, VEN) (18). Nee & Mori 3961 (US, VEN) (27); 4107 (US) (14). Nee & Whalen 17147 (F, VEN) (18).

Oberwinkler 13446 (MER, VEN) (13). Ortega 1671 (MO, MY, PORT) (14); 549 (MY) (12); 631 (MY, PORT) (12). Ortiz 1196 (MY, VEN) (15); 1261 (MY, VEN) (15). Ortiz et al. 1145 (VEN) (12); 1157 (VEN) (12). Osorio (MY-84794) (27). Otto 704 (G, P) (27).

Páez et al. 29 (MY) (14). Pietrangeli (MY-86956), (MY-86957), (MY-86958) (31); (MY-86959) (5); 1226 (MY, VEN) (4); 1243 (MY, VEN) (13); 1269 (MY) (31); 2020 (MY) (13); 2147 (MY) (13); 2149 (MY) (31); 2337 (MY) (13). Pipoly et al. 6478 (MO) (5). Pittier 166 (VEN) (13); 5797 (F, NY, US, VEN) (12); 5925 (P, US, VEN) (27); 9200 (GH, NY, US, VEN) (27); 9245 (US, VEN) (4); 10045 (US, VEN) (21); 10393 (GH, US, VEN) (23); 11215 (VEN) (7); 12094 (NY, US, VEN) (12); 12332 (G, NY, US, VEN) (12); 12639 (GH, NY, VEN) (31); 12858 (US, VEN) (31); 12911 (US, VEN) (5); 12919 (US, VEN) (31); 13029 (G, NY, US, VEN) (18); 13210 (F, MO, US, VEN) (5); 13294 (F, MO, US, VEN) (31); 13323 (F, MO, US, VEN) (31); 13963 (US, VEN) (27); 14075 (VEN); Pittier & Nakichenovitch 15368 (VEN) (4); 15683 (VEN) (4). Plowman 7765 (F, MO) (13). Ponce & Trujillo 634 (MY) (5). Prance 28160 (MO) (15). Pulgar (MY-16420) (27). Pursell et al. 8432 (VEN) (12).

Quintero 70 (MER, MY) (7); 134 (MER, MY) (23); 161 (MER) (12); 526 (MER) (23); 1310 (MER) (31); 2039 (MER) (13); 2292 (MER) (13). Quintero & Carroz 1082 (MER) (13). Quintero & Ricardi 1524 (MER) (14). Quintero et al. 235 (MER) (2).

Ramia & Ortíz 8626 (VEN) (12). Ramirez 2148 (MY) (12); 234 (MY, VEN) (12). Ramirez & López 3162 (MY) (2). Reggio & de Scorza (VEN-118911) (18). Ricardi & Adamo 576 (MY) (31). Ricardi & Carroz 9 (MER) (12). Ricardi & Salcedo 5734 (MER) (13); 5744 (MER) (23); 5756 (MER) (23). Rivero 1678 (MO) (5). Rivero et al. 1888 (MO, MY, PORT) (14). Rodríguez 1 (MER) (4); 71 (MY) (12); 118 (MY) (12); 203 (MY) (12). Rodríguez & Cardozo 1729 (MY) (4). Rodríguez et al. 1357 (MY) (4).

Romero 357 (MY) (12); 750 (MY) (31); 1035 (MY) (31). Ruiz 4183 (MY) (4); 4297 (MY) (4). Ruiz et al. 429 (VEN) (2); 525 (VEN) (2); 532 (VEN) (2); 579 (VEN) (2); 1507 (VEN) (2); 1644 (VEN) (2); 2101 (VEN) (2); 4501 (MY) (12); 4718 (MY) (14); 4719 (MY) (14). Ruiz-Terán 1761 (MER, MO) (12); 1774 (MER) (12); 2205 (MY) (33); 2878 (MER, MERF) (12); 2978 (MER) (4); 3019 (MERF) (13); 3195 (MER, MY) (21); 3548 (MER, MY) (12); 3579 (MER) (2); 3606 (MER) (7); 6312 (MERF) (21); 6819 (MY) (5); 6867 (MERF, MY) (21); 6911 (MERF) (5); 12094 (MERF, MY) (21); 13420 (MY) (5); 13426 (MY) (5); 13430 (MERF, MY) (21); 13516 (MY) (5). Ruiz-Terán & Dugarte 12219 (MY) (5); 14886 (MY) (13); 14539 (MERF, MY) (31); 11999 (MERF, MY) (31); 12935 (MY) (13); 15916 (MERF, MY) (21); 15985 (MERF, MY) (21). Ruiz-Terán & Gallardo 12641 (MERF, MY) (2). Ruiz-Terán & López-Figueiras 279 (MERF, MY) (5); 358 (MY) (5); 731 (MY) (5); 1024 (MY) (5); 1756 (MY) (5); 1998 (MERF) (5); 8306 (MY) (5); 8791 (MERF) (13); 8898 (MY) (5); 949 (MY) (5); 13086 (MY) (5). Ruiz-Terán & López-Palacios 1651b (MY) (5); 7550 (MERF, MY) (21); 7552 (MY) (33); 7615 (MERF) (13); 9925 (MY) (12); 9975 (MY) (18); 10223 (MERF, MY) (2). Ruiz-Terán & Marcano-Berti 1241 (MER) (23); 1325 (MER, MY) (12); 1390 (MY) (5); 1494 (MY) (5). Ruiz-Terán & Ruiz-Pérez 14956 (MERF, MY) (31); 15673 (MY) (13). Ruiz-Terán et al. 3818 (MERF, MY) (31); 3841 (MY) (5); 3859 (MY) (5); 3914 (MERF) (31); 3948 (MERF) (21); 3989 (MERF) (13); 6113 (MERF, MY) (7); 6214 (MY) (2); 6743 (MER, MERF) (13); 8226 (MERF, MY) (5); 10651 (MY) (12); 12357 (MERF, MY) (21); 14230 (MERF, MY) (21); 14266 (MERF, MY) (31); 14677 (MERF, MY) (31); 15135 (MERF, MY) (21); 16114 (MY) (5); 16146 (MERF, MY) (21); 16154 (MY) (25); 16171 (MY) (25); 16303 (MERF, MY) (31). Rusby & Squires 327 (F, G, GH, MO, US) (12). Rutkis 373 (MY, VEN) (12).

Saer 15 (US, VEN) (2); 17 (G, NY) (2); 162 (US, VEN) (27); 184 (MY, US, VEN) (2); 445 (F, VEN) (31); 833 (NY, US, VEN) (12). Schnee 1260 (MY) (12). Schott 123 (F) (7). Schulz et al. 330 (VEN) (5). Smith 3507 (F, US) (13); V1555 (VEN) (31); V165 (VEN) (15); V41 (VEN) (2); V5242 (VEN) (4); V585 (VEN) (2); V7153 (VEN) (23); V7661 (VEN) (7); V8487 (VEN) (31). Spruce 2974 (BR, G, NY) (28). Stergios 821 (MY) (5); 1528 (MY) (31). Stergios & Aymard 7311 (PORT) (28); 7358 (MO) (28); 7606 (PORT) (28); 7770 (MO, MY) (1). Stergios 5630 (MY, PORT) (12). Stergios & Delgado 12910 (MY, PORT) (12). Stergios & Utrera 2465 (MY, PORT) (15). Stergios et al. 3977 (MY, PORT) (12); 5347 (MO, PORT) (12); 6626 (MO, MY, PORT) (15); 8573 (MY, PORT) (12); Steyermark 55008 (MY, VEN) (26); 55689 (MY, VEN) (13); 55695 (F, VEN) (21); 55713 (F, MY, VEN) (5); 55972 (MY, VEN) (31); 56219 (F, VEN) (2); 56322 (F, MY, VEN) (14); 56453 (MY, VEN) (4); 56518 (F, MY, VEN) (5); 57006 (MY, VEN) (22); 57031 (MY, VEN) (13); 57102 (VEN) (13); 59314 (F, MY, VEN) (12); 60925 (F, VEN) (12); 61711 (MY, VEN) (23); 61816 (F, MY, VEN) (31); 61844 (F, VEN) (4); 61974 (MY, VEN) (4); 62371 (F, MY, VEN) (12); 62434 (MY, VEN) (7); 62525 (F, VEN) (2); 75663 (F, VEN) (8); 75682 (F, VEN) (8); 86286 (NY, VEN) (4); 86845 (VEN) (12); 87218 (MO, VEN) (12); 88525 (US, VEN) (2); 88871 (F, US, VEN) (12); 89833 (NY, US, VEN) (4); 90560 (US, VEN) (12); 90566 (US, VEN) (12); 91594 (VEN) (13); 91611 (VEN) (13); 91659 (VEN) (26); 91672 (F, VEN) (13); 92106 (F, US, VEN) (26); 92147 (P, US, VEN) (11); 93274 (F, US, VEN) (8); 95075 (VEN) (20); 95083 (F, P, VEN) (15); 99040 (VEN) (4); 99361 (VEN) (4); 99368 (VEN) (4); 99894 (MO, US, VEN) (23); 101047 (US, VEN) (6); 104947 (VEN) (31); 105035 (P, VEN) (21); 105056 (P, VEN) (5); 106207 (US, VEN) (4); 107001 (VEN) (12); 107414 (MO, US, VEN) (12); 111264 (US, VEN) (8); 120447 (VEN) (12); 122681 (VZU) (12); 125620 (VEN) (26); 127851 (MO) (13); 129677 (MO, MY, VEN) (8). Steyermark & Agostini 91026 (US, VEN) (20). Steyermark & Braun 94598 (P, VEN) (2). Steyermark & Bunting 102318 (VEN) (12). Steyermark & Carreño E. 108771 (VEN) (23); 111662 (F, US, VEN) (12). Steyermark & Liesner 118501 (VEN) (19); 118531 (VEN) (4); 118748 (MO, VEN) (4). Steyermark & Manara 110407 (MO, VEN) (2); 125448 (MY, VEN) (5). Steyermark & Nevling 95906 (VEN) (4). Steyermark & Perkins 122032 (MY, VEN) (15). Steyermark & Rabe 96236 (VEN) (15). Steyermark & Steyermark 95366 (US, VEN) (15); 95463 (NY, P, US, VEN) (29). Steyermark & Wessels-Boer 100397 (MO, VEN) (15); 98775 (MY, VEN, US) (5); 100219 (MO, US, VEN) (4); 100602 (F, US, VEN) (21); 100827 (F, MY, US, VEN) (9); 101047 (MO, VEN, US) (10); 101530 (MO, US, VEN) (1); 103403 (P, VEN) (4); 111522 (VEN) (15); 114590 (MO, VEN) (12); 119545 (MO, VEN) (1); 119881 (VEN) (4); 121278 (VEN) (12); 121518 (MO) (15); 121595 (MO, VEN) (20); 121863 (MO, VEN) (31); 122650 (MO, MYF, VZU) (12); 123025 (MO, VEN, VZU) (2); 123352 (MO, VEN) (12); 124269 (MY, VEN) (12); 124739 (MY, VEN) (15); 124887 (MY, VEN) (12); 127229 (MO, MY) (12); 131034 (CAR, MO) (15). Sugden 1192 (MO) (15).

Tamayo 116 (VEN) (13); 2077 (US, VEN) (12); 2500 (VEN) (2); 2933 (US, VEN) (12); 319 (VEN) (2); 4367 (MY) (5). Tamayo et al. 2504 (VEN) (13). Tate 24 (US) (31); 25 (US) (31); 885 (US) (8). Tengler 3967 (CAR) (18). Tejera 133 (US) (2). Thomas et al. 3392 (MY) (15). Tillett 737-307 (MY) (21); 746-454 (MY) (18); 747-1021 (AAU, MO, MY, MYF, VEN) (30). Tillett & König 737-276 (MY) (21); 738-460 (MY) (21); 738-534 (MY) (21); 747-929 (MY) (30). Tillett & Sayago 843-35 (MY, MYF) (18). Tillett et al. 761-35 (MYF, MY) (15); Torres et al. 19 (MY) (5); 371 (MY) (4). Trujillo 1306 (MY) (13); 1930 (MY) (15); 1962 (MY) (4); 2784 (MY) (31); 3993 (MY) (13); 4629 (MY) (12); 4756 (MY) (2); 4816 (MY) (12); 5121 (MY) (31); 6147 (MY) (27); 6317 (MY) (15); 6549 (MY) (2); 6837 (MY) (2); 7473 (MY) (2); 7635 (MY) (4); 8382 (MY) (21); 9124 (MY) (4); 979 (MY) (31); 14541 (MY) (12). Trujillo & Fernández 30 (MY) (23); 856 (MY) (21); 16351 (MY) (12). Trujillo & Ponce 18282 (MY) (13); 19702 (MY) (18). Trujillo & Rodriguez 17987 (MY) (12).

Valverde & Peña 1061 (MER, MY) (12); 1069 (MER) (14); 1070 (MER, VEN) (14). van der Werff & Ortiz 5859 (MO, VEN) (4). van der Werff & Wingfield 3107 (MY) (2). van der Werff et al. 51 (WIS) (2); 74 (WIS) (2); 576 (CORO, MY) (4); 3209 (WIS) (15); 8771 (MO) (13). Vareschi 5635 (VEN) (5); 7549 (VEN) (5). Vareschi & Lasser 374 (VEN) (5); 6052 (VEN) (5). Vogel 1238 (US) (12); A237 (BM) (26); 406 (BM, M, S, US, VEN) (27).

Weitzman & Boom 95 (MYF) (16). Wessels Boer 2210 (VEN) (5). Wessels Boer et al. 2421 (MER, VEN) (21). Williams 9937 (F, VEN) (13); 9948 (F, US, VEN) (13); 11476 (F, GH, US, VEN) (12); 11544 (F, US, VEN) (12); 11670 (VEN) (12); 13652 (F) (27). Wingfield 5116 (CORO, MY) (7); 5214 (MO, WIS) (2); 6818 (WIS) (2). Wingfield & López-Figueiras 7640 (CORO, MY) (4). Wood 322 (VEN) (22); 412 (VEN) (15); 429 (VEN) (22). Wood & Berry 88 (VEN) (30). Woronov 7079 (F) (13). Wurdack & Steyermark 1083 (VEN) (8); 1366 (VEN) (8).

Xena 583 (MO, MY) (31); 1053 (MY) (15).

Yeffrey 2457 (MY) (5).

Zambrano & Alfonzo 1340 (HERZU, VEN) (12); 1404 (HERZU, VEN) (12). Zambrano & Gutierrez 1529 (HERZU, VEN) (15); 1790 (HERZU) (15). Zambrano et al. 1899 (HERZU) (12); 2217 (HERZU) (23).

INDEX TO SCIENTIFIC NAMES

MATERIALS TOWARD A REVISION OF *GRIMMIA* (MUSCI: GRIMMIACEAE): NOMENCLATURE AND TAXONOMY OF *GRIMMIA LONGIROSTRIS*[1]

Jesús Muñoz[2]

ABSTRACT

Grimmia longirostris Hook. is described and illustrated, and its ecology and phytogeography are considered. A world distribution map is presented. Fifty-five names, at specific and infraspecific rank, are considered synonymous with *G. longirostris*. *Grimmia affinis* Hornsch., the name employed for this taxon in the holarctic, is illegitimate and slightly predated by *G. longirostris* Hook., a name hitherto used only in the Andean region. Cross-section costal morphology is considered the best diagnostic character to distinguish *G. longirostris* from related species. Other useful features are the long, incrassate and nodulose basal paracostal cells of the lamina, the straight setae, and the compound, revoluble annulus. *Grimmia longirostris* grows on all continents except Antarctica and Australia–New Zealand. Its absence in these regions seems not to be an artifact of undercollecting. The preferred habitat is acidic rocks in high mountain ranges or latitudes.

Grimmia is the largest genus in the Grimmiaceae. The difficulty of its study is increased because a vast number of taxa were described at the turn of the century without a critical analysis. In fact, more than half of the taxa in the genus were described in the 50-year period between 1875 and 1925. A critical revisionary study is required to understand the taxonomy and biogeography of the genus. Toward this aim, some years ago I started a nomenclatural database of the genus. The final goal is to present a checklist that could be the starting point of a complete taxonomic revision.

One of my most striking conclusions is that at least 55 validly published names and 10 nomina nuda apply to a single species that has been most commonly known as *Grimmia affinis* Hornsch. Not less surprisingly, this has proven to be an illegitimate homonym predated by the legitimate *Grimmia longirostris* Hook. The legitimate *G. affinis* Hornsch., described five months earlier, is a taxonomic synonym of *G. fuscolutea* (cf. Crum, 1994).

MATERIALS AND METHODS

All names in *Grimmia* found in Crosby et al. (1992), Crosby and Magill (1994), and *Index Muscorum* (Wijk et al., 1962, 1969) and not transferred in these works to other genera have been included in the nomenclatural database. A few taxa excluded from *Grimmia* originally in *Index Muscorum* have been resurrected and included (*G. brandegei* Austin would be an example; cf. Ochyra & Bednarek-Ochyra, 1994). The database now contains 1300 names, which represent a possible maximum of 747 taxa; subsequent taxonomic judgments may reduce this number. The protologue of each name has been checked, involving the review of more than 500 different papers. I have so far been able to study

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the type(s) or original material(s) of 328 taxa (ca. 44% of the total).

Some 900 herbarium specimens from 22 herbaria were studied to determine the geographical distribution and morphological variation of *G. longirostris.* Figure 2 shows data from 733 revised specimens for which geographical coordinates could be established.

I have selected lectotypes whenever necessary. It has been pointed out (Blom, 1996: 11; Horton, 1982: 377) that the only extant specimen in the herbarium of the original author should not automatically be considered the holotype of a name described prior to the establishment of the type concept. I fully agree with this view, but I have followed the designations of previous authors, as did Blom (1996).

Grimmia longirostris Hook., Musci Exot. 1: 62. 1818. TYPE: [Ecuador. Chimborazo: Mt. Chimborazo], *Humboldt 76* (lectotype, designated by Deguchi (1984), BM; isolectotypes, BM, PC).

Grimmia obliqua Hornsch., Flora 2: 84. 1819 [February]. *Grimmia ovata* var. *obliqua* (Hornsch.) Huebener, Muscol. Germ. 183. 1833. *Dryptodon ovatus* var. *obliquus* (Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838. *Grimmia ovalis* var. *obliqua* (Hornsch.) I. Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1909(5): 26. 1909. *Grimmia ovalis* f. *obliqua* (Hornsch.) Mönk., Laubm. Eur. 360. 1927. TYPE: [Austria. Salzburg:] In alpibus Salisburgensibus, *Hornschuch s.n.* (lectotype, here designated, BM).

Grimmia affinis Hornsch., Flora 2: 443. 1819 [July], nom. illeg. [non Hornsch. 1819, Flora 2: 85 [February] (= *Grimmia fuscolutea* Hook.)]. *Dryptodon ovatus* var. *affine* (Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838. *Grimmia ovata* var. *affinis* Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. (fasc. 25–28) 3: 123, Tab. 255ß. 1845. *Grimmia ovalis* var. *affinis* (Hornsch.) Broth., Acta Soc. Sci. Fenn. 19: 86. 1892. *Grimmia ovalis* f. *affinis* (Hornsch.) Mönk., Laubm. Eur. 360. 1927. TYPE: [Austria.] Windissmattrey Tauern, *Hornschuch s.n.* (lectotype, designated by Deguchi (1978), B).

Grimmia affinis var. *ramosissima* Nees & Hornsch., Bryol. Germ. 2: 144, Tab. XXI fig. 13b. 1827. *Grimmia affinis* var. *elongata* Nees & Hornsch. ex Huebener, Muscol. Germ. 709. 1833, nom. illeg. TYPE: [Austria.] Heiligenblut b. Dartl. [*Hornschuch s.n.*] (lectotype, here designated, BM).

Grimmia schimperi Bruch & Schimp. ex Müll. Hal., Syn. Musc. Frond. 1: 792. 1849. TYPE: Ethiopia. Gonder: Semen Mts., 1842, *W. Schimper s.n.* [Schimperi iter abyssinicum, Sectio II, n° 484. 1842] (lectotype, here designated, NY; isolectotype, PC).

Grimmia neilgherriensis Müll. Hal., Bot. Zeitung (Berlin) 11: 62. 1853. TYPE: India. Tamil Nadu: in montibus Neilgheriensibus [Nilghiri Hills], *Perrottet 1583* (lectotype, here designated, PC; isolectotype, PC).

Grimmia columbica De Not., Mem. Reale Accad. Sci. Torino, ser. 2, 18: 447, fig. 7. 1859. TYPE: [Ecuador. Napo:] ad rivum Napo, *Osculati s.n.* (isotype, H-SOL).

Grimmia peruviana Sull., U. S. Expl. Exped., Musc. 8, Tab. 5A. 1860. TYPE: Peru. Andes, 15000 ft., *U.S. Ex. Ex. Wilkes [Rick & Brackenridge] s.n.* (lectotype, here designated, BM; isolectotypes, BM, FH, NY).

Grimmia bogotensis (Hampe) A. Jaeger, Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1872–73: 70 (Gen. Sp. Musc. 1: 352). 1874. *Guembelia bogotensis* Hampe, Linnaea 32: 142. 1863. TYPE: Colombia. Cundinamarca: Bogotá, Los Laches, 2800 m, July 1859, *Lindig 2011* (lectotype, here designated, PC; isolectotype, NY).

Grimmia hausmanniana De Not., Cronac. Briol. Ital. 2(2): 16. 1866. *Racomitrium hausmannianum* (De Not.) Molendo, Ber. Naturhist. Vereins Passau 10: 127. 1875. *Grimmia ovata* subsp. *hausmannii* Kindb., Eur. N. Amer. Bryin. 2: 227. 1898. *Grimmia ovalis* f. *epilosa* Podp., Conspectus Muscorum Europaeorum, 278. 1954, nom. illeg., non Warnst. 1904. TYPE: [Austria. Tirol:] Rittner Horn, *Hausmann s.n.* (isotype, BM).

Grimmia ovata var. *praecox* A. Kern., Flora exsiccata austro-hungarica n° 316, 1881. TYPE: [Austria. Tirol:] ad Trins in valle Gschnitz, 1200 m, *Kern 316* (lectotype, here designated, BM).

Grimmia integridens Müll. Hal., Linnaea 43: 460. 1882. TYPE: Argentina. Tucumán: in der Cienaga, ca. 11000′, 1893, *Lorentz s.n.* (lectotype, here designated, PC).

Grimmia leucophaeola Müll. Hal., Linnaea 43: 456. 1882. TYPE: Argentina. Tucumán: Tafi, 1872, *Lorentz s.n.* (lectotype, here designated, JE; isolectotypes, BM, JE, NY).

Grimmia raphidostega Müll. Hal., Linnaea 43: 459. 1882. TYPE: Argentina. Salta: Nevado de Castillo, 1873, *Lorentz s.n.* (lectotype, here designated, JE).

Grimmia vernicosula Müll. Hal., Linnaea 43: 458. 1882. TYPE: Argentina. Salta: Orán, *Lorentz s.n.* (lectotype, here designated, JE; isolectotype, BM).

Grimmia cavifolia Lindb. & Arnell, Kongl. Svenska Vetenskapsakad. Handl. 23(10): 103. 1890. TYPE: [Russia. Krasnoyarsk Oblast:] Jenisei, Krasnojarsk, 11 June 1876, *Arnell s.n.* (lectotype, here designated, H-SOL; isolectoypes, JE, PC, UPS).

Grimmia nano-globosa Müll. Hal. ex E. Britton, Bull. Torrey Bot. Club 23: 477. 1896. TYPE: Bolivia. La Paz: Mapiri, 5000 ft., May 1886, *Rusby s.n.* (holotype, NY).

Grimmia ortholoma Kindb., Rev. Bryol. 23: 19. 1896. TYPE: Canada. British Columbia: Dear Park, 8 June 1890, *Macoun s.n.* (holotype, S; isotype, S).

Grimmia breviexserta Müll. Hal., Bull. Herb. Boissier 5: 200. 1897. TYPE: Guatemala. Quezaltenango: Quezaltenango, *Bernoulli & Cario 115* (lectotype, here designated, PC).

Grimmia micro-ovata Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 4: 128. 1897. TYPE: Bolivia. Cochabamba: prope

Choquecamata, June 1889, *Germain 1142* (lectotype, here designated, JE; isolectotype, NY).

Grimmia subovata Schimp. ex Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 4: 128. 1897. TYPE: Bolivia. Larecaja: vicinitis Sorata, Ancouma, hacienda Peñas, 3700–4000 m, Apr. 1860, *Mandon 1634* (lectotype, here designated, BM; isolectotype, BM 2 replicates, FH, G).

Grimmia arctophila subsp. *labradorica* Kindb., Eur. N. Amer. Bryin. 2: 221. 1898. TYPE: Canada. Labrador: 21 July 1896, *Macoun s.n.* (lectotype, here designated, S; isolectotype, CANM 198076).

Grimmia itatiaiae Müll. Hal., Bull. Herb. Boissier 6: 109. 1898. TYPE: Brazil. Minas Gerais: Serra do Itatiaia, Agulhas-Negras, 2300 m, Mar. 1894, *Ule 1830* (lectotype, here designated, H-BR).

Grimmia itatiaiensis Broth. ex Müll. Hal., Bull. Herb. Boissier 6: 108. 1898. TYPE: Brazil. Minas Gerais: Serra do Itatiaia, 2100 m, Mar. 1894, *Ule 1913* [Ule & Brotherus, Bryotheca brasiliensis, n° 124] (lectotype, here designated, H-BR; isolectotypes, GOET, JE, NY, PC, UPS).

Grimmia elata Kindb., Rev. Bryol. 32: 33. 1905. TYPE: Canada. Yukon: Hunker creek, 25 July 1902, *Macoun s.n.* (lectotype, here designated, S; isolectotypes, CANM 198084, H-BR).

Grimmia ovataeformis Kindb., Rev. Bryol. 32: 35. 1905. TYPE: Canada. British Columbia: lake Louise, 6000 ft., 13 Sep. 1904, *Macoun s.n.* (holotype, S; isotype, CANM 198092).

Grimmia praetermissa Cardot, Rev. Bryol. 36: 105. 1909. TYPE: Mexico. México: In the crater of the Volcano of Toluca, 13,500 ft., 25 Sep.1892, *Pringle s.n.* [Pringle, Plantae mexicanae n° 26a] (lectotype, here designated, NY; isolectotypes, JE, PC 2 replicates).

Grimmia herzogii Broth., in Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: [Bolivia. Cochabamba:] An Felsen eines Gipfel der Yanakakabastion, 4500 m, Juli 1911, *Herzog 3826* (lectotype, designated by Deguchi (1987), JE; isolectotype, H-BR).

Grimmia nigella Herzog, Biblioth. Bot. 87: 55, fig. 17. 1916. TYPE: Bolivia. Bei der Saittulaguna, 4300 m, June 1911, *Herzog 2679* (lectotype, here designated, JE).

Grimmia speirophylla f. *humilis* Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: Bolivia. Cochabamba: Torreni-Yanakaka, July 1911, *Herzog s.n.* (holotype, JE).

Grimmia speirophylla Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: Bolivia. Cochabamba: Yanakakabastion, 4500 m, June 1911, *Herzog 3827* (lectotype, here designated, JE; isolectotype, JE). SYNTYPES: *Herzog 4871* (JE); *Herzog 3148* (JE); *Herzog 4811* (NY, PC).

Grimmia allionii Broth., Rev. Bryol. 47: 9. 1920. TYPE: [Ecuador.] Azuay: In rupibus montis prope Cañar, 3400 m, 16 Nov. 1909, *Allioni s.n.* (lectotype, here designated, H-BR; isolectotypes, H-BR, PC).

Grimmia afro-ovata Broth. & Thér., Bull. Mus. Hist. Nat. (Paris) 30: 240. 1924. TYPE: Kenya. Kilimanjaro: Kilimanjaro, *Alluaud s.n.* (lectotype, here designated, PC; isolectotype, H-BR).

Grimmia catalinensis E. B. Bartram, Bryologist 27: 62, Pl. 10. 1924. TYPE: U.S.A. Arizona: Pima Co., ravine near top of Mt. Lemon, Santa Catalina Mountains, 9000 ft., 15 Jan. 1923, *Bartram 387* (holotype, FH; isotypes, FH, NY).

Grimmia catalinensis var. *mutica* E. B. Bartram, Bryologist 27: 62. 1924. *Grimmia ovalis* f. *mutica* (E. B. Bartram) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 34. 1933. TYPE: U.S.A. Arizona: Santa Cruz Co., White House Canyon, Santa Rita Mountains, 5500 ft., 18 Feb. 1923, *Bartram 683B* (holotype, FH).

Grimmia trollii Herzog, Hedwigia 74: 102. 1934. TYPE: Bolivia. Oruro: Curahuara, *Troll 58* (lectotype, designated by Deguchi (1987), JE).

Grimmia cinerea Thér., Rev. Bryol. Lichénol. 9: 9, fig. 3. 1936. TYPE: Ecuador. Pichincha: rochers du Condorguachana, 4150 m, 4 Nov. 1930, *Benoist 3153* (holotype, PC).

Grimmia stenopyxis Thér., Rev. Bryol. Lichénol. 9: 8. 1936. TYPE: Ecuador. Pichincha: Pichincha, 24 Oct. 1930, *Benoist s.n.* (lectotype, here designated, PC).

Grimmia sumatrana Dixon, Ann. Bryol. 12: 50. 1939. TYPE: "G. Losir, 3250–3500 m, 4 Feb. 1937; *van Steenis (10152)*; Hb. Bog (4035) [Buitenzorg Botanical Garden] (Syntype, fide Deguchi (1986), L not seen).

Grimmia antillarum Thér., Rev. Bryol. Lichénol. 13: 13. 1944. TYPE: Dominican Republic. Azua: Cordillera Central, Los Vallecitos de Yaque, 2500 m, 2 Oct. 1929, *Ekman 13630* (lectotype, here designated, PC; isolectotype, NY).

Grimmia akaisi-alpina Takaki, Bot. Mag. (Tokyo) 64: 180, fig. 4. 1951. TYPE: [Japan.] South Alps, Sensui pass, 2700 m, 15 Aug. 1950, *Takaki 10137* (holotype, private herbarium of Takaki, not seen).

Grimmia maido Greven, Bryologist 99: 428, fig. 1. 1996. TYPE: Africa. La Réunion: Le Maïdo, at the end of RF 8, 2150 m, 7 Oct. 1995, *Greven & Khoebal 4000/1* (isotype, MO).

Autoicous. Plants forming dense cushions, yellowish green, olive-green to dark green, occasionally rusty, golden yellowish above, brownish to black below, occasionally hoary due to long hair-points of the leaves, only rarely muticous. *Stems* erect, to 3 cm high × 160–220 μm diam., central strand well developed. *Leaves* usually erect and appressed, not flexuous when dry (larger plants can have more flexuous leaves), erect to erect-spreading, rigid when moist, 1.7–2.6 mm long (exclusive of hair-point) × 0.3–0.6 mm wide, lanceolate to ovate-lanceolate, acute, not or weakly keeled, not plicate; *hyaline hair-points* terete, from erect and rigid to moderately flexuous, to 2 mm long, smooth or slightly denticulate; *margins* entire, recurved on one side to ½–⅔ their length, elsewhere plane, seldom recurved on both sides; *costa* percurrent, scarcely prominent on dorsal surface on the upper half of leaves, *in section semi-elliptical to reniform, curved and with the ventral sinus U-shaped,* not always clearly delimited from laminal cells, especially in the 2-stratose upper part of the leaf, *at midleaf with 2–4 ventral guide cells, a medial layer composed of substereids, and a dorsal epidermis, the three layers not clearly differentiated from each other,* usually only the ventral layer composed of large cells, clearly differentiated from the other two, the latter more obscurely delimited from each other; *lamina* 2(3)-stratose in the upper ½, more regularly 2-stratose with 3(4)-stratose areas toward the margins; *upper cells* 4–11 μm along their longest axis, isodiametric, rectangular and transversely rectangular intermingled, incrassate and somewhat sinuate, if long rectangular then more strongly nodulose; *basal paracostal cells* 25–60(90) μm long × 7–13 μm wide, rectangular (3–7(11):1), with thick and nodulose walls; *basal marginal cells* 9–25 μm long × 6–11 μm wide, usually rectangular (1–3:1), hyaline, with straight walls, the transverse walls thicker than longitudinal ones.

Perichaetial leaves convolute, 2.6–3.5 mm long × 0.6–0.7 mm wide, 3–5× larger than vegetative leaves, yellowish or hyaline at the base; *hyaline hair-points* as in vegetative leaves but longer, to 3 mm. *Androecia* terminal, in inflated perigonial buds. *Setae* erect, straight, seldom weakly arcuate, 1–4(5) mm long (including the vaginula). *Capsules* immersed to long-exserted, ovoid to cylindric, 1.0–2.5 mm long × 0.5–0.7 mm wide, smooth, with 7–15 stomata at the base, yellowish when deoperculate, chestnut when empty; *exothecial cells* 18–50 μm long × 18–20 μm wide, mostly rectangular (2:1), although many isodiametric intermingled, with thin walls; *annuli* well developed, compound and revoluble, consisting of 3–4 rows of inflated, hyaline cells; *peristome teeth* 50–80 μm wide at the mouth, entire or fairly broken at the apex, the outer surface nearly smooth below, papillose above, the inner surface papillose throughout, orange to reddish, contrasting in color with the rest of the sporophyte (in recently deoperculate capsules that preserve intact peristome); *opercula* from mammillate to long-rostrate, beak straight, in some populations 0.75 mm long, red. *Calyptrae* mitrate, seldom cucullate, covering only the opercula. *Spores* 8–12 μm, granulose.

Illustrations. Figure 1; Afonina (1986: Ris. 1 figs. 1–8, *sub G. affinis*; Ris. 2 figs. 9–16, *sub G. ovalis*); Cao & Churchill (1995: plate 1); Cao & Vitt (1986: figs. 1, 2); Deguchi (1978: figs. 12, 13; 1984: fig. 6; 1987: figs. 6, 7); Ignatov & Cao (1994: fig. 7); Ireland (1982: pl. 134); Jóhannsson (1993: fig. 36); Maier & Geissler (1995: Abb. 1).

Distribution (Fig. 2). *Grimmia longirostris* is known from the Americas, Eurasia, and Africa, and is not known from Australia and Antarctica. It ranges altitudinally from 530 m at Lake Baikal in Irkutsk to 5300 m at Mururata in Bolivia. It grows on dry and exposed siliceous rocks, mostly above tree line, but also at lower elevations at high latitudes.

Representative specimens examined. U.S.A. **Alaska:** Alaska Range District, Healy Quadrangle, along Denali Highway at Savege River, *Hermann 21555* (BM). **Arizona:** Santa Cruz Co., Baldy Trail, Santa Rita Mountains, *Bartram 1276* (NY). **California:** San Diego Co., ca. 9 mi. from Warner Springs, *Allen 648* (MO). **Colorado:** Rocky Mt. Nat. Park, SW slope of Deer Mountain, *Hermann 27789* (BM). **Hawaii:** Maui, Haleakala National Park, narrow ravine 50 m E of Hosmer's Grove, *Hoe 3462.0* (NY). **Minnesota:** [locality illegible] 10 Aug. 1902, *Bullard s.n.* (FH). **Montana:** Madison Co., 12 mi. E of Ennis, *Hermann 17937* (S). **New Mexico:** Santa Fe Co., Santa Fe Canyon, 14 Oct. 1930, *Arsène s.n.* (FH). **Oregon:** Wasco Co., The Dalles, Sep. 1933, *Frye s.n.* (MO). **South Dakota:** Pennington Co., Black Hills, along Pine Creek, just W of Mount Rushmore, *Churchill 8186* (IBA-7361). **Texas:** Jeff Davis Co., St. Davis, *Orcutt 7073* (FH). **Vermont:** Newfane Mt., 27 Aug. 1902, *Grout s.n.* (FH). **Wyoming:** Sheep Mt., *Goodding 2101* (FH). CANADA. **British Columbia:** head of Summit Lake above Fort Nelson (near mile 108), *Correll 11990* (FH). **Labrador:** Churchill Falls, Bridge Camp area, *Brassard 6511* (BP-156326). **Northwest Territories:** Baffin Island, Pangnirtung, *Polunin 2611A20* (FH); Hunter Bay, E of Sloan River, E end of McTavish Arm, Great Bear Lake, 31 July 1948, *Steere s.n.* (H). **Ontario**: Muskoka Dist. Mun., Foot's Bay, ca. 9 km S of Freeman Township along Moon River, *Ireland 23944* (FH). **Québec:** Ungava Bay, valley slope and rolling upland N of Leaf River and 100 miles from Leaf Bay, 18 Aug. 1948, *Marr s.n.* (FH). **Yukon:** Hunker Creek, 25 July 1902, *Macoun s.n.* (S). **Alberta:** Mount Aylmer, 6 Aug. 1891, *Macoun s.n.* (NY). CHILE. Andes (FH-Sull). GREENLAND. Jacobshavn, Grönland, 1883, *Hastrüp s.n.* (FH); Südgrönland, Narssarssuaq, Fjellgebiete zwischen Qoroq Fjord und Kiagtut Gletscherzunge, 26 Aug. 1979, *Frahm s.n.* (IBA-5072). MEXICO. **Durango:** below El Salto, *Sharp 1833* (FH). **México:** 1.5 km de la desviación al E de Techuchulco, *Castilla 1983* (MO). **Hidalgo:** Dublan, *Pringle 15076* (JE). **Jalisco:** ladera N del Nevado de Colima, 27 July 1983, *Delgadillo s.n.* (ALTA). **Michoacán:** Paracho, about 6 km N on way to Cherán, *Frey 3072* (FH). **Puebla:** ladera NW del Pico de Orizaba, 22 Apr. 1980, *Delgadillo s.n.* (ALTA). **Territorio de Baja California Sur:** summit of Sierra de La Laguna, about 15 mi. E of Todos los Santos, *Delgadillo et al. 3093* (FH). **Veracruz:** cima del Cofre de Perote, 7 Dec. 1979, *Delgadillo s.n.* (ALTA). **Zacatecas**: Cerro de la Bufa, 9 June 1979, *Cárdenas s.n.* (ALTA). GUATEMALA. **Quezaltenango:** Cerro La Pedrera, S of Quezaltenango, *Standley 65530* (FH). **Sacatepéquez:** slopes of Volcán de Agua, above Santa María de Jesús, *Standley 65262* (FH). HONDURAS. **Lempira**: Montaña Celaque, summit of Cerro Mojón, *Allen 12260* (MO). COSTA RICA. **Cartago:** near

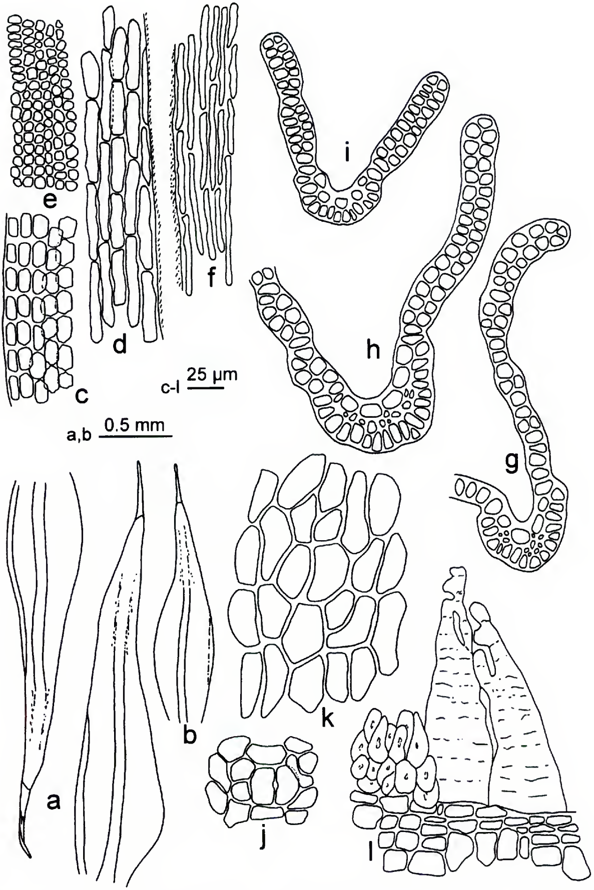

Figure 1. *Grimmia longirostris.*—a, b. Leaves.—c. Basal marginal leaf cells.—d, f. Basal paracostal leaf cells.—e. Apical leaf cells.—g. Transverse section at basal part of leaf.—h. Transverse section at medial part of leaf.—i. Transverse section at apical part of leaf.—j. Basal exothecial cells and stoma.—k. Medial exothecial cells.—l. Annulus and peristome teeth (only contour shown, not papillosity). (b, f: isotype of *Grimmia columbica*, H-SOL; a, c–e, g–i: *Redfearn 34610*, MO; j–l: *Liu 952096*, MO).

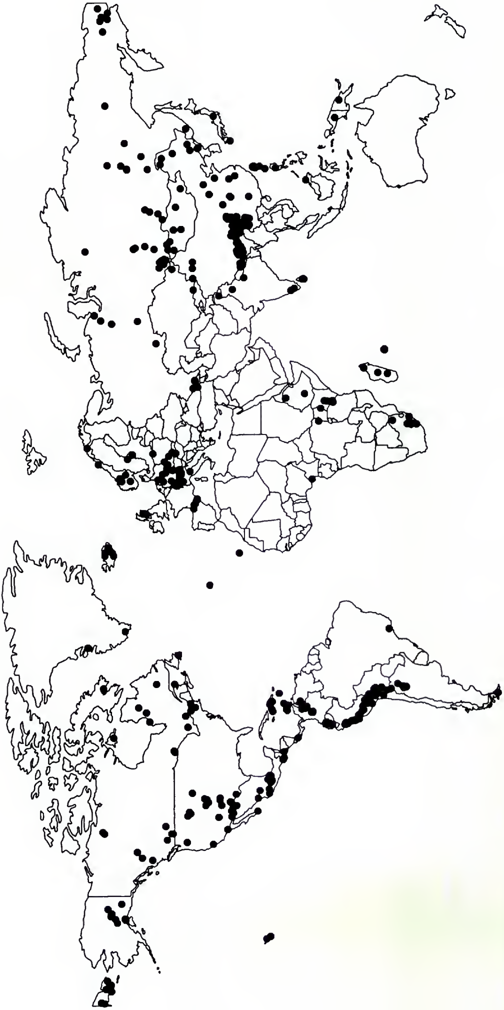

Figure 2. World distribution of *Grimmia longirostris* based on specimens studied.

summit of Inter American Highway at La Ascensión, *Crosby & Crosby 6137* (MO). DOMINICAN REPUBLIC. **La Vega:** 6.3 km S of Valle Nuevo, *Steere 23052* (G). **San Juan:** summit of Pico Duarte, *Buck 8396* (NY).

COLOMBIA. **Cundinamarca:** Bogotá, Los Laches, *Lindig 2011* (PC). **Boyacá:** near the Ritacuba glacier, Sierra Nevada de Cocuy, *Grubb & Guymer B.210* (BM). **Santander:** Páramo Frailejonale, near Vetas, *Killip & Smith 17987* (BM). VENEZUELA. **Mérida:** Distrito Libertador, Sierra Nevada de Mérida, near Laguna de Los Anteojos just below the loma Redonda station, *Griffin et al. 398* (NY); Distr. Rivas Dávila, páramo La Negra, above the town of Bailadores, *Griffin et al. 2047* (NY). ECUADOR. **Pichincha:** Pichincha, *Bell 154* (IBA-4721). **Napo:** Cerro Antisana, *Grubb 2500* (FH). PERU. **Ancash:** Huaraz Province, Monterrey bei Huaraz, *Hegewald & Hegewald 7482* (MO). **Apurimac:** Andahuaylas Province, Pampa Runtojocha bei Chincheros, *Hegewald & Hegewald 5761* (MO). **Cajamarca:** Contumazá Province, 2 km südlich Contumazá, *Hegewald & Hegewald 7280* (MO). **Ayacucho:** Provincia Wanda [Huanta], alrededores de Wanda [Huanta], *Vargas 15863* (NY). **Cuzco:** Provincia Canas, El Descanso, *Vargas 10039* (FH). **Junín:** Jauja Province, La Oroya, Laguna Mesapata bei Canchayllo, *Hegewald & Hegewald 5375* (MO). **La Libertad:** Otuzco Province, Huancamarca, Quebrada Hornillo, *Hegewald & Hegewald 5156* (MO). **Lima:** Canta Province, 2 km vor Canta an der Straße nach Lima, *Hegewald & Hegewald 7425* (MO). **Puno:** Miajachi, Huancané, *Aguilar 150* (FH). BRAZIL. Rio de Janeiro, Serra de Itatiaia, Mar. 1894, *Ule s.n.* (GOET). BOLIVIA. **Cochabamba:** 28 km NW of Cochabamba, NW slope of Mt. Tunari, near Liriuni Aguas Termales Hotel, *Hermann 25149* (ALTA). **Amasuyos:** vicinitis Achacache, Padchani, *Mandon 1635* (BM). **La Paz:** Inquisivi Province, km 2 above Quime, *Lewis 87-958* (MO); Mururata, Sep. 1924, *Jaffuel s.n.* (FH). **Larecaja:** vicinis Sorata, Ancouma, hacienda Peñas, *Mandon 1634* (BM). ARGENTINA. **Tucumán:** Tafi, cumbre del Potrerillo, *Lamb 5288* (FH). **Tierra del Fuego:** lac Cami, base de la Chaloupe, *Skottsberg 370* (PC).

ICELAND. E-Iceland, Egilsstadir, *Aptroot 4961A* (NY). Northeast Iceland, Asbyrg, a glacial valley between Mývatn and Akureyri, 7 July 1964, *Steere s.n.* (NY). S-Iceland, Kirkjubaeklaustur, *Aptroot 4939* (NY). NORWAY. Hamar, Stift Foldaleu, Laughö, 20 July 1890, *Conradi s.n.* (TRH); Trondheim, Stift Dovre, Kongsvold, 24 July 1890, *Conradi s.n.* (TRH); in canyon of Skibotelva River about 20 km from Skibotn, Storfjord, Troms, *Norris 69524* (MO). SWEDEN. Gestriciae [Gästrickland], *Hartman* (H); Holmiam [Stockholm], *Hartman* (H). RUSSIA. **Tomsk Oblast:** Bijskij u., *Kusnezow 2066* (LE). **Krasnoyark Kraj**: Minusinsk, May 1888, *Martinoff s.n.* (H-BR). **Yakutsk A.S.S.R.:** middle course of Indigirka river, near mouth of In'yali Creek, 23 June 1976, *Afonina s.n.* (LE). **Magadan Oblast:** Chukotka, Lake Achchen, 30 July 1970, *Afonina s.n.* (LE). **Gorno Altayskaya Autonomous Oblast:** Altai Mountains, Kayakkatuyarykskij Creek, *Ignatov 8/48* (IBA-7039). **Irkutskaya Oblast:** lacus Bajkal, super pago Bolšije Koty, 16 Aug. 1982, *Pujmanová s.n.* (NICH-391992). **Primorskij Kraj:** Sovetskij rajon, p. Murtto, 25 Aug. 1945, *Kolesnikov s.n.* (LE). **Stavropol' Kraj:** Klukhorskij rajon, Teberda, Teberdinskij Reserve, 17 Aug. 1955, *Abramova & Abramov s.n.* (LE). UNITED KINGDOM. **Scotland:** Arthur's Seat, Edinburgh, Aug. 1866, *Hunt s.n.* (NY). GERMANY. Harz, Falkenstein, 25 July 1898, *Vocke s.n.* (GOET); Pöhlberges b. Annaberg, *Weicker* (FH); Sylvae Nigrae (Hollinthal), 1824, *Braun s.n.* (BM); Westfalen, Rüthen, 13 Jan. 1862, *Müller s.n.* (BP-36103). POLAND. Probsthainer Spitzberges bei Bunzlau, 23 Apr. 1867, *Limpricht s.n.* (FH); Sudeten, *Kaulfuss s.n.* (BM). FRANCE. St. Etienne de Baigorry, 9 May 1908, *Fleischer s.n.* (FH); Vogesen, Dép. Haute-Saône, straße von Col de Croix zum Ballon de Servance, *Frahm 935069* (IBA-5048). SWITZERLAND. Kanton Bern, Gasteren, 3 Sep. 1910, *Culmann s.n.* (IBA-2643); Susten, 25 Aug. 1907, *Culmann s.n.* (BM). AUSTRIA. **Kärnten:** Ublizen in Pölla Alpen, 19 Aug. 1901, *Glowacki s.n.* (JE). **Salzburg:** Alpen, *Funck s.n.* (JE). **Steirmark:** Libija Graben bei Traßberg, 2 Aug. 1898, *Glowacki s.n.* (JE). **Tirol:** ad margines rivi Oetztaler pr. pag. Oetztal, 30 July 1923, *Vajda s.n.* (BP-159024). CZECH REPUBLIC. **Böhmen**: Leitmeritz, Eisberges, Apr. 1901, *Schmidt s.n.* (IBA 5361). **Morava:** Jesenik, Vrbno, July 1949, *Duda s.n.* (BP-159134b). SLOVAKIA. Mala Fatra, prope ruinam Stary hrad, Pilous s.n. June 1935 (BP-112583). PORTUGAL. Azores, Fayal, May 1937, *Persson s.n.* (NY). SPAIN. **Álava:** Sur de Umandia, 7 Sep. 1982, *Heras s.n.* (IBA-1018). **Lérida:** Coll de Cantó, 9 Sep. 1981, *Casas s.n.* (IBA-3965). **Santa Cruz de Tenerife:** Tenerife (BM). ITALY. Südtirol, Kastelruth-Sankt Michael, 25 June 1984, *Heimhold s.n.* (GOET); Vallvellena, *Garovaglio* (RO). GEORGIA. Distr. Chokhatauri, vicinitas pagi Bakhmaro, mons Mzis-chasvlis-mta, 21 July 1980, *Vašák s.n.* (NY); in alpe Kasbek ad fl. Terek, *Brotherus & Brotherus 121* (H-SOL). KAZAKSTAN. **Alma Ata Oblast:** Turgen Gorge, *Allen 10849* (MO). **Semipalatinsk Oblast:** Altai, jug. Narymskij, 22 July 1899, *Ladygin s.n.* (MO). KIRGIZISTAN. **Issyk-Kul' Oblast:** Thian Schan Mts., ad fontes fl. Narym, 27 July 1896, *Brotherus s.n.* (FH). MONGOLIA. **Bulganskij aimak:** Gurvan-bulak somon, S Khugne-Khan, NW slope of Otroga Mt., 23 Nov. 1975, *Tsegmed s.n.* (LE). **Chobd-aimak:** Erdeneburen-somon, Namasuren-ul, *Schubert M183* (MO). **Ubsunurskij ajmak:** Turgen somon, N slope of Turgen Mt., *Tsegmed 248* (NY). **Chubsugul-Aimak:** Sumber-Uul, 19 July 1983, *Huneck s.n.* (JE). **Ubs-aimak:** Chanchöchi-ul, 5 km westlich Chiargas, *Schubert M295* (MO); about 7 km NW of Ulan Bator, head of small valley, *Jeffrey 1535* (BM). TURKMENISTAN. Prope Da-tzzjanj-en montes, 13 June 1893, *Potanin s.n.* (LE). PAKISTAN. Kashmir, Astor Valley, between Doyen and Harcho, 15 Aug. 1892, *Duthie s.n.* (H-BR). TIBET. Nielamu Co., *Zhao 117* (ALTA); Yadong Co., *Zang 373* (ALTA); Zhun Ba, Jie Bei, *Zang 1093* (KUN-3489); Milin Co., *Lang 658* (MO). CHINA. **Anhui:** Mt. Wuang, *D. Li 2227* (ALTA). **Guangxi:** Xingan Co., Mt. Miao Er, *Gao & Chang 1623* (ALTA). **Heilongjiang:** Mangui, *Gao 12896* (ALTA). **Jilin:** Mt. Chang Bai, *Aur 5091* (ALTA). **Shaanxi:** Taibai Co., Taibai Shan, *Li 642A* (MO). **Sichuan:** Songpan Co., hwy. Zhangla to Huanglong, *Redfearn 35234* (MO). **Hubei:** Shennongjia Forest District, vicinity of Xiaoshennongjia, *Bartholomew et al. 990* (FH). **Xinjiang Uygur:** Hejing Co., Gongnaisi Village, Tian Shan Range, *Zhao 953299* (MO). **Yunnan:** Dali Co., E-slope of Diancang Shan Mt. Range, vicinity of Qingbichi, *Redfearn Jr. et al. 1091* (FH). TAIWAN. Ilan Co., Mt. Nan-hu-ta-shan, *Peng Ching-I 83-31* (MO). NEPAL. Moraine droite du camp de base à Lobuje, 24 Apr. 1952, *Zimmermann s.n.* (G). JAPAN. Mt. Kitadake, Ashiyasumura, Nakakoma-gun, Yamaguchi Pref., 21 Aug. 1974, *Deguchi s.n.* (TNS-50119); Simozuke, Mt. Sirane, 13 July 1927, *Sasaoka s.n.* (BM). BHUTAN. *Griffith 127* (MO). INDIA. Kumáun, Kalámoni forest, 4 Aug. 1900, *Iráyot s.n.* (H-BR); Madras State, Madura District, Palni Hills, Kodaikanal and surrounding region, Kodaikanal, 1924, *Foreau s.n.* (MO); Nilghiri Hills (SW India), Doddabetta, 12 Sep. 1907, *Lülti s.n.* (H-BR); Simla, punjab Himalaya, Mahassu, *Doulea 3110* (H-BR). SRI LANKA. Central Province, *Thwaites CM29* (BM). MALAYSIA. **Sabah:** N Borneo, West Coast Res., Mt. Kinabalu, *Meijer B10389* (MO). PHILIPPINES. Luzon Island, Mountain Prov., summit of Mt. Pulog, *Tan 82-195* (FH). PAPUA NEW GUINEA. Eastern Highlands, Bismark Ranges, Mount Wilhelm, *Weber & McVean B-32146* (MO).

ETHIOPIA. Bale, Bale Mountains Natl. Park, Sanetti Plateau near the foot of Tullu Deemtu Peak, *Petelin 37-7* (MO). CAMEROON. Cameroun Mountain, Meoli Ndiva Ridge, Victoria Div., Western Province, *Brenan & Richards 4269* (MO). UGANDA. Between head of Butandiga ridge and Jackson's Summit, Mt. Elgon, N. Bugishu Co., Mbale district, Eastern Province, *Wood 1160* (NY). KENYA. Africa orient., Mt. Kenya, *Troll 5868* (JE). TANZANIA. **Arusha:** Arameru Dist., Mt. Meru, W side of cinder cone, just off trail from end of road from Forestry Training Institute, *Gereau 1649* (MO). **Kilimanjaro:** Mt. Kilimanjaro, near Peters Hut, *Hedberg 1238A* (MO). SOUTH AFRICA. Dolme Hill, Kaffraria, Cape Pr., *Sim 7218* (NY); Natal Drakensberg, Giants Castle Game Reserve, valley below Injasuti Summit Cave, *Rooy 1074* (NY); Transkei, Kwa Matiwana Mountains, NE of Umtata, slopes above Mlanlane Forest Station, *Rooy 2282* (NY). LESOTHO. Maloti Mountains, Moteng Pass (West), between Butha Buthe and Mokhotlong, *Rooy 3124* (MO); Sehlabathebe National Park, hills around sandstone outcrops E of Lodge, *Magill 4269* (MO). MADAGASCAR. Fianarantsoa, Andringitra summit of Anjavidilava, 37 km S of Ambulavao, *Crosby & Crosby 6980* (MO); Mt. Tsaratanana, Apr. 1924, *Perrier de la Bâthie s.n.* (H-BR). REUNION. Arrt. du Vent: Vicinity of "gite" at summit of trail up SW slopes of Cirque de Cilaos, near Caverne Dufour, 22 km S of E of St. Denis, *Crosby & Crosby 9648* (MO).

Grimmia longirostris can be identified with confidence by the shape of the costa in transverse section (Fig. 1g–i). It is reniform and curved, with both the ventral and dorsal surfaces concave. The ventral sinus is U-shaped. It is rather unfortunate that both Sayre (1952: 255) and Greven (1995: 24) neglected the importance of leaf cross sections as a source of taxonomic characters in *Grimmia.* From my studies I realized that information obtained from leaf cross sections is absolutely necessary to name some species correctly and extremely useful to name many others. In the case of *G. longirostris,* the leaf cross section alone serves to identify this taxon with certainty. The leaves of this species are usually described as keeled, but I reserve this term for laminae that are V-shaped in cross section, not U-shaped, as in *G. longirostris.* Characters that give additional support to the identification are long, incrassate, and nodulose basal paracostal cells, the straight seta, and the usually cylindrical capsules with a compound, revoluble annulus of rectangular hyaline cells.

Grimmia longirostris is widely distributed and varies accordingly. Most of this variation involves quantitative features that totally overlap in measurements. Length of setae, capsules, and opercula vary broadly, but there are no correlations among these or with other taxonomic features. Specimens distributed by Sullivant and Lesquereux in their "Musci boreali-americani ed. 2," nº 214, for example, have both long and short setae in the same cushion. Consequently some capsules are relatively long-exserted, whereas others are included among the perichaetial leaves. Populations with immersed capsules from the southwestern United States were denoted as *G. catalinensis* E. B. Bartram, and from China as *G. subimmersa* Broth. (*nom. nud.*). Deguchi (1987: 27) discussed the variation in operculum length and concluded that it is not correlated with other characters.

Hair-point length is, as in many other Grimmiaceae, quite variable. Some taxa were described on the basis of muticous morphs of *G. longirostris* (e.g., *G. hausmanniana* De Not. from the European Alps, and *G. catalinensis* var. *mutica* E. B. Bartram from the southwestern United States).

Cao and Vitt (1986) have previously reported wide variability in all these quantitative characters. They discussed and illustrated seta, capsule, and operculum length variability in Chinese specimens of *G. longirostris* (as *G. affinis* Hornsch.).

Grimmia longirostris also shows variability with regard to some qualitative characters. The calyptrae are usually mitrate, but occasionally also cucullate, even in the same cushion. Some populations, especially from South America, show a rope-like disposition of leaves around the stem, much like *G. funalis* (Schwägr.) Bruch & Schimp. This feature is especially pronounced in Bolivian plants that have been named *G. speirophylla* Herzog and Ecuadorian populations on which *G. columbica* De Not. was based, but there is no correlation between this feature and other sporophytic or gametophytic characters.

In North America *G. longirostris* is more abundant along the Alaskan Range, Sierra Nevada, and the Rocky Mountains in the west and the Adirondacks in the east, with scattered localities in Québec, Newfoundland, the Northwest Territories, and Ontario in Canada. It is absent from the Interior Highlands, the Appalachian Mountains, and most of the interior of Canada.

Southward, *Grimmia longirostris* is a common plant of the high altitudes of the southern part of the Sierra Madre Occidental and transverse ranges between Veracruz and Jalisco states, Mexico. Collections from Guatemala, Honduras, and Costa Rica are from the highest mountains of these countries. *Grimmia longirostris* also grows on several

Caribbean Islands, with most records from high altitudes in Hispaniola.

In South America it is common along the Andean range north of 28°S, with a disjunct locality at Serra do Itatiaia, near Rio de Janeiro in Brazil, and another in South Patagonia. Other localities in the intervening Andean areas are to be expected, where conditions are suitable for *G. longirostris*.

African collections have been made mostly in the ranges along the east coast, with only one disjunct western locality on Mt. Cameroun. This distribution agrees with White's (1978, 1993) pattern of Afromontane vegetation "islands," with a more or less continuous corridor formed by the six main East African ranges (Ethiopian, Usambara, Kivu-Ruwenzori, Uluguru-Mlanje, Chimaimani, and Drakensberg) and disjunct, outlier populations in high elevations of western Africa. The intervening lowland areas, dominated by savanna or tropical rainforest, lack the conditions for the establishment of Afromontane vegetation. *Grimmia longirostris* has not been recorded from the Chimanimani or Uluguru-Mlanje systems; however, its presence in Drakensberg and the northern Ethiopian and Usambara systems suggests that it may be found there. Malagasy collections fit the proposed distribution of Afomontane vegetation for Madagascar (White, 1978). *Grimmia longirostris* may yet be found in the high elevations of the Atlas Mountains in Morocco and Algeria, where conditions are apparently appropriate.

In Europe, *G. longirostris* is rare toward the south, growing only in scattered localities in the Pyrenees and the Caucasus. In central Europe it is relatively common, mostly associated with the Alps and the Carpathian Mountains. It is also known at higher latitudes, in Scotland and Fennoscandia.

In mainland Asia, *Grimmia longirostris* is common along the main Siberian mountain systems and along the Himalayas, Tian Shan, and the Tibetan Plateau.

In tropical Asia, *G. longirostris* is restricted to the highest peaks of the Nilgiri Hills in India, central Sri Lanka, Mt. Kinabalu in Borneo, northern Luzon in the Philippines, New Guinea, and Taiwan.

Strikingly, I was not able to find *Grimmia longirostris* among the Australian and New Zealand collections studied. This is surprising since other common *Grimmia* species, viz., *G. pulvinata* (Hedw.) Sm. and *G. trichophylla* Grev., grow in both areas, where the environmental conditions should likewise support *G. longirostris*.

In this study I have found the following heterotypic names to be new synonyms of *Grimmia longirostris*: *G. affinis*, *G. affinis* var. *ramosissima*, *G. afro-ovata*, *G. allionii*, *G. antillarum*, *G. arctophila* subsp. *labradorica*, *G. breviexserta*, *G. catalinensis* var. *mutica*, *G. columbica*, *G. elata*, *G. hausmanniana*, *G. herzogii*, *G. integridens*, *G. itatiaiae*, *G. leucophaeola*, *G. maido*, *G. nano-globosa*, *G. neilgherriensis*, *G. nigella*, *G. obliqua*, *G. ortholoma*, *G. ovata* var. *praecox*, *G. peruviana*, *G. praetermissa*, *G. raphidostega*, *G. schimperi*, *G. speirophylla*, *G. speirophylla* f. *humilis*, *G. stenopyxis*, *G. subovata*, *G. trollii*, *G. vernicosula*. The following species had been previously considered synonymous with *G. longirostris* or *G. affinis*: *G. bogotensis* (Churchill, 1994), *G. cinerea* (Churchill, 1994), *G. itatiaiensis* (Cao & Churchill, 1995), *G. micro-ovata* (Deguchi, 1987), *G. ortholoma* (Allen, 1995), *G. stenopyxis* (Cao & Churchill, 1995), and *G. sumatrana* (Deguchi, 1986).

The following names had been considered synonyms of *Grimmia ovalis* (Hedw.) Lindb., a species that can be separated from *G. longirostris* by its plane margins and its indistinct costa in the distal half of the leaf: *G. akaisi-alpina* (Takaki et al., 1970); *G. catalinensis* E. B. Bartram (Jones, 1933); *G. cavifolia* (Ignatov & Cao, 1994); *G. ovataeformis* Kindb. (Allen, 1995).

The nomenclature around *Grimmia affinis* has a tortuous history. Three names must be kept in mind: *Grimmia apiculata* Hornsch., *G. affinis* Hornsch., and *G. ovalis* (Hedw.) Lindb. The problems concerning the relationship and differentiation between the two latter species were resolved by Sayre (1951). There is one dioicous taxon, *Grimmia ovalis* (Hedw.) Lindb., and another autoicous taxon, for which Sayre (and most authors thereafter) used the name *G. affinis* Hornsch. But the latter name is an illegitimate homonym that cannot be employed, according to the ICBN (Greuter et al., 1994), because it was applied to two different taxa in two separate issues of the same journal (Hornschuch, 1819a, 1819b).

Hornschuch employed the epithet *affinis* in the first issue of the journal (Flora 19: 85, published 14 Feb. 1819) to describe the taxon currently known as *G. apiculata*, which has an arcuate seta. The same name was again employed by Hornschuch in the second issue of the same journal (Flora 19: 443, published 28 July 1819) to describe the species with a straight seta, for which the epithet *affinis* has been widely used, and he changed the name of the first *G. affinis* to *G. apiculata*. The name change by Hornschuch was not the result of some printing error or mistake (Hornschuch, 1819b: 442). Thus, according to the ICBN (Greuter et al., 1994: art. 51), *G. apiculata* is an illegitimate name because when published it was a superfluous name for the previous valid and legitimate *G. affinis* (curved seta). The second *G. affinis* (straight seta) became an illegitimate homonym, and thus inapplicable (Greuter et al., 1994: art. 53).

All the above problems concerning the use of the name *G. affinis* were pointed out by Mårtensson (1956: 117–118), who hesitated to employ this name for the autoicous plant with a straight seta here recognized as *G. longirostris*. Even without having seen the second Hornschuch paper, Mårtensson was correct in considering the second *Grimmia affinis* (*G. longirostris* in the sense of this paper) as illegitimate. Later, Deguchi (1978: 161) justified his use of the illegitimate name by citing art. 64 of ICBN (Seattle Code, Stafleu et al., 1972), which corresponds with article 53 of the current Tokyo Code. Presumably, he based his argument on the last provision of this article (corresponding with the current art. 53.6, Tokyo Code), assuming that both names were published simultaneously. This is not, however, the case (cf. Sayre, 1959); actually, one was published five months earlier.

NOMINA NUDA (ONLY NAMES ACTUALLY PUBLISHED EITHER IN LITERATURE OR IN EXSICCATAE)

Grimmia commutata f. *brevipila* Broth., in sched. Musci turkestanici, nº 49. 1899.

Grimmia leucophaeoides Müll. Hal. ex Kindb., Enum. Bryin. Exot., Suppl. 1: 91. 1889.

Grimmia micromitria Schimp. ex Müll. Hal., Nuovo Giorn. Bot. Ital. n.s. 4: 165. 1897.

Grimmia obliquata Host ex Brid., Bryol. Univ. 1: 180. 1826.

Grimmia ovata f. *glacialis* P. de la Varde, Ark. Bot., n.s. 3: 147. 1955.

Grimmia preussii Broth. ex Paris, Index Bryol. Suppl.: 175. 1900.

Grimmia semipilosa Hampe ex Müll. Hal., Linnaea 43: 461. 1882.

Grimmia subovata Schimp. ex Müll. Hal., Linnaea 43: 461. 1882.

Grimmia subovata var. *laevipila* Schimp. ex Paris, Index Bryol. 2: 538. 1895.

Grimmia tenuicaulis Hampe ex A. Jaeger, Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1872–73: 72 (Ad. 1: 354). 1874.

Literature Cited

Afonina, O. M. 1986. Additamenta ad bryofloram peninsulae Czukotka. 4. Novosti Sist. Nizsh. Rast. 23: 222–228.

Allen, B. 1995. Eight neglected species of Grimmiaceae (Musci) from North America. Fragm. Florist. Geobot. 40: 159–166.

Blom, H. H. 1996. A revision of the *Schistidium apocarpum* complex in Norway and Sweden. Bryophyt. Biblioth. 49: 1–333.

Cao, T. & S. P. Churchill. 1995. New synonyms in *Grimmia* and *Schistidium* (Bryopsida: Grimmiaceae). Nova Hedwigia 60: 505–513.

——— & D. H. Vitt. 1986. A taxonomic revision and phylogenetic analysis of *Grimmia* and *Schistidium* (Bryopsida; Grimmiaceae) in China. J. Hattori Bot. Lab. 61: 123–247.

Churchill, S. P. 1994. New synonyms and deletions for the moss floras of Colombia and Ecuador. Trop. Bryol. 9: 1–4.

Crosby, M. R. & R. E. Magill. 1994. Index of Mosses 1990–1992. Monogr. Syst. Bot. Missouri Bot. Gard. 50: [i–vi], 1–87.

———, ——— & C. R. Bauer. 1992. Index of Mosses 1963–1989. Monogr. Syst. Bot. Missouri Bot. Gard. 42: [i–vi], 1–646.

Crum, H. 1994. Grimmiales. *In* A. J. Sharp, H. Crum & P. M. Eckel (editors), The Moss Flora of Mexico. Part One. Sphagnales to Bryales. Mem. New York Bot. Gard. 69: 386–415.

Deguchi, H. 1978[1979]. A revision of the genera *Grimmia, Schistidium* and *Coscinodon* (Musci) of Japan. J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 16: 121–256.

———. 1984. Studies on some Patagonian species of Grimmiaceae (Musci, Bryophyta). Pp. 17–72 *in* H. Inoue (editor), Studies on Cryptogams in Southern Chile. Kensei-sha, Tokyo.

———. 1986. Notes on some Asian species of *Grimmia*. Hikobia 9: 327–329.

———. 1987. Studies on some Peruvian species of the Grimmiaceae (Musci, Bryophyta). Pp. 19–74 *in* H. Inoue (editor), Studies on Cryptogams in Southern Peru. Tokai Univ. Press, Tokyo.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill (Editors). 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 131: [i]–xviii, 1–389.

Greven, H. C. 1995. *Grimmia* Hedw. (Grimmiaceae, Musci) in Europe. Backhuys Publishers, Leiden.

Hornschuch, C. F. 1819a. Neue Laubmoose. Flora 2: 81–112.

———. 1819b. Einige botan. Notizen aus England und Schweden. Flora 2: 440–444.

Horton, D. H. 1982. A revision of the Encalyptaceae (Musci), with particular reference to the North American taxa. Part I. J. Hattori Bot. Lab. 53: 365–418.

Ignatov, M. S. & T. Cao. 1994. Bryophytes of the Altai Mountains. IV. The family Grimmiaceae. Arctoa 3: 67–122.

Ireland, R. R. 1982. Moss Flora of the Maritime Provinces. Publ. Bot. (Ottawa) 13: 1–738.

Jóhannsson, B. 1993. Íslenskir mosar. Skeggmosaætt [Grimmiaceae]. Fjölrit Náttúrufraedistofnunar 24: 1–116.

Jones, G. N. 1933. Grimmiaceae. *In* A. J. Grout (editor), Moss Flora of North America 2: 1–66, pl. 1–25. Newfane, Vermont.

Maier, E. & P. Geissler. 1995. *Grimmia* in Mitteleuropa: Ein Bestimmungsschlüssel. Herzogia 11: 1–80.

Mårtensson, O. 1956. Bryophytes of the Torneträsk Area, Northern Swedish Lappland. II. Musci. Kung. Svenska Vetenskapsakad. Avh. Naturskyddsärenden 14: 1–321.

Ochyra, R. & H. Bednarek-Ochyra. 1994. A reconsideration of *Grimmia brandegei* Musci, Grimmiaceae. Fragm. Florist. Geobot. 392: 667–670.

Sayre, G. 1951. The identity of *Grimmia ovalis* and *G. commutata*. Bryologist 54: 91–94.

———. 1952. Key to the species of *Grimmia* in North America. Bryologist 55: 251–259.

———. 1959. Dates of publications describing Musci, 1801–1821. Russell Sage College. Troy, New York.

Stafleu, F. A., C. E. B. Bonner, R. McVaugh, R. D. Meikle, R. C. Rollins, R. Ross, J. M. Schopf, G. M. Schulze, R. de Vilmorin & E. G. Voss (editors). 1972. International Code of Botanical Nomenclature. Regnum Veg. 82: 1–426.

Takaki, N., T. Amakawa, T. Osada & E. Sakuma. 1970. Bryophyte flora of Mt. Kaikoma, Mt. Senjo and Mt. Kitadake (Southern Japan Alps). J. Hattori Bot. Lab. 33: 171–202.

White, F. 1978. The Afromontane Region. Pp. 463–513 *in* M. J. A. Werger (editor), Biogeography and Ecology of Southern Africa. Dr. W. Junk, The Hague.

———. 1993. Refuge theory, ice-age aridity and the history of tropical biotas: An essay in plant geography. Fragm. Florist. Geobot., Suppl. 2: 385–409.

Wijk, R. van der, W. D. Margadant & P. A. Florschütz. 1962. Index muscorum 2. D–Hypno. Regnum Veg. 26: 1–535.

———, ——— & ———. 1969. Index muscorum 5. T–Z, Appendix. Regnum Veg. 65: [I]–xii, 1–922.

Index to Exsiccatae

Aguilar, P. G. 150 (FH), 18454 (FH), 18493 (FH), 18545 (FH), 18709 (FH), 18775 (FH); Allen, B. H. 648 (MO), 9511 (G), 10849 (MO), 12260 (MO); Allioni, M. 8095 (H-BR); Allred, K. W. 6363 (MO), 6376 (MO); Alpert, P. 228 (FH); Amatt, T. 1401 (FH); André, E. 591 (NY); Aptroot, A. 4939 (NY), 4955A (NY), 4961A (NY); Arnell, W. H. 236B (H-SOL); Asplund, E. 13 (JE); 53 (JE); 78 (IBA, JE, UPS); Aur, C.-W. 5091 (ALTA).

Baldwin, D. D. 224 (H-BR); Barclay, H. G. & P. Juajibioy 7350 (IBA); Barnes & Land 368 (JE); Bartholomew, B. et al. 990 (FH); Bartram, E. B. 268 (FH), 283 (FH), 356 (FH), 383 (FH), 446 (FH), 621 (FH), 683 (FH), 683B (FH), 788 (FH), 808 (FH), 819 (FH), 829B (FH), 850A (FH), 855 (FH, NY), 857 (FH), 862 (FH), 1102 (FH), 1197 (FH), 1198 (FH), 1200 (FH), 1250 (FH), 1276 (FH, NY), 1310 (FH), 1695 (FH); Bell, B. G. 154 (BM, G, IBA), 155 (BM, FH, G); Benoist, R. 2276 (NY), 3153 (PC), 3386 (PC); Brass, L. J. 30026 (FH); Brassard, G. R. 6511 (BP), 15284 (FH); Brotherus, A. H. & V. F. Brotherus 121 (H-SOL); Brotherus, V. F. 244 (H-SOL); Buchtien, G. & O. Buchtien 1750 (H-BR); Buck, W. R. 8037 (NY), 8396 (NY), 13341 (NY), 14040 (NY), 14275 (NY), 14277 (NY), 14289 (NY).

Cao, T. & B. Yan 199 (ALTA), 266 (ALTA); Castilla, M. 1983 (MO), 2030 (MO); Chang, J.-W. M750 (ALTA); Chang, K.-C. & J.-Y. Fen 14655 (ALTA); Chen, P.-C. 4744 (ALTA), 5112 (ALTA), 5112 (KUN); Chernyadjeva, I. V. 8 (LE), 35 (LE), 53 (LE); Churchill, S. P. 8186 (IBA); Correll, D. S. 11990 (FH); Cremers, G. 1705 (MO); Crosby, M. R. & C. A. Crosby 6980 (MO), 8438 (MO), 8824 (MO), 9648 (MO), 8430A (MO), 8941 (MO), 6137 (MO); Crum, H. A. & L. E. Anderson 7797 (G).

De Sloover, J. 17934 (MO); Deall & Killik 133 (MO); Delaney, K. S. 1646 (BM); Delgadillo, C. et al. 3093 (FH); Doulea, J. 3110 (H-BR); Dusén, P. 605 (H-BR), 924 (H-BR).

Eddy, A. 2519 (BM), 2520 (BM), 2548 (BM), 2572 (BM), 2651 (BM); Ekman, E. L. 13630 (NY, PC); Elias, T. S. et al. B-65190 (NY).

Frahm, J.-P. 844419 (IBA), 935069 (IBA); Frey, T. C. & E. M. Frey 3072 (FH).

Galeotti, H. G. 6974 (PC); Gao, C. 1194 (ALTA), 1197 (ALTA), 1383 (ALTA), 12881 (ALTA), 12895 (ALTA), 12896 (ALTA), 13092 (ALTA), 13119 (ALTA), 13227 (ALTA), 22186 (MO), 22252 (MO), 22445 (ALTA); Gao, C. et al. 20831 (ALTA); Gao, C. & E.-Z. Bai 34124 (MO); Gao, C. & K.-C. Chang 1623 (ALTA), 9132 (ALTA), 9202 (ALTA); Gardens 4812 (JE); Gereau, R. 1649 (MO); Germain, P. 1142 (JE); Goodding, L. N. 433 (FH), 2101 (FH); Griffin, D. et al. 398 (NY), 2047 (NY); Griffith 127 (MO); Grubb, F. J. 2500 (FH); Grubb, F. J. & D. A. Guymer B.8 (BM), B.216-A (BM), B.210 (BM), L4.A (BM), B8 (IBA); Guo, H.-G. 17 (ALTA).

Handel-Mazzetti, H. 240 (BM), 748 (BM), 966 (JE), 2658 (H-BR, JE), 3183 (JE), 4670 (JE); He, S. 31243 (MO), 31245 (MO), 31248 (MO), 31304 (MO), 31792 (MO), 31800A (MO), 31834 (MO), 951051 (MO), 951156 (MO); Hedberg, O. 1238A (MO); Hegewald, E. & P. Hegewald 7236 (IBA, MO), 5076 (MO), 5104 (MO), 5135 (MO), 5156 (MO), 5274 (MO), 5375 (MO), 5761 (MO), 6018 (IBA, MO), 6029 (MO), 6151 (MO), 6220 (IBA, MO), 6241 (IBA, MO), 6543 (MO), 6553 (MO), 7280 (MO), 7425 (MO), 7482 (MO), 7568 (IBA, MO), 7605 (IBA, MO), 7638 (MO), 7639 (MO), 7667 (IBA, MO), 7918 (MO); Hermann, F. J. 17357 (NY), 17937 (S), 20992 (BM, FH, G), 21555 (BM), 25149 (ALTA), 27789 (BM); Herzog, T. 2584A (JE), 2679 (JE), 3148 (JE), 3579 (H-BR, JE), 3585 (JE), 3587A (JE), 3597 (JE), 3745 (JE), 3826 (H-BR, JE, PC), 3827 (JE), 4811 (NY), 4863 (JE), 4871 (JE), 4912 (BM), 4938 (JE); Hoe, W. J. 3462.0 (NY), 3463.0 (NY); Hu 950144 (MO); Humboldt, A. 76 (BM); Hyvönen, J. & S. Stenroos 4032 (IBA), 3924 (IBA), 3946 (IBA).

Ignatov, M. 0/918 (IBA), 0/475 (MO), 3/103 (IBA), 3/67 (IBA), 3/102 (IBA), 3/273 (IBA), 4/7 (IBA), 5/14 (IBA), 6/36 (IBA), 8/48 (IBA), 8/307 (IBA), 8/147 (IBA), 9/37 (IBA), 17/54 (MO), 17/43 (IBA), 34/161 (IBA), 34/218 (IBA), 36/103 (IBA); Ireland, R. R. 23944 (FH); Ireland, R. R. & G. Bellolio-Trucco 18557 (NY).

Jeffrey, C. 1535 (BM); Jin, Z.-Z. 87A (ALTA).

Kabir Khan 1835 (H-BR); Kiener, W. 18517 (FH); Kil'dyushevski 54/7 (LE); Killip, E. P. & A. L. Smith 17434 (BM), 17985 (BM), 17987 (BM), 17988 (BM); Kolenati 2568 (LE); Koponen, T. 18252 (ALTA); Krivoshapkin, K. K. 010404 (LE), 010602 (LE), 060107 (LE), 060108 (LE), 060110 (LE); Kuchar, P. B8980 (MO); Kunkel, G. 186 (NY).

Lai, H.-J. 80-171 (ALTA), 80-184 (ALTA), 6886 (MO); Lamb, I. M. 5288 (FH); Lang, K.-Y. 311A (ALTA), 321 (ALTA), 324A (ALTA), 654 (ALTA), 658 (MO), 780B (MO), 1102 (ALTA), 1102 (MO), 1192 (ALTA), 5302 (ALTA); LeSeur, H. B2B (FH); Lewis, M. 87-947 (MO), 87-958 (MO); Li, X.-J. 28 (MO), 80-16 (KUN), 80-184 (KUN), 642 (MO), 642A (MO), 799 (MO), 1321 (MO); Li, D.-K., 2227 (ALTA), 2233 (ALTA); Lin, Z.-Q. 00/342 (ALTA), 00/350 (ALTA); Lindig, A. 2011 (PC); Ling, Y.-H. 33106 (ALTA); Liogier, A. & P. Liogier 25032 (FH); Liu, S. 1551 (ALTA), 952096 (MO); Liu, S. et al. 1551 (ALTA); Lobb. 103 (BM); Lundlow, F. et al. 4221 (BM, IBA).

Magill, R. E. 4186 (MO), 4269 (MO), 6607 (MO), 6674 (MO), 6729 (IBA); Mandon, G. 1631 (BM), 1632 (PC), 1634 (BM, FH-Sull, G), 1635 (BM); Matthews, K. I. 1125 (FH); Meijer, W. B10374 (MO), B10389 (MO), B11947 (MO), B11952 (MO); Meyer, F. G. 5435 (JE), 5518 (JE).

Norris, D. H. 69524 (MO).

ôba, T. 103 (NICH); Orcutt, C. R. 5353 (FH), 7073 (FH).

Peng Ching-I 83-31 (MO), 83-34 (MO), 83-35 (MO); Pennell, F. W. 18400D (FH); Petelin, D. A. 37-7 (MO);

Phillips, W. S. 2902 (FH); Pittier, H. 13198 (NY); Polunin, N. 2293A-5 (FH), 2611A20 (FH); Poplavskaya, G. 141 (LE); Preuss 859 (H-BR); Pringle, C. G. 26A (JE), 15076 (JE).

Redfearn Jr., P. L. 34610 (MO), 34945 (MO), 34976 (MO), 35162D (MO), 35213 (MO), 35234 (MO); Redfearn Jr., P. L. et al. 599 (FH, MO), 1079 (MO), 1091 (FH, MO), 1145 (MO), 1153B (MO), 1659 (MO), 1814 (FH, MO); Redfearn Jr., P. L. & D. M. Eggers 16340 (MO); Richards, P. W. 4269 (MO); Robbins, R. G. 706 (FH); Rojkowski, S. 157 (JE); Ruinard, C. & A. H. M. Jayasuriya 17/40 (MO); Rupidera, J. L. 1 (SALA).

Schiffner, V. 461 (H-BR), 773 (FH, H-BR); Schubert, W. M183 (MO), M295 (MO); Selivanova-Gorodkova, E. A. 792 (LE), 5259 (LE); Sharp, A. J. 1833 (FH), 2290A (FH); Shaw, J. 5610 (NY); Shushan, S. 1038 (G); Sim, T. R. 7218 (NY); Skottsberg, C. 370 (PC), 1600 (H-BR), 1603 (H-BR), 1607 (H-BR), 1618 (H-BR), 1628 (H-BR); Standley, P. C. 65262 (FH), 65526A (FH), 65530 (FH); Stark, L. R. & R. Castetter 2055 (MO); Steere, W. C. 72-895A (NY), 10129 (NY), 12436 (NY), 23052 (G), 640703-7 (NY); Stenroos, S. 3050 (IBA).

Takeda, Y. & J. Wang 860420-11 (NICH), 860406-7 (NICH), 860406-8A (NICH), 860412-1A (NICH); Tan, B. C. 82-195 (FH), 89-521 (NY); The Expedition to the Tibet 7446 (ALTA), 7608 (ALTA), 7884 (ALTA); Thwaites, G. H. K. CM29 (BM); Townsend, C. C. 85/860 (ALTA); Troll, C. 64 (JE), 5570 (JE), 5860 (JE), 5868 (JE), 5868 (FH), 5868 (JE); Tsegmed, T. 228 (LE), 248 (NY), 747 (LE), 2442 (LE); Tuomikoski, R. & J. Kucyniak T1472 (JE).

Ule, E. 1830 (H-BR), 1913 (H-BR).

Valcarcel, L. 40 (FH); van Rooy, J. 2294 (NY), 3124 (MO), 1074 (NY), 1104 (NY), 2282 (NY); Vareschi, L. 1274 (NY); Vargas, J. C. 5039 (FH), 7099 (FH), 7676 (FH), 8674 (FH), 8709 (FH), 8780 (FH), 10039 (FH), 15863 (NY).

Wang, M.-Z. 12503 (ALTA), 8141105J (ALTA); Weber, W. A. & D. McVean B-32146 (MO), B-32146 (MO); Weddell, M. H. A. 4 (PC); Weiss, J. 297 (JE, PC); Welch, W. H. 16694 (NY); Williams, R. S. 2815 (BM); Wood 1160 (NY); Wooton, E. O. 1501 (FH); Wu, S.-G. 1076 (ALTA), 1076A,B (KUN).

Xinjiang Biological Institute 47085 (MO); Xizang Team 7761 (MO); Xu, W.-X. 422 (ALTA).

Yang, C. M. S.51 (BM).

Zang, M. 21 (ALTA), 93 (ALTA), 373 (ALTA), 428 (ALTA), 682 (KUN), 890 (ALTA, KUN), 1093 (KUN), 1119 (KUN), 1358 (ALTA), 1728 (ALTA), 1865 (ALTA), 1996 (KUN), 5217 (ALTA), 5230 (ALTA), 5298 (ALTA), 5317 (ALTA); Zhao, K.-Y. 85A (ALTA), 117 (ALTA), 953299 (MO); Zhu, W.-M. 4 (ALTA), 7716 (ALTA), 64020 (ALTA), 64627 (ALTA); Zhu, W.-M. & J.-L. Wu 64067 (ALTA).

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CONTENTS

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A TAXONOMIC REVISION OF *GRIMMIA* SUBGENUS *ORTHOGRIMMIA* (MUSCI, GRIMMIACEAE)[1]

Jesús Muñoz[2]

ABSTRACT

Grimmia subg. *Orthogrimmia* comprises nine species distributed on mountain chains or high latitudes mainly in the Northern Hemisphere. This subgenus is defined by the following combination of characters: leaves V-shaped in transverse section, margins flat (seldom recurved in *G. reflexidens*), proximal marginal cells with the transverse walls thicker than the longitudinal walls, setae erect and straight (curved only in *G. arenaria*), and capsules symmetric and smooth. I recognize two sections: sect. *Donnianae*, including *G. arenaria* Hampe, *G. donniana* Sm., and *G. triformis* Carestia & De Not.; and sect. *Montanae*, comprising *G. alpestris* (F. Weber & D. Mohr) Schleich., *G. caespiticia* (Brid.) Jur., *G. montana* Bruch & Schimp., *G. nivalis* Kindb., *G. reflexidens* Müll. Hal., and *G. ungeri* Jur. *Grimmia brachyphylla* Cardot, considered by other authors to be synonymous with *G. montana*, is shown to be conspecific with *Coscinodon humilis*, and is here lectotypified. *Grimmia sinensianodon* is considered to be synonymous with *Coscinodon cribrosus*, and not with *G. caespiticia*, as previously believed. All taxa are keyed and described, and typified where indicated. Illustrations and distribution maps are provided for each species.

Grimmia Hedw. is the largest genus in the Grimmiaceae (Musci). It is distributed throughout the world, mostly in mountainous areas. Several infrageneric taxa have been proposed within *Grimmia*, always based on the European species.

Grimmia subg. *Orthogrimmia* differs from the other subgenera of *Grimmia* by the following combination of characters: leaves keeled, V-shaped in transverse section; margins flat (rarely recurved in *G. reflexidens*); proximal marginal cells with the transverse walls thicker than the longitudinal walls; setae erect and straight (curved only in *G. arenaria*);

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and capsules ovoid to fusiform, symmetric, and smooth. I have recognized two sections: sect. *Donnianae*, with three species, and sect. *Montanae*, with six. The species of this subgenus are distributed along mountain chains mainly in the Northern Hemisphere. Only *G. reflexidens* is also known from the Southern Hemisphere.

The taxonomic history of *Grimmia* has been reviewed in an excellent manner by Deguchi (1978: 123–126). Table 1 summarizes several major taxonomic treatments of the genus.

Recently, revisions of *Grimmia* have been published for the Altai Mountains (Ignatov & Cao, 1994), China (Cao & Vitt, 1986), Europe (Greven, 1995; Maier & Geissler, 1995), Japan (Deguchi, 1978), and South America (Deguchi, 1984, 1987). However, much more work must be done to resolve the taxonomic and nomenclatural difficulties of this genus.

Traditionally, the species dealt with in the present work have been treated (Hagen, 1909; Limpricht, 1890; Loeske, 1913) in *Grimmia* subg. *Guembelia* (Hampe) Schimp. (Schimper, 1856). However, the lectotype of *Guembelia*, designated by Pfeiffer (1874: 1511), is *Grimmia elliptica* Funck (nom. illeg.≡ *G. ovalis* (Hedw.) Lindb.), which belongs to a different subgenus, usually known by the later and arguably illegitimate name *Grimmia* subg. *Litoneuron* I. Hagen (Hagen, 1909). Therefore, *Grimmia* subg. *Guembelia* is the oldest name for the group usually known as subgenus *Litoneuron*, and the group usually known as subgenus *Guembelia* must be called *Grimmia* subg. *Orthogrimmia* Schimp., here lectotypified by *G. donniana* Sm.

The species in the *G. alpestris–G. donniana* complex of subgenus *Orthogrimmia* have been treated at various taxonomic ranks in the literature. Whereas *G. alpestris*, *G. caespiticia*, *G. donniana*, *G. montana*, and *G. reflexidens* (as *G. sessitana*) have usually been considered worthy of specific rank, *G. arenaria*, *G. nivalis*, *G. triformis*, and *G. ungeri* have rarely merited more than subspecific recognition. Nevertheless, all are discrete entities, without morphological intergradations. These taxa vary across their geographical ranges, but always in secondary features, mostly quantitative and presumably habitat-induced. These quantitative features have been much employed in the literature, yielding disparate taxonomies. On the other hand, major structural characters, such as presence or absence of stomata, have usually been neglected. From *Index Muscorum* (Wijk et al., 1962, 1969) onward, all the species treated in this study have been commonly lumped with *Grimmia donniana* following Habeeb (1950: 75). His knowledge of the group, however, was inadequate, as noted by Crum and Anderson (1981: 429).

MATERIALS AND METHODS

This revision is based on 1939 specimens from BCB, BCC, BM, BP, CANM, COLO, FH, G, GLM, H, JE, KRAM, KUN, LE, LISU, M, MA, MO, MUB, NY, OP, PAV, PC, S, TCD, TNS, TRH, VIT, W, WRSL, Z, as well as from the private herbaria of J.-P. Frahm (Bonn), E. Fuertes (Madrid), and R. B. Pierrot (Dolus). Some type specimens requested from DR, GLM, LZ, MPU, and ROST were not found in these herbaria.

Specimens were moistened in water with domestic detergent and then transferred to clean water. At the beginning of this study and, later, for types and specimens not immediately referable to any taxa, 10 to 15 mature but green leaves from the apical part of the stem (excluding the uppermost ones), transverse sections, the two or three innermost perichaetial leaves, and a capsule sectioned in eight parts were mounted in lactophenol gel (Zander, 1983) or Hoyer's (Anderson, 1954) medium. In this treatment, seta length includes the vaginula. Lamina length excludes hair-point, lamina width has been measured at the broadest part of the leaf, and fractions (e.g., "margin recurved in the proximal ½") always refer to lamina length. Cell measurements include the wall. Proximal paracostal and marginal cells refer to the two or three rows of cells closest to the costa and margin, respectively.

I have distinguished species on the basis of morphological characters. They are "taxonomic species" according to Grant (1981: 78–80). The characters employed are important throughout the genus, and even the family.

For mapping distributions I have used ArcView GIS, which almost automatically loads geographical coordinates from database files with the ".dbf" format. Distribution maps are based solely on examined herbarium specimens. In "Selected specimens examined" I have cited only one specimen per geographical unit, and the total number of specimens parenthetically at the head of the section. A complete list of specimens studied is available upon request.

I have designated lectotypes for all names except those for which the author specifically selected in the protologue a single collection as holotype (Greuter et al., 1994, ICBN 9.1). The common practice of accepting as holotype a specimen kept in the personal herbarium of the original author can be a source of error. Good examples of problematic

Table 1. Various infrageneric divisions of *Grimmia*. An asterisk (*) indicates taxa that include species dealt with in this work.

Bruch & Schimper (1845)	Schimper (1856)	Limpricht (1890)	Kindberg (1898) (ranks not indicated)	Hagen (1909)	Loeske (1930)
Grimmia	*Grimmia*	*Grimmia*	*Grimmia*	*Grimmia*	*Grimmia*
Tribu *Curvisetae*					
sect. *Crinitae*	subg. *Gasterogrimmia*	subg. *Gasterogrimmia*	*Streptophyllum*	subg. *Gasterogrimmia*	subg. *Gasterogrimmia*
Pulvinatae			*Eugrimmia*		
Trichophyllae		subg. *Rhabdogrimmia*	*Molliformes*	subg. *Rhabdogrimmia*	subg. *Rhabdogrimmia*
Elatiores	subg. *Grimmia*		*Velutinae**		subg. *Pulvinatae*
Uncinatae		subg. *Grimmia**	*Pulvinatae**		subg. *Torquatae*
			*Alpestriformes**		
			Andreaeoideae		
		subg. *Guembelia**	*Pseudoracomitrium*		
			Papillosae		
Tribu *Rectisetae*			*Crispulae*		
sect. *Leucophaea**	subg. *Orthogrimmia**		*Trichophylloideae**	subg. *Litoneuron*	subg. *Litoneuron*
*Commutatae**	subg. *Guembelia**		*Ovataeformes**	subg. *Guembelia**	subg. *Alpestres**
			*Unicoloriformes**	sect. *Montanae**	subg. *Alpinae*
				*Ovales**	
				Funales	
			Pseudo-Schistidium		
			*Piliferae**		
			Crinitae		
Atratae		*Dryptodon*		subg. *Streptocolea*	*Dryptodon*
				subg. *Hydrogrimmia*	*Hydrogrimmia*
			Schistidium	subg. *Schistidium*	*Schistidium*
Schistidium	subg. *Schistidium*	*Schistidium*	*Platyphylloideae*		
			Apocarpaeformes		

typification are the many epithets associated with Kindberg or Müller (also cf. Ortiz, 1989).

TAXONOMIC CHARACTERS

This character overview refers to members of *Grimmia* subg. *Orthogrimmia*, except where otherwise indicated.

GAMETOPHYTE

Habit. The plants grow in dense compact cushions on rocks, mainly siliceous. These cushions are usually round and semi-spherical, although when growing in rock crevices they adopt the form of the crevice. The color of the plants varies among nuances of olive-green above, and usually blackish below.

Stem. Stems of *G. triformis* may reach 2 cm high, but most species rarely exceed 1.5 cm. The stem diameter varies between 100 and 210 μm. Stem internal structure in *Grimmia* was studied in depth by Kawai (1965: 113–117) and Deguchi (1978: 128–131). Kawai distinguished three parts in transverse section: an epidermal layer, a cortical layer, and a central strand. According to the degree of differentiation among the three layers, Kawai defined four stem types: "a" type, with no differentiation among the three layers, because of their nearly uniform cells; "b" type, where the epidermal and cortical layers are differentiated but the central strand is not; "c" type, where all three layers are differentiated and the central strand has less than 15 cells; and finally "d" type, as in the previous type but with a more developed central strand, i.e., of more than 15 cells.

Deguchi's system varies from that of Kawai. He joined Kawai's types "c" and "d" into his "Type II," whereas his Types "I" and "III" are identical to Kawai's types "a" and "b," respectively.

In this study the internal structure of the stem in *Grimmia* subg. *Orthogrimmia* was found to be characterized by a weak differentiation between the epidermal and cortical layers (which together form a more or less homogenous layer) on the one hand, and the central strand (which is well developed in nearly all species) on the other. This stem structure is intermediate between Kawai's types "a" and "c" or Deguchi's "I" and "II."

Branching. Branching systems in *Grimmia* have been studied in depth by Deguchi (1978: 128, figs. 1, 2). Branching pattern is usually sympodial, and this is the only type observed in *Grimmia* subg. *Orthogrimmia*. Innovations arise at the base of the perigonia and perichaetia. When these sexual structures are abundant, the stems appear like stairs (Deguchi, 1978: figs. 1, 2). Occasionally, the plants appear monopodial because damaged sexual structures have fallen off. This is especially true for old plants. Rarely, the perigonia can be monopodially attached in cladoautoicous species.

All species of subgenus *Orthogrimmia* except *Grimmia caespiticia* show intricately branched stems resulting in a cohesive net and compact cushions. *Grimmia caespiticia* has less extensively branched stems, and its cushions are easly decomposed.

Some young branches have rhizoids at their base and are easily detached from the stems. This could reflect their role as diaspores in nature (Correns, 1899: 102; Deguchi, 1978: 128).

Rhizoids. Usually, rhizoids are limited to the base of stems. Plants subject to periodic inundation, however, have rhizoids throughout the stem length.

Axillary hairs. Axillary hairs in subgenus *Orthogrimmia* consist of 3–8 hyaline, uniseriate cells, of which the 1–2 most proximal ones are shorter. Length may vary between 50 and 175 μm.

Leaf orientation. When dry, all taxa have erect and appressed leaf bases, whereas the apex can be incurved and appressed (e.g., *G. caespiticia, G. montana*, and *G. ungeri*), variously flexuous (e.g., *G. arenaria, G. donniana*, and *G. triformis*) or appressed (e.g., *G. alpestris, G. nivalis*, and *G. reflexidens*). When moist, the leaves vary from erect to spreading, and *G. montana* exhibits sigmoid leaves in lateral view.

Leaf size and shape. Leaf lengths fall into two groups: shorter than 1.5 mm (e.g., *G. alpestris, G. caespiticia, G. montana, G. nivalis, G. reflexidens*, and *G. ungeri*); and longer than 1.5 mm (e.g., *G. arenaria, G. donniana*, and *G. triformis*). Mean leaf width is more uniform than length, always around 0.35 mm.

Grimmia alpestris, G. caespiticia, G. nivalis, G. reflexidens, and *G. ungeri* (Figs. 8a, b, 10a, 14b, 16a, 18a) have ovate leaves, with a length/width ratio of 2–3 : 1. *Grimmia arenaria, G. donniana, G. triformis*, and *G. montana* (Figs. 2a, 4a, 6a, 12a, b) have narrowly ovate leaves, with a length/width ratio of 3–6 : 1.

Leaf margin. The leaf margins are entire in all species studied, and plane at the base on both sides in most species. An exception to this rule are some populations of *G. reflexidens*, with recurved margins in the proximal half on one side and at the very base on the other side, or occasionally only briefly and narrowly recurved at the base on one side. Unfortunately, in this taxon it is an inconsistent character used profusely in the literature. The distal leaf margins are plane or incurved. Exceptions are the muticous leaves of *G. caespiticia, G. montana,* and *G. nivalis,* which have a more or less cucullate apex.

Leaves in transverse section. Three types of leaves can be distinguished in *Grimmia* according to the shape of their transverse sections: concave, U-shaped (= canaliculate) and V-shaped (= keeled, carinate). Species in subgenus *Orthogrimmia* have strongly keeled leaves, although *G. montana* and more often *G. ungeri* can have only slightly keeled leaves in some populations.

Grimmia alpestris, G. nivalis, and especially *G. caespiticia* have leaves with a longitudinal plication on each side of the costa. The cells of these plicae are usually longer and narrower and have thicker walls, although they can be undifferentiated, mainly in the two former species.

Species of subgenus *Orthogrimmia* have a semiterete costa mostly projecting on the dorsal surface and clearly delimited from the lamina. Costal cross sections consist of three cell layers: ventral epidermis, internal band of stereids or substereids, and dorsal epidermis. Based on the morphology and differentiation of these three layers, Kawai (1965: 111, 1968: 128) recognized four types of costal structure in *Grimmia.* Species in subgenus *Orthogrimmia* belong to Kawai's "C" type, characterized by a more or less clear differentiation of the three layers, and a ventral epidermis two cells wide. Whereas costal structure and morphology are of great taxonomic value in some taxa of Grimmiaceae (e.g., *Racomitrium, Dryptodon,* other *Grimmia* subgenera), they have a limited utility in *Grimmia* subg. *Orthogrimmia.*

The leaf lamina is unistratose in the proximal part and 2(3–4)-stratose in the distal ⅓–⅔, mainly at the margins.

Laminar cells. The distal cells vary greatly in length, width, wall thickness, and sinuosity, and cannot be used to distinguish species. Their shape varies from isodiametric to rectangular or transversely rectangular in the same leaf, without any definite pattern. Length of major diameter ranges between 4 and 8 μm in *G. montana* and 8 and 13 μm in *G. alpestris.* Cell cross-sectional shape, on the other hand, is of great importance in defining taxa: *Grimmia alpestris, G. caespiticia, G. nivalis,* and some populations of *G. reflexidens* have rounded cells bulging on both surfaces, whereas *G. arenaria, G. donniana, G. triformis, G. montana,* and *G. ungeri* have isodiametric or rectangular cells plane on the lamina surface (seldom *G. montana* has cells slightly bulging on the dorsal surface). *Grimmia nivalis* and many populations of *G. caespiticia* have papillose distal laminar cells. The papillae are usually better developed on the dorsal than on the ventral surface.

The proximal laminar cells in *Grimmia arenaria, G. donniana,* and *G. triformis* are alike: hyaline, and long and narrow (length/width ratio 3–10 : 1). Their walls are thin and even, straight and nearly indistinct, although the paracostal cells can have somewhat thickened and sinuous walls (Figs. 2e, 4c, 6c). *Grimmia alpestris, G. caespiticia, G. montana, G. nivalis, G. reflexidens,* and *G. ungeri* have proximal cells that range from isodiametric to rectangular (to 6 : 1 in paracostal cells), with the transverse walls always thicker than the longitudinal ones, which usually are thicker than in the other species of the subgenus (Figs. 8d, 10c, 12d, 14e, 16e, 18d).

Hair-points. As in almost any other species in the genus, the length of the hyaline hair-points varies significantly in subgenus *Orthogrimmia,* and can often be correlated with ecological conditions. Populations from exposed habitats usually have longer hair-points. *Grimmia arenaria* has the longest hair-points in the subgenus despite habitat, and they are always strongly flexuous. *Grimmia caespiticia,* a species of exposed sunny and dry habitats, has the shortest hair-points, at times reduced to as few as one hyaline cell. Male plants of dioicous species always have shorter hair-points than their female counterparts, and when cushions of different sexes grow intermingled, they can appear quite distinct.

The hair-points are usually erect, and their degree of flexuosity depends on their length. Short hair-points are straight, whereas longer ones are often flexuous. *Grimmia arenaria* always has strongly flexuous and homomallous hair-points.

In *Grimmia alpestris, G. caespiticia, G. montana, G. nivalis, G. reflexidens,* and *G. ungeri* the hair-points are always terete, whereas in *G. arenaria* and *G. triformis* they are always flat. The structure of the hair-points in *G. donniana* depends on their length: longer hair-points are flat, whereas shorter ones are more or less terete.

Perichaetial leaves. The inner perichaetial leaves of most species of subgenus *Orthogrimmia* are well differentiated from the apical vegetative ones, i.e., they are 2–3 times larger and convolute. Moreover, the cells in the proximal, sheathing half are enlarged and hyaline-yellowish, with very thin walls, at least along the margins. Exceptions are *G. arenaria,* with undifferentiated perichaetial leaves, and *G. caespiticia,* with convolute but only slightly larger perichaetial leaves.

The hyaline hair-points are always longer in perichaetial than in vegetative leaves.

Reproductive organs. Taxa in subgenus *Orthogrimmia* are dioicous, gonioautoicous (androecium bud-like and axillary on the same stem as the terminal gynoecium) or cladautoicous (androecium on a separate stem). In the last-mentioned case, ramifications and the growth of branches at times produce a notable separation of perichaetium and perigonium-bearing branches. In this case, the plants could seem dioicous.

Androecia can be axillary or terminal. The latter are easy to observe, since they are inflated and bulbiform, giving the stem a clavate appearance. Axillary buds are smaller and very difficult to find, especially in autoicous species. The antheridia are surrounded in both types by strongly differentiated, cochleariform perigonial leaves with acute apexes.

Perichaetia are always terminal, but soon appear axillary due to elongation of the subfloral branch (Deguchi, 1978: figs. 1, 2).

SPOROPHYTE

Autoicous species, i.e., *G. arenaria, G. donniana, G. reflexidens, G. triformis,* and *G. ungeri,* had sporophytes in 70–100% of the studied collections. Dioicous species show important differences in the percentage of fertile collections: *Grimmia nivalis* had sporophytes in all examined samples except one, *Grimmia alpestris* showed a high percentage, near 90%, whereas *G. caespiticia* and *G. montana* exhibited lower percentages, ca. 70%.

Setae. The setae are straight except in *G. arenaria,* which has curved setae. Other species can occasionally have slightly curved setae, particularly *G. reflexidens.* The setae are longer than capsules in all species except *G. triformis.* They range in length from 1 mm in *G. triformis* to 4 mm in *G. alpestris* and *G. montana.* In all species the seta is twisted counterclockwise when dry.

Capsules. Capsules provide important taxonomic characters in subgenus *Orthogrimmia.* Recently dehisced or, better, non-dehisced capsules must be used. Older capsules have greater deposits of wax over their exothecial cells, and most are infected by fungi, making it difficult to recognize important features, like the presence of stomata or the thickness of the exothecial cell walls.

All species of subgenus *Orthogrimmia* have smooth capsules. They are exserted except in *Grimmia arenaria,* which has emergent capsules, and *G. triformis,* which has immersed capsules.

Capsules are mostly ovoid, with a wide base abruptly connected to the seta. The only exception is *G. alpestris,* with ellipsoid-fusiform capsules attenuated at the base and not abruptly connected with the setae (Fig. 8c). The base is usually symmetrical, but in some populations of *G. alpestris, G. montana,* and *G. reflexidens* the base is slightly asymmetrical and the capsule is weakly inclined.

Capsules of *Grimmia arenaria, G. donniana, G. reflexidens, G. triformis,* and *G. ungeri* are usually stramineous, although in the last two species the color can turn to brownish in older capsules. The capsule color of *G. alpestris, G. caespiticia, G. montana,* and *G. nivalis* is castaneous.

At the capsule mouth there are several rows of small, transversely rectangular, usually reddish or brownish, more intensely colored cells with thick walls. This character is uniform in subgenus *Orthogrimmia.* The cells of the rest of the urn are isodiametric, rectangular, or transversely rectangular; usually all types are present, with one of them dominating. The exothecial cell walls are thin (less than 3 μm) in *G. arenaria, G. caespiticia, G. donniana, G. montana, G. reflexidens,* and *G. ungeri,* and thick (more than 3 μm) in *G. alpestris, G. nivalis,* and *G. triformis.*

Stomata can be found in the neck region of the urn in all species of subgenus *Orthogrimmia* except *G. alpestris, G. montana,* and *G. ungeri.* The best procedure for observing the stomata is to cut a capsule in half and then cut the proximal half again (for a total of four parts) and search for stomata (in uncut old capsules it can be hard to see the stomata because of secondary deposits of wax and other substances). The guard cells are reniform, and under the compound microscope appear dotted or colored, with a cellular content different from that of the adjoining exothecial cells. The cells surrounding the guard cells are usually undifferentiated from the other exothecial cells, thus the stomata can be classified as anomocytic. Sometimes, however, the row of subsidiary cells surrounding the guard cells is slightly differentiated and smaller than the other exothecial cells, and such stomata could be considered stephanocytic (Baranova, 1987).

The absence of stomata is a good character to separate *Grimmia alpestris* from the closely related *G. nivalis* and *G. reflexidens.*

Two annular types can be recognized in subgenus *Orthogrimmia* (Deguchi, 1978: 143–144). Annulus cells in the *Schistidium*-type are undifferentiated from the exothecial rim cells and non-revoluble. All species in section *Montana* have this type of annulus (simple and persistent). On the other hand, the *elongata*-type is characterized by having two or three rows of isodiametric, inflated and hyaline, revoluble cells. All species in section *Donnianae* have this type of annulus (compound and revoluble).

The peristome of *Grimmia* subg. *Orthogrimmia* consists of 16 more or less entire, irregularly divided or cribrose teeth. Their width, measured at the outer surface of the peristome base, varies from 35–50 μm in *G. caespiticia* and *G. ungeri* (Figs. 10d, 18f) to 70–100 μm in *G. triformis* (Fig. 6f). The teeth are densely papillose on the inner surface, whereas on the outer surface they are papillose distally and smooth or slightly papillose proximally. Tooth color (castaneous-brown or orange) is constant in each species.

The operculum is conic with a short mammilla in all species except *G. montana*, in which it is rostrate.

Calyptrae. Calyptra morphology is much employed in the taxonomy of Grimmiaceae. All species in *Grimmia* subg. *Orthogrimmia* have smooth calyptrae, which may be mitrate (sect. *Donnianae*) or cucullate (sect. *Montanae*). Only one collection of *Grimmia donniana* out of the 555 fertile specimens of section *Donnianae* studied had some cucullate calyptrae, and I considered this an abnormality.

Spores. The spores of all species of subgenus *Orthogrimmia* are spherical and homogenous in size (isosporic, Mogensen, 1983: 334–336). Under the compound microscope they appear smooth, but are minutely granulose (Cao & Vitt, 1986: fig. 16c, f). Hirohama (1978: 37, figs. 57, 58) described the spores as smooth, but his figures show a minutely granulose surface similar to Cao and Vitt's figure 16c.

Once again, it is possible to separate the group consisting of *G. arenaria*, *G. donniana*, and *G. triformis* (i.e., sect. *Donnianae*), with smaller spores (6.5–11.0 μm), from that comprising *G. alpestris*, *G. caespiticia*, *G. montana*, *G. nivalis*, *G. reflexidens*, and *G. ungeri* (i.e., sect. *Montanae*), with larger spores (9–14 μm).

CHROMOSOME NUMBERS

It has been pointed out that the basic chromosome number in Grimmiaceae is $x = 7$ (Smith, 1978; Vitt, 1984). From this number have been derived the remaining ones in the family: 10, 12, 12+m, 13, 13+m, 14, 14+1–4acc., 22, 26, and 26+m (Fritsch, 1991; Vaarama, 1949).

The most common haploid complement in *Grimmia* is $n = 13$, with $n = 10$, 12+m, 13+m, 14, and 14+1–4acc also common. These numbers were probably derived through doubling of the basic $x = 7$ complement of the Grimmiaceae (primary diploids). Other species have a haploid complement of $n = 26$ or $n = 26+\mathrm{m}$ (Fritsch, 1991), probably resulting from secondary doubling of the $n = 13$ chromosome complement (secondary diploids).

It is generally acknowledged that the duplication of the chromosome number implies a directional transformation from a dioicous to an autoicous sexual condition [but see Wyatt & Anderson (1984) for a thorough discussion on this topic]. Ramsay (1983: fig. 147, see also discussion on pp. 202–206) diagrammed the various ways of maintaining the dioicous condition by aneuploid reduction. Some of the primary diploids in *Grimmia* may have reverted to the dioicous sexual condition (e.g., *G. alpestris*), whereas others have become autoicous (e.g., *G. arenaria* and *G. donniana* (Fig. 1)).

Chromosome counts for the species studied here are scarce (Table 2). Known numbers are $n = 13$ or 13+m for *G. alpestris*, $n = 12+\mathrm{m}$ and $n = 13$ for *G. donniana*, and $n = 13$ for *G. arenaria* and *G. montana*. I was only able to verify the identity of the voucher for the count of *G. donniana* (Khanna, 1964: 348, fig. 5).

TAXONOMIC TREATMENT

Grimmia Hedw., Sp. Musc. Frond. 75. 1801. TYPE: *Grimmia plagiopodia* Hedw. (lectotype, designated by Mårtensson (1956: 106–107).

Autoicous or dioicous. Plants in dense cushions or compact to loose tufts, glaucous, green, greenish yellow, or dark green. *Stems* erect or ascending, with or without central strand. *Leaves* erect, appressed or flexuous, occasionally with homomallous tips when dry, erect to spreading when moist, linear, ovate, lanceolate, ligulate or oblong, obtuse to acuminate, concave, canaliculate or keeled, plane or plicate; *margins* entire, plane, recurved or incurved; *costa* single, percurrent, terete, semi-terete, semi-elliptic, or almost indistinct in cross section; *lamina* 1- to 4-stratose in the distal half, smooth or pseudopapillose; *distal cells* isodiametric to rectangular or transversely rectangular, with straight or sinuous walls, plane or bulging, smooth or papillose; *proximal cells* isodiametric to rectangular or transversely rectangular, the walls straight or sinuous, uniformly thickened or with the transverse walls thicker than the longitudinal walls; with or without *hyaline hair-points. Perichaetial leaves* convolute and larger, or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* entire to dentate, or lacking. *Androecia* axillary or terminal. *Setae* straight, curved, or coiled, longer or shorter than capsules. *Capsules* immersed, emer-

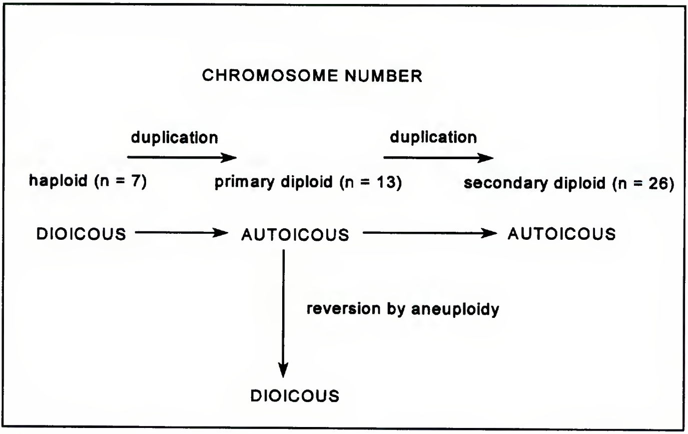

Figure 1. Correlation between chromosome number and sexual condition in *Grimmia.*

gent or exserted, subglobose, ovoid, ellipsoid, or fusiform, symmetric or asymmetric and ventricose at the base, smooth or furrowed, stramineous or castaneous; with stomata at the urn base or lacking stomata; *exothecial cells* isodiametric to rectangular, thin- or thick-walled; *annulus* simple and persistent or compound and revoluble, of 1–3 rows of isodiametric to rectangular cells; *peristome teeth* 16, triangular, entire, perforate in the distal half or cribrose throughout their length and irregularly cleft in the distal ⅔–¾, orange or brown; *opercula* conic to long-rostrate; *calyptrae* mitrate or cucullate, smooth, covering the operculum; *columella* persistent; *spores* usually 8–16 μm, occasionally up to 20 μm, smooth to granulose.

The supraspecific taxonomy of *Grimmia* has yet to be fully resolved. Whereas some recognized supraspecific taxa (cf. Table 1) are natural and well established (e.g., subgenera *Grimmia* and *Orthogrimmia*), others are at present tentative. The following key is intended to separate subgenus *Orthogrimmia* from all other members of *Grimmia,* not to present a taxonomy of the genus. No formal status or circumscription is given to either "Rhabdogrimmia" or "Alpinae" until further work on these groups is carried out.

KEY TO MAJOR SUPRASPECIFIC TAXA OF *GRIMMIA*

1a. Capsules strongly asymmetric at base, ventricose .... *Grimmia* subg. *Grimmia*

Table 2. Chromosome numbers reported for *Grimmia* subg. *Orthogrimmia.*

Species	n =	Origin	Author
Grimmia alpestris	13	California	Steere et al. (1954)
	13+m	Georgia (Republic)	Lazarenko et al. (1971)
	13	Colorado	Khanna (1971)
Grimmia arenaria	13	Great Britain	Smith & Newton (1968)
Grimmia donniana	12+m	New York	Khanna (1964)
	13	Great Britain	Smith & Newton (1966)
	13	Great Britain	Ramsay (1969)
	13	Kazakhstan	Vysotskaya & Lesnyak (1984)
	13	Poland	Kuta et al. (1984)
Grimmia montana	13	Canada	Anderson & Crum (1958)

1b. Capsules symmetric or very slightly asymmetric, not ventricose at base.
  2a. Setae variously curved; capsules mostly ribbed, or if smooth, leaf margins recurved to some degree or leaves variously crisped .... "Rhabdogrimmia"
  2b. Setae straight or, if curved, capsules smooth, leaf margins plane and leaves straight to flexuous, not crisped.
    3a. Leaves concave; costa semi-elliptic, indistinct .... *Grimmia* subg. *Guembelia*
    3b. Leaves canaliculate to keeled; costa semi-terete, clearly delimited from lamina.
      4a. Leaf margins plane or incurved .... *Grimmia* subg. *Orthogrimmia*
      4b. Leaf margins recurved.
        5a. Annulus compound and revoluble .... "Alpinae"
        5b. Annulus simple and persistent *Grimmia* subg. *Orthogrimmia* (*G. reflexidens*)

Grimmia subg. **Orthogrimmia** Schimp., Coroll. Bryol. Eur. 48 1856. TYPE: *Grimmia donniana* Sm. (lectotype, here designated).

Autoicous or dioicous. Plants in dense, compact tufts, glaucous, green, greenish yellow, or dark green. *Stems* erect, to 2 cm tall × 110–210 μm diam., with central strand well developed, sometimes with rhizoids present nearly throughout; *axillary hairs* 3–8-celled, hyaline, 50–175 μm long. *Leaves* erect, appressed to flexuous (occasionally with homomallous tips) when dry, erect-spreading to spreading (occasionally sigmoid in lateral view), flaccid or rigid when moist, 0.8–2.2 × 0.25–0.65 mm, narrowly ovate to ovate, acute to acuminate, keeled, although sometimes only weakly, plane or plicate; *margins* plane, seldom recurved; *costa* semi-terete in cross section, usually prominent on the dorsal surface, slightly to clearly delimited, with 2 cells in the ventral epidermis, an internal band of stereids or substereids, and a dorsal epidermis, the three layers ± differentiated; *lamina* 2–3(4)-stratose in the distal half, mainly along the margins, smooth or pseudopapillose; *distal cells* 4–20 × 7–14 μm, isodiametric to short or transversely rectangular, with straight or sinuous walls, plane or bulging, smooth; *proximal paracostal cells* 10–55 × 7–20 μm, green, isodiametric to rectangular (1–6:1), the walls straight or sinuous, uniformly thickened or the transverse walls thicker than longitudinal walls; *proximal marginal cells* 9–50 × 6–20 μm, isodiametric to rectangular (1–5:1), with transverse walls thicker than longitudinal cell walls; or *proximal and paracostal cells* 35–100 × 5.5–25 μm, alike, hyaline, long and narrow (3–10:1), with even, very thin, straight, scarcely discernible walls; *hyaline hair-points* flat or terete at the base, somewhat to strongly flexuous, at times homomallous and twisted, to 2 mm long, denticulate to dentate. *Perichaetial leaves* 1.5–3.1(–4) × 0.4–0.9 mm, convolute and larger (2–3×) or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* plane or terete, flexuous, to 2.8 mm, entire, denticulate or dentate. *Androecia* axillary or terminal. *Setae* straight or curved, to 1.0–4.5 mm long. *Capsules* immersed, emergent or exserted, ovoid, ellipsoid or fusiform, symmetric (seldom slightly asymmetric at base), smooth, stramineous or castaneous; with stomata at the urn base, or lacking stomata; *exothecial cells* 16–70 × 10–55 μm, isodiametric to rectangular (1–4.5:1), thin- or thick-walled; *annulus* simple and persistent or compound and revoluble of 2–3 rows of mostly isodiametric cells 6–10 μm high; *peristome teeth* 35–100 μm wide at the base, entire, perforate in the distal half or cribrose throughout their length and irregularly cleft in the distal ⅔–¾, orange or brown, concolorous or contrasting in color with the urn, outer surface papillose distally and smooth or slightly papillose proximally, inner surface papillose throughout; *opercula* conic to rostrate; *calyptrae* mitrate or cucullate. *Spores* 6.5–14 μm, minutely granulose.

Distribution. All continents.

KEY TO SECTIONS OF *GRIMMIA* SUBG. *ORTHOGRIMMIA*

1a. Proximal marginal cells of leaf ± hyaline and inflated, length/width ratio 3–10:1, walls thin, scarcely discernible, the transverse walls similar to the longitudinal walls; calyptrae mitrate; annulus compound and revoluble .... I. *Grimmia* subg. *Orthogrimmia* sect. *Donnianae*
  2a. Setae straight, to 1 mm; capsules immersed; exothecial cells thick-walled .... 3. *G. triformis*
  2b. Setae straight or curved, longer than 1 mm; capsules emergent or exserted; exothecial cells thin-walled.
    3a. Setae curved; hyaline hair-points to 2 mm, those of the perichaetial leaves strongly flexuous and twisted .... 1. *G. arenaria*
    3b. Setae straight; hyaline hair-points to 1 mm, those of the perichaetial leaves weakly flexuous and not twisted .... 2. *G. donniana*
1b. Proximal marginal cells of leaf neither hyaline nor inflated, length/width ratio 1–4.5(6):1, walls thick, always distinct, the transverse walls thicker than the longitudinal walls; calyptrae cucullate; annulus simple and persistent .... II. *Grimmia* subg. *Orthogrimmia* sect. *Montanae*
  4a. Laminar cells not bulging (Figs. 12e, 16d, 18c).

5a. Stomata present at the urn base .... 8. *G. reflexidens*
5b. Stomata lacking.
    6a. Opercula long-rostrate; setae 2–4 mm long; peristome teeth 50–90 μm wide at mouth, irregularly splitting above and ± cribrose; proximal paracostal leaf cells mostly long-rectangular, to 4.5 : 1; dioicous .... 6. *G. montana*
    6b. Opercula obtuse to mammillate; setae to 2 mm; peristome teeth 40–50 μm wide at mouth, entire or slightly cribrose at apex; proximal paracostal leaf cells isodiametric to rectangular, to 2 : 1; autoicous .... 9. *G. ungeri*
4b. Laminar cell bulging (Figs. 8e, 16e).
    7a. Laminar cells papillose.
        8a. Leaves strongly plicate on both sides of costa .... 5. *G. caespiticia*
        8b. Leaves plane or weakly plicate .... 7. *G. nivalis*
    7b. Laminar cells not papillose.
        9a. Leaves strongly plicate on both sides of costa .... 5. *G. caespiticia*
        9b. Leaves plane or weakly plicate.
            10a. Stomata lacking at the urn base; capsules usually fusiform, castaneous, concolorous with peristome teeth; exothecial cells isodiametric, thick-walled .... 4. *G. alpestris*
            10b. Stomata present at the urn base; capsules ovoid, stramineous, different in color from the orange peristome teeth; exothecial cells irregularly rectangular, thin-walled .... 8. *G. reflexidens*

I. Grimmia (subg. **Orthogrimmia**) sect. **Donnianae** (Loeske) J. Muñoz, comb. et stat. nov. *Grimmia* [unranked] *Donnianae* Loeske, Biblioth. Bot. 101: 110. 1930. TYPE: *Grimmia donniana* Sm.

Autoicous. Plants in compact tufts, green, greenish yellow, or dark green. *Stems* to 2 cm tall, with central strand well developed, sometimes rhizoids present nearly throughout; *axillary hairs* 3–7-celled, 70–160 μm long. *Leaves* erect and appressed or flexuous (occasionally with homomallous tips) when dry, patent to spreading, and flaccid or rigid when moist, 1.3–2.2 × 0.25–0.65 mm, narrowly ovate, acute to acuminate, keeled, plane; *margins* plane; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, smooth or pseudopapillose; *distal cells* 7–11 × 7–14 μm, isodiametric to rectangular or transversely rectangular, plane, smooth; *proximal paracostal and marginal cells* 35–100 × 5.5–25 μm, alike, hyaline, narrowly rectangular (3–10 : 1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* flat or terete at the base, somewhat to strongly flexuous, at times homomallous and twisted, to 2 mm long, denticulate to dentate. *Perichaetial leaves* 1.8–3.1 × 0.4–0.8 mm, convolute and larger (2–3×) or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* plane, flexuous, to 2.8 mm, entire, denticulate or dentate. *Androecia* axillary or terminal. *Setae* straight or curved, to 3.5 mm long. *Capsules* immersed, emergent or exserted, ovoid or ellipsoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothecial cells* 30–70 × 10–46 μm, isodiametric to rectangular (1–4.5 : 1), thin- or thick-walled; *annulus* compound and revoluble of 2–3 rows of isodiametric cells 6–12 μm high; *peristome teeth* 50–100 μm wide at the base, entire, perforate in the distal half or cribrose throughout, irregularly cleft in the distal ⅔–¾, orange, contrasting in color with the urn; *opercula* conic or with a short mammilla; *calyptrae* mitrate. *Spores* 6.5–11 μm.

Distribution. Northern America, Europe, and temperate Asia.

Grimmia subg. *Orthogrimmia* sect. *Donnianae* is characterized by thin-walled proximal marginal cells, mitrate calyptrae, and a compound and revoluble annulus.

1. Grimmia arenaria Hampe, Linnaea 10: 405. 1836. *Grimmia curvula* Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 113, tab. 238. 1845, nom. illeg. incl. sp. prior. *Grimmia incurva* Schleich. ex Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 113. 1845, nom. inval. pro syn. *Grimmia donniana* var. *curvula* Spruce, Musci pyrenaici n° 281, 1847. *Grimmia donniana* subsp. *arenaria* (Hampe) Dixon, Stud. Handb. Brit. Mosses Ed. 2: 155. 1904. *Grimmia donniana* var. *arenaria* (Hampe) Loeske, Laubm. Eur. Part I: 93, figs. 1c, 17a, 26b, 28. 1913. TYPE: [Germany. Magdeburg:] Regenstein Hercyn[iae], June, *Hampe s.n.* (lectotype, here designated, BM; isolectotype, FH).

Illustrations. Figure 2; Bruch et al. (1845: tab. 238, *sub G. curvula*).

Autoicous. Plants in hoary tufts, dark-green to blackish. *Stems* to 1.5 cm tall, with central strand

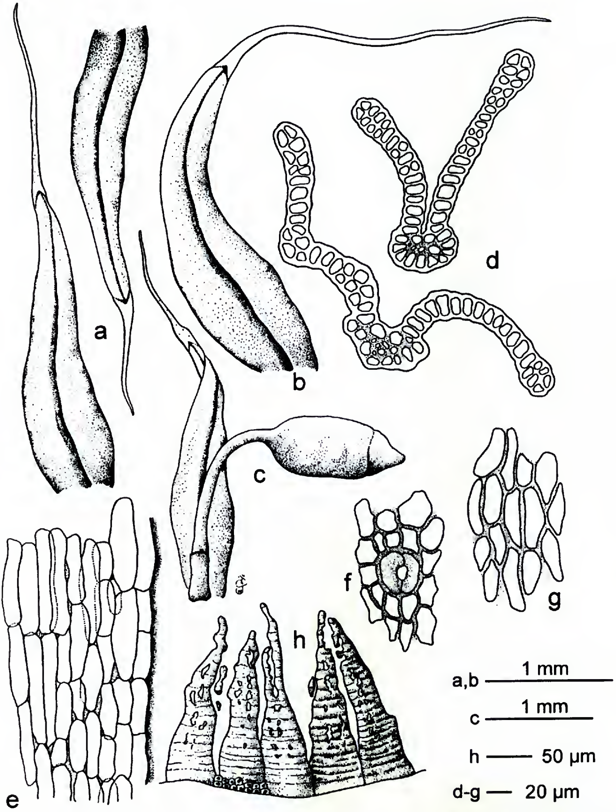

Figure 2. *Grimmia arenaria.* —a. Leaves. —b. Perichaetial leaf. —c. Sporophyte and perichaetial leaf. —d. Transverse sections of leaf. —e. Proximal leaf cells. —f. Proximal exothecial cells and stoma. —g. Medial exothecial cells. —h. Annulus and peristome teeth. [a, d–h, *Garovaglio s.n.* (G); b, *Spruce*, Musci Pirenaici n° 281, (TCD).]

well developed; *axillary hairs* 5–7-celled, 140–160 μm long. *Leaves* erect (occasionally with the tips homomallous) when dry, patent to spreading, flaccid when moist, 1.3–2.2 × 0.25–0.65 mm, narrowly ovate, acute to acuminate, keeled, not plicate; *margins* plane; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, occasionally pseudopapillose; *distal cells* 7–10 μm, transversely rectangular to isodiametric or rectangular, plane, smooth; *proximal paracostal and marginal cells* 35–95 × 8–25 μm, alike, hyaline, narrowly rectangular (3–10 : 1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hairpoints* flat, strongly flexuous, usually homomallous and twisted, to 2 mm long, rarely shorter than 1 mm, denticulate to dentate. *Perichaetial leaves* 1.8–

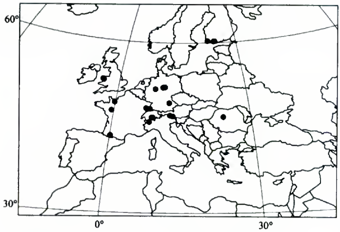

Figure 3. Distribution of *Grimmia arenaria.*

2.6 × 0.4–0.7 mm, similar to vegetative leaves but slightly larger; *hyaline hair-point* similar to those of vegetative leaves but longer, to 2.8 mm. *Androecia* terminal. *Setae* curved, ca. 2 mm long. *Capsules* exserted or, more commonly, emergent among the perichaetial leaves, ovoid, symmetric, stramineous, with stomata at the urn base; *exothecial cells* 30–55 × 10–20 μm, rectangular (1.5–4.5:1), thin-walled; *annulus* compound and revoluble of 2–3 rows of isodiametric cells 10 μm high; *peristome teeth* 50–90 μm wide at the base, perforate in the distal part, eroded and irregularly divided in 2–3 branches, orange, contrasting in color with the urn; *opercula* conic or mammillate; *calyptra* mitrate. *Spores* 6.5–10.5 μm.

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Hyaline hair-points very long, to 2 mm, twisted and usually homomallous. (3) Capsules emergent and facing down among the perichaetial leaves. (4) Setae short and curved. (5) Annulus compound and revoluble. (6) Peristome teeth 50–90 μm wide at the base, perforate in the distal part, eroded and irregularly divided in 2–3 branches.

Distribution (Fig. 3). Central and western Europe, Finland, and Great Britain; open areas from 10 to 1800 m elevation, on dry sandstone and slate. Mature sporophytes were present in 100% of the studied specimens.

This species is distinguished at first sight by the curved setae and small ovoid capsules emerging among the long and twisted hair-points.

With more than half (ca. 68%) of the samples studied from the vicinity of Regenstein (Germany), the type locality, low variability may be expected. Indeed, this taxon varies only in the length of the hyaline hair-points, which only rarely is less than 2 mm. Even the shorter points are strongly curled and flexuous, a feature not seen in other species of the subgenus.

Grimmia arenaria has been treated mostly as an infraspecific taxon of *G. donniana,* both as a subspecies (e.g., Dixon, 1904: 155) and a variety (e.g., Podpěra, 1954: 280). Only recently have Greven (1994, 1995: 44–47) and Touw and Rubers (1989: 212–213) agreed with Limpricht's (1890: 735–736) view that this taxon should be treated at the specific level.

Selected specimens examined (155). AUSTRIA. **Carinthia:** im Kressbrünngraben bei Raibl, *Breidler s.n.* (BP-36050). **Tirol:** Innervillgraten, *Gander s.n.* (BP-36053). FINLAND. **Turku ja Pori:** Lojo, Karkalinniemi, 5 Aug. 1880, *Lindberg s.n.* (G). FRANCE. **Isère:** mt. de Isans, Aug. 1860, *Ravaud s.n.* (TRH). **Maine-et-Loire:** Angers, *Schimper s.n.* (S). **Pyrénées Centrales:** in fauce dict. la Gorge de Labassère, *Spruce s.n.* (NY). **Vosges:** Le Hohneck, *Boulay s.n.* (FH). GERMANY. **Baden-Württemberg:** Südl. Schwarzwald, nahe südwarde du Gipfel des Schauinsland, Aug. 1925, *Schmidt s.n.* (JE). **Magdeburg:** Blankenburg, Regenstein, 23 Mar. 1902, *Janzen s.n.* (JE). ITALY. Biellese ne'monti dell'Oropa e di S. Giovanni d'Andorno, Aug. 1861, *Cesati s.n.* (G). ROMANIA. Siebenbürgen, Alpe Paring, *Péterfi s.n.* (BP-36055). SPAIN. **Lérida:** Vallferrera, *Casas s.n.* (IBA-3952). SWITZERLAND. **Tessin:** Fusio, July 1908, *Trautmann s.n.* (S). UNITED KINGDOM. **Wales:** Merioneth, Talsarnan, Harlech, Sep. 1911, *Rhodes s.n.* (S).

2. Grimmia donniana Sm., Engl. Bot. 18: pl. 1259. 1804. *Grimmia sudetica* Schwägr., Sp. Musc. Frond. Suppl. 1(1): 87, tab. 24. 1811, nom. illeg. incl. sp. prior. *Grimmia donnii* Gray, Nat. Arr. Brit. Pl. 1: 728. 1821, nom. illeg. *Dryptodon donnianus* (Sm.) Hartm., Handb. Skand. Fl. Ed. 3: 270. 1838. *Grimmia obtusa* var. *donniana* (Sm.) Hartm., Handb. Skand. Fl. Ed. 5: 377. 1849 (1850?). *Grimmia donii* Sm. ex Lindb., Musci Scand. 30. 1879, nom. illeg. *Grimmia donniana* var. *eudonniana* Loeske, Laubm. Eur. Part I: 91. 1913, nom. inval. *Guembelia donniana* (Sm.) Loeske, Laubm. Eur. I: 90. 1913, nom. inval. *Grimmia donniana* subsp. *eudonniana* Giacom., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, ser. 5, 4: 221. 1947, nom. inval. TYPE: [United Kingdom. Caernarvon:] North Wales, Beddgelart, July 1802, *Turner s.n.* (lectotype, here designated, BM).

Grimmia obtusa Schwägr., Sp. Musc. Frond. Suppl. 1(1): 88, tab. 25. 1811, nom. illeg., non Brid., 1801. *Grimmia donniana* var. *obtusa* (Schwägr.) Steud., Nomencl. Bot. 2: 189. 1824. *Dryptodon erostris* Hartm., Handb. Skand. Fl. Ed. 4: 374. 1843, nom. illeg. incl. sp. prior. TYPE: [Austria.] Glockner, *Kaulfuss s.n.* (holotype, G; isotype, G).

Grimmia sudetica Spreng. ex Schkuhr, Deutschl. Krypt. Gew. Heft 2: 48, Tab. 22. 1811. *G. donniana* f. *sudetica* (Spreng. ex Schkuhr) Loeske, Biblioth. Bot. 101: 113. 1930, nom. illeg., non Chal. 1882. TYPE:

[Poland. Sudety. *Ludwig s.n.*] "Kryptogamische Gewächse der Riesengebirgen. Laubmoose" [handwritten label, not the original of Ludwig's exsiccata] (lectotype, here designated, M).

Grimmia donniana var. *bohemica* Schkuhr ex Brid., Bryol. Univ. 1: 176. 1826. *Grimmia bohemica* Schkuhr ex Steud., Nomencl. Bot. 2: 188. 1824, nom. inval. pro syn. *Grimmia donniana* var. *bohemica* Schkuhr ex Steud., Nomencl. Bot. 2: 189. 1824, nom. inval. pro syn. TYPE: [Poland.] Schneekoppe Sudetum, 1814, *Ludwig s.n.* (lectotype, here designated, B).

Illustrations. Figure 4; Bruch & Schimper (1845: tab. 249, *sub G. obtusa*); Cao and Vitt (1986: figs. 15, 16a–c); Chałubiński (1882: tab. 7 fig. 11); Deguchi (1978: fig. 27); Ignatov and Cao (1994: fig. 10, but not figs. 8, 9); Jóhannsson (1993: fig. 32); Limpricht (1890: fig. 198); Noguchi (1988: fig. 140B); Nyholm (1956: fig. 69F).

Autoicous. Plants in tufts, greenish yellow above, dark green to blackish below. *Stems* to 1.5 cm tall, with central strand well developed; *axillary hairs* 4–5-celled, 90–125 μm long. *Leaves* erect and appressed (occasionally with the tips somewhat flexuous) when dry, patent and rigid when moist, 1.3–2.2 × 0.25–0.60 mm, narrowly ovate, acute to acuminate, keeled, plane; *margins* plane; *costa* semiterete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, occasionally pseudopapillose; *distal cells* 7–11 × 7–9 μm, isodiametric to rectangular (1–1.5 : 1), plane, smooth; *proximal paracostal and marginal cells* 38–80 × 5.5–15.0 μm, alike, hyaline, narrowly rectangular (4–9 : 1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* terete or flat when longer, slightly flexuous, usually to 1 mm long (seldom to 2 mm and then strongly flexuous), smooth to weakly denticulate. *Perichaetial leaves* 2.0–2.5 × ca. 0.8 mm, convolute and larger than vegetative leaves (2.0–2.5×); *hyaline hair-points* slightly flexuous when short, strongly so when longer, to 2.2 mm, smooth or denticulate. *Androecia* axillary or terminal. *Setae* erect and straight, to 3.5 mm long. *Capsules* exserted, ovoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothecial cells* 35–55 × 24–46 μm, isodiametric to rectangular (1–2 : 1), thin-walled; *annulus* compound and revoluble of 2–3 rows of isodiametric cells 10–12 μm high; *peristome teeth* 50–70 μm wide at the base, entire or weakly broken at the tips, orange, contrasting in color with the rest of the sporophyte; *opercula* conic or mammillate; *calyptrae* mitrate. *Spores* 7–11 μm.

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Hyaline hair-points to 1 mm, slightly flexuous, seldom longer (to 2 mm) and then more flexuous. (3) Capsules exserted. (4) Setae straight, to 3.5 mm. (5) Annulus compound and revoluble. (6) Peristome teeth 50–70 μm wide at the base, entire or only slightly cleft at the tip.

Distribution (Fig. 5). Common in Europe, it is scattered through Siberia, Nepal, Japan, North America, and Greenland; open areas and forests from 80 to 3800 m elevation on all types of noncalcareous rocks. Mature sporophytes were present in 96.5% of the specimens studied.

Grimmia donniana is rather stenotypic and easy to recognize because of its hyaline proximal cells, straight setae, and exserted capsules. The most variable features are the length and twisting of the hair-points, but they are rarely as long and flexuous as in *G. arenaria*. However, I have studied two puzzling specimens in which the variation observed is difficult to interpret. *Chernyadjeva 37* (Kamchatka, Kosheleva volcano, LE) exhibits some cucullate calyptrae, but this is the only deviant feature observed and is here considered an abnormality. Another anomalous specimen is *Sharp 4761 p.p.* (Mexico, Popocatépetl, TENN). It has the shortest setae seen in *G. donniana* (i.e., 1 mm) and the capsules are mostly immersed, approaching *G. triformis*. Nevertheless, it matches typical *G. donniana* in all other respects, especially in the thin-walled exothecial cells and the entire and narrow peristome teeth.

See comments under *Grimmia arenaria* and *G. triformis* for differences between these species and *G. donniana.*

Most collections from eastern North America identified as *G. donniana* are specimens of *G. incurva* Schwägr. with nearly straight seta and autoicous inflorescence. The latter species can be distinguished from *G. donniana* by its longer, narrower, and more acuminate leaves, which are crisped and contorted when dry.

Grimmia sudetica Schwägr. was considered the legitimate name for *G. alpestris* by Geissler and Maier (1995: 503). However, in the original publication, Schwägrichen (1811: 87) cited *G. donniana* as a synonym of his new species, which thereby became illegitimate (Muñoz, 1998).

Grimmia donniana has a non-continuous, circumboreal distribution. It is quite common in mountainous areas in central and northern Europe, but becomes rare toward the south and the east. In North America, it is known from scattered localities in the United States and Mexico. In Asia *Grimmia donniana* is rare, growing on Honshu (as cited hereunder) and Hokkaido (Deguchi, 1978: fig. 28), Japan, and from the Altai Mountains and Tibet in

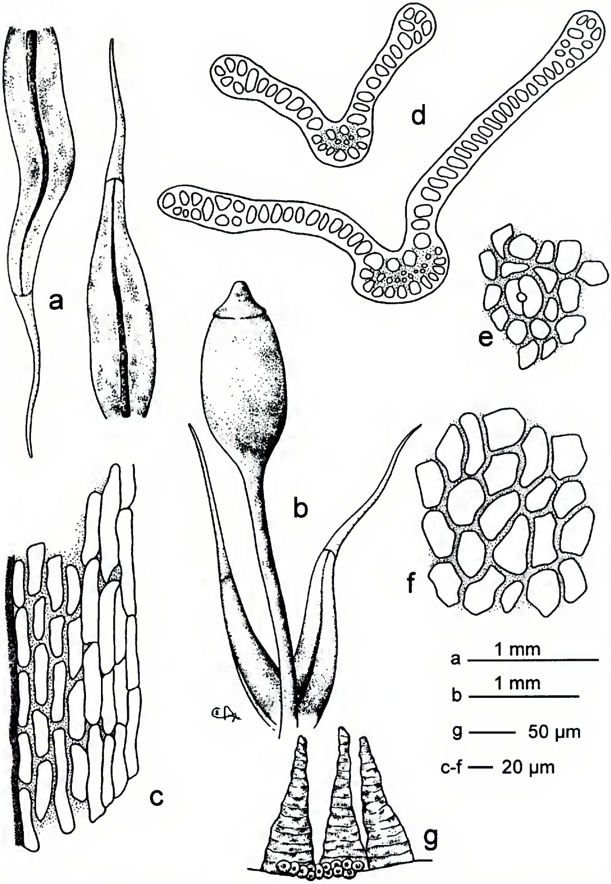

Figure 4. *Grimmia donniana.* —a. Leaves. —b. Sporophyte and perichaetial leaves. —c. Proximal leaf cells. —d. Transverse sections of leaf. —e. Proximal exothecial cells and stoma. —f. Medial exothecial cells. —g. Annulus and peristome teeth. [a–g, *Turner s.n.* (BM).]

continental Asia. Two of the three Tibetan reports (Cao & Vitt, 1986: 161) actually pertain to *G. elongata* Kaulf. (*Lang Kaiyong 598*, ALTA) and *G. longirostris* Hook. (*Lang Kaiyong 5302*, ALTA).

Grimmia donniana has also been reported from Africa (Ochyra & Sharp, 1988: 344) and Antarctica (Bartram, 1957: 141; Kuc, 1969; Savicz-Lyubitskaya & Smirnova, 1969). However, the collections from these areas studied by me represent other taxa (e.g., *G. kidderi*, *G. lawiana*, or *G. reflexidens*).

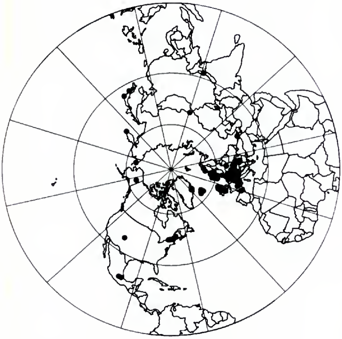

Figure 5. Distribution of *Grimmia donniana.*

Selected specimens examined (380). AUSTRIA. **Carinthia:** im Kremsthale, *Breidler s.n.* (BP-36075). **Salzburg:** Speiereck im Zimgau, 8 Aug. 1887, *Schliephacke s.n.* (GOET). **Steiermark:** im Schöttalgraben bei Oberwölz, *Breidler* (BP-36077). **Tirol:** Innervillgraten, 1 Sep. 1892, *Gander s.n.* (TRH). CZECH REPUBLIC. Bohemia, Montes Krkonoše, vallis Obří důl, Apr. 1949, *Pilous s.n.* (H); Riesengebirge, Felstrümmer der Schneekoppe, July 1887, *Limpricht s.n.* (RO); Tatra Magna, montis Nagymorgár, supra lacu Zelene pleso-Zöldló, *Vajda s.n.* (BP-74869). FRANCE. **Vosges:** prope Lacum viridem, *Mougeot & Nestler s.n.* (FH). **Haute-Loire:** Le Mégal, *Wallace & Cuynet s.n.* (BP-112577). **Puy-de-Dôme:** sous le sommet du Puy-de Dôme, *Pierrot s.n.* (BP-112575). **Pyrénées Centrales:** au sommet du port d'Oo, 5 Sep. 1856, *Zetterstedt s.n.* (TRH). **Savoie:** Pralognan, cirque de l'Arcelin, *Parriat s.n.* (BP-112578). GEORGIA. **South Ossetia Autonomous Oblast:** Dzhavskij rajon, Ermani, 9 Sep. 1946, *Abramov s.n.* (LE). GERMANY. **Bavaria:** Bayerischer Wald, Arberkuppe, *Progel s.n.* (BP-36101). **Bayern:** auf dem Ochsenkopf, *Funck s.n.* (RO); bei Annaberg, *Weicker s.n.* (BP-36102). **Karl-Marx Stadt:** Bärenstein, *Kopsch s.n.* (BP-112572). **Magdeburg:** Regenstein bei Blankenburg, *Itzigsohn s.n. 1843* (S). **Niedersachsen:** Oberharz, Luisenklippen auf dem Quitschenberg zwischen Torfhans und Oderbrücke, 11 July 1988, *Heimhold s.n.* (GOET). **Rhön:** Gipfel der Milseburg, *Anonymous s.n.* (BP-36108). **Saxonia:** prope Altenberg, *Rabenhorst s.n.* (BP-80338). **Thüringia:** *Schmidt s.n.* (GLM-2850). HUNGARY. Montes Szeben, prope Paltanis, *Vajda s.n.* (BP-73974). ICELAND. North Iceland, Bakrangi area, above farm Nipá, NE of Akureyri, 1 July 1964, *Steere s.n.* (NY); South Iceland, Skaftafell, *Aptroot 4974* (NY); hill near Grötta by Rejkjavik, *Andrews 1/2* (NY). IRELAND. Down, Mourne Mts., Slieve Donard, Ballagh Park, 15 Oct. 1884, *Lett s.n.* (TCD). ITALY. Mte. S. Gottardo, July 1853, *Franzoni s.n.* (RO); Rima, precipizii del Mte. Tagliaferro, 19 Aug. 1863, *Carestia s.n.* (RO). JAPAN. Toyama Prefecture, Mt. Tateyama, 11 Aug. 1955, *Iwatsuki s.n.* (G); prov. Iwashiro, mt. Iida, *Ishiba 1331* (H-BR). NORWAY. **Bergen:** Arstad, mellem Haulelandsvadtnet og Kronstad, 9 Sep. 1871, *Wulfsberg s.n.* (TRH). **Kristiams:** Lom, Bäverdalen, Röshejm, 19 Aug. 1887, *Hagen s.n.* (FH). **Sondre Trondhjem:** Stören, Rognes, 16 July 1884, *Hagen s.n.* (TRH). POLAND. Between Wolowiec and Klin, *Chałubiński s.n.* (BP-36084); Beskidy Zachodnie Mts., Babia Gora Mt., ad declivitatem meridionalem sub cacuminem Głwniak, *Wojterski s.n.* (BP-112978); Sudetes Mts., Karkonosze Range, Jelenia Gora-Zaborze, *Prager s.n.* (BP-6071). ROMANIA. **Beszterce-Naszód:** Mt. Rodnai havasok, cacuminis montis Ünökö, *Péterfi s.n.* (BP-112955). **Brasov:** montes Fogarasi havasok, vallis Arpasul, *Vajda s.n.* (BP-70413). **Maramureş :** sept. jugi Lunca ciasa sub monte Toroiaga prope pagum Borsabánya, *Boros s.n.* (BP-112954). **Szeben:** Cibin, ad "Wasserleitungs-Weg" supra Hohe Rinne *Boros s.n.* (BP-112947). RUSSIA. **Gorno Altayskaya Autonomous Oblast:** Altai Mountains, Trekhglavaya Peak, *Zolotukhin s.n.* (IBA-7025). **Kamchatka:** slopes of Kosheleva volcano, *Chernyadjeva 37* (LE). **Magadan:** Chukotka peninsula, Lake Ioni, 5 July 1977, *Afonina s.n.* (LE). SLOVAKIA. **Gömör:** merid. montis Ökörhegy pr. Rozsnyó, *Boros s.n.* (BP-112915). **Špis:** in jugo "Lorenz-Joch" supra lacum "Wahlenberg See," *Degen s.n.* (BP-112900); Liptovské hole, Plačlivé, *Pilous s.n.* (BP-112584). SWEDEN. **Nordvestra:** Härjedalens, Helagsfjället, Aug. 1913, *Smith s.n.* (TRH). **Sule Lappmark:** Rvihhjohk Njammsts, 15 July 1891, *Ryan s.n.* (IBA-4128). SWITZERLAND. **Unterwalden:** Engelberg, bei der Klostersennerei Seerenrüti, July 1859, *Cramer s.n.* (RO). **Tessin:** Fusio, July 1908, *Trautmann s.n.* (TRH). **Valais:** Vallon d'Arpettas, 30 Aug. 1889, *Bernet s.n.* (FH). TIBET. Yatong County, *Zang 669* (ALTA). UKRAINE. Ukrainian Carpathians, Chornogora range, Turkul Mt., *Partyka s.n.* (IBA-6993). UNITED KINGDOM. **England:** Cumberland, Grange, Apr. 1870, *Borrowdale s.n.* (FH). **Wales:** Carnarvonshire, Capel Curig, Feb. 1880, *Bleckelt s.n.* (FH).

MEXICO. **México:** Popocatépetl, *Sharp 4761 p.p.* (TENN). **Veracruz:** monte Orizaba, *Galeotti s.n.* (PC). GREENLAND. Runde Fjeld (the summit), 12 May 1892, *Hartz s.n.* (NY). U.S.A. **Alaska:** Circle Quadrangle: vicinity of Eagle Summit, Mile 105–108 Steese Highway, *Steere 72–895* (NY). **Colorado:** Clear Creek Co., S side, Summit Lake, Mount Evans, *Weber 7769* (FH). **Maine:** Piscataquis Co., Abol Slide, W slope of mt. Katahdin, *Hermann 19276* (G). **New Hampshire:** Mt. Washington, 12 Aug. 1939, *Harring, Wickes & Grout s.n.* (FH). **New York:** Essex County trail from Adirondack Loj to Algonquin Peak of the MacIntyre Mountains, *Redfearn 13325* (MO).

3. Grimmia triformis Carestia & De Not., Comment. Soc. Crittog. Ital. 2: 102. 1866. *Grimmia donniana* var. *triformis* (Carestia & De Not.) Loeske, Laubm. Eur. Part I: 96, figs. 26d, 30. 1913. TYPE: [Italy. Vercelli:] In Tagliaferro, a quelche metro sotto la veta sul versante di Rima, 19 Aug. 1963, *Carestia s.n.* (lectotype, here designated, BM; isolectotypes, BM [2 replicates], BP-37541, JE).

Grimmia ganderi Limpr., Jahresber. Schles. Ges. Vaterl. Cult. 61: 215. 1884. *Grimmia donniana* var. *breviseta* Breidl. ex Loeske, Laubm. Eur. Part I: 95. 1913. TYPE: [Austria.] Tirol, Innervillgraten, "Kalchstein" 4400 ft., 15 Mar. 1884, *Gander s.n.* (lectotype, here designated, BP-37547; isolectotypes, JE [2 replicates], H).

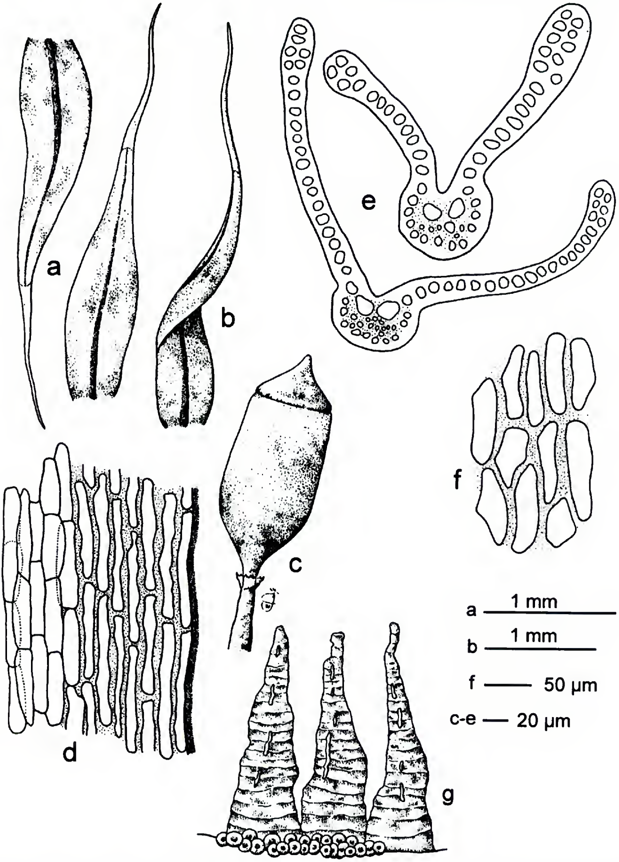

Figure 6. *Grimmia triformis.* —a. Leaves. —b. Perichaetial leaf. —c. Sporophyte. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothecial cells. —g. Annulus and peristome teeth. [a, c, d, f, *Gander s.n.* (BP-37547); b, e, *Gander s.n.* (BP-37549).]

Illustrations. Figure 6; Ignatov and Cao (1994: fig. 5, *sub Coscinodon cribrosus*); Limpricht (1890: figs. 196, 197).

Autoicous. Plants in tufts, green. *Stems* to 2 cm tall, with central strand weakly developed; rhizoids abundant to middle of stems; *axillary hairs* 3-celled, ca. 70 µm long. *Leaves* erect and flexuous when dry, patent and flaccid when moist, 1.5–2.2 × 0.3–0.5 mm, narrowly ovate, acute, keeled, plane; *margins* plane; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half,

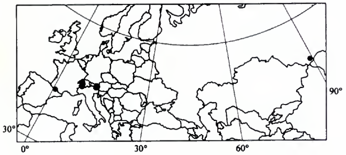

Figure 7. Distribution of *Grimmia triformis.*

occasionally pseudopapillose; *distal cells* 7–9 × 7–14 μm, isodiametric to rectangular (1–1.5 : 1), plane, smooth; *proximal paracostal and marginal cells* 40–100 × 7–18 μm, alike, hyaline, narrowly rectangular (3–10 : 1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* flat, flexuous, to 1.3 mm long, denticulate. *Perichaetial leaves* 2.5–3.1 × 0.8 mm, convolute and larger than vegetative leaves, yellowish at the base; *hyaline hair-points* flat, strongly flexuous, to 2 mm, denticulate. *Androecia* terminal. *Setae* erect and straight, to 1 mm long. *Capsules* immersed, ovoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothecial cells* 46–75 × 10–21 μm, irregularly rectangular (2–4 : 1), thick-walled; *annulus* compound and revoluble of 2 rows of isodiametric cells 6–10 μm high; *peristome teeth* 70–100 μm wide at the base, cribrose throughout and irregularly cleft in the distal ⅔–¾, orange, contrasting in color with the urn; *opercula* conic or mammillate; *calyptrae* mitrate. *Spores* 8–11 μm.

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Capsules immersed. (3) Setae erect and straight and very short (to 1 mm). (4) Annulus compound and revoluble. (5) Peristome teeth 70–100 μm wide at the base, cribrose throughout and irregularly cleft in the apical ⅔–¾.

Distribution (Fig. 7). Very rare, known only from the European Alps and Pyrénées, and from an outlying locality in the Altai Mountains of Siberia; in open areas above the tree-line between 1385 and 4500 m elevation on non-calcareous rocks. Mature sporophytes were present in 100% of the specimens studied.

This seldom-collected taxon hardly varies, and is well characterized by sporophyte features. *Grimmia triformis* can only be confused with *G. donniana*, from which it is nearly indistinguishable gametophytically. The most conspicuous difference is the included sporophytes of *G. triformis*; those of *G. donniana* are exserted. Other characters separating these species are the wider (70–100 μm), cribrose peristome teeth and thick-walled exothecial cells of *G. triformis* versus the narrower (50–70 μm), entire peristome teeth and thin-walled exothecial cells of *G. donniana*. Some collections of *G. triformis* have been identified as *Coscinodon cribrosus* (Hedw.) Spruce (Ignatov & Cao, 1994: 76), which also has included capsules, but the shape of the proximal laminar cells precludes any confusion.

Selected specimens examined (33). AUSTRIA. **Salzburg:** Rauriser Goldberg, *Mielichhofer s.n.* (BP-36855, p.p.). **Tirol:** Innervillgraten, "Kalchstein," *Gander s.n.* (BP-37549). FRANCE. **Haute-Garonne:** Port de Benasque, *Pierrot s.n.* (BCB-2578). ITALY. **Vercelli:** Alpes Penninae Pedemontii, in monte Tagliaferro, prope cacumen, 19 Aug. 1863, *Carestia s.n.* (JE). RUSSIA. **Gorno Altayskaya Autonomous Oblast:** Altai Mountains, Kobiguayuk Creek, *Ignatov 0/474* (IBA-6997). SWITZERLAND. **Bern:** Fungfraujoch am den "Hotelfelsen," *Kol & Chorus s.n.* (BP-80466, p.p.).

II. **Grimmia** (subg. **Orthogrimmia**) sect. **Montanae** I. Hagen, Kongel. Norske Vidensk Selsk. Skr. (Trondheim) 1909(5): 16. 1909. TYPE: *Grimmia montana* Bruch & Schimp.

Autoicous or *dioicous. Plants* in compact tufts, seldom fragile, glaucous, green, olive-green, or brownish green above, blackish below. *Stems* to 1.5 cm tall, with central strand well developed, seldom with rhizoids the entire stem length; *axillary hairs* 3–8-celled, 50–175 μm long. *Leaves* erect and appressed or flexuous when dry, erect to spreading, sigmoid or straight, and flaccid or rigid when moist, 0.8–2.0 × 0.26–0.65 mm, narrowly ovate to ovate, acute to acuminate, keeled (occasionally weakly), plane or plicate; *margins* plane or partially recurved at the base; *costa* semi-terete, usually prominent on the dorsal surface, slightly to distinctly delimited; *lamina* 2–3(4)-stratose in the distal half, smooth; *distal cells* 4–20 μm, isodiametric, plane or bulging, smooth or papillose; *proximal paracostal cells* 10–55 × 7–20 μm, not hyaline, isodiametric to rectangular (1–6 : 1), the walls straight, the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 9–50 × 6–20 μm, isodiametric to rectangular (1–5 : 1), with straight walls uniformly thickened or the transverse walls thicker than longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm long, smooth or denticulate (serrate, with many acute teeth in some populations of *G. montana*). *Perichaetial leaves* 1.5–2.8(–4) × 0.5–0.9 mm, convolute and larger (2–3×) than vegetative leaves; *hyaline hair-points* terete, straight, to 1.5 mm, nearly smooth. *Androecia* axillary or terminal. *Setae* erect and straight or somewhat curved, 1–4.5 mm long. *Capsules* exserted, ovoid, ellipsoid or fusiform, symmetric (seldom slightly asymmetric at base), smooth, stramineous to castaneous, with stomata at the urn base or lacking stomata; *exothecial cells* 16–70 × 10–55 μm, isodiametric to rectangular (1–4:1), thin- or thick-walled; *annulus* simple and persistent; *peristome teeth* 35–90 μm wide at the base, entire, split and cribrose or irregularly 2–3 cleft in the distal half, castaneous or orange, concolorous or contrasting in color with the urn; *opercula* conic, mammillate or rostrate; *calyptrae* cucullate. *Spores* 9–14 μm.

Distribution. All continents.

Grimmia subg. *Orthogrimmia* sect. *Montanae* is characterized by proximal marginal cells with the transverse walls thicker than the longitudinal walls, cucullate cayptrae, and a simple and persistent annulus.

4. **Grimmia alpestris** (Schleich. ex F. Weber & D. Mohr) Schleich., Cat. Pl. Helv. Ed. 2: 29. 1807 [1808]. *Grimmia alpestris* Schleich., Neues J. Bot. 1: 196. 1806 [1805], nom. inval. *Trichostomum pulvinatum* var. *alpestre* Schleich. ex F. Weber & D. Mohr, Bot. Taschenbuch 110. 1807. *Campylopus pulvinatus* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Brid., Muscol. Recent. Suppl. 4: 75. 1819. *Dryptodon pulvinatus* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Brid., Bryol. Univ. 1: 198. 1826. *Grimmia donniana* var. *sudetica* Huebener, Muscol. Germ. 175. 1833, nom. illeg. incl. var. prior. *Grimmia donniana* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Hampe, Flora 20: 281. 1837. *Guembelia alpestris* (Schleich. ex F. Weber & D. Mohr) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. *Grimmia alpestris* var. *eualpestris* Loeske, Laubm. Eur. Part I: 101, figs. 25b, 27a–c. 1913, nom. inval. TYPE: [Switzerland. Valais:] In M[onte]. Sylvio, *Schleicher s.n.* [Schleicher, Plantae cryptogamae helvetiae, n° 13] (lectotype, designated by Muñoz (1998), BM).

Grimmia holzingeri Cardot & Thér., in Holz., Bot. Gaz. 30: 123, tab. 11 fig. 2. 1900. *Grimmia alpestris* var. *holzingeri* (Cardot & Thér.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 31, pl. 9. 1933. *Grimmia donniana* var. *holzingeri* (Cardot & Thér.) Wijk & Margad., Taxon 9: 190. 1960. TYPE: [U.S.A.] Montana: Flathead Co., vicinity of Lake McDonald, 4 mi. N of Belton, a station 30 mi. E of Kalispell, 6000–7000 ft., 25 July 1898, *Holzinger & Blake s.n.* (lectotype, here designated, PC; isolectotypes, NY, PC).

Illustrations. Figure 8; Abramov and Abramova (1983: figs. 27, 9–12); Maier and Geissler (1995: fig. 24, *sub G. sudetica*).

Dioicous. Plants in compact tufts, glaucous or green above and blackish below. *Stems* to 1.5 cm tall, with central strand well developed; *axillary hairs* 5–6-celled, 100–145 μm long. *Leaves* erect, appressed, and straight when dry, patent to spreading and somewhat flaccid when moist, 1–1.6 × 0.3–0.5 mm, ovate, acute, keeled, plicate, sometimes weakly so, plicae cells undifferentiated or more commonly longer and narrower than the other laminar cells; *margins* plane proximally and incurved at the apex; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2(–3)-stratose in the distal ⅔, smooth; *distal cells* 8–13 μm, isodiametric, bulging, smooth; *proximal paracostal cells* 10–35 × 8–20 μm, isodiametric to rectangular (1–3.5:1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* always with the transverse walls clearly thicker than the longitudinal walls, otherwise similar to the proximal paracostal cells; *hyaline hair-points* terete, straight, to 1 mm long, nearly smooth. *Perichaetial leaves* 2–2.5 × 0.75–0.9 mm, convolute and larger than vegetative leaves (2–3×); *hyaline hair-points* straight, to 1.5 mm, nearly smooth. *Androecia* terminal. *Setae* erect and straight, 2–4 mm long. *Capsules* exserted, mostly fusiform, seldom ovoid and then with a narrowed mouth, symmetric, smooth, castaneous, lacking stomata; *exothecial cells* 16–35 × 16–55 μm, isodiametric (1[2]:1), thick-walled; *annulus* simple and persistent; *peristome teeth* 50–70 μm wide at the base, entire or irregularly cleft in the apical part, brownish, concolorous with the urn; *opercula* conic or with a short and obtuse mammilla; *calyptrae* cucullate. *Spores* (9)10–13(–14) μm.

Diagnostic characters. (1) Lamina 2(–3)-stratose and plicate. (2) Cells always bulging. (3) Capsules mostly fusiform, castaneous, lacking stomata. (4) Exothecial cells ± isodiametric with thick walls.

Distribution (Fig. 9). Common in mountain chains in Europe and western North America, but known only from scattered localities in the intervening Asian areas. Mostly in open areas above the tree-line, between 1500 and 3400 m elevation on dry, exposed siliceous rocks. Mature sporophytes were present in 89.6% of the specimens studied.

Grimmia alpestris is somewhat variable. The amount of cuticular wax and consequent glaucous color vary according to habitat conditions. A greater amount of cuticular wax develops in dry and sunny habitats. The capsules are usually fusiform, but ovoid capsules are occasionally found.

Grimmia alpestris is easily distinguished from *G. reflexidens* when sporophytes are present. Diagnostic characters are the color and shape of the cap-

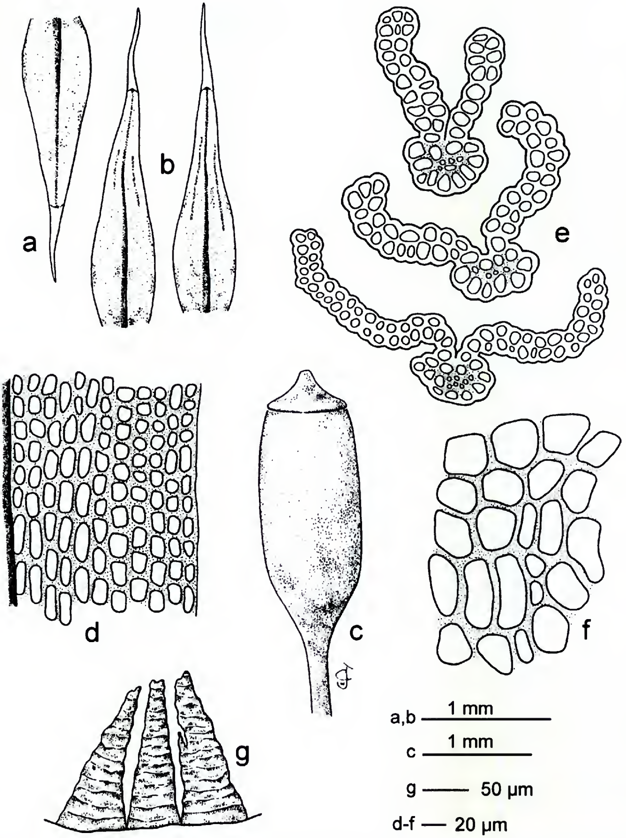

Figure 8. *Grimmia alpestris.* —a. Non-plicate leaf. —b. Plicate leaves. —c. Capsule. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothecial cells. —g. Peristome teeth. [a, c, f, g, *Vajda s.n.* (BP-64281); b, d, e, *Schleicher s.n.* (JE).]

sules: brown and fusiform with the base attenuated into the seta in *G. alpestris* (Fig. 8c); stramineous and ovoid and abruptly connected with the seta in *G. reflexidens* (Fig. 16b). Dissecting capsules to study the shape of the exothecial cells and search for stomata may sometimes be necessary: *G. alpestris* has isodiametric, thick-walled exothecial cells and lacks stomata, whereas the exothecial cells in *G. reflexidens* are rectangular and thin-walled, and 4–8 stomata can be found at the urn base.

On the other hand, sterile specimens can be difficult to name. When present, a diagnostic feature is the recurved margin of *G. reflexidens* (always plane in *G. alpestris*). The axillary hair-points are

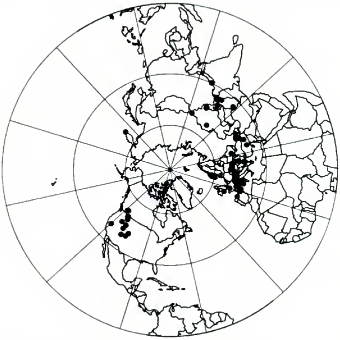

Figure 9. Distribution of *Grimmia alpestris.*

also useful: in *Grimmia alpestris,* they are 5–6-celled and 100–145 μm long, whereas in *G. reflexidens* they are 3–4(–5)-celled and 50–85 μm long.

Geissler and Maier (1995) and Maier and Geissler (1995) have employed the name *G. sudetica* Schwägr. for this taxon. This is an illegitimate name, however, as noted by Muñoz (1998).

Grimmia alpestris has a discontinuous circumboreal distribution pattern. It has a western Europe–western North America disjunct distribution, and is not known from eastern North America or most of Asia. While this species is very likely absent from North America east of the Rocky Mountains, the lack of records from temperate Asian regions probably has more to do with undercollection. This species is typically associated with mountain chains: the Swiss Alps, the Fennoscandian Alps, the Balkans, the Carpathians s.l., and the Pyrenees in Europe, the Rocky Mountains in western North America, and the Altai, Caucasus, and Northwest-Himalayan chains in Asia. Bardunov (1974: 40) reported this species from the western Sayan Mountains (Russia, Krasnoyarsk Kray), but I was unable to obtain these specimens on loan.

Selected specimens examined (234). AFGHANISTAN. Panjskir Valley, Ruka, *Köie s.n.* (IBA-4770). ANDORRA. Grau Roig, *Casas s.n.* (BCB-21724). AUSTRIA. **Carinthia:** Malniksee im Maltathal, *Breidler s.n.* (BP-6190). **Steiermark**: Hochalpe bei Turrach, 16 Aug. 1889, *Breidler s.n.* (FH). **Tirol:** Sulden (am Ortler), lower part of the Rosimtal, *Townsend 92/522* (IBA-6279). BULGARIA. Rila planina, Mussalla, 2 Aug. 1908, *Podpěra s.n.* (TRH). CZECH REPUBLIC. Oester. Schlesien, Gesenke, Kessel, *Limpricht s.n.* (IBA-5468). FRANCE. **Alpes Maritimes:** S. Martin-Vésubie au Boréon, 28 July 1910, *Durand s.n.* (G). **Ariège:** près de l'étang d'Areon, Pozo d'Aula, 5 Sep. 1923, *Culmann s.n.* (Z). **Corsica:** montis Rotondo, supra "il Timozzo," 7 July 1880, *Levier s.n.* (TRH). **Hautes Alpes:** montie du Galibier du chemin à Lantiret, 26 Aug. 1926, *Culmann s.n.* (Z). **Isère**: La Lauvitel, 17 Aug. 1894, *Thériot s.n.* (TRH). **Normandie**: *Montagne s.n.* (RO). **Pyrénées Centrales:** marginem lacus Lac de Gaube dicti, non longe a Cauterets, *Spruce s.n.* (NY, TCD). **Savoie**: Col de la Croix de Fer, *Cuynet 22* (herb. Pierrot). GEORGIA. Gurschevi ad fontes fl. Dschandschachi Tschali, July 1877, *Brotherus s.n.* (H). Svanetia libera or. supra Chaldechi et Kala, montis Djanga-tau, 8 Aug. 1890, *Sommier & Levier s.n.* (G). GERMANY. Kleinhans, *Anonymous s.n.* (TRH). ITALY. Mte. Lineone, *Balsamo-Crivelli s.n.* (RO); Ortler, Martelltal, Cevedalehütte, 30 July 1913, *Kern s.n.* (WRSL). KAZAKSTAN. **Alma-Ata:** Chimbulak to Medeo Dam above Alma Ata, *Allen 10798* (MO). **Kochketav:** Akmolinsk, distr. Atbassar, montes Dshaksy-Arganaty, *Gordjagin 198* (H-BR). NEPAL. NW Himalaya, *Troll 67* (JE). NORWAY. **Christiams:** Jotumheimen, Bukkelaegret, 31 July 1879, *Bryhn s.n.* (TRH). **Sondre Trondhjems:** Opdal, Sliper, 19 May 1882, *Kaurin s.n.* (TRH); Valders, Vang Skogstad, 8 Aug. 1889, *Bryhn s.n.* (TRH). PAKISTAN. **Hindukusch:** Tschitral, Bumboret-Tal, 1935, *Kerstan s.n.* (JE). **Kashmir:** Kalapani, Kamri Nala, Astor Valley, 10 July 1901, *Inayal-Khan s.n.* (H-BR). POLAND. Wysokie Tatry Mts. 1 km W of Czarny Staw tarn, 24 Aug. 1987, *Wójcicki s.n.* (IBA-7417, KRAM). ROMANIA. **Fogaras:** ad lacum Bulea, *Boros s.n.* (BP-112946). **Beszterce-Naszód:** Mt. Radnai havasok, montis Ünökó, ad Ünökói menedékház, *Felföldy s.n.* (BP-112943). RUSSIA. **Altayskaya Autonomous Oblast:** Altai, Stonovajatal in Katunjgebirge, 1 Aug. 1915, *Grand s.n.* (H-BR). **Kamchatka:** slope of Kosheleva volcano, *Chernyadjeva 16* (LE). **North Ossetia:** ad mare glaciale Zei, Aug. 1881, *Brotherus s.n.* (PC). SLOVAKIA. Siroka (Jaworiner-), *Chałubiński s.n.* (BP-36661); versus "Virágoskert" vallis Felkai-völgy, Velická dolina, *Boros s.n.* (BP-112912). SPAIN. **Gerona:** Circ de Concrós, *Lloret s.n.* (BCB-23455). **Huesca:** Benasc, La Renclusa, a l'ermita, *Casas s.n.* (BCB-27596). **Lérida:** Boí, Estany de Cavallers, *Casas s.n.* (BCB-39886). **Cantabria:** Peña Prieta, 14 Aug. 1987, *Muñoz s.n.* (IBA-606). SWITZERLAND. **Bern:** am Abhange des Piz Pischierva, 21 July 1909, *Kern s.n.* (WRSL). **Rhaetia:** Davos, 20 Apr. 1890, *Amann s.n.* (TRH); Grand San Bernard, au Val Soren, 31 July 1895, *Bernet s.n.* (FH). **Graubünden:** Stätrorhorn, 25 June 1888, *Adlerz s.n.* (TRH). **Wallis:** Südabhang des Santschpasses, 11 Aug. 1912, *Culmann s.n.* (FH). **Unterengadin:** Zernez, Munt Baseglia, 16 July 1912, *Kern s.n.* (WRSL). TADZHIKISTAN. N slope of Darvazhski mountain range p. Zhingou, 19 July 1964, *Mamatkulov s.n.* (LE). TURKEY. **Artvin:** Ardanuc, Kordevan-dag (Yalnizçam Deglari), at Kütül yayla, *Davis & Hedge D.30403* (IBA-5098). **Kayseri:** Erciyas-dagh, *Zederbauer s.n.* (W-2486). **Tunceli:** Kurdistan, Masgerth, 1881, *Brotherus s.n.* (H-BR). UKRAINE. Turka, oben Sta. Caterina, *Lorentz s.n.* (BP-36623). **Kirovograd:** Jabar-Syrt ad fontes fl. Vandam-ezai, 23 Aug. 1900, *Alexeenko s.n.* (LE). UNITED KINGDOM. **Wales:** Carmarthenshire, near Marros, 29 Mar. 1907, *Knight s.n.* (FH).

CANADA. **British Columbia:** Revelstoke, 7 May 1890, *Macoun s.n.* (S). U.S.A. **Arizona:** Kaibab, *Mead 990* (FH). **California:** Alpine Co., Monitor, *Lapham s.n.* (FH). **Colorado:** Larimer Co., Dream Lake, Rocky Mountain National Park, 1 Aug. 1929, *Braun s.n.* (MO). **Idaho:** Elmore Co., Atlanta, Boise National Forest, *Anonymous s.n.* (MO). **Montana:** Flathead Co., pr. Lake McDonald, 4 mi. N of Belton, a station 30 mi. E of Kalispell, 25 July 1898, *Holzinger & Blake s.n.* (TRH). **Utah:** San Juan Co., Elk Ridge, at Kigalia Ranger Sta., *Flowers 3633* (MO). **Wyoming:** Evanston, *Degener & Peiler 16928* (FH).

5. Grimmia caespiticia (Brid.) Jur., Laubm.-Fl. Oesterr.-Ung. 172. 1882. *Campylopus caespiticius* Brid., Muscol. Recent., Suppl. 4: 77. 1819 [1818]. *Grimmia funalis* var. *caespiticia* (Brid.) Hampe, Flora 20: 282. 1837. *Guembelia caespiticia* (Brid.) Müll. Hal., Syn. Musc. Frond. 1: 773. 1849. *Grimmia alpestris* var. *caespiticia* (Brid.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 30. 1933. TYPE: [Switzerland. Bern:] St. Bernard, *Bridel s.n.* (holotype, B).

Grimmia sulcata Saut., Flora 24: 39. 1841. *Guembelia sulcata* (Saut.) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. TYPE: [Austria. Salzburg:] Pinzgauer Alpen, *Sauter s.n.* (lectotype, here designated, H-SOL; isolectotype, Z).

Grimmia jacquinii Garov. var. *subimberbis* Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 23: 552. 1866 [1867]. *Grimmia alpestris* var. *subimberbis* (Lindb.) Berggr., Kongl. Svenska Vetenskapsakad. Handl. 13(7): 49. 1875. *Grimmia caespiticia* var. *subimberbis* (Lindb.) Limpr., Laubm. Deutschl. 1: 780. 1889. *Grimmia sulcata* var. *subimberbis* (Lindb.) G. Roth, Eur. Laubm. 1: 431. 1903 [1904]. *Grimmia caespiticia* f. *subimberbis* (Lindb.) Podp., Consp. Musc. Eur. 283. 1954. TYPE: [Norway.] Spitsbergen: Amsterdam Island, 1861, *Holmgren s.n.* (lectotype, here designated, H-SOL).

Grimmia manniae Müll. Hal., Flora 70: 223. 1887. *Grimmia alpestris* var. *manniae* (Müll. Hal.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 31. 1933. *Grimmia donniana* var. *manniae* (Müll. Hal.) Wijk & Margad., Taxon 9: 50. 1960. TYPE: [U.S.A.] California: Napa Soda Springs, 3 May 1886, *Mann s.n.* (lectotype, here designated, NY; isolectotype, PC).

Grimmia pyrenaica Kern, Jahresber. Schles. Ges. Vaterl. Cult. 92: 38. 1915. TYPE: [Spain. Lérida:] Gavernie, auf eisenhalbsigen Felsen dem Port de Boucharo, spanische Seite, 13 July 1914, *Kern s.n.* (lectotype, designated by Bednarek-Ochyra et al. (1992), WRSL; isolectotypes, BP-80423, KRAM, MA-8158, MA-10927).

Illustrations. Figure 10; Bednarek-Ochyra et al. (1992: fig. 1); Bruch et al. (1845: tab. 252, *sub G. sulcata*); Chałubiński (1882: tab. 9 fig. 16); Limpricht (1890: fig. 203); Maier and Geissler (1995: fig. 6); Nyholm (1956: fig. 69C).

Dioicous. Plants in fragile tufts, glaucous or olive-green to blackish. *Stems* to 1 cm tall, with central strand well developed; *axillary hairs* 4-celled, 55–75 μm long. *Leaves* erect and appressed, and with incurved apices when dry, erect and rigid when moist, 0.8–1.8 × 0.3–0.6 mm, ovate, acute, keeled, strongly plicate, the plicae of 2–5 rows of longer and more narrow cells with thicker walls; *margins* plane in the proximal half, incurved in the distal half and cucullate at tip; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2(–3)-stratose in the distal half, smooth; *distal cells* 7–9 μm, isodiametric, bulging, usually papillose; *proximal paracostal cells* 14–35 × 7–18 μm, isodiametric to rectangular (1–3 : 1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 12–32 × 10–14 μm, isodiametric to rectangular (1–3 : 1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.4 mm long, smooth. *Perichaetial leaves* ca. 1.5 × 0.4–0.5 mm, convolute and slightly larger than vegetative leaves; *hyaline hair-points* straight, to 0.5 mm, smooth. *Androecia* terminal. *Setae* erect and straight, 2.5–3.5 mm long. *Capsules* exserted, ovoid, symmetric, smooth, castaneous, with stomata at the urn base; *exothecial cells* 24–70 × 10–28 μm, very irregularly isodiametric to rectangular (1–3 : 1), thin-walled; *annulus* simple and persistent; *peristome teeth* 35–50 μm wide at the base, ± entire, brownish, concolorous with the urn; *opercula* mammillate or rostellate, and then with an oblique beak; *calyptrae* cucullate. *Spores* 10–14 μm.

Diagnostic characters. (1) Leaves with a strongly marked longitudinal plication on each side of costa. (2) Margin involute in the distal half and becoming cucullate at tip. (3) Hyaline hair-point very short, to 0.5 mm on the perichaetial leaves, but usually much shorter. (4) Laminar cells bulging. (5) Distal leaf cells usually papillose. (6) Capsules castaneous, with stomata at the base.

Distribution (Fig. 11). Europe, the Caucasus, Svalbard, and the west coast of North America; in open areas above the tree-line from 1000 and 2797 m elevation on dry, siliceous rocks. Mature sporophytes were present in 77% of the specimens studied.

Grimmia caespiticia is rather invariable in most respects, except glaucousness, which depends on the amount of wax deposited on the leaves. As in *G. alpestris*, this variation correlates with habitat conditions. The degree to which the cells bulge also varies. Usually they bulge prominently, but may be nearly smooth in some populations.

In fertile condition, the combination of plicate leaves, very short hair-points, and exserted capsules clearly distinguishes *G. caespiticia* from any other species in *Grimmia* or *Coscinodon*. Another useful character for separating this taxon from *G. alpestris* is the presence of stomata at the base of the capsule, absent in the latter species. In sterile condition, it is difficult (or at times impossible) to

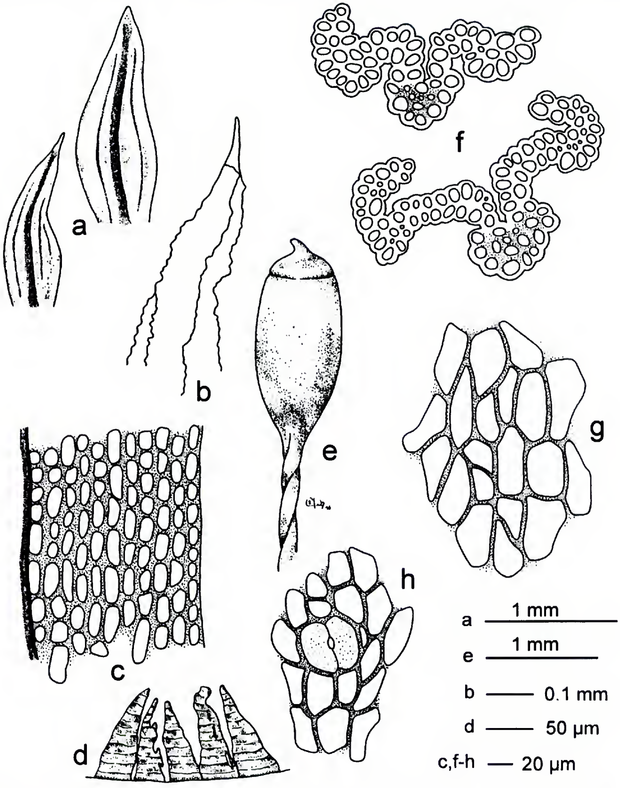

Figure 10. *Grimmia caespiticia.* —a. Leaves. —b. Dorsal view of papillose leaf apex. —c. Proximal leaf cells. —d. Peristome teeth. —e Capsule. —f. Transverse sections of leaf with non-papillose cells. —g. Medial exothecial cells. —h. Proximal exothecial cells and stoma. [a, b, c, f, *Pierrot 201/100* (herb. Pierrot); d, e, g, h, *Rupidera 3* (SALA).]

separate this taxon from *Coscinodon cribrosus,* a species also difficult to distinguish from *G. alpestris* and *G. reflexidens* when sterile. The differences alleged by previous authors (Cao & Vitt, 1986: 168; Nyholm, 1956: 151) are not reliable; the length of the proximal cells, the thickness of the cell walls, and the shape of the leaf apex vary inordinately in both taxa, as can be verified from fertile collections. The only useful character for separating sterile material of *G. caespiticia* and *C. cribrosus* is the usually papillose laminar cells in the former, as opposed to the always smooth laminar cells in the latter. This feature, though noted by Loeske (1913: fig. 32), has been neglected by later authors. Another useful character is the length and shape of the hair-points. *Grimmia caespiticia* has very short hair-points, never longer than 0.5 mm, which are always terete, even on the longest hairs. Hair-points in *Coscinodon cribrosus,* however, are usually longer than 0.5 mm and flat below. From these differences, and af-

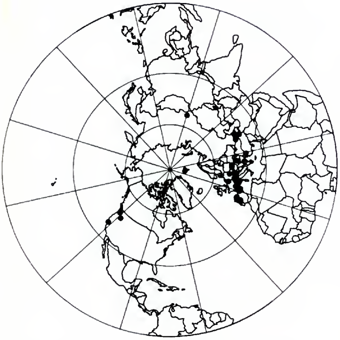

Figure 11. Distribution of *Grimmia caespiticia.*

ter studying the lectotype (H) and two isolectotypes (BM, PC) of *G. sinensianodon* Müll. Hal. (Müller, 1898: 188), I conclude that it is synonymous with *C. cribrosus* (Hedw.) Spruce and not with *G. caespiticia* as proposed by Cao and Vitt (1986: 167). Those authors reported the type locality of *G. sinensianodon* to be the only known Chinese station for *G. caespiticia.* Because I have not found any specimens referable to *G. caespiticia* among the Chinese collections studied, this species must be excluded from the Chinese bryoflora.

The protologue of *Grimmia manniae* states "2 Majo 1886" as the collection date. The only two specimens I can find collected by Martha R. Mann in Soda Springs, the type locality, have "3 Majo 1886" as the collection date (NY, PC). Considering that they agree in every other respect with the protologue and that there are more typographical mistakes in the same paper (Müller, 1887), I have assumed that a mistake could have been made in transcribing the label in the original publication.

Selected specimens examined (163). ANDORRA. Tristaina, *Casas s.n.* (BCB-10537). ARMENIA. Sisianskij rajon, s. Arevis, 5 July 1966, *Manakyan s.n.* (LE). AUSTRIA. **Carinthia:** Monte Caglians, auf dem Piz Ciadin, 8 July 1908, *Kern s.n.* (WRSL). **Steiermark:** Würslingen Höhe bei Stadl, 12 July 1878, *Breidler s.n.* (GOET). **Tirol:** Alpe Rosstall bei Innervillgraten, *Gander s.n.* (BP-36291). BELGIUM. Promenade Annette Lübin à Spa, Feb. 1906, *Cornet s.n.* (NY). BULGARIA. Mt. Pirin, decl. borealium mt. Mangar Tepe, *Simon s.n.* (BP-68488); Wichryn, ad viam Zwusticam, *Kuc s.n.* (BP-70237). FRANCE. **Alpes-Maritimes:** Saint-Dalmas-de-Tende, les Ciappe de Fontanalba, *Parriat s.n.* (BP-112934). **Cantal:** Plomb-du-Cantal, *Cuynet s.n.* (BP-112904). **Hautes Alpes:** plane nord du Combegnot, 21 July 1926, *P. Culmann s.n.* (Z). **Isère:** les Grandes Rousses, environs du lac Blanc, 20 Aug. 1894, *Thériot s.n.* (Z). **Puy de Dôme:** vallée du Chandeferer, 19 Aug. 1919, *Culmann s.n.* (Z). **Pyrénées Centrales:** Port de Bénasque, 12 Sep. 1845, *Spruce s.n.* (NY). GEORGIA. In jugo alpino inter flumina Neusksa et Sckun pr. Svaniae occid. confine, *Sommier & Levier 364* (H). **South Ossetia Autonomous Oblast:** in alpe Zomorasch prope Ress ad fl. Terek, July 1881, *Brotherus s.n.* (H). GERMANY. **Karl-Marx Stadt:** Bärenstein (BP-112894). ITALY. Adamellogruppe, Leipziger Hütte, 27 July 1895, *Kern s.n.* (WRSL); Rizlembrai juxta Côl di Stelvio, *Lorentz s.n.* (BP-36283). NORWAY. **Svalbard:** Amsterdam Island, 1861, *Holmgren s.n.* (H-SOL). POLAND. Kozi-Wirch, den Gipfel, 3 Sep. 1876, *Chałubiński s.n.* (BP-36297). PORTUGAL. **Beira Alta:** Serra da Estrela, Cântaro Raso, pr. da vista para o Covao da Ametade, *Sérgio & Séneca 8164* (IBA-5050). ROMANIA. **Brasov:** vallis Podragu, montes Fogarasi havasok, *Vajda s.n.* (BP-72021). RUSSIA. **Irkutsk:** Western Sayan, the river Ona in the upper part, *Bardunov s.n.* (NICH 306126). **Stavropols'kij Kraj:** Teberdinsky Reserve, 14 Sep. 1954, *Patrabolova s.n.* (LE). SLOVAKIA. Tatra Magna, convallis "Sirkert" sub monte Lomnicki-csucs, *Boros s.n.* (BP-6188); Höher Rücken zwischen den Mengsdorfer und Koprowy-Spitze, *Chałubiński s.n.* (BP-36298); vallis Virágoskerl, supra lacu Felkaitó, *Vajda s.n.* (BP-70417). SPAIN. **Asturias:** Somiedo, pr. El Puerto, La Vega de Peñueta, 4 Nov. 1995, *Muñoz s.n.* (IBA-6750). **Ávila:** bajada a la laguna de El Trampal, 9 Sep. 1995, *Muñoz s.n.* (IBA-6723). **Cantabria:** Peña Prieta, 14 Aug. 1987, *Muñoz s.n.* (BCB-25772). **Gerona:** Coma de l'Orri, *Lloret s.n.* (BCB-28890). **Huesca:** Benasc, La Renclusa, Ibón de Paderna, *Casas s.n.* (BCB-30444). **Lérida:** Areu, roques próximes al refugi, *Casas s.n.* (BCB-33173). **Palencia:** pico Curavacas, 12 July 1988, *Muñoz s.n.* (IBA-681). SWITZERLAND. **Bern:** Urbachtal bei der Gaulihütte, *Culmann s.n.* (MA 5870). **Graubünden:** Pischahorn im Fluelathal, *Amann BH-12* (Z). **Valais:** Distebalp, Saastal, *Amann BH-24* (Z). TURKEY. **Bursa:** Nordabhang des Ulu Dağ, *Walther 3318* (NY).

U.S.A. **California:** Napa, Soda Springs, 3 May 1886, *Mann s.n.* (NY). **Oregon:** Union Co., S shore of Antony Lake, Blue Mts., 17.5 mi. W of North Powder, *Hermann 28821* (G). **Washington:** Pierce County, Mt. Rainier Park, about 0.5 mi. from ranger station, *Lawton 4792* (MO).

6. Grimmia montana Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 128, tab. 250. 1845. *Guembelia montana* (Bruch & Schimp.) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. *Grimmia holmiensis* Lindb. ex Hartm., Handb. Skand. Fl. Ed. 7: 374. 1858, nom. inval. pro syn. TYPE: [Germany. Rhineland-Palatinate:] Donnersberg, Apr. 1843, *Gümbel s.n.* (lectotype, designated by Cao & Vitt (1986), BM).

Grimmia laxa Müll. Hal., Bot. Zeitung (Berlin) 5: 801. 1847. TYPE: Mexico. In monte Orizabae, *Deppe & Schiede s.n.* (lectotype, here designated, PC).

Grimmia fragilis Schimp., Syn. Musc. Eur. Ed. 2: 257. 1876, nom. illeg., non F. Weber, 1804. *Grimmia montana* var. *fragilis* (Schimp.) Loeske, Laubm. Eur. Part I: 99. 1913. TYPE: [Portugal.] Ad rupes granit. in alpestribus Prov. Beira, Aug. 1848, *Welwitsch s.n.* (lectotype, here designated, BM).

Guembelia tenella Müll. Hal., Bot. Centralbl. 44: 388. 1890. *Grimmia tenella* (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 2: 107. 1893. TYPE: [U.S.A.] Idaho: Coeur d'Alene, 6 Aug. 1888, *Röll s.n.* (lectotype, here designated, G; isolectotypes, H-BR, JE, S).

Grimmia montana var. *longifolia* Cardot, in Gasilien, Rev. Bryol. 21: 24. 1893 [1894]. *Grimmia montana* f. *longifolia* (Cardot) Podp., Consp. Musc. Eur. 281. 1954. TYPE: [France. Puy de Dôme:] Auvergne, Pierre sur Haute, 1884, *Gasilien s.n.* (lectotype, here designated, TRH).

Grimmia montana var. *abnoba* H. Schmidt, Mitt. Bad. Landesvereins Naturk. Naturschutz Freiburg 2: 121, fig. 6. 1927. TYPE: [Germany. Württemberg:] Süd. Schwarzwald, südweste dem Schauinslandgipfel, *Schmidt s.n.* (lectotype, here designated, JE).

Grimmia montana f. *submutica* J. E. Zetterst. ex H. Möller, Ark. Bot. 26A(2): 31. 1933 [1934]. TYPE: [Sweden.] Juxta Husbyborg prope Upsaliam, 15 May 1855, *Zetterstedt s.n.* [Zetterstedt, Grimmiae et Andreaeae exsiccatae, n° 21c] (lectotype, here designated, H-BR).

Illustrations. Figure 12; Bruch et al. (1845: tab. 250); Chałubiński (1882: tab. 8 fig. 14); Jóhannsson (1993: fig. 26); Maier and Geissler (1995: fig. 17); Nyholm (1956: fig. 69B).

Dioicous. Plants in flat or bulging cushions or tufts, olive-green at the tips, dark green or blackish below. *Stems* to 1 cm tall, with central strand well developed; *axillary hairs* 5–8-celled, 95–175 μm long. *Leaves* erect, loosely appressed and flexuous when dry, with patent proximal part and incurved apex, sigmoid in lateral view, rigid when moist, 1–2 × 0.3–0.6 mm, abruptly acuminate from an ovate base, apex from somewhat to distinctly keeled, plane or with very weak plicae; *margins* plane proximally and incurved distally, forming a canaliculate apex; *costa* semi-terete, prominent on the dorsal surface, slightly to distinctly delimited; *lamina* 2(3–4)-stratose in the distal half, smooth; *distal cells* 4–8 μm, isodiametric, plane or slightly bulging on the dorsal surface, smooth; *proximal paracostal cells* 20–50 × 8–15 μm, rectangular (2–4.5 : 1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 20–50 × 8–15 μm, rectangular (2–4.5 : 1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm long, obtusely denticulate (rarely serrate). *Perichaetial leaves* 1.7–2.4(–4) × 0.6–0.9 mm, convolute and larger than vegetative leaves (2×), yellowish at the base; *hyaline hair-points* similar to those of vegetative leaves. *Androecia* terminal. *Setae* erect and straight, 2–4 mm long. *Capsules* exserted, ovoid or ellipsoid, symmetric (seldom slightly asymmetric at base), smooth, castaneous, lacking stomata; *exothecial cells* 30–70 × 10–25 μm, rectangular (2–4 : 1), thin-walled; *annulus* simple and persistent; *peristome teeth* 50–90 μm wide at the base, irregularly split and perforate, ± cribrose, castaneous, concolorous with the urn; *opercula* rostrate, the beak oblique; *calyptrae* cucullate. *Spores* 10–14 μm.

Diagnostic characters. (1) Leaves flexuous, sigmoid in lateral view when moist, ending in a long acuminate apex. (2) Laminar cells not bulging. (3) Plants dioicous. (4) Capsules lacking stomata. (5) Opercula rostrate with oblique beak.

Distribution (Fig. 13). Western Europe, the Canary Islands, Greenland, and North America; coniferous and broad-leaved formations, and also open areas, mostly below the tree-line, between 300 and 2000 m elevation on dry, siliceous rocks. Mature sporophytes were present in 69% of the specimens studied.

Grimmia montana is a rather stenotypic taxon throughout its entire distribution range. Some minor gametophytic differences between North American and Eurasian specimens may be observed, but the sporophytes are identical worldwide. Eurasian populations from lower latitudes and/or elevations have longer and more acuminate leaves than those from higher latitudes and/or elevations. North American populations resemble northern Eurasian populations in having leaves with a short leaf acumen. In very exposed places at high altitudes, cells bulge slightly at the dorsal laminar surface, and the acumina are shorter. Male plants are shorter and have leaves with shorter hair-points, sometimes muticous. They are easy to recognize because their stems end in globose perigonia.

Circumboreal but scattered, *Grimmia montana* is the only species of subgenus *Orthogrimmia* known from Greenland and Baffin Island. Oddly, there are no collections from continental eastern North America; all material from that region so identified actually represents *G. incurva* with erect and straight setae. Brodo and Alstrup (1981: 231–233) documented the same distribution pattern for two lichens, *Bryoria subdivergens* (Dahl) Brodo & D. Hawksw. and *Rhizocarpon bolanderi* (Tuck.) Herre, and noted that such a pattern is unknown in other plant groups. Subsequently, Blom (1996: fig. 46) illustrated the same pattern for *Schistidium umbrosum* (J. E. Zetterst.) H. H. Blom (Musci, Grimmiaceae).

Grimmia montana was recorded from China and Tibet by Cao and Vitt (1986: 161–164, fig. 19), but all specimens listed by those authors represent other species, mainly *G. longirostris*; hence *G. montana* can be deleted from the Chinese bryoflora.

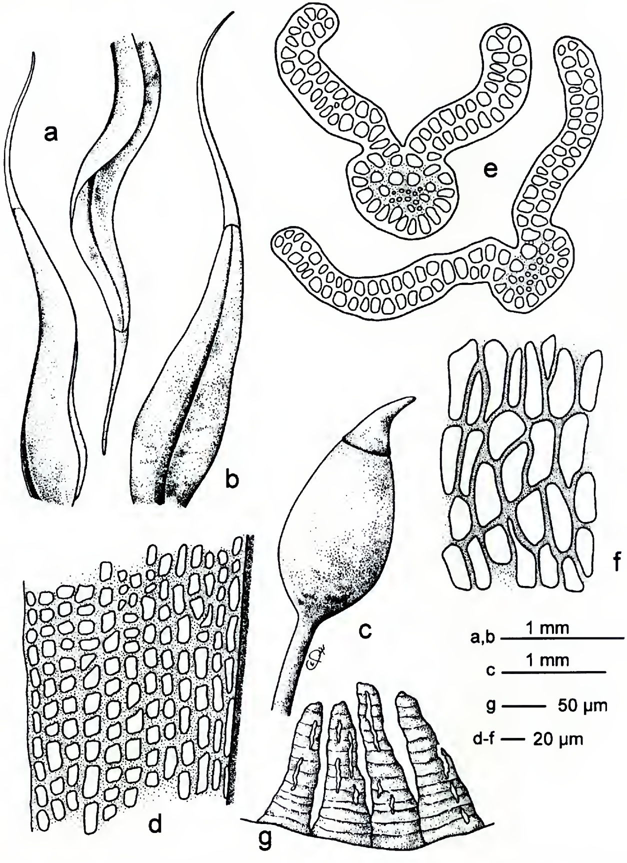

Figure 12. *Grimmia montana.* —a, b. Leaves. —c. Capsule. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothecial cells. —g. Peristome teeth. [a, *Gasilien s.n.* (TRH); b, d, e, *Gümbel s.n.* (BM); c, f, g, *Kaurin s.n.* (TRH).]

Cao and Vitt (1986: 161) also synonymized *G. brachyphylla* Cardot with *G. montana,* based on several character states shared by these two species. Nevertheless, the features listed by these authors are common to many other species in the genus, and thus inconclusive. Based on a study of the types, I conclude that *G. brachyphylla*[3] is synonymous with *Coscinodon humilis* Milde.

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[3] TYPE: South Korea. Pomasa, 800 m, 1906, *Faurie 218* (lectotype, here designated, PC; isolectotypes H, H-BR, NY).

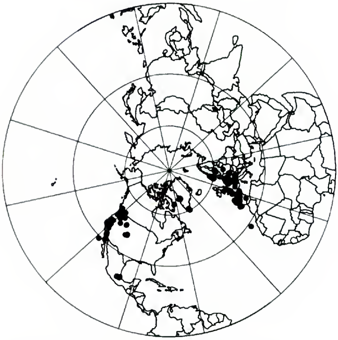

Figure 13. Distribution of *Grimmia montana.*

Grimmia montana has been also reported from the Russian Far East (Afonina, 1986: 223, ris. 2 figs. 1–8; Ignatov & Afonina, 1992: 42); however, all the specimens supporting these reports are *G. longirostris* or *G. reflexidens.*

Selected specimens examined (294). ANDORRA. Tristaina, *Casas s.n.* (BCB-10536). AUSTRIA. **Niederosterreich:** Arndorf, 19 Aug. 1894, *Baumgartner s.n.* (TRH). **Tirol:** Zaithal, Sölden, *Dixon & Nicholson s.n.* (BP-80258). BELGIUM. Ardennas, *Cardot s.n.* (FH); Montagun-russes bei Spa, *Cornet s.n.* (BP-36286). FRANCE. **Maine-et-Loire:** Angers, 10 Apr. 1857, *Perraudiére s.n.* (G). **Calvados:** Condé-sur-Noireau, *Husnot s.n.* (FH). **Pyrénées Centrales:** Pic du Midi, Aug. 1847, *Philippi s.n.* (FH). **Savoie:** pr. Chamonix, loco dicto Pierre à Bérard, *Payot s.n.* (TRH). **Vosges:** *Reinsch s.n.* (FH). GERMANY. **Baden-Württemberg:** circa Heidelbergam, *Braun s.n.* (FH). **North Rhine–Westphalia:** *Bertram s.n.* (IBA-4125). ITALY. Adamellogruppe, Val di Genova, 28 July 1895, *Kern s.n.* (WRSL). NORWAY. **Oppland:** Dovre, Vaarstien ad viam publ. pr. Nestadsvallas, *Kaurin s.n.* (TRH). **Oslo:** montis Egeberg, 18 June 1870, *Zetterstedt & Wickbom s.n.* (TCD). **Sor Trondelag:** Oppdal, Sliper, 1 July 1883, *Hagen s.n.* (TRH). POLAND. Sudetes Mts., Karkonosze Range, Sniezny Kociol, July 1876, *Limpricht s.n.* (FH). PORTUGAL. **Beira Alta:** Serra d'Estrela, in jugis alpinis editionibus, 31 July 1878, *Levier s.n.* (G). **Beira Baixa:** Sabugal, a 2 km de Quadrazais, ponte do río Côa, *Sérgio s.n.* (IBA-4506). **Douro Litoral:** na cima do Serra do Marao, *Ervideira s.n.* (LISU-P53901). **Minho:** Serra de Peneda-Gerêz, Soajo, Branda da Bouça dos Homens, *Sérgio & Sim-Sim s.n.* (LISU-154131). **Trás-os-Montes:** Pitoês das Junias, Montalegre, *Sérgio & Schumacker s.n.* (LISU-154132). SPAIN. **Almería:** Sierra de los Filabres, barranco de la Verruga, 26 May 1990, *García-Zamora & Ros s.n.* (MUB). **Asturias:** Puerto de Leitariegos, 15 July 1835, *Durieu s.n.* (PC). **Ávila:** bajada a las lagunas de El Trampal, 9 Sep. 1995, *Muñoz s.n.* (IBA-6722). **Burgos:** roquedo de Carromata, *Heras s.n.* (VIT 1050/84). **Cantabria:** Puertos de Riofrío, 12 July 1988, *Muñoz s.n.* (IBA-618). **Cáceres:** Acebo, *Cros & Brugués s.n.* (BCB-21766). **Gerona:** torrent de la Llosa, *Lloret s.n.* (BCB-23440). **Granada:** Sierra Nevada, San Gerónimo, *Casares Gil s.n.* (MA 8155). **Huesca:** lago de Urdiceto, *Casas s.n.* (IBA-3984). **Lérida:** Alta Ribagorça, marge esquerre de la Noguera Ribagorçana, *Canalís s.n.* (BCC-1278). **León:** Ancares, subiendo al Cuíña, *Cros & Lloret s.n.* (BCB-20118). **La Rioja:** Posadas, Sierra de la Demanda, *Casas s.n.* (BCB-2472). **Madrid:** Puerto de Navacerrada, *Casares Gil s.n.* (MA 8156). **Navarra:** monte Mendaur, *Arraiza s.n.* (NAU-3284). **Orense:** pr. Casayo, Fonte da Cova, *Aedo s.n.* (IBA-3177). **Palencia:** Valdecebollas, *Aedo s.n.* (IBA-3933). **Salamanca:** Alto de Los Lobos, subiendo a la Peña de Francia, 26 Sep. 1991, *Muñoz s.n.* (IBA-3595). **Tenerife:** Cañadas del Teide, Apr. 1906, *Pitard s.n.* (MO). **Zamora:** San Pedro de las Herrerías, *Rupidera 52* (SALA). SWEDEN. Mt. Huddinges, 2 June 1902, *Arvén s.n.* (FH); Norrkåping, 1878, *Olsson s.n.* (TRH); Stockholm, Lidingo, 30 Apr. 1859, *Zetterstedt s.n.* (TRH); Uppsala, Bârby, 14 June 1859, *Zetterstedt s.n.* (TRH). SWITZERLAND. [No locality given.] 1842, *Anonymous s.n.* (BM). UNITED KINGDOM. **England:** Somerset, near Highbridge, 24 Mar. 1913, *Nicholson s.n.* (FH).

CANADA. **British Columbia:** Sproats Landing, 20 June 1890, *Macoun s.n.* (S). **Northwest Territories:** Cumberland peninsula, *Anonymous s.n.* (NY). GREENLAND. Groenlandia boreal, Claushavn, 1870, *Berggren s.n.* (TRH); SW Greenland, Narssaq, on Narssaqsund at Gronlands Geologiske Undersogelser camp and general vicinity, *Steere 62–982* (NY). MEXICO. **Baja California:** National Park, San Pedro Mártir Mts., *Hammond 10837* (NY). Guadalupe Island, summit, *Moran 5664* (FH). **México:** Popocatépetl, *Sharp 4749* (TENN). **Puebla:** S slope of Ixtaccíhuatl, *Vitt 17520* (TENN). **Veracruz:** Monte Orizaba, *Purpus 4277* (PC). U.S.A. **California:** San Bernardino Co., W face of Cucamonga Mt., *Sweet Jr. 189* (FH). **Colorado:** Eagle Co., 1 mi. W of Wolcott, *Weber B-15354* (MO). **Idaho:** Elmore Co., Hot Springs, Atlanta, Berse National Forest, *MacFadden 18766* (FH). **Montana:** Mineral Co., shore of Clark Fork, Rest Area on US 10, 3 mi. W of Alberton, *Hermann 22562* (FH). **Nevada:** Kings Canyon near Carson, 2 June 1902, *Baker s.n.* (PC). **Oregon:** Multnomah Co., Larch Mountain near summit, *Redfearn 11541* (MO). **Washington:** Spokane, 11 May 1909, *Bonser s.n.* (FH). **Wyoming:** Yellowstone, 2 Sep. 1888, *Röll s.n.* (JE).

7. **Grimmia nivalis** Kindb., in Macoun, Bull. Torrey Bot. Club 17: 271. 1890. TYPE: [Canada.] British Columbia: Gold Range, 7000 ft., 10 Aug 1889, *Macoun s.n.* (lectotype, here designated, S; isolectotypes, CANM-198090, H-BR).

Grimmia papillinervis Kindb., Rev. Bryol. 34: 89. 1907. TYPE: Canada. British Columbia: Skagit summit, 18 July 1905, *Macoun s.n.* (holotype, S).

Illustrations. Figure 14; Allen (1995: figs. 3–5).

Dioicous. Plants in tufts, olive-green. *Stems* to 1.5 cm tall, with central strand weakly developed; *axillary hairs* 5–7-celled, ca. 130 μm long. *Leaves* erect and appressed when dry, patent, rigid when moist, 1.1–1.8 × 0.3–0.5 mm, ovate, acute, strong-

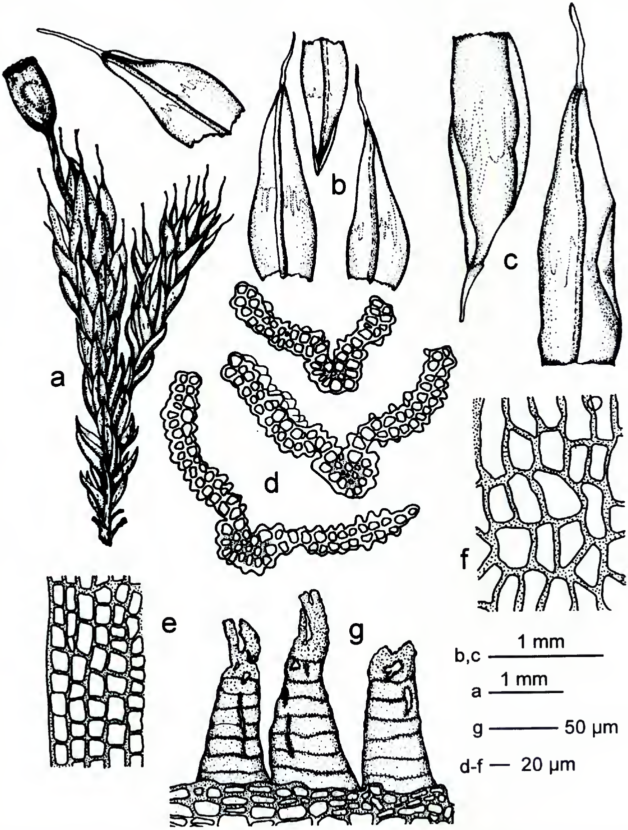

Figure 14. *Grimmia nivalis.* —a. Habit. —b. Leaves. —c. Perichaetial leaves. —d. Transverse sections of leaf. —e. Proximal leaf cells. —f. Medial exothecial cells. —g. Peristome teeth. [*Howell s.n.* (FH).]

ly keeled, plane or weakly plicate; *margins* plane proximally and incurved distally; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose in the distal half, smooth; *distal cells* 6–9(–11) μm, isodiametric, bulging, papillose; *proximal paracostal cells* 17–35 × 15 μm, isodiametric to rectangular (1–2 : 1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 9–14 × 9–11 μm, isodiametric to rectangular (1–1.5 : 1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.5 mm long, smooth. *Perichaetial leaves* 1.7–2.8 × 0.6–0.9 mm, convolute and larger than vegetative leaves (2×); *hyaline hair-points* straight, to 0.75 mm, smooth. *Androecia* not seen. *Setae* erect

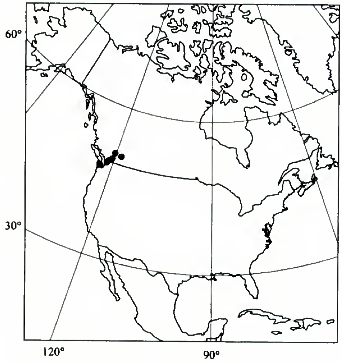

Figure 15. Distribution of *Grimmia nivalis*.

and straight, ca. 3 mm long. *Capsules* exserted, ovoid, symmetric, smooth, castaneous, with stomata at the urn base; *exothecial cells* 28–55 × 10–35 μm, rectangular or (seldom) isodiametric (1.4–4: 1), thick-walled; *annulus* simple and persistent; *peristome teeth* 55–80 μm wide at the base, split in 2–3 branches in the distal ⅓–½, castaneous, concolorous with the urn; *opercula* conic, mammillate or short-rostellate, and then the beak oblique; *calyptrae* cucullate. *Spores* 9–14 μm.

Diagnostic characters. (1) Lamina plane or weakly plicate. (2) Cells bulging and papillose. (3) Plants dioicous. (4) Capsules castaneous with stomata at the base.

Distribution (Fig. 15). Known only from the northwestern United States (Washington) and western Canada (British Columbia); open areas between 620 and 2100 m elevation on siliceous, seemingly dry rocks. Mature sporophytes were present in 94% of the studied specimens.

Both *Grimmia nivalis* and *G. alpestris* have ovate, somewhat glaucous leaves, long hair-points and bulging laminar cells, and their overall macroscopic aspect is quite similar. Nevertheless, microscopic examination distinguishes both species at once: transverse leaf sections of *G. nivalis* reveal scattered thick papillae on the lamina, and stomata on the capsules. Leaf cells of *G. alpestris* are bulging but not papillose, and capsules of this species lack stomata. Moreover, capsules of *G. alpestris* are mostly fusiform in shape, whereas those of *G. nivalis* are ovoid. *Grimmia caespiticia*, the only other species in subgenus *Orthogrimmia* with papillose laminar cells and stomata on the capsule, usually has very short hair-points and strong plicae along both sides of the costa.

Allen (1995: 162–164) considered *Grimmia nivalis* synonymous with *G. tenerrima* Renauld & Cardot (*G. reflexidens* in the sense of this paper). Both species are macroscopically similar, but they can be separated because *G. nivalis* is a dioicous species with papillose cells and castaneous capsules, whereas *G. reflexidens* is autoicous, never has papillose cells, and the capsules are stramineous.

Specimens examined (13). CANADA. **British Columbia:** Gold Range, 10 Aug. 1889, *Macoun s.n.* (CANM-198089, CANM-198090, H-BR, NY [4 replicates], S); Summit Lake, 18 July 1905, *Macoun s.n.* (CANM-135430); Skagit summit, 18 July 1905, *Macoun s.n.* (S); Spence's Bridge, 28 May 1889, *Macoun s.n.* (PC). U.S.A. **Washington:** Mt. Baker, 15 July 1931, *Howell s.n.* (FH); Clallam Co., Mt. Angeles, 23 July 1931, *Howell s.n.* (FH).

8. Grimmia reflexidens Müll. Hal., Syn. Musc. Frond. 1: 795. 1849. TYPE: Chile. *Pöppig s.n.* (lectotype, here designated, BM; isolectotypes, JE, NY, PC).

Grimmia subsulcata Limpr., Laubm. Deutschl. 1: 757. 1889. *Grimmia sessitana* var. *subsulcata* (Limpr.) Breidl., Mitt. Naturwiss. Vereines Steiermark 28: 88. 1892 [1891]. *Grimmia alpestris* subsp. *subsulcata* (Limpr.) Kindb., Eur. N. Amer. Bryin. 2: 221. 1898. *Grimmia alpestris* f. *subsulcata* (Limpr.) Loeske, Laubm. Eur. Part 1: 104. 1913. *Grimmia alpestris* var. *subsulcata* (Limpr.) Broth., in Engl., Nat. Pflanzenfam. Ed. 2, 10: 309. 1924. *Grimmia sessitana* f. *subsulcata* (Limpr.) Loeske, Biblioth. Bot. 101: 117. 1930. TYPE: [Austria.] Steiermark: auf Glimmerschiefer "Speiereben bei Schoder," 9 Aug. 1888, *Breidler s.n.* (holotype, BP).

Guembelia lamellosa Müll. Hal., Bot. Zeitung (Berlin) 12: 318. 1854. *Grimmia lamellosa* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872/73: 72. 1874. TYPE: [France. Haute Garonne:] in Pyrenaeis centralibus, ad lacum Espingo (lectotype, designated by Deguchi (1978), PC; isolectotype, H-SOL).

Grimmia sessitana De Not., Atti Reale Univ. Genova 1: 704. 1869. *Grimmia exannulata* Lindb. ex Broth., Acta Soc. Sci. Fenn. 19(12): 87. 1892, nom. inval. *Grimmia alpestris* var. *stomata* Loeske, Laubm. Eur. Part I: 104 figs. 26e, f, g, 27d, e, i, k. 1913, nom. illeg. *Grimmia alpestris* var. *sessitana* (De Not.) I. Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1909(5): 22. 1909. *Grimmia alpestris* f. *sessitana* (De Not.) Loeske, Laubm. Eur. Part I: 104. 1913. TYPE: [Italy. Vercelli:] Frane alle scaturigini del Vogna, sotto l'ospizio della Valdobbia in Val Sessia, *Carestia s.n.* (lectotype, designated by Cao & Vitt (1986), RO; isolectotypes, BM [2 replicates], FH, WRSL).

Grimmia anceps Boulay, Musc. France 1: 371. 1884. TYPE: [France. Haute-Savoie:] Col de Berard a d'Anchane–Mt. Blanc, *Payot s.n.* (lectotype, here designated, PC; isolectotype, BP-36692).

Grimmia tenerrima Renauld & Cardot, Bot. Gaz. 15: 40, pl. 6 A. 1890. TYPE: [U.S.A.] Oregon: Mt. Hood, *Henderson 1239* (lectotype, here designated, PC; isolectotype, NY).

Grimmia grisea Cardot, Bull. Herb. Boissier sér. 2, 6: 7. 1906. TYPE: South Georgia. Cumberland Bay, *Skottsberg 307* (holotype, PC? not found; isotypes, H-BR, S).

Grimmia subpapillinervis Kindb., Rev. Bryol. 36: 98. 1909. TYPE: [Canada.] British Columbia: Ambean Valley, 10 July 1908, *Brinkman s.n.* (lectotype, here designated, CANM-198100).

Grimmia subcaespiticia Schiffn., Ann. K. K. Naturhist. Hofmus. 27: 490. 1913. TYPE: [Turkey. Malatya:] Kurdistania occidentalis, Taurus Cataonicus, in convallibus subalpinis prope vicum Bekikara inter urbem Malatja et vicum Kjachta, ca. 1600 m, 18 July 1910, *Handel-Mazzetti s.n.* (lectotype, here designated, FH; isolectotype, H-BR).

Grimmia asperitricha Dixon & Sainsbury, Trans. & Proc. Roy. Soc. New Zealand 75: 173. 1945. TYPE: New Zealand. South Island: Tasman Glacier, near De La Beche Hut, *Sainsbury 756* (lectotype, here designated, BM; syntypes, BM [*Sainsbury 753, 757, 771, 772, 799*]).

Grimmia alpestris f. *hybrida* Chal., Pamietn. Fizyogr. 2: 68. 1882. *Grimmia alpestris* var. *hybrida* (Chal.) Chal. Enum. Musc. Frond. Tatr. 56. 1886. *Grimmia sessitana* f. *longifolia* Loeske, Biblioth. Bot. 101: 116. 1930, nom. illeg. incl. f. prior. TYPE: [Slovakia.] Tatra, Polnischer-Kaum, v.d. Felkaër-Thal, 27 Aug. 1879, *Chałubiński s.n.* (lectotype, here designated, BP-36703).

Grimmia donniana f. *antarctica* Kuc, Rev. Bryol. Lichénol. 36: 659, figs. 1, 2, 3d, e, 4, 5. 1969. TYPE: Antarctica. Queen Mary Land: Bunger Hills, in the neighbourhood of the Polish Base, 25 June 1959, *Różycki s.n.* (holotype, KRAM; isotype, IBA-7386).

Illustrations. Figure 16; Cao and Vitt (1986: fig. 20a, c, e–l, n, p, q, s, u; Deguchi (1978: fig. 41, *sub G. subsulcata*); Maier and Geissler (1995: fig. 23, *sub G. sessitana*).

Autoicous. Plants in tufts, yellowish green at the tips, brownish green, brown, or blackish below. *Stems* ca. 1 cm tall, occasionally with rhizoids throughout, with central strand well developed; *axillary hairs* 3–4(5)-celled, 50–85(–100) μm long. *Leaves* erect and appressed when dry, patent to spreading and rigid to somewhat flaccid when moist, 1–1.8 × 0.25–0.45 mm, ovate to narrowly ovate, acute, keeled, plane or very weakly plicate; *margins* plane or recurved to ½ the leaf length on one side and proximally on the other side, occasionally only briefly and narrowly recurved proximally on one side; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose in the distal half, smooth; *distal cells* 8–12 μm, isodiametric, plane or bulging, smooth; *proximal paracostal cells* 20–55 × 8–10 μm, rectangular (2–6 : 1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 20–50 × 8–13 μm, rectangular (2–5 : 1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.5 mm long, smooth or very weakly denticulate. *Perichaetial leaves* 1.8–2.7 × 0.5–0.85 mm, convolute and larger than vegetative leaves (2×); *hyaline hair-points* terete or somewhat flattened proximally in longer hair-points, straight, to 1.5 mm, nearly smooth. *Androecia* axillary or terminal. *Setae* erect and straight, 1.5–3 mm long. *Capsules* exserted, ovoid or ellipsoid, symmetric (rarely slightly asymmetric at the base), smooth, stramineous, with stomata at the urn base; *exothecial cells* 35–70 × 10–35 μm, irregularly rectangular (1.5–3 : 1), thin-walled; *annulus* simple and persistent; *peristome teeth* 45–70 μm wide at the base, entire or split, orange, contrasting in color with the urn; *opercula* conic, obtuse or mammillate; *calyptrae* cucullate. *Spores* 10–14 μm.

Diagnostic characters. (1) Axillary hairs 3–4(5)-celled, 50–85(–100) μm long. (2) Proximal cells mainly rectangular, 2–5 : 1. (3) Capsules stramineous, with stomata at the base. (4) Exothecial cells rectangular, with thin walls.

Distribution (Fig. 17). Known from all continents; woody formations and open areas from 850 to 3500 m, except in Antarctica and surrounding islands, where it grows at sea level. It prefers damp or moistened habitats close to rivulets and snowbeds, and is not uncommon in shaded places. Within section *Montanae,* this species is the least xerophilous member, even growing on rocks that are periodically flooded, mainly from spring thaw. Mature sporophytes were present in 82% of the studied specimens.

Grimmia reflexidens is a widely distributed and gametophytically variable species, and identification of sterile specimens can be impossible. Plants growing in drier and more sunny habitats were described in Europe as *G. subsulcata.* They have shorter and more ovate leaves with (usually) strongly bulging cells, and can also have weak longitudinal plicae. On the other hand, plants from exceedingly moist places have more flaccid leaves and a high number of rhizoids, and are closer to the traditional concept of *G. sessitana.* This distinction of these two taxa is untenable, as the correlation between the observed characters is not absolute. Plants with very long proximal paracostal cells and recurved margins, typical of the *G. sessitana* concept, can exhibit strongly bulging cells, and do not differ from other material in sporophytic features.

The leaf margins of *G. reflexidens* are usually

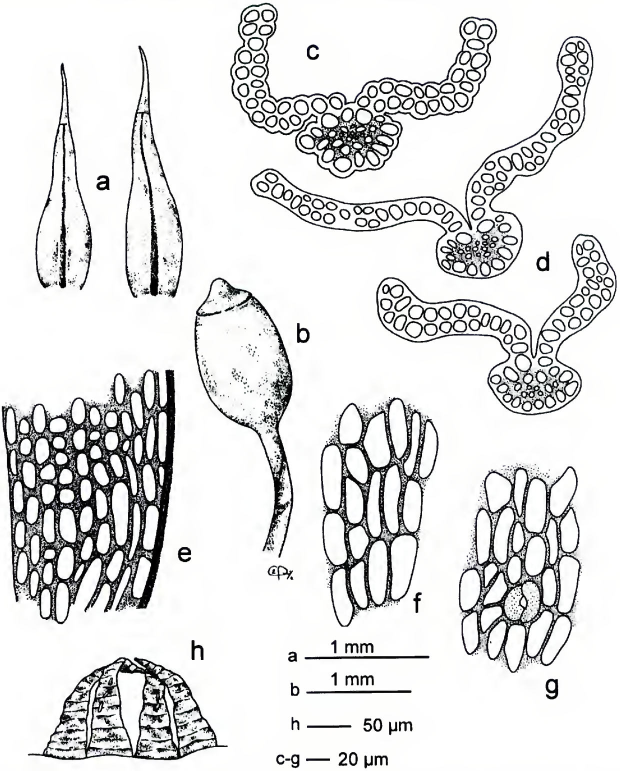

Figure 16. *Grimmia reflexidens.* —a. Leaves. —b. Capsule. —c. Transverse section of leaf with bulging cells. —d. Transverse sections of leaf with smooth cells. —e. Proximal leaf cells. —f. Medial exothecial cells. —g. Proximal exothecial cells and stoma. —h. Peristome teeth. [a, b, e–h, *Carestia s.n.* (PAV); c, *Brinkman s.n.* (CANM-198100); d, *Breidler s.n.* (BP-26598).]

plane in the proximal half. However, some populations have the margins recurved for part of their length, a feature that has been considered stable and of prime taxonomic value, causing many misidentifications.

Grimmia reflexidens was originally described as dioicous, because the perigonia and perichaetia usually occur at the ends of separate branches and so the autoicous condition can be extremely difficult to demonstrate. The sporophyte is rather stenotypic, and when fresh is easy to recognize with a 16–20× hand lens. The combination of straight setae and usually stramineous urns crowned with a distinct orange peristome is diagnostic and makes it unnecessary to dissect capsules to observe stomata. Populations with old capsules, already brown and damaged, are more problematic. In such cases, capsule color can be the same as in *G. alpestris.* The only sporophytic characters that vary to some degree are the orientation of the setae and the

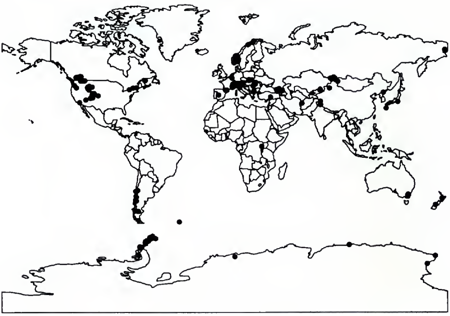

Figure 17. Distribution of *Grimmia reflexidens.*

shape of the opercula. The setae can be straight or weakly inclined, even in the same population. The operculum can be conic and obtuse, or mammillate. Both characters vary randomly, and so are taxonomically uninformative.

Grimmia reflexidens is a bipolar species widespread in the Northern Hemisphere, although uncommon in temperate Asia. In eastern North America it is rare, known only from a few localities in New Hampshire, New York, and Québec. It is the most common and widespread species of *Grimmia* in Antarctica, and it is relatively common in southern South America. Outside these two continents, it is rare in the Southern Hemisphere, known only from scattered localities in Australia, New Zealand, and Uganda.

Grimmia reflexidens (as *G. sessitana*) has been recorded from China by Cao and Vitt (1986: 166, fig. 21). I was able to study the materials on which their reports are based. Whereas some of the specimens from Chang Bai mountain are *G. reflexidens,* other collections from the same locality (e.g., *Cao Tong 199,* ALTA) are *G. longirostris.* The Yunnan specimen (*Zhu & Wu 64082,* ALTA) is *G. elongata.*

All authors except Deguchi (1978: 207) have mistakenly ascribed the authorship of *Grimmia lamellosa* to "Müll. Hal." (e.g., Greven, 1995; Wijk et al., 1962: 390; 1969: 655). In fact, Müller described *Guembelia lamellosa.* The reason for this mistake may be that in the original publication the genus *Guembelia* follows *Grimmia,* and Müller wrote out the full generic name only for the first species of each genus. For the remaining species he used the contractions "*G.*" and "*Gr.*" and this could have escaped the notice of later authors.

Selected specimens examined (533). UGANDA. Ruwenzori, Mijusi Valley, E slope of Mt. Speke, *O. Hedberg 571* (PC, UPS).

ANTARCTICA. **Antarctic Peninsula Region:** Andrée Island, Charlotte Bay, *Lewis-Smith 4018* (IBA-7365). **Melchior Archipelago:** Fysted Island, Water Fanding, *Siple 376.2* (FH). **Queen Mary Land:** Bunger Hills, in the neighbourhood of the Polish Base by the so-called "Totalizator," *Różycki s.n.* (IBA-7384). **Queen Maud Land:** Princess Astrid Coast, Drygalski Mts., NE slopes of the nunatak Malenkiy, *Konovalov s.n.* (IBA-7381). **Ross Sector:** Cape Sastrugi, *Walton 227* (IBA-7382). **South Shetland Islands:** King George Island, Admiralty Bay, Skua Cliff above Petrified Forest Creek, W of Arctowski Station, *Ochyra 627/80* (NY). **Victoria Land:** Cape Adare, *Terra Nova Expedition s.n.* (IBA-7379). SOUTH GEORGIA. Grytocken, "Dammen," 4 Apr. 1933, *Jröim s.n.* (BM).

AUSTRALIA. **New South Wales:** Mt. Kosciusko, Merrits Camp, *Maiden & Forsyth 203* (H-BR). NEW ZEALAND. **North Island:** Pinacles Ridge, Mt. Ruapehu, Feb. 1942, *Sainsbury s.n.* (BM). **South Island:** Tasman Glacier, near De La Beche Hut, *Sainsbury 756* (BM).

AFGHANISTAN. **Parwan:** Panjskir valley, Ruka, 10 Oct. 1948, *Köie s.n.* (ALTA). ANDORRA. Ríu de la Coma del Forcat, *Casas s.n.* (BCB-21723). AUSTRIA. **Carinthia:** in alpe "Fasihaunernik," pr. Malta, 1880, *Breidler s.n.* (TRH). **Salzburg:** Oblitzen bei Muhr im Lungau, *Breidler s.n.* (BP-36694). **Steiermark:** auf Glimmerschiefer "Speiereben bei Schöder," *Breidler s.n.* (BP-26598). **Tirol:** Sölden (am Ortler), Zaital, very near the Dusseldorferhutte, *Townsend 92/547* (IBA-6280). BELGIUM. Spa, promenade Annette et Lubin, *Cornet s.n.* (BP-36284). BULGARIA. **Sofia:** Rila-Geb., Musalla, *Richard s.n.* (GLM-2851). CHINA. **Jilin:** Mt. Chang Bai, *Koponen 36641* (ALTA). **Xinjiang Uygur:** Nileke Co., Haxilegen vicinity along Du-ku Highway, Tian Shan Range, *Zhao 953267* (MO). CZECH REPUBLIC. Tatra Magna, in valle Kistarpatak-völgy, Malá Studená dolina, *Boros s.n.* (BP-112930). FRANCE. **Ariège:** Montereign, 7 Sep. 1923, *Culmann s.n.* (Z). **Hautes Alpes:** Lantaret, Combegnot, 21 July 1926, *Culmann s.n.* (Z). **Isère:** La Lauirtel, 17 Aug. 1894, *Thériot s.n.* (TRH). **Pyrénées Centrales:** au sommet du port d'Oo, 5 Sep. 1856, *Zetterstedt s.n.* (TRH). **Haute-Savoie:** Chamonix, *Payot s.n.* (TRH). GEORGIA. Imeretia, in alpe Chrshein, *Brotherus 232* (H-SOL); distr.

Sukhumi, in vicinitate pagi Omarishara, in valle rivi Klich, 20 June 1986, *Vašák s.n.* (NY). GERMANY. Suythal, *Sendtner s.n.* (GLM-12812). INDIA. **Himanchal Pradesh:** Bara-Lacha-La, Lahul, Kangra, Punjab, *Koelz 6774* (MO). ITALY. **Trento:** Pedergnone di Trento, Oct. 1919, *Sbarbaro s.n.* (BM). JAPAN. **Honshu:** Mt. Tateyama, Toyama Prefecture, 11 Aug. 1955, *Iwatsuki s.n.* (H, JE). **Kyushu:** Kagoshima Pref., Kumage-gun, Isl. Yakushima, Mt. Miyanoura, *Mizokuti 59* (NICH-116232 p.p.). KAZAKSTAN. **Alma Ata:** Big Alma-Atynskoye Gorge and Lake, shore of Lake Alma Atinskoye Zalilisliy Alatau, *Allen 10636* (MO). MONGOLIA. **Chobd-aimak:** Erdeneburen-somon, Pabhöhe, *Schubert M196* (MO). NORWAY. **Opland**: Dovre pr. Kongsvold, *Kaurin s.n.* (BP-36229). **Sondre Trondhjems:** Opdal, pr. Sliper, 24 May 1883, *Kaurin s.n.* (TRH). PAKISTAN. Baltistan, Rimochagma, *Duthie s.n.* (H). POLAND. Dolinka Buczynowa, *Chałubiński s.n.* (BP-36671). ROMANIA. **Hunedoara:** supra lacu Zenoga, montes Retyezát, 3 Aug. 1969, *Vajda s.n.* (BP-74854). **Maramureş :** in alp Pop-Jocac, ad Fochesány, *Margittai s.n.* (BP-112952). RUSSIA. **Dagestan:** Kasi-kumuk, Tschulty, July 1898, *Alexander s.n.* (H-BR). **Gorno Altayskaya Autonomous Oblast:** Altai Mountains, Kayakkatuyarykskij Creek, *Ignatov 8/67* (IBA-7022). **Magadan:** Chukotka, Anadyr river basin, upper course of Ilmyneiveem river, 29 July 1978, *Afonina s.n.* (LE). SLOVAKIA. in jugo "Lorenz-Joch" supra lacum "Wahlenberg See," *Degen s.n.* (BP-86539); Höhe Tatra, Kleines Kohlbachthal auf der Leewald, 10 Aug. 1905, *Gyoffry s.n.* (JE). SPAIN. **Ávila:** circo de Gredos, inmediaciones de là Laguna Grande, *Rupidera s.n.* (IBA-3985). **Gerona:** Coll dels Tres Pics, *Lloret s.n.* (BCB-25784). **Huesca:** Alta Ribagorça, pic de Salenques, *Ballesteros s.n.* (BCC-1276). **Lérida:** Vall de Boí, Comaloforno, *Ballesteros s.n.* (BCC-1277). SWEDEN. Torneträsk-området Abisko Nationalpark, Bergvegg, ovenfor Ridopakte, 11 Aug. 1945, *Gjärevoll s.n.* (TRH). SWITZERLAND. **Bern:** Unteraargletocher, *Trautmann s.n.* (BP-36682). **Graubünden:** 10 Sep. 1930, *Amann s.n.* (FH). **Rhaetia:** Davos, July 1887, *Amann s.n.* (TRH). **Tessin:** au lac de Muzzano, près de Lugano, 6 Sep. 1930, *Amann s.n.* (PC). TURKEY. **Malatya:** Taurus Cataonicus, In convallibus subalpinis prope vicum Bekikara inter urbem Malatja et vicum Kjachta, *Handel-Mazzetti 2422* (FH).

CANADA. **British Columbia:** shoulder of Storm Mountain, Vermilion Pass, 13 Aug. 1913, *Brinkman s.n.* (FH). **Québec:** Gaspé Co., Table-top Mt., *Collins 4378* (FH). U.S.A. **Alaska:** Kenai (A7) Quadrangle, Chisik Island, along shoreline about 0.5 mi. N of Cannery, *Talbot 407* (NY). **Arizona:** Coconino Co., Point Sublime, on Fossil Shell Ridge, *Young 20* (MO). **California:** San Bernardino Mts., South Fork of Santa Ana, *Munz 6250* (FH). **Colorado:** Mesa Verde, *Lutz 4371* (FH). **Montana:** Flathead Co., Glacier National Park, along Sperry Glacier Trail, ¾ mi. E of Sperry Chalet, *Hermann 20709* (FH). **New Hampshire:** Mt. Washington, 10 July 1895, *Kennedy s.n.* (FH). **New York:** Essex Co., Keene, rocky summit of Gothics, *Miller 12045* (IBA). **Oregon:** Mt. Hood, 1 Aug. 1871, *Hall s.n.* (FH). **Washington:** Mason Co., near the summit of Mt. Ellinor, 13 June 1940, *Meyer s.n.* (G). **Wyoming:** Park County, Beartooth Lake Meadow, 20 Aug. 1953, *Conard s.n.* (MO).

ARGENTINA. **Santa Cruz:** in alpinis pr. Rio Tarde, *Halle 369* (BM). CHILE [no locality given]. *Pöppig s.n.* (BM, JE). **La Araucanía:** Lonquimay, *Guenckel 1768* (PC). **Osorno:** Ottoshöhe, S Ufer des Lago Nahuel Huapi, *Schiller 25* (PC). **Santiago:** San Gabriel, Río Maipo, *Looser 1037* (IBA).

9. Grimmia ungeri Jur., in Unger & Kotschy, Ins. Cypern. 169. 1865. *Grimmia alpestris* subsp. *ungeri* (Jur.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7: 112. 1883. *Grimmia alpestris* var. *ungeri* (Jur.) Husn., Muscol. Gall. 129. 1887. TYPE: [Cyprus.] In Olimpo Cypri, Vere [spring] 1862, *Unger s.n.* (lectotype, here designated, BM; isolectotypes, BM [2 replicates], GOET [2 replicates], H-SOL, S).

Grimmia brachyodon Austin, Bull. Torrey Bot. Club 6: 45. 1875. *Grimmia montana* var. *brachyodon* (Austin) Lesq. & James, Man. 145. 1884. TYPE: "*Grimmia montana*, var. Sulliv. & Lesqx. Exsic. Ed. 2, n. 215 pro parte" [Sullivant & Lesquereux, Musci boreali-americani ed. 2, n° 215 (1865 [1866]) (lectotype, here designated, FH; isolectotypes, FH [4 replicates], G, H, NY).

Grimmia jamesii Austin, Bull. Torrey Bot. Club 6: 43. 1875. *Grimmia montana* var. *truncata* Lesq. & James, Man. 145. 1884. TYPE: [U.S.A.] Nevada: Carson, *Watson 1412* (lectotype, here designated, FH; isolectotypes, FH [2 replicates]).

Grimmia microtricha Müll. Hal. & Kindb., in Macoun & Kindb., Cat. Canad. Pl. 6: 70. 1892. TYPE: [Canada.] British Columbia: Revelstoke, 7 May 1890, *Macoun s.n.* (lectotype, here designated, S; isolectotype, CANM-198087).

Grimmia montana var. *idahensis* Renauld & Cardot, Bot. Gaz. 30: 18. 1900. TYPE: [U.S.A.] Idaho: lac Pend d'Oreille, 1892, *Leiberg s.n.* (lectotype, here designated, PC; isolectotypes, CANM-197540, FH [2 replicates], NY).

Grimmia pseudomontana Cardot & Thér., Bot. Gaz. 30: 18, Pl. IV fig. 2. 1900. TYPE: [U.S.A.] Idaho: near Moscow, 24 Mar. 1894, *Henderson s.n.* (lectotype, here designated, PC).

Grimmia canadensis H. Winter [Karl Herman Winter, 1845–1933; as cañadensis], Hedwigia 55: 102, fig. 4. 1914, nom. illeg., non Kindb., 1897. *Grimmia ovalis* subsp. *canadensis* (H. Winter) Podp., Consp. Musc. Eur. 279. 1954. TYPE: [Spain. Santa Cruz de Tenerife:] Tenerife Island, Cañadas del Teide, 2000 m, Apr. 1912, *Winter s.n.* (lectotype, here designated, JE; isolectotypes, JE [5 replicates]).

Illustration. Figure 18.

Autoicous. Plants in tufts, olive-green to blackish. *Stems* to 1.5 cm tall, with central strand weakly developed; *axillary hairs* 5–8-celled, 105–175 μm long. *Leaves* erect and appressed when dry, patent and rigid when moist, 1–1.7 × 0.3–0.5 mm, ovate, acute, weakly keeled in the distal half, plane; *margins* plane proximally and incurved distally; *costa* semi-terete, prominent on the dorsal surface, although only weakly so above, slightly to clearly delimited; *lamina* 2–3(4)-stratose in the distal half, smooth; *distal cells* 5–7 μm, isodiametric, plane or slightly bulging on dorsal surface, smooth; *proximal*

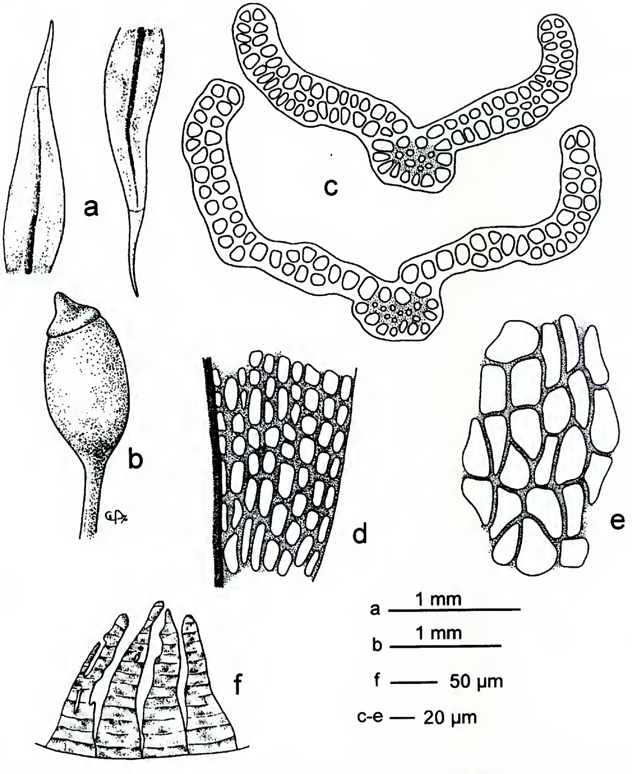

Figure 18. *Grimmia ungeri.* —a. Leaves. —b. Capsule. —c. Transverse sections of leaf. —d. Proximal leaf cells. —e. Medial exothecial cells. —f. Peristome teeth. [a–f, *Unger s.n.* (BM).]

paracostal cells 20–35 × ca. 16 μm, isodiametric to rectangular (1–2 : 1), with straight walls uniformly thickened or the transverse walls thicker than longitudinal walls; *proximal marginal cells* 10–25 × 6–10 μm, isodiametric to rectangular (1–2 : 1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.7 mm long, smooth. *Perichaetial leaves* 1.5–2.5 × 0.5–0.9 mm, convolute and larger than vegetative leaves (2–3×); *hyaline hair-points* terete, straight, to 1.5 mm long, nearly smooth. *Androecia* terminal. *Setae* erect and straight, ca. 2 mm long. *Capsules* exserted, ovoid or ellipsoid, symmetric, smooth, stramineous to brownish, lacking stomata; *exothecial cells* 17–65 × 13–45 μm, isodiametric and rectangular intermingled, thin-walled; *annulus* simple and persistent; *peristome teeth* 40–50 μm wide at the base, entire or moderately cribrose at the apex, orange-brownish, concolorous with the urn; *opercula* mammillate; *calyptrae* cucullate. *Spores* 9–13 μm.

Diagnostic characters. (1) Costa slightly prominent on the dorsal surface. (2) Laminar cells not bulging or only slightly. (3) Plants autoicous. (4)

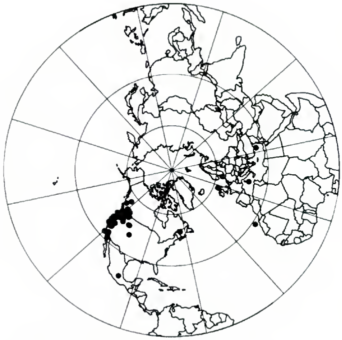

Figure 19. Distribution of *Grimmia ungeri.*

Capsules lacking stomata. (5) Opercula mammillate.

Distribution (Fig. 19). North America, Europe, Cyprus, and Canary Islands; coniferous forests and open areas between 600 and 3900 m elevation, on metamorphic and igneous rocks, (either basalts or granites). Mature sporophytes were present in 89% of the specimens studied.

Grimmia ungeri is the only species in the genus so far known to combine an autoicous sexual condition with capsules lacking stomata. Unfortunately, the perigonia usually arise on different branches than the perichaetia and are usually difficult to find.

Grimmia ungeri has been included in the synonymy of *G. alpestris* almost since its original publication. However, it is closer to *G. reflexidens* or *G. montana* and is only remotely related to *G. alpestris.* From *G. montana* it is distinguished by its autoicous (rather than dioicous) sexual condition and its obtusely mammillate opercula. *Grimmia reflexidens,* also autoicous, has stramineous urns contrasting strongly in color with the orange peristome teeth, and the capsules have stomata at the base. The remaining species in section *Montanae, G. alpestris, G. caespiticia,* and *G. nivalis,* differ in having bulging laminar cells, whereas members of section *Donnianae* are distinguished by their proximal laminar areolation.

Grimmia ungeri exhibits a rather anomalous distribution pattern. In North America, it is common along the Pacific Coast, but very rare on the Atlantic Coast, with only one locality known (in Québec). In Europe, it is known only from single localities in Scotland and Sardinia. From Africa *Grimmia ungeri* is also known from just one locality in the Canary Islands, from where it was described as *G. canadensis.* It also occurs in Cyprus, where it is common.

Greven (1995) considered this species as endemic to Cyprus and suggested that the remaining European records pertained to *G. alpestris* or *G. reflexidens* (as *G. sessitana*). However, the European collections are morphologically identical with Cypriot and North American plants.

The protologue of *G. brachyodon* states "*Grimmia montana,* var. Sulliv. & Lesqx. Exsic. Ed. 2, n. 215 pro parte" as the type of the taxon. The label of the specimen nº 215 of Sullivant and Lesquereux's exsiccata reads: "California: montis Diablo (Bolander); etiam in alpibus Sierra Nevada montium (Brewer)," but in none of the studied sets is the material separated according to either the provenance or the collector.

Selected specimens examined (135). CYPRUS. In Olympo (Troodos) Cypri, *Unger s.n.* (S). ITALY. **Sardinien:** Ostseite der Pta. La Marmara (Mt. Gennargentu), 2 June 1906, *Herzog s.n.* (JE). SPAIN. **Santa Cruz de Tenerife:** Tenerife, Cañadas del Teide, Apr. 1912, *Winter s.n.* (JE). UNITED KINGDOM. **Scotland:** Aberdeenshire, Ballater, Mt. Curtin, July 1870, *Fergusson s.n.* (FH).

CANADA. **British Columbia:** head of Baker Creek, Jakmia River, Cascade Mts., 17 Oct. 1880, *Watson s.n.* (FH). **Québec:** Gaspé Co., Mt. Albert, *Collins 3961* (FH). MEXICO. **Baja California:** Las Cuevitas, Sierra Juárez, ca. 10 mi. S of Laguna Hanson, *Wiggins 9177* (FH). **México:** Mt. Popocatépetl, *Kiener 18591* (FH). U.S.A. **California:** Luyo Co., Rock Creek, *MacFadden 17386* (FH). **Colorado:** Tolland South Boulder Canyon, 18 July 1923, *Roberts s.n.* (FH). **Idaho:** Coeur d'Alène Mountains, Clearwater-St. Joseph divide, *Leiberg 1692* (S). **Montana:** Columbia Falls, 24 June 1895, *Williams s.n.* (S). **Nevada:** Carson City, 1868, *Watson s.n.* (FH). **Oregon:** Klamath Co., Odell Lake, 23 June 1931, *Howell s.n.* (FH). **Washington:** Ellesburg, 23 July 1916, *Bailey s.n.* (FH). **Wyoming:** Park Co., Shoshone Natl. Park, at "Three Mile Campground" area, off Hwy. 16, *Churchill 5845* (G).

PUBLISHED NOMINA NUDA

Grimmia alpestris Schleich., Neues J. Bot. 1: 196. 1806[1805] (= *G. alpestris*).

Grimmia caespiticia f. *epilosa* Pilous, Musci čechoslovenici exsiccati n° 483 (= *G. caespiticia*).

Grimmia holmiensis Lindb. ex Hartm., Handb. Skand. Fl. Ed. 7: 374. 1858 (= *G. montana*).

Grimmia intermedia Fergusson, in Braithw., J. Bot. 10: 198. 1872 (= *G. ungeri*).

Literature Cited

Abramov, I. I. & A. L. Abramova. 1983. Konspect flori mkhov Mongol'skoj Narodnoj Respubliki. Nauka, Leningrad.

Afonina, O. M. 1986. Additamenta ad bryofloram Peninsulae Czukotka. 4. Novosti Sist. Nizsh. Rast. 23: 222–228.

Allen, B. 1995. Eight neglected species of Grimmiaceae (Musci) from North America. Fragm. Florist. Geobot. 40: 159–166.

Anderson, L. E. 1954. Hoyer's solution as a rapid permanent mounting medium for bryophytes. Bryologist 57: 242–244.

——— & H. Crum. 1958 [1959]. Cytotaxonomic studies on mosses of the Canadian Rocky Mountains. Bull. Natl. Mus. Canada 160: 1–89.

Baranova, M. A. 1987. Historical development of the present classification of morphological types of stomates. Bot. Rev. (Lancaster) 53: 53–79.

Bardunov, L. V. 1974. Listostebel'nye mkhi Altaya i Sayan. Nauka, Novosibirsk.

Bartram, E. B. 1957. Mosses from the United States Antarctic Service Expedition, 1940–41. Bryologist 60: 139–143.

Bednarek-Ochyra, H., J. Muñoz & R. Ochyra. 1992. The identity of *Grimmia pyrenaica* (Musci, Grimmiaceae). Fragm. Florist. Geobot. 37: 389–393.

Blom, H. H. 1996. A revision of the *Schistidium apocarpum* complex in Norway and Sweden. Bryophyt. Biblioth. 49: 1–333.

Brodo, I. M. & V. Alstrup. 1981. The lichen *Bryoria subdivergens* (Dahl) Brodo & D. Hawksw. in Greenland and North America. Bryologist 84: 229–235.

Bruch, P. & W. P. Schimper. 1845. Grimmiaceae. *In:* P. Bruch, W. P. Schimper & W. T. von Gümbel, Bryologia europaea 3: 89–147, tab. 230–271. E. Schweizerbart, Stuttgartiae.

Cao, T. & D. H. Vitt. 1986. A taxonomic revision and phylogenetic analysis of *Grimmia* and *Schistidium* (Bryopsida; Grimmiaceae) in China. J. Hattori Bot. Lab. 61: 123–247.

Chałubiński, T. 1882. Grimmieae tatrenses. Pamietn. Fizyogr. 2: 1–118, tab. 1–18.

Correns, C. 1899. Untersuchungen über die Vermehrung der Laubmoose. Gustav Fischer, Jena.

Crum, H. A. & L. E. Anderson. 1981. Mosses of Eastern North America. Columbia Univ. Press, New York.

Deguchi, H. 1978 [1979]. A revision of the genera *Grimmia, Schistidium* and *Coscinodon* (Musci) of Japan. J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 16: 121–256.

———. 1984. Studies on some Patagonian species of Grimmiaceae (Musci, Bryophyta). Pp. 17–72 *in* H. Inoue (editor), Studies on Cryptogams in Southern Chile. Kensei-sha, Tokyo.

———. 1987. Studies on some Peruvian species of the Grimmiaceae (Musci, Bryophyta). Pp. 19–74 *in* H. Inoue (editor), Studies on Cryptogams in Southern Peru. Tokai Univ. Press, Tokyo.

Dixon, H. N. 1904. The Student's Handbook of British Mosses, 2nd ed. V.T. Sumfield, Eastbourne, U.K.

Fritsch, R. 1991. Index to bryophyte chromosome counts. Bryophyt. Biblioth. 40: 1–352.

Geissler, P. & E. Maier. 1995. Lectotypifications of Central European *Grimmia* species (Musci, Grimmiaceae). Candollea 50: 495–514.

Grant, V. 1981. Plant Speciation, 2nd ed. Columbia Univ. Press, New York.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill (editors). 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 131: [i]–xviii, 1–389.

Greven, H. 1994. *Grimmia arenaria* Hampe by the Mawddach estuary in North Wales. J. Bryol. 18: 196–198.

———. 1995. *Grimmia* Hedw. (Grimmiaceae, Musci) in Europe. Backhuys Publishers, Leiden.

Habeeb, H. 1950. Nomenclatural and other notes on mosses. Rhodora 52: 72–75.

Hagen, I. 1909. Forarbejder til en Norsk Løvmosflora. IX Grimmiaceae. X Timmiaceae. XI Schistostegaceae. XII Hedwigiaceae. Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1909(5): 1–114.

Hirohama, T. 1978. Spore morphology of bryophytes observed by scanning electron microscope, IV. Grimmiaceae. Bull. Natl. Sci. Mus., Tokyo, B 4: 33–42, pl. 1–8.

Ignatov, M. & O. M. Afonina. 1992. Check-list of mosses of the former USSR. Arctoa 1: 1–85.

——— & T. Cao. 1994. Bryophytes of the Altai Mountains. IV. The family Grimmiaceae. Arctoa 3: 67–122.

Jóhannsson, B. 1993. Íslenskir mosar. Skeggmosaætt. Fjölrit Náttúrufraedistofnunar 24: 1–116.

Kawai, I. 1965. Studies on the genus *Grimmia*, with reference to the affinity of gametophyte. Sci. Rep. Kanazawa Univ., Biol. 10: 79–132.

———. 1968. Taxonomic studies on the midrib in Musci. Sci. Rep. Kanazawa Univ., Biol. 13: 127–157.

Khanna, K. R. 1964. Cytology of some mosses from the Adirondack Mountains. Bryologist 67: 343–350.

———. 1971. Sex chromosome in Bryophytes. Nucleus (Calcutta) 14: 14–23.

Kindberg, N. C. 1898. European and N. American Bryineae. Linköpings Lithografiska Aktiebolag, Linköping.

Kuc, M. 1969. Some mosses from an Antarctic oasis. Rev. Bryol. Lichénol. n.s. 36: 655–672.

Kuta, E., L. Przywara & R. Ochyra. 1984. Chromosome studies on Polish bryophytes I. Bryol. Beitr. 3: 28–45.

Lazarenko, A. S., E. I. Vysotskaya & E. N. Lesnyak. 1971. [Atlas of chromosome of leafy mosses of the USSR]. Naukova Dumka, Kiev.

Limpricht, K. G. 1890. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. Abth. 1. E. Kummer, Leipzig.

Loeske, L. 1913. Die Laubmooose Europas I. Grimmiaceae. Max Lande, Berlin-Schöneberg.

———. 1930. Monographie der europäischen Grimmiaceen. Biblioth. Bot. 101: [i]–ix, 1–236.

Maier, E. & P. Geissler. 1995. *Grimmia* in Mitteleuropa: Ein Bestimmungsschlüssel. Herzogia 11: 1–80.

Mårtensson, O. 1956. Bryophytes of the Torneträsk Area, Northern Swedish Lappland. II. Musci. Kung. Svenska Vetenskapsakad. Avh. Naturskyddsärenden 14: 1–321.

Mogensen, G. S. 1983. The Spore. *In:* R. M. Schuster (editor), New Manual of Bryology 1: 325–342. Hattori Botanical Laboratory, Nichinan.

Müller, C. 1887. Beiträge zur Bryologie Nord-Amerika's. Flora 70: 219–225.

———. 1898. Bryologia provincia Schen-si sinensis ex collectione giraldiana III. Nuovo Giorn. Bot. Ital. n.s. 5: 158–209.

Muñoz, J. 1998. The correct name of *Grimmia alpestris* (Musci, Grimmiaceae). Bryologist 100: 517–519.

Noguchi, A. 1988. Illustrated Moss Flora of Japan, Part 2. Hattori Botanical Laboratory, Miyazaki-ken.

Nyholm, E. 1956. Illustrated Moss Flora of Fennoscandia. II. Musci. Fascicle 2. CWK Gleerup, Lund.

Ochyra, R. & A. J. Sharp. 1988. Results of a bryogeographical expedition to East Africa in 1968, IV. J. Hattori Bot. Lab. 65: 335–377.

Ortiz, S. 1989. On the correct use of the term "holotype." Taxon 38: 635–636.

Pfeiffer, L. 1874. Nomenclator botanicus 1(2). T. Fischer, Kassel, Germany.

Podpěra, J. 1954. Conspectus Muscorum Europaeorum. Československé Akademie Věd, Prague.

Ramsay, H. P. 1969. Cytological studies on some mosses from the British Isles. Bot. J. Linn. Soc. 62: 85–121.

———. 1983. Cytology of mosses. Pp. 149–221 *in* R. M. Schuster (editor), New Manual of Bryology, Vol. 1. Hattori Botanical Laboratory, Nichinan.

Savicz-Lyubitskaya, L. I. & Z. N. Smirnova. 1969. *Grimmia doniana* Sm. ex Antarctida Orientali. Novosti Sist. Nizsh. Rast. 1969: 249–253.

Schimper, W. P. 1856. Corolarium bryologiae europaeae. E. Schweizerbart, Stuttgart.

Schwägrichen, C. F. 1811. Species Muscorum Frondosorum Supplementum 1(1). J. A. Barth, Leipzig.

Smith, A. J. E. 1978. Cytogenetics, biosystematics and evolution in the Bryopsida. Advances Bot. Res. 6: 195–276.

——— & M. E. Newton. 1966. Chromosome studies on some British and Irish mosses. I. Trans. Brit. Bryol. Soc. 5: 117–130.

——— & ———. 1968. Chromosome studies on some British and Irish mosses. III. Trans. Brit. Bryol. Soc. 5: 462–522.

Steere, W. C., L. E. Anderson & V. S. Bryan. 1954. Chromosome studies on Californian mosses. Mem. Torrey Bot. Club 20: 1–75.

Touw, A. & W. R. Rubers. 1989. De Nederlandse Bladmossen. Stichting Uitgeverig Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht.

Vaarama, A. 1949. Meiosis on the family Grimmiaceae. Portugaliae Acta Biol., Sér. A, Volume R. B. Goldschmidt: 47–78.

Vitt, D. H. 1984. Classification of the Bryopsida Pp. 696–759 *in* R. M. Schuster (editor), New Manual of Bryology, Vol. 2. Hattori Botanical Laboratory, Nichinan.

Vysotskaya, E. I. & E. N. Lesnyak. 1984. [Cytotaxonomic study in leafy mosses of Khybiny (Kolsky Peninsula)]. Bot. Zhurn. (Kiev) 69: 1399–1402.

Wijk, R. van der, W. D. Margadant & P. A. Florschütz. 1962. Index Muscorum (D–Hypno). Regnum Veg. 26: 1–535.

———, ——— & ———. 1969. Index Muscorum (T–Z, Appendix). Regnum Veg. 65: [i]–xii, 1–922.

Wyatt, R. & L. E. Anderson. 1984. Breeding systems in bryophytes. Pp. 39–64 *in* A. F. Dyer & J. G. Duckett (editors), The Experimental Biology of Bryophytes. Academic Press, London.

Zander, R. H. 1983. A rapid microscopic mounting medium for delicate bryophytes. Taxon 32: 618–620.

Index to Scientific Names

(accepted species in roman font)

REVISIÓN SISTEMÁTICA Y ANÁLISIS CLADÍSTICO DEL GÉNERO *CHAETIUM* (POACEAE: PANICOIDEAE: PANICEAE)

Osvaldo Morrone,[1] *Fernando O. Zuloaga,*[1] *Mirta O. Arriaga,*[2] *Raúl Pozner*[1] *y Sandra S. Aliscioni*[2]

RESUMEN

Chaetium (Poaceae: Panicoideae: Paniceae) comprende tres especies, distribuidas desde México y las Antillas hasta el norte de América del Sur. Este género se caracteriza por poseer espiguillas con articulación oblicua, las que tienen asimismo un callo piloso en la base y cariopsis con hilo linear. En este trabajo se analizaron las especies de *Chaetium* desde el punto de vista exomorfológico e histofoliar, hallándose dos patrones anatómicos en el género. Asimismo, se llevó a cabo un análisis cladístico del género, utilizando 29 caracteres morfológicos y anatómicos. Los resultados muestran que *Chaetium* constituye un clado monofilético, sobre la base de los caracteres antes mencionados. En la presente revisión se incluye una descripción de los caracteres morfológicos y anatómicos, una clave de las especies, fotografías de antecios superiores, fotomicrografías de transcortes de hoja y tallo florífero, mapas de distribución, descripciones e ilustraciones de las especies.

ABSTRACT

Chaetium (Poaceae: Panicoideae: Paniceae) is a neotropical genus of three species, ranging from Mexico and the Antilles to northern South America. The genus is mainly defined by having an oblique articulation of the spikelet, a hairy callus at the base of the spikelet, and a linear hilum on the caryopsis. Morphological and anatomical characters were considered in the present treatment; two anatomical patterns were found in the transverse section of the leaves. A cladistic analysis was carried out using 29 morphological characters; the results have shown that *Chaetium* forms a monophyletic clade, based on exomorphological and leaf anatomical data. A key to the species as well as an anatomical description of the genus and photomicrographs of the species, morphological description, illustrations, and a distribution map are presented.

Chaetium Nees (Poaceae) es un género americano perteneciente a la tribu Paniceae, de la subfamilia Panicoideae. Comprende tres especies de distribución neotropical, las que se hallan desde México, América Central y Cuba hasta el norte de América del Sur, en Colombia, Venezuela y noreste de Brasil. Si bien sus especies han sido tratadas parcialmente en floras regionales de México y Centroamérica (Hitchcock, 1930; Swallen, 1955; Pohl, 1980, 1994; McVaugh, 1983), las islas del Caribe (Hitchcock, 1909, 1936; Hitchcock & Chase, 1917) y Sudamérica (Doell, 1877; Smith & Wasshausen, 1981), no existe una revisión sistemática de conjunto de las especies del género, por lo que no han sido propuestas hipótesis filogenéticas para las especies de *Chaetium.*

En el presente tratamiento se estudian las especies de *Chaetium* desde el punto de vista exomorfológico, anatómico, se aportan nuevos datos y se discute, mediante un análisis cladístico, la monofilia y delimitación de *Chaetium.*

MATERIALES Y MÉTODOS

ESTUDIO ANATÓMICO

Se realizaron cortes transversales a la altura del tercio medio del limbo foliar y empleándose material procedente de ejemplares de herbario, previamente tratado con etilenglicol durante 24–48 horas. Los cortes se realizaron a mano alzada y los preparados de epidermis se obtuvieron siguiendo el método de Metcalfe (1960).

Para el estudio de los tallos se realizaron cortes en la zona próxima al último nudo de la caña florífera o en la zona media del entrenudo del estolón.

Algunos cortes se observaron sin vaciar para determinar la posición relativa de los cloroplastos en

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la vaina Kranz. El resto fue vaciado y coloreado con Alcian Blue-safranina (Cutler, 1978).

La presencia y ubicación del almidón de síntesis se detectó mediante la prueba de lugol (Johansen, 1940).

Se aplicó microscopia de fluorescencia para diferenciar por autofluorescencia, los cloroplastos comunes, ubicados en el clorénquima, y los cloroplastos especializados, localizados en la vaina Kranz (Elkin & Park, 1975; O'Brien & McCully, 1981). Para ello, algunos materiales cortados, sin vaciar, se montaron en agua destilada y se observaron con un microscopio de fluorescencia con excitación por luz reflejada IVFI (Epifluorescencia) Zeiss Standard, equipado con filtro de excitación azul BP 450–490; divisor cromático FT 510 y filtro supresor LP 520; la fuente de iluminación consistió en una lámpara de alta presión de mercurio HBO 50W perteneciente a la División Anatomía Vegetal del Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina.

Las fotomicrografías, que se obtuvieron con un equipo Zeiss, fueron realizadas en materiales vaciados.

ANÁLISIS DE ANTECIO SUPERIOR

Para el estudio de la epidermis abaxial de la lemma y pálea se empleó un microscopio de barrido Zeiss 940A, perteneciente al Instituto de Botánica Darwinion (IBODA), Buenos Aires, Argentina.

ESTUDIO EXOMORFOLÓGICO

Este estudio fue realizado sobre materiales pertenecientes a los herbarios BAA, G, LIL, MEXU, MO, SI, UC y US.

Con un asterisco (*) se señalan los ejemplares empleados en el estudio histofoliar y con dos asteriscos (**) aquellos especímenes utilizados en el análisis de la lemma y pálea superior: *Black 55-18634**,**, Davidse & D'Arcy 10412*,**, Díaz Luna 5010*, Eiten & Eiten 4713*, Ekman 7816*,**, *15699*, 16827**, 16474*, Hinton 2418*, Hitchcock s.n.*, 6856**, 6985**, Iltis & Nee 1048*, Iltis et al. 588*, Lyonnet 2447*, Moraes 2217**,**, Pickel 1714*, *Pittier 14926*, Pringle 11736*, Reeder & Reeder 2334*, Swallen 4635**, 4797**, Weatherwax 158*, Weston 2140*, 4145*.*

ANÁLISIS CLADÍSTICO

El análisis de las relaciones filogenéticas de las especies de *Chaetium* se realizó siguiendo los principios de la sistemática filogenética propuestos por Hennig (1966). Para el análisis filogenético se emplearon 29 caracteres morfológicos. Cinco de éstos (1, 2, 3, 24, 29) son caracteres multiestados y fueron tratados como no aditivos (no ordenados). La lista de los caracteres y estados usados para el análisis se muestra en la Tabla 1. La Tabla 2 contiene la matriz de datos (especies por caracteres).

El análisis cladístico fue llevado a cabo utilizando la opción de enumeración implícita (ie*) del Hennig86, versión 1.5 (Farris, 1988). Los árboles fueron re-enraizados al grupo externo más cercano (Nixon & Carpenter, 1993). Para la construcción del árbol de consenso estricto se usó la opción Nelsen del citado programa. Los caracteres fueron analizados sobre la base del estudio morfológico y anatómico de materiales citados en el apéndice 1 y complementados con datos bibliográficos.

Para el análisis de la distribución de los caracteres en los cladogramas y la generación de los mismos se empleó CLADOS (Nixon, 1993).

SELECCIÓN DE LOS GRUPOS EXTERNOS

Diversos autores relacionaron a *Chaetium* con varios géneros de Paniceae, por lo que las relaciones de este género dentro de la tribu son poco claras. Como no existe hasta el momento un estudio filogenético de las Paniceae se siguió el criterio sustentado por Nixon y Carpenter (1993) para la elección de los posibles grupos externos. A tal efecto, se consideraron las referencias bibliográficas con el siguiente criterio: cuando un autor citó uno o más géneros relacionados, se tomó la especie tipo de cada uno de ellos; cuando la publicación menciona una especie en particular, se incluyeron tanto dicha especie como la especie tipo del género correspondiente.

Los grupos externos utilizados en este análisis son:

Echinochloa (Kunth, 1833; Steudel, 1853–1855; Fournier, 1886; Hitchcock & Chase, 1917; Clayton & Renvoize, 1986; Beetle, 1987): dentro de este género se analizaron *Echinochloa crus-galli* (L.) P. Beauv., *E. holciformis* (Kunth) Chase y *E. oplismenoides* (E. Fourn.) Hitchc.
Louisiella (Clayton & Renvoize, 1986): *L. fluitans* C. E. Hubb. & J. Léonard
Melinis (Presl, 1830): *M. minutiflora* P. Beauv.
Panicum (Zuloaga & Soderstrom, 1985): *P. miliaceum* L. y *P. aristellum* Döll
Oplismenopsis (Clayton & Renvoize, 1986): *O. najada* (Hack. & Arechav.) Parodi
Oplismenus (Nees, 1829; Presl, 1830; Kunth, 1833; Steudel, 1853–1855): *O. hirtellus* (L.) P. Beauv.
Oryzidium (Hubbard & Schweickerdt, 1936; Clay-

Tabla 1. Lista de los caracteres y estados de caracteres usados para el análisis cladístico de *Chaetium*.

1. Orden del paracladio elemental: 0 = de 3er. orden; 1 = de 2do. orden; 2 = de 1er. orden. [veáse abajo]
2. Número de espiguillas por nudo: 0 = una; 1 = dos; 2 = variable.

Los caracteres 1 y 2 corresponden a características de la inflorescencia. La inflorescencia de las Poaceae es variable y compleja. Para establecer las homologías se tuvo en cuenta el orden máximo de paracladios presentes en la base de la inflorescencia.

3. Disposición de las espiguillas: 0 = no unilateral; 1 = unilateral.
4. Desarticulación de la espiguilla: 0 = transversal; 1 = oblicua.

El punto de desarticulación es uno de los caracteres más significativos para la distinción de los géneros de Paniceae (Webster, 1988). En este estudio se consideró la orientación de la zona de articulación en relación al eje mayor del pedicelo. A tal efecto se consideró transversal cuando la misma es perpendicular al eje mayor del pedicelo y oblicua cuando es diagonal.

5. Compresión de la espigulla: 0 = dorsiventral; 1 = lateral.

Estes es un carácter válido para distinguir géneros dentro de las Paniceae (Webster, 1988). La determinación de la compresión de la espiguilla se realizó cuando la inflorescencia se halla parcialmente incluida en la vaina foliar, debido a que las espiguillas maduras pueden presentar deformaciones de su estructura en el material herborizado.

6. Pelos de la base de la espiguilla: 0 = pelos ausentes; 1 = pelos presentes.

Se consideró la presencia o ausencia de un denso mechón de pelos (macropelos unicelulares) en la base de la espiguilla junto a la articulación de la misma.

7. Callo: 0 = ausente; 1 = presente.

El término callo es aplicado a cualquier modificación del disemínulo presente en el punto de desarticulación (Webster, 1988). En este estudio se definió callo al estípite formado por la expansión en longitud de la base de la gluma inferior y el nudo donde esta gluma se inserta.

8. Base de la gluma inferior: 0 = foliosa; 1 = reducida.
9. Arista de la gluma inferior: 0 = ausente; 1 = presente.
10. Número de venas de la gluma inferior: 0 = 5–7-nervia; 1 = 0–3-nervia.
11. Apice de la gluma superior: 0 = entero; 1 = hendido.
12. Arista de la gluma superior: 0 = ausente; 1 = presente.
13. Flor inferior: 0 = presente; 1 = ausente.
14. Consistencia de la lemma inferior: 0 = herbácea; 1 = coriácea.
15. Apice de la lemma inferior: 0 = entero; 1 = hendido.
16. Arista de la lemma inferior: 0 = ausente; 1 = presente.
17. Pálea inferior: 0 = presente; 1 = ausente.

Los caracteres 8, 9, 11, 12, 15, 16 incluyen diversas estructuras que comprometen a las brácteas de la espiguilla. Para establecer las homologías se siguió el criterio sustentado por Troll (1967: 1248–1290), donde la porción inferior de las glumas y lemmas es homóloga de la vaina foliar y la arista de las mismas, a la lámina foliar. Se consideró como una arista a toda prolongación superior a 0.4 mm de longitud. La presencia de una porción apical bífida en las glumas o lemmas es homóloga de las aurículas de la hoja vegetativa y, en el caso de las aristas dorsales, la porción de la gluma por encima de la base de arista es homóloga de la lígula. Con estas pautas se interpretó que las aristas son siempre terminales.

18. Compresión del antecio superior: 0 = dorsiventral; 1 = lateral.
19. Apice del antecio superior: 0 = cerrado; 1 = abierto.

Se consideró que el antecio superior es cerrado cuando los márgenes apicales de la lemma superior cubren al ápice de la pálea, y abierto cuando este último se halla libre. Ambos estados se observaron cuando el antecio está maduro.

20. Consistencia del antecio superior: 0 = crustáceo; 1 = cartilaginoso.

Como la consistencia varía a lo largo del desarrollo de la espiguillas, se tuvo en cuenta que el antecio superior se hallara maduro y encerrara una cariopsis desarrollada.

21. Bordes de la lemma superior: 0 = curvos; 1 = planos.

Los márgenes de la lemma superior tienen gran valor diagnóstico a nivel genérico en las Poaceae (Webster, 1988). En este estudio los márgenes de la lemma pueden ser involutos (curvados hacia la cara adaxial de la lemma) o planos cuando los márgenes están aplicados sobre la cara abaxial de la pálea superior.

22. Apice de la pálea superior: 0 = sin diferenciación morfológica; 1 = con 2 líneas verdes.

Los caracteres 18, 19, 20, 21, 22 implican diferentes estructuras del antecio superior. Las características morfológicas del antecio superior han sido utilizadas como uno de los caracteres más importantes a nivel genérico dentro de las Paniceae para establecer relaciones (Chase, 1911; Webster, 1988; Zuloaga & Soderstrom, 1985).

23. Forma del hilo: 0 = puntiforme; 1 = linear 1/1 del largo; 2 = linear 1/2 del largo.

La forma del hilo en la tribu es ampliamente variable, predominando el tipo punctiforme, siendo menos frecuente el tipo linear. La presencia de un hilo linear es utilizada como un carácter genérico distintivo; sin embargo su importancia como carácter diagnóstico ha sido poco explorada (Clayton & Renvoize, 1986). Zuloaga & Soderstrom (1985), Filgueiras (1986), Sendulsky et al. (1987) y Morrone & Zuloaga (1991) consideraron el hilo como un carácter de valor taxonómico. En este estudio se considera el hilo punctiforme cuando no alcanza el 1/4 de la longitud de la cariopsis. Se considera linear 1/1 cuando ocupa toda la longitud de la cariopsis y cuando el hilo presenta una forma intermedia, ocupando el 50% de la longitud de la cariopsis, se trató como linear 1/2.

24. Papilas adaxiales: 0 = ausentes; 1 = presentes.
25. Papilas abaxiales: 0 = ausentes; 1 = presentes.
26. Células parenquimaticas asociadas a las buliformes: 0 = ausente; 1 = presente.
27. Vaina mestomática: 0 = sin cloroplastos; 1 = con cloroplastos.
28. Vaina parenquimática: 0 = con cloroplastos; 1 = sin cloroplastos.
29. Vaina parenquimática: 0 = presente; 1 = ausente.

Los caracteres 27, 28 y 29 están relacionados con el tipo fotosintético y el Síndrome de Kranz. Estos caracteres fueron utilizados para delimitar los géneros de Paniceae por Brown (1977) y su importancia taxonómica fue enfatizada por numerosos agrostólogos (Ellis, 1977; Clayton & Renvoize, 1986; Hattersley, 1987). Para establecer las homologías se siguió el criterio sustentado por Brown (1977) y Dengler et al. (1985), quienes consideraron que la vaina Kranz del tipo anatómico MS es homóloga a la vaina mestomática de las plantas non-Kranz, y la vaina Kranz del tipo PS es homóloga a la vaina parenquimática de las gramíneas C_3.

Tabla 2. Matriz de datos usada para el análisis cladístico de *Chaetium*, con "*" se indican los caracteres polimórficos, con "–" los estados de caracteres no codificables.

	1 2 12345678901234567890123456789
Panicum miliaceum	00000000000000000000000000000
Oryzidium barnardii	10000001010100000011100000000
Melinis minutiflora	11001001011110111111100001000
Lousiella fluitans	10000001010010001011101110000
Panicum aristellum	12001000110100000001100000010
Oplismenus hirtellus	211010001*01*0001001100110010
Oplismenopsis najada	20100000110100010011101000010
Echinochloa crus-galli	211000000*01000100100101101-1
Echinochloa holciformis	221000000101100100100101101-1
Echinochloa oplismenoides	221000000001100100100101101-1
Chaetium bromoides	21010110100111011011102000000
Chaetium festucoides	210101111101100110111020001-1
Chaetium cubanum	210101101101100010111020001-1

ton & Renvoize, 1986): *O. barnardii* C. E. Hubb. & Schweick.

HISTORIA TAXONÓMICA DEL GÉNERO

Nees von Esenbeck en el año 1829 fundó el género *Chaetium* sobre la base de una especie, *C. festucoides*, y relacionó al mismo con *Oplismenus*. Nees von Esenbeck distinguió a *Chaetium* principalmente por tener inflorescencias espiciformes, pedicelos con articulación oblicua, gluma inferior setiforme, gluma superior rostrado-setosa y antecio superior cartáceo.

Posteriormente, Presl (1830) estableció el género *Berchtoldia* para México, describiendo e ilustrando una única especie, *B. bromoides*. Este autor relacionó a *Berchtoldia* con *Panicum*, *Melinis* y *Oplismenus*.

Kunth (1833) transfirió a *Chaetium festucoides* al género *Oplismenus*, ubicándolo dentro de la sección *Echinochloa*, junto con especies actualmente consideradas en los géneros *Echinochloa* y *Anthaenanthia* por tener "glumae inaequales, flos sterilis aristatus, spicae paniculatim, rarius racemosim dispositae." En la misma obra, Kunth trató a *Berchtoldia* como un género válido, citando al final de la descripción del género "Charact. gen. ex Presl." Por ello se deduce que posiblemente Kunth no hubiera visto la especie descripta por Presl, reconociendo a *Berchtoldia* como un género independiente de *Oplismenus* sobre la base de la descripción e ilustración de Presl.

En 1853, Steudel consideró a *Chaetium festucoides* como sinónimo de *Panicum chaetium* Steud. Este autor incluyó a *P. chaetium* en la sección *Echinochloa*, con especies actualmente consideradas en *Echinochloa*, *Oplismenus* y *Panicum*. En la misma obra Steudel consideró a *Berchtoldia* con rango genérico basándose en la obra de Presl.

Doell (1877) trató a *Chaetium* como una sección de *Panicum*, incluyendo una unica especie, *P. chaetium*.

Bentham (1881) reconoció a *Chaetium* como un género distinto de *Oplismenus*, sobre la base de diferencias morfológicas de la espiguilla e inflorescencia. En 1883 Bentham considera por primera vez a *Berchtoldia* sinónimo de *Chaetium*.

Posteriormente, Fournier (1886) trató a *Berchtoldia* (erróneamente citado "*Berchtholdia*") como un género válido para México, caracterizando al mismo por tener "gluma inferiore remota," posiblemente haciendo referencia al entrenudo desarrollado de la raquilla entre la gluma inferior y superior. Fournier reconoció tres especies en *Berchtoldia*: *B. bromoides*, *B. holciformis* (Kunth) E. Fourn. y *B. oplismenoides* E. Fourn., siendo estas dos últimas consideradas actualmente en *Echinochloa*.

Hackel (1887) reconoció a *Chaetium* e incluyó en la sinonimia del género a *Berchtoldia*.

Chase (1911), en su sinopsis de los géneros de Paniceae de América, reconoció a *Chaetium* y lo distinguió de *Echinochloa* por tener espiguillas lanceoladas, con un largo callo en la base y glumas largamente aristadas.

Hitchcock y Chase (1917) relacionaron a *Chaetium* con *Echinochloa* por tener espiguillas escabrosas.

Hsu (1965) trató a *Chaetium* como un género válido por el callo barbado presente en la base de la espiguilla y el patrón epidérmico del antecio superior con costillas longitudinales y depresiones echinadas.

Beetle (1977) citó *C. bromoides* para México y lo ubicó, sin aclarar las razones, dentro de la tribu Andropogoneae. Posteriormente, en 1987, este autor trató *C. bromoides* dentro de la tribu Paniceae y lo relacionó con *Echinochloa*, separando a este último género por tener espiguillas globosas, dorsiventralmente comprimidas, con la base obtusa y glumas desprovistas de largas aristas. A la vez señaló que *C. bromoides* tiene espiguillas angostas, lateralmente comprimidas, con callo basal agudo y ambas glumas con largas aristas.

Clayton y Renvoize (1986) relacionaron a *Chaetium bromoides* con *Echinochloa*, distinguiendo a este último género por tener la gluma inferior corta y aristas rígidas.

Webster y Valdés Reyna (1988) reconocieron a *Chaetium* por tener el ápice de los pedicelos oblicuo y la base de la espiguilla prolongada en un callo oblicuo y piloso. Estos autores indicaron que las evidencias que sostienen la relación de *Chaetium* con *Echinochloa* son dudosas y su relación con otros géneros dentro de la tribu es poco clara.

RESULTADOS

CARACTERES MORFOLÓGICOS Y TAXONÓMICOS

Forma biológica. *Chaetium* incluye especies perennes, con rizomas de entrenudos cortos. *Chaetium bromoides* posee cañas erguidas, simples a ramificadas hacia la base; se pueden hallar en esta especie cañas estoloníferas, de entrenudos cortos y arraigados, los que originan nuevas plantas. *Chaetium cubanum* tiene cañas simples a profusamente ramificadas, que pueden doblarse hacia el suelo, arraigar y propagar la mata a cierta distancia. *Chaetium festudoides* posee cañas simples, erguidas a geniculadas.

Las cañas en las especies del género tienen entrenudos comprimidos y macizos, con médula esponjosa. Las lígulas son membranáceo-pestañosas en *C. cubanum* y *C. festucoides* y pestañosas en *C. bromoides*, y las láminas son lineares, planas a plegadas o involutas, con pilosidad variable, desde glabra a híspidas en ambas caras.

Inflorescencias. Las inflorescencias son contraídas, espiciformes a subespiciformes, parcialmente incluidas en las vainas foliares en *C. cubanum* a exsertas en el resto de las especies.

Espiguillas. *Chaetium* presenta el plan básico de espiguilla de las Paniceae, la que se caracteriza por ser biflora, con dos glumas y articulación en la base de la espiguilla, junto a la inserción con el pedicelo. Las espiguillas son largamente ovoides, comprimidas dorsiventralmente, escabrosas, en pares, sobre pedicelos desiguales. La base de la espiguilla posee un callo como resultado del desarrollo de la raquilla entre las glumas y el antecio superior. El callo es agudo, híspido y con su extremo oblicuo. La espiguilla posee en el nudo basal una gluma inferior, con un cuerpo principal que varía de lanceolado a ovado, terminando en ambos casos en una arista; está reducida a una estructura setácea en *C. festucoides*. La gluma superior es herbácea y aristada. La lemma inferior es herbácea en *C. cubanum* y *C. festucoides* y coriácea en *C. bromoides*, siendo corta a largamente aristada en *C. bromoides* y *C. festucoides*, respectivamente, a acuminada en *C. cubanum*. La pálea y flor inferior se hallan ausentes.

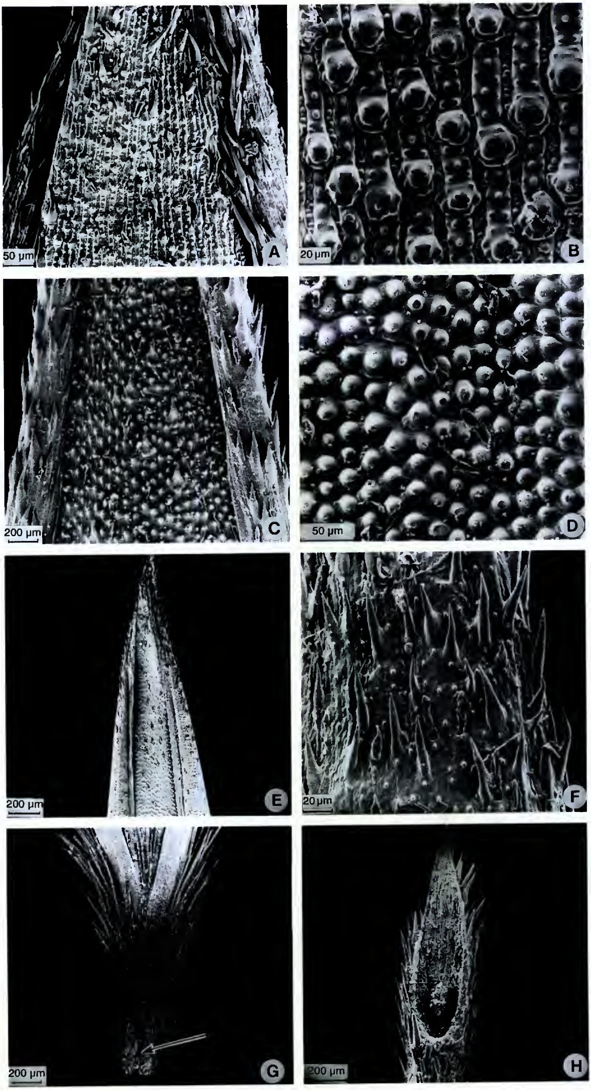
La cariopsis es largamente elipsoide, dorsiventralmente comprimida, con hilo linear, la mitad del largo de la cariopsis.

Textura y ornamentación del antecio superior (Fig. 1). El antecio superior es largamente ovoide, dorsiventralmente comprimido, cartilaginoso, papiloso, pajizo y escabroso hacia el ápice; la lemma posee los márgenes membranáceos y planos, dejando libre el ápice de la pálea. La epidermis abaxial de la lemma y pálea posee células largas rectangulares, agrupadas en hileras longitudinales, tres veces más largas que anchas en *Chaetium festucoides* y *C. cubanum* y más de tres veces más largas que anchas en *C. bromoides*. Las células largas poseen las paredes anticlinales longitudinales onduladas.

La epidermis abaxial de la pálea y lemma posee aguijones hacia el ápice y micropelos bicelulares, fusiformes, en toda su superficie, con mayor número hacia el ápice de la lemma y pálea. Se observaron papilas simples en la lemma y pálea de *Chaetium cubanum* y *C. festucoides*, distribuidas regularmente, una por célula larga, en toda la super-

→

Figura 1. A–F. Fotomicrografías MEB de antecios superiores de especies de *Chaetium*. A, B. *C. bromoides*. —A. Porción superior del antecio visto desde la pálea. —B. Detalle de la epidermis abaxial de la lemma. C, D. *C. festucoides*. —C. Porción superior del antecio visto desde la pálea. —D. Detalle de la epidermis abaxial de la lemma. E, F. *C. cubanum*. —E. Apice del antecio visto desde la pálea. —F. Detalle de E, con aguijones. —G. Base de la espiguilla de *C. bromoides*. La flecha indica el área de inserción oblicua. —H. Apice del pedicelo de *C. bromoides*. (A, B, G, H, *Davidse & D'Arcy 10412*; C, D, *Swallen 4635*; E, F, *Ekman 7816*.)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ficie. La pared tangencial externa es marcadamente convexa en *C. bromoides*, con costillas longitudinales y surcos asociados a las paredes anticlinales longitudinales; en esta especie, las papilas son compuestas, asociadas a la pared transversal distal de las células largas, y se hallan formadas por una papila simple con 2–6 proyecciones equinadas. También posee papilas simples distribuidas a lo largo de los surcos y costillas.

ANATOMIA FOLIAR

Caracteres histofoliares en corte transversal (Figs. 2, 3). *Transcorte*: variable de plano a conduplicado o convoluto; láminas simétricas a ambos lados de la costilla central, con costillas bien marcadas en ambas caras y ápice redondeado en *C. bromoides* o con ambas caras sublisas, con costillas ligeramente insinuadas en las restantes especies. Todas las costillas se hallan limitadas por grupos de células buliformes. *Costilla central*: de estructura variable, conspicua, con un haz vascular primario y dos haces vasculares terciarios, estructuralmente distinguibles de los restantes haces vasculares, asociado o no a células parenquimáticas incoloras hacia la cara adaxial o inconspicua, con un haz vascular primario solitario sin células parenquimáticas incoloras. *Distribución de los haces vasculares*: haces vasculares primarios y secundarios equidistantes de ambas epidermis y asociados a las costillas; haces vasculares terciarios dispuestos por debajo de las células buliformes y próximos a la cara abaxial. *Estructura de los haces vasculares*: haces vasculares *primarios* de contorno subcircular a elíptico, con vasos de metaxilema de contorno angular y diámetro igual o ligeramente mayor que las células Kranz; haces vasculares *secundarios* de contorno angular, con xilema y floema distinguible; haces vasculares *terciarios* de contorno angular, con xilema y floema pobremente desarrollado. *Vaina de los haces vasculares*: compuesta por una única vaina mestomática con cloroplastos de posición centrífuga, en *C. cubanum* y *C. festucoides*, o compuesta por dos vainas en *C. bromoides*, la externa parenquimática con cloroplastos de posición centrífuga, la interna mestomática, compuesta por células de paredes uniformemente engrosadas; vaina perifloemática presente. *Células distintivas Kranz:* ausentes. *Esclerénquima*: pobremente desarrollado, en grupos discontinuos, subepidérmicos, adaxiales y abaxiales. *Mesofilo*: clorénquima formado por células raquimorfas, imperfectamente radiado alrededor de los haces vasculares en *C. cubanum* y *C. festucoides*, y radiado en *C. bromoides*. *Células epidérmicas*: células buliformes presentes en los surcos adaxiales, formando grupos pequeños; células epidérmicas pequeñas y regulares en forma, de pared tangencial externa muy engrosada. *Macropelos*: unicelulares, de base bulbosa, asociada a células epidérmicas isodiamétricas, de paredes más engrosadas.

Epidermis en vista paradermal. *Células largas*, en ambas epidermis, 3 a 5 veces más largas que anchas, de paredes sinuosas, interrumpidas por células cortas alargadas en sentido transversal, a veces silicificadas, en ocasiones cuadrangulares en *C. festucoides*. *Células buliformes*: isodiamétricas a rómbicas. *Aparatos estomáticos*: rómbicos a subrómbicos, distribuidos en dos hileras en la zona intercostal, flanqueados por una hilera de ganchos; células largas interestomáticas de extremos excavados.

Micropelos. bicelulares, tipo “panicoide.” *Macropelos*: unicelulares, distribuidos en las zonas intercostales, de paredes engrosadas y asociados a células epidérmicas sobreelevadas. *Cuerpos de sílice costales*: halteriformes de eje corto, ocasionalmente cruciformes en *C. festucoides*; células suberosas costales de contorno sinuoso, de igual o mayor longitud que las silíceas; pares sílico-suberosos ocasionales en *C. cubanum*.

Autofluorescencia. Los cloroplastos de la vaina Kranz de *Chaetium bromoides* autofluorescen como los típicos cloroplastos de las especies PS, mientras que los cloroplastos de la vaina Kranz de *C. cubanum* y *C. festucoides* autofluorescen como los típicos de las especies MS (Elkin & Park, 1975).

Corte transversal de tallo florífero (Figs. 2G, H, 3C, D). Médula formada por grandes células parenquimáticas sin contenido, con grandes espacios intercelulares, limitada externamente por un anillo de esclerénquima constituido por 3–4 hileras de fibras. Zona medular con haces vasculares primarios, distribuidos en 2–4 ciclos, con vaina perifloemática, rodeados por una vaina esclerosada. Haces vasculares periféricos primarios y terciarios, dispuestos en dos ciclos. Haces vasculares primarios trabados, los terciarios libres. En *C. cubanum* y *C. festucoides* los haces vasculares periféricos se encuentran rodeados por una sola vaina mestomática Kranz, con cloroplastos especializados de posición centrífuga y depósitos de almidón de síntesis; en *C. bromoides* los haces vasculares periféricos poseen una vaina interna esclerenquimática y externa parenquimática Kranz, la que se extiende entre los haces vasculares contiguos, con cloroplastos especializados de posición centrífuga y depósitos de almidón de síntesis.

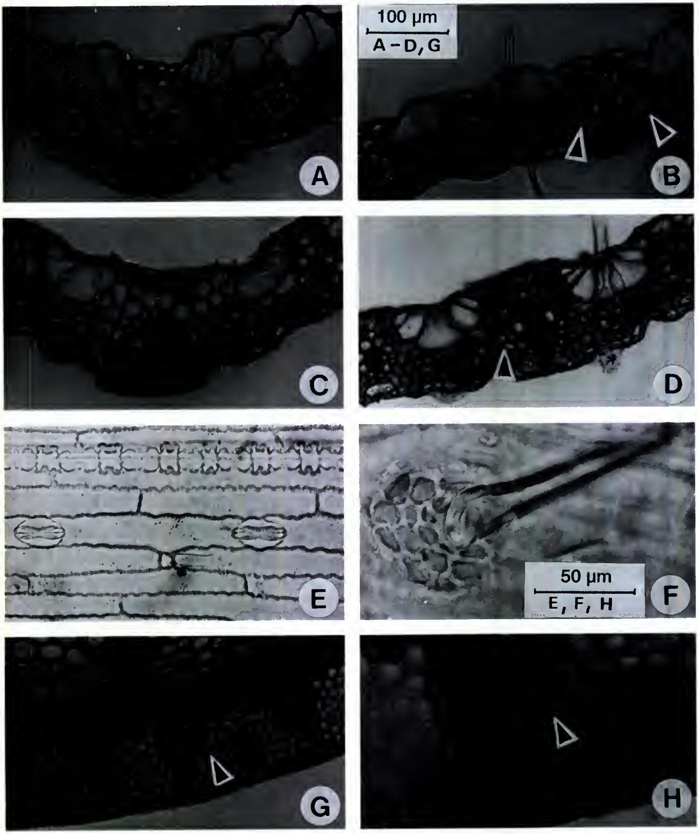

Figura 2. A, B. *Chaetium cubanum*. —A. Transcorte foliar a la altura de la costilla central. —B. Transcorte foliar de una porción de la lámina. C–F. *C. festucoides*. —C. Transcorte foliar a la altura de la costilla central. —D. Transcorte foliar de una porción de la lámina. —E. Epidermis abaxial en vista topográfica. —F. Detalle de macropelo unicelular con base en cojinete. G, H. *Chaetium cubanum*. —G. Haces vasculares periféricos en transcorte de tallo florífero. —H. Detalle aumentado de la fotomicrografía anterior. Las flechas indican restos de una vaina externa, en hoja y tallo. (A, B, G, H, *Ekman 15699*; C, *Pittier 14926*; D–F, *Moraes 2217*).

La única diferencia observada entre la anatomía del tallo florífero y del estolón es un aumento en la cantidad de ciclos en que se presentan los haces vasculares internos, del número de capas de fibras que componen el anillo esclerenquimático y una disminución en el tamaño y calibre de las fibras de dicho anillo que se observa en el transcorte del estolón.

En la Tabla 3 se resumen los caracteres anatómicos distintivos de las tres especies de *Chaetium*.

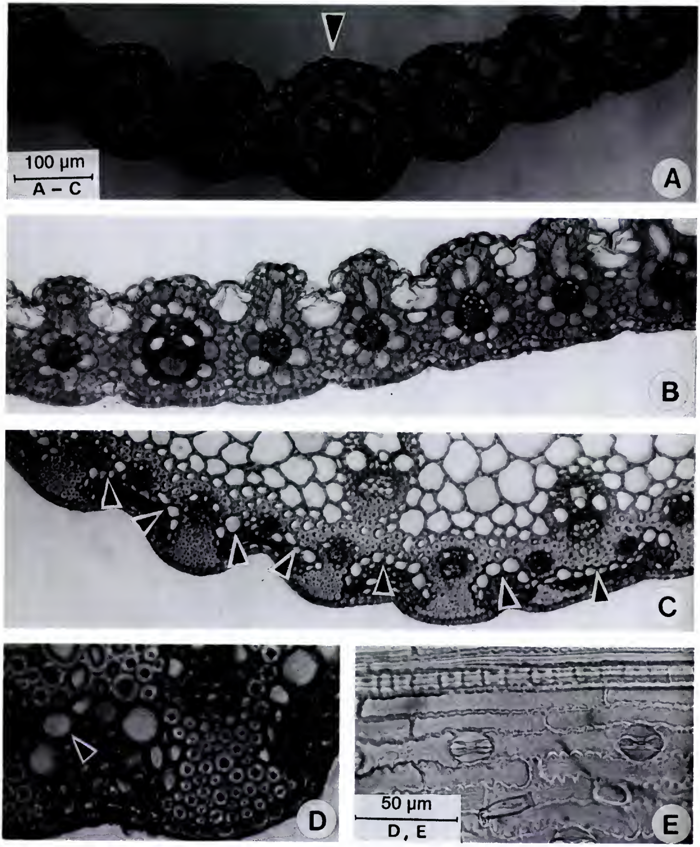

Figura 3. A, B. *Chaetium bromoides*. —A. Transcorte foliar a la altura de la costilla central; se señala la costilla central. —B. Transcorte foliar de una porción de la lámina. —C. Zona periférica de transcorte de tallo florífero. —D. Detalle aumentado de la fotomicrografía anterior. —E. Epidermis abaxial en vista topográfica. Las flechas indican las vainas parenquimáticas en los haces vasculares periféricos de transcorte de tallo (A, *Iltis et al. 588*; B, *Díaz Luna 5010*; C–E, *Hitchcock s.n.*).

Los caracteres anatómicos observados en *Chaetium bromoides* concuerdan con lo previamente señalado por Montiel (1972), siendo esta una especie C$_4$, con vaina Kranz de tipo PS, tanto en hoja como en tallo; en dicha vaina se localizan los cloroplastos especializados, los que autofluorescen de la misma forma que los de otras especies PS. A su vez, del estudio anatómico de *Chaetium cubanum* y *Chaetium festucoides* se desprende que son especies C$_4$, con vaina Kranz de tipo MS, tanto en hoja como en tallo, con cloroplastos de posición centrífuga, los que autofluorescen de igual forma que los de otras

Tabla 3. Comparación de los caracteres anatómicos de las especies de *Chaetium*.

	C. bromoides	*C. festucoides*	*C. cubanum*
Aspecto del transcorte	moniliforme	subliso	subliso
Forma del transcorte	plano a conduplicado	conduplicado	convoluto
Ancho del transcorte	muy ancho	ancho	angosto
Costilla central	inconspicua, con un haz vasc. 1º	conspicua, con 3 haces vasc. (1º y 3º)	conspicua con 3 haces vasc. (1º y 3º)
Células parenquimáticas incoloras en la costilla central	ausentes	presentes	ausentes
Tipo de haces vasculares	1º y 2º	1º, 2º y 3º	1º, 2º y 3º
Vainas completas alrededor de los haces vasculares	dos	una	una
Extensiones de la vaina	presentes adaxialmente	ausente	ausente
Vaina perifloemática	incompleta	completa	completa
Tipo anatómico	PS-PCK	MS	MS
Fluorescencia de los cloroplastos	como en especies PS-NAD-me	como en especies MS	como en especies MS
Vinculación de los haces vasculares	1º y 3º vinculados a las costillas	1º vinculados a las costillas y 3º a cél. buliformes	1º vinculados a las costillas y 3º a las cél. buliformes

especies MS, de tipo bioquímico NADP-me. La presencia de dos vainas alrededor de los haces vasculares, en *Chaetium bromoides,* la externa con cloroplastos centrífugos, tradicionalmente ha sido asociada al tipo fisiológico PEP-ck (Gutiérrez et al., 1976). Sin embargo, dicha correlación debe tomarse con precaución, dadas las excepciones halladas hasta el presente dentro de las Paniceae (Ohsugi & Murata, 1980; Ohsugi et al., 1982; Oguro et al., 1985; Prendergast & Stone, 1987).

En *Chaetium cubanum* y *C. festucoides* puede observarse, por fuera de la vaina Kranz, unas pocas células globosas de paredes algo engrosadas, vacías de cloroplastos; estas células representan restos de una segunda vaina, confirmando lo observado previamente por Renvoize (1987). La presencia de restos de una vaina externa en especies MS fue anteriormente citada para especies de *Panicum* de las sects. *Agrostoidea* Hitchcock & Chase, *Discrepantia* Zuloaga, *Prionitia* Zuloaga y *Tuerckheimiana* (Hitchc.) Zuloaga (Zuloaga et al., 1989) y en el género *Anthaenantiopsis* (Morrone et al., 1993). En especies de *Aristida* (Brown, 1977), *Alloteropsis, Neurachne* y *Paraneurachne* (Hattersley, 1987) se encuentra una vaina externa a la vaina Kranz MS, bien desarrollada, vacía o con unos pocos cloroplastos, de naturaleza parenquimática. Brown (1977) y Dengler et al. (1985) definen este último carácter como intermedio entre una vaina non-Kranz y una vaina Kranz MS.

ANÁLISIS CLADÍSTICO

El análisis cladístico arrojó dos árboles igualmente parsimoniosos (Fig. 4B, C), ambos con una longitud de 58 pasos, un índice de consistencia de 0.55 y un índice de retención de 0.65. *Chaetium* se comportó como un taxón monofilético en todos los casos (Fig. 4A), estando sustentado por cuatro sinapomorfías: desarticulación oblicua de la espiguilla (4), pelos presentes en la base de la espiguilla (6), callo presente (7) e hilo linear ½ (23). En ambos árboles originales *Chaetium* presenta la misma topología interna; el clado *Chaetium festucoides* y *C. cubanum* forma un grupo monofilético por la presencia de vaina mestomática con cloroplastos (27), que corresponde al subtipo fotosintético C_4 MS y por la ausencia de vaina parenquimática (29). *Chaetium festucoides* se distingue por la base reducida de la gluma inferior (8) y *C. cubanum,* por la lemma inferior aristada (16). *Chaetium bromoides* está definido por la nerviación de la gluma inferior 5–7-nervia (10) y la lemma inferior de consistencia coriácea (14).

El número básico de cromosomas fue excluido del análisis debido a que de las tres especies del género sólo se conocen recuentos cromosómicos para *Chaetium bromoides,* con $2n = 26$ (Gould, 1958, 1966; Reeder, 1967; Pohl & Davidse, 1971; Montiel, 1972). El número básico $x = 13$ es poco frecuente en las Poaceae, especialmente en las Panicoideae, por lo que deberían realizarse estudios cromosómicos en *C. cubanum* y *C. festucoides* para confirmar este carácter. De confirmarse este número básico de $x = 13$, el mismo agregaría un carácter adicional para la monofilia de este género.

Brown (1977), sobre la base del estudio anatómico en géneros de Poaceae propuso, que los tipos

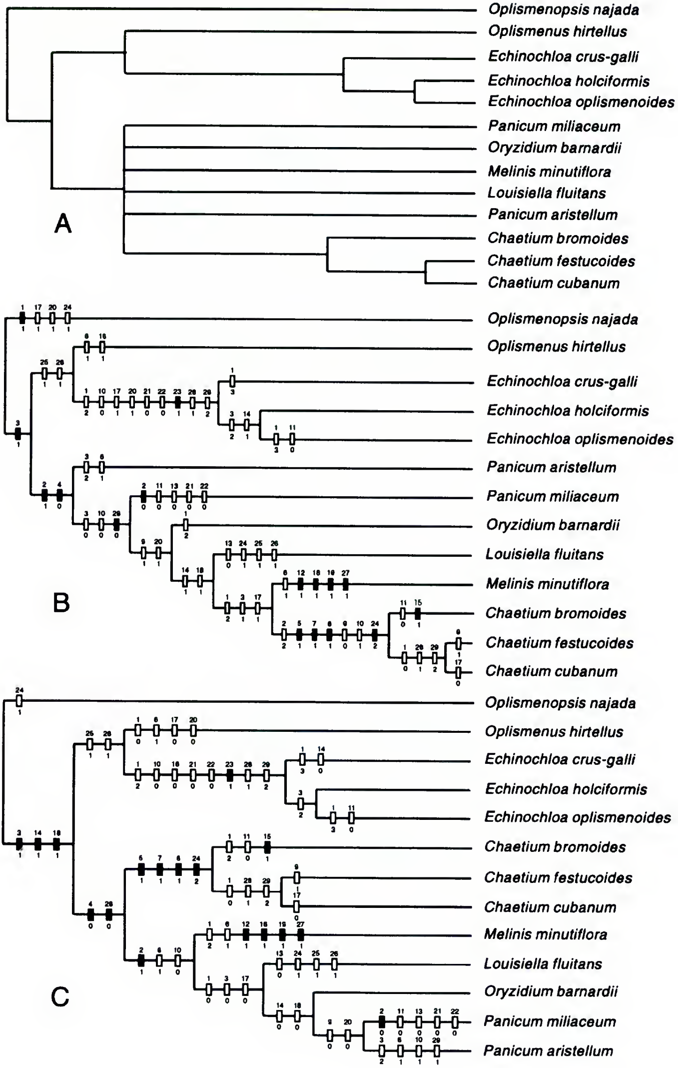
Oplismenopsis najada
Oplismenus hirtellus
Echinochloa crus-galli
Echinochloa holciformis
Echinochloa oplismenoides
Panicum miliaceum
Oryzidium barnardii
Melinis minutiflora
Louisiella fluitans
Panicum aristellum
Chaetium bromoides
Chaetium festucoides
Chaetium cubanum
A
Oplismenopsis najada
Oplismenus hirtellus
Echinochloa crus-galli
Echinochloa holciformis
Echinochloa oplismenoides
Panicum aristellum
Panicum miliaceum
Oryzidium barnardii
Louisiella fluitans
Melinis minutiflora
Chaetium bromoides
Chaetium festucoides
Chaetium cubanum
B
Oplismenopsis najada
Oplismenus hirtellus
Echinochloa crus-galli
Echinochloa holciformis
Echinochloa oplismenoides
Chaetium bromoides
Chaetium festucoides
Chaetium cubanum
Melinis minutiflora
Louisiella fluitans
Oryzidium barnardii
Panicum miliaceum
Panicum aristellum
C

Figura 5. Distribución de las especies de *Chaetium*.

anatómicos PS y MS evolucionaron independientemente en la tribu Paniceae y correlacionan ambos tipos con los subtipos fisiológicos NAD-me y NADP-me respectivamente. Consecuentemente, Brown señaló que *Chaetium*, que posee especies PS y MS, debería segregarse en dos géneros. Más recientemente, Hattersley y Watson (1992), indicaron que existe una marcada diversificación fotosintética en las Poaceae y postularon la hipótesis de que las gramíneas NADP-me (= MS) podrían haber evolucionado a partir de las NAD-me (PS). El presente estudio corrobora el estatus monofilético de *Chaetium* y sustenta la hipótesis antes mencionada por Hattersley y Watson (1992), pues el análisis cladístico muestra que las especies MS, *C. festucoides* y *C. cubanum*, son derivadas de un antecesor hipotético PS. A la vez, se descarta la posibilidad de segregar al género de acuerdo a la anatomía foliar que presentan las especies.

DISTRIBUCIÓN GEOGRÁFICA

Chaetium es un género neotropical cuya área se extiende aproximadamente desde los 23° de latitud Norte hasta los 10° de latitud Sur (Fig. 5). Sus especies poseen una distribución alopátrica: *Chaetium bromoides*, crece desde el centro y sur de México hasta el sur de Panamá. *Chaetium cubanum* sólo se la halla en Cuba. *Chaetium festucoides* habita en el norte de América del Sur, presentando un área discontinua: se encuentran poblaciones en el noreste de Brasil (en los estados de Ceará, Mara-

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Figura 4. —A. Cladograma de consenso estricto obtenido a partir de dos cladogramas igualmente parsimoniosos B y C. Los caracteres indicados con barras negras señalan sinapomorfías, las barras vacías homoplasias.

nhão, Paraíba y Rio Grande do Norte) y otras crecen en el norte de Colombia (en el estado de Bolívar) y Venezuela (en el estado de Guárico).

De esta distribución alopátrica se puede deducir que la posibilidad de que los grupos fotosintéticos representados por *Chaetium bromoides* (PS) y *C. cubanum–C. festucoides* (MS) al quedar aislados geográficamente pudieran haber evolucionado en forma vicariante (Hedges et al., 1994).

TRATAMIENTO TAXONÓMICO

Chaetium Nees, in Mart., Fl. Bras. Enum. Pl. 2: 269. 1829. *Panicum* sect. *Chaetium* (Nees) Döll, in Mart., Fl. Bras. 2(2): 149. 1877. TIPO: *Chaetium festucoides* Nees.

Berchtoldia J. Presl, in C. Presl, Reliq. haenk. 1: 323. 1830. TIPO: *Berchtoldia bromoides* J. Presl.

Plantas perennes, cespitosas, en ocasiones estoloníferas, con *cañas* de entrenudos macizos, con médula esponjosa. *Lígulas* membranáceo-pestañosas a pestañosas. *Láminas* lineares. *Inflorescencias* espiciformes a subespiciformes, con ramificaciones ascendentes, adpresas, terminando en una espiguilla desarrollada; espiguillas en pares, con desarticulación oblicua en la base de la espiguilla junto al pedicelo. *Espiguillas* largamente ovoides, dorsiventralmente comprimidas, plano-convexas, glabras; callo puntiagudo, formado por la base de la gluma inferior y el entrenudo de la raquilla, híspido. *Gluma inferior* largamente lanceolada a setácea, aristada, no abrazadora, separada de la gluma superior por un entrenudo conspicuo. *Gluma superior* aristada. *Lemma inferior* acuminada a aristada. *Pálea inferior* y flor inferior ausentes. *Antecio superior* largamente ovoide, cartilaginoso; papiloso, escabroso junto al ápice; lemma con los márgenes membranáceos, planos, dejando libre el ápice de la pálea; pálea binervia; estambres 3; lodículas 2; estilos libres desde la base; estigmas plumosos. *Cariopsis* largamente elipsoide, dorsiventralmente comprimida, pálida; hilo linear, ½ del largo de la cariopsis; embrión ⅓–⅔ del largo de la cariopsis.

Género americano con tres especies, desde México e islas del Caribe hasta Brasil.

CLAVE PARA LA IDENTIFICACIÓN DE LAS ESPECIES

1a. Espiguillas de 8–11 mm de largo (sin las aristas); gluma inferior largamente lanceolada, cubriéndo totalmente el dorso del antecio superior, 7-nervia, con 3 nervios centrales, los restantes equidistantes; lemma inferior coriácea; vainas aquilladas; lígulas pestañosas [México hasta Panamá] .... *Chaetium bromoides*

1b. Espiguillas de 4.8–9.2 mm de largo (sin las aristas); gluma inferior reducida a una seta a ovada, dejando libre el dorso del antecio superior o cubriéndolo hasta ¾ del mismo, enervia a 3-nervia, con un nervio central, los restantes próximos a los márgenes; lemma inferior herbácea; vainas de dorso redondeado; lígulas membranáceo-pestañosas.

  2a. Gluma inferior ovada; lemma inferior acuminada; plantas erectas a apoyantes, con láminas de 4–12 × 0.1–0.2 cm, poco divergentes del caule; Cuba ...... *Chaetium cubanum*

  2b. Gluma inferior reducida a una seta; lemma inferior aristada, la arista de 0.6–1.5 cm de largo; plantas erectas a geniculadas, con láminas de 10–35 × 0.5–1 cm, divergentes del caule; Colombia, Venezuela y Brasil .... *Chaetium festucoides*

1. Chaetium bromoides (J. Presl) Benth. ex Hemsl., Biol. cent.-amer., bot. 3: 503. 1885. *Berchtoldia bromoides* J. Presl, in C. Presl, Reliq. haenk. 1: 324, pl. 43. 1830. TIPO: México. Sin localidad, 1836, *Haenke s.n.* (holótipo, PR no visto; isótipos, MO-1837508, US-865574 no visto). Figuras 5, 6.

Plantas cortamente rizomatosas, con *cañas* estoloníferas, arraigadas y ramificadas en los nudos basales a erectas, simples o ramificadas hacia la base; porción erecta 40–120 × 0.2–0.3 cm; entrenudos de 15–30 cm de largo, comprimidos, longitudinalmente surcados, glabros, pajizos; nudos glabrescentes a barbados. *Vainas* de (3–)5–15 cm de largo, menores que los entrenudos, glabras a esparcidamente papiloso-pilosas, aquilladas, las basales flojas, los márgenes pestañosos, más densamente hacia la porción distal. *Lígulas* pestañosas, de 1.6–2.6 mm de largo; porción membranácea de 0.1–0.3 mm de largo, pestañas formada por un arco de densos pelos blanquecinos de 1.2–2.5 mm de largo; cuello híspido. *Láminas* 10–30 cm × 0.4–0.9 mm, ascendentes, planas a plegadas, esparcidamente papiloso-pilosas en ambas caras, de base redon-

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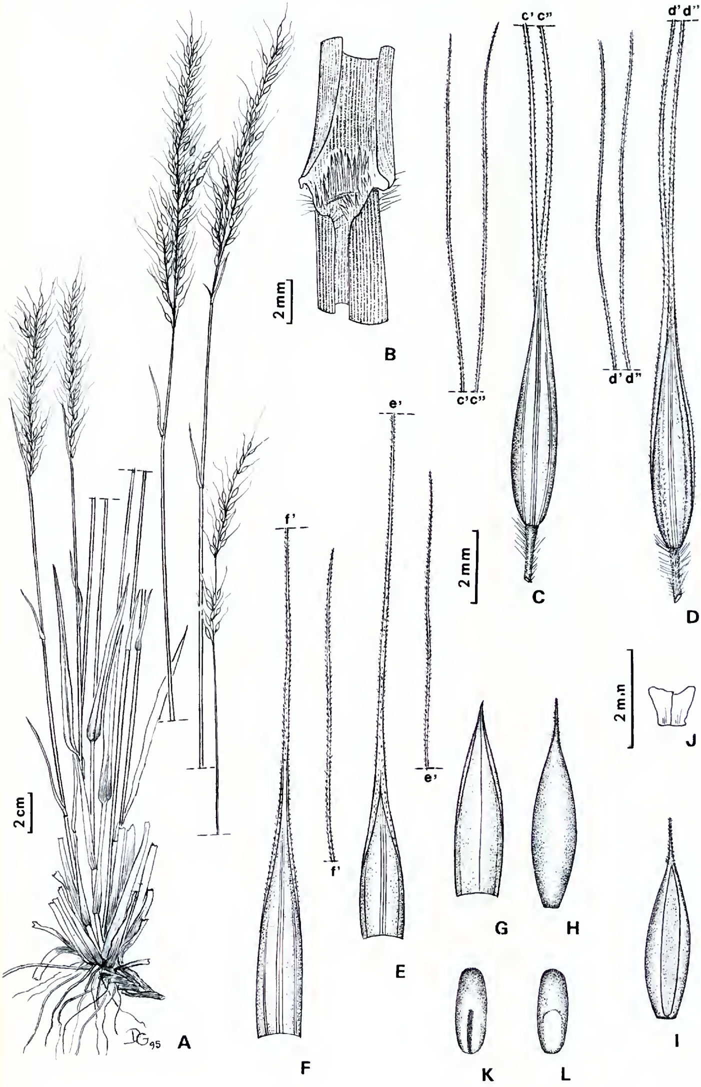
Figura 6. *Chaetium bromoides.* —A. Hábito. —B. Detalle de la región ligular. —C. Espiguilla vista del lado de la gluma inferior. —D. Espiguilla vista del lado de la gluma superior. —E. Gluma inferior. —F. Gluma superior. —G. Lemma inferior. —H. Antecio superior visto del lado de la lemma. —I. Antecio superior visto del lado de la pálea. —J. Lodículas. —K. Cariopsis, vista hilar. —L. Cariopsis, vista escutelar. En c', c'', d', d'', e' y f' se indica la continuación de las aristas. (*Weston 4145.*)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deada y ápice agudo, con los márgenes escabrosos, pestañosos. *Pedúnculos* subincluidos en las vainas foliares a exsertos, hasta de 45 cm de largo, comprimidos, glabros a esparcidamente pilosos. *Inflorescencias* subespiciformes, 9–26 × 1–2.5 cm, terminales, multifloras; eje principal y ejes de las ramificaciones triquetros, glabros, escabrosos; pulvínulos glabros a pilosos; pedicelos en pares, desiguales, triquetros, escabrosos. *Inflorescencias* axilares en ocasiones presentes, similares a las terminales. *Espiguillas* de 8–11 mm de largo (sin las aristas), 1–1.2 mm de ancho, escabrosas, verdes a púrpuras. *Gluma inferior* herbácea, largamente lanceolada, de 7–10 mm de largo (sin la arista), 7-nervia, con 3 nervios centrales aproximados, los restantes submarginales, escabrosa sobre los nervios, espacios internervales escabriúsculos, cara interna escabrosa hacia la porción distal, luego lisa, lustrosa; arista de 1.8–2.5 cm de largo, pálida a púrpura, escabrosa. *Gluma superior* herbácea, de 6.4–8 mm de largo (sin la arista), el dorso ligeramente concavo, 7-nervia, con 3 nervios centrales, los restantes submarginales, escabrosa sobre los nervios y espacios internervales, la cara interna escabrosa hacia el ápice, lisa y lustrosa hacia la base; arista de 1–2 cm de largo, pálida a púrpura, escabrosa. *Lemma inferior* de 6–8 mm de largo, coriácea, lisa, el ápice acuminado a cortamente aristado, arista de 1–1.5 mm de largo, escabriúscula, 3(–5)-nervia. *Antecio superior* largamente ovoide, 6–8.8 × 1.2 mm, cartilaginoso, pajizo, papiloso, escabroso hacia el ápice; lemma aristada, arista de 1.2–2 mm de largo, escabrosa; lodículas de 0.4–0.6 mm de largo, hialinas, conduplicadas, abrazando los bordes de la lemma; anteras 1.5–2 mm de largo. *Cariopsis* 2.6–2.8 × 1 mm; embrión ⅔ del largo de la cariopsis.

Nombres vulgares. "Granillo" (en México); "setilla" (en Costa Rica).

Distribución y ecología. Habita desde México hasta Panamá desde el nivel del mar hasta 2100 m de elevación. Se halla en laderas montañosas en bosques de *Quercus* y *Pinus*; también en áreas modificadas junto a malezas o en bordes de caminos.

Material representativo citado. COSTA RICA. **Alajuela**: In and around Zarcero, Cantón Alfaro Ruíz, Highway 15, 1700–2000 m, *Weston et al. 3073* (UC). **Cartago**: 6 km SW of Pacayas, 1700 m, *Pohl & Davidse 10891* (UC); San Ramón, E of San José, 1400 m, *Pohl & Gabel 13677* (MO); W side of Cartago, 1450 m, *Pohl & Calderón 10238* (MO). **Puntarenas**: forest along trail between Las Alturas and Cotonsito, along the Río Cotón, 8°56′N, 82°48′W, 1400 m, *Davidse 24656* (MEXU, MO). **San José**: 3 km SW of Tarbaca, 1650 m, *Weston et al. 2659* (UC); 5 km N of Buenavista, 1450 m, *Pohl & Davidse 10972* (UC).

EL SALVADOR. San Andrés, 1700 ft., *Walkins 45* (US).

GUATEMALA. **Quezaltenango:** in mountains near Santa María, just S of Quezaltenango, *Weatherwax 158* (US).

MÉXICO. **Chiapas**: Mun. Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, 1900 m, *Breedlove 40213* (US); Mun. Amatenango del Valle, 14 km SE of Teopisca along hwy. to Comitán, 2100 m, *Davidse et al. 29802* (MEXU). **Colima**: Mun. Comala, Rancho El Jabalí, 20 km (airline) NNW of Colima in the SW foothills of the Volcán de Colima, ca. 19°26.2′N, 103°41.8′W, 1450 m, *Sanders et al. 10284* (MO). **Distrito Federal**: Pedregal de San Angel, *Lyonnet 1661* (MEXU, US); Cerro Xochitepec, cerca de Xochitepec, *Rzedowski 23292* (MEXU). **Guanajuato**: S. Andrés, S. Miguel, *Liebmann* 595 (US); Inter S. Andrés et S. Miguel, *Liebmann 866* (US). **Guerrero**: cerca de Cacahuamilpa, Piedras Negras, 1100 m, *Matuda 29718* (US). **Jalisco**: Guadalajara, *Jones 27442* (UC); Guadalajara, *Jones 27662* (US); Mun. Tecalitán, Barranca de San Juan de Dios, cerca de Los Corrales, Sierra de Los Corrales, *Rzedowski 17381* (US); gravelly banks near Guadalajara, 5000 ft., *Pringle 11736* (LIL, MEXU, US); about 9 mi. S of Guadalajara along roadside right of way, 1765 m, *Reeder & Reeder 2334* (MEXU); plains of Guadalajara, *Pringle 2331* (LIL, MEXU, US); Barrio of Ciudad Granja, 8 km W of Guadalajara, ca. 100 m S of Avenida Vallarta, 1560 m, *Iltis & Nee 1048* (MEXU, US), forming dense clumps up to ½ m diam, ca. 1–1.2 m tall; Club de Golf Santa Anita, km 7 del Periférico, carretera a Morelia, 1550 m, *González & Carvajal 559* (MEXU); 1.5 km E of El Depósito, ca. 10 km WSW of Ciudad Guzmán, 19°39′N, 103°32′W, 1800 m, *Iltis et al. 588* (MEXU, US); Lomas del Valle, Guadalajara, 1610 m, *Díaz Luna 5010* (MEXU). **México**: Temascaltepec, 1750 m, *Hinton 2418* (BAA, US); Temascaltepec, Pungaranche, 13 Oct 1934, *Hinton 6748* (MO, US). **Michoacán**: Morelia, *Arsène* 5445 (MEXU, US); Uruápan, 5600 ft., *Hitchcock 6985* (US). **Morelos**: Cuernavaca, *Woronow & Juzepczuk 948* (US); 5 mi. N of Cuernavaca, *Gould 7018* (UC); Valle del Tepeite, *Lyonnet 2447* (MEXU, US); Cuernavaca, 4500 ft., *Hitchcock 6856* (US). **Nayarit**: 2 mi. W of Guadalajara on Highway 15 towards Tepic, 5000 ft., *Soderstrom 596* (US). **Veracruz**: Cerro Macuiltepec, just outside Jalapa, 5300 ft., *Reeder & Reeder 5982* (MO); Río Blanco near Orizaba, *Hitchcock s.n.* (LIL-39361, UC, US); Río Blanco, June–Oct. 1886, *Palmer 619* (MEXU, US); Orizaba, *Botteri s.n.* (US-976996, -821224); Izuatlanchillo près Orizaba, *Bourgeau 2597* (US).

PANAMA. **Chiriquí**: ca. 3 km NE of El Hato del Vol-

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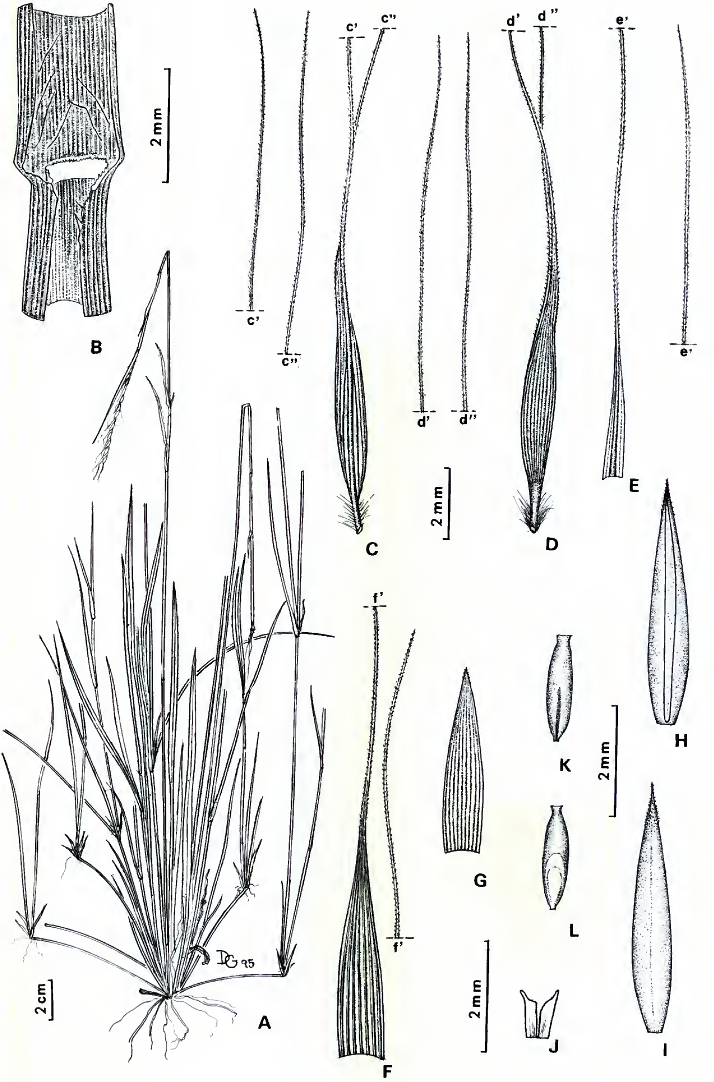
Figura 7. *Chaetium cubanum.* —A. Hábito. —B. Región ligular. —C. Espiguillas vista del lado de la gluma inferior. —D. Espiguilla vista del lado de la gluma superior. —E. Gluma inferior. —F. Gluma superior. —G. Lemma inferior. —H. Antecio superior visto del lado de la pálea. —I. Antecio superior visto del lado de la lemma. —J. Lodículas. —K. Cariopsis, vista hilar. —L. Cariopsis, vista escutelar. En c′, c″, d′, d″, e′ y f′ se indica la continuación de las aristas. (A, *Ekman 16474*; B–L, *Ekman 7816*.)


B
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cán at base of Volcán de Chiriquí (Barú), 3 km E of highway, 1800 m, *Davidse & D'Arcy 10412* (MO, US).

Chaetium bromoides es exomorfológicamente similar a *C. festucoides*; se distingue de esta especie por la gluma 7-nervia, lígulas pestañosas y espiguillas de mayor tamaño.

Un ejemplar con caracteres morfológicos discordantes de *Chaetium bromoides* es *Matuda 29718*, coleccionado en el estado de Guerrero, México, el que posee la gluma inferior y superior esparcidamente pilosas en los bordes y panojas más laxas, con menos espiguillas.

2. **Chaetium cubanum** (C. Wright) Hitchc., Contr. U.S. Natl. Herb. 12: 232. 1909. *Perotis cubana* C. Wright, Anales Acad. Ci. Méd. Habana 8: 288. 1871. TIPO: Cuba. Región oriental, 1856–1857, *Wright 735* (isótipos MO-2095218, -1837473). Figuras 5, 7.

Plantas con rizomas nodosos, de entrenudos cortos, con *cañas* largamente estoloníferas, arraigadas y con numerosas innovaciones extravaginales a erectas a apoyantes con ramificaciones prolíferas; porción erecta 40–70 × 0.1–0.3 cm; entrenudos de 4–12 cm de largo, cilíndricos, glabros, finamente estriados; nudos pubérulos. *Vainas* de 2–3.5 cm de largo, menores que los entrenudos, de dorso redondeado, glabras, con pelos esparsos junto a la unión con la lámina, los márgenes ciliados. *Lígulas* de 0.2–0.6 mm de largo, membranáceo-pestañosas, castañas, glabras; cuello castaño, cortamente piloso. *Láminas* 4–12 × 0.1–0.2 cm, planas a involutas, ascendentes, cortamente híspidas en la cara adaxial y con cara abaxial glabra o con ambas caras cortamente híspidas, de base atenuada continuándose con la vaina y ápice largamente agudo, los márgenes cartilaginosos, glabros, esparcidamente papiloso-pilosos hacia la base. *Pedúnculos* subincluidos en las vainas foliares. *Inflorescencias* terminales, subespiciformes, paucifloras, subexsertas, parcialmente incluidas en las vainas foliares, 3–9 × 0.5 cm; eje principal y ejes de las ramificaciones triquetros, escabrosos; pulvínulos pilosos; pedicelos en pares, triquetros, escabrosos. *Espiguillas* de 7–9.2 mm de largo (sin las aristas), 0.8–1 mm de ancho, escabrosas, glabras, verde pálidas o con tintes purpúreos. *Gluma inferior* ovada, de 1.8–3 mm de largo (sin la arista), herbácea, 3-nervia, escabrosa sobre los nervios; arista de 1.4–3 cm de largo, pálida a púrpura, escabrosa. *Gluma superior* de 5.6–6.5 mm de largo (sin la arista), herbácea, 9–13-nervia, los nervios escabrosos, cara interna escabrosa hacia la porción distal, luego lisa, lustrosa; arista de 2–2.5 cm de largo, escabrosa. *Lemma inferior* glumiforme, de 6.4–7.2 mm de largo, herbácea, 7–9-nervia, de ápice acuminado, cortamente hispídula entre los nervios, escabrosa hacia la porción superior de la cara interna, lisa en el resto de la superficie. *Antecio superior* largamente ovoide, 4.4–6.4 × 0.8 mm, cartilaginoso, pajizo, papiloso, escabroso junto al ápice; lemma 5-nervia, cortamente aristada, la arista hasta de 0.8 mm de largo, escabrosa; pálea de igual largo que su correspondiente lemma o ligeramente mayor, lodículas de 0.6–0.8 mm de largo, hialinas, no conduplicadas, glabras; anteras de 0.8 mm de largo. *Cariopsis* 3.2 × 0.6 mm de ancho; embrión ½ del largo de la cariopsis.

Distribución y ecología. Endémica de Cuba, crece desde el nivel del mar hasta los 800 m, en laderas secas.

Material adicional examinado. CUBA. **Sin Provincia**: Región oriental, *Wright 734* (MO). **Matanzas**: al S de Canasí, *Ekman 16474* (US). **Santiago de Cuba**: El Cobre, *Ekman 15699* (BAA, LIL, UC, US); El Cobre, near the mine, *Ekman 7816* (US). **Villa Clara**: Santa Clara, Motembo, *Ekman 16827* (US).

Chaetium cubanum se distingue de las restantes especies del género por comprender plantas largamente estoloníferas, con cañas profusamente ramificadas y apoyantes en la vegetación; sus láminas son ascendentes, poco divergentes del caule. Esta especie ha sido escasamente coleccionada en la isla de Cuba existiendo especimenes en los herbarios de más de 70 años de antigüedad.

3. **Chaetium festucoides** Nees, in Mart., Fl. Bras. Enum. Pl. 2: 270. 1829. *Oplismenus festucoides* (Nees) Kunth, Enum. Pl. 1: 146. 1833. TIPO: Brasil. "Habitat in graminosis et in cultis ad lumen S. Francisci, ad Joazeiro, etc. Provinciarum Pernambucanae et Bahiensis," *Martius s.n.* (holótipo, M no visto; isótipo, US-3049472). Figuras 5, 8.

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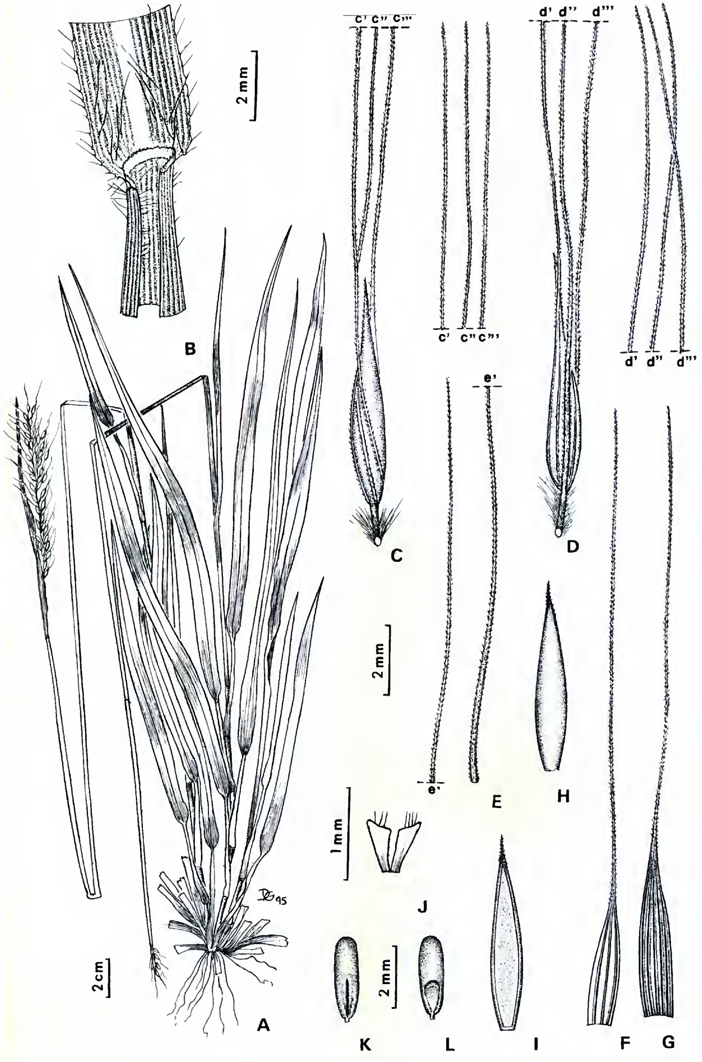
Figura 8. *Chaetium festucoides.* —A. Hábito. —B. Región ligular. —C. Espiguilla vista del lado de la gluma superior. —D. Espiguilla vista del lado de la gluma inferior. —E. Gluma inferior. —F. Gluma superior. —G. Lemma inferior. —H. Antecio superior visto del lado de la lemma. —I. Antecio superior visto del lado de la pálea. —J. Lodículas. —K. Cariopsis, vista hilar. —L. Cariopsis, vista escutelar. En c′–c‴, d′–d‴ y e′ se indica la continuación de las aristas. (A, *Pittier 14926*; B–L, *Pickel 1714*.)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Plantas cortamente rizomatosas, de 70–110 cm de alto, con *cañas* erectas a geniculadas, simples; entrenudos 9–22 × 0.2–0.3 cm, cilíndricos, glabros, los basales más cortos; nudos castaños, glabros. *Vainas* de 5–11 cm de largo, usualmente menores que los entrenudos, de dorso redondeado, glabras a papiloso-hirsutas hacia la porción distal, con un margen ciliado, el restante glabro. *Lígulas* de 0.4–0.6 mm de largo, membranáceo-pestañosas, con la cara externa esparcidamente pilosa; cuello hirsuto. *Láminas* 10–35 × 0.5–1 cm, planas, de base redondeada y ápice largamente agudo, papiloso-hirsutas en ambas caras, con largos pelos rígidos junto a la lígula, hasta de 5 mm de largo, los márgenes escabrosos. *Pedúnculos* exsertos a subincluidos en las vainas foliares, hasta de 30 cm de largo, cilíndricos, glabros. *Inflorescencias* espiciformes, 5–20 × 0.5–2 cm, terminales, exsertas; eje principal y ramificaciones triquetros, glabros, escabrosos; pulvínulos con un mechón de pelos blanquecinos; pedicelos delgados, triquetros, glabros a esparcidamente pilosos, escabrosos. *Espiguillas* de 4.8–7.2 mm de largo (sin las aristas), 0.8–1 mm de ancho, glabras, escabrosas, verde pálidas o con tintes purpúreos. *Gluma inferior* setácea, reducida a una arista escabrosa de 1.2–3.5 cm de largo, excéntrica, pajiza a púrpura, enerve. *Gluma superior* de 2.4–3 mm de largo (sin la arista), herbácea, 3-nervia, con los nervios manifiestos, escabrosos, uno central, los restantes submarginales, espacios internervales hialinos, delicados; arista de 1–1.7 cm de largo, escabrosa. *Lemma inferior* glumiforme, herbácea, de 4–5 mm de largo (sin la arista), 5-nervia, con los nervios manifiestos, uno central, los restantes equidistantes; arista de 0.6–1.5 cm de largo, escabrosa. *Antecio superior* largamente ovoide, de 4–4.8 mm de largo (sin la arista), 0.8–2 mm de ancho, cartilaginoso, papiloso, escabroso hacia la porción superior; arista hasta de 0.8 mm de largo, escabrosa; lodículas de 0.5 mm de largo, hialinas, truncadas, no conduplicadas, con una cara pilosa; anteras de 0.6–0.8(–1.6) mm de largo. *Cariopsis* 2.8 × 0.7 mm, pálida; embrión ⅓ o un poco más del largo de la cariopsis.

Distribución y ecología. Se encuentra en el noreste de Brasil y en Colombia y Venezuela, desde el nivel del mar hasta los 500 m de elevación, en lugares abiertos, secos o en bordes de monte.

Material representativo examinado. BRASIL. **Ceará:** Mun. Parangaba, Tapereóba, *Black 55-18634* (BAA, US); Martinópolis, *Swallen 4635* (US). **Maranhão:** Mun. Lorêto, Ilha de Balsas region, between the Rios Balsas and Parnaíba, about 200 m W of Riacho da Simiana, *Eiten & Eiten 4713* (US). **Paraíba:** sin localidad, *Moraes 2217* (US). **Piauí:** sin localidad, *Gardner 2346* (US). **Pernambuco:** Tapera, Pedras de Fogo, *Pickel 1714* (US). **Rio Grande do Norte:** Estremoz to Natal, *Swallen 4797* (US).

COLOMBIA. **Bolívar:** N of Arjona, 30–50 m, *Killip & Smith 21194* (MO).

VENEZUELA. **Guárico:** Llanos de Calabozo, entre la Encrucijada y la Misión de Arriba, *Pittier 14926* (US); Estación Biológica de los Llanos, *Trujillo 8639* (MO).

Doell (1877) cita erróneamente la presencia de *Chaetium festucoides* en Cuba, sobre la base del ejemplar *Wright 735*, correspondiendo este último al tipo de *C. cubanum*.

Se observaron flores cleistógamas en los ejemplares *Eiten & Eiten 4713, Black 55-18634, Swallen 4797* y *Pittier 14926* los que poseen cariopsis desarrolladas y anteras pequeñas, de 0.6–0.8 mm de largo, presentes en el ápice de la cariopsis. El único ejemplar que posee anteras de 1.6 mm de largo es *Gardner 2346*, pero no se halló cariopsis desarrollada.

La distribución geográfica de *Chaetium festucoides* es disyunta; la mayoría de sus colecciones son de la región nordeste del Brasil habiéndose hallado ocasionalmente en savanas de Venezuela y en zonas costeras del estado de Bolivar en Colombia, junto al mar Caribe. Nuevas colecciones permitirán comprobar si esta especie crece en áreas intermedias del norte del Brasil y las Guyanas.

En el herbario US se examinó un duplicado del tipo de esta especie, correspondiente a un fragmento del holótipo depositado en Munich. Cabe destacar que si bien en el protólogo de la especie se cita "Provinciarum Pernambucanae et Bahiensis," lo cual podría indicar que existe más de un ejemplar tipo de *C. festucoides*, los datos antes mencionados del protólogo coinciden exactamente con la información de un único ejemplar de herbario coleccionado por Martius en el Brasil. Esta situación se repite en otras especies de Poaceae coleccionadas por Martius y descriptas por Nees von Esenbeck, en géneros como *Panicum, Paspalum* y otros.

Literatura Citada

Beetle, A. A. 1977. Noteworthy grasses from Mexico. V. Phytologia 37: 317–407.

———. 1987. Las Gramíneas de México, tomo II. Secretaría de Agricultura y Recursos Hídraúlicos, México.

Bentham, G. 1881. Notes on Graminae. J. Linn. Soc., Bot. 19: 14–134.

———. 1883. Gramineae. Pp. 1074–1215 *en* G. Bentham & J. D. Hooker, Genera Plantarum. J. Cramer, Weinheim (reimpresión, 1965).

Brown, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. Mem. Torrey Bot. Club 23: 1–97.

Chase, A. 1911. Notes on genera of Paniceae. IV. Proc. Biol. Soc. Wash. 24: 103–160.

Clayton, W. D. & S. A. Renvoize. 1986. Genera Graminum. Kew Bull. 13: 1–389.

Cutler, D. 1978. Applied Plant Anatomy. Academic Press, London.

Dengler, N. G., R. E. Dengler & P. W. Hattersley. 1985. Differing ontogenetic origins of PCR ("Kranz") sheaths in leaf blades of C_4 grasses (Poaceae). Amer. J. Bot. 72: 284–302.

Doell, J. C. 1877. Tribe 3, Paniceae. *En:* C. F. P. von Martius (editor), Flora Brasiliensis 2(2): 33–340. Munich, Vienna, Leipzig.

Elkin, L. & R. B. Park. 1975. Chloroplast fluorescence of C_4 plants. I. Detection with infrared color film. Planta 127: 243–250.

Ellis, R. P. 1977. Distribution of the Kranz Syndrome in the Southern African Eragrostoideae and Panicoideae according to bundle sheath anatomy and cytology. Agroplantae 9: 73–110.

Farris. J. S. 1988. Hennig86. Reference, version 1.5. Port Jefferson Station. J. S. Farris, New York.

Filgueiras, T. S. 1986. O conceito do fruto em gramineas e seu uso na taxonomia da família. Pesq. Agropecu. Brasil. 21: 93–100.

Fournier, E. 1886. Mexicanas Plantas. Pars secunda Gramineae: 1–160. Ex Typographeo Reipublicae, Paris.

Gould, F. W. 1958. Chromosome numbers in southwestern grasses. Amer. J. Bot. 45: 757–767.

———. 1966. Chromosome numbers of some Mexican grasses. Canad. J. Bot. 44: 1683–1696.

Gutiérrez, M., G. E. Edwards & W. V. Brown. 1976. PEP carboxykinase containing species in the *Brachiaria* group of the subfamily Panicoideae. Biochem. Syst. & Ecol. 4: 47–49.

Hackel, E. 1887. Gramineae. *En:* A. Engler & K. Prantl (editores), Die natürlichen Pflanzenfamilien 2(2): 1–97. Engelmann, Leipzig (reimpresión).

Hattersley, P. W. 1987. Variations on photosynthetic pathway. Pp. 49–64 *en* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

——— & L. Watson. 1992. Diversification of photosynthesis. Pp. 38–116 *en* G. P. Chapman (editor), Grass Evolution and Domestication. Cambridge Univ. Press, London.

Hedges, S. B., C. A. Hass & L. R. Maxson. 1994. Reply: Towards a biogeography of the Caribbean. Cladistics 10: 43–53.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana.

Hitchcock, A. S. 1909. Catalogue of the grasses of Cuba. Contr. U.S. Natl. Herb. 12: 183–258.

———. 1930. The grasses of Central America. Contr. U.S. Natl. Herb. 24: 557–762.

———. 1936. Manual of the grasses of the West Indies. U.S.D.A. Bur. Pl. Industr. Misc. Publ. 243: 1–439.

——— & A. Chase. 1917. Grasses of the West Indies. Contr. U.S. Natl. Herb. 18: 261–494.

Hsu, C. C. 1965. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 9: 43–150.

Hubbard, C. E. & H. G. Schweickerdt. 1936. *Oryzidium*, a new genus from South West Africa. Bull. Misc. Inform. Kew 5: 326–329.

Johansen, D. A. 1940. Plant Microtechnique. McGraw-Hill, New York.

Kunth, C. S. 1833. Enumeratio Plantarum: 1–606. J. G. Cottae, Stuttgart & Tübingen.

McVaugh, R. 1983. Gramineae. *En:* W. R. Anderson (editor), Flora Novo-Galiciana. A Descriptive Account of the Vascular Plants of Western Mexico 14: 1–436. Univ. Michigan Press, Ann Arbor.

Metcalfe, C. R. 1960. Anatomy of Monocotyledons. I. Gramineae. Oxford Univ. Press, Oxford.

Montiel, M. B. 1972. Determinación taxonómica de la especie *Chaetium bromoides* (Presl) Benth. basada en el estudio anatómico. Revista Biol. Trop. 20: 45–79.

Morrone, O. & F. O. Zuloaga. 1991. Revisión del género *Streptostachys* (Poaceae–Panicoideae), su posición sistemática dentro de la tribu Paniceae. Ann. Missouri Bot. Gard. 78: 359–376.

———, T. S. Filgueiras, F. O. Zuloaga & J. Dubcovsky. 1993. Revision of *Anthaenantiopsis* (Poaceae: Panicoideae: Paniceae). Syst. Bot. 18: 434–453.

Nees von Esenbeck, C. G. 1829. *En:* C. F. P . von Martius (editor), Flora brasiliensis se enumeratio plantarum, Vol. 2(1). J. G. Cottae, Stuttgart & Tübingen.

Nixon, K. C. 1993. Clados, versión 1.38 [32 bit] beta version. Programa de computación distribuido por el autor.

——— & J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413–426.

O'Brien, T. P. & M. E. McCully. 1981. The Study of Plant Structure Principles and Selected Methods. Termacarphi, Melbourne, Australia.

Oguro, H., K. Hinata & S. Tsunoda. 1985. Comparative anatomy and morphology of leaves between C_3 and C_4 species in *Panicum*. Ann. Bot. (Oxford) 55: 859–869.

Ohsugi, R. & T. Murata. 1980. Leaf anatomy, post-illumination CO_2 burst and Nad-malic enzyme activity of *Panicum dichotomiflorum*. Pl. Cell Physiol. 21: 1329–1333.

———, ——— & N. Chonan. 1982. C_4 syndrome of the species in the *Dichotomiflora* group of the genus *Panicum*. Bot. Mag. (Tokyo) 95: 339–347.

Pohl, R. W. 1980. #15, Gramineae. *En:* W. Burger (editor), Flora costaricensis. Fieldiana, Bot., n.s. 4: 1–608.

———. 1994. *Chaetium*. Pp. 330–331 *en* G. Davidse, M. Sousa & A. O. Chater (editors), Flora Mesoamericana, Vol. 6. Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, México, D.F.; Missouri Botanical Garden, St. Louis; The Natural History Museum, London.

——— & G. Davidse. 1971. Chromosome numbers of Costa Rica grasses. Brittonia 23: 293–324.

Prendergast, H. D. V. & N. E. Stone. 1987. New structural/biochemical associations in leaf blades of C_4 grasses (Poaceae). Austral. J. Pl. Physiol. 14: 403–420.

Presl, J. 1830. Gramineae. *En:* C. Presl, Reliquiae Haenkeneae: 207–356. A. Asher, Amsterdam (reimpresión, 1973).

Reeder, J. R. 1967. Notes on mexican grasses. VI. Miscellaneous chromosome numbers. Bull. Torrey Bot. Club. 94: 1–17.

Renvoize, S. A. 1987. A survey of leaf-blade anatomy in grasses XI. Paniceae. Kew Bull. 42: 739–768.

Sendulsky, T., F. S. Filgueiras & A. G. Burman. 1987. Fruits, embryos and seedlings. Pp. 31–36 *en* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

Smith, L. B. & D. Wasshausen. 1981. Chave para os gêneros das Gramíneas Brasileiras. Bradea 3: 1–36.

Steudel, E. G. 1853–1855. Synopsis Plantarum Graminearum. *En:* Synopsis Plantarum Glumacearum 1: 1–475. J. B. Metzler, Stuttgart.

Swallen, J. R. 1955. Flora of Guatemala, part II: Grasses of Guatemala. Fieldiana, Bot. 24: 1–390.

Troll, W. 1967. Vergleichende Morphologie der höheren Pflanzen, 2 Teil, IV Abschnitt. Gebrüder Borntrager, Berlin.

Webster, R. D. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). Syst. Bot. 13: 576–609.

——— & J. Valdés Reyna. 1988. Genera of Mesoamerican Paniceae (Poaceae: Panicoideae). Sida 13: 187–221.

Zuloaga, F. O. & T. R. Soderstrom. 1985. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). Smithsonian Contr. Bot. 59: 1–63.

———, O. Morrone & J. Dubcovsky. 1989. Exomorphological, anatomical, and cytological studies in *Panicum validum* (Poaceae: Panicoideae: Paniceae): Its systematic position within the genus. Syst. Bot. 14: 220–230.

ÍNDICE DE COLECCIONES NUMERADAS

Cada especimen es citado por el primer nombre del colector en el caso en que otros coleccionistas participen de la colección. Se indica entre paréntesis el número de la especie: *Chaetium bromoides* (1); *C. cubanum* (2); *C. festucoides* (3).

Arsène Bro. 5445 (1).

Black, G. A. 55-18634 (3); *Bourgeau, M. 2597* (1); *Breedlove, D. E 40213* (1).

Davidse, G. 10412 (1), *24656* (1), *29802* (1); *Díaz Luna 5010* (1).

Eiten, G. 4713 (3); *Ekman, E. L. 7816* (2), *15699* (2), *16474* (2), *16827* (2).

Gardner, G. 2346 (3); *González 559* (1); *Gould, F. W. 7018* (1), *11697* (1).

Hinton, G. B. 2418 (1), *5043* (1), *6748* (1); *Hitchcock, A. S., Amer Gr. Nat. Herb. 307* (1), *6856* (1), *6985* (1), *7114* (1), *7287* (1).

Iltis, H. H. 588 (1), *1048* (1).

Jones, M. E. 27442 (1), *27662* (1).

Killip, E. P. 21194 (3).

Liebmann, F. M. 594 (1), *595* (1), *866* (1), *12912* (1); *Lyonnet, E. 1661* (1), *2447* (1).

Martínez Pérez 149 (1); *Matuda, E. 1591* (1), *25920* (1), *29718* (1); *Moraes 2217* (3); *Müller 2126* (1).

Nee, M. 264 (1).

Palmer, E. 619 (1); *Pickel, B. J. 1714* (3); *Pittier, H. 14926* (3); *Pohl, R. W. 9908* (1), *10238* (1), *10364* (1), *10891* (1), *10972* (1), *11040* (1), *13677* (1); *Pringle, C. G. 2331* (1), *11736* (1).

Reeder, J. 2334 (1), *4169* (1), *5982* (1); *Rzedowski, J. 17381* (1), *23292* (1).

Sanders 10284 (1); *Soderstrom, T. R. 596* (1); *Stevens, W. D. 13645* (1); *Swallen, J. R. 4635* (3), *4797* (3).

Trujillo, B. 8639 (3).

Vázquez 1064 (1); *Vera Santos, J. 3105* (1).

Walkins, J. M. 45 (1); *Weatherwax, P. 158* (1); *Weston, A. S. 2140* (1), *2659* (1), *3073* (1), *3341* (1), *3555* (1), *4145* (1); *Woronow, G. 948* (1); *Wright, C. 734* (2).

APÉNDICE 1. MATERIAL ADICIONAL EXAMINADO

Echinochloa crus-galli. ARGENTINA. **Buenos Aires:** Pergamino, *Boelcke 506* (SI). **Córdoba:** *Castellanos 465* (SI). **Entre Ríos:** Concepción del Urugnay, *Sorarú 168* (SI). PARAGUAY. **Central:** Itá, *Ramírez 69* (BAA). URUGUAY. Sin localidad, *Felippone 5466* (SI).

Echinochloa holciformis. MÉXICO. **Jalisco:** Lake Chapala near Tuxcueca, *Leavenworth & Leavenworth 1848* (US); Orozco, *Hitchcock 7375* (US). **Michoacán:** Cerro Santa María, *Feddema 96* (US); Cerro Potrerillos, *King & Soderstrom 4604* (US); 3 mi. E of Morelia, *Soderstrom 546* (US). **Morelia:** Morelia, *Arsène s.n.* (LIL-39358).

Echinochloa oplismenoides. MÉXICO. **Aguascalientes:** Aguascalientes, *Hitchcock 7441* (US), *Archer 3991* (US). **Jalisco:** 36 km Ojuelos-Aguascalientes, *Xolocotzi X-2503* (US). **Puebla:** 6 mi. E of Puebla, *Soderstrom 394* (US), *Arsène 5444* (US).

Louisiella fluitans. REPÚBLICA CENTRAL AFRICANA. Manovo Gounda–St. Floris National Park, *Fay 6160* (MO), *7353* (MO).

Melinis minutiflora. ARGENTINA. **Buenos Aires:** La Plata, *Burkart 12484* (SI). **Misiones:** El Dorado, *Martínez Crovetto 10032* (SI). BRASIL. **Paraná:** Porto da Cima, *Jonsson 569a* (SI). **Pernambuco:** Tapera, *Pickel 97* (SI). VENEZUELA. **Cojedes:** San Carlos, *Burkart 16166* (SI). **Miranda:** Miranda, *Burkart 16012* (SI).

Oplismenoides najada. ARGENTINA. **Buenos Aires:** Delta del Paraná, *Burkart 4509* (SI), *7598* (SI); Médanos, *Burkart 3564* (SI). **Corrientes:** La Cruz, *Burkart 8105* (SI). **Santa Fe:** Los Amores, *Lewis & Pire 815* (SI).

Oplismenus hirtellus. ARGENTINA. **Entre Ríos:** La Paz, *Burkart 21063* (SI). **Jujuy:** El Fuerte, *Kiesling et al. 5500* (SI). **Salta:** Rosario de Lerma, *Venturi 8219* (SI). **Tucumán:** Siambón, *Burkart 5294* (SI).

Oryzidium barnardii. BOTSWANA: near Mboma Island road in Moremi Wildlife Reserve, *Smith 1944* (MO).

Panicum miliaceum. ARGENTINA. **Buenos Aires:** Ensenada, *Zuloaga 1890* (SI); San Isidro, *Pastore 849* (SI). BRASIL. **Rio Grande do Sul:** São Leopoldo, *Rambo 1937* (BAA).

Panicum aristellum. BRASIL. **Paraná:** Foz do Rio Taquaral, *Hatschbach 337* (US). **Rio Grande do Sul:** Tupaceretan, *Araujo 338* (US). **Santa Catarina:** 6 km of Porto União, *Smith & Klein 15279* (US). **São Paulo:** Mun. Salesópolis, Boraceia, *Kuhlmann 2774* (SI).

REVISIÓN DEL GÉNERO *CUCURBITELLA* (CUCURBITACEAE)[1]

Raúl Pozner[2]

RESUMEN

De acuerdo con la literatura, el género sudamericano *Cucurbitella* comprende seis especies cuyos caracteres diagnósticos son de escaso valor. Este estudio demuestra que la estructura de los primordios foliares, el grado de exserción de los estambres y la forma y el tamaño de los pétalos y el hipanto son los únicos caracteres morfológicos variables entre los especímenes. La variación de estos caracteres es continua y no correlacionada. Por ello se reconoce sólo una especie polimórfica: *Cucurbitella asperata* (Gillies ex Hook. & Arn.) Walp. La distribución geográfica de las frecuencias de los primordios foliares sugiere la existencia de tres razas ecológicas. Pero en vista de los numerosos especímenes intermedios estas razas no reciben nombres científicos formales. Por la misma razón no se incluye una clave para su identificación. *Cucurbitella ecuadorensis* Cogn. queda excluida de *Cucurbitella* porque su holótipo es en realidad un ejemplar de *Posadaea sphaerocarpa* Cogn.

ABSTRACT

According to previous authors, the South American genus *Cucurbitella* (Cucurbitaceae) includes six species, ostensibly separated by several diagnostic characters of dubious value. This study establishes the morphology of foliar primordia, the degree of stamen exsertion, and the shape and size of the petals and hypanthium as the only morphological characters with significant variation among specimens. These characters vary continuously and independently, and any internal partitions would be arbitrary. Thus, *Cucurbitella* consists of only one polymorphic species: *C. asperata* (Gillies ex Hook. & Arn.) Walp. The geographic distribution of foliar primordium characters suggests three ecological races, but due to intermediate specimens, these races do not merit formal scientific recognition, and a key to identify them is not included. *Cucurbitella ecuadorensis* Cogn. is removed from *Cucurbitella* because the holotype represents *Posadaea sphaerocarpa* Cogn.

El nombre *Cucurbitella* Walp. (Cucurbitaceae) está basado en *Cucurbita asperata* Gillies ex Hooker & Arnott (1833). Fue publicado como "*Curcubitella*" (Walpers, 1846) y corregido posteriormente por el mismo autor (Walpers, 1847: 769). *Cucurbita asperata* había sido combinado anteriormente bajo *Schizostigma* Arn. (1840), homónimo ilegítimo de *Schizostigma* Arn. ex Meisn. (1838, Rubiaceae). *Prasopepon* Naudin (1866), con sus dos especies *P. durieui* Naudin y *P. cucumifolius* Griseb., fue transferido a *Cucurbitella* por Cogniaux (1878). A estas tres especies se agregaron *Cucurbitella integrifolia* Cogn. y *Cucurbitella ecuadorensis* Cogn. Más tarde Jeffrey (1978) transfirió *Cucurbita urkupinana* Cárdenas, de modo que, hasta hoy, *Cucurbitella* se considera un género de seis especies: *Cucurbitella ecuadorensis*, endémica de Ecuador, *C. urkupinana*, endémica de Bolivia, y las especies restantes, con su área principal de distribución en la Argentina. *Cucurbitella durieui* se ha citado también para Paraguay, sur de Brasil y Uruguay, *C. integrifolia*, para Bolivia y Paraguay, y *C. asperata*, para Chile. Los caracteres utilizados para identificar las supuestas especies de *Cucurbitella* son: la consistencia, la pubescencia y el grado de división de las hojas (Cogniaux, 1916; Martínez Crovetto, 1965, 1974; Cabrera, 1993), la forma del fruto (Cogniaux, 1916; Cabrera, 1993), el tamaño de las hojas (Cabrera, 1993), la presencia o ausencia de brácteas en las inflorescencias estaminadas, la forma del hipanto y la presencia de pelos en la garganta del hipanto (Cogniaux, 1916). La revisión de casi 600 ejemplares de *Cucurbitella*, en su mayoría de la Argentina, mostró que los caracteres utilizados para reconocer las especies, no permiten la identificación precisa de más de la mitad de los ejemplares. Jeffrey (1978, 1990 y com. pers.) duda de la identidad de *C. cucumifolia*, *C. urkupinana* y de los límites entre *C. durieui* y *C. asperata*. Por otro lado, la identidad de *C. ecuadorensis* plantea serias du-

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das pues su distribución está alejada y aislada del área de distribución del género, y sólo se cuenta con la colección del tipo. Por todos estos motivos, y a raíz de la preparación de las Cucurbitaceae para el proyecto Proflora de Argentina, se realizó la revisión de este género.

MATERIALES Y MÉTODOS

Se estudiaron las colecciones de *Cucurbitella* de los herbarios BAA, BAB, BBB, CORD, CTES, LP, MERL, SI, SRFA, material fijado en FAA, y ejemplares cultivados a partir de semillas para conocer la sucesión foliar del tallo principal. Para el estudio de los primordios foliares se eligió el primer primordio en dirección apical que tuviera su zarcillo no elongado (no sensible en el momento de la herborización). Los cortes anatómicos fueron hechos a mano alzada y coloreados con safranina o azul de algodón. La identificación de las sustancias pécticas se realizó con rojo de rutenio (Jensen, 1962). Todas las ilustraciones son originales, han sido realizadas por el autor y corresponden a material de herbario, fijado, cultivado o fotografías. Para los esquemas anatómicos se utilizaron los símbolos de Metcalfe y Chalk (1950). Las medidas de las flores y sus partes corresponden a flores totalmente abiertas.

MATERIAL FIJADO

Forma foliar "*asperata*": *Pozner 62, 63, 65* (BAB); *A. A. Cocucci s.n.* (CORD); *J. H. Hunziker 13116* y *13084* (SI). Forma foliar "*cucumifolia*": *Pozner 50* y *88* (BAB); *Hoc 63* (BAFC); *A. A. Cocucci s.n.* (CORD). Forma foliar intermedia entre "*asperata*" y "*durieui*": *A. A. Cocucci s.n.* (CORD). Forma foliar "*durieui*": *Pozner 82* (BAB).

MATERIAL CULTIVADO

Forma foliar "*asperata*": *Pozner 62, 63, 65* (BAB) y *106* (SI). Forma foliar "*cucumifolia*": *Pozner 87* (BAB).

ANÁLISIS DE LOS CARACTERES

RAÍZ

Todo el sistema radical de *Cucurbitella* es de origen primario y forma una estructura reservante junto con el hipocótilo, los primeros nudos del epicótilo y la porción basal de las ramas de los años siguientes (año dos en adelante), por medio de su desarrollo secundario en diámetro. La raíz principal y sus primeras ramificaciones son napiformes. El resto del sistema radical tiene porciones no tuberosas y tuberosas (tubérculos radicales) que pueden alcanzar hasta 20 cm de diámetro. El ritidoma posee numerosas lenticelas pulviniformes, notorias y en general alineadas horizontalmente, de modo que semejan un repliegue como los que se observan en las raíces contráctiles, aunque no es éste el caso. Un corte transversal de una porción no tuberosa de la raíz muestra un súber de 6–7 capas celulares, felógeno, una felodermis de 4–5 capas con grupos, esclereidas subyacentes, el floema secundario, el xilema secundario con vasos aislados o en grupos, con parénquima vasicéntrico. Los tubérculos radicales presentan la misma estructura secundaria pero con un gran desarrollo de los radios parenquimáticos, ricos en granos de almidón compuesto, y la formación de cámbium supernumerario (Fig. 1E).

Este sistema radical combina el desarrollo napiforme de la raíz principal como en *Bryonia* y la capacidad de desarrollar tubérculos radicales como *Thladiantha dubia* Bunge (Troll, 1967). Según Ruíz Leal (1975) el sistema radical de *C. asperata* puede formar unas 8 a 10 tuberosidades de más de 1 kg, y son éstas más abundantes cuanto más árido es el lugar donde crece esta especie. De acuerdo con Cárdenas (1945), *Cucurbitella asperata* (sub *Cucurbita urkupinana*) posee un tubérculo radical formado por la raíz principal. El desarrollo del parénquima del xilema secundario como tejido reservante se conoce en los tubérculos radicales de *Coccinia engleri* Gilg y en los rizomas de *Melothria argyrea* A. Zimm. (Zimmermann, 1922). No se ha observado variación en la estructura de la raíz.

TALLO

La porción basal del vástago, que junto con la raíz, forma el sistema reservante, es perenne y porta las yemas hibernantes para la próxima estación de crecimiento. Todo el resto del vástago es anual y dura sólo el verano y el otoño. La porción anual de los tallos suele desarrollar un crecimiento secundario incipiente (Fig. 1H, I) sin formar felógeno. La epidermis, el colénquima y el clorénquima subepidérmicos acompañan el crecimiento en diámetro. Los tallos con estructura primaria son cilíndricos, carecen de costillas y tienen 10 haces vasculares anficribales: cinco internos mayores y cinco externos menores (Fig. 1G). La actividad del cámbium comienza primero en los cinco haces internos, y en esta etapa los tallos son generalmente 5-angulados o con cinco costillas (Fig. 1H). Cuando el cámbium comienza su actividad en los cinco haces externos, los tallos muestran un número mayor de costillas (Fig. 1I). Esta estructura del tallo es uniforme en

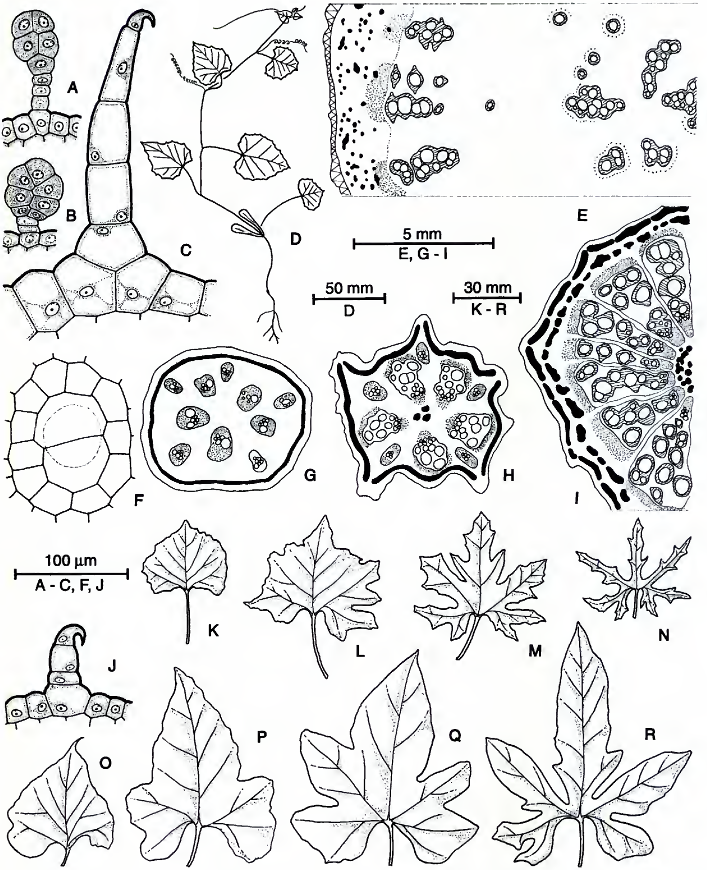

Figura 1. —A, B. Tricomas glandulares foliares (*Hoc 63*). —C, J. Tricomas uncinulados (*Hoc 63*). —D. Plántula del tipo foliar "*asperata*" (*Pozner 106*). —E. Detalle de la sección transversal de un tubérculo radical (*Pozner 87*). —F. Dos células basales de un tricoma uncinulado y su corona de células adyacentes (*Pozner 65*). —G. Sección transversal de un tallo joven (*Hoc 63*). —H. Idem G pero de un tallo más desarrollado (*Pozner 87*). —I. Detalle de una sección transversal de un tallo hacia el final del verano (*Cabrera 34534*). —K, L, M, N. Sucesión foliar del tipo foliar "*asperata*," catafilo (K), hojas de transición (L, M), nomofilo (N) (*MERL 42789*). —O, P, Q, R. Sucesión foliar del tipo foliar "*durieui*," catafilo (O), hojas de transición (P, Q), nomofilo (R) (*Zuloaga 1305*). En los esquemas G, H, I no se representa el colénquima y el clorénquima subepidérmico por razones de escala.

todo el material estudiado y relativamente frecuente en las Cucurbitaceae (Zimmermann, 1922).

PUBESCENCIA

La superficie de los tallos y las hojas varía desde casi glabra (especialmente la cara adaxial de las hojas) hasta densamente hirsuta (en la abaxial de las hojas). Los tricomas más abundantes son uniseriados, 3–5-celulares, con la célula apical uncinulada (Fig. 1C, J) y las células anexas dispuestas en una corona que rodea la célula basal del tricoma (Fig. 1C , F), y sobresale por encima del nivel del resto de la epidermis. Estos tricomas uncinulados varían entre 60 y 200 μm (Fig. 1C, J), y son los responsables del tacto áspero de esta pubescencia. Por otro lado, y con menos frecuencia, hay tricomas glandulares, sin células anexas diferenciadas, con un pie 1–4-celular y una cabezuela 2–8-celular (Fig. 1A, B). Por tratarse de las únicas estructuras secretoras de los tallos y las hojas, y aunque no se ha identificado la naturaleza química de su secreción, son los probables responsables del olor fétido típico de estas plantas. De hecho estos pelos glandulares faltan en el las flores, que son inodoras.

HOJAS

Con el objetivo de facilitar la descripción de la variación de la estructura foliar, se distinguen tres formas básicas de nomofilos a las que se hará referencia como:

Tipo "*cucumifolia*": nomofilos enteros, cordiformes (incluye las formas foliares de *C. cucumifolia* y *C. integrifolia*, Fig. 2A, B);
Tipo "*durieui*": nomofilos 3–5-palmatipartidos con lóbulos enteros (incluye las formas foliares de *C. durieui* y *C. urkupinana*, Fig. 2D, E);
Tipo "*asperata*": nomofilos 3–5-palmatipartidos con lóbulos pinnatífidos hasta casi disectos (incluye las formas foliares de *C. asperata*, Fig. 2H, I).

Variación intra-individual. La variación dentro de un mismo individuo se debe a la sucesión foliar y afecta la forma y el grado de división de la lámina (los detalles de la variación de las brácteas y de las hojas florales se analizan bajo los títulos de Inflorescencias y Flores). La sucesión foliar del eje principal parte siempre de cotiledones elípticos, trinervados, epígeos, y catafilos enteros 5-angulados (Fig. 1D). En los individuos con nomofilos tipo "*cucumifolia*" se suceden hojas de transición más o menos cordiformes o imperfectamente y levemente trilobuladas. En los individuos con nomofilos tipo "*asperata*" se suceden hojas de transición paulatinamente más divididas hasta los nomofilos profundamente palmatipartidos con segmentos pinnatipartidos (Fig. 1K–N), y en los individuos con nomofilos tipo "*durieui*" las hojas de transición son 3–5-palmatipartidas y culminan con nomofilos 5-palmatipartidos con lóbulos enteros de ápice obtuso o redondeado (Fig. 1O–R). En general, en los brotes hibernantes se repite la misma sucesión de catafilos y nomofilos observada en el eje principal, pero en las ramificaciones de estos brotes hibernantes casi no hay diferencias en la forma de los catafilos y los nomofilos. En algunos ejemplares con nomofilos tipo "*durieui*" o "*cucumifolia*" la sucesión foliar es al revés y lleva de hojas lobuladas a enteras.

La sucesión foliar observada en *Cucurbitella* es una de las más frecuentes en las Cucurbitaceae (Zimmermann, 1922). A través del cultivo de algunos ejemplares (*Pozner 62, 63, 65, 87, 106*) en condiciones hídricas diferentes a las naturales se ha observado que la forma de la hoja de un individuo no cambia con el régimen hídrico.

Variación interindividual. La variación interindividual de los nomofilos afecta la forma, el grado de división de la lámina, el margen, la consistencia y la pubescencia.

Entre los individuos con nomofilos tipo "*cucumifolia*," con nomofilos tipo "*durieui*" y aquéllos con nomofilos tipo "*asperata*," existen individuos con todas las formas foliares intermedias, que se corresponden con las respectivas estructuras intermedias de sus primordios foliares (Fig. 2A–I). La ontogenia foliar de los tres tipos foliares principales muestra a los primordios más jóvenes enteros y cordiformes (Fig. 2a, d, g). Los nomofilos tipo "*cucu-*

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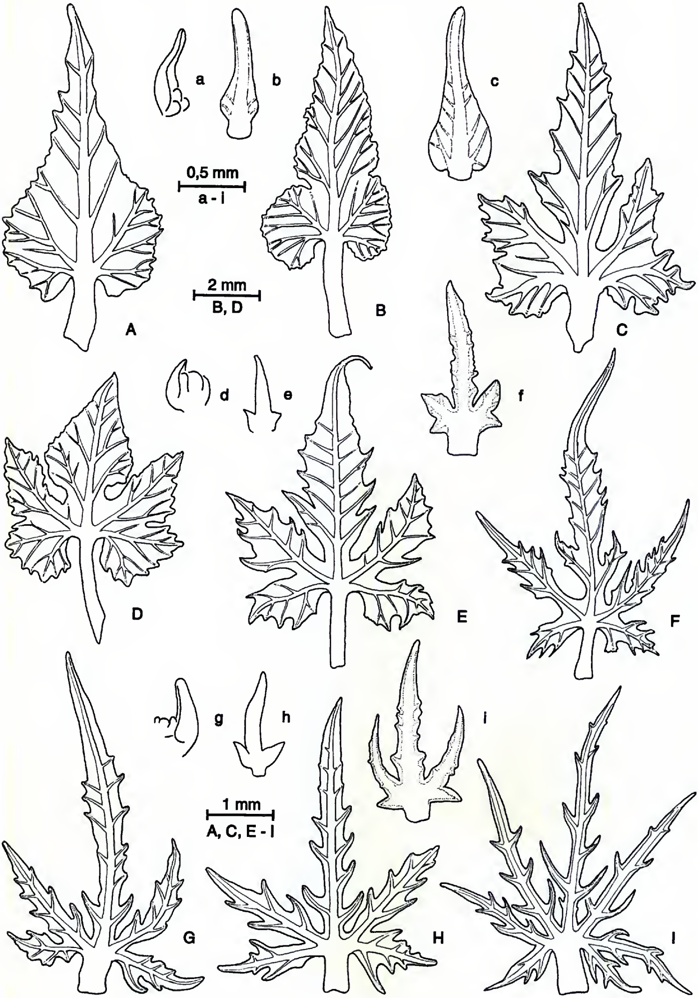
Figura 2. Primordios foliares. —A, B. Tipo foliar "*cucumifolia*" (*Cristóbal 2160, Venturi 3133* respectivamente). —C. Forma intermedia entre los tipos foliares "*cucumifolia*" y "*durieui*" (*A. T. Hunziker 4709*). —D, E. Tipo foliar "*durieui*" (*Novara 2884, Schulz 6323* respectivamente). —F, G. Formas intermedias entre los tipos foliares "*durieui*" y "*asperata*" (*Venturi 7734* y *7665* respectivamente). —H, I. Tipo foliar "*asperata*" (*Pedersen 15211, Krapovickas 14631* respectivamente). —a, b, c. Tres etapas de la ontogenia de un primordio del tipo foliar "*cucumifolia*" (*Cristóbal 2160*). —d, e, f. Idem a, b, c para un primordio del tipo foliar "*durieui*" (*BAB 752730*). —g, h, i. Idem a, b, c para un primordio del tipo foliar "*asperata*" (*Piccinini 1721*).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mifolia" mantienen esta forma inicial durante todo su desarrollo (Fig. 2a–c, A). En los nomofilos lobulados surgen, en la base del primordio foliar, primero los dos lóbulos medianos y luego los dos lóbulos basales (Fig. 2d–i). Los nomofilos tipo "*durieui*" y "*asperata*" comparten más etapas en común durante su desarrollo que con los nomofilos "*cucumifolia*." Quizás por esta razón los individuos con tipos foliares intermedios entre "*asperata*" y "*durieui*" tienen una sucesión foliar poco marcada, mientras que los individuos con tipos foliares intermedios entre "*durieui*" y "*cucumifolia*" tienen una sucesión foliar marcada que combina ambos tipos de hojas. Existe una gran variación en el margen foliar, que puede ser desde casi liso con dientes remotos hasta serrado con dientes de bordes rectos, convexos o cóncavos (margen obcrenado en este último caso). Con excepción de las hojas casi disectas de algunos individuos, donde los segmentos de los lóbulos se corresponden siempre con los dientes, existen individuos con todas las combinaciones posibles de formas foliares y tipo de margen.

El tamaño de los nomofilos de *Cucurbitella* varía entre 1 × 1 cm hasta 18 × 16 cm, y los ejemplares estudiados sugieren que el tamaño de los nomofilos depende del ambiente. En efecto, ejemplares de los suelos arenosos de la Salina de Mascasín, La Rioja (*Piccinini 1721* y *1744*), poseen nomofilos de sólo 1 cm de longitud y anchura. Algo similar ocurre con algunos ejemplares de suelos arenosos y pedregosos de Salta (*Novara 2884*), con nomofilos de 1.5 × 1.5 cm. Incluso un mismo ejemplar puede combinar hojas muy pequeñas y grandes.

La consistencia y la pubescencia de los hojas están afectadas por el ambiente. Individuos coleccionados en Córdoba (600–700 mm de precipitación media anual, *Pozner 62, 63, 65*) con hojas rígidas y pubescentes, desarrollaron hojas delgadas y casi glabras cuando fueron cultivados en Buenos Aires (900–1000 mm de precipitación media anual).

ZARCILLOS

En la mayoría de las Cucurbitaceae el zarcillo es una estructura compuesta por una porción caulinar (unifacial), denominada portazarcillo ("Rankenträger"), y una o más partes foliares (bifaciales y con la misma filotaxis que las hojas normales) que forman las ramas del zarcillo. La primera rama de estos zarcillos compuestos corresponde al profilo de la yema vegetativa lateral, que es la hoja tectriz del portazacillo. Los zarcillos de *Cucurbitella* son simples con prefoliación recta. De acuerdo con Kumazawa (1964), son de naturaleza foliar (con estructura bifacial en toda su longitud), sin portazarcillo, y homólogos al profilo anódico de la yema vegetativa lateral. Estos zarcillos simples no son raros en las Cucurbitaceae, se conocen también en *Cucumis* y *Trichosanthes* (Kumazawa, 1964).

ESPORIDAD

El período de floración se extiende desde noviembre hasta abril, y su comienzo varía entre noviembre y febrero según el inicio de la época lluviosa en cada región. El material estudiado vivo y herborizado incluye ejemplares con flores carpeladas, con flores estaminadas o con ambos tipos de flores dentro de cada tipo foliar. Asimismo, individuos que en condiciones naturales producen ambos tipos de flores, una vez trasplantados sólo forman flores estaminadas (cfr. Naudin, 1866). Los mecanismos que determinan la esporidad ("sex expression") en las Cucurbitaceae son complejos y variados (Condon & Gilbert, 1990; Delesalle, 1989; Roy & Saran, 1990). Por ahora es posible afirmar que *Cucurbitella* es siempre monoica. Pero no se sabe si las poblaciones combinan individuos perfectos con individuos estaminados y/o carpelados.

INFLORESCENCIAS

Las flores carpeladas y las inflorescencias estaminadas se forman generalmente en nudos dife-

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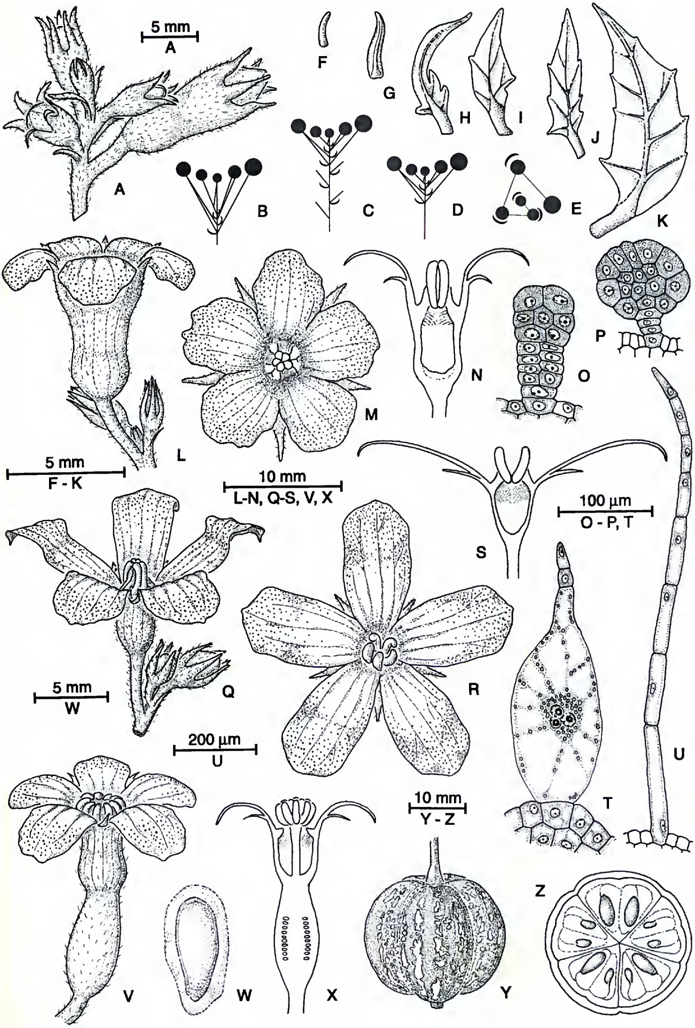
Figura 3. —A. Inflorescencia estaminada (*Pozner 82*). —B, C, D. Variación de la inflorescencia estaminada, fascículo sésil (B, *Pozner 82*), monocasio racimiforme (C, *Krapovickas 20592*), fascículo pedunculado (D, *Krapovickas 5931*). —E. Esquema en planta de A. —F, G, H, I, J, K. Variación de las brácteas de la inflorescencia estaminada (*Pozner 82*). —L, M, N. Flor estaminada tipo "*cucumifolia*," vista lateral (L), vista superior (M) y sección longitudinal esquemática (N), (*Pozner 88*). —O, P. Tricomas glandulares de los pétalos (*Pozner 65, Pozner 88* respectivamente). —Q, R, S. Flor estaminada tipo "*asperata*," vista lateral (Q), vista superior (R) y sección longitudinal esquemática (S) (*J. H. Hunziker 13084*). —T. Tricomas ampuliforme conectival (*Pozner 88*). —U. Tricoma de la garganta del hipanto (*Pozner 65*). —V, X. Flor carpelada, vista lateral (V), sección longitudinal esquemática (X) (*J. H. Hunziker 13084*). —W. Semilla con saco ariloideo (*Pozner 106*). —Y, Z. Fruto, vista lateral (Y), sección transversal (Z), (*Pozner 106*). En los esquemas B, C, D, los pedicelos triangulares indican que la flor se encuentra hacia adelante (▽) o hacia atrás (△) respecto del plano del esquema (se trata de la misma convención utilizada en los esquemas de las fórmulas moleculares).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rentes de una misma rama. Las flores carpeladas son solitarias o excepcionalmente geminadas. En este último caso las dos flores carpeladas carecen de brácteas y tienen distinto grado de desarrollo. Si se compara con la inflorescencia estaminada de este género y con las inflorescencias cimosas típicas de las Cucurbitaceae, estos casos de flores carpeladas geminadas pueden interpretarse como monocasios bifloros. Las flores estaminadas se agrupan en monocasios (bóstrix) 3–10-floros (Fig. 3A–E), donde algunas veces sólo desarrolla una sola flor. Estos monocasios poseen un pedúnculo de longitud variable entre 1 y 30 mm, y los nudos interflorales pueden estar reducidos (fascículo, Fig. 3B, D) o desarrollados (monocasio racimiforme, Fig. 3C). En general, cuanto más largo es el pedúnculo del monocasio, más cortos son los pedicelos florales y viceversa (Fig. 3B, D), de modo que la longitud total de la inflorescencia estaminada siempre es igual o menor que el pecíolo de su hoja tectriz. Las flores estaminadas marchitas se desprenden de su pedicelo, que persiste y se engruesa sobre la inflorescencia. En los ejemplares con monocasios racimiformes, los entrenudos que separan a las flores desarrollan a medida que las flores se abren y marchitan (Fig. 3C). Por esta causa un mismo ejemplar puede tener fascículos (monocasios que recién comienzan a abrir sus flores) y monocasios racimiformes (monocasios que están abriendo sus últimas flores). Además de este caso particular, la longitud del pedúnculo, de los entrenudos y los pedicelos florales suele ser variable dentro de un mismo ejemplar. Las brácteas de las flores estaminadas pueden estar presentes o ausentes en distintas inflorescencias del mismo ejemplar. En general las brácteas son pequeñas, subuladas a lineares (Fig. 3F, G), y pueden pasar desapercibidas. En algunos ejemplares las brácteas son foliosas (Fig. 3H–K).

FLORES

El cáliz tiene prefloración abierta (Fig. 3A). Los sépalos varían entre lineares a triangulares y, del mismo modo que la cara externa del hipanto, están cubiertos por pelos uncinulados. La corola tiene prefloración coclear distal (sensu Weberling, 1992), los pétalos son orbiculares, elípticos u oblongos (Fig. 3M, R), están libres entre sí o levemente soldados en su base. Los pétalos tienen vernación plana en su porción basal y media, y vernación involuta en el ápice. Su color varía entre el blanco, blanco-verdoso, amarillo, amarillo-verdoso y amarillo-anaranjado. La cara adaxial de los pétalos está cubierta de tricomas glandulosos, moruliformes, con un pie 1–2-seriado 2–8-celular y una cabezuela con 3 a 6 células de diámetro, ricas en almidón compuesto (Fig. 3O, P). La base de los estambres (y los estaminodios en las flores carpeladas) y la garganta del hipanto sobre la cual se insertan, está rodeada por tricomas uniseriados, 6–10-celulares (Fig. 3U), con cutícula verrucosa y aspecto algodonoso en conjunto. Estos tricomas forman un nectarostegio que cierra la porción del hipanto donde se acumula el néctar. El nectario es mesenquimático, formado por la base del hipanto engrosada. En las flores estaminadas el androceo es claramente 2+2+1. Cada estambre conserva su hacecillo vascular y puede ser separado de su par por simple tracción. El conectivo de las anteras posee pelos ampuliformes explosivos (Fig. 3T), cuyo producto de liberación actúa como un aglutinante del polen, como ocurre también en otros géneros de Cucurbitaceae (Zimmermann, 1922; Vogel, 1981; Dieringer & Cabrera, 1994). Los granos de polen son tricolporados reticulados, con un diámetro ecuatorial de 42 a 54 μm y polar de 61 a 71 μm (Marticorena, 1963). No hay pistilodio. Las flores carpeladas tienen un hipanto campanulado, cinco estaminodios mameliformes, y un gineceo 5-carpelar (Fig. 3V, X, Z). El ovario contiene numerosos rudimentos seminales horizontales, el estilo es recto y el estigma está ubicado al nivel de la garganta del hipanto (Fig. 3V, X) y formado por 10 ramas cilíndricas (2 por carpelo) unidas en pares entre carpelos vecinos (estigmas comisurales, sensu Weberling, 1992). La superficie del estigma está cubierta de emergencias papiliformes. Tanto las flores estaminadas como las carpeladas se abren desde la mañana temprana y sólo duran abiertas un día.

Así como la estructura floral carpelada es uniforme, existe una amplia variación del hipanto y la posición de los estambres en la flor estaminada (Fig. 3L–N, Q–S). En general el hipanto es campanulado, raramente es tubular y excepcionalmente urceolado. Los estambres pueden insertarse sobre la garganta del hipanto y estar exsertos, o bien se insertan en la mitad superior del hipanto y están completamente insertos (Fig. 3N, S). Existen individuos con flores con todas las formas descriptas de hipanto e inserciones y exserciones intermedias de los estambres.

FRUTOS

El fruto de *Cucurbitella* es una baya esférica, levemente deprimida o alargada, con epicarpo glabro o pubescente, verde con manchas blancas o verdoso-blanquecinas, alineadas en vetas longitudinales (Fig. 3Y). El meso- y el endocarpo son mucilaginosos y de color verde intenso. Los frutos alcanzan su madurez, generalmente después de que los tallos y las hojas de esa temporada se han marchitado. Según Martínez Crovetto (1965, sub *C. durieui*), los frutos son amarillentos a la madurez, rasgo que no se ha observado en ninguna de las plantas estudiadas. Definitivamente se trata de una observación errónea pues el material citado por Martínez Crovetto (1965) corresponde a *Apodanthera sagittifolia* (Griseb.) Mart. Crov. var. *dissecta* (Cogn.) Mart. Crov.

SEMILLAS

Las semillas son ovoideas, comprimidas, lisas y de color castaño. Están envueltas por una porción del endocarpio, denominada saco ariloideo (Font Quer, 1982), que se separa del resto del tejido del fruto y rodea a cada semilla como si fuera un arilo (Fig. 3W). El saco ariloideo es mucilaginoso, rico en sustancias pécticas, de color verde y adhesivo. Por tales causas habría que considerar la endozoocoria y la epizoocoria por mixospermia en la dispersión de las semillas.

RELACIONES

RELACIONES INTERGENÉRICAS

De acuerdo con la clasificación más reciente (Jeffrey, 1990), el género *Cucurbitella* está incluido dentro de la subfamilia Cucurbitoideae, tribu Melothrieae, subtribu Dendrosicyinae. No hay opiniones publicadas sobre las relaciones entre *Cucurbitella* y los géneros restantes de las Dendrosicyinae. En el presente estudio se considera que *Cucurbitella* está definido por el conjunto de las siguientes características: flor carpelada con gineceo 5-carpelar, estigmas bisectos (en total 10 ramas estigmáticas lineares), y 5 estaminodios; pedúnculo de la inflorescencia estaminada igual o menor que el pecíolo de la hoja tectriz; y flor estaminada con estambres dobles separables por tracción en sus componentes y conectivo con pelos ampuliformes explosivos. Ninguno de estos caracteres es una autapomorfía de *Cucurbitella*. Tomados individualmente, estos caracteres relacionan a *Cucurbitella* con *Apodanthera*, y con un grupo de géneros afines a *Apodanthera*, como *Wilbrandia*, *Guraniopsis* y *Melothrianthus*, cuyos límites y relaciones deben ser revisados (cfr. Martínez Crovetto, 1954a; Jeffrey, 1978). El género *Apodanthera* necesita una revisión integral, particularmente las especies de la sect. *Apodanthera*, para algunas de las cuales se desconoce la información de las flores carpeladas. La relación de *Cucurbitella* con *Apodanthera* parece ser muy estrecha, particularmente con *A. ferreyrana* Mart. Crov. (sect. *Apodanthera*), por sus cinco estigmas bífidos, y con *A. lasiocalyx* Cogn. (sect. *Apodanthera*), por sus cinco estaminodios (carácter que está relacionado con la posibilidad de separar los componentes de los estambres dobles por tracción). Los pelos conectivales ampuliformes están presentes en *A. undulata* A. Gray (sect. *Cucurbitopsis*) pero son frecuentes también en otros géneros de Cucurbitaceae (Zimmermann, 1922). En este contexto, *Cucurbitella* se distingue de *Apodanthera* sects. *Apodanthera* y *Cucurbitopsis* por sus monocasios cortamente pedunculados, y de *Apodanthera* sect. *Pseudoapodanthera* por sus flores carpeladas solitarias. A continuación se agrega una clave para reconocer los taxones principales americanos de las Dendrosicyinae:

1a. Androceo formado por dos estambres dobles (A 2+2) .... *Guraniopsis*
1b. Androceo formado por dos estambres dobles y uno simple (A 2+2+1).
  2a. Flores estaminadas sésiles, en monocasios espiciformes; zarcillos circinados en la yema .... *Wilbrandia*
  2b. Flores estaminadas pediceladas, en monocasios racimiformes o en fascículos (raro flores solitarias); zarcillos rectos en la yema.
    3a. Pétalos bipartidos, los lóbulos circinados en el capullo .... *Ceratosanthes*
    3b. Pétalos enteros, no circinados en el capullo.
      4a. Anteras basifijas .... *Melothrianthus*
      4b. Anteras dorsifijas.
        5a. Ovario y fruto transversalmente oblongos; rudimentos seminales 8; semillas piriformes, con el tegumento escrobiculado .... *Halosicyos*
        5b. Ovaro y fruto longitudinalmente oblongos; rudimentos seminales 8 ó más; semillas ovoideo-comprimidas, con el tegumento liso o con excrecencias esponjosas.
          6a. Flores carpeladas en fascículos .... *Apodanthera* sect. *Pseudoapodanthera*
          6b. Flores carpeladas solitarias (raro geminadas).
            7a. Gineceo 5-carpelar, los estigmas 5, bisectos; pedúnculo de la inflorescencia estaminada menor o igual que el pecíolo de la hoja tectriz .... *Cucurbitella*
            7b. Gineceo bi- o tricarpelar, los estigmas 2 ó 3, bisectos o de formas variadas; pedúnculo de la inflorescencia estaminada mayor que el pecíolo de la hoja tectriz (excepciones: *Apodanthera ferreyrana*, con gineceo 5-carpelar y 5 estigmas bífidos;

Apodanthera anatuyana (Mart. Crov.) Pozner; con pedúnculo de la inflorescencia estaminada igual al pecíolo de la hoja tectriz).
8a. Hojas membranáceas .... *Apodanthera* sect. *Apodanthera*
8b. Hojas suculentas .... *Apodanthera* sect. *Cucurbitopsis*

RELACIONES INFRAGENÉRICAS

La revisión de los caracteres morfológicos de *Cucurbitella* muestra que la estructura de la raíz, del tallo, del fruto y de la semilla es uniforme entre los ejemplares estudiados. El tamaño, la pubescencia y la consistencia de las hojas están estrechamente relacionados con los factores ambientales. La inflorescencia estaminada, en cuanto al desarrollo del pedúnculo, los entrenudos, los pedicelos florales y las brácteas, varía dentro de un mismo individuo. Sólo la forma del primordio foliar de los nomofilos, la exserción de los estambres, la longitud del hipanto y de los pétalos son los caracteres constantes en cada ejemplar y más variables entre ejemplares. En todos los casos la variación de estos caracteres es continua y no correlacionada ($-0.34 <$ índice de Spearman < 0.23 y $-0.35 <$ índice de Kendall < 0.18). La distribución geográfica de las frecuencias relativas de las formas foliares primordiales muestra que los individuos con primordios foliares de tipo "*asperata*" (Fig. 2H, I) son más frecuentes en el centro, oeste y una pequeña parte del este de la Argentina, dentro de las provincias fitogeográficas del Monte, Espinal y el sur del distrito Chaqueño Serrano de la provincia Chaqueña (Fig. 4). En esta misma área son más frecuentes los individuos con estambres exsertos. Hacia el norte son más frecuentes los individuos con primordios de transición entre los tipos "*asperata*" y "*durieui*," y con primordios foliares del tipo "*durieui*," cuyas frecuencias dominan en las provincias fitogeográficas Prepuneña y Puneña, Pampeana y el distrito Chaqueño Occidental de la provincia Chaqueña (Fig. 4). Dentro de estas mismas áreas fitogeográficas predominan los individuos con estambres semiexsertos. Los individuos con primordios de tipo "*cucumifolia*" dominan en las provincias fitogeográficas de las Yungas, Paranense y en el norte del distrito Chaqueño Serrano de la provincia Chaqueña (Fig. 4). Asimismo predominan los individuos con estambres insertos. El distrito Chaqueño Oriental de la provincia Chaqueña combina frecuencias similares de individuos con primordios foliares "*cucumifolia*" y "*durieui*." La longitud del hipanto tiene su máxima frecuencia entre los 5 y 7 mm en toda la distribución del género, pero el rango de variación aumenta de sur (4–6 mm) a norte (4–12 mm).

Aunque ciertas formas foliares predominan en cada una de las áreas fitogeográficas mencionadas, casi todas las formas foliares restantes están también presentes (Fig. 4). Dentro de esta variación, los tipos nomenclaturales de *C. asperata*, *C. cucumifolia* y la ilustración de *C. durieui* publicada por Naudin (1866, pl. 2, sub *Prasopepon durieui*), corresponden a formas foliares bien diferenciables. El tipo nomenclatural de *C. urkupinana* coincide con la ilustración de *C. durieui* publicada por Naudin (1866, pl. 2, sub *Prasopepon durieui*), y el tipo nomenclatural de *C. integrifolia* con el de *C. cucumifolia*. El tipo nomenclatural de *C. ecuadorensis* queda excluido del género (véase más abajo).

Este análisis de caracteres permite establecer un único taxón con un amplio rango de variación continua, donde es arbitrario colocar límites internos. La distribución geográfica de las frecuencias de los caracteres sugiere la distinción de tres grupos o razas:

1. Estambres exsertos, pétalos largos (8–12 mm), hipanto corto (4–5 mm), primordios foliares H y I (Fig. 2). Se incluye aquí el tipo de *C. asperata.*
2. Estambres semiexsertos, pétalos medianos (6–8 mm), hipanto mediano (6–7 mm) y primordios foliares D y E (Fig. 2). Se incluyen aquí el tipo de *C. urkupinana* y la ilustración de *C. durieui* publicada por Naudin (1866, pl. 2, sub *Prasopepon durieui*).
3. Estambres insertos, pétalos cortos (4–6 mm), hipanto largo (8–12 mm), primordios foliares J y K (Fig. 2). Se incluyen aquí los tipos de *C. cucumifolia* y *C. integrifolia.*

Los diferentes tipos de razas poseen una distribución geográfica de sus poblaciones y una distribución de las frecuencias de las variantes polimórficas dentro de cada población, que les son características (cfr. Grant, 1989). El presente estudio de frecuencias de las formas foliares primordiales se ha basado en ejemplares de herbario y no en censos de poblaciones. A pesar de esta limitación, la distribución de las frecuencias de las formas foliares primordiales de este género tiene un patrón en mosaico (Fig. 4) característico de la distribución de las razas ecológicas (Grant, 1989), con la particularidad que existe un cambio paulatino de frecuencias en las direcciones norte-sur y oeste-este. En general, cuanto más árido es el ambiente, son más frecuentes los ejemplares con hojas tipo "*asperata*," con menor tamaño de las hojas, y pu-

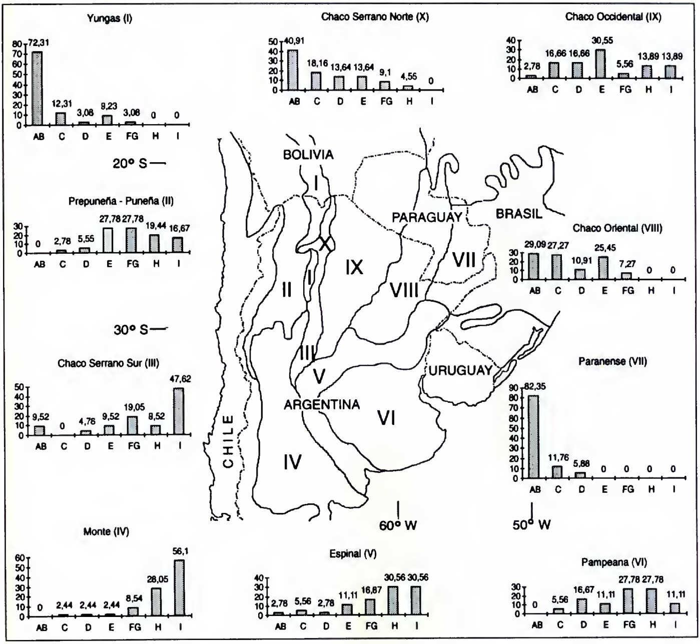

Figura 4. Frecuencias relativas de los tipos de primordios foliares ilustrados en la Figura 2, calculados para las diferentes provincias y distritos fitogeográficos donde se distribuye el género *Cucurbitella*. Los límites de las provincias y distritos fitogeográficos están marcados con línea llena y se han basado en Cabrera y Willink (1980), Morello y Adámoli (1968), Spichiger et al. (1995) y Prado (1993). Cada gráfico de frecuencia está acompañado por el nombre del área fitogeográfica correspondiente y una refererencia (I, II, III, IV, V, VI, VII, VIII, IX, X) que permite ubicar el área en el mapa. Las provincias Puneña y Prepuneña se han reunido en una sola unidad y no se ha indicado el área de la provincia Altoandina para simplificar la representación gráfica. Los límites políticos internacionales están indicados con línea interrumpida. Las abreviaturas A, B, C, D, E, F, G, H, I corresponden a las formas foliares ilustradas en la Figura 2, de modo que la barra AB corresponde a la frecuencia relativa de las formas foliares A y B de la Figura 2 para cada una de las áreas fitogeográficas en cuestión, y así sucesivamente.

bescencia más densa. A pesar de que los individuos con primordios foliares tipo "*asperata*" son dominantes en el centro y oeste de la Argentina (clima regional árido o semiárido) su presencia, y la de individuos con formas de transición, alcanza el norte de la Argentina (clima regional subtropical) en hábitats localmente áridos por sus condiciones edáficas (salares, bosque xerófilo, médanos y pedregales). Y viceversa con los individuos con primordios foliares de tipo "*durieui*" y "*cucumifolia.*" La variación continua de los caracteres en este género coincide con una variación paulatina de la frecuencia de hábitats áridos regionales con ambientes locales más húmedos a subtropicales regionales con ambientes semi-áridos locales, según las condiciones del suelo.

El cultivo de individuos en condiciones hídricas distintas a las de su lugar de origen mostró que la forma foliar tiene una base genética y no es una respuesta morfogenética al ambiente. La distribución de las frecuencias de los caracteres morfológicos sugiere que el género *Cucurbitella* comprende una única especie polimórfica, *C. asperata* (Gillies ex Hook. & Arn.) Walp., con tres posibles razas ecológicas. Según Stace (1993), las razas ecológicas suelen denominarse bajo la categoría de *variedad.* En este caso particular se considera que la denominación formal de estas razas de *Cucurbitella asperata* no tiene aplicación práctica debido a los numerosos individuos con variantes intermedias. Por el mismo motivo carece de sentido proponer una clave para distinguir las razas. En consecuencia se establece el siguiente tratamiento taxonómico.

Tratamiento Taxonómico

Cucurbitella Walp. ["Curcubitella"], Repert. Bot. Syst. 6: 50. 1846. TIPO: *Cucurbitella asperata* (Gillies ex Hook. & Arn.) Walp. (*Cucurbita asperata* Gillies ex Hook. & Arn.).

Schizostigma Arn., Madras J. Lit. Sci. 12: 50. 1840, non Arn. ex Meisn. 1838. TIPO: *Schizostigma asperatum* (Gillies ex Hook & Arn.) Arn. (*Cucurbita asperata* Gillies ex Hook & Arn.).

Prasopepon Naudin, Ann. Sci. Nat., Bot. sér. 5, 5: 26. 1866. TIPO: *Prasopepon durieui* Naudin ["*duriaei*"].

Hemicriptófitos diclimonoicos, fétidos. Raíz reservante, napiforme, con tuberosidades esféricas u ovoideas, ritidoma con lenticelas pulviniformes, en general alineadas horizontalmente. Vástago anual con pubescencia áspera de tricomas uncinulados y glandulares. Porción basal de las ramas perenne, portadora de las yemas hibernantes. Hojas simples, suborbiculares, enteras a 3–7-palmati- o pedatipartidas, base cordada, segmentos enteros o pinnatipartidos, hasta disectos; margen serrado, obcrenado, o con dientes remotos. Zarcillos simples, de vernación recta. Flores estaminadas en monocasios (bóstrix) sésiles o cortamente pedunculados 2–10-floros, fasciculiformes o racimiformes; brácteas subuladas o lineares, foliosas o ausentes. Hipanto tubular a infundibuliforme; garganta vellosa. Cáliz abierto; sépalos triangulares a subulados. Corola imbricada (coclear distal); pétalos amarillos, amarillo-anaranjados, amarillo-verdosos, blancos o blanco-verdosos, cara adaxial con pubescencia glandulosa. Androceo 2+2+1; estambres exsertos, insertados en la garganta del hipanto, hasta inclusos, insertados en la mitad superior del hipanto; anteras dorsifijas, levemente adheridas entre sí; tecas rectas; filamentos breves; conectivo con pelos ampuliformes explosivos cuya secreción actúa como aglutinante del polen; polen 3-colporado reticulado; pistilodio ausente. Flores carpeladas solitarias, raramente geminadas. Hipanto, cáliz y corola como en la flor estaminada. Estaminodios 5, mameliformes. Gineceo 5-carpelar; ovario ovoideo o fusiforme, con numerosos rudimentos seminales horizontales; estilo recto; estigma divido en cinco ramas bisectas, segmentos lineares cubiertos de emergencias papiliformes. Baya subesférica, verde con vetas longitudinales formadas por máculas blanquecinas. Semillas aovadas, comprimidas, pardas, lisas, envueltas en un saco ariloideo verde, mucilaginoso y adhesivo.

1. **Cucurbitella asperata** (Gillies ex Hook. & Arn.) Walp., Repert. Bot. Syst. 6: 50. 1846. *Cucurbita asperata* Gillies ex Hook. & Arn., Bot. Misc. 3: 324. 1833. *Schizostigma asperatum* (Gillies ex Hook. & Arn.) Arn., Madras J. Lit. Sci. 12: 50. 1840. TIPO: Argentina. Mendoza: "in travesia or uncultivated places," *Gillies s.n.* (lectótipo, aquí designado, GL; fotografía SI).

Prasopepon durieui Naudin ["*duriaei*"], Ann. Sci. Nat., Bot. sér. 5, 5: 26. 1866. *Cucurbitella durieui* (Naudin) Cogn., en Mart., Fl. bras. 6(4): 40. 1878. TIPO: "Hab. In regione uruguayensi Americae australis. Plantam reperimus abunde floriferam fructiferamque in horto burdigalensi a clar. Durieu feliciter cultam, unde viva in hortum parisiensem transmigravit" (P? no visto).

Prasopepon cucumifolius Griseb., Pl. lorentz. 98, Abh. Königl. Ges. Wiss. Göttingen 19: 98. 1874. *Cucurbitella cucumifolia* (Griseb.) Cogn., en Mart., Fl. bras. 6(4): 70. 1878. TIPO: Argentina. Tucumán: "frequens in fruticetis et sepibus pr. Siambon," *Lorentz 309* (holótipo, GOET; fotografía de F-8987, SI).

Cucurbitella integrifolia Cogn., en A. DC. & C. DC., Monogr. phan. 3: 733. 1881. TIPO: Paraguay, "l'Assomption dans les nois," *B. Balansa 1112* (lectótipo, aquí designado, K; fotografía, SI).

Cucurbita urkupinana Cárdenas, Revista Agric. (Cochabamba) 3: 76. 1945. *Cucurbitella urkupinana* (Cárdenas) C. Jeffrey, Kew Bull. 33: 349. 1978. TIPO: Bolivia. Cochabamba: Cerro del Calvario near Quillacollo, 2560 msnm, sobre colinas secas con arbustos y piedras, XII-1945, *Cárdenas 3600* (isótipo, SI).

Tubérculos radicales hasta de 20 cm de diámetro. Tallos plurimetrales. Pecíolo de 1.5–10 cm; lámina de 1–18 × 1–16 cm. Inflorescencia estaminada con pedúnculo de 1–30 mm; pedicelos de 5–25 mm. Flor estaminada con hipanto de 4–12 × 3–6 mm; sépalos de 2–6 mm; pétalos de 7–12 × 3–5 mm; anteras de 3 mm. Flor carpelada con pedicelo de 10–55 mm; ovario de 8–15 × 3–6 mm y estilo de 4 mm. Baya de 30–35 × 30–40 mm. Semillas (sin saco ariloideo) de 5–6 × 2–3 × 0.75–1 mm.

Nombres vulgares. Sandillo del Campo (Mendoza: Hooker & Arnott, 1833), *Sandía del Campo* (Catamarca: *Jörgensen 1247*), *Sandía de la Zorra* (Mendoza: *Ruiz Leal 8530,* San Juan: *Spegazzini 344*), *Sandía del Zorro* (San Juan: *Haene 162,* La Rioja: *Krapovickas 5931*), *Sandía del Diablo* (Buenos Aires: *Schulz 9372*, Mendoza: *Kurtz 1339*, Tucumán: *Venturi 321*), *Angola de Zorro* (Jujuy: *Krapovickas 17619*), *Sandía de la Víbora* (Salta: *Saravia Toledo 1532*), *Zapallito* (Santiago del Estero: *Pire 1115*), *Zapallito de la Víbora* (Catamarca: *Troncoso 1865*), *No'otalán* (Paraguay: *Arenas 1750*).

Distribución. Argentina, Uruguay, Paraguay, Bolivia y Sur de Brasil. El género *Cucurbitella* no está incluido en la *Flora Chilena* (Muñoz Pizarro, 1959; Navas, 1979). La cita de Arnott (1841) para Chile se considera dudosa, basada en una confusión en la ubicación de la provincia de Mendoza, pues Arnott sólo menciona los ejemplares de Gillies. Asimismo la presencia de este género parece dudosa en Brasil. Aunque se mencionó en la *Flora brasiliensis* (Cogniaux, 1878), no figuró en la *Flora Ilustradada Rio Grande do Sul* (Porto, 1974). Hasta el momento, los únicos ejemplares citados para Brasil son los de *Engler, Arechavaleta* (Augusto, 1946) y *Sello 896, 897* (Cogniaux, 1878). El material citado para Uruguay fue publicado por Cogniaux (1878), Herter (1930) y Martínez Crovetto (1954b).

Material representativo examinado. ARGENTINA. **Buenos Aires:** San Pedro, 29 dic. 1945 (fl, fr), *Nicora 3550* (SI). **Catamarca:** Andalgalá, La Playa, 25 feb. 1916 (fr), *Jörgensen 1247* (SI). **Córdoba:** Punilla, falda oeste de la Sierra Chica, ruta 38 a Capilla del Monte, 11 ago. 1961 (fr), *A. E. Cocucci 352* (CORD). **Corrientes:** Saladas, San Lorenzo, 19 ene. 1983 (fl, fr), *Pedersen 13490* (CTES). **Chaco:** 1ro. de Mayo, Colonia Benítez, 20 ene. 1969 (fl), *Schulz 16497* (SI). **Entre Ríos:** Paraná, bajada grande al sur de la ciudad de Paraná, 4 feb. 1973 (fl), *Burkart 29608* (SI). **Formosa:** Pilcomayo, Parque Nacional Pilcomayo, 16 dic. 1988 (fl, fr), *Guaglianone 2291* (SI). **Jujuy:** El Carmen, Los Lapachos, 4 nov. 1984 (fl), *Ahumada 5064* (CTES). **La Pampa:** Rancul, entre El Tala y Chamaico, 2 sep. 1983, *Troiani 7249* (SRFA). **La Rioja:** Chilecito, Valle de los Talas, 1 ene. 1948 (fl, fr), *Sosa s.n.* (MERL 11505). **Mendoza:** Las Heras, Parque aborigen, 4 dic. 1942 (fr), *Ruiz Leal 8010* (MERL). **Salta:** Orán, Tabacal, 4 feb. 1943 (fl), *A. T. Hunziker 2778* (CTES). **San Juan:** Jachal, San Roque y Fuerte, 3 dic. 1937 (fl), *Spegazzini 344* (BAB). **San Luis:** Ayacucho, Santa Rosa, 29 ene. 1944 (fl), *Burkart 13957* (SI). **Santa Fe:** San Jerónimo, Arroyo Colastiné, ruta 11, 15 km al sur de Coronda, 27 ene. 1971 (fl, fr), *Krapovickas 17801* (BAA). **Santiago del Estero:** Carlos Pellegrini, Cerro del Remate, 23 dic. 1927 (fl), *Venturi 5681* (SI). **Tucumán:** Tafí, Yerba Buena, 3 ene. 1919 (fl), *Venturi 321* (SI). BOLIVIA. **Santa Cruz:** Andrés Ibáñez, 3 km al sudoeste de Angostura, 25 ene 1987 (fl, fr), *Nee 38825* (CTES); Cordillera, Santa Cruz 200 km al sur del Río Grande, 12 mar. 1981 (fl, fr), *Beck 6490* (SI); Florida, 10 km al nornoroeste de Maratal a San Juan del Potrero, 30 ene. 1994, *Nee & Vargas 44783* (SI); Florida, Maidana, 31 ene. 1984 (fl, fr), *Nee & Vargas 44809* (SI). **Tarija:** Arce, 108 km de Tarija a Bermejo, 22 nov. 1986 (fl), *Ehrich 242* (SI); Gran Chaco, Cototo, 7 km al este de Villa Montes, 11 abr. 1977 (fr), *Krapovickas & Schinini 31180* (SI); entre Narbáez y Entre Ríos, 24 oct. 1980 (fl), *Zuloaga et al. 1305* (SI). PARAGUAY. **Alto Paraguay:** Puerto Diana, 6 km al norte de Bahía Negra, 7 ene. 1974 (fr), *Arenas 300* (SI). **Boquerón:** Misión Santa Rosa, 1 feb. 1981 (fl), *Arenas 1750* (SI). **Concepción:** Puerto Casados, 1 dic. 1916 (fl), *Rojas 2354* (SI). **Chaco:** Parque Nacional Defensores del Chaco, 1 nov. 1984 (fl), *Duré 429* (CTES). **Nueva Asunción:** ruta Trans-Chaco, 21°26'S, 61°25'W, 7 mar. 1979 (fr), *Schinini & Bordas 16402* (SI). **Presidente Hayes:** Colonia menno, 28 ene. 1976 (fl), *Arenas 1450* (SI).

Iconografía. Cogniaux, 1878: tab. 19; Cogniaux, 1916: 232, fig. 51; Martínez Crovetto, 1974: 71–72, figs. 31–32; Roig, 1981: 143, fig. 86; Cabrera, 1993: 504–505, figs. 205–206. Conviene aclarar aquí que en la ilustración de *C. asperata* publicada por Martínez Crovetto, 1965: 395, fig. 130A y Cabrera, 1993: 501, fig. 204A, se ha basado en un ejemplar de *Apodanthera sagittifolia* (Griseb.) Mart. Crov. var *dissecta* (Cogn.) Mart. Crov. (probablemente *Cabrera 2062*, LP).

En la publicación original de *Cucurbita asperata* no se citaron explícitamente ejemplares de herbario sino una breve nota de campo: "uncultivated places in the province of Mendoza, J. Gillies, nom. vernac. Sandillo del Campo." En dicha publicación se aclaró además que Gillies encontró una segunda variedad: ". . . that growing in travesia, or more arid places, has the segments of the leaves less deeply sinuated than the other," pero sin asignarle un nombre. Se han encontrado tres ejemplares de Gillies identificados como *Cucurbita asperata:*

1. Un primer ejemplar (GL) cuya etiqueta dice "*Cucurbita asperata* n. sp. Gillies. In Travesia or arid uncultivated places in province of Mendoza. J. Gillies," con la anotación B/H 751471 en la cartulina, y cuyas hojas responden a la descripción de la variedad con los segmentos menos profundamente sinuados.
2. Un segundo ejemplar (K) cuya etiqueta dice "*Cucurbita asperata* n. sp. var. *dissecta* Gillies, Sandillo del Campo nom. vernac. Jarillal or uncultivated places. Mendoza. J. Gillies" y cuyas hojas tienen segmentos más profundamente sinuados que el ejemplar anterior. La cartulina de este ejemplar también posee la inscripción B/H 751471 e incluye una descripción latina manuscrita en el ángulo superior derecho.
3. Un tercer ejemplar (GL) con ambas etiquetas (1 y 2) pegadas en la misma cartulina, y cuyas hojas se ajustan mejor al ejemplar 2.

Según las etiquetas de los ejemplares 1 y 2, la variedad típica de *C. asperata* corresponde al ejemplar 1. Y aunque tales variedades no tienen valor (nomenclatural ni taxonómico), permiten conocer la intención del autor. Por este motivo se designa como lectótipo de *Cucurbita asperata* Gillies ex

Hook. & Arn. al ejemplar 1, pues coincide con la variedad típica en el sentido de Gillies. En cuanto a *Cucurbitella integrifolia* Cogn., se designa como lectótipo el sintipo *Balansa 1112* (K) por ser más completo que *Gibert 73* (K).

El material tipo de *Prasopepon durieui* Naudin fue solicitado al Muséum National d'Histoire Naturelle (P), pero no pudo ser localizado con certeza (G. G. Aymonin, com. pers.). Sin embargo, la ilustración publicada por Naudin (1866: pl. 2) permite identificar sin dudas las características del material tipo de *Prasopepon durieui.*

NOMBRE EXCLUIDO

Cucurbitella ecuadorenis Cogn., en Engl., Pflanzenr. IV. 275 I (Heft 66): 233. 1916. = *Posadaea sphaerocarpa* Cogn., Bull. Acad. Roy. Sci. Belgique sér. 3, 20: 477. 1890. TIPO: Ecuador. "Felsen am Fluss Pilaton 900 m. u. M.," *Sodiro 516* (holótipo, BR).

Literatura Citada

Arnott, G. A. W. 1840. Remarks on the fruit of the natural order Cucurbitaceae. Madras J. Lit. Sci. 12: 43–54.

———. 1841. On the Cucurbitaceae. J. Bot. (Hooker) 3: 271–280.

Augusto, Hermano. 1946. Flora do Rio grande do Sul. Oficinas Graficas da Imprensa Oficial. Porto Alegre.

Cabrera, A. L. 1993. Cucurbitaceae. *En:* A. L. Cabrera (editor), Flora de la provincia de Jujuy. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 13(9): 472–515.

——— & A. Willink. 1980. Biogeografía de América Latina. Colección de Monografías Científicas de la Organización de Estados Americanos, Secretaría General de la OEA, serie Biología, monografía nro. 13.

Cárdenas, M. 1945. Notas sobre taxonomía de plantas económicas de Bolivia. Revista Agric. (Cochabamba) 3: 76–77.

Cogniaux, A. 1878. Cucurbitaceae. *En:* C. F. P. Martius, Flora brasiliensis 6(4): 1–126. F. Fleischer, Leipzig.

———. 1916. Cucurbitaceae: Fevilleae et Melothrieae. *En:* A. Engler (editor), Das Pflanzenreich IV. 275 I (Heft 66): 1–277. W. Engelmann, Leipzig.

Condon, M. A. & L. E. Gilbert. 1990. Reproductive biology and natural history of the neotropical vines *Gurania* and *Psiguria*. Pp. 150–166 *en* D. M. Bates, R. W. Robinson & C. Jeffrey, Biology and Utilization of the Cucurbitaceae. Cornell Univ. Press, Ithaca.

Delesalle, V. A. 1989. Year-to-year changes in phenotypic gender in a monoecious cucurbit *Apodanthera undulata*. Amer. J. Bot. 76: 30–39.

Dieringer, G. & L. Cabrera. 1994. Sexual selection of anther trichomes and sexual dimorphism in *Ibervillea lindheimeri* (Cucurbitaceae–Melothrieae). Amer. J. Bot. 81: 111–118.

Font Quer, P. 1982. Diccionario de Botánica. 8 ed. Labor, Barcelona.

Grant, V. 1989. Evolución Vegetal. 2 ed. Limusa, México.

Herter, G. 1930. Florula Uruguayensis. Plantas Vasculares. Imprenta Nacional, Montevideo.

Hooker, W. J. & G. A. W. Arnott. 1833. Contributions towards a Flora of South America and the Islands of the Pacific. Bot. Misc. 3: 129–211, 303–367.

Jeffrey, C. 1978. Further notes on Cucurbitaceae: IV, Some New World Taxa. Kew Bull. 33: 347–380.

———. 1990. An outline classification of the Cucurbitaceae. Pp. 449–463 *en* D. M. Bates, R. W. Robinson & C. Jeffrey, Biology and Utilization of the Cucurbitaceae. Cornell Univ. Press, Ithaca.

Jensen, W. A. 1962. Botanical Histochemistry. W. H. Freeman, San Francisco.

Kumazawa, M. 1964. Morphological interpretations of axillary organs in the Cucurbitaceae. Phytomorphology 14: 287–298.

Marticorena, C. 1963. Material para una monografía de la morfología del polen de Cucurbitaceae. Grana Palynol. 4: 78–91.

Martínez Crovetto, R. 1954a. Sur les organes femelles de quelques espèces du genre *Apodanthera* (Cucurbitaceae). Notul. Syst. (Paris) 15: 41–43.

———. 1954b. Synopsis des Cucurbitacées de l'Uruguay. Notul. Syst. (Paris) 15: 47–55.

———. 1965. Cucurbitaceae. *En:* A. L. Cabrera, Flora de la provincia de Buenos Aires. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 4(5): 390–407.

———. 1974. Cucurbitaceae. *En:* A. Burkart, Flora Ilustrada de la provincia de Entre Ríos. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 6(6): 63–94.

Meisner, C. F. 1838. Plantarum vascularium genera, Vols. 1–2. Libraria Weidmannia, Leipzig.

Metcalfe, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

Morello, J. & J. Adámoli. 1968. Las grandes unidades de vegetación y ambiente del Chaco argentino. Primera parte: objetivos y metodología. Ser. Fitogeogr. Minist. Agric. Ganad. 10: 1–125.

Muñoz Pizarro, C. 1959. Sinopsis de la Flora Chilena. Ed. Universidad de Chile.

Naudin, M. Ch. 1866. Cucurbitacées nouvelles cultivées au Muséum d'Histoire Naturelle en 1863, 1864 et 1865. Ann. Sci. Nat., Bot. sér. 5, 5: 5–43, pl. 1–6.

Navas Bustamante, L. E. 1979. Flora de la Cuenca de Santiago de Chile. Ed. Universidad de Chile, 3 vols.

Porto, M. L. 1974. Cucurbitaceae. *En:* A. R. Schulz (editor), Flora Ilustrada do Rio Grande do Sul. Bol. Inst. Centr. Bioci. Univ. Fed. Rio Grande do Sul, Sér. Bot. 31: 1–64.

Prado, D. E. 1993. What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. Candollea 48: 145–172.

Roig, F. A. 1981. Flora de la Reserva Ecológica de Ñacuñán. Cuad. Técn. Inst. Argent. Invest. Zonas Aridas 3–80.

Roy, R. P. & S. Saran. 1990. Sex expression in the Cucurbitaceae. Pp. 251–268 *en* D. M. Bates, R. W. Robinson & C. Jeffrey, Biology and Utilization of the Cucurbitaceae. Cornell Univ. Press, Ithaca.

Ruiz Leal, A. 1975. Flora Popular Mendocina. Deserta 3: 1–299, f. 1–86.

Stace, C. A. 1993. Plant Taxonomy and Biosystematics, 2nd ed. Cambridge Univ. Press, Cambridge, U.K.

Spichiger R., R. Palese, A. Chautems & L. Ramella. 1995. Origin, affinities and diversity of hot spots of the Paraguayan dendrofloras. Candollea 50: 515–537.

Troll, W. 1967. Vergleichende Morphologie der höhren

Pflanzen. Band I, Teil 1–3. Gebrüder Borntraeger, Berlin.

Vogel, S. 1981. Die Klebstoffhaare an den Antheren von *Cyclanthera pedata* (Cucurbitaceae). Pl. Syst. Evol. 137: 291–316.

Walpers, G. G. 1846–1847. Repertorium Botanices Systematicae, Vol. 6. F. Hofmeister, Leipzig.

Weberling, F. 1992. Morphology of Flowers and Inflorescences. Cambridge Univ. Press.

Zimmermann, A. 1922. Die Cucurbitaceen. Beiträge zur Anatomie, Physiiologie, Morphologie, Biologie, Pathologie und Systematik. Heft 1 und 2. Gustav Fischer, Jena.

ÍNDICE DE EXSICCATAE

D. Abbiatti 211, 517; O. Ahumada 3408, 4425, 4677, 4874, 4974, 5064; M. M. Arbo 540, 559; P. Arenas 300, 1450, 1750, 2014; J. L. Argañarás 57; L. Artico 38.

J. R. Báez 29; H. H. Bartlett 19839, 20252; S. Beck 6490; M. Birabén 30, 229; F. Biurrum 1407, 3055, 3137, 3304, 3323, 3371, 4000; O. Boelcke 74, 6629, 14630, 14631, 14632; Bridarolli 639, 3224; A. Brown 1694; A. Burkart 12586, 12588, 12747, 13245, 13370, 13957, 20116, 20134, 20166, 22316, 23514, 25304, 25307, 25308, 25478, 25764, 27386, 27833, 29536, 29608.

A. Cabral 253, 965, 1146; A. L. Cabrera 1133, 4359, 5795, 5975, 12850, 13701, 16201, 16742, 17247, 17898, 20648, 20992, 21768, 21826, 22357, 22413, 23350, 23420, 24635, 27227, 29852, 29894, 31387, 31389, 31424, 33994, 34534, 34580, 34582, 34614, 34628, 34629a, 34660; C. Calderón 1260; E. Cano 4379, 4626, 5149; P. Cantino 545, 597, 613; E. Carette 104, 153, 181; R. R. Carnevali 2092; J. A. Castiglioni 6872, 7189, 7301, 7951, 7980; E. C. Clos 4063; A. E. Cocucci 352; A. Correa 319; N. Correa 4300; N. E. Crespo 159; S. 2943; C. Cristóbal 2160; L. Cusato 3603; S. Chalukian 1784; A. Charpin 20438.

G. Dawson 3326; N. Deginani 6, 810; E. Dinelli 757; R. Duré 429.

R. Ehrich 242; C. Ezcurra 1403.

H. A. Fabris 5036, 6254, 6430; A. Flossdorf *s.n.* 20 nov. 1908 (BAB-25200), *s.n.* 20 nov. 1908 (BAB-25201); R. Fortunato 631, 1571, 1708, 2024; Franceschi 505, 707, 784; J. Frenguelli 529.

M. L. Giardelli 766½, 1262; Gibert 73; E. R. Guaglianone 1369, 1375, 1818, 2291.

E. Haene 162; C. M. Hicken 25306, 25309, 25310; G. Hieronymus (Fotografía de F-8988); Hoffmann 1863; C. C. Hosseus 2643; A. T. Hunziker 1055, 2778, 4709, 5774, 9144, 11703, 13583, 13584, 14081, 17669, 17830, 18516, 18645, 20557, 24105; J. H. Hunziker 11253, 9535, 9547, 11668.

Job 826, 1847; P. Jörgensen 165, 273, 1241, 1247, 2773, 2776, 2778a; J. Jozami 874; Juárez de Varela 1723.

E. Kermes 389; R. Kiesling 148, 1196b, 4256, 4468, 5022, 5354, 5585, 5846, 5947, 6577; R. King (LP 896296); A. Krapovickas 1626, 5008, 5136, 5931, 11503, 11897, 13819, 13829, 14631, 14761, 15375, 17503, 17619, 17725, 17801, 18414, 20592, 21827, 24565, 24566, 27663, 27836, 27837, 28375, 28625, 30449, 30591, 30885, 31180, 32970, 46327, 46363; F. Kurtz 200, 1339, 2409, 3354, 11862, 13219, 13245.

H. Lagiglia 1963; A. Lanfranchi 1182; P. Legname 5058; Leguiza 51; J. P. Lewis 1350; P. G. Lorentz 750, 1248.

Maldonado 236, 1145, (LP 46736); L. Malmierca 2065; R. Martínez Crovetto 3694, 9880, 10302; V. Maruñak 469, 517; D. Medán 284; A. M. Molina 2985, 2897, 3197, 3216, 3426, 3454, 3953; Morici 8; M. Múlgura 683.

M. Nee 33825, 44783, 44809; E. Nicora 3550, 9058; L. Novara 2884, 2887, 4044, 4082, 4097, 4686, 5557, 5626, 8900, 9317, 9501, 10086.

C. Palací 391; Palán 385, 391; L. Parodi 6033, 14865, 15216; T. M. Pedersen 13490, 15211; J. Pensiero 4589; J. B. Pesce 122; Petersen 2589; C. A. Petetin 1056, 1359, 1531, 1664, 1831; B. G. Piccinini 1134, 1720, 1721, 1744, 4091, 4347; S. M. Pire 1115, 1503; R. Pozner 50, 88; Prado 405.

C. Quarín 826, 2324, 3038, 3250.

A. Ragonese 7131, 7139, 7987, 8744, 9655; F. Rial Alberti 190, 203; Rodríguez 269; A. Rodrigo 2548; F. A. Roig 562, 1521, 2253, 3501, 3558, 3567, 5449, 6436, 6598, 8512; T. Rojas 2354; A. Rotman 872; A. Ruiz 113; A. Ruiz Leal 904, 5761, 6472, 8010, 8530, 8809, 9011, 9096, 9237, 11348, 13418, 15908, 16487, 16736, 17203, 18434, 21124, 21369, 22559, 27023.

C. Saravia Toledo 1532; A. Scala (LP); F. Schickendantz 116, 288; A. Schinini 8709, 10988, 12136, 12465, 12520, 12584, 13021, 13702, 13863, 16402, 19547, 19554, 19565, 20023, 22248, 22446, 22480, 22508, 24175; A. G. Schulz 101, 2863, 2865, 2866, 2868, 2871, 2874, 4079, 4086, 5916, 6323, 6353, 6358, 6375, 6425, 6429, 7400, 7404, 8263, 8271, 8466, 8648, 8985, 8988, 9372, 14556, 15240, 15650, 15828, 15830, 15832, 15853, 15868, 16257, 16497, 17064, 17352, 17999; H. Schwabe 357; C. Spegazzini 3131, *s.n.* 12 Mar. 1937 (BAB-58011), *s.n.* 5 Mar. 1904 (BAB-11229), *s.n.* 11 Mar. 1905 (BAB-13841), *s.n.* 18 Mar. 1905 (BAB-14235), *s.n.* 9 Feb. 1906 (BAB-15471), *s.n.* 17 Jan. 1908 (BAB-22248), 17 Jan. 1908 (BAB-22250), *s.n.* 17 Jan. 1908 (BAB-22276), *s.n.* 1 Feb. 1908 (BAB-22664), *s.n.* 1 Feb. 1908 (BAB-22675), *s.n.* 1 Feb. 1908 (BAB-22676), *s.n.* 1 Feb. 1908 (BAB-22682), *s.n.* 1 Feb. 1908 (BAB-22683), *s.n.* 1 Feb. 1908 (BAB 22773), P. L. Spegazzini *s.n.* 1 Dec. 1909 (BAB 28732); R. A. Spegazzini 344; P. Steibel 3886, 3921, 4058, 5468, 6544, 10109.

C. M. Taylor 11366; S. G. Tressens 3212; Troiani 4129, 7246, 7249, 7878, 7954, 9537, 9538, 9547, 9871, 6750b; N. Troncoso 1865, 1902.

E. Ulibarri 305, 1401.

Varela 242, 306, 345; S. Venturi 321, 1159, 1602, 4405, 5680, 5681, 7665, 7687, 7734; Vignati 244, 526; C. Villamil 7678.

J. Williamson 3233.

Zapata 92; F. Zuloaga 300, 352, 1305, 2615, 2704, 2890, 2891, 3514, 3650, 3652, 3663, 3698, 3700, 3762.

A TAXONOMIC REVISION OF *DICOMA* (ASTERACEAE: CICHORIOIDEAE: MUTISIEAE) FOR THE HORN OF AFRICA[1]

Santiago Ortiz,[2] Juan Rodríguez-Oubiña,[2] and Mesfin Tadesse[3]

ABSTRACT

A revision of the genus *Dicoma* (Asteraceae: Cichorioideae: Mutisieae) in the Horn of Africa (Djibouti, Eritrea, Ethiopia, and Somalia) is provided. This area is probably a major center of radiation for this genus, and nine of the twelve species present are endemic here. The revision is based on both field observations and micro- and macromorphological study of herbarium specimens. Six of the twelve species recognized have been described recently by the first two authors. For each species, data are presented on morphological characteristics, area of distribution (of particular interest in view of the incorrect information previously published for several of the species), ecology, and local names. One new species, *D. thuliniana,* is described and illustrated, one new combination, *D. schimperi* subsp. *cinerea,* is proposed, and *D. lanuginosa* is lectotypified.

The genus *Dicoma* Cass. (Asteraceae: Cichorioideae: Mutisieae) consists of about 50 species of herbs, shrubs, and small trees. Most species are from tropical and southern Africa and Madagascar, though one species reaches the Arabian Peninsula and India and Pakistan.

Traditionally, *Dicoma* has been included in the tribe Mutisieae (Jeffrey, 1967; Cabrera, 1977). Recently, Hansen (1991) has suggested its exclusion from this tribe, largely because (a) the surface morphology of the corolla cells does not show the typical Mutisieae pattern, (b) the corolla is clearly divided into a narrow tube and a broad limb, and (c) in species with bilabiate flowers the upper lobes are absent or short and uncoiled. However, recent cladistic analyses of the subfamily Cichorioideae have suggested that *Dicoma* should be included in the Mutisieae despite these differences (Karis et al., 1992; Bremer, 1994).

The Horn of Africa (Djibouti, Eritrea, Ethiopia, and Somalia), which is probably a major center of radiation for *Dicoma,* is one of the least known areas of the continent floristically (cf. Hedberg & Edwards, 1989; Thulin, 1993; Edwards et al., 1995). Until recently, only four species of *Dicoma* were known from this area; Cufodontis (1967) cited five species, but these included *D. gnaphaloides,* which is merely a synonym of *D. tomentosa.* More recent work, and particularly study of herbarium material collected from the 1970s onward (especially in ETH, K, and UPS), has revealed the presence of twelve species, most of which have not been described previously (Ortiz & Rodríguez-Oubiña, 1994, 1995, 1996a, b; Rodríguez-Oubiña & Ortiz, 1995). We have also recently typified *D. bangueolensis* (Ortiz & Rodríguez-Oubiña, 1996a), thus resolving the nomenclatural problems and confusion arising from the erroneous reports of Buscalioni and Muschler (1913): as a result of this confusion, all the herbarium material of this species examined by us had been previously identified incorrectly or unidentified, despite this being one of the commonest species in Somalia.

It is also necessary to clear up a confusion deriving from Cufodontis (1967), who stated that *D. bangueolensis, D. somalensis,* and *D. schimperi* extended into Ethiopia, when in fact these species are known only from Somalia.

In response to these recent developments, we here present a revision of *Dicoma* for the Horn of Africa, accounting for all the species previously known together with those described recently.

MATERIAL AND METHODS

A total of 120 herbarium specimens from BM, ETH, FT, G, K, OXF, P, PAL, PI, S, UPS, and W,

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Table 1. Composition of the sections of *Dicoma* proposed by Hoffmann (1893) (considering only those species present in the Horn of Africa).

sect. *Eudicoma*	sect. *Hochstetteria*	sect. *Psilocoma*	sect. *Pterocoma*
D. bangueolensis *D. tomentosa*	*D. schimperi*	*D. aethiopica* *D. gillettii* *D. hindiana* *D. paivae* *D. popeana* *D. scoparia* *D. somalensis* *D. thuliniana*	*D. sessiliflora*

collected in Eritrea, Ethiopia, and Somalia, were studied, and all type material was examined by the authors; it was not possible to obtain herbarium material on loan from EA and MOG. We saw no *Dicoma* collections from Djibouti, although we know of one literature reference for the presence of *D. schimperi* subsp. *schimperi* in that country (Audru et al., 1994). All material was studied with the aid of a light microscope. We also studied other micromorphological and anatomical characters with a compound light microscope; for this part of the study, floral parts were first boiled in water and placed in Hoyer's solution (Anderson, 1954) for observation. Testa morphology was classified following Grau (1980), and epidermal cell surface, twin hairs, and superficial achene gland morphology following Karis et al. (1992). In the species descriptions, anther length includes the length of the apical appendage and the anther tails.

PHYLOGENY

Very little is known about the phylogenetic relationships of *Dicoma*. A cladistic analysis of the subfamily Cichorioideae indicated that *Dicoma* is closely related to *Pleiotaxis* and *Erythrocephalum* (Karis et al., 1992). This conclusion was supported by Bremer (1994), who assigned these three genera plus the African genera *Pasaccardoa*, *Achyrothalamus*, and *Gladiopappus* to the "*Dicoma* group," which he considered to be monophyletic.

We are currently performing the first cladistic analysis of *Dicoma* in which the species considered include not only members of *Dicoma* but also members of the other genera of the *Dicoma* group sensu Bremer. Our preliminary conclusions indicate that *Dicoma* is paraphyletic with respect to *Pasaccardoa*, and that *Pleiotaxis*, *Achyrothalamus*, and *Erythrocephalum* are sister to *Dicoma* plus *Pasaccardoa*. In general, the most primitive species of *Dicoma* appear to be those of southern Africa and Madagascar. Most of the species of the Horn of Africa form part of more advanced lineages resulting from radiation into more arid regions. *Dicoma sessiliflora* appears to form part of a lineage that underwent secondary adaptation to shadier, wetter sites.

If we accept Hoffman's (1893) division of *Dicoma* into eight sections, the species of the Horn of Africa fall into four sections: *Eudicoma* DC. (*Dimorphae* F. C. Wilson), *Hochstetteria* (DC.) O. Hoffm., *Psilocoma* Harv. (*Barbellatae* F. C. Wilson), and *Pterocoma* DC. (*Plumosae* F. C. Wilson), as detailed in Table 1. However, Hoffman's division of the genus does not appear to be a good reflection of phylogeny. A more useful approach might be to consider all species present in the Horn of Africa, except *D. sessiliflora*, as members of a single group.

DIAGNOSTIC CHARACTERS

In what follows, we discuss the principal diagnostic characters used in the systematics of *Dicoma*, and, in particular, those relevant to the species of the Horn of Africa.

Habit. *Dicoma* includes annual and perennial herbs, shrubs, and (Madagascar only) small trees. Some species, such as *D. aethiopica*, are variable in habit, with some individuals being annual herbs and others biennial or perennial. Other species, such as *D. sessiliflora*, are rootstock perennials. Some shrub species form dense cushions.

Stem. Gross stem morphology is of little diagnostic value: stems range from scarcely to highly branched, and the branches range from straight to highly twisted. Stem pubescence (or lack thereof) is a more useful character, ranging from glabrous or glabrescent to very densely tomentose, with interlaced, long, flexuose, simple hairs. Stem color ranges from greenish or stramineous to whitish or grayish white, or in some cases purplish.

Leaves. Leaf arrangement is always alternate, and spacing ranges from well separated to subfasciculate. Leaf shape ranges from linear to suborbicular, and the leaves may or may not be conduplicate. The leaf margin is generally entire or slightly serrate, and is in some cases highly revolute. A pseudopetiole may or may not be present. The leaf apex ranges from acute to obtuse, with or without a spine or a mucro. Leaf pubescence and color are generally similar to those of the stem, and leaves may be concolorous or discolorous, depending on whether the pubescence of the lower surface is markedly denser than that of the upper surface.

Capitulum. The capitulum has a variable number of subtending leaves. The shape and size of the involucre, ranging from narrow cylindrical to broadly campanulate, is useful for diagnosis.

The number of phyllaries and phyllary rows is also important, and whether the inner phyllaries are longer or shorter than the adjacent outer phyllaries is of particular value. The phyllaries can be erect, patent, or squarrose. Reflexed phyllaries are an important diagnostic characteristic, particularly in section *Pterocoma,* but *Dicoma* rarely has phyllaries of this type in the Horn of Africa (only the outermost phyllaries in *D. schimperi*). Phyllary shape is variable, ranging from linear or linear-lanceolate to deltate, while the apex may be acuminate or aristate. The phyllaries may be scarious at the margins or over their entire surface. The presence or absence of a conspicuous midrib is important. Pubescence ranges from glabrous to densely tomentose, and is generally similar to that of the stem and leaves.

Florets. The number of florets, which is of course related to capitulum size, shows great variation among species. The corolla may be white, cream, yellowish, violet, or lilac. The corolla lobes are recurved apically in all except one species in the Horn of Africa, and the veins along the edge may be slender and submarginal, or thick and marginal. The epidermis of the corolla shows either an "intestine-like" surface (i.e., a rugose pattern of longitudinal bands) or is slightly transversely undulate-striate or smooth. The indument is made up of short or long, twin, glandular hairs (see Karis et al., 1992: 418, figs. 4I, H, respectively).

The sizes of the different parts of the stamens and the shape of the anther appendages are likewise variable, but of little diagnostic value; the presence or absence of antrorse hairs on the tail apex is, however, important.

The most useful characteristics of the style are (a) the extent of the area occupied by sweeping hairs (hairs that brush the pollen through the anther tube for pollination), and (b) whether or not the basal sweeping hairs are longer than the rest.

Fruit. The achenes have (5–)8–10 prominent ribs, or are not conspicuously ribbed. The achene hairs are situated between the ribs or all around the achene; in the latter case, they have a conspicuous bulbous, glandular base. Most species have epidermal glands and superficial biseriate glands, always located between the ribs.

The testa may be of two types: the *Dicoma* type, with the external layer of the testa prosenchymatic and strengthened with ribs; or the *Gochnatia* type, with the lateral and basal walls of the testa epidermis strengthened and u-shaped in cross section (Grau, 1980).

The pappus may be isomorphic or dimorphic. In the latter case, there is an inner row of scales in addition to the various outer rows of bristles. In species in which the pappus is isomorphic, it may comprise a single row of about 10 rigid flattened bristles or bristle-like scales (as in *D. schimperi*), or several rows of bristles that may be either barbellate or plumose. In general, the number of pappus rows and the length of the pappus bristles are important diagnostic characters.

TAXONOMIC TREATMENT

Only synonyms relevant to species occurring in the Horn of Africa are included. Likewise, the genus description includes only those species present in the Horn of Africa.

Dicoma Cass., Bull. Sci. Soc. Philom. Paris 1817: 12. 1817. TYPE: *Dicoma tomentosa* Cass.

Hochstetteria DC., Prodr. 7: 287. 1838. TYPE: *Hochstetteria schimperi* DC.

Annual or perennial herbs and shrubs. Stem simple to branched, sericeous to lanate, the branches generally striate. Leaves alternate, often with a pseudopetiole, the margins entire to serrulate. Capitula obconic to campanulate, sessile or pedunculate, discoid and homogamous (or radiate and heterogamous outside the Horn of Africa), often with subtending leaves; phyllaries multiseriate, acuminate to aristate, coriaceous, sometimes with scarious margins. Receptacle alveolate; pits surrounded by a membrane, generally with an irregular margin; paleae absent. Corollas white, cream, yellowish, violet, or lilac, actinomorphic, deeply 5-lobed, with short-glandular or long-glandular twin hairs. Anthers with lanceolate, acute to acuminate apical appendages and long-tapering, retrorse-pilose tails. Style swollen at the base, the branches connivent, with obtuse apex and short, generally subapical, acute, sweeping hairs. Achenes obovoid to turbinate, with (5–)8–10 obscure to prominent ribs, often glutinous between the ribs, with ascending hispid hairs inserted between the ribs or all around the achene, the basal hairs shorter and spreading; testa of the *Dicoma* or *Gochnatia* type. Pappus of barbellate to plumose bristles arranged in several rows with or without one internal row of scales; in one species (*D. schimperi*) the pappus is only of scales arranged in one row.

KEY TO THE SPECIES OF *DICOMA* OCCURRING IN THE HORN OF AFRICA

1a. Pappus conspicuously dimorphic, with external capillary bristles and ca. 10 innermost scales.

2a. Shrub; leaves broadly elliptic to suborbicular, not conduplicate; phyllaries with short (0.2–0.5 mm) acuminate apex; achenes 1.3–1.5(–2.5) mm long .... 2. *D. bangueolensis*

2b. Annual herb; leaves linear-elliptic to linear-oblanceolate, often conduplicate; phyllaries with long (1–7 mm), acuminate-aristate apex; achenes 1.6–3 mm long .... 12. *D. tomentosa*

1b. Pappus isomorphic, made up solely of bristles, those of the innermost series sometimes somewhat broader toward the base.

3a. Pappus uniseriate, of ca. 10 rigid, flattened bristles .... 7. *D. schimperi*

3b. Pappus multiseriate, of more than 10 bristles.

4a. Phyllaries without median vein, the innermost shorter than the adjacent series; pappus of plumose bristles .... 9. *D. sessiliflora*

4b. Phyllaries with a conspicuous median vein, the innermost longer than the other series; pappus of barbellate bristles.

5a. Phyllaries squarrose.

6a. Phyllaries 35–70 per capitulum, pubescent; corolla ca. 5 mm long; achenes 2.7–3 mm long, narrowly turbinate; pappus of 60–70 bristles, 4.5–5.2 mm long .... 4. *D. hindiana*

6b. Phyllaries 100–140 per capitulum, glabrous; corolla ca. 9 mm long; achenes 1.5–2 mm long, broadly turbinate; pappus of 100–130 bristles, 7–9 mm long .... 10. *D. somalensis*

5b. Phyllaries not squarrose.

7a. Leaves linear-revolute, often with an apical spine.

8a. Branches twisted, forming dense whitish cushions; leaves often subfasciculate, 7–17 mm long, slightly curved; capitula sessile to subsessile, apex of the phyllaries acuminate, 0.2–1 mm long; pappus 3–5 mm long .... 5. *D. paivae*

8b. Branches erect, straight; leaves solitary, (5–)15–22(–26) mm long, straight; capitula on leafy peduncles, apex of the phyllaries acuminate, 1.2–3.5 mm long; pappus 6–7 mm long .... 11. *D. thuliniana*

7b. Leaves linear-elliptic to elliptic, oblanceolate or spathulate, with flat margins, without an apical spine.

9a. Annual or perennial herb; achenes 1.5–2.5 mm long; pappus 4–6 mm long.

10a. Leaves 15–90 × 2–17 mm; involucre 7–11 × 12–20 mm; corolla (5–)6.5–8.2 mm long; pappus of 40–100 bristles arranged in 3(–4) rows .... 1. *D. aethiopica*

10b. Leaves 15–25 × 2–3 mm; involucre 6–7 × 7–10 mm; corolla (4–)5 mm long; pappus of 25–40 bristles arranged in 1–2(–3) rows .... 6. *D. popeana*

9b. Shrub; achenes 2.8–3.7 mm long; pappus 6.5–7(–8) mm long.

11a. Leaves narrowly elliptic, 10–130 × 2–12.5 mm; involucre 13–15 × 22–23 mm, broadly campanulate; pappus of 100–120 bristles .... 3. *D. gillettii*

11b. Leaves squamiform, to 3 × 1 mm; involucre 6.5–8 × 3.8–5.5 mm, narrowly cylindric; pappus of 65–75 bristles .... 8. *D. scoparia*

1. **Dicoma aethiopica** S. Ortiz & Rodr. Oubiña, Nordic J. Bot. 16: 279. 1996. TYPE: Ethiopia. Bale: at the Sof Omar Caves, 6°55′N, 40°50′E, ca. 1400 m, 31 Oct. 1985, *Friis, Gilbert & Vollesen 3686* (holotype, K; isotype, ETH).

Annual or perennial herb to 40 cm high. Taproot slightly ramified. Stem ramified; the branches striate, greenish to purple, moderately grayish white-tomentose, with simple hairs and sessile to subsessile glands. Leaves 15–90 × 2–17 mm, linear-elliptic to oblanceolate, attenuate at base on a decurrent pseudopetiole 2–20 mm long; the margins serrulate, slightly callose; apex acute; both surfaces greenish to purple, rugose, slightly to moderately tomentose, with sessile glands in some cases on the upper surface slightly darker and slightly more glabrescent. Capitula numerous per plant, on erect-patent peduncles, 30–90 mm long, with 3–5(–8) subtending leaves; involucre 7–11 × 12–20 mm, campanulate, with 70–100 phyllaries arranged in 4–5(–6) rows, stramineous to purple, with a darker stripe on either side of the midrib, acuminate, pungent, glabrous to glabrescent, the margins entire to shortly serrulate principally toward the apical part; not scarious or with very narrow scarious margins; outermost phyllaries 3.5–4.5 × 0.7–0.8 mm, ovate-lanceolate, erect-patent, with an acuminate apex

1.5–2 mm long; middle phyllaries 6–8 × 1.2–1.5 mm, lanceolate, erect-patent, with an acuminate apex (3–)4–5 mm long; innermost phyllaries 9–11 × 1.5–1.7 mm, longer than the outer phyllaries and projected ca. 2 mm beyond the pappus or shorter than the pappus, oblong-lanceolate, erect, with an acuminate apex 1.2–3 mm long; receptacle concave, alveolate, pits surrounded by a membrane with an irregular dentate margin 1–1.3 mm high. Florets 15–25 per capitulum. Corolla (5–)6.5–8.2 × 1.8–3 mm, white, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 2.8–4.8 × 0.4–0.9 mm; lobes 3.3–3.5 × 0.4–0.5 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 0–2.5 mm beyond the corolla; filaments 1.3–2 mm long; collar 0.4–0.5 mm long; anthers 3.9–4.1 mm long; apical appendages ca. 1 mm long, conspicuously apiculate; anther tails 1.2–1.3 mm long, with retrorse hairs 0.2–0.4 mm long and some shorter antrorse hairs at the apex. Style 6.5–9 mm long, stylar branches 2.3 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.4 mm long, the basal ones longer than the others. Achenes 1.5–2.5 × 0.7–1.2 mm, turbinate, 10-ribbed, hispid, with ascending hairs 0.2–2.5 mm long, inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 40–80(–100) barbellate bristles arranged in 3(4) series, the innermost bristles broadened toward base, the longest bristles 4–6 mm long, the shortest ca. 1 mm long; barbellae 0.1–0.2 mm long.

Habitat and distribution (Fig. 1). Known only from Ethiopia, at 1400–1500 m. Limestone or granitic outcrops; dense to open *Acacia–Commiphora* bushland and open areas with *Combretum molle*, *Terminalia brownii*, etc. Endemic.

Additional specimens examined. ETHIOPIA. **Bale:** 13 km from Ginir on road to Robi via Sof Omar, 7°5′N, 40°48′E, 1500 m, *Gilbert, Ensermu & Vollesen 7870* (ETH, K, UPS). **Sidamo:** Bitata, 20 km from Negele on road to Kibre Mengist, 5°29′N, 39°28′E, 1450 m, *Gilbert, Ensermu & Vollesen 7781* (ETH, K, UPS).

The principal diagnostic characters of this species are its concolorous, generally rugose, elliptic to oblanceolate leaves with more or less long pseudopetioles, and the pappus of 40–100 barbellate bristles that are slightly broadened at the apex arranged in 3(–4) rows. In the Horn of Africa, the most closely related species is undoubtedly *D. popeana*, which has smaller leaves (15–25 × 2–3 mm), a smaller involucre (6–7 × 7–10 mm), and a smaller corolla ((4–)5 mm long), as well as fewer pappus bristles (< 40) arranged in 1–2(–3) rows. In the genus as a whole, the most similar species morphologically is *D. anomala* Sond., one of the most widely distributed species of the genus. This species can be distinguished from *D. aethiopica* by its sessile or short-pseudopetiolate leaves, these discolorous with the lower surface densely tomentose, and by the 7–12-mm-long pappus made up of more than 100 bristles that are conspicuously narrower at the apex.

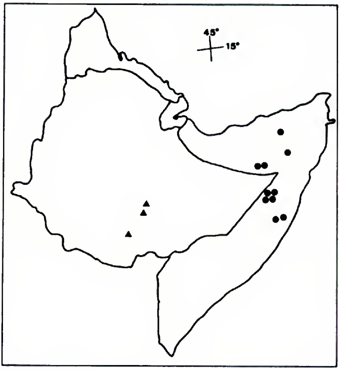

Figure 1. Distribution of *Dicoma aethiopica* (▲) and *D. bangueolensis* (●) in the Horn of Africa.

The color of dried *D. aethiopica* specimens shows great variability: some specimens (such as the holotype) are basically greenish to stramineous, while *Gilbert, Ensermu & Vollesen 7781* (K) exhibits a strong purplish coloration of the stem, leaves, and phyllaries.

2. **Dicoma bangueolensis** Buscal. & Muschl., Bot. Jahrb. Syst. 49: 514. 1913. TYPE: Somalia. Between Hobyo and Wuarandi and in Merehan, *Robecchi-Briquetti s.n.* (lectotype, designated by Ortiz & Rodríguez-Oubiña (1996), K).

Dicoma somalensis O. Hoffm. ex Engl., Sitzungsber. Königl. Preuss. Akad. Wiss. 1904: 371. 1904, nom. illeg., non S. Moore, 1899. TYPE: Somalia (without precise locality or collector; see Ortiz & Rodríguez-Oubiña, 1996).

Vernacular names. Darran (*Beckett 242*), Gedaad (*Kazmi, Celmi, Mahmund & Sulaiman 5*), Ghedhad, uadad (Cufodontis, 1967).

Shrub or shrublet to 60 cm high. Taproot slightly ramified. Stem often highly ramified; the branches nearly quadrangular in section, covered with a grayish white tomentum of simple hairs, especially on young branches, with sessile to subsessile glands. Leaves (6–)12–17(–23) × (3.5–)5–7(–10) mm, alternate, sometimes fasciculate, elliptic to broadly elliptic, sometimes suborbicular, with a pseudopetiole (1.5–)3–5(–8) mm long; the margins entire to denticulate; apex with a mucro up to 1 mm long; both surfaces with sessile glands, densely grayish white tomentose. Capitula numerous per plant, arranged in corymbiform synflorescences, on erect-patent peduncles 1–3(–9) mm long with linear bracts at the base, without subtending leaves; involucre 6–7(–9) × 4–6(–7) mm, obconic, with 20–30 phyllaries arranged in 4–5 rows, stramineous, with a darker stripe on either side of the midrib, acuminate, pungent, densely tomentose on the whole surface of the outer phyllaries and on the distal part of the median and innermost phyllaries, the margins shortly serrulate principally toward the apical part; outermost phyllaries 1–1.5(–2) × 0.5–0.7 mm, deltate, erect-patent, without acuminate apex, the margins not scarious; middle phyllaries 4–5 × 1–1.7 mm, deltate to oblong-lanceolate, erect, with an acuminate apex 0.2–0.3 mm long, the scarious margin 0.2–0.5 mm wide; innermost phyllaries 5–6 × 1.5–2(–2.5) mm, longer than outer phyllaries, projected 2–3(–4) mm less than the pappus, oblong-lanceolate, erect, with an acuminate apex 0.2–0.5 mm long, the scarious margin 0.3–0.8 mm wide; receptacle concave, alveolate, the pits surrounded by a membrane with a scarcely dentate margin 0.05–0.1 mm high. Florets 3–7 per capitulum, whitish pink. Corolla 7 × 1.5–1.7(–2) mm, purple or bluish, with epidermal cell surface "intestine-like" and glabrous or with short glandular twin hairs, especially toward the basal part; tube 2–3 × 0.4–0.6(–0.8) mm; lobes 4–4.5 × 0.4–0.5 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 0.7–1.5 mm beyond the corolla; filament 1.5–2 mm long; collar 0.2–0.5 mm long; anthers 4–5 mm long; apical appendages ca. 1.3 mm long, conspicuously apiculate or not apiculate; anther tails 1.2–1.5 mm long, with retrorse hairs ca. 0.3 mm long and 3–5 antrorse hairs at the apex. Style 6–7.5 mm long, stylar branches 1.3–1.7 mm long, with sweeping hairs forming a subapical ring covering a surface 0.4–0.7 mm long, the basal ones conspicuously longer than the others. Achenes 1.3–1.5(–2.5) × 0.8–1.7(–2.5) mm, turbinate, (8–)10-ribbed, hispid, covered with ascending, white hairs 0.2–2.5 mm long, these inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus dimorphic, of 110–130 barbellate bristles arranged in 2–3 external series, the longest bristles (5–)6.5–7.5 mm long, the shortest 1 mm long; barbellae ca. 0.05 mm long; ca. 10 scales arranged in a single internal series, these 5.5–6.5 × 0.5–0.8(–1) mm, barbellate toward the apex.

Habitat and distribution (Fig. 1). Known only from northeastern Somalia, at 130–1300 m. Principally on gypseous soils, but also on limestone soils, stony or not; in *Acacia–Commiphora* bushland. Endemic.

Additional specimens examined. SOMALIA. **Mudug**: 23 km E of Baxdo, 5°71′N, 47°26′E, 145 m, *Beckett 242* (FT, K); 6 km NW of Gaalkacyo, 6°49′N, 47°22′E, 300 m, *Beckett 397* (K); 23 km E of Baxdo on road to Hobyo, 5°48′N, 47°28′E, 130 m, *Gillett, Hemming & Watson 22381* (K); 8 km E of Bacaadweyn on road to Baardale, 7°09′N, 47°37′E, 360 m, *Gillett, Hemming & Watson 22028* (K); 1 km from Gaalkacyo toward Garoowe, *Kazmi, Celmi, Mahmund & Sulaiman 5* (FT); 10 km from Gaalkacyo along road to Belet Uen, 300 m, *Thulin 5635* (K, UPS); **Nugaal**: 1 mi. N of Laascaanood, 2400 ft., *Bally B10873* (K); ca. 8 km NE of Xalin on road to Qardho, 9°05′N, 48°41′E, 675 m, *Gillett & Beckett 23352* (K); 3 km E of Laascaanood, 8°25′N, 47°20′E, *Hansen & Heemstra 6322* (K); **Sanaag**: 10°37′N, 48°11′E, 1300 m, *Gillett & Watson 780* (K).

The principal distinguishing morphological characters of *Dicoma bangueolensis* are its concolorous densely grayish-tomentose, elliptic to broadly elliptic, sometimes suborbicular leaves, obconic involucres, and dimorphic pappus of 110–130 barbellate bristles in 2–3 rows with an inner row of 10 scales. In the Horn of Africa, *D. tomentosa* is the only other *Dicoma* species with a dimorphic pappus, of similar characteristics; however, this species is very different as regards habit, leaf morphology, and the size and morphology of its phyllaries and achenes. The only other *Dicoma* species with an obconic involucre is *D. dinteri* S. Moore (from Namibia); however, this species has linear leaves and an isomorphic pappus.

Wilson (1923) cited *D. bangueolensis* as a member of his section *Dimorphae*, characterized by a dimorphic pappus (though he stated that this species occurs in the Tanganyika region, as erroneously reported by Buscalioni & Müschler, 1913). Cufodontis (1967) reported this species from Somalia, probably on the basis of Volkens (1915), and also from Ethiopia, though we have yet to see a specimen from the latter country.

We have recently (Ortiz & Rodríguez-Oubiña, 1996a) resolved the nomenclatural problems and confusion arising from the erroneous reports of Buscalioni and Muschler (1913). In fact, all specimens of *D. bangueolensis* seen by us in the course of our herbarium studies of *Dicoma* had been incorrectly identified or left unidentified.

3. **Dicoma gillettii** Rodr. Oubiña & S. Ortiz, Bot. J. Linn. Soc. 119: 59. 1995. TYPE: Somalia. Shabeellaha Dhexe: 30 km S of Aadan Yabaal, 3°27′N, 46°12′E, 170 m, 6 June 1981, *Gillett & Beckett 23263* (holotype, K; isotype, UPS).

Shrub to 40 cm high, ramified; the branches striate, covered with a dense grayish white tomentum of simple hairs covered externally with a membranaceous pellicle, with sessile to subsessile glands. Leaves (10–)30–110(–130) × (2–)4–9(–12.5) mm, narrowly elliptic, attenuate at base and decurrent on a slightly stem-clasping pseudopetiole 7–25 mm long; the margins irregularly callose denticulate; apex acute; upper surface greenish, glabrous and covered with a membranaceous pellicle, with sessile glands; lower surface densely grayish white-tomentose, with sessile glands. Capitula several per plant, solitary on erect to erect-patent peduncles, 40–70 mm long, with 3–5 subtending leaves; involucre 13–15 × 22–23 mm, broadly campanulate, with 65–80 phyllaries arranged in 5–6 rows, stramineous, rigid, acuminate, pungent, scarcely tomentose to glabrescent, the margins shortly serrulate-fimbriate toward the basal part; outermost phyllaries 4–5 × 1.5–2 mm, ovate, widening sharply and becoming scarious in their basal third, patent to erect-patent, with an acuminate apex 3–5 mm long; middle phyllaries 10–12 × 2–2.5 mm, ovate-lanceolate, erect-patent, with an acuminate apex 2–3 mm long; innermost phyllaries 9–12 × 2–3 mm, longer than the outer phyllaries, as long as the pappus, lanceolate, erect to slightly patent, with an acuminate apex 0.5–1.5 mm long. Florets (25–)30–35 per capitulum. Corolla 9–12 × 1.2–2.5 mm, yellowish, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 5–6 × 0.7–1.5 mm; lobes 5–6 × 0.4–0.7 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 0.5–1 mm beyond the corolla; filaments 2–2.5 mm long; collar 0.5–0.7 mm long; anthers 5.8–6.5 mm long; apical appendages 1.5–2 mm long, conspicuously apiculate; anther tails 2.3–2.5 mm long, with retrorse hairs 0.3–0.5(–0.8) mm long and some shorter antrorse hairs at the apex. Style 9–11.5 mm long, stylar branches 2.5–2.7 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.3–0.7 mm long, the basal ones conspicuously longer than the others. Achenes 2.8–3.1 × 1.7–1.9 mm, turbinate, 8- to 10-ribbed, hispid, with ascending hairs 0.3–2 mm long, these inserted between the ribs in the basal ¾–⅘ of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 100–120 barbellate bristles arranged in 2–3(–4) series, the innermost bristles broadened toward the base, the longest bristles 7(–8) mm long, the shortest 0.1–0.5 mm long; barbellae 0.1–0.2 mm long.

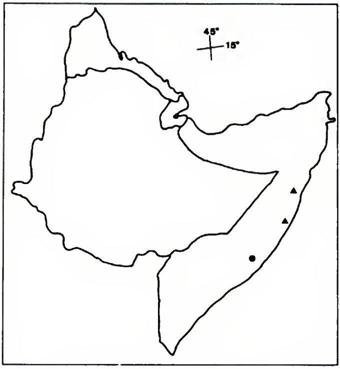

Figure 2. Distribution of *Dicoma gillettii* (●) and *D. hindiana* (▲) in the Horn of Africa.

Habitat and distribution (Fig. 2). Known only from the type locality, at ca. 170 m. On yellowish level sand; *Acacia–Commiphora* bushland. Endemic.

The most important distinguishing characteristics of *Dicoma gillettii* are the presence of a membranaceous pellicle entirely covering the tomentum of the stem, and the broadly campanulate involucre with the outermost phyllaries widening abruptly and becoming scarious in their basal third. None of the other *Dicoma* species of the Horn of Africa exhibit a close morphological relationship with *D. gillettii*. Considering the genus as a whole, *D. anomala* Sond. is somewhat similar in leaf morphology and the shape and size of the involucre. However, *D. anomala* lacks a membranaceous pellicle covering the tomentum of the stem, and has considerably fewer phyllaries. Furthermore, the outermost phyllaries are deltate-lanceolate, without the widened, scarious, basal third that characterizes *D. gillettii*.

4. **Dicoma hindiana** S. Ortiz & Rodr. Oubiña ("hidana"), Nordic J. Bot. 15: 187. 1995. TYPE: Somalia. Mudug: near Hobyo, 14 Oct. 1912, *Drake-Brockmann 960* (holotype, K).

Shrub to 30 cm high. Taproot slightly ramified. Stem ramified; the branches striate, moderately grayish white-tomentose, with simple hairs, with sessile to subsessile glands, often with glabrescent to glabrous areas. Leaves (2–)8–18(–19) × (1.2–)2–5(–7) mm, elliptic to obovate, attenuate at base and decurrent on a pseudopetiole 0.5–4 mm long; the margins serrulate, often somewhat revolute; apex mucronate; upper surface greenish, tomentose, with sessile glands; lower surface generally densely grayish white-tomentose, with sessile glands. Capitula numerous per plant, 1–5 arranged in lax subcorymbose synflorescences, on erect-patent peduncles, 3–30 mm long, with 1–3(–4) subtending leaves; involucre 7–9 × 7–13 mm, campanulate, with (35–)45–60(–70) phyllaries arranged in (4–)5–7 rows, stramineous, with a darker stripe on either side of the midrib, acuminate-pungent, slightly tomentose, especially in the apical third, the margins entire to shortly serrulate-ciliolate principally toward the apical part, not scarious; outermost phyllaries 1–1.5 × 0.5–0.7 mm, deltate to ovate, erect-patent; middle phyllaries 2.5–4 × 0.7–1 mm, lanceolate, squarrose, with an acuminate-aristate apex 0.2–0.6 mm long; innermost phyllaries 5.5–7(–8) × 0.7–1.1 mm, longer than the outer phyllaries and projected (0–)1.5–3(–4) mm beyond the pappus, lanceolate to oblong-lanceolate, squarrose, with an acuminate apex 0.5–1 mm long; receptacle concave, alveolate, the pits surrounded by a membrane with irregular denticulate margin 0.2–0.3 mm high. Florets 10–17 per capitulum. Corolla 5 × 1.6 mm, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 1–1.5 × 0.6–1 mm; lobes 2.5–3 × 0.4 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 1 mm beyond the corolla; filaments ca. 1 mm long; collar 0.4 mm long; anthers 3.2–4 mm long; apical appendages ca. 1 mm long, conspicuously apiculate; anther tails 1 mm long, with retrorse hairs 0.2–0.4 mm long and some shorter antrorse hairs at the apex. Style 4.8–5 mm long, stylar branches 1.3 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.2–0.3 mm long, the basal ones conspicuously longer than the others. Achenes 2.7–3 × 0.8 mm, turbinate, 10-ribbed, hispid, with ascending hairs 0.3–1.5 mm long, these inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 60–70 barbellate bristles arranged in 4–5 series, stramineous, the innermost bristles broadened toward the base, the longest bristles 4.5–5.2 mm long, the shortest 0.2–0.3 mm long; barbellae 0.05 mm long.

Distribution (Fig. 2). Known only from Mudug province in Somalia at ca. 90 m. Endemic.

Additional specimen examined. SOMALIA. **Mudug:** on road to Hobyo, 48 km S of Jirriiban, 90 m, *Gillett, Hemming & Watson 22104* (K).

The principal diagnostic characteristics of *Dicoma hindiana* are its squarrose phyllaries, narrowly turbinate achenes, and pappus of 60–70 barbellate bristles, these 4.5–5.2 mm long. The most morphologically similar species in the Horn of Africa is *D. somalensis*; indeed, all of the specimens of *D. hindiana* at K were labeled as *D. somalensis*. However, there are clear morphological differences between the two taxa. *Dicoma somalensis* has more phyllaries per capitulum ((100–)120–140); these are glabrous, and the innermost are erect. Furthermore, *D. somalensis* has a longer corolla (ca. 9 mm), shorter (1.5–2 mm), broadly turbinate achenes, and longer (7–9 mm) and more numerous (100–130) pappus bristles. Considering *Dicoma* as a whole, the only other species with consistently squarrose phyllaries as in *D. hindiana* and *D. somalensis* is *D. squarrosa* Wild, endemic to Angola (though some of the outermost phyllaries may be squarrose in some specimens of *D. anomala*). However, *D. squarrosa* can be clearly distinguished from *D. hindiana* by its elliptical leaves up to 50 mm long and its dimorphic pappus with both bristles and five broadly alate inner setae.

Note that we here use the epithet "hindiana," despite having originally described this species as "hindana"; this change is in accordance with the spelling recorded in *Index Kewensis* (Davies, 1996: 95).

5. **Dicoma paivae** S. Ortiz & Rodr. Oubiña, Canad. J. Bot. 72: 1478. 1994. TYPE: Somalia. Nugaal: about 80 km N of Eyl, 8°30′N, 50°7′E, 110 m, 11 June 1981, *Gillett & Watson 23375* (holotype, K).

Woody perennial, highly ramified; old branches very thick, twisted, forming cushions, young branches striate, covered with a whitish tomentum of simple hairs, old branches glabrous to glabrescent, without or with very scarce sessile to subsessile glands. Leaves sessile, subfasciculate, 7–17 × 0.7–1 mm, linear, slightly curved; leaf margins revolute, entire; apex with a short spine 0.5–0.8 mm

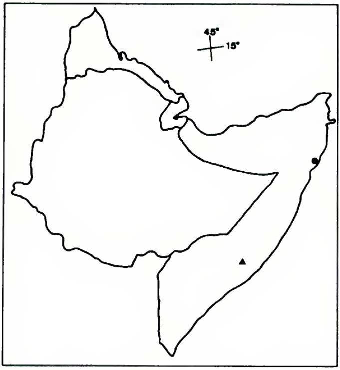

Figure 3. Distribution of *Dicoma paivae* (●) and *D. popeana* (▲) in the Horn of Africa.

long; both surfaces densely whitish-tomentose. Capitula numerous per plant, solitary, sessile or subsessile on up to 10-mm-long peduncles, with 1–3 subtending leaves; involucre 6–6.5 × 3–4 mm, obconic-campanulate, with 25–30 phyllaries arranged in 5–6 rows, stramineous, with a darker stripe on either side of the midrib, rigid, slightly acuminate, pungent, tomentose, the margins entire to shortly serrulate principally toward the apical part, not scarious or with a very narrow scarious border; outermost phyllaries 0.8–1 × 0.4–0.5 mm, deltate, patent to erect-patent, with an acuminate apex 0.2–0.3 mm long; middle phyllaries 3 × 1.3 mm, deltate-lanceolate, erect-patent, with an acuminate-aristate apex 0.5–0.7 mm long; innermost phyllaries 4–5 × 1.2–1.5 mm, longer than the outer phyllaries and shorter than the pappus, deltate-lanceolate, erect, with an acuminate-aristate apex 0.7–1 mm long. Florets unknown. Achenes 1.5–1.6 × 1–1.2 mm, turbinate, 8- to 10-ribbed, hispid, with ascending hairs 0.5–2 mm long, these inserted between the ribs from the base to near the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 80–100 barbellate bristles arranged in 3–5 series, the innermost bristles broadened toward base, 0.1–0.5 mm wide, the longest bristles 3–5.5 mm long, the shortest 1–1.5 mm long, barbellae 0.05–0.1 mm long.

Habitat and distribution (Fig. 3). Known only from the type locality at ca. 110 m. Low gypseous limestone ridges, very stony and windswept; common with prostrate species of *Commiphora, Caesalpinia, Ochradenus, Acacia,* and cushions of *Oldenlandia saxifragoides.* Endemic.

The most important distinguishing characteristics of *Dicoma paivae* are its twisted branches forming dense white cushions, frequently subfasciculate, linear-revolute, slightly recurved leaves with an apical spine, and sessile or subsessile capitula. The most similar species in the Horn of Africa is *D. thuliniana,* which can be distinguished from *D. paivae* by its erect, straight branches, straight, solitary leaves longer ((5–)15–22(–26) mm) than those of *D. paivae,* long, leafy capitular peduncles, and longer pappus (6–7 mm). In the genus as a whole, *D. cana* Balf. f., from Socotra, shows some similarities to *D. paivae,* particularly in leaf morphology and general habit (it likewise forms dense, white cushions). However, the capitula of the former species are very different: all phyllaries lack a midrib, the outer phyllaries have a long, acuminate-aristate, patent apex, and the inner phyllaries are white and membranaceous-papery (Ortiz & Rodríguez-Oubiña, 1994).

6. **Dicoma popeana** S. Ortiz & Rodr. Oubiña, Nordic J. Bot. 16: 277. 1996. TYPE: Somalia. Hiiraan: 12 km from Ceel Baraf, 3°21′N, 45°49.5′E, 190 m, 14 Dec. 1987, *Kuchar 17653* (holotype, K; isotype, UPS).

Vernacular name. Reexaan (*Kuchar 17653*).

Annual herb to 25 cm high. Taproot slender, slightly ramified. Stem highly ramified; the branches quadrangular in transverse section, moderately grayish white-tomentose, with simple hairs and sessile to subsessile glands. Leaves 15–25 × 2–3 mm, linear-elliptic, attenuate at base on a pseudopetiole 2–4(–5) mm long; the margins serrulate; apex with a mucro 0.2–0.5 mm long; both surfaces greenish, rugose, slightly to moderately tomentose, in some cases the upper surface slightly darker and slightly more glabrescent. Capitula numerous per plant, on erect-patent peduncles, 10–30 mm long, with 3–5 subtending leaves; involucre 6–7 × 7–10 mm, campanulate to broadly cylindrical, with 40–60 phyllaries arranged in 4–5 rows, stramineous, with a darker greenish to brownish stripe on either side of the midrib, acuminate, pungent, glabrescent to slightly tomentose, minutely strigulose, the margins entire to shortly serrulate toward the apical part; outermost phyllaries 2.5–4 × 0.4–0.7 mm, lanceolate, erect-patent, with an acuminate apex 0.7–2 mm long; middle phyllaries 6–7 × 1–1.3 mm, oblong-lanceolate, erect-patent, with an acuminate apex 1.5–2 mm long; innermost phyllaries 6.5–7.5

× 1–1.4 mm, longer than the outer phyllaries and projected 0–1.5 mm beyond the pappus, oblong-lanceolate, erect, with an acuminate-aristate apex 1–1.7(–2) mm long, and a scarious margin 0–0.4 mm wide; receptacle concave to flat, alveolate, the pits surrounded by a membrane with a very irregular dentate margin 1.5–2 mm high. Florets 8–12 per capitulum. Corolla (4–)5 × 1.2–1.5 mm, yellowish, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 2.2–2.5 × 0.3–0.4 mm; lobes 2.8–3.5 × 0.4–0.5 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 0–1 mm beyond the corolla; filaments 1–1.1 mm long; collar 0.3–0.5 mm long; anthers 3.3–3.6 mm long; apical appendages ca. 1 mm long, not conspicuously apiculate; anther tails 1 mm long, with retrorse hairs 0.3 mm long and some shorter antrorse hairs at the apex. Style 4.6–6 mm long, stylar branches 1.3–1.5 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.2–0.3 mm long, the basal ones conspicuously longer than the others. Achenes 1.5–2 × 1 mm, turbinate, 10-ribbed, hispid with ascending hairs 0.2–1.8(–2.5) mm long, these inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 25–40 barbellate bristles arranged in 1–2(–3) series, the longest bristles 4–5 mm long, the shortest ca. 1 mm long; barbellae 0.15–0.2 mm long.

Habitat and distribution (Fig. 3). Known only from the type locality, at 190 m. In gently rolling orange sandhills; bushland with *Commiphora* cf. *velutina* and *Indigofera ruspolii.* Endemic.

The principal distinguishing characteristics of *Dicoma popeana* are its concolorous, generally rugose, linear-elliptic leaves with a more or less long pseudopetiole and a pappus of 25–40 barbellate bristles, broadened slightly at the apex and arranged in 1–2(–3) rows. The most morphologically similar species in the Horn of Africa is *D. aethiopica*; in the latter species, however, the leaves (15–90 × 2–17 mm), involucre (7–11 × 12–20 mm), and corolla ((5–)6.5–8.2 mm long) are all larger, and the pappus comprises 40–100 bristles arranged in 3(–4) rows. Considering the genus as a whole, the most similar species is *D. anomala* Sond., which differs from *D. popeana* in the same ways as *D. aethiopica.*

7. **Dicoma schimperi** (DC.) Baill. ex O. Hoffm., in Engl. & Prantl, Nat. Pflanzenfam. 4(5): 339. 1893. *Hochstetteria schimperi* DC., Prodr. 7: 287. 1838. TYPE: Saudi Arabia. "In Montibus ad Vallem Fatmensem," *Schimper 864* (holotype, G).

Annual herb to 45 cm high. Taproot slightly ramified. Stem scarcely to highly ramified; the branches striate, glabrous to densely grayish white-tomentose, tomentum of simple hairs, with sessile to subsessile glands. Leaves (8–)15–50 × (2–)5–16(–18) mm, elliptic-lanceolate to broadly ovate or suborbicular, with a pseudopetiole (2–)4–8(–15) mm long and auricles at the base; the margins serrulate, with teeth bulbous or not; apex with a 0.3–1 × 0.2–1-mm mucro; both surfaces green to grayish white, glabrous to densely tomentose, with sessile glands. Capitula numerous per plant, generally solitary or 2–12 in lax corymbiform synflorescences, on erect-patent peduncles, 0.5–10 cm long, with 1–4 subtending leaves; involucre (4–)5–12(–13) × (10–)15–20(–23) mm, obconic-campanulate, with 40–70(–100) phyllaries arranged in 4–5(–6) rows, linear-deltate, stramineous to whitish colored, with a greenish stripe on either side of the midrib, rigid, with an acuminate apex 0.5–1 mm long, pungent, glabrescent to densely tomentose, with broadly scarious margins 0.2–0.5 mm wide, serrulate principally toward the apical part; the outermost phyllaries 2–5 × 0.3–1 mm, patent to reflexed, the margins not scarious; the middle phyllaries (3–)5–7(–9) × 0.5–1(–1.3) mm, erect-patent; innermost phyllaries 8–11 × 1–1.5 mm, erect, longer than the outer phyllaries and projected 2–4 mm beyond the pappus, all of the phyllaries becoming reflexed when the achenes are ripe; receptacle flat, alveolate, the pits surrounded by a membrane with a highly irregular dentate to fimbriate margin 0.2–0.3 mm high. Florets (10–)20–40(–50) per capitulum. Corolla 5.5–9 × 0.5–2(–2.5) mm, greenish yellow or greenish white to bluish, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 2.6–5.5 × 0.4–1 mm; lobes 2.8–3.7 × 0.5 mm, becoming recurved, with thin slender submarginal veins. Stamens exserted for 0.5–1.5(–2.2) mm beyond the corolla; filament 0.8–2.5 mm long; collar 0.4–0.5 mm long; anthers 3.4–4.7 mm long; apical appendages ca. 1–1.7 mm long, apiculate; anther tails 1–1.3 mm long, with retrorse hairs 0.3–0.5 mm long and some shorter antrorse hairs at the apex. Style 5–8.3 mm long, the branches 1–1.5 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.4–0.6 mm long, the basal ones longer than the others. Achenes 1.5–2.5 × 1–2.2 mm, turbinate, (8–)10(–12)-ribbed, hispid, with ascending hairs 0.3–2 mm long, inserted between the ribs from the base to near the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of (4–)8–10(–11) rigid, barbellate bristles, broadened toward base (or bristlelike

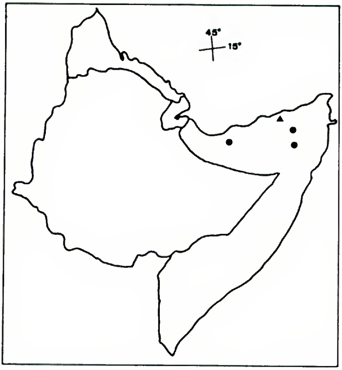

Figure 4. Distribution of *Dicoma schimperi* in the Horn of Africa: *D. schimperi* subsp. *schimperi* (●). D. *schimperi* subsp. *cinerea* (▲).

scales), arranged in one series, each bristle (4–)5–7 × 0.2–0.5(0.6) mm.

The most characteristic feature of *Dicoma schimperi* is its pappus, comprising (4–)8–10(–11) rigid, flattened bristles (or scales). Other characters worthy of note are its phyllaries, which become reflexed when the achenes are ripe, and the relatively narrow depressions between the ribs of the achenes. Most other characters show considerable intraspecific variation. No other species of *Dicoma* shows particular morphological similarities with *D. schimperi.*

Some authors, such as Cabrera (1977), have considered the above-mentioned characters, particularly those relating to pappus morphology, to be sufficient grounds for placing this taxon in a separate genus, namely the monotypic *Hochstetteria.* Nevertheless, more recent treatments (Hansen, 1991; Bremer, 1994) have maintained *Hochstetteria* as a synonym of *Dicoma,* in accordance with Hoffman (1893), who considered *Hochstetteria* as a section of *Dicoma.*

Cufodontis (1967) cited *D. schimperi* from Ethiopia, though we have not seen any specimens of this taxon from that country.

Habitat and distribution (Fig. 4). In the Horn of Africa, known only from Djibouti (Audru et al., 1994) and the north of Somalia at 714–2000 m. Principally in gypseous and limestone soils; in *Acacia–Commiphora* bushland. Djibouti, Egypt, Sudan, Somalia, and the Arabian Peninsula.

In our description of *Dicoma cinerea* (Ortiz & Rodríguez-Oubiña, 1994), we stated that it was closely related to *D. schimperi.* Subsequently, however, we have become aware of the existence of intermediate specimens [Yemen. Hadhramaut, *Popov GPH610* (BM), 11 Dec. 1947, *Thesiger s.n.* (BM)], suggesting that *D. cinerea* should be considered a subspecies or variety of *D. schimperi.* We favor the subspecies option, since *D. schimperi* consistently exhibits a number of distinctive features (glabrous or glabrescent stems, leaves, and phyllaries; elliptic-lanceolate leaves with non-pustulate teeth; etc.) throughout its geographic range (Djibouti, Egypt, Sudan, Somalia, and the Arabian Peninsula). Individuals that deviate from this pattern are found only in two small areas, in the northeast of its range in the Horn of Africa (see Fig. 4), and in the region of Hadhramaut in Yemen. These two areas were contiguous until their separation at the end of the Miocene (Mattauer, 1967), by which time the Asteraceae were already fully differentiated (Graham, 1996). Individuals of *D. schimperi* from Hadhramaut are densely tomentose and have some ovate leaves, and appear to be intermediate between this taxon and *D. cinerea.* In our opinion, the treatment of *D. cinerea* at subspecies rank is justified purely by the geographic distribution of the two taxa. In addition, the specimens from northeastern Somalia that we described as *D. cinerea* are sharply defined by their densely tomentose stems, leaves, and phyllaries, and broadly ovate to suborbicular leaves with pustulate teeth.

KEY TO THE SUBSPECIES OF *DICOMA SCHIMPERI*

1a. Plants glabrous or glabrescent; leaves elliptic-lanceolate with non-pustulate teeth; apical mucro 0.3–0.5 × 0.2–0.3 mm .... *D. schimperi* subsp. *schimperi*

1b. Plants densely tomentose; leaves broadly ovate to suborbicular with pustulate teeth; apical mucro 0.5–1 × 0.3–1 mm .... *D. schimperi* subsp. *cinerea*

7a. **Dicoma schimperi** subsp. **schimperi**

Plant glabrous to glabrescent. Leaves (8–)15–50 × (2–)5–13(–18) mm, elliptic-lanceolate; leaf margins serrulate, with non-pustulate teeth and an apical mucro 0.3–5 × 0.2–0.3 mm; both surfaces greenish, glabrous to glabrescent. Involucre with (40–)70–100 phyllaries, glabrous to glabrescent. Corolla 5.5–9 mm long. Achenes 1.8–2.5 × 1.2–1.8 mm; pappus of (5–)9–10 bristles, 4–5 mm long.

Habitat and distribution (Fig. 4). In the Horn of Africa, known only from Djibouti (Audru et al., 1994) and the north of Somalia at 714–1000 m.

Principally in gypseous and limestone soils, stony or not; in *Acacia–Commiphora* bushland. Djibouti, Egypt, Sudan, Somalia, and the Arabian Peninsula.

Specimens examined. SOMALIA. Without exact locality: Goda, 1000 m, *Chedeville 411* (FT), *518* (FT). **Bari:** 3 km below Galgallo on road to Boosaaso, *Bally & Melville 15857* (K); Gardo, 9°32′N, 49°07′E, 714 m, *Gillett 23405* (K). **Togdheer**: Wagga Mountain, 1897, *Lort Phillips s.n.* (BM, K).

7b. Dicoma schimperi subsp. **cinerea** (S. Ortiz & Rodr. Oubiña) S. Ortiz & Rodr. Oubiña, comb. nov. Basionym: *Dicoma cinerea* S. Ortiz & Rodr. Oubiña, Canad. J. Bot. 72: 1479. 1994. TYPE: Somalia. Sanaag: Einand, 11°02′N, 48°55′E, 2000 m, 21 Aug. 1957, *Newbould 1013* (holotype, K).

Plant densely tomentose. Leaves 5–10 × 6–16 mm, broadly ovate to suborbicular; leaf margins serrulate, with pustulate teeth and an apical mucro 0.5–1 × 0.3–1 mm; both surfaces grayish white, densely tomentose. Involucre with 40–60 phyllaries, densely tomentose. Corolla 7.5–7.7 mm long. Achenes 1.5–2.5 × 1–2 mm. Pappus of (4–)8–10(–11) bristles, 4–7 mm long.

Habitat and distribution (Fig. 4). Known only from the type locality in the north of Somalia at ca. 2000 m. Limestone scree and boulders. Endemic? There are morphologically intermediate specimens between this subspecies and subspecies *schimperi* in the Arabian Peninsula.

8. Dicoma scoparia Rodr. Oubiña & S. Ortiz, Bot. J. Linn. Soc. 119: 61. 1995. TYPE: Somalia. Mudug: Central Massif, about 18 km from the sea, 6°01′N, 48°47′E, 35 m, 27 May 1989, *Gillett, Hemming & Watson 22175* (holotype, K).

Shrub to 25 cm high. Taproot slightly ramified. Stem highly ramified; the branches striate, with a grayish white tomentum of simple hairs, principally along the grooves. Leaves (0.8–)1.1–1.9(–3.1) × 0.5–0.9(–1) mm, sessile, deltoid to spathulate; the margins entire; apex acute; upper surface greenish, glabrous to tomentose; lower surface greenish, glabrous, with 3 conspicuous veins. Capitula numerous per plant, solitary or two on erect to erect-patent peduncles 6–50 mm long, with 1–2 subtending leaves; involucre 6.5–8 × (3.8–)4–4.5(–5.5) mm, narrowly cylindric, with 20–30 phyllaries arranged in 5–6 rows, stramineous, with a broad greenish stripe on either side of the midrib and brownish purple at the apex, rigid, acuminate, pungent, glabrous to scarcely tomentose, the margins entire to shortly serrulate-fimbriate, principally toward the apical part, not scarious or with very narrow scarious margins; the outermost phyllaries 0.5–1.5 × 0.8–1.5 mm, broadly deltate, patent to erect-patent; middle phyllaries 3–4 × 1.3–1.5 mm, deltate-lanceolate, erect, with an acuminate-aristate apex 0.2–0.3(–0.5) mm long; innermost phyllaries 5–5.5(–6) × (1.3–)1.5–1.7(–1.9) mm, longer than the outer phyllaries and 3–4(–5) mm shorter than the pappus, oblong-lanceolate, erect, with an acuminate-aristate apex 0.4–0.5(–0.6) mm long, the scarious margin 0–0.1 mm wide; receptacle concave, alveolate, the pits surrounded by a membrane with an irregular dentate margin 0.2–0.5 mm high. Florets 5–7 per capitulum. Corolla 6.5 × 1.5 mm, pale lilac to purple, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 2.5–3 × 0.4–1 mm; lobes 3–3.8 × 0.5–0.6 mm, becoming recurved, with slender, submarginal veins. Stamens exserted for 1–1.5 mm beyond the corolla; filaments 2 mm long; collar 0.5–0.6 mm long; anthers 3.9–4.2 mm long; apical appendages ca. 1 mm long, conspicuously long apiculate; anther tails 1.3–1.5 mm long, with retrorse hairs 0.4–0.6 mm long and some shorter antrorse hairs at the apex. Style 7–7.5 mm long, stylar branches 1–1.1(–1.2) mm long, with sweeping hairs forming a subapical ring, covering a surface 0.4 mm long, the basal ones slightly longer than the others. Achenes 3.5–3.7 × 1 mm, turbinate, 10-ribbed, hispid with ascending hairs (0.3–)0.4–2 mm long, these inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 65–75 barbellate bristles arranged in 3–4 series, the innermost bristles broadened toward the base, the longest bristles 6.5–7 mm long, the shortest bristles 0.3–0.5 mm long; barbellae 0.1–0.15 mm long.

Habitat and distribution (Fig. 5). Known only from the Mudug region near the sea at 35–200 m. Limestone; low grassy vegetation. Endemic.

Additional specimen examined. SOMALIA. **Mudug**: E of Gawen, ca. 3 km on road from Hobyo to Wisil, 150–200 m, *Thulin & Abdi Dahir 6620* (K).

Dicoma scoparia is one of the most morphologically distinctive of all species of the genus. Important characters include the very small (generally less than 2 mm long), deltate to spathulate leaves with three longitudinal nerves, and the one or two long-pedunculate capitula with narrowly cylindrical involucres conspicuously overtopped (by (3–)4–5 mm) by the pappus. The achenes (3.5–3.7 × 1 mm) are turbinate, but considerably narrower than is

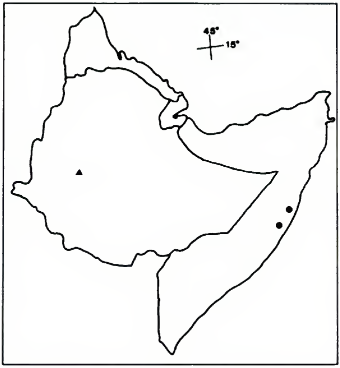

Figure 5. Distribution of *Dicoma scoparia* (●) and *D. sessiliflora* subsp. *stenophylla* (▲) in the Horn of Africa.

typical for the genus. No other species of *Dicoma* shows particular similarities with *D. scoparia.*

9. **Dicoma sessiliflora** Harv. subsp. **stenophylla** G. V. Pope, Kew Bull. 46: 701. 1991. TYPE: Nigeria. Lokoja, Mt. Patti, *Dalziel 33* (holotype, K).

Perennial herb to 95 cm high, from woody rootstock. Stems annual, simple, solitary, with 4–6 sides in transverse section, covered with a tomentum of long, mixed, grayish white, simple hairs which form a sheath around the stem, with sessile to subsessile glands, often with glabrous to glabrescent areas. Leaves 110–130 × 15–37 mm, elliptic to oblanceolate, sessile to subsessile; the margins sparsely serrulate; apex acute to subobtuse; upper surface green, glabrous to glabrescent; lower surface with sessile to subsessile glands, densely grayish white-tomentose. Capitula solitary, terminal (in the sole specimen known from the Horn of Africa) or few per plant, sessile (in this specimen) or short-stalked, with 0–1 subtending leaf; involucre 33 × 33 mm, obconic-campanulate, with 100–120 phyllaries arranged in 10–12 rows, greenish-stramineous, rigid, acuminate, pungent, glabrous; the margins slightly revolute, entire to shortly serrulate principally toward the apical part, with an acuminate apex 1–1.5 mm long; outermost phyllaries 6.5–7 × 2.3–2.5 mm, deltate, patent to erect-patent, the margins not scarious; middle phyllaries 20–23 × 3–5 mm, lanceolate, erect to erect-patent, the scarious margin 0–1 mm wide; innermost phyllaries 18–20 × 4–5 mm, shorter than the adjacent outer phyllaries, as long as the pappus, lorate, erect, white scarious; longest phyllaries projected (3–)5–10(–15) mm beyond the pappus; receptacle concave, alveolate, the pits surrounded by a membrane with an irregular dentate-fimbriate margin 1–2 mm high. Florets 30–50(–65) per capitulum. Corolla 9.3–9.6 × 1.5–1.6 mm, yellowish, with epidermal cell surface slightly transversely undulate-striate to smooth and long glandular twin hairs; tube 3–4 × 0.6–1.2 mm; lobes 6 × 0.5–0.6 mm, straight, with thick marginal veins. Stamens little or not exserted; filaments 1.5–2.5 mm long; collar 1 mm long; anthers 8.5–9 mm long; apical appendages ca. 1.7–2 mm long, not apiculate; anther tails 4.5–4.6 mm long, with retrorse hairs 0.3–0.5 mm and without antrorse hairs at the apex. Style 9–9.1 mm long, stylar branches 2.2–3 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.5 mm long, all the sweeping hairs of a similar length. Achenes (immature) 3 × 2–2.5 mm, obovoid, not conspicuously ribbed, hispid, with ascending hairs 0.3–4(–5) mm long, with a bulbous, glandular base, inserted all around the achene from its base to near its top; without epidermal glands and superficial biseriate glands; testa of *Gochnatia* type, with lateral and basal walls of the testa epidermis strengthened, u-shaped in cross section; pappus isomorphic, of 70–80(–90) plumose bristles arranged in 3–4 series, the longest bristles 9–10 mm long, the shortest 2–3 mm long; plumose barbellae 0.5–1 mm long.

Habitat and distribution (Fig. 5). Known from Ethiopia from only one locality, at 1500 m. Savanna. Senegal, Guinea Bissau, Ghana, Togo, Nigeria, Central African Republic (Pope, 1991), Sudan, Ethiopia, and Uganda.

Specimen examined. ETHIOPIA. **Welega:** Neke'mte, near bridge crossing Didessa river, 1500 m, *W. J. J. O. de Wilde 8941* (K).

The principal diagnostic characters of *Dicoma sessiliflora* subsp. *stenophylla* include its elliptic to oblanceolate leaves, very large by comparison with those of other species of our area (110–130 × 15–37 mm), together with its very large involucres (33 × 33 mm in the single capitulum examined), phyllaries without a midrib, white, scarious innermost phyllaries shorter than the adjacent outer phyllaries, florets with straight corolla lobes, slightly transversely undulate-striate to smooth epidermal cell surfaces, long anthers (8.5–9 mm), anther tails without apical antrorse hairs, stylar sweeping hairs of uniform length, achenes not conspicuously ribbed, without epidermal glands or superficial biseriate glands and with hairs with a bulbous, glandular base inserted all around the achene, *Gochnatia*-type testa, and pappus of plumose hairs. Most of these characters are shared with other species of section *Pterocoma*, all of which have very similar morphology; differentiation is largely on the basis of vegetative characters, particularly leaf morphology (see Pope, 1991). Of the taxa of this section, the most similar to *D. sessiliflora* subsp. *stenophylla* is obviously *D. sessiliflora* subsp. *sessiliflora*; however, this taxon has phyllaries with a conspicuously scarious border, while the outermost phyllaries are reflexed. *Dicoma elliptica* Pope is very close to *D. sessiliflora*, and can be differentiated from *D. sessiliflora* subsp. *stenophylla* by the same characters that distinguish subspecies *stenophylla*; in addition, its leaves are generally linear-elliptic and subcoriaceous with a conspicuously revolute margin (see Pope, 1991).

We know of only one sheet of *Dicoma sessiliflora* subsp. *stenophylla* from Ethiopia, though one of us (Mesfin Tadesse) considers that it is probably not uncommon there. Pope (1991) did not cite this subspecies from Sudan, Ethiopia, or Uganda.

The single Ethiopian specimen has only one capitulum and this is immature, so it was not possible to assess the relative length of the pappus ensemble, the shape of the receptacle pits, the number of florets per capitulum, etc., without damaging the specimen. These data were thus evaluated from specimens from other countries.

10. Dicoma somalensis S. Moore, J. Bot. 37: 60. 1899. TYPE: Somalia. Togdheer: Wagga Mountain, above Upper Shiikh, 6000 ft., 1 Feb. 1897, *Lort Phillips s.n.* (holotype, BM; isotype, K). Figure 6.

Vernacular names. Adah (*Gillett 4002*), Gundre (*Godding 87*), Ma-adadi (*Gillett 4620*, Cufodontis (1967)), Bastireh (*Drake-Brockmann s.n.*).

Shrub 50 cm high, highly ramified; the branches striate, glabrescent or covered with a grayish white tomentum of simple hairs, with sessile to subsessile glands. Leaves (3–)8–20(–30) × (0.8–)1–1.5(–2.5) mm, linear to linear-oblanceolate, attenuate at base and decurrent on a pseudopetiole 0–2(–3) mm long; the margins somewhat revolute, scarcely serrulate to the apical part; apex mucronate; upper surface green, glabrescent to tomentose, rugose, with sessile glands; lower surface generally densely grayish white-tomentose, without sessile glands. Capitula numerous per plant, on peduncles erect to erect-patent, 2–10 cm long, normally without subtending leaves; involucre 5–13 × (10–)15–20 mm, broadly campanulate, with (100–)120–140 phyllaries, these mainly squarrose, arranged in 6–8(–10) rows, stramineous, with a darker stripe on either side of the midrib, acuminate-pungent, glabrous, minutely strigose, the margins entire to shortly ciliolate or fimbriate principally toward the apical part; outermost phyllaries 1.5–2 × 1 mm, deltate, patent to erect-patent, with an acuminate apex ca. 1 mm long, the margins not scarious; middle phyllaries 5–7 × 1.5–2 mm, oblong-lanceolate, squarrose, with an acuminate apex 2–2.5 mm long, the scarious margin 0.2–0.3(0.5) mm wide; innermost phyllaries (7–)8–10(–13) × 1.5–2 mm, linear-lanceolate, erect, longer than the outer phyllaries and projected (0–)1–2 mm beyond the pappus, with an acuminate-aristate apex 0.5–2 mm long, the scarious margin 0.3–0.5 mm wide; receptacle flat, very slightly alveolate, pits surrounded by a membrane 0–0.15 mm high. Florets (13–)16–20 per capitulum. Corolla 7–8 × 1.5 mm, white to purplish white, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 4–5 × 0.5–0.6 mm; lobes 3–3.5(–4) × 0.5–0.7 mm, becoming recurved, with slender submarginal vein. Stamens exserted for 1–2.5 mm beyond the corolla; filaments 1.7–1.8 mm long; collar 0.6–0.8 mm long; anthers 5.5–7 mm long; apical appendages ca. 1.2 mm long, narrowly apiculate; anther tails ca. 2 mm long, with retrorse hairs 0.1–0.2 mm long and some shorter antrorse hairs at the apex. Style 9–10 mm long, stylar branches 2–3 mm long, with sweeping hairs forming a subapical ring, covering a surface 0.3–0.5 mm long, all hairs of similar length or the basal ones longer than the others. Achenes 1.5–2 × 1–1.3 mm, turbinate, (8–)10-ribbed, hispid, with ascending hairs 0.3–2.5 mm long, these inserted between the ribs on the inferior third of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 100–130 barbellate bristles arranged in 4–5 series, the innermost bristles broadened toward the base, the longest bristles 7–8(–9) mm long, the shortest 1 mm long; barbellae 0.1–0.2 mm long.

Habitat and distribution (Fig. 7). Known only from northwestern Somalia at 1250–1868 m. Principally on rocky slopes in limestone areas. Endemic.

Additional specimens examined. SOMALIA. Without exact locality: 26 Feb. 1913, *Drake-Brockmann s.n.* (K); Golis Range, *Drake-Brockmann 164* (K). **Sanaag:** 10°11′N, 47°28′E, 1300 m, *Gillett & Watson 23761* (K); Medishe Valley (Midhisho?), *Glover & Gilliland 942* (BM, K). **Togdheer:** 9°57′N, 45°61′E, 1460 m, *Gillett & Watson 23616* (K); Upper Shiikh, 4900 ft., *Godman 75* (BM);

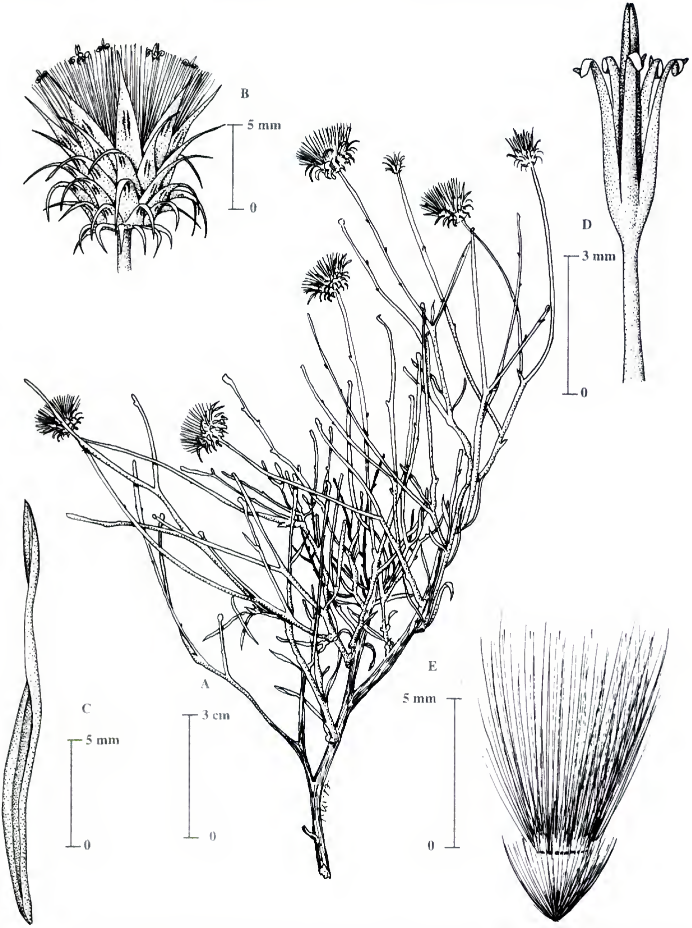

Figure 6. *Dicoma somalensis* (*Gillett 4620* (K)). —A. Habit. —B. Capitulum. —C. Leaf. —D. Floret. —E. Achene with pappus.

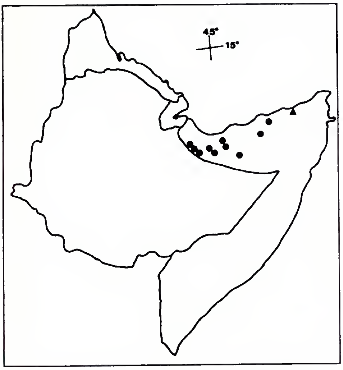

Figure 7. Distribution of *Dicoma somalensis* (●) and *D. thuliniana* (▲) in the Horn of Africa.

Shiikh, 4500 ft., *Ironside Wood S/73/2* (K). **Woqooyi Galbeed**: Abassa, on road from Boorama to Djibouti, 4900 ft., *Bally B9967* (K); Hargeysa, 9°33′N, 44°0′E, 4300 ft., *Gillett 4002* (K); Andoba, 10°6′N, 43°0′E, 5400 ft., *Gillett 4620* (FT, K); 35 km NW of Hargeysa, 9°41′N, 44°19′E, 1250 m, *Gillett 22845* (K); Dardode, 10°07′N, 2°58′E, 1868 m, *Godding 87* (K).

The principal diagnostic characters of *Dicoma somalensis* are its linear to linear-oblanceolate leaves, involucre with numerous ((100–)120–140), glabrous, mainly squarrose phyllaries arranged in 6–8(–10) rows, and pappus of 100–130 barbellate bristles 7–9 mm long. The most morphologically similar species in the Horn of Africa is *D. hindiana*; indeed, as mentioned above, all specimens of *D. hindiana* at K had been labeled as *D. somalensis*. However, there are marked morphological differences between the two species: *D. hindiana* has fewer phyllaries per capitulum (35–70); these are pubescent, and the innermost are squarrose. In addition, *D. hindiana* has a shorter corolla (ca. 5 mm), longer (2.7–3 mm), narrowly turbinate achenes, and fewer (60–70) and shorter (4.5–5.2 mm) pappus bristles. Outside the Horn of Africa, the only species with clearly squarrose phyllaries (like *D. somalensis* and *D. hindiana*) is the Angolan endemic *D. squarrosa*; as noted for *D. hindiana*, however, *D. squarrosa* shows a number of clear differences.

Cufodontis (1967) cited *D. somalensis* from Ethiopia, but we have not seen any specimens from that country.

11. **Dicoma thuliniana** S. Ortiz, Rodr. Oubiña & Mesfin, sp. nov. TYPE: Somalia. Bari: 20 km from Dhurbo on road toward El Gal, 11°33′N, 50°19′E, 900 m, 22 Nov. 1986, *Thulin & Warfa 5975* (holotype, UPS). Figure 8.

Differt a simili *Dicoma paivae* caulibus erectis, foliis rectis atque (5–)15–22(–26) mm longis, bracteis involucralibus longis acuminatis, acumine (1.2–)1.5–3.5 mm longo, atque pappo 6–7 mm longo.

Shrub to 20 cm high, ramified; the branches striate, covered with a dense grayish white tomentum of simple hairs, with sessile to subsessile glands. Leaves sessile, (5–)15–22(–26) × 7–10 (–12) mm, linear; the margins revolute, entire; apex with a short spine 0.2–1(–1.2) mm long; both surfaces densely grayish white-tomentose, with sessile to subsessile glands. Capitula numerous per plant, solitary, on leafy, erect to erect-patent peduncles, 20–50 mm long, with (0–)1–3 subtending leaves; involucre 10–11 × 11–12 mm, campanulate, with 40–50 phyllaries arranged in 5–6 rows, stramineous, with a darker stripe on either side of the midrib, long acuminate-aristate, pungent, tomentose, the margins entire to shortly serrulate principally toward the apical part, not scarious; outermost phyllaries 2–2.5 × 0.8–1.2 mm, deltate-oblong, erect-patent, with an acuminate apex 1.2–2 mm long; middle phyllaries 3–6 × 0.8–1.2(–1.5) mm, ovate-lanceolate, erect-patent, with an acuminate-aristate apex 1.5–3 mm long; innermost phyllaries 6–8 × 1.5–3 mm, longer than the outer phyllaries and projected 1.5–2 mm beyond the pappus, oblong-lanceolate, erect-patent, with an acuminate-aristate apex 2.5–3.5 mm long. Florets unknown. Achenes (2–)3–3.5 × 1.5–2 mm, turbinate, 10-ribbed, hispid, with ascending hairs 0.3–2.5(–3) mm long, inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus isomorphic, of 100–130 barbellate bristles arranged in (4–)5–6 series, the innermost bristles broadened toward base, ca. 0.4 mm wide, the longest bristles 6–7 mm long, the shortest ca. 1 mm long, barbellae 0.05–0.15 mm long.

Habitat and distribution (Fig. 7). Known only from the type locality, at ca. 900 m. South-facing limestone slopes; vegetation of sparse low bushes. Endemic.

The most distinctive characters of *Dicoma thuliniana* are its solitary, linear leaves with revolute margins and short, apical spine, capitula on leafy, erect to erect-patent, peduncles 20–50 mm long, large (10–11 × 11–12 mm) campanulate involucres

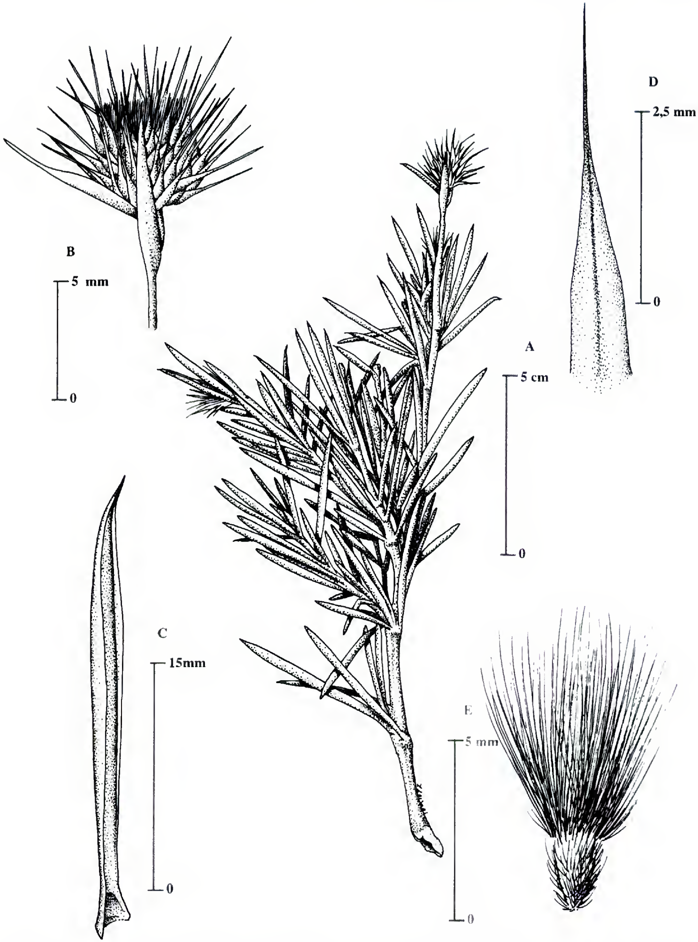

Figure 8. *Dicoma thuliniana* (*Thulin & Warfa 5975* (UPS)). —A. Habit. —B. Capitulum. —C. Leaf. —D. Phyllary apex. —E. Achene with pappus.

with 40–50 phyllaries, and deltate to oblong-lanceolate phyllaries with an acuminate-aristate apex 1.2–3.5 mm long. The most morphologically similar species in the Horn of Africa is *D. paivae*, which can be readily distinguished by its twisted branches forming dense whitish cushions, slightly recurved and often subfasciculate leaves, sessile or subsessile capitula, obconic-campanulate involucres (6–6.5 × 3–4 mm), 25–30 deltate to deltate-lanceolate phyllaries with pungent, acuminate apices 0.2–1 mm long (this feature being particularly distinctive), and shorter pappus (3–5 mm). Of the species of *Dicoma* from outside our area, *D. cana* Balf. f., from Socotra, has leaves showing certain morphological similarities, though in other respects exhibits clear differences (mostly similar to those observed between *D. cana* and *D. paivae*). Furthermore, *D. thuliniana* does not appear to form the dense cushions characteristic of *D. paivae* and *D. cana*.

This species is named after Mats Thulin (UPS), one of the collectors of the type, one of the most knowledgeable experts on the Somalian flora, and editor/author of the *Flora of Somalia*.

12. Dicoma tomentosa Cass., Bull. Sci. Soc. Philom. Paris. 1818: 47. 1818. TYPE: Senegal, *Adanson s.n.* (holotype, P).

Dicoma lanuginosa DC., Prodr. 7: 36. 1838. TYPE: "Eastern India," *Wallich s.n.* (lectotype, here designated, G).

Dicoma gnaphaloides Mattei, Boll. Reale Orto Bot. Palermo 7: 112. 1908. TYPE: Somalia. Goscia, Torda, 21 Aug. 1907, *Macaluso 96* (holotype, PAL).

Vernacular names. Bisciar (Cufodontis, 1967), Gaiocum (Cufodontis, 1967), Tebe-mro (*Mateos Er. 68*), Yset-melase (*Soda Ash Project 2*).

Annual herb to 60 cm high. Taproot slender, lightly ramified. Stem scarcely to highly ramified; the branches striate, generally reddish purple, covered with a grayish white tomentum of simple hairs, with sessile to subsessile glands, often with glabrous to glabrescent areas. Leaves (10–)20–50(–80) × (2–)4–10(–16) mm, linear to linear-oblanceolate, rarely linear-elliptic, conduplicate, attenuate at base and decurrent on a pseudopetiole 0–5 mm long; the margins callose-serrulate; apex 0.5–1.5 mm long, apiculate to aristate with a short spine; upper surface greenish, glabrescent, with sessile glands; lower surface with sessile glands, generally densely grayish-white-tomentose, rarely greenish and glabrescent. Capitula numerous per plant, generally solitary in leaf axils, with 1(–4) subtending leaves, sessile or on peduncles, erect-patent, 1–5 (–8) mm long; involucre (11–)12–15(–17.5) × (10–)12–20(–25) mm, obconic-campanulate, with 30–45(–50) phyllaries arranged in 5–6 rows, stramineous to purple, with a darker stripe on either side of the midrib, rigid, long-acuminate, pungent, glabrescent to densely tomentose, minutely strigose, the margins entire to shortly serrulate-ciliolate, principally toward the apical part; outermost phyllaries 2–4.5 × (0.5–)0.7(–1) mm, deltate to ovate-oblong, patent to erect-patent, with an acuminate apex 1–3.5 mm long, the margins not scarious; middle phyllaries 9–17 × 1.5–2.5 mm, oblong-lanceolate, erect-patent, with an acuminate-aristate apex 4–7 mm long, the scarious margin 0.2–0.3(–0.5) mm wide; innermost phyllaries 11–14 × 2–3 mm, generally of similar length to or shorter than the adjacent outer phyllaries and projected 2–5(–6) mm beyond the pappus, oblong-lanceolate, erect, with an acuminate-aristate apex 2–5 mm long, the scarious margin up to 0.5 mm wide; receptacle concave, alveolate, the pits surrounded by a membrane with a highly irregular dentate margin 0.7 mm high. Florets (7–)10–12(–15) per capitulum. Corolla 6.5–7 × 1.5–2 mm, white, lilac, or violet, with epidermal cell surface "intestine-like" and with short glandular twin hairs; tube 3.4–3.7 × 0.7–1 mm; lobes 3–3.7 × 0.3–0.5 mm, becoming recurved, with slender submarginal veins. Stamens exserted for 0.2–1.5 mm beyond the corolla; filaments 1.7–2 mm long; collar 0.6–0.7 mm long; anthers 3–3.8 mm long; apical appendages ca. 1.2–1.3 mm long, not conspicuously apiculate; anther tails 1–1.3 mm long, with retrorse hairs 0.2–0.5 mm long and some shorter antrorse hairs at the apex. Style 7.5–8 mm long, stylar branches 1–1.5 mm long, with sweeping hairs covering a surface 0.5–0.8 mm long, the basal ones conspicuously longer than the others. Achenes 1.6–3 × 1–1.5 mm, turbinate, (8–)10-ribbed, hispid, with ascending hairs 0.3–2.5 mm long, these inserted between the ribs from the base to the top of the achene, with epidermal glands and superficial biseriate glands between the ribs; testa of *Dicoma* type; pappus dimorphic, of 50–80 barbellate bristles arranged in 1–3 external series, the innermost bristles broadened toward the base, the longest bristles 5–6(–7.5) mm long; the shortest 2 mm long; barbellae 0.1–0.2 mm long; ca. 10 scales arranged in a single internal series, these (5–)6–6.5 (–7.5) × 0.5–1 mm, barbellate toward the apex.

Habitat and distribution (Fig. 9). Widespread in Eritrea, Ethiopia, and Somalia at 230–1700 m. Sandy, gravelly, and rocky granitic or calcareous soils, lava flows; in open *Acacia* woodland, *Acacia–Commiphora* bushland, *Acacia* grassland, open habitats, roadsides. Widespread in north Africa

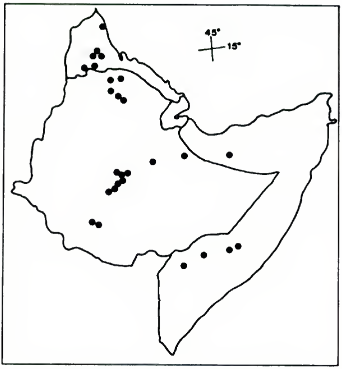

Figure 9. Distribution of *Dicoma tomentosa* in the Horn of Africa.

(Egypt) and tropical and southern Africa; also in Socotra, Pakistan, and India.

Additional specimens examined. ERITREA. Between Galeb Zagle and Malekte, 17°7′N, 38°45′E, 850 ft., *Bally 6786* (ETH, K); Cheren, Do-Longoroc, *Gandussio 79* (FT); Bogos, Moccada, *Pappi 2484* (FT, K); Bogos, Tzabab, *Pappi 8468* (FT); Keren, 10–25 Nov. 1902, *Tellini s.n.* (FI); Keren, *Tellini 781* (FT). ETHIOPIA. Without exact locality: 1853, *Schimper 426* (G, K, P, W). **Gamo Gofa**: without exact locality, 610 m, *Sebsebe & Amha 653* (ETH); Nechsar National Park, Arba Minch, *Mateos Er. 68* (ETH); between Lake Ch'amo and Lake Abaya, 6°30′N, 37°38′E, 1250–1300 m, *Gilbert, Thulin & Aweke 295* (ETH, K, UPS); **Harerge**: Errer Valley, 4 km E of the river, 9°14′N, 42°15′E, 1300 m, *Burger 3566* (K); about 30 km N of bridge crossing Awash River along road to Gewane, 800 m, *Seegeler 2794* (ETH). **Shewa**: Sodere, 8°25′N, 39°24′E, N bank of Awash River, ca. 28 km S of Nazreth, *Ash 2106* (K); Erer, *IECAMA H-9* (K); Gala Aruss, 1909, *Negri 911* (FT); Awash National Park, 950 m, *Nystrom 77* (ETH); 1 km W of Birrta, on track to Koye, ca. 10 km from Meki, 8°14′N, 38°55′E, 1700 m, *Gilbert & Gelahun Abate 3121* (ETH, K); Awash National Park, 8°55′N, 39°55′E, *Gilbert & Gilbert 1256a* (ETH, K); 1–2 km W of Metahara, 8°55′N, 39°54′E, 1050 m, *Gilbert & Thulin 219* (ETH, UPS); Abyjata, 1650 m, *Soda Ash Project 2* (ETH). **Sidamo**: near Murle Lake, *Corradi 1762* (FT); Atana–Murle road, *Corradi 1814* (FT). **Tigray**: Haramat, Cianduch Plain, *Pappi 226* (FT); "ad montes prope Dscheladscheranne," Tekeze Valley, 3 Nov. 1839, *Schimper s.n.* (G, K, OXF, P, PI, S, W); "in montibus prope Gageros," Agow, 3500 ft., 18 Oct. 1854, *Schimper s.n.* (G, K, P, S, W); Temben Awraja, 11.7 km along Yechila–Abiy Adi road, 1500 m, *Mesfin T. 8551* (ETH); Yechila, ca. 94 km from Mek'ele, 1600 m, *Mesfin T. & Tewolde 8520* (ETH). SOMALIA. **Bay**: Baydhabo, 2°59′N, 44°16′E, 230 m, *Thulin & Bashir Mohamed 7105* (K, UPS). **Gedo**: 20 km along road between Garbahaarrey and Qansaxdeheere, 300 m, *Thulin & Bashir Mohamed 6917* (UPS); 5 km along road between Garbahaarrey and Luuq, 250 m, *Thulin & Bashir Mohamed 6924* (K, UPS). **Hiiraan**: 5.5 km S of Dharyo on road to Gobyaxas, 3°37′N, 44°54′E, 275 m, *Kuchar 17329* (K, UPS). **Togdheer**: 8°50′N, 45°34′E, 870 m, *Beckett 1361* (K); Buulobarde, ½ km SW of Aborey, 4°0′N, 45°41′E, 195 m, *Kuchar 17601* (K).

The principal diagnostic characters of *Dicoma tomentosa* are its linear-elliptic to linear-oblanceolate often conduplicate leaves, apically apiculate to aristate with a short spine, its sessile or short-pedunculate, generally solitary axillary capitula with obconic-campanulate involucres, deltate to oblong-lanceolate phyllaries with long (1–7 mm) pungent acuminate-aristate apices, style with sweeping hairs covering a surface 0.5–0.8 mm long, and dimorphic pappus of 50–80 barbellate bristles and ca. 10 scales arranged in a single internal series. Of the *Dicoma* species in the Horn of Africa, only *D. bangueolensis* has a dimorphic pappus of similar composition; as noted elsewhere, however, that species shows marked differences as regards habit, leaf morphology, and the morphology and size of the phyllaries and achenes. A number of other species, including *D. cana* and *D. spinosa* (L.) Druce, and to a lesser extent *D. latifolia* DC. and *D. relhanioides* Less., have phyllaries with a long-pungent, acuminate apex; however, all of these are shrubs, and in addition present other clear differences from *D. tomentosa*, including the absence of a phyllary midrib, straight corolla lobes, achenes without prominent ribs and without epidermal glands or superficial biseriate glands between the ribs, and an isomorphic pappus.

Within the study area, *Dicoma tomentosa* shows relatively little morphological variability, though some variation is observed in growth habit (more or less prostrate), degree of ramification, pubescence and coloration of the stems and phyllaries (which may in some cases be purplish), leaf width, and length of peduncles, and number of capitula.

The type of *Dicoma gnaphaloides* Mattei, a name accepted by both Wilson (1923) and Cufodontis (1967), is indistinguishable from *D. tomentosa*, and we thus include the former name here as a synonym.

Literature Cited

Anderson, L. E. 1954. Hoyer's solution as a rapid permanent mounting medium for bryophytes. Bryologist 57: 242–247.

Audru, J., J. C. Lebrun & P. Lebrun. 1994. Les Plantes Vasculaires de la République de Djibouti. Flore Illustrée. CIRAD, Paris.

Bremer, K. 1994. Asteraceae. Cladistics & Classification. Timber Press, Portland, Oregon.

Buscalioni, L. & R. Muschler. 1913. Beschreibung der von Ihrer Königlichen Hoheit der Herzogin Helena von Aosta in Zentral-Afrika gesammelten neuen Arten. Bot. Jahrb. Syst. 49: 457–515.

Cabrera, A. L. 1977. Mutisieae–Systematic review. Pp. 1039–1066 *in* V. H. Heywood, J.-B. Harborne & B. L. Turner (editors), The Biology and Chemistry of the Compositae. II. Academic Press, London.

Cufodontis, G. 1967. Enumeratio plantarum Aethiopae Spermatophyta (sequentia). Bull. Jard. Bot. Natl. Belgique 37, Suppl.: 115–1193.

Davies, R. A. (editor). 1996. Index Kewensis, suppl. 20. Royal Botanic Gardens, Kew.

Edwards, S., Mesfin T. & I. Hedberg (editors). 1995. Flora of Ethiopia and Eritrea, Vol. 2(2). The National Herbarium of the Addis Ababa University and the Department of Systematic Botany of the Uppsala University, Addis Ababa and Uppsala.

Graham, A. 1996. A contribution to the geologic history of the Compositae. Pp. 123–140 *in* D. J. N. Hind & H. J. Beentje (editors), Compositae: Systematics. Proceedings of the International Compositae Conference, Kew. Royal Botanic Gardens, Kew.

Grau, J. 1980. Die Testa der Mutisieae und ihre systematische Bedeutung. Mitt. Bot. Staatssaml. München 16: 269–332.

Hansen, H. V. 1991. Phylogenetic studies in Compositae tribe Mutisieae. Opera Bot. 109: 1–50.

Hedberg, I. & S. Edwards (editors). 1989. Flora of Ethiopia, Vol. 3. The National Herbarium of the Addis Ababa University and the Department of Systematic Botany of the Uppsala University, Addis Ababa and Upsala.

Hoffmann, O. 1893. Tubiflorae–Mutisieae. *In:* H. G. A. Engler & K. A. E. Prantl, Die natürlichen Pflanzenfamilien 4(5): 333–350. W. Engelmann, Leipzig.

Jeffrey, C. 1967. Notes on Compositae: 2. The Mutisieae in East Tropical Africa. Kew Bull. 21: 177–223.

Karis, P. O., M. Källersjö & K. Bremer. 1992. Phylogenetic analysis of the Cichorioideae (Asteraceae), with emphasis on the Mutisieae. Ann. Missouri Bot. Gard. 79: 416–427.

Mattauer, M. 1967. Les deformations de materiaux de l'ecorce terrestre. Herman Editeurs des Sciences et des Arts, Paris.

Ortiz, S. & J. Rodríguez-Oubiña. 1994. *Dicoma paivae* and *Dicoma cinerea* (Asteraceae), two new species from Somalia. Canad. J. Bot. 72: 1478–1481.

——— & ———. 1995. *Dicoma hindana* (Asteraceae), a new species from Somalia. Nordic J. Bot. 15: 187–189.

——— & ———. 1996a. The identity of *Dicoma bangueolensis* (Asteraceae). Taxon 45: 519–520.

——— & ———. 1996b. Two new species of *Dicoma* (Asteraceae) from Somalia and Ethiopia. Nordic J. Bot. 16: 277–281.

Pope, G. V. 1991. Notes on *Dicoma* Cass. (Compositae). Kew Bull. 46: 699–709.

Rodríguez-Oubiña, J. & S. Ortiz. 1995. Two new species of the genus *Dicoma* (Asteraceae) from Somalia. Bot. J. Linn. Soc. 119: 59–64.

Thulin, M. (editor). 1993. Flora of Somalia, Vol. 3. Royal Botanic Gardens, Kew.

Volkens, G. L. A. 1915. Berichtigungen zu den von R. Muschler in Engl. Bot. Jahrb. XLIII. (1909), XLVI (1911), XLIX (1913) und L. Suppl. (1914) veröffentlichten Diagnosen afrikanischer Pflanzen. II. Die "von Ihrer Königlichen Hoheit der Herzogin Helena von Aosta in Zentral-Afrika gesammelten neuen Arten," Compositae. Bot. Jahrb. Syst. 53: 373–375.

Wilson, F. C. 1923. Revision of the genus *Dicoma*. Bull. Misc. Inform. Kew 1923: 377–388.

A REVIEW OF THE GENUS *PARAGONIA* (BIGNONIACEAE)[1, 2]

Warren D. Hauk[3]

ABSTRACT

Paragonia (Bignoniaceae) is a genus of two species, *P. brasiliensis* and *P. pyramidata*, the latter containing two varieties (var. *pyramidata* and var. *tomentosa*). Both species are lianas with subulate-appressed pseudostipules, lavender to magenta, tubular-campanulate corollas, linear-oblong fruit, and winged seeds. *Paragonia pyramidata* var. *pyramidata* is distributed from southern Mexico to southern Brazil and Uruguay, whereas *P. pyramidata* var. *tomentosa* is restricted to southern Brazil. *Paragonia brasiliensis* is known only from a few states in eastern Brazil. A key to flowering and fruiting material, maps of species distributions, graphs of flowering and fruiting phenology, and an illustration of *P. pyramidata* var. *pyramidata* are provided.

Paragonia Bureau (Bignoniaceae) is a ditypic genus of lianas with lavender to magenta, tubular-campanulate corollas, linear-oblong fruit, and winged seeds (Fig. 1). It is distinguished from other genera of the liana tribe Bignonieae by a combination of characters that includes stems with four phloem arms in cross section, subulate-appressed pseudostipules, bifid or trifid tendrils, moniliform-puberulent corolla tubes, psilate 3-colporate pollen, and the absence of interpetiolar glandular fields (Gentry, 1973, 1977, 1978, 1982a, b; Gentry & Tomb, 1979). *Paragonia* is generally found in lowland portions of Central and South America and is a common component of tropical moist forest, tropical wet forest, and premontane wet forest environments.

Paragonia brasiliensis (Baill.) A. H. Gentry is a poorly known species restricted to portions of eastern Brazil (Fig. 2). *Paragonia pyramidata* (Rich.) Bureau var. *pyramidata* is more wide-ranging (Fig. 3) and morphologically variable than the geographically restricted *P. pyramidata* var. *tomentosa* Bureau & K. Schum., of south-central Brazil (Fig. 2).

This treatment attempts to compile all information available on *Paragonia*, notably that obtained by the late Alwyn H. Gentry during his extensive investigations of Bignoniaceae. The maps of geographic distribution and graphs of flowering and fruiting phenology presented here were derived from a database initiated during Gentry's studies of the family.

HISTORY

Paragonia was described by Bureau in 1872 based on *Bignonia lenta* Mart. ex DC. (1845). However, *Bignonia lenta* is considered synonymous with a previously described species, *Bignonia pyramidata* Rich. (1792), and thus the epithet *pyramidata* takes precedence. A second species, *Paragonia brasiliensis*, was originally described by Baillon in 1888 as the sole member of the genus *Sanhilaria*. *Paragonia* was monotypic until 1976, when Gentry transferred *Sanhilaria brasiliensis* into *Paragonia*. Gentry (1976a) evaluated the type of *P. brasiliensis* and concluded that it was specifically distinct from *P. pyramidata* because of its softly puberulous, short-petioled leaves, trifid tendrils, narrower inflorescence, acute corolla lobes, costate calyx, and compressed fruit that lack the sandpaper-like surface of fruit of *P. pyramidata* (Table 1). However, the puberulence of the type specimen of *P. brasiliensis* is not manifest in all collections (Gentry, 1976a).

SYSTEMATICS

According to Gentry and Tomb (1979), the genera *Paragonia*, *Leucocalantha* Rodr., *Spathicalyx* J. C. Gomes, *Manaosella* J. C. Gomes, *Ceratophytum*

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[1] This paper is number 5 of the GENTRY INVITATIONAL SERIES, in acknowledgment of contributions to the study of the Bignoniaceae made by Alwyn H. Gentry.

[2] I thank Peter Raven and the Missouri Botanical Garden for the opportunity to conduct this research. I thank two anonymous reviewers for helpful comments, and the curators of NY and US for providing loans of herbarium specimens. In particular, I am grateful to William G. D'Arcy, whose advice and guidance were an invaluable contribution to this work. Susan A. Moore provided the illustration. A special thanks to Linda Wellsey for her volunteer support of the project. Financial support was provided by the National Science Foundation (grant DEB-9509270).

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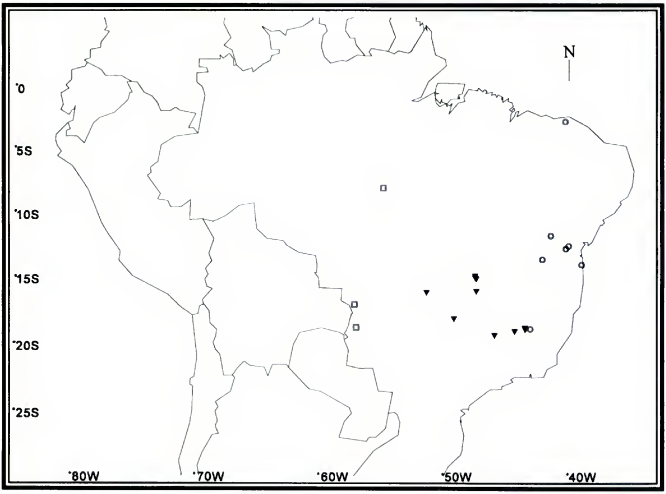
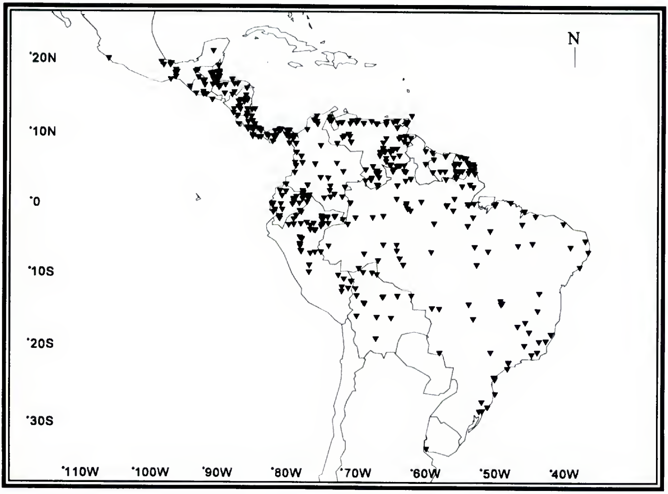
ANN. MISSOURI BOT. GARD. 85: 460–474. 1998.

Figure 1. *Paragonia pyramidata* var. *pyramidata*. —A. Inflorescence and leaves (after *Steinbach 428*). —B. Seed (after *Kirkbride 3580*). —C. Fruit (after *Martínez 15747*).





Figures 2, 3. Geographic distributions. —Figure 2 (top). *Paragonia brasiliensis* (circles), *P. pyramidata* var. *tomentosa* (triangles), and collections of anomalous specimens of *P. pyramidata* (squares). —Figure 3 (bottom). *Paragonia pyramidata* var. *pyramidata*.

Table 1. Features used to differentiate *Paragonia pyramidata* and *P. brasiliensis* (after Gentry, 1976).

P. pyramidata	*P. brasiliensis*
1. Tendril tip minutely bifid (rarely trifid)	Tendril tip minutely trifid
2. Petioles and petiolules well developed	Petioles and petiolules reduced, obsolescent
3. Leaflets elliptic or ovate-elliptic, the apex obtuse to acuminate	Leaflets narrowly elliptic to oblanceolate, the apex obtuse
4. Calyx ecostate	Calyx conspicuously ribbed
5. Inflorescence broadly paniculate	Inflorescence racemose-paniculate
6. Capsule subterete, sandpaper-surfaced, moderately lepidote	Capsule strongly compressed, smooth-surfaced, densely lepidote (when immature)
7. Corolla lobes rounded	Corolla lobes acute
8. Mexico to southern Brazil	Eastern Brazil (Bahia and Minas Gerais)

Pitt., *Tynanthus* Miers, and *Periarrabidaea* A. Samp. may form a natural group because they share pubescent corolla tubes, 2–3(multi)-fid tendrils, and "more or less psilate 3(–4)-colpate pollen." *Paragonia pyramidata* has psilate, microperforate, 3-colporate pollen with narrow colpi (Tomb & Gentry, unpublished), whereas the pollen of *P. brasiliensis* is unstudied.

Simmonds (1954) reported a chromosome count of $2n = 40$ for *Paragonia pyramidata.* Of the 23 genera of Bignonieae cited by Goldblatt and Gentry (1979), only 2 (*Mansoa* and *Pachyptera*) have diploid chromosome numbers other than $2n = 40$. The near uniformity of chromosome numbers in Bignonieae supports the monophyly of this lineage (Goldblatt & Gentry, 1979), but provides little information regarding relationships among genera of the tribe.

DISTRIBUTION

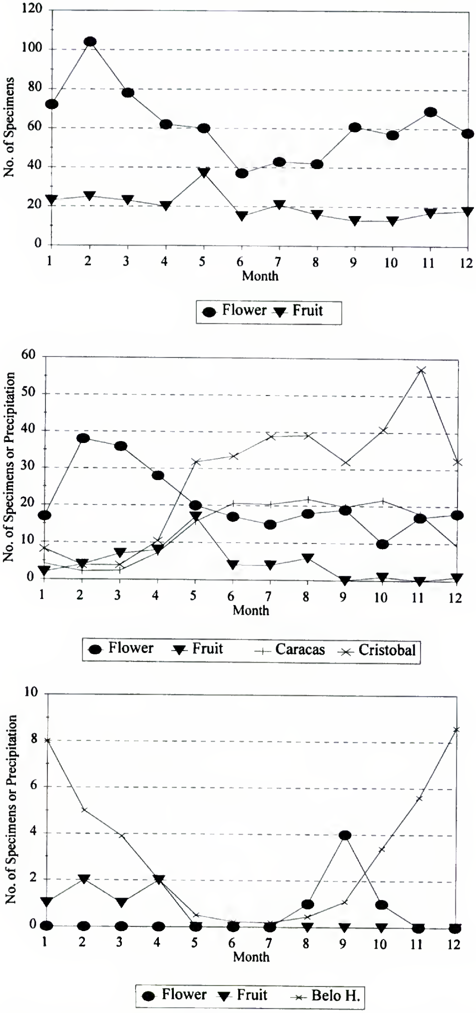
Paragonia pyramidata is wide-ranging throughout the Neotropics (Figs. 2, 3), typically below 1000 m, although collections extend to 2066 m. Common through all of Central America and the northern half of South America, *P. pyramidata* var. *pyramidata* extends southward to the eastern Andes in Peru and Bolivia, and across Brazil to the eastern shore of South America. The northernmost collections are from Mexico, in Colima and the Yucatán Peninsula. The southernmost collection examined was from Uruguay (adjacent to Buenos Aires, Argentina), with other collections from the Brazilian states of Paraná and São Paulo. Gentry (1973, 1977) reported that *P. pyramidata* occurs in Argentina, but no collections from Argentina were seen in the present investigation. Gentry (1973, 1977, 1978, 1982a, 1982b) reported collections from Guadeloupe (West Indies), but other collections from the Caribbean are not documented. *Paragonia pyramidata* var. *tomentosa* is more restricted than variety *pyramidata* and is found only in south-central Brazil (Fig. 2).

Paragonia brasiliensis is more restricted geographically than *P. pyramidata* var. *pyramidata* and occupies higher (500–1000 m) and drier portions of eastern Brazil (Fig. 2), i.e., the states of Ceará, Bahia, and Minas Gerais. It is likely that *P. brasiliensis* occurs in Pernambuco, Piauí, Rio Grande do Norte, and Paraíba, but collections from these states were not seen.

PHENOLOGY

Large bees are the primary pollinators of *Paragonia pyramidata,* and flower production follows the "cornucopia" strategy (Gentry, 1976b). "Cornucopia" species produce numerous flowers over a period of several weeks, and a wide range of pollinators are attracted during this period. The cornucopia strategy is the most widespread and generalized of the five flowering patterns typical of Central American Bignoniaceae (Gentry, 1974). Gentry (1976b) documented the cornucopia pollination strategy for *P. pyramidata* in tropical moist forest, tropical wet forest, and premontane wet forest environments.

Graphs of flowering and fruiting phenology for *P. pyramidata* var. *pyramidata* show that flower and fruit production occur throughout the year (Figs. 4, 5). Peaks in the number of flowering and fruiting collections were in February and May, respectively. However, the wide geographic range of *P. pyramidata* var. *pyramidata* (Fig. 3) may obscure more localized phenological patterns. Figure 5 presents flowering and fruiting phenology for collections from Panama, Colombia, and Venezuela only. Mean monthly precipitation in centimeters for Cristóbal, Panama, and Caracas, Venezuela, was plotted to assess floral and fruiting phenology relative to precipitation. A marked peak in flowering occurs in February during the dry season, with a smaller peak in fruit production occurring in May during the first part of the wet season. However, numbers of collections from south of the equator did not peak during the dry season (not graphed). Thus, the floral and fruiting phenology of *P. pyramidata* var.



Figures 4–6. —Figure 4 (top). Flowering and fruiting phenology of *P. pyramidata* var. *pyramidata* for all collections. —Figure 5 (middle). Flowering and fruiting phenology of *P. pyramidata* var. *pyramidata* from Panama, Colombia, and Venezuela. Mean monthly precipitation in cm is plotted (1×) for Caracas, Venezuela, and (2×) for Cristóbal, Panama. —Figure 6 (bottom). Flowering and fruiting phenology of *P. pyramidata* var. *tomentosa*. Mean monthly precipitation in cm is plotted (0.25×) for Belo Horizonte, Brazil.

pyramidata appears to be influenced by regional climatic conditions.

There were few fertile collections of *P. pyramidata* var. *tomentosa* (Fig. 6). The six flowering specimens were all collected at the beginning of the wet season, between August and September. Fruiting collections were limited to the latter part of the wet season, from January to April. Although these data are preliminary, they indicate that *P. pyramidata* var. *tomentosa* differs phenologically from *P. pyramidata* var. *pyramidata.*

Assessments of flowering and fruiting phenology of *P. brasiliensis* did not reveal clear trends because of the limited number of fertile collections available; four flowering collections are known from January, one from June, and two from November. Of the two known fruiting collections, one is from January and the other is from February. Flowering and fruiting probably peak during the first few months of the year, but additional collections are needed to confirm this.

ECONOMIC AND ETHNOBOTANICAL USES

Reports of uses for *Paragonia* are limited. Gentry (1992) cited the use of *Paragonia* as a treatment for stomach and intestinal problems. *Paragonia pyramidata* is one of several lianas used by native peoples "para tomar agua" (Gentry, in press). Macbride (1961) reported that the stems of *P. pyramidata* are used for lashings.

MATERIALS AND METHODS

Gentry compiled a private database of label information from herbarium specimens he collected and from specimens at other herbaria that he examined personally. Gentry's database has been incorporated into the Missouri Botanical Garden database-management system, TROPICOS, which also contains label information for all other *Paragonia* specimens housed at MO. All types were assumed to have been seen by Gentry unless otherwise noted. Gentry did not always designate types as "holotype," "isotype," or "syntype," and the designations presented here are based upon inferences drawn from Gentry's work and the original literature; these type designations were not based on personal verification of specimens at the various herbaria. Uncertainty of the type designation is indicated by a question mark.

Data used for mapping and phenology were downloaded from TROPICOS. For records with no latitude/longitude coordinates in TROPICOS, approximate coordinates were obtained from gazetteers produced by the U.S. Board on Geographic Names, Office of Geography, Dept. of the Interior. Distribution maps were produced using the computer program VERSAMAP 1.51 (C.H. Culberson, Newark, Delaware, 1991–1995). Graphs of flowering and fruiting phenology were generated using the computer program Quattro Pro 7.00 (Corel Inc., 1996). Phenology is reported as the number of flowering specimens collected during each month of the year; detailed studies of flower production (per plant, per population, per species, or per time period) have not been conducted. Amounts of precipitation used in the graphs of phenology were obtained from *Agroclimatological Data for Latin America and the Caribbean* (FAO, 1985).

TAXONOMIC TREATMENT

Paragonia Bureau, Bull. Soc. Bot. France 19: 17. 1872. TYPE: *Bignonia lenta* Mart. ex DC. [= *Paragonia pyramidata* (Rich.) Bureau].

Sanhilaria Baill., Hist. Pl. 10: 27. 1888 [1891], non Leandro (1838). TYPE: *Sanhilaria brasiliensis* Baill. [= *P. brasiliensis* (Baill.) A. H. Gentry].

Hilariophyton Pichon, Bull. Soc. Bot. France 92: 228. 1945. TYPE: *Sanhilaria brasiliensis* Baill. [= *P. brasiliensis* (Baill.) A. H. Gentry].

Lianas; stems woody with 4 phloem arms in cross section; branchlets terete, lenticellate, with interpetiolar glandular fields lacking, glabrate to lepidote or densely puberulent; pseudostipules subconical, subulate (basally expanded with acuminate tips), curved inward and appressed or nearly appressed to branchlets or angled away from branchlet and nearly appressed to the subtending petiole, eglandular, glabrate to puberulent. *Leaves* opposite, petiolate, estipulate, 2-foliolate with oppositely arranged simple leaflets and a bifid or trifid (rarely simple) terminal tendril (or tendril scar); petioles and petiolules puberulent, the petiolules sulcate; distal adaxial petiolar glandular fields present or absent; leaflets entire, chartaceous, glabrate to densely puberulent beneath, venation brochidodromous, the midrib and secondary veins prominent, glandular fields in axils lacking, margins slightly undulate. *Inflorescences* elongate terminal or axillary panicles, many-flowered; rachis and peduncles minutely bracteate, the axes minutely scurfy to densely puberulent. *Flowers* ovoid in bud, the calyx expanding before corolla emergence; calyx cupular-campanulate, minutely and densely lepidote to sparingly lepidote or moniliform-pubescent, the calyx apically truncate except for minute, mucronate teeth, costate or ecostate, the margin frequently split and/or reflexed, often ciliate; corolla zygomorphic, tubular-campanulate, lavender to magenta, frequently with a white throat, the outer surface densely moniliform-pubescent and the inner surface glabrate with a ring of elongate, dense, moniliform pubescence immediately below insertion of stamens; corolla lobes 5 (2 upper and 3 lower), short-orbicular, rounded to acute, the inner and outer surfaces moniliform-pubescent; fertile stamens didynamous with a single staminode present, stamens and staminode adnate to the corolla; fertile anthers glabrous, with two spreading thecae, included; disk present; ovary cylindrical, usually densely lepidote; ovules 2-seriate in each locule; stigma bipartite, the divisions laterally flattened or partially fused and appearing hollow, included. *Fruit* a compressed, woody, linear-oblong septicidal capsule, dark brown to tan, the valves dehiscing parallel to the septum, the midline inconspicuous, and the surface conspicuously tuberculate to nearly smooth, many-seeded; seeds oblong, flattened, bialate, the body ovoid and frequently bipartite.

Paragonia contains two species and ranges from Mexico to Brazil and Uruguay. Collections are also reported from Guadeloupe (Gentry, 1973, 1977, 1978, 1982a, b).

KEY TO SPECIES OF *PARAGONIA*

1a. Petioles < 10 mm long; petiolules ≤ 6 mm long; petiolar glandular field absent or obscured by pubescence; tendrils trifid; pseudostipules usually angled sharply away from the branchlet; inflorescence axes glandular-puberulent; calyx costate; fruit surface nearly smooth .... 1. *P. brasiliensis*

1b. Petioles ≥10 mm long; petiolules ≥10 mm long; petiolar glandular fields present and evident; tendrils generally bifid, rarely trifid or simple; pseudostipules appressed or nearly appressed to the branchlet; inflorescence axes lepidote-puberulent to densely tomentose-puberulent; calyx smooth; fruit surface tuberculate .... 2. *P. pyramidata*

1. **Paragonia brasiliensis** (Baill.) A. H. Gentry, Ann. Missouri Bot. Gard. 63: 70. 1976. *Sanhilaria brasiliensis* Baill., Hist. Pl. 10: 27. 1888 (1891). *Hilariophyton brasiliensis* (Baill.) Pichon, Bull. Soc. Bot. France 92: 228. 1945. TYPE: Brazil. Minas Gerais: *St. Hilaire 745* (holotype, P).

Lianas; branchlets terete, drying brown, puberulent; pseudostipules angled away from branchlet and nearly appressed to the subtending petiole, puberulent. *Leaves* 6–10 cm long, 2-foliolate with a single, minutely trifid, terminal tendril (or tendril scar); petioles 6–8 mm long, lepidote-puberulent to densely puberulent, glandular fields lacking; petiolules 3–6 mm long, sulcate, lepidote-puberulent to densely puberulent; leaflets 4–9 × 1.5–4.0 cm, elliptic, apices acute with minute mucronate tips lacking, bases acute to obtuse, with 5–8 principal secondary vein pairs, the lamina frequently punctate, glabrate above and glabrate to densely puberulent below. *Inflorescences* to 12 cm long, glandular-puberulent, several-flowered; rachis and peduncles minutely bracteate, the bracts linear-triangular, 2–3 × 1 mm, ± persistent, eglandular, puberulent; pedicels 4–9 mm long, densely puberulent. *Flowers* ovoid in bud; calyx 5–6 × 8 mm, costate, densely lepidote to moniliform-pubescent, apically truncate except for 5 minute, mucronate teeth, dark glands present on distal half of calyx, the margin smooth to ciliate; corolla exserted ca. 45 mm beyond the calyx lip, 3–4 mm wide at the calyx lip, 15 mm wide at the mouth, the outer surface densely moniliform-pubescent and the inner surface glabrate with a ring of dense uniseriate pubescence at the level of the calyx lip; corolla lobes 15 × 12 mm, the apices acute; fertile stamens 12 or 16 mm long, inserted into the inner ring of corolla pubescence, the single staminode 4 mm long, inserted beyond the ring of corolla pubescence; disk 1 × 2 mm; ovary 3 mm long; style ca. 21 mm long. *Capsule* 40 × 1 cm, drying dark, the outer surface nearly smooth or minutely lepidote; seeds 1.0 × 3.5 cm.

Paragonia brasiliensis is a poorly known species from the eastern Brazilian states of Bahia, Minas Gerais, and Ceará (Fig. 2). All collections known are from 500 to 1000 m, typically in the caatinga. Patterns of flowering and fruiting phenology are not evident because only nine fertile collections were available (flowering collections: four from January, one from June, and two from November; fruiting collections: one each from January and February). Peak flowering probably occurs from November to January. However, because a single flowering collection is known from June, *P. brasiliensis* may not have a rigidly constrained flowering period.

Additional specimens. BRAZIL. **Bahia**: Mun. Caetite. 20 km E de Caetite, 14°08'S, 42°15'W, 500 m, *Arbo et al. 5652* (MO); Rodovia BR 4, 60 km N da divisa com Minas Gerais, 14°50'S, 39°00'W, *Belem 1196* (CEPEC, H, MO); Rod. BR-116 (Mun. Candido Sales), *Hatschbach & Silva 50026* (MO); Jequie, 13°05'S, 40°04'W, *Heringer 10277* (IAN, NY, UB); Serra da Agua de Rega 28 km N of Seabra, road to Agua de Rega, 12°25'S, 41°46'W, 1000 m, *Irwin et al. 31159* (MO, NY, UB); BR 4, km 966, *Pabst & Pereira 8364* (MO); 6 km antes de Planalto Bahiana, *Pereira & Pabst 9539* (MO); 9 km de Maracas rumo a Caatinga, 13°26'S, 40°27'W, *Pereira & Pabst 9705* (MO). **Ceará**: Serra da Meruoca, Sitio J. Antonio, 03°28'S, 40°30'W, *Fernándes s.n.* (EAC-1950).

The stems and leaves of *Paragonia brasiliensis* are often dark and densely puberulent, particularly on the short petioles and petiolules. The tendrils of *P. brasiliensis* are trifid rather than bifid as is usually observed in *P. pyramidata.* Petiolar glandular fields were not observed in *P. brasiliensis,* and these are a nearly ubiquitous feature of *P. pyramidata.* The inflorescence axes of *P. brasiliensis* are glandular-puberulent, whereas those of *P. pyramidata* are lepidote-puberulent to densely tomentose-puberulent. The costate calyces of *P. brasiliensis* are distinct from the smooth calyces of *P. pyramidata.* Gentry (1976; Table 1) reported that the inflorescences of *P. brasiliensis* are narrower than those of *P. pyramidata.* However, fertile collections of *P. brasiliensis* are few, and it is difficult to assess whether inflorescence width is a useful character to distinguish the two species. Gentry (1976) reported that the fruit of *P. brasiliensis* are "strongly compressed," whereas those of *P. pyramidata* are subterete. The few fruiting collections of *P. brasiliensis* that are available possess immature fruit, and any generalizations based on these collections would be somewhat speculative. Despite the immaturity of the *P. brasiliensis* fruiting collections, the nearly smooth fruit surface of *P. brasiliensis* appears distinct from the tuberculate surface of *P. pyramidata* fruit.

2. **Paragonia pyramidata** (Rich.) Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 104. 1894. *Bignonia pyramidata* Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792. *Tabebuia pyramidata* (Rich.) DC., in A. DC., Prodr. 9: 214. 1845. TYPE: French Guiana, *Leblond 292* (holotype, P-LA).

Lianas; branchlets terete, drying gray, tan, or occasionally dark brown, the younger growth glabrate to densely tomentose and the older stems often rough-surfaced. *Leaves* 10–30 cm long, 2-foliolate with a single, minutely bifid or trifid (rarely simple) terminal tendril (or tendril scar); petioles 10–20 mm, glabrate to lepidote or densely tomentose-puberulent, the distal adaxial glandular fields usually present and either evident or obscured by pubescence; petiolules 1–2 cm, lepidote to densely tomentose-puberulent; leaflets 7–26 × 3.5–13.0 cm, narrowly to broadly elliptic, elliptic-orbicular or ovate-elliptic, apices acute with minute mucronate tips present, bases broadly acute to obtuse or rounded, with 4–5(6) principal secondary vein pairs, the lamina punctate, nearly glabrate above and glabrate to sparsely puberulent or densely tomentose-puberulent below. *Inflorescences* to 18 cm long, lepidote-puberulent to densely tomentose-puberulent, many-flowered; rachis and peduncles minutely bracteate, the bracts linear-triangular, 2 × 1 mm, caducous, eglandular, puberulent to densely tomentose-puberulent; pedicels to 12 mm long, lepidote or tomentose-puberulent. *Flowers* ovoid in bud; calyx 5–7 × 6–7 mm, ecostate, glabrate to lepidote, mealy, or densely tomentose-puberulent, occasionally sparsely and minutely puberulent, apically truncate except for 5 mucronate teeth, the margin ciliate; corolla tubular-campanulate, exserted 35–40 mm above calyx lip, 2–4 mm wide at calyx lip, 15–20 mm wide at mouth, the outer surface densely moniliform-pubescent and the inner surface glabrate with a ring of dense uniseriate pubescence at the level of the ovary apex; corolla lobes 12–15 × 16–20 mm, the apices rounded; fertile stamens 16 or 19 mm long, inserted at inner ring of corolla pubescence, the single staminode 4 mm long, inserted beyond the ring of corolla pubescence; disk 1 × 3 mm; ovary 3 mm long; style 20–25 mm long. *Capsule* 32–52 × 1.0–1.5 cm, dark to light brown or uniformly tan to silvery-tan, the outer surface tuberculate to finely tuberculate and lepidote; seeds 1 × 4 cm. Figures: Gentry (1973, fig. 24), Gentry (1982a, fig. 19), Gentry (1982b, fig. 31), Gentry (1997, fig. 339), Sprague (1903, figs. 2771, 2772).

Paragonia pyramidata ranges from southern Mexico through Central America and South America east of the Andes, to southern Brazil and Uruguay (Fig. 3). Gentry (1973, 1977) included Argentina in the distribution of *P. pyramidata,* but no collections from Argentina were located during this investigation. It typically ranges from 0 to 1000 m, with collections reported to 2066 m. *Paragonia pyramidata* is common in tropical and premontane wet forests, and thrives in a diversity of ecological conditions from dry hillsides to swamps (Gentry, 1973).

The subulate, appressed (or nearly appressed) pseudostipules, large "lauraceous" leaflets, and distinctive, sweet smell of the freshly crushed leaves are important field characters for *P. pyramidata* (Gentry, 1973, 1978). The minutely bifid (versus trifid) tendrils and absence of interpetiolar glandular fields distinguish *P. pyramidata* from the vegetatively similar *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw. (Gentry, 1973).

Although Bureau described *Paragonia pyramidata* var. *elliptica* in 1845, and Bureau and Schumann described *P. pyramidata* var. *tomentosa* in 1896, Gentry (1973, 1977, 1982a, b) did not recognize varieties of *P. pyramidata,* and regarded variation in pubescence as "taxonomically unimportant" (Gentry, 1976a). However, my inspection of specimens from South America revealed forms clearly identifiable as variety *tomentosa*, and these are restricted to a specific geographic area (Fig. 2). Variety *tomentosa* apparently grows intermixed with the glabrate variety *pyramidata*. However, no intermediates were identified.

The characters of the glabrate and pubescent varieties differ more in frequency of expression than in fundamental structure, e.g., all characters of variety *tomentosa* are present in variety *pyramidata* but at different frequencies. The principal difference between the two varieties is in the overall pubescence; variety *pyramidata* is usually glabrate and variety *tomentosa* is typically densely tomentose-puberulent. The leaflets of variety *tomentosa* are generally wider and more nearly ovate than the elliptic leaflets typical of variety *pyramidata*. Typically, variety *pyramidata* has minutely puberulent inflorescence axes, whereas those of variety *tomentosa* are densely tomentose-puberulent. The calyces of variety *tomentosa* are densely tomentose-puberulent, whereas those of variety *pyramidata* are glabrate to lepidote (rarely mealy; see below). The fruit surface of variety *tomentosa* is uniformly tan, whereas that of variety *pyramidata* varies from dark brown to light tan and is generally less lustrous and more coarsely tuberculate. The fruit surface of variety *tomentosa* is often more finely textured and more lustrous than that of variety *pyramidata*.

Anomalous collections of *Paragonia pyramidata* that do not fit clearly into either variety *tomentosa* or variety *pyramidata* are known from the Brazilian states of Pará, Mato Grosso, and Mato Grosso do Sul. These anomalous collections are well removed from the main range of variety *tomentosa* (Fig. 2). The Pará collection (*Prance et al. P25318*) has glabrate-mealy calyces and elliptic leaflets, and inflorescence and leaflet pubescence reduced in density and length. The Mato Grosso do Sul collection (*Hatschbach et al. 52475*) has tomentose-puberulent leaflets (indistinguishable from those of variety *tomentosa*), short-tomentose inflorescence axes, and glabrate-mealy calyces. The Mato Grosso collection (*Prance et al. 26131*) has evenly but sparsely short-pubescent leaves (no young inflorescence axes or calyces are present because the specimen is fruiting). These anomalous collections were excluded from the variety descriptions and key. Additional collections are needed to assess the taxonomic status of the anomalous specimens.

The correlation among character states (of leaflet shape, leaf pubescence, and fruit surface) for some collections warrants recognition of variety *tomentosa* as distinct from variety *pyramidata*. However, the absence of character state discontinuities (in individual characters) between the taxa argues against recognition of variety *tomentosa* as a species or subspecies. More detailed investigations may provide additional characters to support recognition of this variety at a higher taxonomic level.

KEY TO VARIETIES OF *P. PYRAMIDATA*

1a. Leaflets glabrate or nearly so, narrowly to broadly elliptic, only occasionally ovate-elliptic or elliptic-orbicular, the bases broadly acute to obtuse; calyx glabrate to lepidote, occasionally sparsely and minutely puberulent .... 2a. *P. pyramidata* var. *pyramidata*

1b. Leaflets puberulent to densely tomentose-puberulent beneath, ovate-elliptic or less commonly broadly elliptic, the bases rounded to broadly obtuse; calyx densely tomentose-puberulent .... 2b. *P. pyramidata* var. *tomentosa*

2a. Paragonia pyramidata var. pyramidata

Bignonia laurifolia Vahl, Eclog. Amer. 2: 44. 1798. TYPE: Trinidad. *von Rohr s.n.* (holotype, C).

Bignonia ehretioides Cham., Linnaea 7: 704–705. 1833 ['1832']. TYPE: Brazil. *Sellow s.n.* (holotype?, B not seen by Gentry).

Bignonia rupestris Gardner, London J. Bot. 1: 179. 1842. TYPE: Brazil. Rio de Janeiro: *Gardner 78* (holotype?, K).

Bignonia lenta Mart. ex DC., in A. DC., Prodr. 9: 159. 1845. TYPE: Brazil. Amazonas: *Martius 2977* (holotype, M; isotype, G-DC).

Bignonia martiusiana DC., in A. DC., Prodr. 9: 156–157. 1845. TYPE: Brazil. Pará: 1817, *Martius s.n.* (holotype, BR).

Pachyptera dasyantha DC., in A. DC., Prodr. 9: 176. 1845. TYPE: Brazil. Rio São Francisco, *Blanchet 2903* (holotype, G-DC; isotype, K).

Pachyptera perrottetii DC., in A. DC., Prodr. 9: 176. 1845. TYPE: French Guiana. *Perrottet 2851* (holotype, G-DC).

Pachyptera striata DC., in A. DC., Prodr. 9: 176. 1845. TYPE: Brazil. São Paulo: *Lund 783* (holotype?, G-DC).

Pachyptera umbelliformis DC., in A. DC., Prodr. 9: 175–176. 1845. SYNTYPES: Brazil. São Paulo: *Martius s.n.* (M not seen by Gentry); Rio Paraibia, *Neuwied s.n.* (M not seen by Gentry).

Pithecoctenium reticulare DC., in A. DC., Prodr. 9: 197. 1845. TYPE: Brazil. Without locality or collector (holotype?, G-DC).

Zeyheria ["Zeyheria?"] *surinamensis* Miq., Linnaea 18: 250. 1845 ["1844"]. TYPE: Suriname. *Focke 230* (holotype, U, excluding leaves of *Cydista aequinoctialis* (L.) Miers; isotype, K).

Bignonia sinclairii Cerón, Bot. Voy. Sulphur 129. 1845. TYPE: Panama. *Sinclair s.n.* (holotype, K).

Arrabidaea dichasia Donn. Sm., Bot. Gaz. 20: 6. 1895. TYPE: Honduras. San Pedro Sula: *Thieme 5393* (isotypes?, NY, US).

Paragonia schumanniana Loes., Bot. Jahrb. Syst. 23: 130. 1897. TYPE: Nicaragua. Matagalpa: *Rothschuh 230* (holotype?, B).

Adenocalymna densiflora Rusby, Mem. New York Bot.

Gard. 7: 355. 1920. TYPE: Bolivia. Cataracts of Bopi River, *Rusby 484* (isotypes?, NY, US).

Petastoma leiophyllum Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 58. 1921. TYPE: Brazil. Paraná: *Dusén 8633* (isotype?, K).

Petastoma macrocalyx Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 59. 1921. TYPE: Brazil. São Paulo: *Heiner 569* (holotype, S; photo, K).

Young branchlets glabrate to lepidote; petioles and petiolules glabrate to lepidote, with distal adaxial petiolar glandular fields usually present and conspicuous; leaflets narrowly to broadly elliptic, infrequently elliptic-orbicular or ovate-elliptic, the leaflet bases acute to obtuse or infrequently rounded, the surface glabrate or nearly so above, glabrate to sparsely puberulent below; rachis and peduncles glabrate to lepidote or puberulent; pedicels and calyces lepidote, occasionally sparsely and minutely puberulent or glabrate; outer surface of capsule dark to light brown or (less commonly) tan.

Paragonia pyramidata var. *pyramidata* ranges from southern Mexico through Central America and South America east of the Andes, to southern Brazil and Uruguay (Fig. 3). Collections of *Paragonia pyramidata* var. *pyramidata* are known from 0 to 2066 m. It is common in tropical and premontane wet forests and thrives in a diversity of ecological conditions from dry hillsides to swamps (Gentry, 1973). Flowering occurs throughout the year, and collections peak in February (Figs. 4, 5). Fruiting collections increase from January to April and peak in May.

Representative specimens. MEXICO. **Campeche**: 5 km S de Ulmal, *Cabrera 2308* (MO). **Chiapas**: 6 km al sur de la desviacion a Chancala, *Cabrera & Cabrera 6216* (MO). **Colima**: W of Manzanillo Bay, 5 mi. W of Santiago, Peña Blanca, 19°00′N, 104°00′W, 90–150 m, *McVaugh 15707* (MICH). **Oaxaca**: Mpio. Sta. Maria Chimalapa, 16°55′00″N, 94°40′30″W, 300 m, *Hernández 180* (MO). **Quintana Roo**: 10 km al oeste de La Pantera, *Cabrera & Cabrera 4252* (MO). **Tabasco**: Balancan, Finca la Esperanza, 17°48′N, 91°32′W, 50 m, *Calzada et al. 2651* (MO). **Veracruz**: 10 km N of Sontecomapan, vic. Playa Escondida, 18°35′N, 95°03′W, 100 m, *Nee 24741* (MO). **Yucatán**: Tzucacab, 20°04′N, 89°03′W, *Enríquez 645* (MEXU). BELIZE. **Belize**: N of Hwy. S of Altunha, 0 m, *Gentry 8259* (MO). **Cayo**: Sibun River near Hummingbird Hwy., 17°26′N, 88°16′W, 66–100 m, *Gentry 8432* (MO). **Corozal**: 1 mi. N of Buena Vista, 16°34′N, 88°32′W, *Gentry 8547* (MO). **Orange Walk**: 10 mi. S of Orange Walk, 17°15′N, 88°47′W, *Whitefoord 2599* (MO). **Stann Creek**: Carib Reserve, 16°57′N, 88°15′W, *Gentle 3100* (MICH). **Toledo**: Río Temash, 15°59′N, 88°55′W, *Dwyer 12924* (MO). GUATEMALA. **Alta Verapaz**: Cubilquitz, 15°40′N, 90°25′W, 350 m, *von Tuerckheim 7648* (MO). **Escuintla**: Río Michatoya, SE of Escuintla, 14°48′N, 90°47′W, *Standley 89136* (F). **Izabal**: Puerto Méndez, bank of Río Gracias a Dios, 15°53′N, 89°13′W, *Contreras s.n.* (F). **Jutiapa**: between San José Acatempa and Río de Los Esclavos, 14°15′N, 90°08′W, 900–1200 m, *Standley 60621* (F). **Petén**: Camino para El Remate, km 69, parque Tikal, 17°00′N, 89°42′W, *Tun 1214* (F, MO). **Retalhuleu**: between Nueva Linda and Champerico, 14°25′N, 91°49′W, 120 m, *Standley 87669* (F). EL SALVADOR. **La Libertad**: El Amatalito, 13°29′N, 89°16′W, *Villacorta et al. 844* (MO). HONDURAS. **Atlántida**: between Tela & Pajuiles, 15°44′N, 87°27′W, 200 m, *Molina & Molina 25719* (F). **Colón**: Río Guaimoreto, 4.5 mi. NE of Trujillo, 15°57′N, 85°54′W, *Saunders 299* (MO). **Comayagua**: 19 km NW of Siguatepeque, 14°25′N, 87°37′W, 566 m, *Webster et al. 12748* (LL). **Cortés**: Cerca de Choloma, carretera San Pedro Sula–Cortés, 15°30′N, 88°00′W, 100 m, *Molina 6667* (F, LL). **El Paraíso**: valley of Río Dantas, barranco El Muro, 14°10′N, 86°30′W, 733 m, *Webster et al. 12048* (MO). **Gracias a Dios**: Mosquitia, Río Plátano, 0–4 hrs. upriver from village of Ras, 15°30′N, 84°40′W, 0 m, *Gentry et al. 7521* (F, MO). **Islas de la Bahía**: Isla de Roatán, camino entre Roatán y Sandy Bay, 16°23′N, 86°30′W, 0–50 m, *Nelson & Romero 4495* (MO). **Olancho**: Culmi, 14°45′N, 86°00′W, 500 m, *Nelson & Romero 4634* (MO). **Santa Bárbara**: Montana al mineral del Mochita, 15°10′N, 88°20′W, 900 m, *Molina 5603* (F). NICARAGUA. **Carazo**: 1 km E of San Marcos, 11°55′N, 86°12′W, *Neill 260* (MO). **Chontales**: Cerro Oluma, Cordillera Amerisque, 750 m, *Gentry et al. 43918* (MO). **Jinotega**: below Peñas Blancas via El Tuma, 13°15′N, 85°41′W, 1200 m, *Neill 7139* (MO). **Managua**: El Zapotal E of Managua, 12°09′N, 86°07′W, 15 m, *Garnier 1049* (K). **Matagalpa**: 7 km al NO de Esquipulas, 12°40′N, 85°43′W, 800 m, *Moreno 25421* (MO). **Río San Juan**: between Río Santa Cruz and Caño Santa Crucita, 11°03′N, 84°25′W, 50 m, *Stevens 23408* (MO). **Zelaya**: 12 km SW of Bonanza near Lago Siempreviva, 14°02′N, 84°34′W, 300 m, *Neill 4037* (MO). COSTA RICA. **Alajuela**: Bord de la route à Carrillo, 09°54′N, 83°33′W, 300 m, *Pittier 2497* (CR, G, US). **Cartago**: Las Vueltas, Tucurrique, 635 m, *Tonduz 7481* (BM, CR, GH, K, US). **Guanacaste**: 17 km SW of Nicoya, 12 km SW of Curime, 10°03′N, 85°32′W, 100–300 m, *Liesner 5027* (MO). **Heredia**: Finca La Selva, the OTS Field Station, 100 m, *Wilbur 34424* (MO). **Limón**: Río Colorado between Caño Bravo and Caño Pereira, 10°43′N, 83°42′W, 5 m, *Stevens 24058* (MO). **Puntarenas**: Osa Peninsula near Rincón, 09°55′N, 84°13′W, *Gentry 1210* (F, MO). **San José**: El General Viejo, El General Valley, 09°11′N, 83°30′W, 750 m, *Williams et al. 28484* (F, MO). PANAMA. **Bocas del Toro**: Lower Río San Pedro Valley, 08°49′N, 81°33′W, *Gordon 20D* (MO). **Canal Zone**: Barro Colorado Island, Fuertes Cove, 09°11′N, 79°57′W, *Croat 8136* (MO). **Chiriquí**: W of Río Chorchita, 08°22′N, 82°15′W, *Gentry 5849* (MO). **Cocle**: 1 mi. N of El Valle, 08°36′N, 80°33′W, *Gentry & Dwyer 3572* (MO). **Darién**: Río Balsas between Manene and Río Coasi, 08°15′N, 77°59′W, *Hartman 12523* (MO). **Herrera**: 1.4 mi. S of Ocú, 07°57′N, 80°47′W, *Gentry 3129* (MO). **Los Santos**: 10 mi. N of Tonosí, 07°24′N, 80°27′W, *Tyson et al. 2941* (MO, SCZ). **Panamá**: Río Corona, along Pan Am Hwy., 08°27′N, 80°01′W, *Gentry 2903* (MO). **San Blas**: Ailigandi, 09°14′N, 78°01′W, 0–66 m, *Hammel & D'Arcy 4997* (MO). **Veraguas**: 2 mi. S of Santa Fe, 08°31′N, 81°05′W, *Gentry 2942* (MO).

TRINIDAD AND TOBAGO. **Trinidad**: Tamana, 10°20′N, 61°05′W, *Broadway 5600* (MO). **Tobago**: The Widow, 11°15′N, 60°44′W, *Broadway 4576* (U).

COLOMBIA. **Amazonas**: Puerto Nariño, 03°29′N, 70°30′W, 100 m, *Rudas et al. 2023* (MO). **Atlántico**: Barranquilla, Juanmina, 10°58′N, 74°54′W, 10 m, *Dugand*

6926 (COL). **Boyacá:** El Humbo, 1333 m, *Laurance 800* (MO). **Caquetá:** 21–22 km E of Morelia, 01°31′N, 75°41′W, 260–280 m, *Gentry et al. 9074* (MO). **Chocó:** 31 km E of Quibdó, ca 14 km E of Tutunendo, 05°45′N, 76°32′W, *Gentry & Brand 36887* (MO). **Córdoba**: Río Sinu, 09°24′N, 75°49′W, 120–200 m, *Cuadros 4175* (MO). **Cundinamarca**: Guaduas, 1040–1320 m, *García-Barriga 12338* (COL). **Guaviare**: Río Ranchería, 02°35′N, 72°38′W, 100 m, *Haught 4023* (COL). **Magdalena**: Rincón Hondo, *Allen 412* (MO). **Meta:** Sierra la Macarena, Río Guapaya, 02°45′N, 73°55′W, 475 m, *Philipson et al. 1689* (COL). **Nariño**: Mun. Tumaco, Llorente, 01°49′N, 78°46′W, *de Benavides 627* (COL). **Putumayo**: Río Putumayo opposite mouth of Río Gueppi, 00°30′N, 76°00′W, 200 m, *Gentry et al. 22117* (MO). **Santander**: Barranca Bermeja (El Centro), 07°03′N, 73°52′W, 100 m, *Haught 2212* (MO). **Valle**: Río Naya, Puerto Merizalde, 03°16′N, 77°25′W, *Cuatrecasas 14296* (COL). **Vaupés**: Mitu, lower Río Kubiyu, 01°08′N, 70°03′W, *Zarucchi 1261* (MO). ECUADOR. **El Oro**: Road Zaracay–Las Piedras, 250 m, *Harling et al. 15624* (MO). **Esmeraldas**: W of San Mateo, Reserva Forestal de Jardín Tropical, Universidad Técnica Luis Vargas Torres, 00°54′N, 79°37′W, 100–130 m, *Gentry & Lajones 73057* (MO). **Guayas**: 2–4 km W of Bucay, 02°10′S, 79°06′W, 170 m, *Gentry 12287* (MO). **Los Ríos**: 12.5 km E of Patricia Pilar, Centinela, 02°45′S, 80°33′W, 466 m, *Hansen et al. 7784* (MO). **Manabí**: Cuchilla Seca above Estero Perro Muerto, Machalilla National Park, 01°36′S, 80°42′W, 480 m, *Gentry & Josse 72645* (MO). **Napo**: Coca, Coca–Yuca road 15 km SE of Coca, 03°03′S, 79°40′W, 250 m, *Harling et al. 19877* (MO). **Pastaza**: Río Capihuari, 02°30′S, 76°50′W, 285 m, *Øllgaard et al. 35079* (AAU, MO). **Pichincha**: 35 km N of Santo Domingo de los Colorados, 00°15′S, 79°09′W, 250 m, *Gentry 9593* (MO). PERU. **Amazonas**: 65 km N de Pinglo, Río Santiago, 04°26′S, 77°39′W, 200 m, *Huashikat 1813* (MO). **Cusco**: Quispicanchis Province, 13°13′S, 70°45′W, 643 m, *Núñez 13813* (MO). **Huánuco**: San Martín–Río Sion, 07°40′S, 76°46′W, *Schunke 2359* (COL, MO). **Junín**: E de La Merced, 11°03′S, 75°19′W, 1000 m, *Schunke 6213* (LA). **Loreto**: Alto Amazonas, Río Pastaza, lago Rimachi, 04°20′S, 76°35′W, 200 m, *Díaz & Ruiz 936* (MO). **Madre de Dios**: Manú National Park, Cocha Cashu, 11°45′S, 71°00′W, *Emmons 1025* (MO). **Pasco**: Oxapampa, Palcazu valley, on Río Palcazu, 10°10′S, 75°13′W, 300 m, *Smith 3929* (MO). **Puno**: ridge between Río Candamo and Río Guacamayo, 13°30′S, 69°50′W, 400–600 m, *Gentry et al 77002* (MO). **San Martín**: Puerto Pizana, Mariscal Cáceres, Tocache Nuevo, 08°11′S, 76°30′W, 350 m, *Schunke 6872* (MO). **Ucayali**: Yarinacocha (Cano a Pucallpa), 250 m, *Vásquez & Jaramillo 1542* (MO). BOLIVIA. **Beni**: Cercado Province Trinidad, 14°49′S, 64°48′W, 150 m, *Gentry & Perry 77504* (MO). **Cochabamba**: Todos Santos–Chapare, 17°30′S, 65°40′W, 300 m, *Steinbach 428* (F, MO, NY, U, WIS). **La Paz**: Chaquimayo, 17 km NW of Apolo near Río Marchariapo, 14°34′S, 68°28′W, 1000 m, *Gentry 71118* (MO). **Pando**: Nicolás Suárez Río Tahuamanu, 11°06′S, 67°36′W, *Fernández & Susanna 8498* (MO). **Santa Cruz**: Parque Amboro, 17°42′S, 63°35′W, 530 m, *Seidel 3045* (MO). VENEZUELA. **Amazonas**: Dept. Atabapo, Río Cunucunuma, 03°40′N, 65°45′W, 180–210 m, *Steyermark et al. 126165* (MO). **Anzoátegui**: Río León by Quebrada Danta, 10°01′N, 64°13′W, 500 m, *Steyermark 61076* (VEN). **Apure**: Distr. Muñoz, 5 km W of Bruzual–San Fernando Hwy., 07°45′N, 69°17′W, 70 m, *Davidse & González 14793* (MO). **Aragua**: Chuao, 10°13′N, 67°33′W, 50 m, *Pittier 12121* (M, VEN). **Bolívar**: Mpio. Raul Leoni, 04°18′N, 62°05′W, 490 m, *Delgado 83* (MO). **Delta Amacuro**: E of Río Grande and El Palmar, 08°20′N, 61°40′W, *Gentry & Berry 14975* (MO). **Distrito Federal**: between La Sabana and Caruao, 10°37′N, 66°23′W, *Berry 924* (MO). **Falcón**: Cerro Socopo, 10°30′N, 70°45′W, 440–1200 m, *Liesner et al. 8295* (MO). **Lara**: Serranía de Terapaima, S de Barquisimeto, 10°10′N, 69°30′W, 800–1000 m, *Saer 443* (VEN). **Maracay**: 10°15′N, 67°36′W, *Vogl 817* (M). **Miranda**: S of Santa Cruz, 10 km W of Cupira, 10°09′N, 65°48′W, 18–20 m, *Steyermark & Davidse 116416* (MO). **Monagas**: Reserva Forestal de Guarapiche, 09°53′N, 62°53′W, 10 m, *Castillo 719* (MO). **Portuguesa**: T. F. Amazonas, Dpto. Atabapo, alto Río Orinoco, 30 km al SE de La Esmeralda, 03°05′N, 65°52′W, *Aymard 8017* (MO). **Sucre**: Distr. Benítez, Serranía de la Paloma, 10°30′N, 63°07′W, 45–50 m, *Steyermark et al. 121402* (MO). **Yaracuy**: entre San Felipe & Marín, 10°20′N, 68°44′W, *Pittier 12093* (M, VEN). **Zulia:** Dtto. Mara, Río Cocuy, 10°52′N, 72°29′W, *Hayward 201* (MO). SURINAME. **Nickerie**: area of Kabalebo Dam project, 03°34′N, 55°59′W, 30–130 m, *Lindeman et al. 15* (MO). **Saramacca**: Saramacca River, Toekoemoetoe Creek, 05°51′N, 55°53′W, *Maguire 24918* (IAN, MICH, MO). FRENCH GUIANA. **Cayenne**: 2 ième saut de Marouini près d'Antecume Pata, 03°18′N, 54°04′W, *Cremers 4999* (MO). **Saül**: 03°38′N, 53°12′W, 220 m, *Gentry et al. 63076* (MO). BRAZIL. **Acre**: Km 60 from Rio Branco on Rio Branco-Brasileia Rd., 10°50′S, 68°00′W, *Lowrie et al. 425* (MO). **Amapá**: Oiapoque, BR 156, 109 km SSE of Oiapoque O-Calcoene, 03°00′N, 51°30′W, *Mori et al. 17241* (MO). **Amazonas**: Aeroporto de Barcelos, 00°58′S, 62°57′W, *Silva et al. s.n.* (INPA-38180) (MO). **Bahia**: Estrada Canavieiras-Ouricana, 14°00′S, 42°00′W, *Almeida 572* (CEPEC). **Ceará**: Pico Alto, Pacoti, 04°13′S, 38°56′W, *Angelica s.n.* (EAC-11712). **Distrito Federal**: Corrego Papuda, *Heringer et al. 11172* (MO). **Espirito Santo**: Reserva Florestal da CVRD, 20°51′N, 41°07′W, *Peixoto et al. 3354* (MO). **Goiás**: Estrada Alto Paraiso-Teresina, 17°52′S, 51°48′W, *Heringer et al. 2400* (MO). **Maranhão**: Engenho, Mun. de Vitoria do Arari, 04°25′S, 44°45′W, *Rosa 2463* (MO). **Mato Grosso**: MT. BR 158, depois na Rod. para o Provoado de Vila Rica, 10°S, 51′W, *Cid et al. 6448* (MO). **Minas Gerais**: 15 km W of Para de Minas, 19°15′S, 44°37′W, 760 m, *Davidse & Ramamoorthy 10808* (MO); 2 km downstream from Bela Vista, on Rio Mocoes, 03°22′S, 51°50′W, *Sobel et al. 4859* (MO). **Paraiba**: Areias, 01°21′N, 53°15′W, *Moraes 1539* (MO). **Paraná**: Parque Marumbi, 25°28′S, 48°52′W, *Gentry & Zardini 49763* (MO). **Pernambuco**: Cabo, 08°17′S, 35°02′W, *Lima 61–3725* (MO). **Piauí**: R. Napuera, abaixa do Taboleirinho, 07°00′S, 43°00′W, *Ducke s.n.* (MG-9134). **Rio Grande do Sul**: Faz. do Arroio p. Osorio, 29°54′S, 50°16′W, *Rambo 45133* (B). **Rio de Janeiro**: Petropolis Mata do Judau, 22°31′S, 43°10′W, 700 m, *Sucre & Braga 4255* (MO). **Rondônia**: Km 16 on road to Saldana close to Guajara-Mirin, *Kirkbride & Lleras 2710* (MO). **Santa Catarina**: Isla Santa Catarina, Saco Grande, 27°36′S, 48°30′W, 200–400 m, *Lourteig 2343* (MO). **São Paulo**: Cananeia, Parque Estadual da Ilha do Cardoso, 23°33′S, 46°39′W, *Kirizawa & Romaniuc 1259* (MO). URUGUAY. Playa S. Domingo, Río Uruguay, 34°12′S, 58°18′W, *Tweedie 1347* (P).

2b. Paragonia pyramidata var. **tomentosa** Bureau & K. Schum., in Mart., Fl. Bras. 8, pt. 2, fasc. 118: 182. 1896. TYPE: Brazil. Minas Gerais: Uberabá, Formigas, *Regnell III-48* (holotype?, UPS).

Young stems moderately to densely tomentose-puberulent; petioles and petiolules densely tomentose-puberulent, the distal adaxial petiolar glandular fields absent or present but obscured by pubescence; leaflets elliptic-orbicular to ovate-elliptic, infrequently narrowly to broadly elliptic, the bases rounded to broadly obtuse, or infrequently acute, the lamina nearly glabrate above and moderately to densely puberulent or tomentose-puberulent below (especially along veins); rachis and peduncles moderately to densely tomentose-puberulent; pedicels and calyces densely puberulent to tomentose-puberulent; outer surface of the capsule uniformly tan to silvery-tan or (less commonly) dark.

Paragonia pyramidata var. *tomentosa* is known from the Brazilian states of Goiás and Minas Gerais, and the Distrito Federal, as well as Paraguay (Fig. 2). Collections are known from 410 to 950 m. The few reports available indicate that *P. pyramidata* var. *tomentosa* grows on rocky forested slopes or in forested areas associated with streams or meadows. The few fertile specimens were collected at the beginning of the wet season, between August and September (Fig. 6). Fruiting collections were limited to the latter part of the wet season, from January to April.

Additional specimens examined. COUNTRY UNKNOWN. Without exact locality, *Macedo 5450* (US). BRAZIL. **Distrito Federal**: Brasilia, *Heringer et al. 1172* (MO); Brasilia, bacia do Rio São Bartolomeu, *Heringer et al. 5990* (MO); vicinity of Sobredinho, *Prance & Silva 59085* (NY); ca. 25 km N of Brasilia, *Irwin et al. 13999* (MO, NY, US); na margem do Rio das Salinas, *Kirkbride 3580* (NY), *3639* (NY). **Goiás**: ca. 20 km S of Caiaponia, *Anderson et al. 9440* (MO, NY); between Jataí and Caiaponia. 40 km from Caiaponia, *Hunt & Ramos 6272* (NY). **Minas Gerais**: ca. 15 km W of Pará de Minas, *Davidse & Ramamoorthy 10808* (MO, NY); km 618 Rodovia Uberaba-B. Horizonte, *Duarte 44873* (MO); entre Lagoa Santa e Serra do Cipó, *Duarte 6389* (MO); Rio Doce, Mun. Jaboticatubas, *Hatschbach 35255* (MO); Beira do corregodo Carmo, Ituintaba, *Macedo 586* (NY, US); Fundas, Ituiutaba, *Macedo 2608* (US); Uberabá, *Regnell s.n.* (US). PARAGUAY. In regione cursus superioris fluminis Apa., *Hassler 8418* (NY).

Nomina Nuda

Bignonia striata DC., in A. DC., Prodr. 9: 174. 1845, nomen nudum.
Temnocydia elliptica Mart. ex DC., in A. DC., Prodr. 9: 156. 1845, nomen nudum.
Temnocydia lenta Mart. ex DC., in A. DC., Prodr. 9: 159. 1845, nomen nudum.

Literature Cited

Baillon, H. E. 1888 [1891]. Bignoniacées. Histoire des Plantes 10: 1–112. Dessins de Faguet. Paris.
Bureau, L. E. 1872. Valeur des caractères tirés de la structure de la tige pour la classification des Bignoniacées. Bull. Soc. Bot. France 19: 17.
Candolle, A. P. de. 1845. Bignoniaceae. *In*: A.L.P.P. de Candolle, Prodromus 9: 142–248. Treuttel et Würtz. Paris, Strasbourg, London.
FAO (Food and Agricultural Organization of the United Nations). 1985. Agroclimatological Data for Latin America and the Caribbean. Rome.
Gentry, A. H. 1973. Bignoniaceae. *In*: R. E. Woodson, Jr. & R. W. Schery (editors), Flora of Panama. Ann. Missouri Bot. Gard. 60: 781–977.
———. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica 6: 64–68.
———. 1976a. Studies in Bignoniaceae 19: Generic mergers and new species of South American Bignoniaceae. Ann. Missouri Bot. Gard. 63: 46–80.
———. 1976b. Bignoniaceae of southern Central America: Distribution and ecological specificity. Biotropica 8: 117–131.
———. 1977. Fam. 178. Bignoniaceae. *In*: G. Harling & B. Sparre (editors), Flora of Ecuador. Opera Bot. 7: 1–173.
———. 1978. The botany of the Guyana Highland: Bignoniaceae. Mem. New York Bot. Gard. 29: 245–283.
———. 1982a. Bignoniaceae. Pp. 1–222 *in* A. Gómez-Pompa & V. Sosa (editors), Flora de Veracruz. Fasc. 24. Instituto Nacional de Investigaciones sobre Recursos Bióticos. Xalapa, Mexico.
———. 1982b. Bignoniaceae. *In*: Z. Luces de Febres & J. A. Steyermark (editors), Flora de Venezuela. 8(4): 7–433. Instituto Nacional de Parques, Caracas.
———. 1992. A synopsis of Bignoniaceae ethnobotany and economic botany. Ann. Missouri Bot. Gard. 79: 53–64.
———. 1997. Bignoniaceae. Pp. 403–491 *in* J. A. Steyermark, P. E. Berry & B. K. Holst (general editors), Flora of the Venezuelan Guayana, Vol. 3. Missouri Botanical Garden, St. Louis.
———. In press. Bignoniaceae. *In*: Flora de Colombia.
——— & A. S. Tomb. 1979 [1980]. Taxonomic implications of Bignoniaceae palynology. Ann. Missouri Bot. Gard. 66: 756–777.
Goldblatt, P. & A. H. Gentry. 1979. Cytology of Bignoniaceae. Bot. Not. 132: 475–482.
Leandro do Sacramento, P. 1820. Nova plantarum genera e Brasilia. Denkschr. Königl.-Baier. Akad. Wiss. 7: [229]–244, pl. 12–15.
Macbride, J. F. 1961. Bignoniaceae. *In*: Flora of Peru. Field Mus. Nat. Hist., Bot. Ser. 13: 3–103.
Pichon, M. 1945. Notes sur les Bignoniacées. Bull. Soc. Bot. France 92: 222–229.
Simmonds, N. W. 1954. Chromosome behavior in some tropical plants. Heredity 8: 129–146.
Sprague, T. A. 1903. *Paragonia pyramidata* Bur. Bignoniaceae. Tribe Bignonieae. Hooker's Icon. Pl. 28: t. 2771, 2772.

Index to Numbered Exsiccatae

1 = *Paragonia brasiliensis* (Baill.) A. H. Gentry; **2a** = *Paragonia pyramidata* (Rich.) Bureau var. *pyramidata*; **2b** = *Paragonia pyramidata* var. *tomentosa* Bureau & K. Schum. Collections are listed alphabetically by the principal collector. All specimens entered into TROPICOS were assumed to have been examined by A. H. Gentry. Specimens examined by the author were primarily those duplicates housed at MO, although loans of Brazilian specimens from NY and US were also examined. All collections examined by the author are indicated by a "!" in superscript.

Agostini 1626$^{!}$ **2a**; *Alencar 47* **2a**; *Allen 412*$^{!}$ **2a**, *898*$^{!}$ **2a**, *1751*$^{!}$ **2a**, *4166*$^{!}$ **2a**, *5505* **2a**; *Almeida 572* **2a**; *Alston 8715* **2a**; *Amaral et al. 439*$^{!}$ **2a**; *Anderson 11979*$^{!}$ **2a**; *Anderson et al. 9440*$^{!}$ **2b**; *Antonio & Hahn 4224*$^{!}$ **2a**; *Araquistain & Moreno 2384*$^{!}$ **2a**; *Arbo et al. 5652*$^{!}$ **1**; *Aronson 856* **2a**; *Asplund 18904* **2a**, *20398* **2a**; *Austin et al. 7162*$^{!}$ **2a**; *Ayala 2461*$^{!}$ **2a**, *2496*$^{!}$ **2a**, *2511*$^{!}$ **2a**, *3715* **2a**; *Ayala & Arevalo S. 4249*$^{!}$ **2a**; *Ayala et al. 3380*$^{!}$ **2a**, *3382*$^{!}$ **2a**, *3925*$^{!}$ **2a**, *5672*$^{!}$ **2a**, *5773*$^{!}$ **2a**; *Aymard 6213* **2a**, *8017*$^{!}$ **2a**; *Aymard et al. 6911*$^{!}$ **2a**, *6942*$^{!}$ **2a**.

Balee 1961$^{!}$ **2a**, *1963!* **2a**; *Balick et al. 2218*$^{!}$ **2a**; *Balslev & Madsen 10597*$^{!}$ **2a**; *Bangham 339* **2a**; *Barbour 5402*$^{!}$ **2a**; *Barclay 2777* **2a**; *Barfod et al. 48413*$^{!}$ **2a**; *Barreto 1500* **2a**; *von Bayern 330* **2a**; *Beaman & del Alvarez 6353* **2a**; *Beck 3456*$^{!}$ **2a**, *15135*$^{!}$ **2**, *18802*$^{!}$ **2a**, *20046*$^{!}$ **2a**; *Belem 1196*$^{!}$ **1**; *Belshaw 3120* **2a**; *Berg et al. BG756* **2a**; *Berlin 378* **2a**, *673* **2a**; *Bernardi 2914*$^{!}$ **2a**, *6653*$^{!}$ **2a**; *Berry 681*$^{!}$ **2a**, *924*$^{!}$ **2a**; *Billiet & Jadin 1610*$^{!}$ **2a**, *4602*$^{!}$ **2a**; *Black 47-1945*$^{!}$ **2a**, *49-8412* **2a**, *49-8486* **2a**; *Black & Foster 48-3394* **2a**; *Black & Ledoux 50-10726* **2a**; *Blanchet 2903* **2a**; *Bonifaz 275*$^{!}$ **2a**; *Boyan 217* **2a**; *Brandbyge et al. 30552*$^{!}$ **2a**; *Bravo H. 1* **2a**; *Breteler 3531* **2a**; *Bristan 1157p.p.* **2a**; *Broadway 2273* **2a**, *4576* **2a**, *5600*$^{!}$ **2a**; *Brown 86* **2a**; *Bunting 11611*$^{!}$ **2a**; *Bunting & Licht 835* **2a**; *Bunting & Stoddart 8904* **2a**; *Burger et al. 10602* **2a**.

Cabrera 2308$^{!}$ **2a**, *6216*$^{!}$ **2a**; *Calzada et al. 2651*$^{!}$ **2a**, *2692*$^{!}$ **2a**; *Carauta 853*$^{!}$ **2a**; *Cardona 6* **2a**, *74* **2a**, *504* **2a**, *1410* **2a**; *Carpio 1675* **2a**; *Castillo 719*$^{!}$ **2a**; *Cavalcante 1636* **2a**, *1911* **2a**, *2399*$^{!}$ **2a**; *Cavalcante & Silva 1637* **2a**; *Cazalet & Pennington 5182* **2a**; *Cedillo 3638*$^{!}$ **2a**; *Cedillo T. 2611*$^{!}$ **2a**, *3283*$^{!}$ **2a**, *3377*$^{!}$ **2a**; *Cerón 6052* **2a**; *Cerón et al. 2009*$^{!}$ **2a**; *Cerón & Cerón 4585* **2a**; *Cid & Lima 3675* **2a**, *107690* **2a**; *Cid et al. 189!* **2a**, *369*$^{!}$ **2a**, *632*$^{!}$ **2a**, *679*$^{!}$ **2a**, *6448*$^{!}$ **2a**, *6927*$^{!}$ **2a**; *Clewell & Cruz 4136*$^{!}$ **2a**; *Colella et al. 1671* **2a**; *Conrad & Conrad 3013*$^{!}$ **2a**; *Contreras 2644*$^{!}$ **2a**, *2884*$^{!}$ **2a**, *9188* **2a**, *9750*$^{!}$ **2a**; *Conzatti et al. 3070*$^{!}$ **2a**; *Cordeiro 1018*$^{!}$ **2a**; *Correa 1762*$^{!}$ **2a**; *Cowan 38330*$^{!}$ **2a**, *38458*$^{!}$ **2a**, *38556*$^{!}$ **2a**; *Cowell 193* **2a**; *Cremers 4999*$^{!}$ **2a**, *5400*$^{!}$ **2a**, *7266*$^{!}$ **2a**, *7965*$^{!}$ **2a**, *8125*$^{!}$ **2a**; *Cremers & Feuillet 12430* **2a**; *Croat 271* **2a**, *4762*$^{!}$ **2a**, *4805*$^{!}$ **2a**, *4917*$^{!}$ **2a**, *5591*$^{!}$ **2a**, *5615*$^{!}$ **2a**, *5641*$^{!}$ **2a**, *5645*$^{!}$ **2a**, *5705* **2a**, *6538*$^{!}$ **2a**, *6584*$^{!}$ **2a**, *7131*$^{!}$ **2a**, *7695*$^{!}$ **2a**, *7744*$^{!}$ **2a**, *7895*$^{!}$ **2a**, *7896*$^{!}$ **2a**, *8136*$^{!}$ **2a**, *8309A*$^{!}$ **2a**, *8370*$^{!}$ **2a**, *9106*$^{!}$ **2a**, *9227*$^{!}$ **2a**, *9510*$^{!}$ **2a**, *10161* **2a**, *10212 p.p.* **2a**, *10358* **2a**, *11932* **2a**, *14626* **2a**, *14940* **2a**, *19671*$^{!}$ **2a**, *44243* **2a**, *49782*$^{!}$ **2a**; *Cuadros 4175*$^{!}$ **2a**; *Cuatrecasas 8986* **2a**, *10835* **2a**, *14296* **2a**, *16141* **2a**, *17691* **2a**; *Cuatrecasas & Willard 26027* **2a**; *Cuatrecasas & Llano 24117* **2a**; *Cumana 1357* **2a**, *1546* **2a**; *Cuming 1179* **2a**.

Daly et al. 1408$^{!}$ **2a**; *Davidse 32184*$^{!}$ **2a**; *Davidse & González 14793*$^{!}$ **2a**, *14860*$^{!}$ **2a**; *Davidse & Ramamoorthy 10808*$^{!}$ **2b**; *Davis 818*$^{!}$ **2a**; *de Benavides 627* **2a**; *de Cabrera 4252*$^{!}$ **2a**; *de Granville 5164*$^{!}$ **2a**, *8161* **2a**; *de Granville et al. 8161*$^{!}$ **2**, *9589*$^{!}$ **2a**, *9648*$^{!}$ **2a**, *10034*$^{!}$ **2a**; *de Mello 38* **2a**; *de Moraes 1539*$^{!}$ **2a**; *de Morsie 1539* **2a**; *de Nevers 4749* **2a**; *de Nevers et al. 7628*$^{!}$ **2a**; *de Paula 1081* **2a**; *Delascio C. & Guánchez 10988*$^{!}$ **2a**; *Delgado 83*$^{!}$ **2a**; *Deward 158*$^{!}$ **2a**; *Díaz S. 793*$^{!}$ **2a**; *Díaz S. & Ruiz 871*$^{!}$ **2a**, *936*$^{!}$ **2a**; *Díaz S. et al. 213*$^{!}$ **2a**, *604*$^{!}$ **2a**, *617*$^{!}$ **2a**; *Dionizia et al. 195*$^{!}$ **2a**; *Dodson & Gentry 6436*$^{!}$ **2a**; *Dodson et al. 7105*$^{!}$ **2a**; *Duarte 763A*$^{!}$ **2a**, *4082!* **2a**, *6389*$^{!}$ **2b**, *44873*$^{!}$ **2b**; *Duarte & Falcão 3310* **2a**; *Ducke 2583* **2a**; *Dugand 6926* **2a**; *Dugand & Jaramillo 4078* **2a**; *Dugue-Jaramillo 2017* **2a**; *Duke 14251*$^{!}$ **2a**; *Duke & Nickerson 14910*$^{!}$ **2a**; *Dusén 8633!* **2a**, *12034*$^{!}$ **2a**; *Dwyer 2892*$^{!}$ **2a**, *4377A*$^{!}$ **2a**, *12924*$^{!}$ **2a**, *12996*$^{!}$ **2a**, *13053* **2a**, *14795*$^{!}$ **2a**, *Dwyer & Dieckman 13018*$^{!}$ **2a**; *Dwyer et al. 13037*$^{!}$ **2a**.

Echeverry E. 3340 **2a**; *Egler 47638!* **2a**; *Eiten & Eiten 3936*$^{!}$ **2a**; *Elcoro 317*$^{!}$ **2a**; *Emmons 51*$^{!}$ **2a**, *99*$^{!}$ **2a**, *102*$^{!}$ **2a**; *Encarnación 1269*$^{!}$ **2a**; *Enríquez 645* **2a**, *6762* **2a**; *Eugenio 216* **2a**; *Euler Marín 6* **2a**.

Fagerlind & Wibom 2344 **2a**; *Fagerlind et al. 2487b* **2a**; *Fendler 519* **2a**; *Fernández 673* **2a**, *1720* **2a**, *2555*$^{!}$ **2a**, *8498*$^{!}$ **2a**; *Ferreyra 18508*$^{!}$ **2a**; *Feuillet 123* **2a**; *Flores 62*$^{!}$ **2a**; *Florschutz & Maas 2465*$^{!}$ **2a**; *Focke 930* **2a**; *Foldats 365-App* **2a**; *Folsom 9456*$^{!}$ **2a**; *Forero et al. 1878*$^{!}$ **2a**, *2508*$^{!}$ **2a**, *3506*$^{!}$ **2a**, *4149*$^{!}$ **2a**, *4597*$^{!}$ **2a**, *5015*$^{!}$ **2a**, *6349*$^{!}$ **2a**; *Fosberg 29110*$^{!}$ **2a**; *Foster 689* **2a**, *1090* **2a**; *Foster & Terborgh 6112* **2a**; *Foster et al. 3348*$^{!}$ **2a**; *von Friedrichsthal 517* **2a**; *Froes 11739!* **2a**, *12537–231* **2a**, *26674* **2a**, *34095a* **2a**, *34095 p.p.* **2a**, *34267* **2a**; *Fromm et al. 1290* **2a**; *Fuchs & Zanella 21812*$^{!}$ **2a**.

García-Barriga 10650 **2a**, *12338* **2a**, *13844* **2a**; *Gardner 78* **2a**; *Garnier 1049* **2a**; *Garwood 1000*$^{!}$ **2a**; *Gentle 1415*$^{!}$ **2a**, *1943*$^{!}$ **2a**, *2764* **2a**, *2831* **2a**, *3100* **2a**, *3837* **2a**, *6583*$^{!}$ **2a**, *8010*$^{!}$ **2a**, *8246*$^{!}$ **2a**, *8666*$^{!}$ **2a**, *8669*$^{!}$ **2a**, *8906*$^{!}$ **2a**, *9243*$^{!}$ **2a**; *Gentry 430*$^{!}$ **2a**, *433* **2a**, *451*$^{!}$ **2a**, *719*$^{!}$ **2a**, *721*$^{!}$ **2a**, *725*$^{!}$ **2a**, *1037* **2a**, *1158*$^{!}$ **2a**, *1179* **2a**, *1180* **2a**, *1210* **2a**, *1237* **2a**, *1245* **2a**, *1282* **2a**, *1307* **2a**, *1316* **2a**, *1417*$^{!}$ **2a**, *1544*$^{!}$ **2a**, *1580*$^{!}$ **2a**, *1764*$^{!}$ **2a**, *1789*$^{!}$ **2a**, *1835*$^{!}$ **2a**, *1899*$^{!}$ **2a**, *2170*$^{!}$ **2a**, *2210*$^{!}$ **2a**, *2311*$^{!}$ **2a**, *2459*$^{!}$ **2a**, *2527*$^{!}$ **2a**, *2588*$^{!}$ **2a**, *2694*$^{!}$ **2a**, *2903*$^{!}$ **2a**, *2942*$^{!}$ **2a**, *3030*$^{!}$ **2a**, *3129*$^{!}$ **2a**, *3710*$^{!}$ **2a**, *3759*$^{!}$ **2a**, *3782*$^{!}$ **2a**, *3801*$^{!}$ **2a**, *4109*$^{!}$ **2a**, *4183*$^{!}$ **2a**, *4187*$^{!}$ **2a**, *4258*$^{!}$ **2a**, *4406*$^{!}$ **2a**, *4501*$^{!}$ **2a**, *4690*$^{!}$ **2a**, *5002*$^{!}$ **2a**, *5020* **2a**, *5246*$^{!}$ **2a**, *5588*$^{!}$ **2a**, *5849*$^{!}$ **2a**, *6384*$^{!}$ **2a**, *7795*$^{!}$ **2a**, *8070*$^{!}$ **2a**, *8080*$^{!}$ **2a**, *8223*$^{!}$ **2a**, *8247*$^{!}$ **2a**, *8259*$^{!}$ **2a**, *8286*$^{!}$ **2a**, *8432*$^{!}$ **2a**, *8462*$^{!}$ **2a**, *8491*$^{!}$ **2a**, *8547*$^{!}$ **2a**, *8579*$^{!}$ **2a**, *9348*$^{!}$ **2a**, *9560*$^{!}$ **2a**, *9593*$^{!}$ **2a**, *9666*$^{!}$ **2a**, *9732*$^{!}$ **2a**, *9990*$^{!}$ **2a**, *10065*$^{!}$ **2a**, *12287*$^{!}$ **2a**, *12465*$^{!}$ **2a**, *12484*$^{!}$ **2a**, *12501*$^{!}$ **2a**, *28195*$^{!}$ **2a**, *41242*$^{!}$ **2a**, *55611D*$^{!}$ **2a**, *69436*$^{!}$ **2a**, *70799*$^{!}$ **2a**, *71118*$^{!}$ **2a**, *78597*$^{!}$ **2a**, *79281* **2a**; *Gentry & Berry 14975*$^{!}$ **2a**; *Gentry & Brand 36887*$^{!}$ **2a**; *Gentry & Dwyer 3572*$^{!}$ **2a**; *Gentry & Estensoro 70516*$^{!}$ **2a**, *70591*$^{!}$ **2a**; *Gentry & Josse 72382* **2a**, *72645*$^{!}$ **2a**; *Gentry & Lajones 73057*$^{!}$ **2a**; *Gentry & Lott 30799*$^{!}$ **2a**; *Gentry & Mostacedo 75610*$^{!}$ **2a**; *Gentry & Núñez 66001*$^{!}$ **2a**; *Gentry & Perry 77504*$^{!}$ **2a**; *Gentry & Revilla 16319*$^{!}$ **2a**, *16364*$^{!}$ **2a**, *20498*$^{!}$ **2a**, *20794*$^{!}$ **2a**; *Gentry & Smith 44942*$^{!}$ **2a**, *45097*$^{!}$ **2a**, *45106*$^{!}$ **2a**; *Gentry & Zardini 49763*$^{!}$ **2a**, *49839*$^{!}$ **2a**; *Gentry et al. 7521*$^{!}$ **2a**, *7527*$^{!}$ **2a**, *9074*$^{!}$ **2a**, *10440*$^{!}$ **2a**, *10680*$^{!}$ **2a**, *15680*$^{!}$ **2a**, *18442*$^{!}$ **2a**, *18485*$^{!}$ **2a**, *19633*$^{!}$ **2a**, *21298*$^{!}$ **2a**, *21756*$^{!}$ **2a**, *22117*$^{!}$ **2a**, *25850*$^{!}$ **2a**, *26853*$^{!}$ **2a**, *27160*$^{!}$ **2a**, *31296a*$^{!}$ **2a**, *32497*$^{!}$ **2a**, *38143*$^{!}$ **2a**, *43918*$^{!}$ **2a**, *44316*$^{!}$ **2a**, *53813*$^{!}$ **2a**, *56186*$^{!}$ **2a**, *58807*$^{!}$ **2a**, *60149*$^{!}$ **2a**, *63076*$^{!}$ **2a**, *68772*$^{!}$ **2a**, *73879*$^{!}$ **2a**, *74306*$^{!}$ **2a**, *77002*$^{!}$ **2a**, *77250A*$^{!}$ **2a**; *Gillespie 1420*$^{!}$ **2a**, *2435*$^{!}$ **2a**, *2437*$^{!}$ **2a**; *Gilmartin 698* **2a**; *Ginés 4255* **2a**; *Glaziou 4702*$^{!}$ **2a**, *6720*$^{!}$ **2a**, *12986!* **2a**, *12971*$^{!}$ **2a**, *15159*$^{!}$ **2a**; *Gómez et al. 20363* **2a**, *21095* **2a**; *Gonggrijp 13042* **2a**; *González & Davidse 930*$^{!}$ **2a**; *Gordon 20D*$^{!}$ **2a**, *80C–b*$^{!}$ **2a**, *118C*$^{!}$ **2a**; *Goulding 75A* **2a**, *1156* **2a**, *1295* **2a**, *1325* **2a**, *1393* **2a**; *Grández 829*$^{!}$ **2a**, *1014*$^{!}$ **2a**, *1037*$^{!}$ **2a**, *1685*$^{!}$ **2a**, *2055*$^{!}$ **2a**; *Grández et al. 1088*$^{!}$ **2a**; *Grant 11002 p.p.* **2a**; *Guánchez 773*$^{!}$ **2a**;

Gudiño 1339' **2a**; *Gutiérrez 1095* **2a**; *Gutiérrez & Schultes 568* **2a**, *829* **2a**; *Gutte et al. 1627C* **2a**.

Hammel & D'Arcy 4997' **2a**; *Hansen et al. 7784'* **2a**; *Harling & Andersson 11948'* **2a**, *11965'* **2a**, *16525'* **2a**; *Harling et al. 15624'* **2a**, *19877'* **2a**; *Hartman 12523'* **2a**; *Harvey 5285* **2a**; *Hassler 8418* **2a**; *Hatschbach 1704'* **2a**, *7405* **2a**, *8630* **2a**, *25790'* **2a**, *33560* **2a**, *35255'* **2b**, *39324'* **2a**, *44498'* **2a**, *45753'* **2a**, *45978'* **2a**; *Hatschbach & Guimaraes 19067'* **2a**; *Hatschbach & Silva 50026'* **1**; *Hatschbach et al. 52475'* **2a**; *Haught 2212'* **2a**, *2725'* **2a**, *3599'* **2a**, *3988* **2a**, *4023* **2a**; *Hayes 413* **2a**, *915* **2a**, *1043* **2a**; *Hayward 192'* **2a**, *201'* **2a**; *Heringer 7214* **2a**, *8730'* **2a**, *8877* **2a**, *9483* **2a**, *10277'* **1**, *10586'* **2a**, *10635'* **2a**; *Heringer et al. 330'* **2a**, *1172'* **2b**, *2400'* **2a**, *5990'* **2b**; *Hernández G. 180'* **2a**; *Herrera 4591* **2a**, *5087* **2a**; *Heyde 419'* **2a**, *731'* **2a**; *Holm-Nielsen et al. 21080* **2a**, *21125'* **2a**, *21451'* **2a**, *21651* **2a**, *21925B* **2a**; *Holst 2031* **2a**, *4371'* **2a**, *4406'* **2a**; *Holt & Blake 686'* **2a**; *Hoogte & Roersch 3430* **2a**; *Hopkins et al. 650'* **2a**, *676'* **2a**; *Horner et al. 165'* **2a**; *Huashikat 1083'* **2a**, *1193'* **2a**, *1239'* **2a**, *1526'* **2a**, *1813* **2a**; *Huber 581* **2a**; *Huft 1925'* **2a**; *Hunt & Ramos 6272* **2a**.

IFAT 7783 **2a**; *Ibarra M. 733'* **2a**, *1107'* **2a**, *3142'* **2a**; *Irwin & Soderstrom 6851'* **2a**; *Irwin et al. 8145!* **2a**, *9464!* **2a**, *13999'* **2b**, *31159'* **1**, *55547'* **2a**, *55548'* **2a**, *57646'* **2a**.

Jacobs 2963 **2a**; *Jansen-Jacobs 1661'* **2a**; *Jaramillo & Coello 4149 p.p.* **2a**; *Jaramillo-Mejía & Palacios 7914* **2a**; *Játiva & Epling 931'* **2a**; *Jones 306* **2a**; *Kayap 105'* **2a**, *116'* **2a**, *151'* **2a**; *Kennedy & Steiner 2454'* **2a**; *Kerber 178* **2a**; *Kernan 119* **2a**, *130'* **2a**, *1107* **2a**; *Killeen 2853'* **2a**; *Killip 35078'* **2a**, *37242* **2a**, *37531* **2a**; *Killip & Smith 30593'* **2a**; *Kirizawa & Romaniuc N. 1259'* **2a**; *Kirkbride 3639'* **2b**; *Kirkbride & Kirkbride 3580'* **2a**; *Kirkbride & Lleras 2710'* **2a**; *Klein 1142'* **2a**; *Klug 1283'* **2a**, *1676'* **2a**, *1996'* **2a**, *2623'* **2a**, *3409'* **2a**; *Knab 18'* **2a**; *Knapp & Alcorn 7426'* **2a**; *Kohkemper 931* **2a**; *Krukoff 6213'* **2a**, *6272!* **2a**, *8739'* **2a**; *Kuhlmann 594* **2a**, *1102* **2a**, *2272'* **2a**, *6117* **2a**, *7160'* **2a**, *41414'* **2a**.

Lanjouw 1169 **2a**; *Lasser & Foldats 3010* **2a**; *Lathrop 6766* **2a**, *6773* **2a**; *Laughlin 269* **2a**; *Lawesson et al. 43471* **2a**, *43549* **2a**; *Lawrance 800'* **2a**; *Lent 3304* **2a**; *León 459'* **2a**, *719* **2a**; *Lescure 241'* **2a**, *798'* **2a**, *2385* **2a**; *Lewis 4048'* **2a**, *12490* **2a**, *12719* **2a**, *12933* **2a**, *37628'* **2a**, *37669'* **2a**; *Lewis et al. 171'* **2a**; *Liesner 1978* **2a**, *5020* **2a**, *5027* **2a**; *Liesner & Carnevali 22766'* **2a**; *Liesner & González 9180'* **2a**; *Liesner & Morillo 13974'* **2a**, *14021'* **2a**; *Liesner et al. 7673'* **2a**, *8295'* **2a**; *Lima 61–3725'* **2a**; *Lima & Nelson 755'* **2a**; *Lindeman et al. 15'* **2a**, *99'* **2a**; *Lizot 73* **2a**; *Londoño et al. 1608'* **2a**; *Long 118* **2a**; *Lourteig 2342* **2a**, *2343'* **2a**; *Lowrie et al. 425'* **2a**; *Luetzelburg 114* **2a**, *327* **2a**; *Lugo 2922'* **2a**, *3010'* **2a**; *Lund 783* **2a**, *2047* **2a**; *Lundell 6463'* **2a**, *16060'* **2a**, *16351'* **2a**.

Maas et al. 5477' **2a**, *5546'* **2a**; *Macedo 586* **2b**, *2608* **2b**; *Maguire 24918'* **2a**; *Maguire & Fanshawe 23366* **2a**; *Maguire & Stahel 25001* **2a**; *Maguire et al. 36759* **2a**, *53989'* **2a**; *Marcano-Berti 281* **2a**; *Maria 101* **2a**; *Marín 3'* **2a**, *6* **2a**, *731'* **2a**; *Martinelli 7151'* **2a**; *Martínez 13387'* **2a**, *13399'* **2a**; *Martínez S. 15066'* **2a**, *15215'* **2a**, *15220'* **2a**, *15741'* **2a**, *15747'* **2a**; *Martins & Nunes 7660'* **2a**; *Martius 2976* **2a**, *2977* **2a**, *20464* **2a**; *Matuda 1477 p.p.'* **2a**, *16610* **2a**, *17822* **2a**; *Maxon 4795* **2a**; *McDaniel & Rimachi 17622'* **2a**, *26563'* **2a**, *26603'* **2a**; *McDowell 3282'* **2a**; *McVaugh 15707* **2a**; *Meave 1277'* **2a**; *Melo 597'* **2a**; *Mendonca 1014'* **2a**; *Mexía 6077'* **2a**, *6181'* **2a**, *6369'* **2a**, *6471 p.p.'* **2a**; *Miranda 6762* **2a**; *Mitchell 75* **2a**; *Molina R. 1807* **2a**, *5603* **2a**, *6667* **2a**; *Molina & Molina 25719* **2a**; *Molina et al. 18242* F **2a**; *Montgomery 18'* **2a**; *Morales 3542* **2a**, *3867* **2a**, *4015* **2a**, *4181* **2a**; *Moran 29* **2a**; *Moreno 14654A* **2a**, *23825'* **2a**, *23969'* **2a**, *25421'* **2a**; *Moreno & Sandino 14651'* **2a**; *Mori & Gracie 21969'* **2a**; *Mori & Souza 17619'* **2a**; *Mori et al. 17241'* **2a**, *20400'* **2a**, *21029'* **2a**; *Morillo & Liesner 9000'* **2a**.

Nee 24741' **2a**, *34287'* **2a**, *37060'* **2a**; *Nee & Mori 4049'* **2a**; *Nee & Taylor 29338'* **2a**; *Nee & Tyson 10898'* **2a**; *Neill 260'* **2a**, *3693'* **2a**, *4037'* **2a**, *4583'* **2a**, *7135'* **2a**, *7139'* **2a**, *8719'* **2a**, *9187'* **2a**, *9661'* **2a**, *9902'* **2a**; *Neill & Zaruma 7047'* **2a**; *Neill et al. 8331'* **2a**; *Nelson 2098'* **2a**, *7141'* **2a**; *Nelson & Romero 4495'* **2a**, *4634'* **2a**; *Nelson & Vargas 2706'* **2a**; *Neto et al. 125* **2a**; *Nijenhuis 642'* **2a**; *Núñez 6010'* **2a**, *6895'* **2a**, *12101'* **2a**, *12732'* **2a**, *13813'* **2a**, *14011'* **2a**, *14025'* **2a**; *Núñez et al. 8019'* **2a**, *10823'* **2a**, *11049'* **2a**.

Oldeman 1733 **2a**, *2304'* **2a**, *B-1236'* **2a**, *B-3607'* **2a**, *B-4195'* **2a**, *T-223'* **2a**, *T-647'* **2a**, *T-736'* **2a**; *Oldeman & Sastre 114'* **2a**, *126'* **2a**; *Oliveira 3776'* **2a**, *4181!* **2a**; *Øllgaard et al. 35079'* **2a**; *Opler 602* **2a**, *603* **2a**, *713* **2a**, *804* **2a**, *1613* **2a**, *1718* **2a**, *1877* **2a**, *1882* **2a**; *Ortiz 1097'* **2a**, *2122'* **2a**.

Pabst & Pereira 8364' **1**; *Pacheco 1496* **2a**; *Palacios 2476'* **2a**; *Peixoto 3515* **2a**; *Peixoto et al. 3354'* **2a**, *3515'* **2a**; *Peña 410* **2a**; *Pereira 771'* **2a**; *Pereira & Pabst 9539'* **1**, *9705'* **1**; *Pereira et al. 4291* **2a**; *Perrottet 2851* **2a**; *Philipson et al. 1689* **2a**; *Pickel 884!* **2a**; *Pinesta 4* **2a**; *Pipoly 4445'* **2a**; *Pipoly et al. 14765'* **2a**; *Pires 3891'* **2a**; *Pires & Belem 12210* **2a**; *Pires & Silva 10845* **2a**; *Pires et al. 623'* **2a**, *16837'* **2a**, *50877'* **2a**, *51544* **2a**; *Pittier 2497* **2a**, *5577* **2a**, *6688* **2a**, *7568* **2a**, *12093* **2a**, *12121* **2a**, *12162* **2a**, *12178* **2a**; *Pizziolo 162* **2a**, *271'* **2a**; *Plowman et al. 6943'* **2a**, *9037'* **2a**; *Pontual 46–64* **2a**; *Poveda 1103* **2a**; *Prance & Silva 59085* **2a**; *Prance et al. 1139* **2a**, *2728* **2a**, *3981'* **2a**, *4171* **2a**, *6857'* **2a**, *8131'* **2a**, *8817'* **2a**, *9760'* **2a**, *9770'* **2a**, *10705'* **2a**, *10732'* **2a**, *11073'* **2a**, *11139'* **2a**, *13997'* **2a**, *14022'* **2a**, *15090'* **2a**, *15231'* **2a**, *16318'* **2a**, *24610'* **2a**, *25601'* **2a**, *25781'* **2a**, *25887'* **2a**, *26131'* **2**, *28749'* **2a**, *28820'* **2a**, *P25318'* **2**, *P25601'* **2a**, *P25710'* **2a**, *P25781'* **2a**, *P25887'* **2a**; *Prevost 1465'* **2a**; *Prevost & Grenand 2010'* **2a**; *Pulle 391* **2a**, *462 p.p.* **2a**.

Rabelo & Nonato 1389' **2a**; *Rabelo et al. 1837'* **2a**, *2018'* **2a**; *Rambo 45133* **2a**, *45309* **2a**; *Ramírez 208'* **2a**; *Regnell III-48* **2a**; *Reitz & Klein 8110!* **2a**, *8622'* **2a**, *9383* **2a**; *Restrepo 485'* **2a**; *Revilla 465'* **2a**, *500'* **2a**, *511'* **2a**, *604'* **2a**, *615'* **2a**, *720'* **2a**, *731'* **2a**, *774'* **2a**, *786'* **2a**, *799'* **2a**, *1335'* **2a**, *1797'* **2a**, *1803'* **2a**, *1850'* **2a**, *1866'* **2a**, *2012'* **2a**, *2100'* **2a**, *2284'* **2a**; *Ribeiro 450* **2a**, *1573'* **2a**; *Riedel & Langsdorff 179A* **2a**; *Rimachi Y. 688'* **2a**, *4339'* **2a**, *5794'* **2a**, *8175'* **2a**; *Riviere 296'* **2a**; *Robleto 575'* **2a**, *609* **2a**; *Rodrigues 223* **2a**; *Rohr 69* **2a**; *Rombouts 642* **2a**, *821* **2a**; *Romero-Casteñeda 1053* **2a**, *2079* **2a**, *2110* **2a**, *2126* **2a**, *2674* **2a**, *6160* **2a**; *Rosa 2463'* **2a**; *Rudas et al. 2023'* **2a**; *Ruiz 1405'* **2a**; *1507'* **2a**; *Ruiz & Jaramillo 1129'* **2a**; *Rusby 485* **2a**; *Rusby & Squires 12'* **2a**; *Rutkis & Foldats 87* **2a**; *Rutkis & Udris K. 986* **2a**, *1033* **2a**.

Saddi 7083 **2a**, *7187* **2a**; *Saddi & de Lamonica-Freire 2859* **2a**; *Saer 443* **2a**; *Sandino 4801'* **2a**; *Santos et al. 202'* **2a**; *dos Santos 352* **2a**; *dos Santos et al. 40'* **2a**, *78'* **2a**, *101'* **2a**, *139'* **2a**, *168'* **2a**, *201'* **2a**, *228'* **2a**, *230'* **2a**, *273'* **2a**, *436'* **2a**; *Sastre 1792'* **2a**, *5965'* **2a**; *Sastre & Echeverry 659'* **2a**; *Saunders 188'* **2a**, *299'* **2a**, *380'* **2a**, *449'* **2a**; *Schipp 347'* **2a**, *S-71'* **2a**; *Schmalzel & Schupp 959'* **2a**; *Schultes 3990* **2a**, *5421* **2a**, *5423* **2a**, *5498* **2a**;

Schultes & Cabrera 12825 **2a**, *13242* **2a**, *14942A* **2a**, *16229* **2a**; *Schunke V. 31'* **2a**, *2359'* **2a**, *4885'* **2a**, *6213'* **2a**, *6872'* **2a**, *8500'* **2a**, *12337'* **2a**, *12371'* **2a**; *Seemann 400* **2a**; *Sehnem 7995* **2a**; *Seibert 1513* **2a**, *1890'* **2a**, *2010'* **2a**, *3045'* **2a**; *Sendulsky 504'* **2a**; *Serv. For. Cayenne 7783* **2a**; *Sessé & Mociño 2393* **2a**, *2399* **2a**, *2405* **2a**; *Seymour 21404* **2a**; *Silva 445* **2a**; *Silva & Hatschbach 789'* **2a**; *da Silva 213* **2a**, *7106'* **2a**; *Skutch 3884* **2a**, *4133* **2a**, *4697* **2a**, *4885* **2a**; *Smith 756'* **2a**, *1645'* **2a**, *3929'* **2a**, *6656* **2a**; *Sobel et al. 4859'* **2a**; *Soeprata 45J* **2a**; *Solomon et al. 8159* **2a**; *Sousa & Magallanes 7263* **2a**; *Sparre 18888* **2a**, *19984* **2a**; *Spruce 2408'* **2a**, *3192'* **2a**; *St. Hilaire B745* **1**; *Standley 19915* **2a**, *40941* **2a**, *55566* **2a**, *56622* **2a**, *60621* **2a**, *87669* **2a**, *89136* **2a**, *89232* **2a**; *Stannard & Arrais 683'* **2a**; *Starry 150'* **2a**; *Steege 366'* **2a**, *550'* **2a**; *Stein et al. 3973'* **2a**; *Steinbach 428'* **2a**, *6904'* **2a**; *Stelle 50'* **2a**; *Stergios 10319* **2a**, *10755* **2a**, *11001A* **2a**, *11975* **2a**; *Stergios & Aymard 7633'* **2a**, *7655'* **2a**, *9051'* **2a**, *9189'* **2a**; *Stergios & Delgado 12927* **2a**; *Stergios & Ortega 2453'* **2a**; *Stergios & Taphorn 4845'* **2a**; *Stergios et al. 5091'* **2a**, *6065'* **2a**, *8277'* **2a**, *9892'* **2a**; *Stern et al. 1875* **2a**, *33686'* **2a**; *Stevens 7482'* **2a**, *8007'* **2a**, *8278'* **2a**, *12031'* **2a**, *19954'* **2a**, *23408'* **2a**, *23840* **2a**, *24058* **2a**, *24394* **2a**, *24600* **2a**; *Stevens et al. 18741'* **2a**, *19504'* **2a**, *19707'* **2a**, *24860* **2a**; *Stevenson 3'* **2a**; *Steyermark 38674* **2a**, *44932* **2a**, *61076* **2a**, *61137* **2a**, *61498* **2a**, *87784* **2a**, *89115* **2a**, *90761* **2a**; *Steyermark & Davidse 116252'* **2a**, *116416'* **2a**; *Steyermark & Gibson 95642* **2a**; *Steyermark & Liesner 121012'* **2a**; *Steyermark & Manara 110992'* **2a**; *Steyermark et al. 102023 p.p.* **2a**, *117140'* **2a**, *120660* **2a**, *121402'* **2a**, *122660* **2a**, *123272'* **2a**, *126165'* **2a**, *131912'* **2a**; *Strudwick et al. 3365'* **2a**; *Sucre & Braga 4255'* **2a**; *Sytsma 1948'* **2a**, *3502'* **2a**.

Tahe 230 **2a**; *Tamara Núñez 206* **2a**; *Terborgh 6112'* **2a**; *Thieme 903'* **2a**, *5393* **2a**; *Timaná 745'* **2a**, *754'* **2a**, *1182'* **2a**, *1847'* **2a**; *Timaná & Rubio G. 2262'* **2a**; *Tonduz 6857* **2a**, *7481* **2a**, *8249* **2a**, *13864* **2a**; *Torres et al. 3066* **2a**; *Triana J. 4124-7* **2a**; *Trujillo 17326* **2a**; *von Tuerckheim 7648'* **2a**; *Tulleken 323* **2a**, *402* **2a**, *415* **2a**; *Tun O. 1116* **2a**, *1214'* **2a**, *1274* **2a**, *1885'* **2a**, *1912'* **2a**; *Tunqui 342'* **2a**, *500'* **2a**, *619'* **2a**; *Tutin 1551* **2a**; *Tweedie 1347* **2a**; *Tyson et al. 2941'* **2a**, *3102'* **2a**.

Ubiratan 202' **2a**; *Ugent 75'* **2a**; *Ule 5216* **2a**, *5276* **2a**, *5697* **2a**.

Vargas 539 **2a**; *Vásquez 745'* **2a**, *3848'* **2a**, *10509* **2a**, *10599* **2a**, *11262* **2a**, *11742* **2a**; *Vásquez & Jaramillo 1252'* **2a**, *1542'* **2a**, *3645'* **2a**, *7228* **2a**, *8101'* **2a**, *8489'* **2a**, *9140'* **2a**, *9354'* **2a**; *Vazquez et al. V838* **2a**, *V1560* **2a**; *Versteeg 141* **2a**, *267* **2a**; *Villacorta et al. 844'* **2a**; *Vinda 279'* **2a**; *Vogl 817* **2a**.

Wagner 34 **2a**; *Wawra 997* **2a**; *Webster et al. 12048'* **2a**, *12748* **2a**, *16422'* **2a**; *von Wedel 1345 p.p.'* **2a**, *2377'* **2a**; *Wendt et al. 2518'* **2a**, *2812'* **2a**, *4016'* **2a**; *Went 557* **2a**; *Wetmore & Abbe 210* **2a**; *Wetmore & Woodworth 1* **2a**, *847* **2a**; *Whitefoord 2599'* **2a**; *Wiggins 10900* **2a**; *Wilbur 34424'* **2a**; *Williams 263* **2a**, *9747 p.p.* **2a**, *11449* **2a**, *11509'* **2a**, *11562* **2a**, *11604* **2a**, *11788* **2a**, *12619* **2a**, *13656* **2a**, *15185* **2a**, *15212* **2a**, *15673* **2a**, *15743* **2a**, *28484* **2a**; *Williams & Molina 14624* **2a**; *Williams et al. 28484* **2a**; *Woodworth & Vestal 454'* **2a**, *576* **2a**; *Woytkowski 6215'* **2a**, *6301'* **2a**, *7110'* **2a**, *35010'* **2a**, *35164'* **2a**; *Wurdack 225* **2a**; *Wurdack & Adderley 43007'* **2a**.

Yuncker et al. 8498 **2a**.

Zarucchi 1261' **2a**.

INDEX TO SCIENTIFIC NAMES

SYNOPSIS OF *CRATAEGUS* SERIES *APIIFOLIAE*, *CORDATAE*, *MICROCARPAE*, AND *BREVISPINAE* (ROSACEAE SUBFAM. MALOIDEAE)[1]

J. B. Phipps[2]

ABSTRACT

This paper revises four monotypic North American series of *Crataegus* (Rosaceae subfam. Maloideae). Of these, series *Apiifoliae*, *Cordatae*, and *Microcarpae* all possess short-shoot and extension shoot leaves with secondary veins to both the lobes and the sinuses, while series *Brevispinae* only exhibits this attribute on extension shoot leaves. The brilliantly red-fruited *C. marshallii* of series *Apiifoliae* is widespread and common in the southeastern United States and is most closely related to European species, particularly in foliage characters. The species-pair *C. phaenopyrum* (ser. *Cordatae*) and *C. spathulata* (ser. *Microcarpae*) have glossy foliage and small, orange-red, orbicular fruits, and are a little less closely related to European species. *Crataegus phaenopyrum* is mid-Atlantic in range, westward to the Ozarkian area, while *C. spathulata* is a common southeastern species. *Crataegus brachyacantha* (ser. *Brevispinae*) is the most distinctive of the species treated, being black-fruited with different short-shoot foliage and restricted to Louisiana and the bordering parts of adjacent states. Line drawings and distribution maps are presented for each species described, and representative specimens are cited. The selection of taxa for this paper also reflects the fact that the author had been intending to treat *Crataegus* for the now defunct *Vascular Flora of the Southeastern United States* (vol. 1, Cronquist, 1980).

This paper is a further one of mine revising *Crataegus* (Rosaceae subfam. Maloideae) of North America. The first (Phipps, 1988) was devoted to series *Aestivales* (Sarg. ex C. K. Schneid.) Rehder and introduced the genus. This was followed by my monograph of northern Mexican *Crataegus* (Phipps, 1997) and an introduction to the red-fruited *Crataegus* of western North America (Phipps, 1998). The current paper assembles a group of monotypic series all with greater or lesser affinities to European subgenus *Crataegus*. This subgenus was established by El-Gazzar (1980) on the basis of its deeply lobed short-shoot leaves with veins to the sinuses. The taxa treated here comprise the native North American species with deeply lobed short-shoot leaves, as well as one in which the long-shoot leaves alone are deeply lobed.

El-Gazzar (1980) mistakenly held that all *Crataegus* taxa with deeply lobed short-shoot leaves possessing veins to the sinuses were Eurasian. However, there are American series with this attribute, including series *Apiifoliae* (Loudon) Rehder, which fits very comfortably into subgenus *Crataegus* as perceived by El-Gazzar. Its foliage is of the typical monogynoid shape, by which I imply a shape like that of *C. monogyna* Jacq., characteristic of many European species of section *Crataegus*. Further American series possessing lobed short-shoot leaves with veins to the sinuses are series *Cordatae* (Beadle) Rehder and series *Microcarpae* (Loudon) Rehder, each of which has small flowers, small fruit (often orange-red in color), and 3–5 nutlets. These last two series have no very close relatives outside North America. In addition to North American *Crataegus* species with short-shoot leaves lobed to their sinuses, there are also native American taxa of *Crataegus* that include elements intermediate between subgenus *Crataegus* and subgenus *Americanae* El Gazzar—a reason that I am not using El-Gazzar's subgeneric taxa in this revision. The intermediate kinds are principally a group of series normally lacking veins to the si-

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nuses on the short-shoots, but usually possessing these veins on the extension shoots. It should be noted that nearly all hawthorns can produce at least a few extension-shoot leaves that are both deeply lobed and with veins to the sinuses. Clearly the distinction involved is not nearly as sharp as was once believed. Possessing such intermediate characteristics but not closely related to the above three series are series *Lacrimatae* J. B. Phipps, *Virides* (Beadle ex Sarg.) Rehder, and *Brevispinae* (Beadle) Rehder. Series *Brevispinae* is treated in this paper. Due to taxonomic complexity, however, treatment of the series *Virides* is reserved for a separate article. The same is true for series *Lacrimatae*, which is also particularly complex, as evidenced by Beadle's (1903) having included 77 species in this group. The taxonomy of series *Lacrimatae* is under active revision by the author.

Of the species considered here, *Crataegus marshallii* Eggl. (ser. *Apiifoliae*) is very close to members of series *Crataegus*; *C. phaenopyrum* (L. f.) Medik. (ser. *Cordatae*) has large, distinctive leaves, with rather triangular lobes and veins to the sinuses, but otherwise very unlike those of other hawthorns; *C. spathulata* Michx. (ser. *Microcarpae*) has curiously lobed, very small leaves, often somewhat blue to dull green, of a shape unique in *Crataegus.* Finally, *C. brachyacantha* Sarg. & Engelm. (ser. *Brevispinae*) is treated here somewhat for convenience. With black fruits, short recurved thorns, and entire short-shoot leaves, it is a very distinct American hawthorn. However, even in series *Brevispinae*, the presumably plesiomorphic (Phipps, 1983; Phipps et al., 1991) veins to the sinuses show up in the deeply lobed leaves of the long shoots.

Taxonomic difficulties in *Crataegus* are frequently held to be due to hybridization. This has been extensively documented in Europe, but while it occurs in North America, for this continent there is little documentation. Indeed, the four species treated here yield very few examples of putative hybrids, these being restricted to a handful of apparently non-persistent specimens of probable *C. marshallii* × *C. mollis* (s.l.) parentage, as discussed after *C. marshallii.*

MATERIALS AND METHODS

This study has been made possible by the loan of over 2000 herbarium specimens from 43 different herbaria. Thereby the great majority of variation within the species studied should have become evident. Typification of all species and their synonyms was attempted, although in a few cases it was too difficult to complete. These exceptions are clearly indicated in the text.

The numbering of the species in this paper is continuous with that of Phipps (1988). The depth of lobing of leaves is quantified as the "leaf incision index" (LII), widely referred to in the text. LII is a percentage value lying between unlobed (0%) and lobed to the mid vein (100%). The flowering season is given relative to other sympatric species of *Crataegus* and ranges from "early" to "very late." Distribution maps for each species have been created by computer on the basis of recording latitude/longitude coordinates for the very large number of exsiccatae studied. Due to the few taxonomic problems encountered with the *Crataegus* species here only a reduced list of exemplary exsiccatae (one per county) is appended, while the maps show all the locations that can be separated at the scale used.

TAXONOMIC TREATMENT

The taxonomic treatment commences with a key to series and is followed by taxon descriptions with lists of representative exsiccatae. [Note: "leaves" throughout key and taxonomic descriptions refer to short-shoot leaves, unless otherwise specified. Square brackets indicate those series to be treated in other papers by the author.]

1a. Short-shoot leaves deeply lobed (LII ≥ 35%); veins to sinuses always present.
    2a. Leaf blades 2–4 cm wide; lobes and sinuses triangular .... III. *Crataegus* ser. *Cordatae*
    2b. Leaf blades less than 2 cm wide; lobes and sinuses various.
        3a. Leaf blades < 1.3 × longer than wide, the sinuses narrow; bark rough, not exfoliating.
            4a. Inflorescences subglabrous; thorns indeterminate, often becoming branchlets; petals orbicular .... [I. *Crataegus* ser. *Crataegus*]
            4b. Inflorescences tomentose; thorns of determinate origin; petals elliptic .... II. *Crataegus* ser. *Apiifoliae*
        3b. Leaf blades > 1.5 × longer than wide, the sinuses relatively shallow and broad; bark smooth, exfoliating .... IV. *Crataegus* ser. *Microcarpae*
1b. Short-shoot leaves shallowly lobed (LII ≤ 35%) or unlobed; veins to sinuses absent.
    5a. Fruit black or deep purple when fully ripe.
        6a. Short-shoot leaves unlobed; extension-shoot leaves usually deeply lobed, with veins to sinuses; petals turning orange with age; thorns ≤ 1.5 cm long, conspicuously recurved; fruit with a strong bluish bloom unless abraded; nutlets unpitted .... V. *Crataegus* ser. *Brevispinae*
        6b. Short-shoot leaves lobed or not; extension-shoot leaves not usually deeply

lobed, usually lacking veins to sinuses; petals never turning orange with age; thorns usually 1.5–4 cm long, slightly recurved to straight; fruit not usually so strikingly bloomy before full ripeness, when black to deep crimson-purple; nutlets usually laterally pitted .... [*Crataegus* ser. *Douglasii*]

5b. Fruit usually red when fully ripe, occasionally greenish, yellow, orange, pink or purple (if pink, usually eventually becoming bright red underneath a bloom) .... [all other North American *Crataegus* series]

II. **Crataegus** series **Apiifoliae** (Loudon) Rehder, Man. cult. trees Ed. 2: 367. 1940. *Crataegus* sect. *Apiifoliae* Loudon, Arbor. frutic. brit. 824. 1835–1838. TYPE: *Crataegus marshallii* Eggl.

Bushes or small *trees* usually 2–8 m tall; usually with crown of somewhat tabulate branches; *trunk* to 20 cm diam., usually much less, lacking branched thorns; bark grayish, flaking; thorny, with simple thorns. *Leaves* long-petiolate, small, broad-ovate to deltate in outline, deeply lobed with 3 or 4 main lobes each side; veins to major sinuses and lobes at wide (45°–70°) angle with midrib. *Inflorescence* many-flowered; pedicels pubescent; anthesis season mid–early. *Flowers* medium-sized; calyx lobes narrowly triangular, margins slightly lobed; petals elliptic; stamens 20, anthers red; styles 1–3. *Fruit* commonly 6 × 3 mm, ellipsoid to occasionally spherical, glossy, bright red, flesh mealy when ripe; *pyrenes* 1–3, convex dorsally.

One species, southeastern United States; widespread and common.

Crataegus ser. *Apiifoliae* has obvious similarities to the European series *Crataegus* in its distinctive leaf shape, relatively small flowers, and small and few-pyrened fruit. However, it differs from the latter series in only possessing fully developed thorns of definite growth. Differences from series *Crataegus* are sufficiently large to postulate a moderately long period of separation, a point of view also supported by fossil *Crataegus* materials from the Pacific Northwest Tertiary with somewhat similar foliage (e.g., Chaney, 1927). However, one cannot discount the alternative possibility of origin by mid-Tertiary long-distance dispersal of ancestral *Crataegus* with these leaf types across the Atlantic from Europe.

4. **Crataegus marshallii** Eggl., Rhodora 10: 79. 1908. *Mespilus apiifolia* Marshall, Arbust. amer. 89. 1785, non Medik., 1793. *Crataegus apiifolia* (Marshall) Michx., Fl. bor.-amer. Ed. 1. 1: 287. 1803. TYPE: Not located.

Parsley Haw. Figure 1.

Bushes or small *trees* usually 2–8 m tall, usually single trunked with larger specimens having a crown of somewhat tabulate branches; *trunks* to 20 cm diam., usually much less, lacking compound thorns; *bark* grayish, flaking; *branchlets* unarmed or sparsely to moderately thorny with usually simple thorns[3]; extending shoots densely appressed pubescent; 1-year-old shoots pubescent or glabrescent, gray-brown; older gray; *thorns* straight or slightly recurved, slender, (1–)2–3(–5) cm long. *Leaves* deciduous; petioles slender, 1–2 cm long, pubescent; blades small (1.5–3 cm long), broad-ovate to deltate in outline, densely pubescent on both sides when young, ± glabrescent with age except on the main veins below; deeply lobed with (2–)3 or 4(–5) main lobes on each side, sinuses often closed distally by overlapping lobe margins, the margins toothed; veins extending to major sinuses and lobes at a wide (45°–70°) angle with midrib. *Inflorescence* 3–8-flowered; pedicels very pubescent; anthesis mid–early. *Flowers* 12–17 mm diam.; hypanthium glabrous to slightly pubescent externally; calyx lobes 3–4 mm long, narrowly triangular, pubescent adaxially, glabrous abaxially, margins glandular-serrate; petals elliptic, commonly 6–8 mm long, white or very rarely pink; stamens 20, filaments ca. 7 mm, anthers red, 0.5 mm long; styles 1–2(–3). *Fruit* commonly 4–6 mm long, ellipsoid to occasionally spherical, glossy bright red (rarely dull orange) at maturity, flesh mealy when ripe; *pyrenes* 1–2(–3), convex dorsally.

One of the commonest of southern United States hawthorns, *C. marshallii* has a wide distribution from Arkansas to Virginia (Fig. 2) southward to eastern Texas and central Florida, with a few outliers in Oklahoma, southern Missouri, and southern Illinois. It is absent from the southern and eastern parts of Florida. It is found in a variety of open wooded habitats, in woodland openings and edges, successional habitats, fence lines, etc., although not normally in dense shade. It occurs both in quite wet and obviously well-drained soils. *Crataegus marshallii* is known to be hardy to USDA Zone 5, but this may not be true for all provenances. Flowering mostly late March to early April, but as early as mid-February in some seasons in central Florida.

Crataegus marshallii is the only representative of series *Apiifoliae* and as such is not very closely related to other native North American hawthorns

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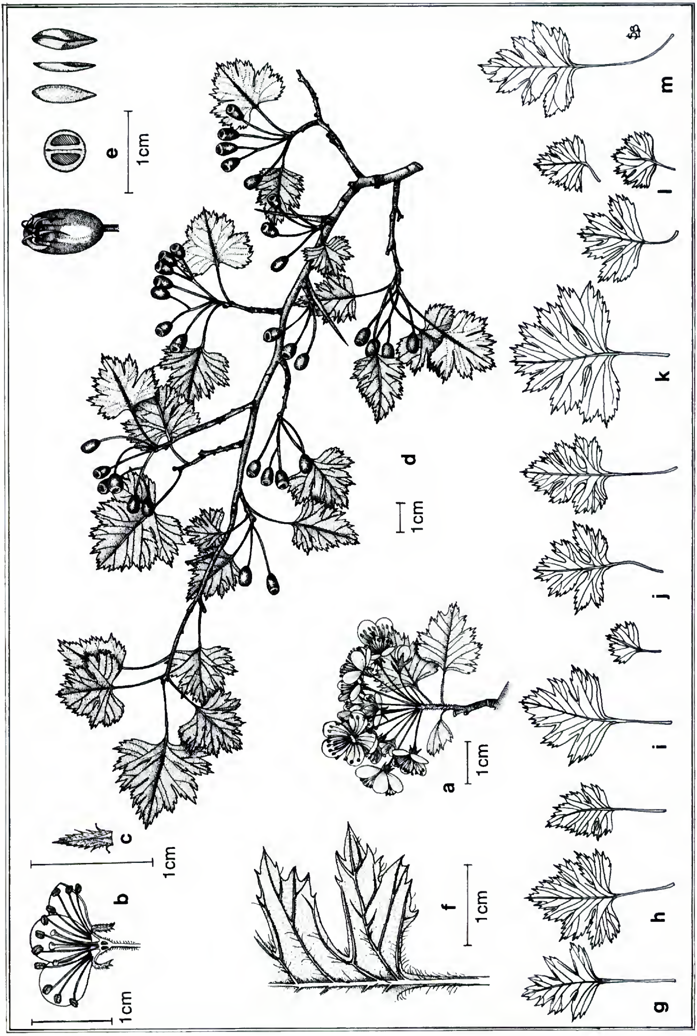
[3] The young shoots are sometimes thorn-like but with small distal herbaceous appendages. These structures may either elongate or become true thorns.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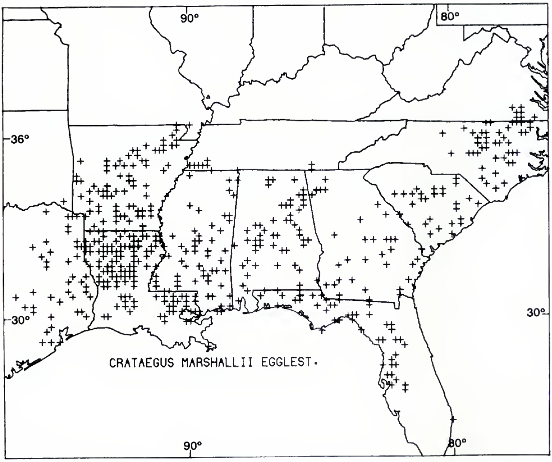

Figure 2. Distribution of *Crataegus marshallii.* Based on collated herbarium records for *The Vascular Flora of the Southeastern United States* (Cronquist, 1980) area; incomplete northward. + = exsiccatae seen by me, △ = literature records.

(Phipps, 1983). I have been unable to access Humphrey Marshall's herbarium at West Chester University, West Chester, Pennsylvania, where there may be type material. However, there is no doubt that Marshall's protologue exactly fits the accepted concept of *C. marshallii* Eggl.

Variation in *Crataegus marshallii* is not sharply segmented into often readily identifiable local populations, as can occur in apomictic forms, and the species therefore appears to be sexual, although critical evidence is lacking. As a 20-stamen species, it is probably also diploid. Variation in length and density of foliar pubescence occurs, and there is substantial variation in plant size and habitat, which could well have a genetic base. There are also slight variations in leaf shape and size, especially in the sharpness of lobes and teeth and the relative width and depth of the sinuses, but this study did not detect infraspecific variants based on any combination of such characters. Much of the variation in leaf shape can be found on one specimen, i.e., *Thieret & Williams 17369* (LAF) from Tangihapoa Parish, Louisiana. The elliptic petal shape of *C. marshallii* is quite unusual in *Crataegus,* as are the small anthers. A form with flowers turning pink at late anthesis has been discovered in northeastern Texas by the late Houston nurseryman Lynn Lowrey, and was being assessed for the retail trade.

Representative specimens examined. U.S.A. **Alabama:** Baldwin: Mobile, *Mohr s.n.* (MSC-43853, US). Calhoun: ca. ½ mi. NE of Nesbit Lake, *Morelle s.n.* (JSU-10086). Cherokee: county road 19, ca. 6.5 mi. S Centre, *Kral 34476* (TENN). Chilton: near Cadena, *Palmer 38920a* (A). Dallas: 1 mi. WNW Cahaba ravine, *Kral 45352* (VDB). Etowah: Attalla, *Anonymous H532* (A, US). Fayette: Mount Vernon, *Mohr s.n.* (A, US). Geneva: swamp of Choctawhatchee River, ca. 1.2 mi. NW of Highbluff jct., *Clark 7589* (NCU). Greene: 5 mi. SE from Eutaw by picnic area

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Figure 1. *Crataegus marshallii.* —a–c. Inflorescence and flower parts from *Phipps 5318* (UWO). —d. Fruiting branch from *Phipps 5180* (UWO). —e. Fruit and parts from *Moreland 991* (NLU). —f. Leaf, abaxial surface from *Phipps 5180* (UWO). —g–m. Leaf variation from several sources (sequence from left to right): g, *Thieret & Williams 17286* (FSU); h, *Phipps 5180* (UWO); i, *Moreland 991* (NLU); j, *Phipps 5113* (UWO); k, *Phipps 5178* (UWO); l, *Phipps 5318* (UWO); m, *Thieret & Williams 17969* (USLH).

of Lock 7, *J. L. Thomas et al. T1058* (NCU, UNA). Hale: by Co. road 10, at jct. Ala. 61, 9 mi. N of Uniontown, *Kral 45385* (VDB). Lee: Auburn, *Earle et al. s.n.* (GH, US). Lowndes: near Mt. Sinai Church on N side of Hwy. 6, *Phipps et al. 5318* (UWO). Marengo: right-of-way of Co. road 44, ca. 4 mi. E of Dayton, *Clark 13714* (NCU). Montgomery: along Alabama River, Montgomery, *Harbison 25* (A). Morgan: *Smith s.n.* (GH, US). Perry: 3.5 mi. E of Uniontown, *J. L. Thomas 1930* (NCU, NLU, UNA, USF). Pike: Conecuh R. bottoms by US 231, NW side Troy, *Kral 47327* (VDB). St. Clair: 2.5 mi. S Asheville on US 231, *Kral 30380* (GAM, VDB). Sumter: 6 mi. N of York, hwy. 17, RR crossing, Flatwoods region, *Jones 15548* (LSU, NCU, VDB). Tallapoosa: Concord Church and Cemetery area, 4.5 mi. N of Dadeville, *Rutland 1997* (AUA). **Arkansas:** Bradley: P.O. Warren, *Demaree 24819* (FSU, GH, NCU). Calhoun: P.O. Hampton, *Demaree 14403* (GH, MO). Clark: N side of I-40, rest area at Arkadelphia, *Phipps 5884* (UWO). Clay: Moark, *Palmer 4787* (A, MO, US). Cleburne: Heber Springs, *Palmer 6971* (A, MO). Columbia: P.O. Waldo, *Demaree 39231* (GH, NCU). Craighead: Crowleys Ridge, *Demaree 28795* (GAM, GH, NCU, NO). Desha: near Dumas, *Ashe s.n.* (NCU-8465). Drew: low hills, *Demaree 4376* (US). Faulkner: near Conway, *Palmer 26493* (A, MO). Franklin: lower end of Devils Hollow near Mill Creek, *Barber 583* (UARK). Garland: Lake Hamilton island, *Demaree 39481* (FSU, GH, NCU). Grant: banks of Saline River, *Demaree 16313* (A, MO, NO, WVA). Greene: P.O. Walcott, Crowleys Ridge State Park, *Demaree 27946* (GH). Hempstead: Fulton, *Bush 53* (MO). Hot Springs: Magnet Cove, *Palmer 26613* (A, UARK). Howard: Bakers Springs, *Kellogg 18* (A, MO). Independence: Batesville, *Palmer 29769* (A, MO, UARK). Jackson: Newport, *Letterman s.n.* (A). Lafayette: S of Walnut Hill, *Montz 4191* (LSU). Miller: Texarkana, *Bush 2226* (A). Montgomery: P.O. Hopper, *Demaree 55131* (USLH, WVA). Nevada: Prescott, *Bush 71* (MO). Ouachita: Twin Bayou bottoms, P.O. Camden, *Demaree 14417* (A, GH, MO, US). Pike: Rosboro, *Demaree 9473* (A, GH, MO). Polk: Hwy. 8 W from Mena, *Patterson 96* (UARK). Pulaski: behind the Little Rock University botany greenhouse, *Sinclair 1730* (NLU). Scott: near Upper Black Fork Basin of Poteau River, *Lynn s.n.* (UARK). St. Francis: N side of I-40, 2 km W of Ark. 78, *Phipps 5883* (UWO). Warren: Warren Prairie, *Kral 64781* (VDB). White: Bald Knob, *Anonymous H2863* (US). **Florida:** Alachua: Gainesville, *Murrill s.n.* (DUKE, GAM-2311, UWO). Calhoun: Chipola R., W of Blountstown, *Godfrey 63072* (FSU, MSC, USLH, VDB). Dixie: Old Town, *Harbison 5605* (A). Escambia: E edge of Bluff Springs, *Beckner et al. 1086* (DUKE, FLAS). Gadsden: River Junction, *Curtiss 5983* (DOV, GAM, FLAS, GH, MO, US). Gilchrist: ca. 7 mi. N of Fanning Springs, at the end of the road to Hart Springs, County Park, along the Suwannee River, *Hansen et al. 10838* (USF). Hernando: vicinity of Brooksville, *Jones s.n.* (US-1086801). Hillsborough: along Morris Bridge Road, *Cooley et al. 5857* (FLAS, USF). Jefferson: ½ mi. rise near Girardeau's Camp, *Exploration Party 1939* (FLAS). Leon: banks of Ochlochnee R., 10 mi. W Tallahassee, *Coker et al. s.n.* (NCU-77619). Marion: 10 mi. N of Ocala, *W. A. Murrill s.n.* (FLAS-43415). Suwannee: S of Luraville, *Arnold et al. s.n.* (FLAS-45214). Taylor: near Gulf Coast, *Harbison 10* (A). Wakulla: near Aucilla R. Rt. 98, *Williams s.n.* (FSU-15214). **Georgia:** Baker: Flint River above junction with Ichawaynochaway Creek, *Thorne 7143* (GAM). Bartow: along S side of Green Pond 6.8 mi. 58° E of Adairsville, *Duncan et al. 12769* (GAM). Charlton: St. Mary's River at Traders Hill S of Folkston, *Duncan 1975* (GAM). Dodge: Ocmulgee River swamp along US highway 280, W of Rhine, *Bozeman 5472* (NCU). Emanuel: 1.3 km (0.8 mi.) S of Interstate Route 16 on US Route 1, *Wood et al. 4365* (CI). Floyd: Rome, *Anonymous B1436* (US). **Louisiana:** Caldwell: clay soil on hillside E of Copenhagen and La. 849 of the Ouachita River, Sec. 13, T12N, *R. D. Thomas et al. 95071* (UWO). Lasalle: Northern half of Sec. 11 in old Bartram's Prairie, SW of U.S. 84 and SE of U.S. 165 S, *R. D. Thomas 94590* (UWO). Orleans: New Orleans, *Drummond 105* (UWO). Union: closed Spencer School along road W of La. 143, *R. D. Thomas et al. 87883,* (USCH, UWO). Vernon: 6 mi. NW of Leesville, *Wolff s.n.* (MSC). **Mississippi:** Clay: Tibbee Creek bottoms S of West point, *McDaniel 2328* (IBE). Covington: 2.5 mi. W of Collins, *McDaniel 2960* (IBE). Forrest: NW Corner Marble St. and 39th Ave., Hattiesburg, *Woofer 2707* (FSU). Forrest & Lamar: Hattiesburg, *Harbison 36* (A). George: in White Bluff area of University of Mississippi, *Pullen 63159* (GAM, NCU). Greene Co.: roadside near McLain on US 98, *Phipps et al. 5337* (UWO). Grenada: 5 mi. W of Holcomb, *McDaniel 2340* (IBE). Harrison: Biloxi, *Seymour et al. 36* (DUKE, GH, MSC, NCU, NO). Itawamba: 17 mi. S of Belmont, Senter place, *Martin II-181* (IBE). Jackson: Ocean Springs, *Skehan s.n.* (MO). Lauderdale: Meridian, *Anonymous H4156* (US). Lowndes: Columbus, *Anonymous H4189* (US). Marion: at old Oxbow Lake along Pearl River at Columbia, Hwy. 98, *Jones et al. 6496* (GAM). Newton: 5 mi. W of Newton, Jackson Prairie Region, *Ray 7785* (FLAS, GH, NCU, USF). Oktibbeha: 15 mi. S of Starkville, Noxubee Game Refuge, *McDaniel 1687* (FSU, NO, UNA). Pearl River: Walkiak Bluff, Pearl River ca. 8 mi. NW of Picayune, *Sargent et al. 11389* (GAM). Simpson: Saratoga, *Trach 8697* (MO). Smith: Bienville National Forest ca. 6.25 mi. NE of Pineville, NE4 S22 ca. 0.5 mi. W of Co. Rd., *Mitchell 29* (IBE). Stone: 7 mi. E Wiggins, *Ray 7689* (FSU, NSU, USF, VDB). Wayne: Waynesboro, *Pollard 1224* (GH, MO, US). Wilkinson: N of Woodville near Doloroso, *Ray 7962* (GH). Winston: ca. 4.0 mi. NW of Louisville, *Smith 502* (UWO). **North Carolina**: Bladen: near Clarkton, *Anonymous 2091a* (US, MO). Cumberland: 2.8 mi. N of jct. US 301 and NC. 24 on river road, *Ahles 36666* (NCU). Durham: along Little Creek near NC 54, 2 mi. E of Chapel Hill, *Britt 1213* (NCU). Edgecombe: near Tar River 1.5 mi. NNE of Rock Mount, *Radford 32032* (NCU). Franklin: along Tar River, about 3 mi. E/SE of Bunn, *Ahles et al. 11388* (NCU, VDB). Granville: Camp Butler, *Batson 747* (DUKE). Halifax: phone line road at a point 0.2 mi. NE of intersection of 1327, *Wickland 1192* (NCU). Hertford: 3.3 mi. NNE of Union, *Ahles et al. 52351* (FLAS, NCU). Johnston: bank of Neuse R., Boone Twp, 9 mi. below Smithfield, *Fox et al. 1277* (GAM, GH, NCSC, TENN). Lenoir: bank of Neuse River, near Kinston, *Totten s.n.* (NCU). Northampton: 1.3 mi. NW of Bryantown, *Ahles 41875* (CM, NCU). Orange: US rte. 70 W of Linden Road, Hillsborough, *Boufford 12037* (CM). Pender: Cape Fear River above Holly Shelter Lodge, *Fox et al. 180* (NCSC). Wayne: close to Neuse R., *Phipps 5113* (UWO). Wilson: Contentnea Creek, near Rock Ridge, *Radford 40810* (NCU). **Oklahoma:** McCurtain: 10 mi. E of Idabel on Okla. 3, *Citty 144* (NLU). **South Carolina:** Bamberg: 5.1 mi. ENE of Ehrharot on County Rt. 21, *Ahles et al. 22221* (NCU). Barnwell: Sta. 64 of Atomic Energy Commission, Savannah River Operations Area, *Kelley et al. s.n.* (USCH). Berkeley: Wambaw Creek at highway bridge, 6 mi. NW of McClellanville, *Little 14337* (NCU). Charleston: Ravenel, vicinity of Charleston, Bear Swamp, *Hunt 3189* (CLEMS, NCU). Chesterfield: highway between Cheraw and Society Hill, 2 mi. from Cheraw, *Coker et al. s.n.* (NCU). Colleton: 5 mi. S of Ruffin, on US 21, *Batson s.n.* (USCH). Darlington: slopes of Lynches River W of Hartsville, *Smith 953* (NCU). Fairfield: ¾ mi. NE of Blairs, *Freeman 5675* (NCU). Florence: 4 mi. E of Olanta & S of Byrds Crossroads, *Bell 6090* (NCU). Jasper: 5.5 mi. S of US Rt. 321 on Co. Rt. 90, *Ahles et al. 10341* (FSU, GAM). Kershaw: S of Lugoff along US 601 about 1 mi. N of jct. with Co. Rt. 28-47, *Leonard 1261* (AUA, CLEMS, DHL, LYN, MARY, NLU, NO, TENN, UNA, USCH, VCU, WILLI, WVA). Lexington: Congaree River, West Columbia, *Radford 9022* (NCU). Marion: along Co. Rt. 49 ca. 15 mi. S of Britton Neck, *Bell 11033* (NCU). Orangeburg: 0.4 mi. N of jct. of Co. Rts. 164 & 42 on Co. Rt. 42 (S of Bowman), *Ahles et al. 21674* (NCU). Richland: Columbia, Bower's Beach, *Philson s.n.* (A, DUKE, USCH). **Tennessee:** Fayette: Creek bottom, shaded, 1.25 mi. WSW Mason, *Kral 19895* (VDB). Hamilton: Lookout Creek at base of Lookout Mtn. on or near Chamblin property, *Sharp et al. 15923* (TENN). Hardeman: Ames Plantation—1 mi. SW Ed. McKinney house, *Hebb 26958* (TENN). Shelby: bottoms of Wolf River, NE of Germantown *Sharp et al. 6592* (TENN). **Texas:** Anderson: 2.3 mi. NW of Palestine, *Shinners 12976* (SMU). Angelina: 6 mi. W of Lufkin, *Parks 8012* (TAEM). Bowie: N-side I-20 5 km E of Texas 8, *Phipps et al. 5255* (UWO). Galveston: 1/2 mi. E of I.H. 45, Dickinson, *Waller et al. 3370* (TEX). Grimes: on Rt. 30, 0.5 mi. E of Navasota R., *P. Fryxell 2883* (SMU, TEX, UWO). Hardin: SW of Kountze, *Lundell & Lundell 10900* (TEX). Harris: Buffalo Bayou, a mi. S of Memorial Drive, *Smith 35* (SMU). Henderson: off 175, NW of Poynor, *Lundell & Lundell 11111* (SMU). Jasper: about 8 mi. N of Jasper on US 96 r.h.s., *Phipps et al. 6074* (UWO). Lamar: 2.5 mi. W of Paris, *McVaugh 7144* (SMU). Madison: 3 mi. S of Normangee on Farm Rd. 39, *Clark 378* (TAEM). Nacogdoches: Nacogdoches, *Parks 28074* (TAES). Newton: 4 ⅔ mi. S of Newton, along Big Cow Creek, *Cory 52598* (SMU, TEX, UWO). Polk: at edge of "Gumbo Glade," *Tharp et al. s.n.* (SMU). San Jacinto: mixed pine-hardwood forest around Double Lade campground, *Hartman 1171* (TAEM). Shelby: 7.7 mi. NW of Aiken, *Correll & Correll 29070* (TEX). Van Zandt: Silver Lake, *Reverchon s.n.* (SMU). **Virginia:** Dinwiddie: near Carson, *Fernald et al. 5793* (MO). Greensville: 1 mi. NW of Dahlia (near Pleasant Hill), *Mikula 8643* (WILLI). Southampton: near Branchville, *Heller 965* (A, MO). Sussex: along Nottoway R., SW of Homeville, *Fernald et al. 10280* (GH).

Putative hybrids:

Crataegus ×*notha* Sarg., J. Arnold Arbor. 3: 9. 1922. TYPE: U.S.A. Arkansas: Hempstead Co., hills abt. 5 mi. NE of Fulton, 26 Sep. 1921, *E. J. Palmer 20646* (A) [suspected *C. marshallii* Eggl. × *C. brachyphylla* Sarg. (ser. *Molles*)].

Five specimens were known in 1922.

Crataegus lacera Sarg., Bot. Gaz. 33: 123. 1902. SYNTYPES: U.S.A. Arkansas: Fulton, 2 Oct. 1900, *C. S. Sargent s.n.* (A); 23 Apr. 1901, *W. M. Canby, B. F. Bush & C. S. Sargent s.n.* (A); Aug. and Oct. 1901, *B. F. Bush s.n.* (A) [possibly *C. marshallii* Eggl. × *C. mollis* (Torr. & A. Gray) Scheele].

This rare taxon is more similar to *C. mollis* than is *C* ×*notha.*

Neither of these putative hybrids has been observed since their original collections.

III. Crataegus series **Cordatae** (Beadle) Rehder, Man. cult. trees Ed. 2: 367. 1940. *Crataegus* [subgroup] *Cordatae* Beadle [without rank], in Small, Fl. s. e. U.S. Ed. 1: 532. 1903. *Crataegus* sect. *Cordatae* (Beadle) Eggl., in A. Gray, B. L. Rob. & Fernald, Manual Ed. 7: 476. 1908. TYPE: *Crataegus cordata* (Mill.) Aiton [= *C. phaenopyrum* (L. f.) Medik.].

Small *trees,* 4–8 m tall; *trunks* with branched thorns or unarmed, bark fibrous-shredding; young *branches* with simple thorns 2–5 cm long. *Leaves* ± glabrous, ± deltate, palmately 3–5-lobed, veins extending to sinuses. *Inflorescence* 20–30-flowered; anthesis season very late. *Flowers* small, glabrous; *calyces* triangular, small; *petals* small, circular; *stamens* 20, anthers ivory; *stigmas, styles,* and carpels 3–4. Fruits 5–8 mm diam., ± orbicular, glossy, vermilion; *calyx* remnants present; *pyrenes* 3, dorsally grooved.

One species, Missouri and Arkansas to North Carolina. Found in woodlands on moist soil, generally in moderate but not very heavy shade.

This distinctive series shows some relationships, as discussed at the beginning of this paper, to series *Microcarpae, Apiifoliae,* and *Virides* in its leaf venation and small fruits.

5. Crataegus phaenopyrum (L. f.) Medik., Gesch. Bot. 84. 1793. *Mespilus phaenopyrum* L. f., Suppl. pl. 254. 1782. TYPE: *Ehrhart s.n.* (holotype, GOET).

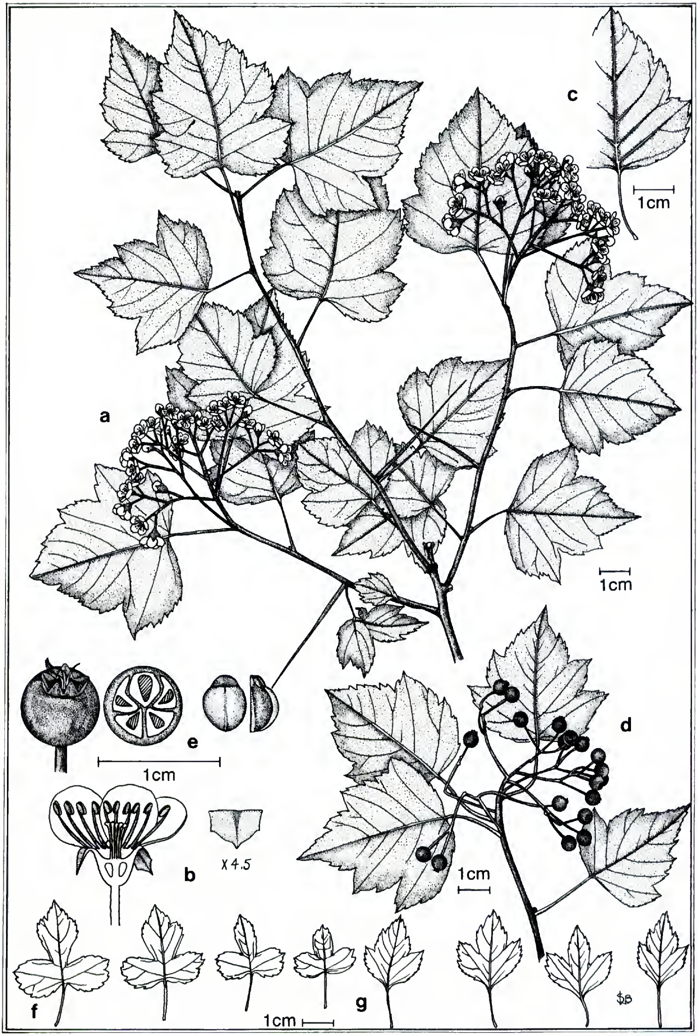
Mespilus cordata Mill., Gard. dict., Ed. 8., 1768. *Crataegus cordata* (Mill.) Aiton, Hort. kew. 2: 168. 1789, nom. prop. rej. *Phaenopyrum cordatum* (Mill.) M. Roem., Fam. nat. syn. monogr. 3: 157. 1847. TYPE: tab. 179 in Mill., Fig. pl. Gard. Dict. Ed. 1., vol. 2. 1760.

? = *Crataegus acerifolia* Lodd. ex Moench, Verz. ausländ. Bäume 31. 1785. *Mespilus acerifolia* (Lodd. ex Moench) Poir., in Lam., Encycl. 4: 442. 1798. TYPE: unknown.

Crataegus populifolia Walter, Fl. carol.: 147. 1788. TYPE: BM? (not seen).

Crataegus youngii Sarg., J. Arnold Arbor. 4: 105. 1923. TYPE: *Harbison 6028a* (holotype, A).

Washington Thorn. Figure 3.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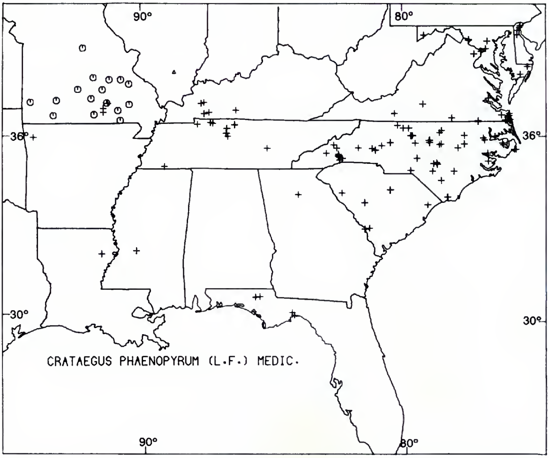

Figure 4. Distribution of *C. phaenopyrum* from collated herbarium records. Essentially complete for *The Vascular Flora of the Southeastern United States* area; incomplete northward. + = exsiccatae seen by me; △ = literature records; octagon with re-entrant tail = Steyermark records, centered by county.

Small *trees*, 4–10 m tall, usually with a single trunk; *trunks* with compound thorns, bark fibrous-shredding; extending shoots subglabrous, becoming dark purple-brown; 1-year-old shoots deep purple or brown; older grayer; young *branches* with simple ± straight thorns 2–5 cm long. *Leaves* deciduous; petioles mainly 1.5–2.5 cm long, slender, glabrous; blades usually 3–6 cm long, broadly to narrowly deltate, ± glabrous, palmately 3–5(–7)-lobed, sometimes very shallowly so, base truncate to more rarely cordate or cuneate, or leaves smaller and ovate in outline (but still lobed) in some plants from central North Carolina; *veins* extending to sinuses. *Inflorescence* 20–30-flowered; branches glabrous; anthesis very late. *Flowers* 10–12 mm diam.; hypanthium glabrous externally; *calyx lobes* broad-triangular, 2 mm long, margins entire, glabrous adaxially; *petals* circular, white; *stamens* 20, anthers ivory; *styles* 3(–4). *Fruits* numerous, globose, glossy, vermilion, 5–8 mm diam.; calyx remnants present or abscissile; *pyrenes* usually 3, dorsally grooved.

Occurring in a broad band from Missouri to North Carolina (Fig. 4), with outliers in all states southward except Alabama, from which earlier records (Clark, 1971) have proven to be vegetative *C. viridis*. Many other *Crataegus* species may possess, particularly in vegetative shoots, a more or less deltate leaf shape, and extreme caution is required in identifying such material. Possibly non-native in Delaware, D.C., and Maryland. Found in woodlands on rich soil, generally in moderate but not very heavy shade. Flowering very late, after all congeners.

This distinctive species shows some relationships to series *Microcarpae*, *Apiifoliae*, and *Virides* in its leaf venation and small fruit. The leaves of sprout shoots of *C. phaenopyrum* are often different from the mature leaves described above, tending to be both smaller and more bluntly lobed (Fig. 3, lower left). Also the terminal lobe is "waisted." Forms differentiated as *C. youngii* Sarg. on the basis of an abscissile fruiting calyx and narrower and

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Figure 3. *Crataegus phaenopyrum*. —a–c. Inflorescence, flower section and calyx lobe, and single leaf (upper right), from *Barrows 2* (UWO). —d, e. Infructescence and fruit parts from *Gattinger 803* (BM). —f, g. Variation in leaf shape is illustrated by: f, *Godfrey 81202* (UWO), lower left; and g, *Skean 377* (UWO), lower right. The Godfrey specimens are typical for sprout shoots, and the Skean specimen illustrates the "*youngii*" tendency (see text) with mature leaves.

smaller leaf blades cannot be sustained because of intermediates. These forms are found in central North Carolina, where they are quite common, with several records from Greensboro, Guilford Co., and Chapel Hill, Orange Co., as well as a few records from South Carolina and southern Virginia.

Crataegus phaenopyrum is an important woody ornamental valued for its tree-like habit, glossy, ivy-shaped leaves, fine fall color, and brilliant, persistent vermilion berries. It is widely cultivated in the central and northeastern United States and through the southern Great Lakes area. It is hardy to USDA Zone 5.

I have not considered the species *C. acerifolia* Lodd. ex Moench or *C. populifolia* Walter worth typifying. *Crataegus acerifolia* is usually considered to be a synonym of *C. phaenopyrum,* presumably on the basis of the name, and is therefore considered here for synonymy. However, Moench's herbarium no longer exists, and the protologue is poor and seemingly contradictory. Relevant detail, translated from the German (Moench, 1785), reads, "The trunk is 12 feet high and thornless. The leaves are alternate, round and of varying form, the (margins) deeply sawtoothed, . . .dark green and not shiny above, below pale green, somewhat hairy on both sides, 5 inches long and 4 broad. The petioles are 1½ inches long from which the leaves hang loosely. The 3-inch-long inflorescences. . .common flower stalks, which are hairy. . . . The five calyx lobes are lance-shaped, mostly with entire margins, and stand upright. The five petals are white, concave, oval and as long as the calyx lobes. Stamens 16–20, never more, white (e.g., filaments), as long as the petals. Anthers yellowish. Pistil is split into two diverging halves (= 2 styles?). Hypanthium is campanulate. Fruit red, ripening in October, the same size as round-leaved hawthorns, 2 pyrenes with compartments." About the only diagnostic points agreeing with *C. phaenopyrum* are leaf color, calyx margin, stamen number, and anther color. Leaf size, shape, inflorescence indumentum, and carpel number are different. The subequal calyx lobe and petal length are implausible as is the leaf size unless for sucker shoots. The deficiencies of the protologue are typical of the period. In the case of *C. populifolia,* the only *Crataegus* that could be found at HUH among the photostats of Walter's herbarium is *C. marshallii,* but the type description, though brief, is pertinent. It reads, "With trilobed subcordate leaves, the lobes incised-serrate, smooth on both sides, with long smooth petioles." *Crataegus phaenopyrum* is so distinct a species that this diagnosis probably applies. Neither of these names has any modern currency.

The name *Crataegus phaenopyrum* has been regularly in use on this continent for the Washington Thorn since Eggleston (1908) argued that Aiton's *C. cordata* (1789) represented another species, perhaps of series *Tenuifoliae.* Aiton's *C. cordata* is based on Philip Miller's *Mespilus cordata,* illustrated (tab. 179) and described in his *Figures of Plants. . .* (1760). This illustration, however, does not compare very well with *C. phaenopyrum,* the flowers being too large, and having 10 instead of 20 stamens. In addition, the toothing of the leaf margins is stronger than is normal for *C. phaenopyrum.* It is clear that the illustration is somewhat inadequate for *C. phaenopyrum.* On the other hand, the deltate leaf of the illustrated specimen does indeed resemble that of *C. populnea* Ashe or *C. iracunda* Beadle (both of ser. *Silvicolae*), and the fairly large flowers are in line with this. These taxa would have fallen within Eggeston's view of series *Tenuifoliae.* However, the illustrations are also somewhat poor for the two last-mentioned species and also Miller explicitly stated that his *Mespilus cordata* flowered in late June, which is so late as to definitely exclude series *Tenuifoliae* (sensu Eggleston) by a good month. It is clear to me that the identity of Philip Miller's *Mespilus cordata* is unknowable with any certainty, on present knowledge of American hawthorns, unless one were to embark on the arbitrary process of epitypification. Consequently, I have submitted a proposal to reject the name *Crataegus cordata* (Mill.) Aiton.

Representative specimens examined. U.S.A. **Arkansas:** Washington: river banks, NW area, *Harvey s.n.* (UARK). **Delaware:** New Castle: hedgerows and fields, *Canby 36* (CM, DOV, GH). **Florida:** Wakulla: Wakulla Springs along Wakulla R., *Palmer 38573* (A, MO). Washington: rd. C-280 about 2 mi. from its jct. with C-277, *Godfrey et al. 81275* (FLAS). **Georgia:** Gwinnett: from Buford to Cumming just E of bridge, Chattahoochee River, *Duncan 3604* (GAM). **Kentucky:** Christian: along small streams, Hopkinsville, *Palmer 17648* (A). **Maryland:** College Park Campus, *Hayden 235* (MARY). Frederick: along stream off Garfield Rd. 1 mi. from Rt. 153, N of Wolfeville, *Norris 364* (CM). Worcester: roadside 5 mi. NE of Pocomoke City on Rt. 113, *Tatnall 1822* (COV). **Mississippi:** Hinds:

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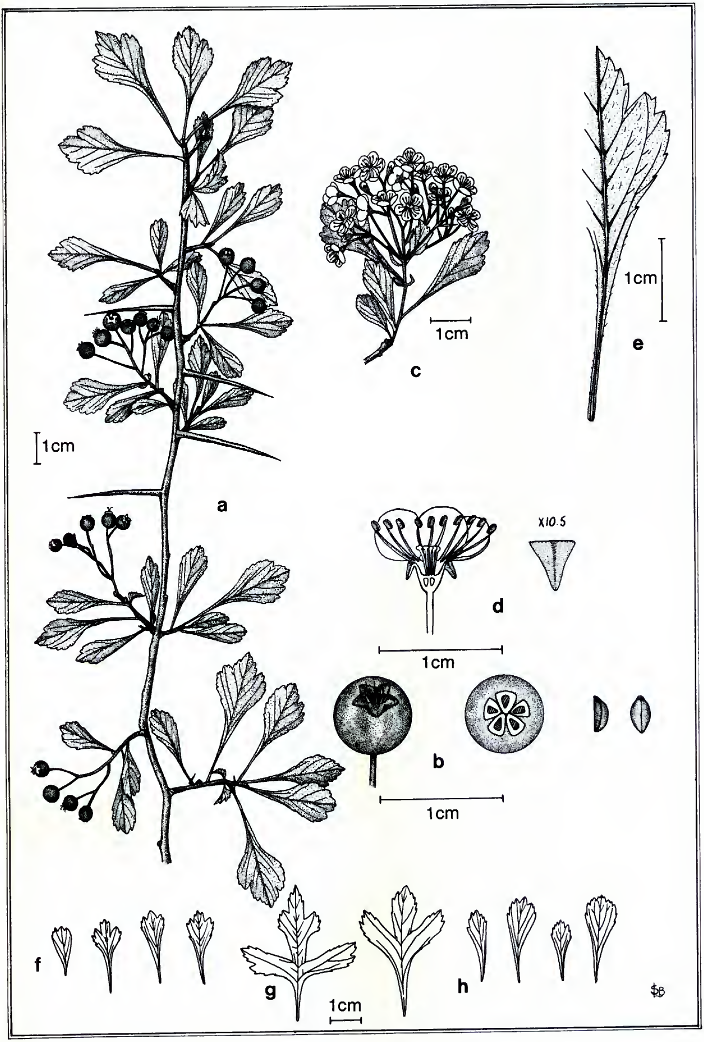
Figure 5. *Crataegus spathulata.* —a, b. Infructescence and fruit parts from *Phipps 5282* (UWO). —c–e. Inflorescence, flower parts, and magnified leaf from *Phipps 5174* (UWO). —f–h. Range of short-shoot leaves from: f, *Phipps 5303* (UWO); g, two deeply lobed long-shoot leaves from *Phipps 5174* (UWO); h, *Thomas et al. 82031* (UWO).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Jackson, *Harbison 6051* (NCU). **North Carolina:** Beaufort: 3 mi. SE of Aurora, *Blair 665* (NCSC). Buncombe: low grounds, Biltmore, *Anonymous 333b* (NCU). Catawba: Lyle Creek, between Newton & Statesville, *W. C. Coker s.n.* (NCU-77650). Chowan: 1.7 mi. ESE of Yeopin in the vicinity of Middleton Creek, *Ahles et al. 51082* (GAM). Cumberland: Methodist College Campus, *Crutchfield 5600* (AUA, CM, DHL, FLAS, KY, LYN, MARY, NCU, NO, UNA, USLH, WILLI, WVA). Davie: near foot of hill, W of Bear Creek on Statesville road near Mocksville, *Totten* (NCU). Durham: swamp of New Hope Creek by Chapel Hill-Raleigh Rd., *Totten 1* (NCU). Guilford: near SW limits of Greensboro, NW corner of intersection of I.95 and E Lee Rd., *Phipps 5120* (UWO). Henderson: NW of US. 6 5 ¼ mi. NE of Hendersonville, *Pittillo 115* (FSU, KY, NCU). Iredell: Statesville, *Patterson s.n.* (MSC-43895). Orange–Durham: Chapel Hill, swamp of Bowlins' Creek near Handcock's bridge, *Totten s.n.* (NCU). Tyrrell: by roadside canal, 5 ½ mi. W of Sandy Point Landing, *Fox et al. 4463* (NCSC). Wilson: near Contentnea Creek, 2 mi. E of Black Creek, *Radford 35682* (NCU). **Ohio:** Hamilton: near a park in Glendale, *Adams 81* (KY). Warren: Bowling Green-southern, *Price s.n.* (A). **Tennessee:** Davidson: around Nashville, *Gattinger sub Curtiss 803* (BM).

IV. Crataegus series **Microcarpae** (Loudon) Rehder, Man. cult. trees, Ed. 2: 367. 1940. *Crataegus* sect. *Microcarpae* Loudon, Arbor. frutic. brit. 825. 1835–1838. TYPE: *Crataegus microcarpa* Lindl. (= *C. spathulata* Michx.).

Small *tree* to 7 m or *bush*, often with very tabulate branching when open grown; main *trunk* erect, bark smooth with thin flakes, cream to cinnamon-brown or light gray-brown in patches; *thorns* simple, abundant to few, straightish, of medium length, 3–4(–5) cm long, blackish. *Leaves* barely petiolate; blades small, coriaceous, long-persistent, lobed, somewhat glaucous, glabrous; those on short shoots elliptic to obovate, lobes 2–3, acute to rounded, LII about 5% to 30%, veins extending to sinuses, those on rapidly elongating shoots generally more diverse in shape, more deeply lobed and larger. *Inflorescence* multi(20–30)-flowered, glabrous; anthesis late. *Flowers* small; *calyx* short-triangular; *petals* small, circular, white; *stamens* 20, anthers pale yellow; *styles* 3–5. *Fruit* small, 3–5 mm diam., globose, often numerous in a corymb, bright orange-red with 3–5 pyrenes obscurely dorsally grooved, their top quarters exposed.

One species, common and widespread in the southeastern United States, west to Texas.

6. Crataegus spathulata Michx., Fl. bor.-amer. Ed. 1: 288. 1803. *Mespilus spathulata* (Michx.) Poir., in Lam., Encycl., suppl. 4: 68. 1816. TYPE: U.S.A. North Carolina: *Michaux s.n.* (P photostat).

Crataegus microcarpa Lindl., Bot. Reg. 22: t. 1846. 1836. TYPE: U.S.A. *Lindley s.n.* (CGE not seen).

Littlehip Hawthorn. Figure 5.

Small *tree* to 7 m or *bush*, often with very tabulate branching when open grown. Main *trunk* usually erect; *bark* smooth with thin flakes, greenish when younger, then cream to cinnamon-brown or light gray-brown in patches; branchlets with extending shoots pubescent or glabrous, becoming dull reddish; 1-year-old shoots dull gray; older gray; *thorns* simple, abundant to few, straightish, of medium length, 3–4(–5) cm long, blackish. *Leaves* deciduous; petioles ± lacking; blades 1.5–3 cm long, ± coriaceous, long-persistent, lobed, somewhat glaucous; those of short shoots elliptic to obovate, narrowly cuneate below, lobes usually 0–2 per side, acute to rounded, LII about 5% to 30%, veins extending to sinuses, if present, those on rapidly elongating shoots generally more diverse in shape, more deeply lobed and larger; glabrous abaxially; adaxially somewhat hairy above especially near the midvein, becoming glabrous; rarely overall pubescent. *Inflorescence* multi(20–30)-flowered; branches glabrous; anthesis medium–late. *Flowers* ca. 10 mm diam.; hypanthium glabrous; *calyx* lobes broad-triangular, 1.5–2.0 mm long, subentire, adaxially and abaxially glabrous; *petals* 4–5 mm long, ± circular, white; *stamens* 20, anthers usually pale yellow, anthers 0.5 mm long; *styles* 3–5. *Fruit* ca. 3–5 mm diam., globose, often numerous in a corymb, bright red or orange; *calyx* present, lobes reflexed; *pyrenes* 3–5, obscurely dorsally grooved.

South-central Texas to northern Florida and north to Arkansas and Virginia (Fig. 6). A distinct and locally common species of the south, but hardly recorded from Mississippi. The fairly high frequency of collection overall for *C. spathulata* suggests that this Mississippi gap is not a collection artifact but has natural causes in which case the hypothesis may be entertained that the separate eastern and western populations derive from different Pleistocene refugia. Woods, fence-lines, and brushy places, on a variety of soils, apparently relatively heliophilous.

Crataegus spathulata exhibits considerable variation in leaf shape and fruit color. In addition, rare forms possess quite pubescent foliage. It appears to be most closely related to *C. phaenopyrum* (ser. *Cordatae*) and is possibly related to *C. viridis* (ser. *Virides*). It is very easily recognized. This is the only species of *Crataegus* known to the author regularly possessing such strikingly thin, flaking outer bark, a characteristic by which it may be easily recognized even in winter. However, *C. viridis* L.

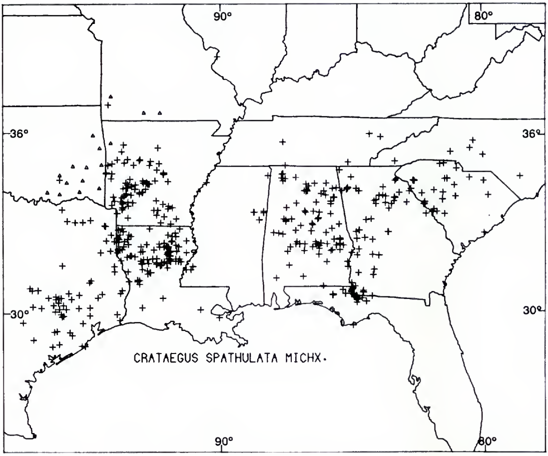


Figure 6. Distribution of *Crataegus spathulata* from collated herbarium records. Nearly all records seen for *The Vascular Flora of the Southeastern United States* area; inexact northward. + = exsiccatae seen by me; △ = literature records.

also possesses this feature in a less marked degree. The chromosome number is not known, but the variation pattern suggests that *C. spathulata* is mainly a sexual diploid.

Representative specimens examined. U.S.A. **Alabama:** Autauga Co.: Prattville, *Smith 444* (UNA). Bullock: ca. 4.5 mi. NW of Union Springs, *Clark 16384* (NCU). Cherokee: county road 18, ca. 1–3 mi. N of Calhoun-Cherokee county line, *Whetstone et al. 12239* (JSU). Colbert: ca. 3 mi. E of Littleville, in upper portion of Rosebud Hill, *Webb 4979* (TENN, UWO). Cullman: covering low banks, *Mohr s.n.* (A). Dallas: near Selma, *Palmer 38917* (A, MO). DeKalb: Al. 35, ca. 2 mi. N of junction of Little River, R-O-W under power line, *Whetstone et al. 13122* (JSU). Elmore: Wetumpka, *Churchill 73-42788* (MSC). Greene: Warrior River by Ala. 14, ca. 4.2 mi. E of Eutaw, *Kral 46853* (VBD). Jefferson: Birmingham, *Harbison 25* (A). Lee Co.: Auburn, *Earle et al. s.n.* (MO-1917666, NCU, US). Lowndes: US 80, 14 mi. E of Dallas County line, *Kral 55038* (VDB). Macon: 2 mi. S of Hardaway, *Grant 087* (AUA). Marshall: along Short Creek, *Clark 12094* (UNC). Montgomery: 2 mi. S of Sellers, *Uttal 10972* (NCU). Shelby: Oak Mountain State Park, towards the summit of mountain, *Kral 41513* (VDB). Talladega: on Ala. 76, just E of Childerburg, location "Coosa Pines," *Phipps 5488* (UWO). Tuscaloosa: 11 mi. S of city of Tuscaloosa, *Cooley et al. 3595* (USF). **Arkansas:** Ashley: P.O. Mist, *Demaree 14703* (GH). Bradley: P.O. Warren, *Demaree 24836* (GH). Calhoun: P.O. Hampton, Champagnolle Bayou Bottoms, *Demaree 16861* (TENN). Clark: between Gum Springs and Hollywood, *Phipps et al. 5244* (UWO). Drew: P.O. Wilmar, *Demaree 24109* (FSU, GH). Garland: Rifes Landing, P.O. Lake Hamilton, *Demaree 39443* (GH). Hempstead: Tokio, *Demaree 10048* (GH, MO). Hot Springs: P.O. Magnet Cove, *Demaree 124854* (GH). Howard: 5 mi. SE of Mineral Springs (ca. 35 mi. NNW of Texarkana), *Iltis et al. 684* (UARK). Miller: Texarkana, *Pringle s.n.* (GH). Montgomery: vicinity of Housley Point on Lake Ouachita National Forest, ca. 10 mi. E of Mount Ida, *Thieret 18216* (FSU, USLH). Pike: Murfreesboro, *Demaree 9963* (CI, GH). Pulaski: P.O. Natural Steps, Maumelle Mountain, *Demaree 8560* (A, GH, MO, NCU). Scott: P.O. Mansfield, *Demaree 18166* (MO). Sebastian: near Hartford, *Palmer 39328* (A, MO, US). Sevier: P.O. Ben Lomond, *Demaree 41649* (GH). Yell: on Lower road 10 mi. SW of Dardanelle, *Henbest s.n.* (UARK-36275). **Florida:** Gadsden: River Junction, *Curtiss 5989* (DOV, FLAS, GAM, GH, MO, NCU, US). Jackson: ca. 9 mi. NW of Marianna, *Godfrey et al. 54275* (FSU, DUKE, NCSC). Liberty: Torreya State Park, *Baker s.n.* (FSU). **Georgia:** Barrow: Gay's Acres, *Morgan 38* (GAM). Clarke: Athens, Agricultural Campus, *Miller E3281* (UNA). Columbia: S of eastern summit of Rosemont Mountain, *Duncan 28969* (GAM). Decatur: 1 mi. N of Chattahoochee, *Muenscher et al. 3077* (MO). Dougherty: along Flint River at Albany, *Small s.n.* (A, US). Dade: on Sand Mountain 4.1 mi. W 6°S of Trenton, *Whetstone 96* (GAM). Early: between Saffold and the Chattahoochee River, *Godfrey 79085* (FSU, MISSA). Floyd: Horseleg Mtn., *Phipps 5303* (UWO). Gwinnett: Yellow River Valley, near McGuire's Mill, *Anonymous 2095* (A, GH, NCSC, US). Hall: E of Gainsville by 7 mi., *W. H. Duncan 3232* (GAM). Harris: Blackman Place near Cataula just S of Ossahatchie Creek, *Jones et al. 22322* (FLAS, GH, USF, VDB). Madison: 4 mi. E of Danielsville, *Hume s.n.* (DUKE, FLAS). Meriwether: near Durand, *Jones 20941* (UNA, WVA). Richmond: Augusta, *Harbison 6080* (A). Seminole: N side Ga. route 91 of Chattahoochee R., *Phipps 5225* (UWO). Stephens: Curahee Mountain off Ga. route 23—U.S. route 123, *Boufford et al. 17745* (CI, MO, NCU). Sumter: near Flint R., *Harper 628* (GH, MO, US). Talbot: 3 mi. SE of Talbottom, *Duncan 5124* (GAM). Walton: 8 mi. E of Monroe, *Wiegand et al. 1377* (GH). **Louisiana:** Bossier: 2.5 mi. NW of Plain Dealing, *Allen et al. 8039* (DUKE, FSCL, GAM, NCU, NO, USLH, WVA). Caddo: Jack Price residence N of Blanchard-Shipp Road, W of Blanchard, *R. D. Thomas et al. 41810* (NLU). Calcasieu: along the Calcasieu River, *Nogle s.n.* (USLH). Caldwell: hills N of Copenhagen, E of La. 849, *R. D. Thomas et al. 35884* (NLU). Catahoula: woods beside La. 124, 3 mi. W of Duty Ferry, *R. D. Thomas et al. 43282* (NLU). DeSoto: 3.2 mi. S of US 84, S of Logansport, *R. D. Thomas et al. 68418* (NLU), *D. Dixon 2088* (NLU). Grant: roadside of Bear Creek Rd., Parish road 521, *Parker 88* (NLU). LaSalle: SW of US 84 and SE of US 165 SW of Tullos, *R. D. Thomas 94592* (TENN, UWO). Morehouse: Spyker Estate, *Crow et al. 551* (NLU). Natchitoches: Natchitoches, *Bush 5442* (CI, US). Ouachita: W of La. 557 between Cypress Creek and Caldwell Parish line, *R. D. Thomas et al. 93836* (UWO). Red River: E of Coushatta, *R. D. Thomas 45635* (NLU). Richland: Alto, *R. S. Cocks 22* (A). Winn: Kisatchie National Forest, *Kessler 1213* (NLU). **North Carolina:** Macon: Clar Creek section, on Highlands-Wallkalla road, *Wright s.n.* (NCU-11425). Montgomery: E of Narrows Dam on Yadkin River 2 mi. NW of town of Uwharrie, *Wells 3048* (NCU). Rowan: *Small et al. 47* (US). **South Carolina:** Aiken: roadside clearings along Co. Rt. 66, vicinity of jct. of Co. Rt. 103 and Co. Rt. 47, *Leonard et al. 4943* (CLEMS, MO, NCU, NLU, VCU). Anderson: Anderson, *Davis 198* (CI, NCU, US). Cherokee: SE of Gaffney, *Ahles et al. 26959* (NCU, USF). Chester: where SC 72 crosses Broad River, *Phipps 5124* (UWO). Henderson: *Davis s.n.* (CI-245197). Lexington: vicinity of Batesburg, *McGregor 107* (US). McCormick: dry pine-oak ridge 1 mi. NE of the Savannah River on S.C. 28, *Bozeman et al. 8845* (AUA, CI, DHL, FLAS, FSU, GAM, KY, LYN, MARY, NCU, NO, TENN, UNA, USCH, USLH, UWO, VDB, WILLI). Newberry: 3 mi. NW of Chappels, *Bell 9184* (NCU). Richland: old Salada Dam near Columbia, *Coker s.n.* (NCU-83574). **Tennessee:** Knox: Knoxville, *Bright 13283* (CI, UWO). **Texas:** Brazos: Bryan, *Anonymous H8076* (US). Fort Bend: few mi. WSW of Rosenburg and 1 mi. E of 541 exit, *Phipps et al. 6083* (UWO). Harris: ENE of Huffman on F.M. 1960, *Phipps et al. 6067* (UWO). Hopkins: 7 mi. W of Sulphur Springs, *Shinners 13045* (GAM, SMU). Newton: Saw Mill Road about 1.5 km W of Saw Mill Town, *Phipps et al. 6078* (UWO). Shelby: 7 mi. S of Center, *Shinners 18463* (SMU). Trinity: *Chambers s.n.* (TEX). Walker: 33 on Nature Trail, Huntsville State Park, *Mahler 8926* (SMU, UWO).

V. **Crataegus** series **Brevispinae** (Beadle) Rehder, Man. cult. trees, Ed. 2: 366. 1940. *Crataegus* [subgroup] *Brevispinae* Beadle [without rank], in Small, Fl. s. e. U.S. Ed. 1: 532. 1903. *Crataegus* sect. *Brevispinae* Beadle ex C. K. Schneid., Ill. Handb. Laudbholzk. 1: 791. 1906. TYPE: *Crataegus brachyacantha* Sarg. & Engelm.

Bush to medium-sized *tree*, commonly 6–10 m tall; *trunk* with plated grayish bark, when older with branched *thorns*; branches thornless to thorny, thorns short, recurved, usually < 1.5 cm long. *Leaves* deciduous, short-petiolate; blades coriaceous and shiny, those of spur shoots small (ca. 2 cm) elliptic, crenate-margined, of elongation shoots often much larger (> 6 cm) and variously lobed, sometimes to the sinuses. *Inflorescences* with 15–25 flowers; branches glabrous; anthesis mid season. *Flowers* small, *calyx lobes* small; *petals* small, white until old; *stamens* 20, anthers cream; *styles* 4–5. *Fruit* ± globose, mealy, black to bluish black, usually with a heavy, waxy bloom at maturity; *pyrenes* 5, with slight dorsal grooving.

One species, Louisiana and neighboring states, disjunct in Georgia.

A very distinct series on account of its unusual, short, recurved thorns, very large plant size in some specimens, glossy leaves, among the smallest flowers in the genus, turning orange with age, and black fruit. The limited distribution range is remarkable and difficult to account for.

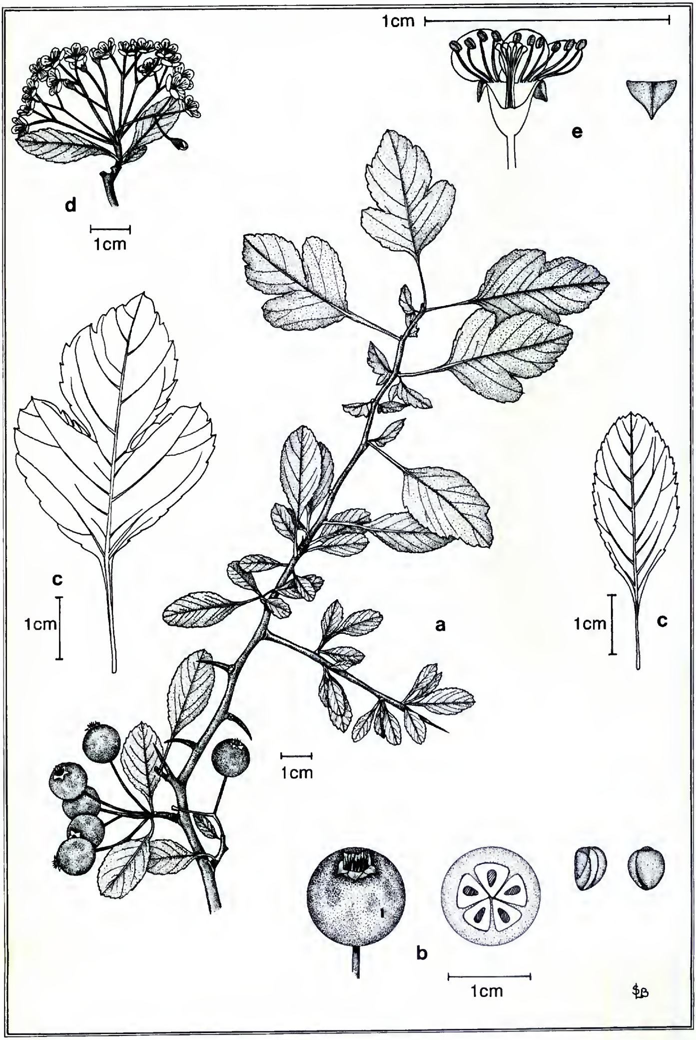
7. **Crataegus brachyacantha** Sarg. & Engelm., Bot. Gaz. 7: 128. 1882. TYPE: U.S.A. Texas: Longview, 19 Aug. 1882, *G. W. Lettermann s.n.* (lectotype, here designated, A).

Blueberry Haw, Hoghaw, Pomette Bleue. Figure 7.

Bush to medium-sized *tree* commonly 6–10(–15) m tall; trunk with plated gray bark; thornless to thorny, thorns short, recurved, usually < 1.5 cm long or branched on larger trunks. *Leaves* deciduous; petioles 3–8 mm long, glabrous; blades coriaceous and shiny, those of spur shoots 2–3 cm long, elliptic, unlobed, crenate-margined, those of vegetative shoots often much larger (> 6 cm long) and variously lobed, sometimes to the sinuses. *Inflores-*

→

Figure 7. *Crataegus brachyacantha.* —a–c. Fruiting branch and infructescence, fruit parts, and leaves from *Duncan & Duncan 4128* (DUKE). —d, e. Inflorescence and flower section with calyx lobe from *J. C. Chaffe s.n.* (DOV).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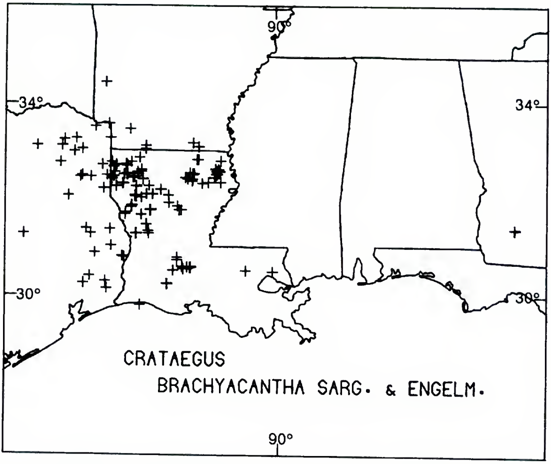

Figure 8. Distribution of *Crataegus brachyacantha*; main range essentially complete from collated herbarium records, somewhat incomplete for Texas.

cences with 15–25 flowers; branches glabrous; anthesis mid season. *Flowers* 7–9(–11) mm diam.; *hypanthium* glabrous externally; *calyx lobes* 1.5 mm long, triangular, margins entire, glabrous adaxially and abaxially; *petals* ca. 3 mm, circular, white until old; *stamens* 20, anthers cream, 0.5 mm; *styles* 4–5. *Fruit* ± oblate, 8–14 mm diam., flesh mealy, black to bluish black, with heavy, waxy bloom before maturity; *calyx* remnants erecto-patent to obsolete; *pyrenes* 4–5, with slight dorsal grooving.

The distribution of *Crataegus brachyacantha* is centered in Louisiana, where this species is locally common. It is also found in southeastern Oklahoma, eastern Texas, southern Arkansas, and southwestern Mississippi. A disjunct population has been collected from Georgia (Fig. 8), but specimens from there cannot be found now. Although *C. brachyacantha* has often been reported as a tree of wet prairies, alluvial flats, etc., I have frequently seen it, though generally as a smallish tree, on well-drained mesic sites in various parts of its natural range. This species is seemingly more shade-tolerant than many species of hawthorn. It flowers during mid season.

Crataegus brachyacantha is a very distinct species; the flowers turn orange with age or on drying, and are remarkable in this respect. The short, recurved thorns and bitter, oblate, black fruits are also distinctive. A very heavy bloom on the somewhat immature fruit, when the skin is purplish, gives rise to a bluish appearance and also to two of the common names. However, the fruit is nearly always full black at maturity. The fall foliage, brilliantly colored lustrous orange, bronze, and red, suggests potential ornamental use. The frequently deeply lobed leaves with veins to their sinuses on elongating shoots constitute a presumptively ancestral character that helps relate *C. brachyacantha* as well as such groups as series *Virides* to the other species treated in this paper. This species may be the tallest species of hawthorn in the United States.

According to Sargent (1890), *Crataegus brachyacantha* is not hardy in the north. The chromosome number is unknown.

Crataegus brachyacantha f. *leucocarpa* Sarg. (J. Arnold Arbor 3: 10. 1922) is a white-fruited form that was collected at Nachitoches, Nachitoches Parish, Louisiana, in September 1915 (*Palmer 8719*, A). The holotype is the only known collection of this forma.

Representative specimens examined. U.S.A. **Arkansas:** Ashley: P.O. Crossett, 160 ft., *Demaree 22033* (A, MO). Little River: Ashdown, *Palmer 8386* (A). Miller: Texarkana, *Palmer 22459* (A, MO, UARK, US). **Georgia:** Baker: 4 mi. N of Newton, *Duncan & Duncan 4128* (A, DHL, DUKE, FLAS, GAM, NCSC, NCU, US). **Louisiana:** Bienville: off Louisiana 4, ca. 2 mi. W of Friendship, *Robinette 212* (NO). Caddo: ca. 4 mi. N of Keatchie, *Thieret 22549* (USLH). DeSoto: ca. 1 mi. E of Naborton, ca. 8 mi. E of Mansfield, *Thieret 27468* (DUKE, FSU, GAM, USLH). Franklin: Murphy Woods property S of Old Mixon School S of La. 132 and NW of Archibald, *R. D. Thomas et al. 88742* (UWO), *7032* (UWO). Nachitoches: Nachitoches, *Cocks s.n.* (A). Ouachita: cultivated, Purchase Gardens & Zoo, Monroe, *R. D. Thomas et al. 30771* (NLU). Richland: E of La. 17 and S of La. 877 and Mitchiner, *R. D. Thomas et al. 59400* (NO, NLU, LSU), *1864* (LSU). Sabine: Toro, *Demaree 48200* (NCU, NO, UWO). St. Landry: Opelousas, *Mohr s.n.* (US-139229). St. Tammany: Glen Gordon, Covington, *Cocks s.n.* (A, NO). Webster: Lake Bistinean State Park campground ca. 8 mi. NW of Ringgold, *Thieret 26621* (DUKE, FSU, GAM, USLH). West Carroll: N of La. 134 at curve E of Little Colewa Creek 4 mi. W of Epps, *R. D. Thomas 84381* (NLU). **Texas:** Franklin: 10 km SE of Mt. Vernon, Farm Road 21, *Phipps et al. 5260* (UWO). Liberty: on FM 162, about 5 mi. E of Moss Hill & W of Batsford, *Phipps et al. 6069* (UWO). Smith: C. C. McDonald Farm, along Bedsprings Rd. in area "B," NE side of Lake Tyler East, ca. 2 mi. SW of Swinneytown, *Wilkinson 360* (SRH). Wood: near Longview, NE Texas, *Letterman s.n.* (A, MO, UWO).

Literature Cited

Aiton, W. 1789. Hortus Kewensis. George Nicol, London.

Chaney, R. W. 1927. Geology and paleontology of the Crooked River Basin, with special reference to the Bridge Creek flora. Pp. 45–122 *in* R. Kellogg et al. (editors), Contributions to Palaeontology from the Carnegie Institute of Washington. Additions to the Paleontology of the Pacific Coast and Great Basin Regions of North America IV. Carnegie Institute of Washington, Washington, D.C.

Clark, R. C. 1971. The woody plants of Alabama. Ann. Missouri Bot. Gard. 58: 99–242.

Cronquist, A. 1980. Vascular Flora of the Southeastern United States, Vol. 1. Univ. North Carolina Press, Chapel Hill.

Eggleston, W. W. 1980. The *Crataegi* of the northeastern United States and adjacent Canada. Rhodora 10: 73–84.

El-Gazzar, A. 1980. The taxonomic significance of leaf morphology in *Crataegus* (Rosaceae) Bot. Jahrb. Syst. 101: 457–469.

Miller, P. 1760. Figures of Plants Described in the Gardener's Dictionary, 1st ed., Vol. 2. Rivington et al., London.

———. 1768. Gardeners' Dictionary, 8th ed. London.

Moench, C. 1785. Verzeichniss ausländicher Bäume und Stauden. J. G. Fleischerischen Buchhandlung, Frankfurt.

Phipps, J. B. 1983. Biogeographic, taxonomic and cladistic relationships between Asiatic and North American *Crataegus*. Ann. Missouri Bot. Gard. 70: 667–700.

———. 1988. *Crataegus* (Maloideae, Rosaceae) of the southeastern United States, Introduction and series *Aestivales*. J. Arnold Arbor. 69: 401–431.

———. 1997. Monograph of northern Mexican *Crataegus*. Sida, Bot. Miscell. 15: 1–94.

———. 1998. Introduction to the red-fruited *Crataegus* (Rosaceae) of western North America. Canad. J. Bot. 56 (in press).

——— & M. Muniyamma. 1980. A taxonomic revision of *Crataegus* (Rosaceae) in Ontario. Canad. J. Bot. 56: 1621–1699.

———, ———, J. Rohrer & P. G. Smith. 1991. Origins and evolution of subfamily Maloideae (Rosaceae). Syst. Bot. 16: 303–332.

Sargent, C. S. 1890. The Silva of North America, Vol. 4. Houghton, Mifflin, Boston and New York.

———. 1922. Manual of the Trees of North America, 2nd ed., Vols. I, II. Houghton, Mifflin, Boston and New York.

ADAPTIVE RADIATION OF BEE-POLLINATED *GLADIOLUS* SPECIES (IRIDACEAE) IN SOUTHERN AFRICA[1]

Peter Goldblatt,[2] John C. Manning,[3] and Peter Bernhardt[4]

ABSTRACT

Observations on the flowers of 45 of 166 species of southern African *Gladiolus* (in sects. *Blandus, Densiflorus, Hebea, Heterocolon, Homoglossum, Linearifolius, Ophiolyza*) show that 42 species are pollinated largely by polylectic bees in the family Apidae, 2 species by bees of the families Andrenidae or Halictidae, and 1 by a combination of hopliine beetles (Scarabaeidae) and Andrenidae. The floral phenology, attractants, diversity of floral foragers, and sometimes the rewards, vary according to geography and are not correlated with taxonomy. Flowering in most *Gladiolus* species in the southern African winter-rainfall zone coincides with the end of the wet season, August to October, but a few flower from February to April at the end of the dry season. They have sweetly fragrant flowers with a wide range of colors and markings. These species receive a diversity of floral foragers including bees in the genera *Allodape, Amegilla, Andrena, Anthophora, Apis,* and *Pachymelus.* Most *Gladiolus* species of the summer-rainfall zone flower from December to April, from the middle to the end of the wet season, but a few species bloom from August to November, at the end of the dry season. Their flowers have no discernible fragrance and are colored mostly in shades of pink to mauve or white. Most floral foragers collected on these species were bees in the genus *Amegilla,* but other bee genera, as well as flies in the genera *Prosoeca* and *Stenobasipteron,* were captured. Among the southern African species of *Gladiolus* pollinated by bees, there are two distinct pollination strategies. The majority have bilabiate, "gullet" flowers or "flag" flowers that secrete sucrose-rich nectar at the base of an obliquely funnel-shaped floral tube 9–20 mm long with the lower, narrow part 5–15 mm long. *Apis mellifera* and large-bodied anthophorine bees (especially *Amegilla* and *Anthophora*) contact dehiscent anthers and/or receptive stigmas while probing the tube for nectar with elongated probosces. In contrast, *G. brevitubus, G. quadrangularis,* and *G. stellatus* have rotate, actinomorphic (or subactinomorphic) perianths offering little or no nectar at the base of tubes less than 7 mm long. *Andrena* species or *Apis mellifera* contact both dehiscent anthers and receptive stigmas of *G. stellatus* or *G. quadrangularis,* respectively, while foraging for pollen.

An additional 53 *Gladiolus* species also have bilabiate, gullet or flag flowers with obliquely funnel-shaped tubes 9–20 mm long (the most common flower type in the genus), and are presumed also to be adapted for pollination by long-tongued anthophorine and honey bees. The actinomorphic, rotate floral form is present in 2 more species. Thus, 60% of the *Gladiolus* species in southern Africa may be regarded as being pollinated by bees, and the overwhelming majority of these species (95%) have gullet or flag flowers and are visited primarily by long-tongued anthophorine bees that are foraging for nectar. The remaining species of *Gladiolus* in southern Africa have flowers with elongate perianth tubes and are adapted for pollination by sunbirds or insects other than bees, most importantly long-tongued flies (Nemestrinidae, Tabanidae), moths, and the large satyrid butterfly, *Aeropetes.*

Gladiolus, the largest genus of Iridaceae subfam. Ixioideae, consists of approximately 250 species (Goldblatt, 1996; Goldblatt & Manning, 1998) distributed throughout Africa, Madagascar, and western Eurasia. Southern Africa is the center of diversity of the genus, and some 166 species occur in Africa south of the Zambezi River, over 95% of them endemic (see Goldblatt, 1996). The southern African species are currently divided into seven sections (sects. *Blandus* (21 spp.), *Densiflorus* (20 spp.), *Hebea* (31 spp.), *Heterocolon* (10 spp.), *Homoglossum* (51 spp.), *Linearifolius* (17 spp.), and *Ophiolyza* (16 spp.)) based on vegetative, floral, and fruiting characteristics (Goldblatt & Manning, 1998). Species of the genus, especially those from southern Africa, have been favorite horticultural subjects in Europe since the beginning of the 19th century, and cultivars based on interspecific hybrids have been marketed since the 1820s (Goldblatt, 1996).

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Despite a long history of cultivation, data on the reproductive biology of *Gladiolus* are meager. Information on intraspecific compatibility in the genus has been derived primarily from experiments on cultivars and a few hardy species. Available literature suggests that species are self-incompatible (Darwin, 1876; Goldblatt, 1971; Ohri & Khoshoo, 1981), while self-compatibility is frequently correlated with interspecific cultivars and/or high levels of ploidy (Knox et al., 1976; Ohri & Khoshoo, 1981). The self-incompatibility so far reported in *Gladiolus* is in marked contrast to the situation in *Ixia, Romulea, Sparaxis,* and *Watsonia.* Most species so far examined of these four genera, also members of subfamily Ixioideae, are self-compatible, but show reduced fertility (Horn, 1962; de Vos, 1972) when selfed as compared with xenogamous crosses. A few species of *Sparaxis,* however, are fully self-incompatible and others are autogamous (Goldblatt, 1992).

The pollination ecology of *Gladiolus* species has until now been barely investigated. Cultivated specimens in India have been reported to be pollinated by the Indian honey bee, *Apis indica* (Ohri & Khoshoo, 1981). Observations of wild species are few and scattered, and with hindsight, often unreliable. Scott Elliot (1891) first commented that the hairy bodies of a hopliine (Scarabaeidae) beetle, *Anisonyx ursus,* carried the pollen of flowers of *G. gracilis* and *G. hirsutus* (as *G. pilosus*) in South Africa. Marloth (1908) reported a long-tongued fly (*Philoliche rostrata,* Tabanidae) foraging for nectar presumably on *G. bonaspei* Goldblatt & de Vos (as *Antholyza merianella* L.), an observation that is erroneous since that fly is not on the wing when *G. bonaspei* blooms. Vogel (1954) suggested that the *Gladiolus* species of southern Africa could be subdivided into four different pollination groups based on floral characters believed to be associated with either bee, sphinx moth, bird, or combined butterfly and long-tongued fly pollination. Unfortunately, Vogel's field observations on *Gladiolus* species were evidently limited to his sighting of a sunbird (Nectarinidae) foraging on the flowers of *G. dalenii* van Geel.

More recent and reliable observations on the pollination of *Gladiolus* have been made in the course of studies of pollination guilds in southern Africa. Johnson and Bond (1994) have recorded the large butterfly, *Aeropetes tulbaghia,* as a visitor and likely pollinator of a few *Gladiolus* species with large, red flowers, including the well-known *G. cardinalis* Curt. Manning and Goldblatt (1995, 1997) recorded the long-tongued flies *Moegistorhynchus longirostris* (Nemestrinidae) and *Philoliche rostrata* (Tabanidae) foraging for nectar on *G. angustus* L. and *G. undulatus* L. and *Prosoeca longipennis* (Nemestrinidae) foraging on *G. bilineatus* G. J. Lewis and *G. engysiphon* G. J. Lewis. The anthers and stigmas brush the dorsal surface of the thorax of these flies and deposit large quantities of pollen when the flies probe the floral tubes with their hyper-elongated mouthparts. *Gladiolus meliusculus* has been reported to be pollinated by a combination of andrenid bees (*Andrena* sp.) and hopliine beetles (*Lepisia, Pachycnema*; Goldblatt et al., 1998). Both bees and beetles carried the pollen of *G. meliusculus* and contacted the stigma lobes during foraging, while beetles also brushed against dehisced anthers and stigmas while mating or engaging in agonistic behavior. Thus, existing observations are either unreliable or involve unusual and highly specialized pollination systems based on a small sample of species, all from the southern African winter-rainfall zone. Available information does, however, indicate that pollination in *Gladiolus* is extremely diverse.

This apparent diversity in pollination biology is matched by a broad range of colors and marking patterns in the flowers of southern African *Gladiolus* species. The predominance of bilabiate, "gullet" flowers (sensu Faegri & van der Pijl, 1979) with relatively short floral tubes, however, suggests that bees should be the dominant pollinators in the genus, and our aim has been to examine this hypothesis. Bees are known to contribute to the pollination of some species of Iridaceae in southern Africa, including *Moraea* (Goldblatt et al., 1989), *Nivenia* (Goldblatt & Bernhardt, 1990), and *Lapeirousia* (Goldblatt et al., 1995). The bees apparently most important in the pollination of these taxa have long tongues and large bodies exceeding 10 mm in length (e.g., *Apis, Amegilla,* and *Anthophora*). We present the following information as part of a broader survey of pollination in *Gladiolus* that aims to document the different pollination strategies that occur in the genus.

MATERIALS AND METHODS

Species examined. We present direct observations made during the years 1993 to 1998 in the field in southern Africa and in living collections at the Missouri Botanical Garden, St. Louis, and Kirstenbosch Botanic Gardens, Cape Town, on aspects of the floral biology of the 80 species of southern African *Gladiolus* that have short-tubed, gullet, flag or rotate (stellate) flowers (Table 1). Some 19 more species have flowers closely resembling those examined, but the remaining 67 species of the genus in southern Africa have flowers with elongate floral

Table 1. Species of southern African *Gladiolus* with flowers adapted for pollination by bees, with field sites and voucher information for species examined for pollinators and/or floral characters (sites marked * if no pollinators captured). Study sites are in South Africa unless otherwise indicated. Species are arranged taxonomically according to Goldblatt and Manning (1998). Vouchers are housed at MO (Goldblatt) or at NBG (other collectors).

Species	Study site Province, Locality	Voucher
Gladiolus **sect.** *Densiflorus*		
series *Paludosus*		
G. paludosus Baker	Mpumalanga, near Belfast(*)	*Goldblatt & Manning 10133*
G. papilio Herb.	Mpumalanga, near Dullstroom	*Goldblatt & Manning 8941*
series *Densiflorus*		
G. crassifolius Baker	Free State, Witzieshoek	*Goldblatt & Manning 9861*
	Zimbabwe, Nyanga	*Goldblatt 9077*
G. densiflorus G. J. Lewis	Mpumalanga, Long Tom Pass(*)	*Goldblatt & Manning 9840*
G. exiguus G. J. Lewis	Mpumalanga, Long Tom Pass	*Goldblatt & Manning 9838*
G. ferrugineus Goldblatt & J. C. Manning	Mpumalanga, Long Tom Pass	*Manning 2109*
	Mpumalanga, Graskop	*Goldblatt & Manning 9826*
G. hollandii L. Bolus	Mpumalanga, near Barberton(*)	*Goldblatt & Manning 9845*
G. serpenticola Goldblatt & J. C. Manning	Mpumalanga, Barberton–Nelspruit(*)	*Goldblatt & Manning 9844*
series *Calcaratus*		
G. appendiculatus G. J. Lewis	Mpumalanga, Long Tom Pass	*Goldblatt & Manning 10644*
series *Scabridus*		
G. brachyphyllus F. Bolus	Mpumalanga, Tshokwane(*)	*Goldblatt & Manning s.n.*
G. ochroleucus Baker	Eastern Cape, near East London(*)	*Goldblatt & Manning 9534*
G. pavonia Goldblatt & J. C. Manning	Mpumalanga, Abel Erasmus Pass(*)	*Goldblatt & Manning 9831*
Gladiolus **sect.** *Ophiolyza*		
series *Oppositiflorus*		
G. dolomiticus Oberm.	Northern Province, Makapansgat	*Goldblatt & Manning 10472*
G. elliotii Baker	Gauteng, Bronkhorstspruit(*)	*Goldblatt & Manning 10134*
G. pole-evansii Oberm.	Mpumalanga, Denilton(*)	*Goldblatt & Manning 9808*
G. sericeovillosus Baker	Mpumalanga, Amersfoort	*Goldblatt & Manning 9850*
	Zimbabwe, Nyanga	*Goldblatt 9083*
series *Ecklonii*		
G. ecklonii Lehm.	Mpumalanga, near Dullstroom	*Goldblatt & Manning 9803*
G. vinosomaculatus Kies	Gauteng, Pretoria hills(*)	*Goldblatt & Manning 9801*
Gladiolus **sect.** *Blandus*		
series *Phoenix*		
G. crispulatus L. Bolus	not studied	
G. phoenix Goldblatt & J. C. Manning	Western Cape, Bain's Kloof	*Goldblatt & Manning 10122*
G. oreocharis L. Bolus	not studied	
series *Sabulosus*		
G. gueinzii Kuntze	Western Cape, Great Brak River(*)	*Goldblatt & Manning 9522 & 9523*
series *Floribundus*		
G. grandiflorus Mill.	Western Cape, Burger's Pass	*Goldblatt & Manning 10017*
G. rudis Roem. & Schult.	Western Cape, Die Galg(*)	*Lewis 6104*

Table 1. Continued.

Species	Study site Province, Locality	Voucher
Gladiolus **sect.** *Linearifolius*		
series *Pubigerus*		
G. malvinus Goldblatt & J. C. Manning	Mpumalanga, Dullstroom(*)	*Goldblatt & Manning 10075*
G. pardalinus Goldblatt & J. C. Manning	Mpumalanga, Stoffberg(*)	*Goldblatt & Manning 10094*
G. parvulus Schltr.	KwaZulu-Natal, Underberg(*)	*Goldblatt & Manning 10061*
G. pubigerus G. J. Lewis	Mpumalanga, Graskop(*)	*Goldblatt & Manning 10085*
	KwaZulu-Natal, Underberg(*)	*Goldblatt & Manning 10062A*
G. woodii Baker	Mpumalanga, Dullstroom(*)	*Goldblatt & Manning 10125*
G. zimbabweensis Goldblatt	not studied	
series *Linearifolius*		
G. aureus Bolus	Western Cape, Cape Peninsula	no voucher
G. brevifolius Jacq.	Western Cape, Glencairn	*Goldblatt & Manning s.n.*
	Near Riviersonderend	*Goldblatt & Manning s.n.*
G. hirsutus Andr.	Western Cape, Sir Lowry's Pass	*Goldblatt 2035*
Gladiolus **sect.** *Heterocolon*		
series *Unguiculatus*		
G. oatesii Rolfe	Mpumalanga, near Warmbad(*)	*Goldblatt & Manning 10095*
series *Heterocolon*		
G. pretoriensis Kuntze	Mpumalanga, Pretoria(*)	*Goldblatt & Manning 9799*
G. rubellus Goldblatt	not studied	
series *Vernus*		
G. juncifolius Goldblatt	not studied	
G. kamiesbergensis G. J. Lewis	Western Cape, Kamiesberg(*)	*Goldblatt & Manning 9768*
G. marlothii G. J. Lewis	Western Cape, Ganaga Pass	*Goldblatt & Manning 10360*
G. mostertiae L. Bolus	Northern Cape, Bokkeveld Mts.	*Goldblatt & Manning 10107*
G. rufomarginatus G. J. Lewis	Mpumalanga, Lydenburg	*Manning 2115*
G. vernus G. J. Lewis	not studied	
Gladiolus **sect.** *Hebea*		
series *Involutus*		
G. involutus D. Delaroche	Western Cape, near Heidelberg	*Manning s.n.*
G. loteniensis Hilliard	KwaZulu-Natal, Loteni Valley(*)	*Goldblatt & Manning 10143*
series *Permeabilis*		
G. inandensis Baker	KwaZulu-Natal, Nchanga(*)	*Goldblatt & Manning 10057*
G. permeabilis D. Delaroche		
subsp. *permeabilis*	Western Cape, Barrydale	*Goldblatt & Manning 10015*
subsp. *edulis* Ker Gawl.	Gauteng, Bronkhorstspruit	*Goldblatt & Manning 9904*
G. stellatus G. J. Lewis	Western Cape, Heidelberg	*Goldblatt & Manning 10024*
G. uitenhagensis Goldblatt	not studied	
G. wilsonii (Baker) Goldblatt & J. C. Manning	not studied	
series *Deserticola*		
G. arcuatus Klatt	Western Cape, Vredendal	*Goldblatt & Manning 9904, 10006*
G. deserticola Goldblatt	Northern Cape, Richtersveld(*)	*Goldblatt & Manning 9950*
G. salteri L. Bolus	Northern Cape, E of Springbok(*)	*Goldblatt & Manning 9649*
G. scullyi Baker	Northern Cape, Calvinia	*Goldblatt & Manning 9964*
G. venustus Klatt	Western Cape, S of Clanwilliam	*Steyn 525*
G. viridiflorus G. J. Lewis	Northern Cape, Anenous flats(*)	*Goldblatt & Manning 9288*

Table 1. Continued.

Species	Study site Province, Locality	Voucher
series *Hebea*		
G. alatus L.	Western Cape, near Porterville	*Goldblatt & Manning 9336*
	Western Cape, Cape Town	*Goldblatt s.n.* no voucher
G. ceresianus L. Bolus	Western Cape, Klein Roggeveld	*Goldblatt & Manning 10308A*
G. equitans Baker	Northern Cape, Spektakel Mts.	*Goldblatt & Manning 10003*
G. meliusculus (G. J. Lewis) Goldblatt & J. C. Manning	Western Cape, Waylands, Darling	*Goldblatt & Manning 10386A*
G. orchidiflorus Andr.	Northern Cape, Spektakel Mts.	*Goldblatt & Manning s.n.*
G. pulcherrimus (G. J. Lewis) Goldblatt & J. C. Manning	Western Cape, Sandberg(*)	*Goldblatt & Manning 10328*
G. speciosus (G. J. Lewis) Goldblatt & J. C. Manning	Western Cape, Botterkloof	*Goldblatt & Manning 10546*
G. uysiae G. J. Lewis	Northern Cape, Bokkeveld Plateau	*Goldblatt & Manning 10294A*
G. virescens Thunb.	Western Cape, Swellendam(*)	*Goldblatt & Manning 9750A*
	Western Cape, Cold Bokkeveld	*Goldblatt s.n.* no voucher
G. watermeyeri L. Bolus	Northern Cape, Bokkeveld Mts.	*Lewis 5890*
Gladiolus **sect.** *Homoglossum*		
series *Carinatus*		
G. atropictus Goldblatt & J. C. Manning	Western Cape, Die Galg(*)	*Manning 2010*
G. carinatus Aiton	Western Cape, Pakhuis Mts.	*Goldblatt & Manning 9922*
	Western Cape, Aurora	*Goldblatt s.n.* no voucher
	Western Cape, Darling(*)	*Grant 4649*
G. comptonii G. J. Lewis	Western Cape, Heerenlogement Mt.(*)	*Manning 2006*
G. griseus Goldblatt & J. C. Manning	Western Cape, near Blouberg Strand	*Manning s.n.*
G. quadrangulus (D. Delaroche) T. T. Barnard	Western Cape, Rondeberg(*)	*Goldblatt & Manning 10542*
	Western Cape, Edgemead	*Goldblatt & Manning 11024*
G. violaceolineatus G. J. Lewis	Western Cape, Pakhuis Pass(*)	*Goldblatt & Manning 9921*
series *Mutabilis*		
G. exilis G. J. Lewis	Western Cape, Bain's Kloof	*Manning 1079*
G. mutabilis G. J. Lewis	Western Cape, Albertinia(*)	*Manning 2018*
G. vaginatus L. Bolus	Western Cape, Drayton(*)	*Manning 1048*
series *Brevitubus*		
G. brevitubus G. J. Lewis	Western Cape, Vogelgat	*Manning s.n.*
series *Gracilis*		
G. bullatus G. J. Lewis	Western Cape, near Elim(*)	*Goldblatt & Manning 9916A*
G. blommesteinii L. Bolus	Western Cape, Sir Lowry's Pass	*Goldblatt 2505*
G. caeruleus Goldblatt & J. C. Manning	Western Cape, Langebaanweg(*)	*Goldblatt & Manning 9928*
G. gracilis Jacq.	Western Cape, Aurora	*Goldblatt & Manning 10227*
	Western Cape, Darling	*Goldblatt s.n.* no voucher
G. inflexus Goldblatt & J. C. Manning	Western Cape, Worcester	*Manning 2010*
G. jonquilliodorus Eckl. ex G. J. Lewis	Western Cape, near Glencairn	*Goldblatt 10603A*
G. martleyi L. Bolus	Western Cape, Hermanus(*)	*Goldblatt & Manning 9875*
	Western Cape, Glencairn	*Goldblatt 10921*
G. ornatus Klatt	not studied	
G. rogersii Baker	Western Cape, Arniston(*)	*Manning 2034*
G. taubertianus Schltr.	not studied	

Table 1. Continued.

Species	Study site Province, Locality	Voucher
series *Teretifolius*		
G. delpierrei Goldblatt	not studied	
G. inflatus Thunb.	Western Cape, Jonaskop	*Goldblatt 10791*
G. patersoniae F. Bolus	Western Cape, Worcester	*Goldblatt & Manning 10504*
	Western Cape, Die Galg	*Manning s.n.*
G. pritzelii Diels	not studied	
G. subcaeruleus G. J. Lewis	Western Cape, near Riviersonderend	*Goldblatt & Manning 10186*
G. sufflavus (G. J. Lewis)	Northern Cape, Bokkeveld Mts.	*Goldblatt & Manning 9783*
G. trichonemifolius Jacq. Goldblatt & J. C. Manning	Western Cape, Camphill road	*Goldblatt 2175*
series *Tristis*		
G. symonsii F. Bolus	not studied	

tubes and are known or assumed to be pollinated by other organisms, including long-tongued flies, birds, a satyrid butterfly, or moths (Goldblatt & Manning, 1998), and will be the subject of separate papers. Plant vouchers (Table 1) are deposited at the Missouri Botanical Garden Herbarium, St. Louis (MO), and/or the Compton Herbarium, Cape Town (NBG).

Seasonality, floral phenology, floral longevity, and reproductive success. Data on seasonality are taken from Goldblatt and Manning (1998) and are summarized below under Results. Observations of the mode and timing of anthesis (opening of individual buds), anther dehiscence, expansion of stigmatic lobes, and withering of the perianth were made on plants in cultivation or in the laboratory on cut stems placed in water. Reproductive success in terms of number of capsules developed per spike compared to the number of flowers produced was determined for one species, *Gladiolus venustus*. Individual fruiting spikes were sampled at 1-m intervals along a transect. Incompletely developed or malformed capsules were not scored.

Fragrance. Floral scent was noted with the human nose in the field and in cultivated plants. Presence of scents too weak to be discerned in the open air was recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar were sniffed after a minimum of 60 minutes (Buchmann, 1983). Site of scent production was determined by immersing flowers in aqueous neutral red stain. Scent chemistry was examined by R. Kaiser, Givaudan-Roure Research Ltd., Switzerland, by gas chromatography using a DB-Wax Capillary column (Kaiser, 1993). Scents were captured in capsules though which air was drawn by a vacuum pump from a small, lidded chamber containing open flowers.

Nectar analysis. Nectar-volume measurements were taken primarily from unbagged flowers in the field, reflecting both rates of secretion and depletion. In addition, nectar samples were removed from *Gladiolus appendiculatus*, *G. brevifolius*, *G. crassifolius*, and *G. involutus* using potted plants or cut stems placed in water in the laboratory for a minimum of 24 hours. Evidence that we have accumulated on some *Gladiolus* species and other Iridaceae indicates that using flowers from cut stems does not affect nectar quality for the first one to two days after harvesting. To collect nectar whole flowers were picked and nectar was withdrawn from the base of the perianth tube with 3-μl capillary tubes after separating the ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory on a Bellingham & Stanley hand-held refractometer (0–50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman's filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HTLC sugar analysis.

Insect observation and pollen-load analyses. Observations of insects on *Gladiolus* flowers of 45 species involved 4–20 hours per species at over 50 sites, and included the mode of foraging and whether insects contacted anthers and stigmas while foraging. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Pollen was removed from insects after specimens were pinned. To prevent contamination of insect bodies with pollen on other insects in the same jar, the bodies of insect specimens were isolated by wrapping them in tissue prior to pinning. Capturing a single bee at any site appeared to reduce the local bee population significantly. We therefore captured only enough bees as necessary to obtain individuals for identification and pollen-load analysis. Removal of pollen from insect bodies involved either gentle scraping with a dissecting needle or gentle washing in drops of 95% ethanol. The residue from needle probes or washes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). Pollen grains were identified by comparison with reference pollen-grain preparations made from plants flowering at study sites. Pollen of a species was recorded as present if more than 10 grains were counted. *Gladiolus* pollen grains are recognized by their large size, monosulcate aperture with prominent 2-banded operculum, and perforate-scabrate exine. Body length and length of mouthparts of insects were measured from pinned specimens.

Insect body length was measured from the base of the labrum to the tip of the abdomen. Mouthpart length was measured from the base of the labrum to the tip of the proboscis (flies) or the extended tongue (bees). Insect specimens were identified by R. W. Brooks (Apidae), C. D. Michener (Halictidae), both of Kansas State University, and V. Whitehead (Melittidae), South African Museum, Cape Town. Voucher specimens are deposited at the South African Museum, or the Snow Entomological Museum, Lawrence, Kansas. The bee classification used here is that of Roig-Alsina and Michener (1993).

RESULTS

Seasonality, floral phenology, and longevity. Species of *Gladiolus* are seasonal, corm-bearing geophytes of small to moderate size, typically 20–45 cm high, but in some species up to 1.5 m. Individuals produce a single, simple or few-branched flowering stem annually, and flowering is closely synchronized in a population. Inflorescences are spikes with the flowers usually secund, rarely distichous (only sect. *Ophiolyza* ser. *Oppositiflorus*) or spiral (species with actinomorphic flowers) (Figs. 1, 2).

Flowering in the *Gladiolus* species of southern Africa is correlated with their geographic ranges in one of two separate rainfall zones (Goldblatt & Manning, 1998). Species of the winter-rainfall zone mostly flower in spring (August to October), toward the end of the wet season, whereas most species of the summer-rainfall zone flower in early to late

Figure 1. Inflorescence form, flower shape, and style-stigma maturation in *Gladiolus alatus*. The upper two flowers opened last and have the style reaching to the base of the anthers with the style branches lying among the anthers and the adaxial surface conduplicate; the stigmatic areas are thus not exposed. In the lowermost flower, open for three days, the style has elongated, the style branches have diverged, and the conduplicate surfaces have unfolded, exposing the stigmatic surfaces, held distant from the anther apices. Arrows indicate position of style branches. Scale approx. ×⅔.

Figure 2. Inflorescences and flowers of southern African *Gladiolus*, with half flowers for some species. —A. *G. papilio* (sect. *Densiflorus*). —B. *G. rufomarginatus* (sect. *Heterocolon*). —C. *G. gracilis* (sect. *Homoglossum*). —D. *G. uysiae* (sect. *Hebea*). —E. *G. stellatus* (sect. *Hebea*). —F. *G. quadrangulus* (sect. *Homoglossum*). Scale approx. ×⅔.

summer (December to April), again coinciding with the wet season (Table 2). In both cases this coincides with the period of optimal plant growth, during or soon after the main rainy period.

Flowering near the end of the dry season is, however, characteristic of several species of both climate zones (Goldblatt & Manning, 1998). In the winter-rainfall zone, several species (Table 2) flower in the late summer and autumn (mainly March to May), and these species typically have reduced leaves on the flowering stem (foliage leaves for the accumulation of food reserves in the corm may be produced later, on separate shoots). In the summer-rainfall zone, flowering in the dry winter is largely precluded by cold temperatures, but several species flower in the spring (September to November), before or shortly after the first rains have fallen. These species also have reduced leaves on the flowering stem, but typically do not produce separate foliage leaves; instead, the leaves and stems remain green for months after flowering.

The pattern of flower buds opening on an inflorescence is acropetal. In all *Gladiolus* species, a mature bud expands just before mid morning and the open flower typically lasts three or four days, and in some species up to five days. Flowers open one to two days apart, hence there are often two or three flowers open at any time on an inflorescence (Figs. 1, 2). The flowers of most species partly close at sunset, loosely enclosing the exserted anthers and stigmas. More precise flowering times occur in two species, *Gladiolus quadrangulus* and *G. stellatus.* Flowers of *G. quadrangulus* close completely at 1500 hours and open at 1000, while those of *G. stellatus* close at 1230 and open at 0700–0800.

Flowers of all species studied show mechanical protandry, a condition first described for southern African species of *Gladiolus* by Scott Elliot (1891). The anthers dehisce longitudinally within one to four hours after the flowers open. This depends to some extent on ambient temperature and humidity, and anthers dehisce later in wet, cool conditions. At this time the three style branches remain loosely clasped to each other and lie against the adaxial surfaces of the dehisced anthers, with the stylar lobes, the distal adaxial surfaces of which comprise the stigmas, folded together. The male phase of flowers of most species lasts at least two days, and a maximum of three days, as flowers wither after three or four (occasionally five) days.

The male phase is then followed by a female phase that lasts either one or two days, during which the stylar lobes diverge and arch outward away from the dehisced anthers. At the same time, stigmatic surfaces at the distal ends of the stylar lobes unfold, and the visibly papillate and moist stigmatic areas are exposed and available for pollen deposition. Thus, species typically pass two days in an exclusively male phase, during which time pollen is usually removed by insects. In undisturbed field sites it could readily be seen that no pollen remained in flowers by the time the stigma lobes unfolded, leaving the flowers in an exclusively female phase for the last one or two days of anthesis. An exception to this pattern, *G. trichonemifolius,* has flowers that last just two days, the first in the male phase with dehisced anthers displaying pollen, and the second in the female phase with the stigma lobes exposed (Fig. 1). As observed by Scott Elliot (1891), mechanical self-pollination cannot readily occur because of the physical separation of the pollen and stigmatic surfaces, even if pollen remains in the anthers by the time the stigmatic surfaces are exposed. We have no data on the biochemistry of stigmatic receptivity.

A significant exception to the general pattern is *Gladiolus gueinzii,* a coastal strand species. The style divides between the base and middle of the anthers, and the stylar lobes remain entangled in the dehisced anthers. It has been found to be autogamous in cultivation, with 80% of flowers setting capsules in the absence of hand manipulation or insect activity (Goldblatt & Manning, 1998).

Population density. Our impression is that population density falls into two categories. Some *Gladiolus* species typically occur in fairly dense populations consisting of flowering individuals standing about 20–30 cm apart. These include species of specialized habitats, e.g., *Gladiolus papilio* and *G. trichonemifolius,* which favor marshy sites, and *G. gueinzii,* which grows on sandy beaches close to the high-tide mark. The majority of species, however, usually form populations in which flowering individuals stand about 1–2 m apart (ignoring obviously disturbed habitats where density may be quite high due to recolonization). We have encountered sites with less than 10 individuals in flower (e.g., *G. sufflavus, G. watermeyeri*), and others with many hundreds of plants in flower (*G. alatus, G. meliusculus*), the latter usually in habitats disturbed by wild fires, partial clearing, or heavy grazing.

Floral presentation and attractants. There are three more or less distinct floral forms in the *Gladiolus* species visited by bees. The most common is the "gullet" flower, with a zygomorphic and bilabiate perianth and arcuate, unilateral stamens (Figs. 2A–C, 3A–C), present in 85 species of southern African *Gladiolus.* The dorsal (posterior) tepal ("tepal" is used throughout this paper for lobe of the perianth) is always slightly larger than the others, and grades in orientation from arched to hooded and spooned. In flowers with a hooded and spooned dorsal tepal, the anthers are concealed and lie horizontally, close to or against the inner surface of the dorsal tepal. The upper lateral tepals are directed forward proximally and flare outward in the distal half. The lower three tepals are typically narrower than the upper three and are oriented horizontally or gently inclined. The distal parts of the lower tepals together form what resembles a landing platform, and have contrasting markings of various shapes and colors (nectar guides). The floral tube is typically obliquely funnel-shaped and 12–20 mm long (Figs. 2A–C, 3A–C). The proximal portion is hollow, suberect, and cylindric, mostly 5–15 mm long (Table 2) and 1–1.5 mm in diameter, thus too narrow to permit entry for the bodies of most insects. The distal part of the tube is flared and more or less horizontally oriented. Collectively the bases of the tepals and the distal part of the tube form a tapering throat leading to the narrow part of the tube. The throat readily accommodates the head and thorax of a large bee. In the sense of Faegri and van der Pijl (1979) these are gullet flowers. An unusual feature of the flowers of members of series *Hebea* (sect. *Hebea*) is ridges of unpigmented, iridescent papillae in the throat.

Pigmentation in these zygomorphic and bilabiate flowers is extremely variable (Table 2), particularly in species of the winter-rainfall zone. Flowers of species in section *Homoglossum* are typically shades of blue to mauve or purple, sometimes pink, or occasionally yellow. The lower tepals often have strongly contrasting nectar guides. *Gladiolus sufflavus* is exceptional in having greenish flowers, and *G. griseus* has a gray-green perianth with yellow nectar guides. In some species of section *Hebea*, flowers are brilliant scarlet to orange or, in a few other species (including *G. arcuatus*, *G. scullyi*, and *G. watermeyeri*), dull greenish, brown, or muddy purple. Flowers with the latter range of colors tend to merge with the background colors of the surrounding vegetation and terrain and seem camouflaged. Notably, these flowers always have a particularly strong fragrance. In the summer-rainfall zone flowers are often pale pink, lilac, or mauve, and only occasionally brightly colored. In these species the tepals are poorly or not at all marked.

Gullet flowers may be modified by atypical development of the tube or of the sexual organs in relation to the floral tube. First, *Gladiolus aureus*, of the winter-rainfall zone, has flowers with subequal tepals lacking contrasting markings. The lower part of the perianth is extremely narrow and tightly sheaths the style. In the summer-rainfall zone, *G. pubigerus* and *G. parvulus* also have subequal tepals without markings and a short perianth tube. Perhaps better termed pseudo-gullet flowers, they produce only traces of nectar in quantities too small to measure. Second, the bases of the anthers of *G. appendiculatus* (sect. *Densiflorus* ser. *Calcaratus*) have elongated to form hard, green, sterile appendages. These appendages extend downward across the floral throat, effectively closing off entry to the proximal part of the floral tube. As a large-bodied insect pushes its head and thorax into the flower, the appendages are elevated and the anthers pulled downward, swabbing the thorax with pollen.

A second flower type conforms more closely to the definition of "flag" rather than to that of "gullet" sensu Faegri and van der Pijl (1979) and has been identified in eight species. The flag flowers of *Gladiolus* differ from gullet flowers mainly in having an erect, enlarged dorsal tepal and widely flaring upper lateral tepals (Figs. 2D, 3D). Like gullet flowers, they also have an obliquely funnel-shaped tube. Flag flowers are most common in series *Hebea* (sect. *Hebea*; Table 2), and in these species the stamens and style are strongly arched so that the anther apices are tilted downward and the style lobes face the ground. Large-bodied bees visiting these flowers typically contact the anthers or stigmas with the dorsal surface of their thorax or abdomen as they exit, but smaller bees do not contact the anthers at all. The ridges of iridescent papillae in the throats of these flowers are especially prominent. Flag flowers often have bright coloring, usually pink, orange-red, or bright purple, and the lower tepals are marked or streaked with contrasting colors (Fig. 4). However, a few species of series *Hebea* with flag flowers, including *G. ceresianus* and *G. uysiae*, have dull-colored, purple-brown perianths always accompanied by particularly strong odors. *Gladiolus meliusculus* is remarkable in having unusually conspicuous, dark purple markings, which may be "beetle marks" (Goldblatt et al., 1998).

The third flower type is the rarest and has been identified in only five species, 5% (Table 2) of the short-tubed species. This is the rotate flower, in which the perianth is held more or less upright and the tepals spread horizontally, sometimes forming a shallow cup (Figs. 2E, F, 3E). This flower type is restricted to *G. brevitubus*, *G. deserticola*, *G. quadrangulus*, and *G. stellatus* of the winter-rainfall zone, and *G. parvulus* in the southern African summer-rainfall zone. *Gladiolus brevitubus* and *G. deserticola* have a more or less actinomorphic perianth, but unilateral stamens. Visible contrasting markings (nectar guides) are lacking in *G. quad-*

Table 2. Floral and phenological data for southern African *Gladiolus* species with flowers adapted for pollination by bees. Species are arranged according to the sectional classification of Goldblatt and Manning (1998). Note that only the length of the proximal, narrow and cylindric part of the perianth tube is listed to facilitate direct comparison with the mouth parts of visiting insects. Measurements of tube length are the range for the species. Scent is scored according to the typical condition of a species: ++ = strong scent; + = weak scent, − = no scent. Flowering times are from Goldblatt and Manning (1998), and an asterisk (*) indicates species flowering out of phase with the prevailing flowering peak for the rainfall zone.

Species	Flower		Proximal tube (mm)	Scent	Main reward	Main flowering time	Rainfall zone
	Shape	Color					
Gladiolus **sect.** *Densiflorus*							
G. appendiculatus	gullet	pale pink	ca. 7	−	nectar	Apr.–May	summer
G. brachyphyllus	flat	purple	ca. 10	−	nectar	Nov.–Dec.	summer
G. crassifolius	gullet	pink, mauve, or orange	5–8	−	nectar	Feb.–Mar.	summer
G. densiflorus	gullet	pink, mauve, or orange	ca. 6	−	nectar	Feb.–Mar.	summer
G. exiguus	gullet	pink	ca. 7	−	nectar	Feb.–Mar.	summer
G. ferrugineus	gullet	white–pinkish	6–15	−	nectar	Jan.–Apr.	summer
G. hollandii	gullet	pink	9–12	−	nectar	Mar.–Apr.	summer
G. ochroleucus	gullet	pink	7–8	−	nectar	Dec.–Feb.	summer
G. paludosus	gullet	pink	ca. 6	−	nectar	Nov.–Dec.	summer
G. papilio	gullet	pink, gray, or cream	10–12	−	nectar	Dec.–Feb.	summer
G. pavonia	flag	pink	ca. 8	−	nectar	Dec.–Jan.	summer
G. serpenticola	gullet	pink	ca. 5.5	−	nectar	Feb.–Mar.	summer
Gladiolus **sect.** *Ophiolyza*							
G. dolomiticus	gullet	pink	9–12	−	nectar	Feb.–Mar.	summer
G. ecklonii	gullet	pink, red, or mauve	8–10	−	nectar	Dec.–Mar.	summer
G. elliotii	gullet	pink–mauve	ca. 8	−	nectar	Nov.–Dec.	summer
G. pole-evansii	gullet	pink	ca. 8	−	nectar	Dec.–Jan.	summer
G. sericeovillosus	gullet	pink, cream, or purple	5–8	−	nectar	Dec.–Feb.	summer
G. vinosomaculatus	gullet	cream and purple	7–8	−	nectar	Dec.–Jan.	summer
Gladiolus **sect.** *Blandus*							
G. crispulatus	gullet	pink	12–16	−	nectar	Dec.–Jan.	winter
G. grandiflorus	gullet	cream–pink	13–20(–40)	−	nectar	Sep.–Oct.	winter
G. gueinzii	star	mauve	10–12	−	?nectar	Oct.–Nov.	summer/winter
G. oreocharis	gullet	pink	10–15(–20)	−	nectar	Dec.–Jan.	winter
G. phoenix	gullet	pink	ca. 10	−	nectar	Oct.–Nov.	winter
G. rudis	gullet	pink	8–10	−	nectar	Sep.–Oct.	winter
Gladiolus **sect.** *Linearifolius*							
G. aureus	pseudo-gullet	yellow	10–15	−	pollen	Aug.–Sep.	winter
G. brevifolius	star	pink or occ. cream	6–7	−/+	nectar	Mar.–Apr.	winter*
G. hirsutus	gullet	pink–mauve	8–12	−	nectar	July–Sep.	winter
G. malvinus	gullet	mauve	ca. 5	−	nectar	Oct.–Nov.	summer*
G. pardalinus	gullet	yellow or mauve	ca. 4	−	nectar	Oct.–Nov.	summer*
G. parvulus	star	pink	ca. 3	−	?pollen	Oct.–Dec.	summer*
G. pubigerus	gullet	green	7–8	−/+	?nectar	Oct.–Nov.	summer*
G. woodii	gullet	purple or yellow	4–6	−	nectar	Oct.–Nov.	summer*

Table 2. Continued.

Species	Flower		Proximal tube (mm)	Scent	Main reward	Main flowering time	Rainfall zone
	Shape	Color					
Gladiolus **sect.** *Heterocolon*							
G. kamiesbergensis	gullet	blue	ca. 5	+	nectar	Sep.–Oct.	winter
G. marlothii	gullet	blue	ca. 4	–	nectar	Oct.–Nov.	winter
G. mostertiae	gullet	pink	ca. 5	+	nectar	Nov.–Dec.	winter
G. oatesii	gullet	mauve	ca. 4	–	nectar	Oct.–Nov.	summer*
G. pretoriensis	gullet	pink	ca. 6	–	nectar	Dec.–Jan.	summer
G. rubellus	gullet	orange	ca. 7	–	nectar	Nov.–Dec.	summer
G. rufomarginatus	gullet	pink	ca. 4	–	nectar	Mar.–Apr.	summer
G. vernus	gullet	pink	4–6	–	nectar	Aug.–Sep.	summer*
Gladiolus **sect.** *Hebea*							
G. alatus	flat	scarlet	7–9	+	nectar	Aug.–Sep.	winter
G. arcuatus	gullet	brown	10–15	++	nectar	June–July	winter
G. ceresianus	flag	brown–purple	8–10	++	nectar	Sep.–Oct.	winter
G. deserticola	star	blue	ca. 9.5	–	nectar	Aug.–Sep.	winter
G. equitans	gullet	scarlet	9–11	++	nectar	Aug.–Sep.	winter
G. inandensis	gullet	white	5–8	–	nectar	July–Sep.	summer*
G. involutus	gullet	white–pink	16–18	–	nectar	Sep.–Oct.	winter
G. loteniensis	gullet	mauve	ca. 5	–	nectar	Nov.–Dec.	summer
G. meliusculus	flag	pink	5–6	+	nectar	Sep.–Oct.	winter
G. orchidiflorus	gullet	green or brown	7–10	++	nectar	Aug.–Sep.	winter
G. permeabilis							
subsp. *edulis*	gullet	cream	7–10	++	nectar	Sep.–Oct.	summer
subsp. *permeabilis*	gullet	mauve	7–10	++	nectar	Sep.–Oct.	winter
G. pulcherrimus	flag	scarlet	5–8	+	nectar	Sep.	winter
G. salteri	gullet	pink	15–18	++	nectar	Sep.	winter
G. scullyi	gullet	brown–mauve	8–9	++	nectar	Aug.–Sep.	winter
G. speciosus	gullet	scarlet	5–7	+	nectar	Sep.–Oct.	winter
G. stellatus	star	white–mauve	5–7	++	pollen	Sep.–Oct.	winter
G. uitenhagensis	gullet	mauve	15–20	?	?nectar	Oct.	winter
G. uysiae	flag	brown–purple	5–7	++	nectar	Sep.–Oct.	winter
G. venustus	gullet	mauve or pink	8–11	+	nectar	Aug.–Sep.	winter
G. virescens	flag	yellow–brown	6–9	++	nectar	Sep.–Oct.	winter
G. viridiflorus	gullet	green	9–12	++	nectar	May–July	winter
G. watermeyeri	gullet	green	ca. 10	++	nectar	Aug.–Sep.	winter
G. wilsonii	gullet	white	3–6	–	nectar	Oct.–Nov.	winter
Gladiolus **sect.** *Homoglossum*							
G. atropictus	gullet	blue	ca. 8	++	nectar	Sep.–Oct.	winter
G. blommesteinii	gullet	pink	7–13	+	nectar	Sep.–Oct.	winter
G. brevitubus	star	orange	ca. 2	+	pollen	Oct.–Dec.	winter
G. bullatus	gullet	blue	5–8	+	nectar	Sep.–Oct.	winter
G. caeruleus	gullet	blue	6–8	++	nectar	Sep.	winter
G. carinatus	gullet	blue or yellow	5–8	++	nectar	Aug.–Sep.	winter
G. comptonii	gullet	yellow	7–9	–	nectar	July–Aug.	winter
G. delpierrei	gullet	yellow	ca. 4	+	nectar	Dec.	winter*
G. exilis	gullet	blue	7–10	++	nectar	May–June	winter*
G. gracilis	gullet	blue	8–10	++	nectar	Aug.–Sep.	winter
G. griseus	gullet	green-gray	3–5	–	nectar	June–July	winter
G. inflatus	gullet	purple or pink	5–12	–	nectar	Sep.–Oct.	winter

Table 2. Continued.

Species	Flower		Proximal tube (mm)	Scent	Main reward	Main flowering time	Rainfall zone
	Shape	Color					
G. inflexus	gullet	blue	6–8	++	nectar	July–Aug.	winter
G. jonquilliodorus	gullet	yellow	ca. 5	++	nectar	Dec.–Feb.	winter*
G. martleyi	gullet	pink	ca. 7.5	++	nectar	Mar.–Apr.	winter*
G. mutabilis	gullet	blue or brown	8–12	++	nectar	July–Aug.	winter
G. ornatus	gullet	pink	ca. 12	−	nectar	Sep.–Oct.	winter
G. patersoniae	gullet	blue	5–10	++	nectar	Aug.–Sep.	winter
G. pritzelii	gullet	yellow	ca. 6	++	nectar	Sep.–Oct.	winter
G. quadrangulus	star	white or purple	4–6*	−	pollen	Sep.–Oct.	winter
G. rogersii	gullet	blue	5–8	+/−	nectar	Sep.–Oct.	winter
G. subcaeruleus	gullet	blue	8–10	−/+	nectar	Mar.–Apr.	winter*
G. sufflavus	gullet	green	7–8	++	nectar	Aug.–Sep.	winter
G. symonsii	gullet	pink	4–5	?	?	Dec.–Jan.	summer
G. taubertianus	gullet	blue	5–7	+	nectar	Aug.–Sep.	winter
G. trichonemifolius	gullet	yellow	7–10	++	nectar	Aug.–Sep.	winter
G. vaginatus	gullet	blue	3.5–12	++	nectar	Apr.–May	winter*
G. violaceolineatus	gullet	blue	7–9	++	nectar	Sep.–Oct.	winter

rangulus and *G. stellatus,* the actinomorphic flowers of which are arranged spirally on the spikes. These two species also have prominently displayed anthers and short perianth tubes. In the case of *G. quadrangulus,* the tube is extremely narrow and completely occluded by the tightly sheathed style. Flowers of all species with a rotate perianth produce reduced amounts of nectar and are often odorless, but flowers of *G. stellatus* are strongly scented. Pigmentation in species with rotate flowers is usually pale pink, whitish, or lilac, but some populations of *G. quadrangulus* have mauve flowers, and *G. deserticola* has dark blue flowers with white markings. *Gladiolus brevitubus* (sect. *Homoglossum*) has a bright orange perianth with yellow markings on the lower tepals. The flowers are lightly sweet-scented and have a filiform perianth tube, 2.5–4 mm long, and too narrow to permit entry to an insect's tongue.

Scent. Discernible scent production in *Gladiolus*

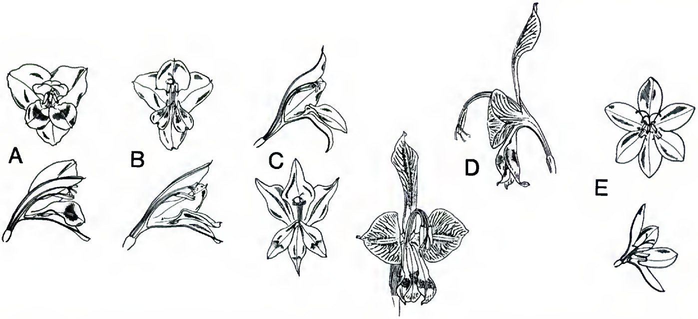

Figure 3. Front view and vertical section (or side view) of flowers of selected species of *Gladiolus* pollinated by bees, showing details of representative gullet (A–C), flag (D), and rotate (E) flowers. —A. *G. crassifolius* (sect. *Densiflorus*). —B. *G. woodii* (sect. *Linearifolius*). —C. *G. permeabilis* (sect. *Hebea*). —D. *G. uysiae* (sect. *Hebea*). —E. *G. brevitubus* (sect. *Homoglossum*). Scale approx. full size.

Figure 4. Floral foraging in southern African *Gladiolus.* —A. *Amegilla obscuriceps* on *G. brevifolius.* —B. *Amegilla spilostoma* on *G. rufomarginatus.* —C. *Anthophora diversipes* on *G. alatus.* —D. *Amegilla spilostoma* on *G. crassifolius.* Arrows indicate position of anthers.

is correlated with phylogeny and geography (Table 2). Fragrance is released during the day and is suppressed at night. To the human nose, most species of the southern African winter-rainfall zone in sections *Hebea* and *Homoglossum* have strong, sweet, but variable fragrances reminiscent of commercial cultivars of *Rosa centifolia*, *Viola odorata*, or *Freesia* spp. The flowers of *G. alatus* (sect. *Hebea*) and a few other species in sections *Hebea* and *Homoglossum* produce a distinctive, somewhat acrid odor, reminiscent of the terrestrial orchid genus *Pterygodium*. Within section *Homoglossum*, isolated populations of *G. carinatus*, *G. gracilis*, and *G. trichonemifolius* were found to have flowers lacking discernible scent. Species of section *Blandus* produce no apparent odor, and those of section *Linearifolius* in the winter-rainfall zone may have sweet, rose-like scents or no apparent odor.

In contrast, most *Gladiolus* species of the summer-rainfall zone, including those species belonging to sections *Hebea* and *Homoglossum*, produce no discernible scent. *Gladiolus pubigerus* (sect. *Linearifolius*) produces a scent similar to flowers of tuberose (*Polianthes*) in the southern populations in KwaZulu-Natal. We have recorded unscented flowers elsewhere in its range.

Neutral red tests indicate a correlation between scent production in *Gladiolus* flowers and epidermal vestiture of the tepals. Within 18 hours of soaking in aqueous neutral red, papillae on the lower tepals and ventral throat of *Gladiolus* flowers stain red. These papillate zones are restricted to regions of pale pigmentation. Flowers of species that lack these papillate zones appear unscented.

Biochemical analysis of floral fragrance in selected *Gladiolus* species in sections *Hebea* and *Homoglossum* identifies 16 major constituents (Table 3). However, the scents of most of these species contain only four to seven major constituents. *Gladiolus virescens* is unusual in producing only two scent constituents. Fragrances dominated by geraniol, citronellol, and nerol, or their acetates, have a rose-like odor. Fragrances dominated by B-ionone and dihydro-B-ionone smell like a combination of violet and freesia (Table 3). The orchid-like odor of *G. alatus* appears to be produced primarily by linalool, balanced with a combination of four lesser constituents.

Nectar. Nectar glands are septal in *Gladiolus* species, as in the entire subfamily Ixioideae (Goldblatt, 1990, 1991; Manning & Goldblatt, unpublished). Nectar is secreted from pores at the top of the ovary directly into the base of the perianth tube and is retained in the proximal part of the tube. The

Table 3. Scent characteristics of selected species of southern African *Gladiolus* with flowers adapted for bee pollination.

		Scent composition (% constituents above 1%)															
Species	Scent description	Geraniol	Geraniol acetate	Citronellol	Citronellyl acetate	Nerol	Neryl acetate	Nerolidol	Limonene	Ocimene	a-farnesine	B-pinene/ (a-)	Caryophyllene/ (-epixide)	Benzyl acetate	B-ionone	Dihydro-B-ionone	Linalool
Gladiolus **sect.** *Hebea*																	
G. alatus	floral orchid	—	—	—	—	—	—	12.5	—	—	8.5	7 (3)	11 (4.5)	—	—	—	45
G. orchidiflorus	rosy sweet	7	39.5	—	—	36	8	—	—	—	—	2	4	—	—	—	—
G. scullyi	rosy	27	—	4	—	45	—	2	—	—	15	—	—	—	—	—	—
G. virescens	violet–freesia	—	—	—	—	—	—	—	—	—	—	—	—	—	88	7	—
Gladiolus **sect.** *Homoglossum*																	
G. carinatus	violet–freesia	—	—	—	—	—	—	—	—	4.5	—	—	6	—	71	10.5	—
G. jonquilliodorus	rosy	26	—	30.5	10	4	—	3.5	—	—	—	—	—	16	—	—	2
G. patersoniae	rosy	34	—	6.5	—	41	—	—	1	1.5	—	4	—	—	1.5	—	—

Table 4. Nectar characteristics of selected species of southern African *Gladiolus* with flowers adapted for bee pollination. Sample number, from different individuals, (n) for nectar volume and concentration (conc.) is the same. Fru = fructose, Glu = glucose, Suc = sucrose.

Species	Nectar		Range of sugars %			Ratio of sucrose to F + G (n)
	Volume µl (n)	Conc. % (±SD)	Fru	Glu	Suc	
G. alatus	0.6–1.2 (6)	27.5 (3.6)	4	13–16	80–83	4.41 (2)
G. appendiculatus	2.7–3.8 (2)	29.0–34.0	—	—	—	—
G. arcuatus	2.1–3.1 (5)	43.2 (2.1)	—	—	—	—
G. aureus	quantity too small to measure		6	16	78	3.55 (1)
G. blommesteinii	0.8–1.6 (3)	25.0 (3.1)	—	—	—	—
G. brachyphyllus	—	—	2	10	88	7.33 (1)
G. brevifolius	0.8–1.5 (5)	30.2 (3.2)	—	—	—	—
G. brevitubus	no measurable nectar produced					
G. carinatus (Darling)	1.0–2.9 (5)	30.0 (0.9)	1	10	89	8.09 (1)
(Aurora)	0.5–0.8 (8)	25.6 (1.5)	12	4–9	79–84	4.41 (2)
G. crassifolius	1.8–2.7 (3)	27.7 (1.2)	7–15	15–22	63–78	2.39 (2)
G. ferrugineus	2.7–3.5 (3)	29.3 (2.1)	3–11	9–21	68–89	3.65 (2)
G. gracilis (Darling)	0.8–1.8 (10)	36.6 (3.1)	1–6	7–12	82–93	7.51 (4)
(Aurora)	0.6–1.1 (10)	26.1 (2.6)	8–12	1–3	87–89	7.33 (2)
G. grandiflorus	4.1–6.9 (5)	28.6 (2.7)	—	—	—	—
G. hirsutus	1.2–1.9 (2)	25.0–27.0	—	—	—	—
G. inflatus	1.3–2.5 (6)	30.1 (2.3)	—	—	—	—
G. inflexus	1.7–4.6 (6)	36.3 (7.5)	—	—	—	—
G. involutus	3.1–3.8 (2)	29.0	18–21	22–24	57–58	1.35 (2)
G. jonquilliodorus	1.6–2.7 (6)	33.7 (2.2)	—	—	—	—
G. malvinus	2.6–3.0 (2)	44	0	10–11	89–90	8.55 (2)
G. marlothii	2.1–2.9 (4)	26.0 (2.2)	0–5	17–18	77–83	4.00 (2)
G. mostertiae	2.7–3.8 (3)	29.0 (2.0)	0	10–18	82–90	6.14 (2)
G. ochroleucus	2.4–4.9 (5)	27.1 (1.3)	?	3–13	87–97	11.50 (2)
G. ornatus	1.8 (1)	—	7	18	75	4.00 (1)
G. patersoniae (Die Galg)	1.3–2.5 (5)	28.0 (2.5)	—	—	—	—
(Worcester)	0.9–1.7 (8)	33.4 (2.6)	—	—	—	—
G. pavonia	1.5 (1)	36	8	26	66	1.94 (1)
G. permeabilis subsp. *permeabilis*	2.8 (1)	29	—	—	—	—
G. pulcherrimus	—	—	7–8	22	70–71	2.39 (2)
G. quadrangulus	no measurable nectar produced					
G. rogersii	2.4–3.9 (2)	24–26	—	—	—	—
G. scullyi	2.6–3.9 (3)	28.7 (1.5)	9–15	31–36	49–60	1.20 (2)
G. speciosus	—	—	6–8	16	76–78	3.35 (2)
G. stellatus	0.4–0.5 (4)	45.8 (2.6)	10–15	20–27	63–70	1.88 (3)
G. sufflavus	1.4–1.9 (2)	36.0	0–5	17–19	78–81	3.88 (2)
G. trichonemifolius	0.5–1.3 (10)	30.9 (4.2)	—	—	—	—
G. uysiae	0.4–0.8 (2)	40	10–33	18–22	49–68	1.41 (2)
G. venustus	0.8–2.9 (10)	26.3 (2.1)	5–12	24–30	58–69	1.80 (3)
G. violaceolineatus	2.6–5.5 (2)	28.0	14–22	31–44	34–55	0.78 (3)
G. watermeyeri	0.7–1.3 (2)	25–32	10–28	17–39	33–73	0.97 (4)

length of the perianth tube varies among the *Gladiolus* species studied from 7 to 30 mm long, with the proximal, slender part mostly 4.5–15 mm (Table 2). All but 2 of 39 species examined for this character were observed to secrete nectar. Nectar volumes are modest, mostly 1.5–3 μl, and rarely exceed 5 μl (Table 4).

Nectars are sucrose-rich to sucrose-dominant, with sugar solute making up 25–35% of the total volume of fluid (Table 4). The nectar of *Gladiolus aureus*, *G. brevitubus*, and *G. quadrangulus* is produced in such small quantities that the volumes could not be measured. Nectar of *G. stellatus*, which has short-tubed flowers and is visited by short-tongued andrenid bees, shows no difference as regards nectar sugars from species visited only by long-tongued bees, but it does produce nectar of the highest concentration of all *Gladiolus* species in this study, with a mean of 45% sucrose equivalents (Table 4). Nectar recorded here for *Gladiolus* species is similar in quality to that reported for other Iridaceae pollinated by active, long-tongued insects, including long-tongued flies and sphinx moths (Goldblatt et al., 1995; Manning & Goldblatt, 1995, 1997). Nectar volumes are, however, considerably larger in long-tongued fly flowers. Some bird-pollinated species of *Gladiolus* may also have sucrose-rich nectar, while others have hexose-dominant nectar with only trace amounts of sucrose (B.-E. van Wyk, pers. comm.).

Pollinators, pollination mechanisms, and pollen-load analysis. Insect visitors collected on short-tubed species of *Gladiolus* were mostly bees, but in a few cases also flies, or hopliine beetles (Table 5). Bees included *Andrena* sp. (Andrenidae); *Allodape* (1 sp.), *Amegilla* (5 spp.), *Anthophora* (3 spp.), *Apis* (1 sp.), *Pachymelus* (1 sp.), *Tetralonia* (1 sp.), and *Xylocopa* (1 sp.) (Apidae); *Lasioglossum* (2 spp.), *Lipotriche* (2 spp.), and *Patellapis* (1 sp.) (Halictidae); and *Rediviva* (1 sp.) (Melittidae). Bees were predominantly female, but some males were also captured.

Gullet and flag flowers are pollinated primarily by bees with large bodies and long tongues in the family Apidae (Figs. 4, 5), including *Amegilla*, *Anthophora*, and *Pachymelus* (Tables 5, 6). These bees appeared to be foraging solely for nectar, and no anthophorine bees were found visiting *Gladiolus* flowers to collect pollen. Nemestrinid and acrocerid flies, *Prosoeca*, *Psilodera*, and *Stenobasipteron*, with moderately long mouthparts (10–12 mm; Table 6), were also captured on flowers of some *Gladiolus* species visited by bees. They also appeared to pollinate these species in their foraging for nectar, and, like the captured anthophorine bees, were found to carry *Gladiolus* pollen. Both bees and flies landed on the lower tepals and inserted their probosces into the floral tube (Fig. 4). As the insect pushed its head into the floral throat, its thorax made dorsal contact with the anthers and/or the stigma lobes. In *G. orchidiflorus* and flag flowers of section *Hebea* ser. *Hebea*, the dorsal surface of the thorax and abdomen contacted the anthers or stigma lobes as an insect exited a flower.

The native and commercial strains of the honey bee, *Apis mellifera*, appear to be significant pollinators of a few *Gladiolus* species of the winter-rainfall zone. Individuals mostly behaved like anthophorine bees, visiting flowers for nectar, but were also seen actively foraging for pollen.

Our observations show that both anthophorine and honey bees display moderate floral constancy. Anthophorine bees consistently visited flowers of several plants of a particular *Gladiolus* species in succession before shifting their attention to the flowers of other plant species. Where we were able to track individual bees, the same bee was seen to revisit the same series of flowers several times during a morning. Honey bees exhibited stronger floral constancy, and numerous individuals could be observed visiting flowers of different individuals of a *Gladiolus* species for over an hour before shifting their foraging activity to other species.

Gladiolus species of the southern African winter-rainfall zone receive a greater diversity of bee foragers than those of the summer-rainfall zone. Summer-rainfall species were visited primarily by *Amegilla* species (mostly *A. aspergina*, *A. capensis*, *A. fallax*), but also by *Xylocopa rufitarsis* and two species of long-tongued flies in the family Nemestrinidae (Table 5). In the winter-rainfall zone, the most common pollinators were *Anthophora diversipes* and *A. krugeri*, both large bees (Table 5) active in the spring (August to October). Visits to spring-flowering *Gladiolus* species of the winter-rainfall zone by *Pachymelus peringueyi* (Apidae), the short-tongued *Rediviva aurata* (Melittidae), and *Xylocopa rufitarsis* (Apidae) have also been recorded. *Apis mellifera* appears to be an important pollinator only early in the season (June to August), when cool ambient temperatures often make it the only bee on the wing. *Apis mellifera* was the sole pollinator of the winter-flowering *G. griseus* and early spring-flowering *G. aureus*, *G. quadrangulus*, and *G. tenellus*. Later in the season, this bee is rarely seen on *Gladiolus* species. In the summer and autumn, the most common pollinator in the winter-rainfall zone is *Amegilla spilostoma*.

Gladiolus aureus is one of the few species studied with trace amounts of nectar. Although the proximal part of the floral tube is 10–15 mm long, it is extremely narrow, forming a tight sheath around the style, and contains virtually no nectar, only traces of which are present at the mouth of the tube. *Apis mellifera* was the only insect visitor observed, and individuals were seen collecting pollen from the anthers. *Gladiolus aureus* has bright yellow flowers that resemble blooms of yellow-flowered, nectariferous *Oxalis pes-caprae* L., a favorite plant resource of this bee (unpublished observation). Active pollen collection, involving *A. mellifera*, was noted in only two other *Gladiolus* species, *G. gracilis* and *G. quadrangulus*.

A striking exception to the pattern of bee pollination in short-tubed *Gladiolus* species is *G. brevifolius,* on which the acrocerid fly, *Psilodera valida,* was captured while foraging for nectar. This fly is a remarkable mimic of *Amegilla obscuriceps* and *A. spilostoma,* the most common insect visitors of *G. brevifolius,* in appearance, flight, and foraging behavior (Goldblatt et al., 1997). Another exceptional species, *G. meliusculus,* is visited by both female andrenid bees and hopliine beetles (Goldblatt et al., 1998). The exceptionally large landing platform and unusually dark tepal markings are often hallmarks of hopliine beetle pollination, a common strategy in the southern African winter-rainfall zone. Although common in other genera of Iridaceae, including *Ixia, Sparaxis,* and *Tritonia* (Goldblatt et al., 1998), hopliine beetle pollination is not known in other species of *Gladiolus.*

Observations and bee collections on *Gladiolus* species with rotate flowers (*G. brevitubus, G. quadrangulus,* and *G. stellatus*) indicated pollination by small-bodied *Patelapis* and *Lasioglossum* species (Halictidae), *Apis mellifera* (Apidae), and a large *Andrena* sp. (Andrenidae) (Table 5). *Apis* and the *Andrena* sp. landed directly on the anthers, while the halictids landed on the tepals and crawled onto the anthers. While both the *Andrena* sp. and the halictid bees were observed visiting the bases of the flowers for nectar, these bees spent most of their time during visits collecting pollen. Only *Apis* and the *Andrena* sp. were seen to contact the stigma lobes while foraging. The sweetly scented flowers of *G. stellatus* are unusual in opening at sunrise and closing completely soon after midday. *Gladiolus stellatus* would appear to optimize the number of insect visits by partitioning the diurnal timing of flowering with the seasonally coblooming *Moraea polyanthos* Thunb. The flowers of *M. polyanthos* open shortly after those of *G. stellatus* close and fade in the late afternoon. Both plants receive visits by the same bee species.

The morphology of the bilabiate *Gladiolus* flower optimizes pollinator effectiveness because the insect is forced to push its upper body into the distal part of the floral tube as it inserts its mouthparts down the narrow proximal tube in search of nectar. The distal tube conforms closely to the shape and size of the pollinator's body, and the anthers, with their load of pollen, come into close contact with the dorsal surface of the thorax of the insect. Pollen deposition is thus passive, and confined to the dorsal parts of the head and thorax. As flowers of *Gladiolus* species are primarily sources of nectar, it is no surprise that both male and female anthophorine bees visit them, although female bees are recorded more often. In the case of flowers that offer pollen, only female bees were captured. The majority of bees captured on *Gladiolus* species were found to have pollen of *Gladiolus* on the dorsal surface of the thorax. Female anthophorines and halictids also carried *Gladiolus* pollen in their scopae, while *Gladiolus* pollen was usually present in the corbiculae of captured *Apis mellifera.*

The hundreds of hours spent in the field, always at optimal times for pollinator activity, suggest low rates of visitation to *Gladiolus* flowers by anthophorine bees. Visitation rates to species with gullet or flag flowers ranged from no visits to a maximum of three bees per flower per hour. These rates seemed highest in undisturbed sites, where flowering individuals are relatively widely dispersed over the landscape (usually 1–2 m apart). At sites where fire or clearing had occurred in the past one to two years, flowering individuals were often at relatively high density (ca. 20–30 cm apart) and visits seemed to be reduced, so that although bee individuals were seen visiting some flowers, many flowers did not receive visits during the hours we spent at such sites. Typically, female anthophorines begin a foraging bout by visiting flowers of *Gladiolus,* but then forage on coblooming plants of other taxa offering either pollen or nectar, e.g., Asteraceae, *Lachenalia, Lobostemon, Salvia.* Female anthophorines returned to *Gladiolus* flowers repeatedly during the day, visiting three or more *Gladiolus* flowers and alternating these visits with bouts of foraging on flowers of nectariferous species in the families Asteraceae, Boraginaceae (*Lobostemon*), Fabaceae, Hyacinthaceae (especially *Lachenalia*), Iridaceae, Lamiaceae, and Sterculiaceae (*Hermannia*) (Table 5), as well as nectarless species in the families Asphodelaceae (*Bulbine, Trachyandra*) and Hyacinthaceae (*Tenicroa*).

Apis mellifera was observed to forage on *Gladiolus trichonemifolius* more frequently and consistently than any female anthophorine. More than 20 bees were noted foraging on *G. trichonemifolius* between 1100 and 1200 hours. However, after 1200, *Apis mellifera* abandoned flowers of this species and shifted foraging to *Trachyandra* and other coblooming genera.

Reproductive success. For one species where this was estimated, *Gladiolus venustus,* reproductive success was 88%. In a sample size of 61 plants that collectively produced 253 flowers, 202 well formed, full capsules were produced. Our general impression is that species with flowers adapted for pollination by bees almost always produce numerous capsules per plant. Failure to set capsules is

Table 5. Pollen-load analysis of bees and other insects captured on *Gladiolus* species with short-tubed flowers. Number of individuals of either sex indicated in parentheses. *Gladiolus* species are arranged by section according to Goldblatt and Manning (1998). Taxonomic associations of insects are as follows: Hymenoptera (bees): *Allodape, Amegilla, Anthophora, Apis, Pachymelus, Tetralonia, Xylocopa* (Apidae); *Andrena* (Andrenidae); *Lasioglossum, Lipotriche, Patellapis* (Halictidae); *Rediviva* (Mellittidae). Diptera (flies): *Prosoeca, Stenobasipteron* (Nemestrinidae); *Philoliche* (Tabanidae); *Psilodera* (Acroceridae). Coleoptera (beetles): *Lepisia, Pachycnema* (Scarabaeidae: Rutelinae). Abbreviations: UM = unidentified monocot; UD = unidentified dicot. Families of plant taxa: *Aristea, Homeria, Ixia, Hesperantha, Lapeirousia, Moraea, Romulea* (Iridaceae); *Bulbine, Trachyandra* sp. (Asphodelaceae); *Cyphia* (Campanulaceae); *Erica* (Ericaceae); *Hermannia* (Sterculiaceae); *Lachenalia, Tenicroa* (Hyacinthaceae); *Lobostemon* (Boraginaceae); *Oxalis* (Oxalidaceae); *Protea* (Proteaceae); *Salvia* (Lamiaceae); *Satyrium* (Orchidaceae); *Spiloxene* (Hypoxidaceae); *Wachendorfia* (Haemodoraceae).

	Number of insects carrying pollen of		
Plant and insect taxon	*Gladiolus*	Other species	Pollen species carried (excl. *Gladiolus*)
SUMMER-RAINFALL ZONE			
Gladiolus **sect.** *Densiflorus*			
G. appendiculatus			
Amegilla aspergina (2 ♀ 1 ♂)	3	0	n/a
G. crassifolius			
Amegilla capensis (3 ♂)	3	2	*Moraea brevistyla*, UD (1)
A. spilostoma (2 ♀)	2	2	UD × 2 (?Lamiaceae)
Prosoeca sp. (1)	1	1	UD × 4 (?Gentianaceae, Fabaceae)
G. densiflorus			
Amegilla fallax (2 ♀)	2	2	Lamiaceae, Fabaceae
G. exiguus			
Amegilla fallax (2 ♂)	2	2	UM (1), Fabaceae
A. spilostoma (3 ♀)	3	1	Fabaceae, UM (1)
G. ferrugineus			
Amegilla capensis (1 ♀)	1	1	*Chlorophytum* sp., *Hesperantha rupestris*, Lamiaceae, ?Fabaceae
Amegilla aspergina (1 ♀)	1	0	n/a
G. papilio			
Amegilla capensis (2 ♀)	2	0	n/a
Amegilla aspergina (1 ♀)	1	0	n/a
Tetralonia sp. (1 ♀)	1	1	*Hibiscus* sp.
Gladiolus **sect.** *Ophiolyza*			
G. dolomiticus			
Amegilla spilostoma (2 ♀)	2	2	Fabaceae, Lamiaceae
Xylocopa rufitarsis (2 ♀)	2	2	Fabaceae, Lamiaceae
Allodape variegata (2 ♀)	0	1	Asteraceae
Lasioglossum sp. (1 ♀)	1	0	n/a
G. ecklonii			
Amegilla aspergina (2 ♂)	2	2	Lamiaceae (?*Hemizygia*), UD
G. sericeovillosus			
Amegilla spilostoma (2 ♀)	2	1	Asteraceae, Ericaceae, UD (2), UM (1)
Prosoeca sp. (1)	1	0	n/a
Gladiolus **sect.** *Hebea*			
G. permeabilis subsp. *edulis*			
Amegilla fallax (2 ♀)	2	2	UD (2)
Gladiolus **sect.** *Heterocolon*			
G. rufomarginatus			
Amegilla langi (1 ♀)	1	1	Asteraceae, UD (2) (?Lamiaceae)
Amegilla spilostoma (1 ♀)	1	1	?Lamiaceae, UD (1)
Stenobasipteron difficile (2)	2	1	Asteraceae

Table 5. Continued.

	Number of insects carrying pollen of		
Plant and insect taxon	*Gladiolus*	Other species	Pollen species carried (excl. *Gladiolus*)
WINTER-RAINFALL ZONE			
Gladiolus **sect.** *Blandus*			
G. grandiflorus			
Anthophora diversipes (4 ♀)	4	4	*Hermannia* sp., *Lobostemon*, *Pelargonium* sp., UM (1)
Bombyliidae (1)	1	1	*Hermannia* sp., *Lobostemon*, UM (1)
G. phoenix			
Amegilla spilostoma (2 ♀)	2	2	*Lapeirousia neglecta*, UD (?Fabaceae)
Gladiolus **sect.** *Linearifolius*			
G. aureus			
Apis mellifera (4)	4	0	n/a
G. brevifolius			
Allodape exoloma (1 ♀)	1	1	Asteraceae, *Salvia* sp., Fabaceae
Al. pictifrons (1 ♀)	1	1	Asteraceae, Fabaceae
Amegilla obscuriceps (1 ♀ 1 ♂)	2	2	*Bulbine favosa*, *Salvia* sp., Fabaceae
Am. spilostoma (5 ♀ 2 ♂)	7	7	*Bulbine favosa*, *Pelargonium* sp., *Salvia* sp., Fabaceae, Asteraceae
Lipotriche (1 ♀)	0	0	n/a
Psilodera valida (4)	4	4	*Bulbine favosa*, *Salvia* sp.
G. hirsutus			
Apis mellifera (2)	2	2	*Protea* sp., Asteraceae
Gladiolus **sect.** *Heterocolon*			
G. marlothii			
Anthophora diversipes (3 ♀)	3	3	*Tenicroa*, Fabaceae (?*Wiborgia* sp.), Lamiaceae
G. mostertiae			
Amegilla obscuriceps (2 ♀)	2	0	n/a
Gladiolus **sect.** *Hebea*			
G. alatus			
Anthophora diversipes (2 ♀)	2	2	*Aristea inaequalis* (Iridaceae), *Wachendorfia* sp. (Haemodoraceae), UM (1)
An. diversipes (2 ♀)	2	2	*Babiana disticha*, Asteraceae, UD (1) (?Fabaceae)
An. diversipes (1 ♀ 1 ♂)	2	2	*Lachenalia* sp., *Lobostemon* sp., *Oxalis* sp. Asteraceae
Rediva aurata (1 ♀)	1	1	*Lachenalia*, Asteraceae
G. ceresianus			
Anthophora diversipes (1 ♀)	1	1	Asteraceae, ?Lamiaceae
G. equitans			
Pachymelus peringueyi (1 ♀)	1	1	*Hermannia* sp., UM (1)
G. meliusculus			
Andrena sp. (2 ♀)	1	?	*Homeria* sp., *Oxalis* sp., Asteraceae
Lepisia rupicola (7)	6	4	*Romulea* ?*eximia*, *Spiloxene capensis*
Pachycnema crassipes (6)	6	6	*Drosera* sp., *Spiloxene capensis*, Asteraceae
G. orchidiflorus			
Anthophora diversipes (2 ♀)	2	2	*Lobostemon*, Asteraceae
G. permeabilis subsp. *permeabilis*			
Anthophora diversipes (2 ♀)	2	2	*Hermannia* sp., Asteraceae
G. scullyi			
Anthophora diversipes (1 ♂ 1 ♀)	2	1	*Lobostemon* sp., UM (1)
G. speciosus			
Rediviva aurata (1 ♀)	1	1	*Diascia* sp., *Ornithogalum* (?*thyrsoides*)

Table 5. Continued.

Plant and insect taxon	Number of insects carrying pollen of		Pollen species carried (excl. *Gladiolus*)
	Gladiolus	Other species	
G. stellatus			
Andrena sp. (2 ♀)	2	2	*Moraea* (*?polyanthos*), *Lobostemon* sp.
G. uysiae			
Anthophora diversipes (1 ♀)	1	1	*Lachenalia* (*?elegans*), UD (1) (?Fabaceae)
G. venustus			
Anthophora diversipes (3 ♀ 1 ♂)	4	4	*Lobostemon* sp., *Lachenalia* sp.
A. krugeri (1 ♀)	1	1	UD (2), Orchidaceae
G. virescens			
Anthrophora diversipes (1 ♀)	1	1	*Ixia* (*?latifolia*), *Satyrium* sp. (Orchidaceae)
G. watermeyeri			
Anthophora diversipes (2 ♀)	2	2	*Lobostemon* (Boraginaceae)
A. krugeri (1 ♀)	1	1	*Lachenalia* (Hyacinthaceae), 1 (UD)
Gladiolus **sect.** *Homoglossum*			
G. blommesteinii			
Anthophora diversipes (1 ♀ 1 ♂)	2	2	*Lachenalia* sp., Lamiaceae (*?Salvia* sp.), *Lobostemon* sp., UD (*?Cyphia* sp.)
G. brevitubus			
Lasioglossum sp. (2 ♀)	2	2	Asteraceae
G. carinatus			
Anthophora diversipes (2 ♂ 1 ♀)	3	3	*Lobostemon* sp., *Hermannia* sp., *Homeria*
A. schulzei (2 ♀)	2	2	*Hermannia* sp., *Homeria* sp.
A. krugeri (1 ♂)	1	1	*Lobostemon* sp., *Hermannia* sp., *Homeria*
Apis mellifera (2)	2	2	*Moraea* sp.
Lasioglossum sp. (1 ♀)	1	1	Asteraceae
G. exilis			
Amegilla fallax (1 ♀)	1	1	*Trachyandra* sp.
G. gracilis			
Anthophora diversipes (2 ♀)	2	2	*Lobostemon* sp., Fabaceae (*?Aspalathus*)
Apis mellifera (5)	5	4	*Lobostemon* sp., *Erica* sp.
Xylocopa rufitarsis (1 ♂)	1	1	Fabaceae (*?Aspalathus*)
G. griseus			
Apis mellifera	4	4	Asteraceae (*?Chrysanthemoides monilifera*), *Oxalis* sp.
G. inflatus			
Amegilla obscuriceps (1 ♀ 1 ♂)	2	1	*Lobostemon* sp.
G. inflexus			
Anthophora krugeri (1 ♂)	1	0	n/a
Apis mellifera (3)	3	3	*Oxalis* sp., *Romulea* sp.
Patellapis sp. (1 ♀)	1	1	Asteraceae
G. jonquilliodorus			
Amegilla spilostoma (1 ♀)	1	1	*Aristea*
Apis mellifera (1)	1	1	*Aristea*, UD (1)
G. martleyi			
Amegilla spilostoma (2 ♀)	2	2	Rutaceae, UM (1)
G. patersoniae			
Anthophora krugeri (3 ♀)	3	1	*Lobostemon* sp.
Anthophora diversipes (1 ♀)	1	1	*Lobostemon* sp.
Apis mellifera (3)	3	3	*Lachenalia* sp., *Lobostemon* sp., *Oxalis* sp., UD (1)
G. quadrangulus			
Apis mellifera	5	5	*Oxalis* sp., *Hermannia* sp.
G. sufflavus			
Anthophora diversipes (2 ♀)	2	2	*Ixia* (*?brunneobracteata*), *Homeria* sp., *Lobostemon* sp.
G. trichonemifolius			
Apis mellifera (7)	7	7	Asteraceae, *Oxalis* sp., *Romulea* sp., *Trachyandra* sp.

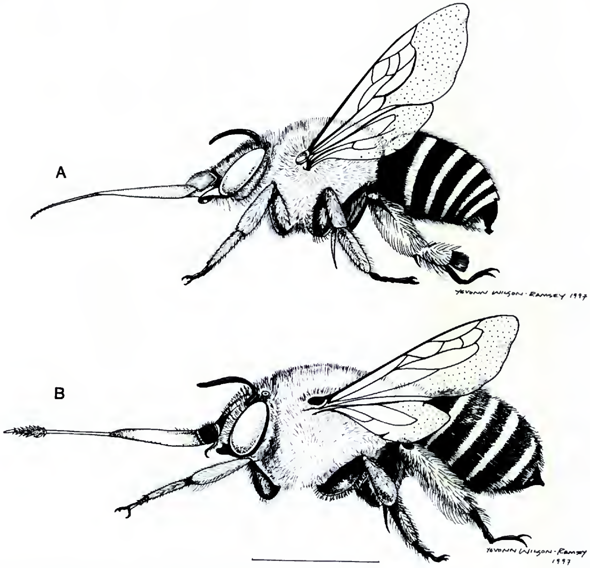

Figure 5. Representative long-tongued anthophorine bee species captured on flowers of *Gladiolus*, showing tongue length relative to body size. —A. *Amegilla fallax*. —B. *Amegilla capensis*. Scale bar 5 mm.

more likely to be the result of unfavorable weather conditions than ineffectiveness of pollinators.

DISCUSSION

Bee pollination in southern African *Gladiolus* comprises two different systems. A few species offer meager quantities of nectar or none at all, and have what appear to be derived, short-tubed, rotate flowers with actinomorphic perianths. These flowers are adapted for a relatively unspecialized pollination strategy of active pollen collection by female andrenids, honey bees, and possibly halictid bees. In the second mode of bee pollination, flowers have zygomorphic perianths and obliquely funnel-shaped floral tubes containing appreciable amounts of sucrose-rich nectar. They are adapted for pollen dispersal by anthophorine and honey bees seeking nectar. In this mode, bees must navigate zygomorphic perianths, and the transfer of pollen to the body of the bee is passive (sensu Bernhardt, 1996). In both these modes of bee pollination, bees are always polylectic foragers. *Apis mellifera* and some large-bodied anthophorines are known to be generalist foragers in southern Africa (Goldblatt et al., 1989, 1995) and on other continents (Armstrong, 1979; Michener, 1974; Bernhardt & Weston, 1996). Another aspect of both modes of bee pollination is that the combination of floral dichogamy, herkogamy, self-incompatibility (inferred), and fairly diffuse population patterns would appear to encourage outbreeding, with large-bodied bees acting as pollen vectors.

The zygomorphic, gullet or flag flower offering nectar and pollinated by large-bodied, hairy, long-tongued bees is the most common floral type among the bee-pollinated *Gladiolus* species studied. This pollination system has now been established for 41 species of the genus in southern Africa. An additional 53 species have flowers similar in size, shape, and coloring, and may be assumed to have the same pollination system. Thus 95% of bee-pollinated species and 94 of the 166 species (56%) of

Table 6. Body dimensions of bee and fly species captured on flowers of *Gladiolus* species. Measurements are the range for each species that was captured, thus covering different study sites.

Taxon	Body length mm	Mouth-part length mm
	HYMENOPTERA	
ANDRENIDAE		
Andrena sp.	14–15	2–3
ANTHOPHORIDAE		
Amegilla capensis	ca. 12.5	9–10
Am. fallax	10–12	4–6
Am. langi	ca. 11	ca. 10
Am. obscuriceps	10–11	5–6
Am. spilostoma	10–14	6–9
Am. sp.	ca. 10	ca. 7.5
Anthophora diversipes	14–17	6.5–8
An. krugeri	11–14	6–7.5
An. schulzei	12–13	5–6
Pachymelus peringueyi	17	ca. 8
Xylocopa rufitarsus	14–15	ca. 4
APIDAE		
Apis mellifera	10–12	3–4
HALICTIDAE		
Patellapis sp.	ca. 9	ca. 2
Lasioglossum sp.	ca. 10	ca. 2
Lipotriche sp.	ca. 11	ca. 2
MELLITIDAE		
Rediviva aurata	ca. 12	ca. 2
	DIPTERA	
ACROCERIDAE		
Psilodera valida	9–10	8–12
NEMESTRINIDAE		
Prosoeca sp.	ca. 15	ca. 12
Stenobasipteron difficile	12–13	ca. 13

Gladiolus in southern Africa, including Zimbabwe, are known or assumed to be pollinated primarily by large, long-tongued bees foraging for nectar. This pollination strategy is also the most widespread within the genus, and predominates in six of the seven sections of *Gladiolus* in southern Africa (according to the infrageneric classification of the genus by Goldblatt & Manning, 1998). In the remaining section *Ophiolyza,* pollination by sunbirds is inferred as most common, given the elongated floral tubes and red or orange flower color of most species. The most parsimonious interpretation would suggest that bee pollination is the ancestral pollination syndrome in the genus.

Just five *Gladiolus* species in southern Africa have rotate perianths and are known or inferred to be pollinated by bees, in this case short-tongued bees foraging for pollen.

The gullet and flag flowers of many *Gladiolus* species show the same type of bee pollination as the bilabiate flowers of such dicot genera as *Pedicularis* (Scrophulariaceae; Macior, 1984), *Aconitum* (Ranunculaceae; Proctor et al., 1996), and the vast majority of papilionoid legumes (Kalin Arroyo, 1989). Both types of flowers exhibit passive collection of pollen. More important, floral evolution in *Gladiolus* exhibits a pattern noted in the flowers of a few other plant genera (e.g., *Pedicularis*), in which passive pollen deposition appears labile. Within such taxa as *Pedicularis* (Macior, 1982), Ranunculaceae tribe Cimicifugeae (Pellmyr, 1985), and the Lecythidaceae (Mori & Prance, 1990), nectariferous bilabiate flowers may be derived from nectarless actinomorphic flowers, or vice versa (Bernhardt, 1996). In *Gladiolus,* as in *Pedicularis,* nectarless species appear to have been derived from ancestors with nectar-producing, bilabiate flowers, but nectarless or nectar-poor species remain in the minority. In *Gladiolus,* this appears to have happened repeatedly, with examples in three separate sections (*G. aureus* being a striking transitional example with its nectar-poor, but gullet-like flowers with an actinomorphic perianth).

There are notable differences between the floral characteristics of summer- and winter-rainfall species of *Gladiolus.* In the summer-rainfall zone, flowers tend to be less variable and less strikingly colored, have obscure tepal markings, and lack scent. They are usually also somewhat smaller in size, and more numerous per inflorescence than in the winter-rainfall zone. The diversity of insect pollinators is lower, and pollinators have a smaller body size. In the winter-rainfall zone, the range of floral color is considerable, and floral markings usually show strong color contrasts. The flowers are often strongly scented, comparatively large, and few per inflorescence. The diversity of pollinators is greater than in the summer-rainfall zone, and pollinator body size is often larger. Irrespective of geography, the selection of large anthophorines pollinating *Gladiolus* flowers does not reflect the diversity of the large anthophorine bee fauna of southern Africa (Eardley, 1994; Eardley & Brooks, 1989). Only a fraction of the total number of *Amegilla, Anthophora,* and *Pachymelus* species represented in the region have been captured foraging for nectar on *Gladiolus* flowers. The same bee species have been captured on several different species of *Gladiolus,* and sometimes the same bee species has been captured in both the summer- and winter-rainfall zones.

Exclusive pollination by long-tongued bees, especially anthophorines, has not often been documented as a specialized mode of pollination in the southern African flora. Large-bodied anthophorines have been associated with *Nivenia* and *Lapeirousia* spp., but a large proportion of species in these genera are pollinated by long-tongued flies in the Nemestrinidae and/or Tabanidae (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995). The bilabiate, nectariferous flowers of *Gladiolus* species appear to exploit long-tongued bees as pollinators in much the same manner as *Nivenia* and *Lapeirousia* exploit long-tongued flies.

The relationship between the bee-pollination system of the majority of *Gladiolus* species and the long-tongued fly pollination system of the minority of *Gladiolus* species (Manning & Goldblatt, 1997; Goldblatt & Manning, 1998) is of particular interest. In contrast to flowers of bee-pollinated *Gladiolus* species, flowers adapted for pollination by long-tongued flies are scentless, have much longer floral tubes, are pink to white with red nectar guides, and are at best weakly bilabiate (Manning & Goldblatt, 1995, 1997). These floral differences, while minor, are entirely consistent within the genus. Consequently, the adaptive radiation of pollination systems in *Gladiolus* appears to be the inverse of that in *Lapeirousia* subg. *Lapeirousia*, where bee pollination is derived in some species.

A specialized pollination system? Pollination by long-tongued anthophorine bees is not normally considered a specialized pollination strategy among African plants. More often (e.g., in *Lapeirousia*, Goldblatt et al., 1995), anthophorine bees participate in more generalized pollination systems that include honey bees, bee flies (Bombyliidae), butterflies, and hopliine beetles. The vast majority of *Gladiolus* species with moderate-sized flowers and obliquely funnel-shaped tubes show a close fit between the size of the flower and that of the anthophorine pollinator—more specifically, between the shape, diameter, and length of the floral tube and the shape and size of the anthophorine's head and thorax. This leads to direct contact between the dorsal surface of the bee's thorax and the sexual organs of the flower. The fit is refined in *G. appendiculatus*, where bees gain access to the floral tube by contact with the anther appendages. Evolution of these appendages in *G. appendiculatus* converges with the evolution of anther awns in the zygomorphic flowers of *Viola* and its allies (Beattie, 1974) and of the sterile anther locule in *Salvia*. The pollinators of *Viola* or *Hybanthus* flowers cannot feed on the nectar in the floral spur without tripping the anther awns that deposit pollen on the insects' bodies (Bernhardt, 1996).

Most other insects that we have occasionally captured visiting *Gladiolus* flowers do not come close to matching this fit. Smaller bees, including Halictidae, and hopliine beetles, are usually too small to be effective pollinators, and seldom carry *Gladiolus* pollen, except in the case of *G. meliusculus*, which appears to be specifically adapted for pollination by hopliine beetles, evidently in combination with andrenid bees (Goldblatt et al., 1998). Long-tongued flies, including *Psilodera* (Acroceridae), *Prosoeca* and *Stenobasipteron* (Nemestrinidae), with large bodies and tongues 10–15 mm long, behave much like anthophorine bees and appear to be potential pollinators, but are much less frequently observed than bees and thus seem to be of minor importance in the pollination ecology of *Gladiolus*. These flies are nectar feeders and are not known to consume pollen, nor do the females collect pollen to provision nests.

We have only rarely seen anthophorine bees or *Apis mellifera* collecting pollen actively from *Gladiolus* species with zygomorphic flowers. The accumulation of *Gladiolus* pollen in the scopae or corbiculae of these bees thus must result from the grooming process. Analyses of pollen loads removed from the bodies of female bees, including the thorax and corbiculae or scopae, combined with field observation of bee activity, indicate that honey bees and female anthophorines depend on *Gladiolus* for nectar but visit many other plants for a combination of pollen and nectar. In some cases, these bees visit nectarless flowers (*Bulbine*, *Tenicroa*, *Trachyandra*) exclusively for their pollen. Since *Apis* and anthophorines visit both nectar-rich and nectar-poor flowers in southern Africa, their foraging parallels the behavior of female anthophorines and halictids in southern Australia (Bernhardt, 1984, 1986, 1989, 1995). In southern Africa, *Gladiolus* species produce nectar, satisfying the energy requirement of the adult bees, while other species offer pollen required by the bees' larvae. Thus *Gladiolus* species with short-tubed, zygomorphic flowers appear to be specifically adapted for a type of bee pollination in which nectar is the consistent reward, and which involves one or very few insect species. There is no indication that this strategy is part of a generalist system involving long-tongued bees and other unspecialized pollinators.

Interestingly, the suppression of both zygomorphy and nectar production in *Gladiolus* species does not make them more attractive to anthophorine bees. Instead, these floral modifications appear to have resulted in a pollinator shift in which the usual pollinators (anthophorines) are replaced by bees belonging to different taxonomic associations (Andrenidae, *Apis*, and possibly Halictidae) and, in one case, hopliine beetles.

A consequence of the limited selection of anthophorine bee species that visit flowers of *Gladiolus* species is the constraint this imposes on the geographic ranges of these plants. Species of *Gladiolus* sharing anthophorine bee pollinators rarely co-occur, except when their flowering times do not overlap. Otherwise, they would compete directly for the same pollinator(s) and be at risk not only of having the wrong pollen deposited on their stigmas, thereby reducing or preventing seed production, but also of having their gene pools disturbed by hybridization (many *Gladiolus* species are interfertile; Herbert, 1847; Goldblatt, 1971, and unpublished). Different species using the same pollination system may be isolated reproductively either by edaphic preferences or by flower shape, color, markings, and/or scent. We speculate that the reason floral variation is so great in *Gladiolus* species pollinated primarily by large-bodied bees in the winter-rainfall zone is that flowering there is concentrated in the spring. The coincident flowering of so many species puts a premium on pollinators. By contrast, species of the genus that have shifted their flowering time significantly exhibit limited floral variability. They have comparatively small flowers of unspecialized form, often virtually identical even in different sections, and more typical of species of the southern African summer-rainfall zone.

In conclusion, pollination by anthophorines in *Gladiolus* shows both expected and unexpected trends. As expected, zygomorphic flowers coupled with high-sucrose nectars are often predicted in plants pollinated by bees with large bodies and long tongues (Baker & Baker, 1983, 1990). In contrast, it is unusual to find two floral forms, flag and gullet, in the same plant genus and in association with the same pollinators. The floral forms of *Gladiolus* species pollinated by bees alone are as variable as those of some neotropical orchid genera pollinated by euglossine bees (Dressler, 1981). The diversity of *Gladiolus* in southern Africa is accounted for largely by species using long-tongued bees as specialist pollinators. Other pollination strategies occur in less than half the species in the region. A final and unexpected feature of bee pollination in *Gladiolus* is the correlation between floral crypsis and strong odor. To the human eye, the flowers of several species of section *Hebea* (e.g., *G. arcuatus*, *G. orchidiflorus*, *G. scullyi*, and *G. watermeyeri*) appear well camouflaged, and while large, are dull colored and merge remarkably well with the terrain. One is more likely to be able to find such flowers by tracing the source of their rich odors than by sight. Could this be an adaptation to restrict the diversity of floral visitors, including those that might damage or consume flowers?

Literature Cited

Armstrong, J. 1979. Biotic pollination mechanisms in the Australian flora—A review. N. Zealand J. Bot. 17: 467–508.

Baker, H. G. & I. Baker. 1983. Floral nectar sugar constituents in relation to pollinator type. Pp. 117–141 *in* C. E. Jones & R. J. Little (editors), Handbook of Experimental Pollination Biology. Scientific and Academic editions, New York.

——— & ———. 1990. The predictive value of nectar chemistry to the recognition of pollinator types. Israel J. Bot. 39: 157–166.

Beattie, A. J. 1974. Floral evolution in *Viola*. Ann. Missouri Bot. Gard. 61: 781–793.

Bernhardt, P. 1984. The pollination biology of *Hibbertia stricta* (Dilleniaceae). Pl. Syst. Evol. 147: 267–277.

———. 1986. Bee pollination in in *Hibbertia fasciculata* (Dilleniaceae). Pl. Syst. Evol. 152: 231–241.

———. 1989. The floral ecology of Australian *Acacia*. Ann. Missouri Bot. Gard. 74: 42–50.

———. 1995. Buzz-pollination of *Dianella caerulea* var. *assera* (Phormiaceae). Cunninghamia 4: 9–20.

———. 1996. Anther adaptation in animal pollination. Pp. 192–220 *in* W. G. D'Arcy & R. C. Keating (editors), The Anther: Form, Function, and Phylogeny. Cambridge Univ. Press, Cambridge, U.K.

——— & P. H. Weston. 1996. The pollination ecology of *Persoonia* (Proteaceae) in eastern Australia. Telopea 6: 775–784.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. Pp. 73–113 *in* C. E. Jones & R. J. Little (editors), Handbook of Experimental Pollination. Van Nostrand Reinhold, New York.

Darwin, C. R. 1876. The Effect of Cross- and Self-Fertilization in the Vegetable Kingdom. John Murray, London.

Dressler, R. L. 1981. The Orchids. Natural History and Classification. Harvard Univ. Press, Cambridge, Massachusetts.

Eardley, C. D. 1994. The genus *Amegilla* Friese (Hymenoptera: Anthophoridae) in southern Africa. Entomol. Mem. Dept. Agric. S. Africa 91.

——— & R. W. Brooks. 1989. The genus *Anthophora* Latreille in southern Africa. Entomol. Mem. Dept. Agric. Water Supply S. Africa 76.

Faegri, K. & L. van der Pijl. 1979. The Principles of Pollination Ecology, 3rd ed. Pergamon Press, New York.

Goldblatt, P. 1971. Cytological and anatomical studies on the southern African Iridaceae. J. S. African Bot. 37: 317–460.

———. 1990. Phylogeny and classification of Iridaceae. Ann. Missouri Bot. Gard. 77: 607–627.

———. 1991. An overview of the systematics, phylogeny and biology of the southern African Iridaceae. Contr. Bolus Herb. 13: 1–74.

———. 1996. *Gladiolus* in Tropical Africa. Timber Press, Portland, Oregon.

——— & P. Bernhardt. 1990. Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. Israel J. Bot. 39: 93–111.

——— & J. C. Manning. 1998. *Gladiolus* in Southern Africa. Fernwood Press, Cape Town.

———, P. Bernhardt & J. C. Manning. 1989. Notes on the pollination mechanisms of *Moraea inclinata* and *M. brevistyla* (Iridaceae). Pl. Syst. Evol. 163: 201–209.

———, ——— & ———. 1997. Notes on the pollination of *Gladiolus brevifolius* (Iridaceae) by bees (Anthophoridae) and bee mimicking flies (*Psilodera*: Acroceridae). J. Kansas Entom. Soc. 70: 297–304.

———, P. Bernhardt & J. C. Manning. 1998. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae:Hopliini) in Southern Africa. Ann. Missouri Bot. Gard. 85: 215–230.

———, J. C. Manning & P. Bernhardt. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa: Floral divergence and adaptation for long-tongued fly-pollination. Ann. Missouri Bot. Gard. 82: 517–534.

Herbert, W. 1847. On hybridisation amongst vegetables. J. Hort. Soc. London 2: 81–107.

Horn, W. 1962. Breeding research on South African plants: III. Intra- and interspecific compatibility in *Ixia* L., *Sparaxis* Ker., *Watsonia* Mill. and *Zantedeschia* Spreng. J. S. African Bot. 28: 269–277.

Johnson, S. D. & W. A. Bond. 1994. Red flowers and butterfly pollination in the fynbos of South Africa. Pp. 137–148 *in* M. Arianoutsou & R. Grooves (editors), Plant Animal Interactions in Mediterranean-Type Ecosystems. Kluwer Academic Press, Dordrecht.

Kaiser, R. 1993. The Scent of Orchids: Olfactory and Chemical Investigations. Elsevier, Amsterdam.

Kalin Arroyo, M. T. 1989. Breeding systems and pollination biology in the Leguminosae. Pp. 723–769 *in* R. Polhill & P. H. Raven (editors), Advances in Legume Systematics. 2. Royal Botanic Gardens, Kew.

Knox, R. B., A. Clarke, S. Harrison, P. Smith & J. J. Marchalonis. 1976. Cell recognition in plants: Determinants of the stigma surface and their pollen interactions. Proc. Natl. Acad. Sci. U.S.A. 73: 2788–2792.

Macior, L. W. 1982. Plant community and pollinator dynamics in the evolution of pollination mechanisms. Pp. 29–45 *in* J. A. Armstrong et al. (editors), Pollination and Evolution. Royal Botanic Garden, Sydney.

———. 1984. Behavioral coadaptation of *Bombus* pollinators and *Pedicularis* flowers. Vème Symposium International sur la Pollinisation. Colloq. I.N.R.A. 21: 257–261.

Manning, J. C. & P. Goldblatt. 1995. Cupid comes in many guises: The not so humble fly and a pollination guild in the Overberg. Veld & Flora 81: 50–52.

——— & ———. 1997. The *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) pollination guild: Long-tubed flowers and a specialized long-proboscid fly pollination system in southern Africa. Pl. Syst. Evol. 206: 51–69.

Marloth, R. 1908. Some observations on entomophilous flowers. S. African J. Sci. 5: 110–113.

Michener, C. D. 1974. The Social Behavior of the Bees. A Comparative Study. Belknap Press, Harvard Univ. Press, Cambridge, Massachusetts.

Mori, S. A. & G. T. Prance. 1990. Flora Neotropica. Lecythidaceae. II. Zygomorphic-flowered New World genera. New York Botanical Garden, New York.

Ogden, E. C., G. S. Raynor, J. V. Hayers & D. M. Lewis. 1974. Manual of Sampling Airborne Pollen. Hafner Press, London.

Ohri, D. & T. N. Khoshoo. 1981. Cytogenetics of garden *Gladiolus*. I. Pollination mechanism and breeding system. Proc. Indian Natl. Sci. Acad., B 47: 510–515.

Pellmyr, O. 1985. Pollination adaptations in the Cimicifugeae and the evolutionary origin of pollinator-plant mutualism. Acta Univ. Uppsal. 2: 1–34.

Proctor, M., P. Yeo & A. Lack. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon.

Roig-Alsina, A. & C. D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 123–162.

Scott Elliot, G. 1891. Notes on the fertilisation of South African and Madagascan flowering plants. Ann. Bot. (Oxford) 5: 333–405.

Vogel, S. 1954. Blütenbiologische Types als Elemente der Sippengliederung. Bot. Stud. 1: 1–338.

Vos, M. P. de. 1972. The genus *Romulea* in South Africa. J. S. African Bot., Suppl. 9: 1–307.

POME ANATOMY OF ROSACEAE SUBFAM. MALOIDEAE, WITH SPECIAL REFERENCE TO *PYRUS*[1]

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ABSTRACT

Two anatomical features of the pome in Rosaceae subfam. Maloideae are investigated: sclereid type and epidermal structure. The large and irregular groups of sclereids in *Pyrus* are different from those in *Sorbus* subgenera *Aria*, *Chamaemespilus*, and *Cormus*, and similar to those in *Cydonia*. In addition, multilayered epidermis, hitherto unreported from *Pyrus*, is documented in *Pyrus* sect. *Pashia*. Consequently, both the monophyly of *Pyrus* and its current sectional classification are supported.

The taxonomy of Rosaceae subfam. Maloideae is problematic in terms of generic delimitation. The inconsistency of the main generic characters has generated a great deal of disagreement in the taxonomic treatment of the group. A representative of the more synthetic view was de Candolle (1825), who included in *Pyrus* species now usually referred to *Malus*, *Photinia*, *Eriolobus*, and *Sorbus*. This classification was followed by Sax (1931) and Robertson (1974). Conversely, Decaisne (1874) and Koehne (1890) used smaller generic concepts. They treated *Pyrus* in a more restricted sense, and split off *Photinia*, *Malus*, and *Sorbus*. A comprehensive review of taxonomic treatments applied to these genera was provided by Robertson et al. (1991).

Malus, *Cydonia*, *Sorbus* subg. *Aria* Pers., and *Sorbus* subg. *Chamaemespilus* (Medik.) K. Koch have all been advanced as close relatives of *Pyrus* (Weber, 1964; Iketani & Ohashi, 1991; Campbell et al., 1995). According to Decaisne (1874), pomes of both *Sorbus* subg. *Aria* and *S.* subg. *Chamaemespilus* are characterized by their heterogeneous flesh. Flesh heterogeneity of pomes in subfamily Maloideae was studied by Kovanda (1961) and Iketani and Ohashi (1991), who showed that it was caused by groups of parenchyma cells filled with tannic substances. *Cydonia*, formerly included in *Pyrus* by Linnaeus (1753), and closely related to it according to Robertson et al. (1991), is easily distinguishable by its solitary flowers and numerous ovules per locule. *Malus* is separated by its connate styles (free in *Pyrus*). This feature is consistent, but may be difficult to evaluate in practice. Thus, Bailey (1949) reported the structure of the flower cluster as the most obvious distinction between *Pyrus* and *Malus*: the *Pyrus* inflorescence has a rachis from which the pedicels emerge, while that of *Malus* has an umbellate structure. Nevertheless, Robertson et al. (1991) showed that both *Pyrus* and *Malus* could have corymbs, panicles, or umbels. Finally, the supposed scarcity or absence of sclereids in the pomes of *Malus* was contested by several authors, including Rehder (1940), Browicz (1969), Terpó (1968), and Iketani and Ohashi (1991). Robertson et al. (1991) reported that *Malus* may have abundant sclereids under the skin and around the core of the pomes. Hybridization and grafting experiments provide additional data about *Pyrus* relationships. According to Taylor (1983) *Pyrus* and *Malus* do not hybridize and cannot be grafted one to the other. They also differ in flavonoid composition (Williams, 1982). However, Weber (1964) and Robertson (1974) reported that *Pyrus*, *Malus*, and *Cydonia* can and do hybridize among themselves.

According to Rohrer et al. (1991: 78), the skin of the pomes of subfamily Maloideae "consists of a single epidermal layer of tightly packed, anticlinally flattened, rectangular cells covered with a cuticle." Such an epidermal structure has been described for *Crataegus* (Akhunova, 1986), *Malus* (Clements, 1935), and *Amelanchier* (Olson &

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ANN. MISSOURI BOT. GARD. 85: 518–527. 1998.

Steeves, 1982). On the other hand, Miller (1984) reported a multilayered epidermis in *Mespilus germanica* L. Our survey of anatomical characteristics of pomes of subfamily Maloideae has documented the occurrence of a multilayered epidermis in both *Pyrus* and *Sorbus torminalis* (Aldasoro et al., 1998).

The supraspecific taxonomy of *Pyrus* is also controversial. Decaisne (1871–1872) recognized 23 species arranged in six informal groups. Koehne (1890) described two sections: *Pashia* and *Achras.* Fedorov (1954) recognized four sections: *Pashia, Pyrus* (= sect. *Achras* Koehne), *Xeropyrenia* Fed., and *Argyromalon* Fed. Tuz (1972) reduced these to two, *Pashia* and *Pyrus,* each with several subsections. Terpó (1985) added his section *Pontica,* but the classification of Tuz (1972) was accepted by Browicz (1993), who pointed out that the two sections could be distinguished by certain obscure characters. According to Browicz (1993) the more operative ones are: the sepal persistence on the pome, the presence or absence of whitish lenticels, and the thickness and flexibility of the pedicels in fruit. The character states of section *Pyrus* are: sepals persistent, white lenticels absent, and thick, stiff pedicels; and of section *Pashia:* sepals deciduous, white lenticels present, and thin, flexible pedicels. Nevertheless, these characters showed some inconsistency; for example, several species of section *Pashia* may have thick pedicels.

The aim of the present work is to investigate some anatomical features of subfamily Maloideae pomes with special reference to *Pyrus,* and to discuss their bearing on the taxonomic issues detailed above. The currently accepted concept of *Pyrus* is that of Decaisne (1874), and the sectional division of the genus that proposed by Tuz (1972), because they are better supported by morphological and anatomical data (Robertson et al., 1991; Browicz, 1993; Aldasoro et al., 1996).

MATERIAL AND METHODS

Pomes were collected (see Table 1) and preserved in Kew mixture (Forman & Bridson, 1989). They were cut with a razor blade both longitudinally and transversely in order to examine the internal structure. Thin hand-cuts were taken in the proximal third of the pome and photographed by light microscopy. Other cuts were made with a SLEE-MAINZ-MTC microtome and stained with Fasga mixture (Tolivia & Tolivia, 1987). In some cuts, malachite green was used to stain the sclereids. For scanning microscopy, dried pomes were cut, glued to aluminum stubs, coated with 40–50 nm gold and examined in a JEOL-TSM T330A scanning electron microscope at 20 kV.

RESULTS

Usually, sclereids are present in the flesh of pomes of subfamily Maloideae. They may occur under the skin, in the core or spread throughout the flesh, isolated or in groups, and vary considerably in shape and size.

Four main sclereid types could be distinguished in the flesh (Table 1): isolated sclereids, as in *Rhaphiolepis;* small groups (less than 10), as in *Amelanchier, Chaenomeles, Cotoneaster, Crataegus, Eriobotrya, Malus, Photinia,* and *Sorbus* subgenera *Sorbus* and *Torminaria;* large but irregular groups, as in *Pyrus* (Fig. 1A, B) and *Cydonia;* and large and rounded groups, as in *Sorbus* subgenera *Aria, Chamaemespilus,* and *Cormus* (Fig. 1C, D).

The groups of sclereids in *Pyrus* and *Cydonia* are remarkably dense (over 50 sclereids can be counted in an equatorial section) and have an irregular outline, while in *Sorbus* subgenera *Aria, Chamaemespilus,* and *Cormus* they comprise less than 40 sclereids and have an elliptic outline (Fig. 1C, D). Some consistent differences in the size and shape of these sclereids were observed (Table 1). *Pyrus* and *Cydonia* sclereids are smaller and have a smaller lumen (40–80 μm long; lumen diameter 10–51 μm; wall thickness 10–20 μm) than those of *Sorbus* subgenera *Aria, Chamaemespilus,* and *Cormus* (110–240 μm long; lumen diameter 76–180 μm; wall thickness 6–32 μm) (Fig. 1). Sclereids in pomes of *Malus* were isolated or in small groups, and were larger and with a greater lumen diameter (75–360 μm long; lumen diameter 12–310 μm; wall thickness 15–80 μm) than those of *Pyrus* pomes.

We were able to study the pomes of 16 of the 38 species of *Pyrus* accepted by Browicz (1993): 9 belonging to section *Pyrus,* and 7 to section *Pashia* (Table 1). A multilayered epidermis was found only in *Pyrus* sect. *Pashia,* while species of section *Pyrus* had only a single layer of epidermal cells that produced a thick cuticle (Fig. 2C, D). The remaining species of subfamily Maloideae showed a single-layered epidermis, except for *Mespilus germanica* and *Sorbus torminalis* (Table 1; Miller, 1984; Aldasoro et al., 1998).

In *Pyrus,* the multilayered epidermis has 3–6 layers of cells, each layer with a cuticular membrane. These cells are tangentially compressed and filled with tannic substances (Fig. 2A, B). They develop from a tangential meristem layer that is somewhat similar to the phellogen, a meristem that ap-

Table 1. Pome epidermal type and sclereid features in Rosaceae subfam. Maloideae. The data are means of five samples from the specimens cited.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
Amelanchier canadensis (L.) Medik.	small groups	67	35	12	SL	this study	cult. MA, *Aldasoro 561* (MA)
Chaenomeles japonica (Thunb.) Lindl.	small groups	55	35	10	SL	this study	cult. MA, *Aldasoro 544* (MA)
Cotoneaster buxifolius Wall. ex Lindl.	small groups	63	40	11	SL	this study	cult. MA, *Aedo 3891* (MA)
C. integerrimus Medik.	small groups	40	10	7	SL	this study	cult. MA, *Aldasoro 580* (MA)
Crataegus azarolus L.	small groups	98	90	10	SL	this study	Spain, *Soler 779* (MA)
C. ×ruscinonensis Gren. & Blanc	small groups	100	70	15	SL	this study	Spain, *Soler 777* (MA)
Cydonia oblonga Mill.	large and irregular groups	50	25	10	SL	this study	Spain, *Aldasoro 561* (MA)
Eriobotrya bengalensis (Roxb.) Hook.	small groups	80	40	22	SL	this study	cult. MA, *Aldasoro 717* (MA)
E. japonica (Thunb.) Lindl.	small groups	100	20	24	SL	this study	cult. MA, *Aldasoro 715* (MA)
E. petiolata Hook.	small groups	120	70	25	SL	this study	cult. MA, *Aldasoro 714* (MA)
E. tengyuehensis W. W. Sm.	small groups	110	12	45	SL	this study	cult. MA, *Aldasoro 716* (MA)
Hesperomeles ferruginea Lindl.	absent	—	—	—	SL	this study	Colombia, *Cuatrecasas 28890* (MA)
H. lanuginosa Hook.	absent	—	—	—	SL	this study	Peru, *Cano 4179* (MA)
H. salicifolia (C. Presl) Abrams	absent	—	—	—	SL	this study	California: USA, *Bartholomew 1479* (MA)
Malus baccata (L.) Borkh.	small groups	127	82	20	SL	this study	cult. K, *Aldasoro 691* (MA)
M. florentina (Zucc.) C. K. Schneid.	small groups	90	40	24	SL	this study	cult. K, *Aldasoro 634* (MA)
M. fusca (Raf.) C. K. Schneid.	small groups	80	55	20	SL	this study	cult. MA, *Aldasoro 539* (MA)
M. halliana Koehne	small groups	75	30	20	SL	this study	cult. Hillier Gardens, *Aldasoro 606* (MA)
M. ioensis (Wood) Britton	small groups	153	120	20	SL	this study	cult. K, *Aldasoro 719* (MA)
M. kansuensis (Batalin) C. K. Schneid.	small groups	100	12	80	SL	this study	cult. K, *Aldasoro 681* (MA)
M. sieboldii Rehder	small groups	78	35	20	SL	this study	cult. K, *Aldasoro 648* (MA)
M. sikkimensis Koehne ex C. K. Schneid.	small groups	127	95	15	SL	this study	cult. K, *Aldasoro 689* (MA)
M. trilobata (Labill.) C. K. Schneid.	small groups	360	310	25	SL	this study	cult. K, *Aldasoro 665* (MA)
M. tschonoskii (Maxim.) C. K. Schneid.	small groups	150	120	18	SL	this study	cult. K, *Aldasoro 643* (MA)
M. yunnanensis (Franch.) C. K. Schneid.	small groups	180	100	40	SL	this study	cult. Hillier Gardens, *Aldasoro 635* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
Mespilus germanica L.	absent	—	—	—	ML	Miller (1984), and this study	Spain, *Navarro 1166* (MA)
Photinia beauverdiana C. K. Schneid.	small groups	100	35	25	SL	this study	cult. K, *Aldasoro 658* (MA)
Ph. davidiana (Decne.) Cardot	small groups	64	40	12	SL	this study	cult. MA, *Aldasoro 709* (MA)
Ph. melanocarpa (Michx.) K. R. Robertson & J. B. Phipps	small groups	100	25	12	SL	this study	cult. MA, *Aldasoro 710* (MA)
Ph. pyrifolia (Lam.) K. R. Robertson & J. B. Phipps	small groups	70	40	14	SL	this study	cult. Hillier Gardens, *Aldasoro 594* (MA)
Ph. serratifolia (Desf.) Kalkman	small groups	45	10	18	SL	this study	cult. MA, *Aldasoro 708* (MA)
Pyrus sect. *Pyrus*							
P. armeniacus Mulk.	large and irregular groups	64	34	16	SL	this study	Armenia, unknown collector (MA-474349)
P. bourgeana Decne.	large and irregular groups	60	10	15	SL	this study	cult. MA, *Aldasoro 131* (MA)
P. communis L.	large and irregular groups	—	—	—	SL	this study	Spain, *Monasterio et al. 1168* (MA)
P. elaeagnifolia Pall.	large and irregular groups	42	25	10	SL	this study	cult. K, *Aldasoro 690* (MA); Macedonia: [Yugoslavia] *Frost-Olsen 2634* (MA)
P. georgica Kuth.	large and irregular groups	56	24	16	SL	this study	Georgia, unknown collectors (MA-417326, MA-417326)
P. nivalis Jacq.	large and irregular groups	78	40	20	SL	this study	cult. Hillier Gardens, *Aldasoro 641* (MA)
P. salicifolia Pall.	large and irregular groups	50	10	15	SL	this study	cult. MA, *Aldasoro 690* (MA); Armenia, unknown collector (MA-298629)
P. spinosa Forssk.	large and irregular groups	58	20	20	SL	this study	Spain, *Navarro et al. 1405* (MA)
P. syriaca Boiss.	large and irregular groups	70	31	19	SL	this study	cult. K, *Aldasoro 668* (MA)
Pyrus sect. *Pashia*							
P. betulifolia Bunge	large and irregular groups	58	30	20	ML	this study	cult. K, *Aldasoro 670* (MA)
P. calleryana Decne.	large and irregular groups	—	—	—	ML	this study	cult. K, *Aldasoro 707* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
P. cordata Desv.	large and irregular groups	50	10	20	ML	this study	Spain, *Aedo 2477* (MA)
P. pashia Buch.-Ham.	large and irregular groups	76	51	10	ML	this study	cult. Hillier Gardens, *Aldasoro 641* (MA); cult. K, *Aldasoro 683* (MA)
P. phaeocarpa Rehder	large and irregular groups	—	—	—	ML	this study	cult. K, *Aldasoro 669* (MA)
P. pyrifolia (Burm. f.) Nakai	large and irregular groups	60	25	17	ML	this study	cult. K, *Aldasoro 667* (MA)
P. ussuriensis Maxim.	large and irregular groups	60	28	17	ML	this study	cult. K, *Aldasoro 676* (MA)
Rhaphiolepis ×delacourii André	isolated	90	60	15	SL	this study	cult. K, *Aldasoro 666* (MA)
R. umbellata (Thunb.) Makino	isolated	60	20	10	SL	this study	cult. MA, *Aldasoro 545* (MA)
Sorbus subg. *Sorbus*							
Sorbus aucuparia L.	small groups	55	30	10	SL	Aldasoro et al. (1998)	Spain, *Aedo 3383* (MA)
S. conmixta Hedl.	small groups	60	35	12	SL	this study	cult. MA, *Aldasoro 553* (MA)
S. esserteauiana Koehne	small groups	120	35	12	SL	this study	cult. MA, *Aldasoro 541* (MA)
S. forrestii McAlister & Gillham.	small groups	122	100	10	SL	this study	cult. K, *Aldasoro 602* (MA)
S. hupehensis C. K. Schneid.	small groups	70	40	13	SL	this study	cult. MA, *Aldasoro 550* (MA)
S. hybrida L.	small groups	60	30	10	SL	Aldasoro et al. (1998)	Spain, *Aldasoro 453* (MA)
S. vilmorinii C. K. Schneid.	small groups	124	100	13	SL	this study	cult. NSS, *Aldasoro 629* (MA)
Sorbus subg. *Aria*							
Sorbus alnifolia (Siebold & Zucc.) K. Koch	large and rounded groups	150	110	21	SL	this study	cult. K, *Aldasoro 672* (MA)
S. aria (L.) Crantz	large and rounded groups	140	100	14	SL	Aldasoro et al. (1998)	Spain, *Aedo 3380* (MA)
S. folgneri (C. K. Schneid.) Rehder	large and rounded groups	127	76	25	SL	this study	cult. MA, *Aldasoro 711* (MA)
S. hajastana Gabrielian	large and rounded groups	165	135	15	SL	this study	cult. K, *Aldasoro 679* (MA)
S. hedlundii C. K. Schneid.	large and rounded groups	134	95	20	SL	this study	cult. Hillier Gardens, *Aldasoro 639* (MA)

Table 1. Continued.

Taxon	Flesh sclereid groups	Sclereid length (µm)	Sclereid lumen diameter (µm)	Sclereid wall thickness (µm)	Pome epidermis (ML: multilayered, SL: single-layered)	Source of data	Material studied
S. hemsleyi (C. K. Schneid.) Rehder	large and rounded groups	120	100	25	SL	this study	cult. K, *Aldasoro 651* (MA)
S. japonica (Decne.) Hedl.	large and rounded groups	140	90	20	SL	this study	cult. K, *Aldasoro 704* (MA)
S. keissleri (C. K. Schneid.) Rehder	large and rounded groups	240	180	21	SL	this study	cult. K, *Aldasoro 652* (MA)
S. lanata (D. Don) Schauer	large and rounded groups	130	100	15	SL	this study	cult. NSS, *Aldasoro 624* (MA)
S. pallescens Rehder	large and rounded groups	140	100	21	SL	this study	cult. K, *Aldasoro 700* (MA)
S. subfusca (Ledeb.) Boiss.	large and rounded groups	140	120	20	SL	this study	cult. K, *Aldasoro 687* (MA)
S. takhtajanii Gabrielian	large and rounded groups	178	112	32	SL	this study	cult. K, *Aldasoro 680* (MA)
S. vestita (Wall. ex G. Don) Lodd.	large and rounded groups	205	160	27	SL	this study	cult. K, *Aldasoro 658* (MA)
S. yuana Spongberg	large and rounded groups	110	98	18	SL	this study	cult. Wakehurst Garden, *Aldasoro 703* (MA)
S. zahlbruckneri C. K. Schneid.	large and rounded groups	123	90	20	SL	this study	cult. K, *Aldasoro 702* (MA)
Sorbus subg. *Chamaemespilus*							
S. chamaemespilus (L.) Crantz	large and rounded groups	140	120	30	SL	Aldasoro et al. (1998)	Spain, *Aedo 3140* (MA)
Sorbus subg. *Cormus*							
Sorbus domestica L.	large and rounded groups	130	120	6	SL	Aldasoro et al. (1998)	Spain, *Aldasoro 560* (MA)
Sorbus subg. *Torminaria*							
Sorbus torminalis (L.) Crantz	small groups	70	60	20	ML	Aldasoro et al. (1998)	Spain, *Navarro 1380* (MA)

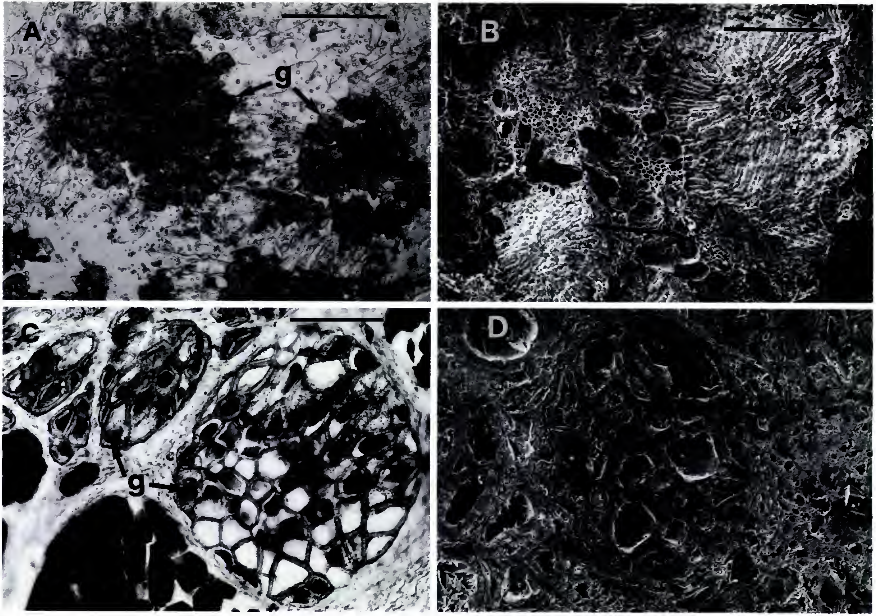

Figure 1. SEM and optical photomicrographs of the groups of sclereids (g) in *Pyrus* and *Sorbus* pomes. —A. Optical photomicrograph of *Pyrus syriaca* (*Aldasoro 668*) showing large irregular groups of sclereids. —B. SEM photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing large irregular groups of sclereids. —C. Optical photomicrograph of *Sorbus lanata* (*Aldasoro 624*) showing large rounded groups of sclereids. —D. SEM photomicrograph of *S. pallescens* (*Aldasoro 700*) showing large rounded groups of sclereids. Scale bars: A = 500 μm; B: 500 μm; C: 200 μm; D: 100 μm.

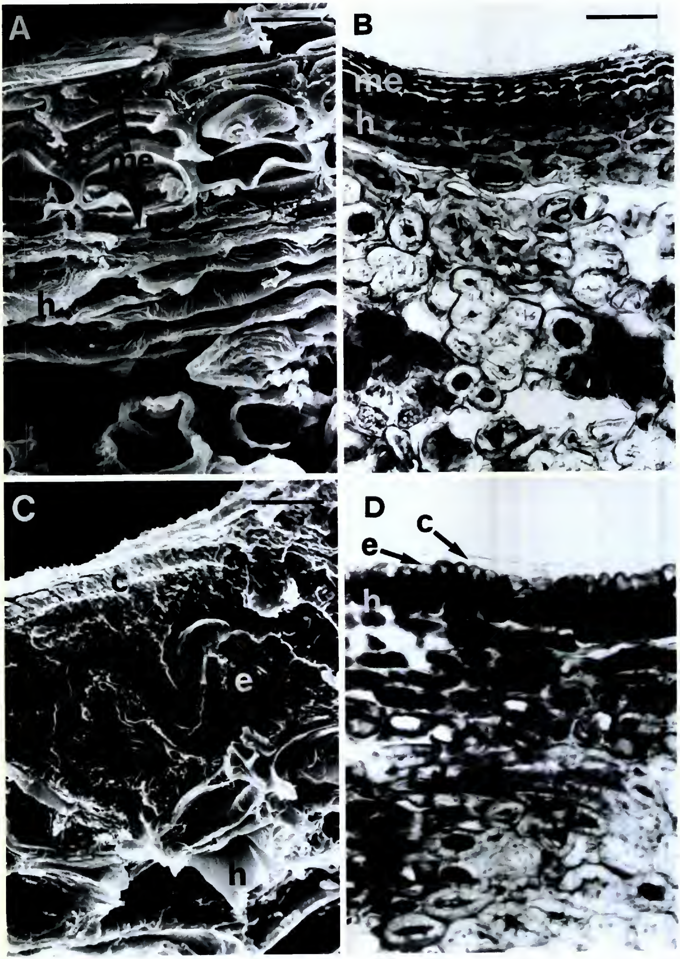

Figure 2. SEM and optical photomicrographs of the epidermis in *Pyrus* pomes. —A. SEM photomicrograph of *Pyrus pashia* (*Aldasoro 641*) showing the multilayered epidermis (me) and the hypodermis (h). —B. Optical photomicrograph of *P. pashia* (*Aldasoro 641*) showing the multilayered epidermis (me) and the hypodermis (h). —C. SEM photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing the one-layered epidermis (e), the cuticle (c) and the hypodermis (h). —D. Optical photomicrograph of *P. spinosa* (*Navarro et al. 1405*) showing the one-layered epidermis (e), the cuticle (c) and the hypodermis (h). Scale bars: A = 10 μm; B: 25 μm; C: 5 μm; D: 20 μm.

pears in the subepidermal region of the incipient lenticel. Like the phellogen, the tangential meristem of the multilayered epidermis divides periclinally, producing layers of cells that undergo a progressive exfoliation. In some cases, it was observed that lenticel concrescence occurred prior to the development of a multilayered cuticle.

DISCUSSION

The hypothesis that *Pyrus* and *Cydonia* are sister taxa was advanced by Rohrer et al. (1994) on the basis of a single presumed synapomorphy: a pit in the floral cup surrounding the style group. The data contributed by Campbell et al. (1995) on ITS DNA sequences also support this view. Our studies show that these genera have sclereids similar in size, structure, and arrangement, which strengthens this idea. However, several other characters uphold the continued recognition of *Cydonia* and *Pyrus* as separate genera: *Cydonia* has pluriovulate carpels, leaves with no adaxial glands, and solitary, pink flowers. In contrast, *Pyrus* has biovulate carpels, adaxial leaf glands, and corymbose, white flowers. Iketani and Ohashi (1991), Sterling (1966a, b), and Kalkman (1988) proposed that *Pyrus* may have branched from the ancestor of *Cydonia* before the latter acquired the pluriovulate condition. Thus, the previously mentioned characters would support the monophyly of *Pyrus* sensu Decaisne (1874). This would be of remarkable interest in subfamily Maloideae, the genera of which have rather few apomorphic character states. However, our data do not support a close relationship between *Pyrus* and *Malus*, since they have different types of sclereid groups.

The distribution of the multilayered pome epidermis in *Pyrus* seems to support the infrageneric classification proposed by Tuz (1972) and Browicz (1993), at least in terms of the sectional division. This is interesting because, as mentioned previously, some of Browicz's sectional characters, such as pedicel thickness, are variable: the pedicels of *P. pyrifolia* and *P. pashia* (sect. *Pashia*) are thicker than those of some species in section *Pyrus*.

Some other taxa of subfamily Maloideae (*Mespilus*, *Sorbus*) may also have a multilayered pome epidermis. According to Phipps et al. (1991) and Campbell et al. (1995), *Mespilus*, *Pyrus*, and *Sorbus* (subg. *Torminaria*) are not closely related. Moreover, pomes with a multilayered epidermis were not present in any of the primitive genera of Maloideae studied (i.e., *Cotoneaster*, *Eriobotrya*, *Heteromeles*, *Photinia*, and *Rhaphiolepis*; primitive according to Phipps et al., 1991; Campbell et al., 1995). Consequently, a multilayered epidermis is most parsimoniously viewed as derived, and it seems an independently acquired character state in these genera. The adaptative role of the multilayered epidermis is unknown, but it may be related to seed dispersal by mammals. All pomes of subfamily Maloideae studied with a multilayered epidermis present traits associated with mammalian zoochory syndromes: green or brown skin inconspicuous to birds, copious lenticels permitting scent to emanate, seeds protected against mammal-stomach gastric juices by many sclereids, tannins inhibiting bacterial or fungal damage in the ground, and high fiber content (Herrera, 1989).

Literature Cited

Akhunova, S. S. 1986. On systematic significance of pericarp anatomical characters in some members of the genus *Crataegus* (Rosaceae). Bot. Zhurn. (Moscow & Leningrad) 72: 778–780. [In Russian.]

Aldasoro, J. J., C. Aedo & F. Muñoz Garmendia. 1996. The genus *Pyrus* L. (Rosaceae) in south-west Europe and North Africa. Bot. J. Linn. Soc. 121: 143–158.

———, ———, C. Navarro & F. Muñoz Garmendia. 1998. The genus *Sorbus* (Maloideae, Rosaceae) in Europe and in North Africa: Morphological analysis and systematics. Syst. Bot. (in press).

Bailey, L. H. 1949. The *Pyrus–Malus* puzzle. Gentes Herb. 8: 40–43.

Browicz, K. 1969. Distribution of woody Rosaceae in W. Asia III. Arbor. Kórnickie 14: 5–19.

———. 1993. Conspect and chorology of the genus *Pyrus* L. Arbor. Kórnickie 38: 17–33.

Campbell, C. S., M. J. Donoghue, B. G. Baldwin & M. F. Wojciechowski. 1995. Phylogenetic relationships in Maloideae (Rosaceae): Evidence from sequences of the internal transcribed spacers of nuclear ribosomal DNA and its congruence with morphology. Amer. J. Bot. 82: 903–918.

Candolle, A. P. de. 1825. Prodromus systematis naturalis regni vegetabilis, Vol. 2. Treuttel & Würtz, Paris.

Clements, H. F. 1935. Morphology and physiology of the pome lenticels of *Pyrus malus*. Bot. Gaz. 97: 101–117.

Decaisne, J. 1871–1872. Le jardin fruitier du Museum, Vol. 1. F. Didot, Paris.

———. 1874. Mémoirs sur la famille des Pomacées. Nouv. Arch. Mus. Hist. Nat. 10: 113–192, pl. 8–15.

Fedorov, A. A. 1954. *Pyrus* L. *In:* S. J. Sokolov (editor), Dereva i kustarniki SSSR, Vol. 3. Academy of Science Press, Moscow & Leningrad. [In Russian.]

Forman, L. & D. Bridson. 1989. The Herbarium Handbook. Royal Botanic Gardens, Kew.

Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55: 250–262.

Iketani, H. & H. Ohashi. 1991. Anatomical structure of fruits and evolution of the tribe Sorbeae in the subfamily Maloideae (Rosaceae). J. Jap. Bot. 66: 319–351.

Kalkman, C. 1988. The phylogeny of the Rosaceae. Bot. J. Linn. Soc. 98: 37–59.

Koehne, E. 1890. Die Gattungen der Pomaceen. R.

Gaertners Verlagsbuchhandlung Hermann Heyfelder, Berlin.

Kovanda, M. 1961. On the generic concepts in the Maloideae. Preslia 37: 27–34.

Linnaeus, C. 1753. Species plantarum. Impensis Laurentii Salvii, Stockholm.

Miller, R. H. 1984. The multiple epidermis–cuticle complex of medlar fruit *Mespilus germanica* L. (Rosaceae). Ann. Bot. (Oxford) 53: 779–792.

Olson. A. R. & T. A. Steeves. 1982. Structural changes in the developing fruit wall of *Amelanchier alnifolia*. Canad. J. Bot. 60: 1880–1887.

Phipps, J. B., K. R. Robertson, J. R. Rohrer & P. G. Smith. 1991. Origins and evolution of subfam. Maloideae (Rosaceae). Syst. Bot. 16: 303–332.

Rehder, A. 1940. Manual of Cultivated Trees and Shrubs Hardy in North America Exclusive of the Subtropical and Warmer Temperature Regions, 2nd ed. Macmillan, New York.

Robertson, K. R. 1974. The genera of Rosaceae in the southeastern United States. J. Arnold Arbor. 55: 303–332, 344–401, 611–662.

———, J. B. Phipps, J. R. Rohrer & P. G. Smith. 1991. A synopsis of genera in Maloideae (Rosaceae). Syst. Bot. 16: 376–394.

Rohrer, J. R., K. R. Robertson & J. B. Phipps. 1991. Variation in structure among fruits of Maloideae (Rosaceae). Amer. J. Bot. 78: 1617–1635.

———, K. R. Robertson & J. B. Phipps. 1994. Floral morphology of Maloideae (Rosaceae) and its systematic relevance. Amer. J. Bot. 81: 574–581.

Sax, K. 1931. The origin and relationships of the Pomoideae. J. Arnold Arbor. 12: 3–22.

Sterling, C. 1966a. Comparative morphology of the carpel in the Rosaceae. VII Pomoideae: *Chaenomeles, Cydonia, Docynia*. Amer. J. Bot. 53: 225–231.

———. 1966b. Comparative morphology of the carpel in the Rosaceae. IX. Spiraeoideae: Quillajeae, Sorbarieae. Amer. J. Bot. 53: 951–960.

Taylor, N. P. 1983. *Malus sikkimensis* 'Rockii.' Bot. Mag. 184: 168–173.

Terpó, A. 1968. *Malus* Miller. Pp. 66–67 *in* T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (editors), Flora Europaea, Vol. 2. Univ. Press, Cambridge.

———. 1985. Studies on taxonomy and grouping of *Pyrus* Species. Feddes Repert. 96: 73–87.

Tolivia, D. & J. Tolivia. 1987. Fasga: A new polychromatic method for simultaneous and differential staining of plant tissues. J. Microscopy 148: 113–117.

Tuz, A. S. 1972. K voprosu klassifikacii roda *Pyrus* L. Trudy Prikl. Bot. 46: 70–91. [In Russian.]

Weber, C. 1964. The genus *Chaenomeles* (Rosaceae). J. Arnold Arbor. 45: 161–205.

Williams, A. H. 1982. Chemical evidence from flavonoids relevant to the classification of *Malus* species. Bot. J. Linn. Soc. 84: 31–39.

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CONTENTS

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1998

Volume 85
Number 4

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AN ORDINAL CLASSIFICATION FOR THE FAMILIES OF FLOWERING PLANTS

The Angiosperm Phylogeny Group[1]

ABSTRACT

Recent cladistic analyses are revealing the phylogeny of flowering plants in increasing detail, and there is support for the monophyly of many major groups above the family level. With many elements of the major branching sequence of phylogeny established, a revised suprafamilial classification of flowering plants becomes both feasible and desirable. Here we present a classification of 462 flowering plant families in 40 putatively monophyletic orders and a small number of monophyletic, informal higher groups. The latter are the monocots, commelinoids, eudicots, core eudicots, rosids including eurosids I and II, and asterids including euasterids I and II. Under these informal groups there are also listed a number of families without assignment to order. At the end of the system is an additional list of families of uncertain position for which no firm data exist regarding placement anywhere within the system.

Why rearrange families, still less formalize orders? Higher-level classifications, the grouping of species into families, orders, etc., are needed as reference tools not only in systematics but also in many other branches of biology. Knowledge of phylogenetic relationships of major groups of organisms, that is, a phylogenetic perspective, is becoming increasingly important, and hence the need for a phylogenetic classification as a reference tool is also becoming imperative.

Our primary focus is on orders with a secondary emphasis on families of flowering plants. The family is central in flowering plant systematics. For example, in studying an unknown plant we usually first identify it to family. The orders, on the other hand, have until quite recently been of little importance, either being morphologically unrecognizable or in most cases lacking any evolutionary coherence (Heywood, 1977; Merxmüller, 1977). However, orders are useful in teaching, for studying

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ANN. MISSOURI BOT. GARD. 85: 531–553. 1998.

family relationships, and in positioning genera of doubtful affinity. The didactic value of suprafamilial groupings has been emphasized by various authors (e.g., Dahlgren, 1975; Thorne, 1976; Davis, 1978; Takhtajan, 1997). This value is even more evident now that the phylogeny of flowering plants is being disclosed in increasing detail. Many of the orders recognized by earlier authors are not monophyletic, yet there is a pressing need for names to communicate the knowledge of monophyletic groupings of families that are becoming evident. With the major branching sequence of flowering plant phylogeny becoming clearer, a revised familial and ordinal classification is feasible.

Flowering plant classification systems from the late 1970s seemed to be stable and show substantial agreement, but this stability has been rudely shattered as new kinds of data and new methods of analyzing conventional data have become firmly established (Stevens, 1986). Classifications such as those by Cronquist (1981) and Takhtajan (1980), although still in frequent use, have become outdated. Of more recent classifications, that by Goldberg (1986) of the dicotyledons predates the advent of molecular studies at higher levels, as does that by Dahlgren et al. (1985) of the monocotyledons. However, the latter incorporated much new data and provided synapomorphy schemes for many groups. The recent system of Takhtajan (1997), although extremely elaborate, is made less useful because his propensity for splitting often results in well-known families being dismembered, then reassembled as orders. Furthermore, the findings of recent molecular studies, despite being cited, have hardly influenced his classification.

We conclude that there is a great need for a new, phylogenetic classification of flowering plants, providing names for major monophyletic groups of families. Obviously, it is not possible, nor is it desirable, to name all clades in the entire phylogeny. Any such complete classification would be so cumbersome that it would be useless for general communication. Systematists need to come to some kind of agreement concerning which clades to recognize and name, so that a reference tool of broad utility can be formulated and used to discuss diversity. An ordinal classification of flowering plant families is here proposed for that purpose (pp. 538–542). It recognizes a selected number of monophyletic suprafamilial groups, that is, clades in the phylogeny of flowering plants that are supported by at least one, and often several, lines of evidence. These are clades to which we find it useful to refer when we communicate information about higher-level interrelationships of the flowering plants.

We note that the selection of clades to be represented in a formal classification is different from the procedure of naming these clades. The latter issue of biological nomenclature in phylogenetics is currently much debated (e.g., Cantino et al., 1997; de Queiroz, 1997; Lidén et al., 1997), but we have not adopted any "phylogenetic naming" sensu de Queiroz and Gauthier (1994). We operate under the current *International Code of Botanical Nomenclature* (Greuter et al., 1994) and choose to emphasize the ranks of family and order. The Linnaean categories serve as a convenient mnemonic device for remembering hierarchical relationships, but it should of course be realized that groups of the same rank are evolutionarily non-comparable units unless they are sister groups.

There are noteworthy problems when establishing the names for taxa at ordinal and other higher taxonomic levels. Until recently, little attention has been paid to the nomenclature at these levels, and our knowledge of the early literature in which such names were used is imperfect. This situation has in considerable part been rectified by Reveal's (1998) Herculean labors. The principle of priority is not mandatory for taxa above the rank of family, although authors are exhorted "generally" to follow this principle (Greuter et al., 1994). We have tried to balance priority with general usage when assigning names to orders, but even if future bibliographic work discloses earlier ordinal names, changes are not mandated.

Which clades should be recognized in classification, or in our case, how should the orders be circumscribed? Given the primary principle of monophyly, that of recognizing clades and not grades in classification, there are nevertheless many considerations to be taken into account when circumscribing taxa at ordinal as well as all other hierarchical levels above that of species. Classification is not only a matter of grouping according to the principle of monophyly, but it is also a matter of communication (note that whatever philosophy of naming is adopted, there has to be some consensus as to the clades we are going to use in general botanical communication). For us, this raises the question of ranking, that is, after having selected clades in the phylogeny to be named, they have to be assigned an appropriate place in the hierarchy, in our case, family and order (e.g., Backlund & K. Bremer, 1998; Stevens, 1998). In choosing between alternative circumscriptions it is desirable to recognize groups that are well supported. It is also useful to select groups that have some kind of easily observed morphological synapomorphies, although this may be difficult at the ordinal level and even sometimes at the family level. Synapomorphies also often include (sometimes exclusively) anatomical, biochemical, and developmental characters.

Many of our ordinal names are already well established and used in earlier classifications and systematic treatments. So far as they represent monophyletic groups, we retain well-known orders in the interest of preserving stability. In other cases, the size of the orders comes into consideration. However, what is reasonably broad circumscription? From the point of view of memorization of names, groups of 2–6 or a few more would seem to be ideal, and there is evidence that systematists in the past have commonly recognized groups of this size (Stevens, 1997). However, with the discoveries of new species, genera, and families, the sizes of genera, families, and orders have increased, and many orders now comprise 10–20 families, or even more. Other orders contain a few families only, and if there are only two or three families in an order, "one is not far from leaving the families unplaced" (Copeland, 1957). Concerns about the doubtful value of recognizing similarly small groups have also been expressed by others (e.g., Burtt, 1977). Nevertheless, we have chosen to recognize a number of small orders because these represent clades for which monophyly and relationships are well supported, and this better conveys the interrelationships of the families included rather than leaving them unclassified to order.

In general, we adopt a broad circumscription of the orders. We recognize 462 families and 40 orders of flowering plants. Cronquist (1981) recognized 321 families and 64 orders, Thorne (1992) 440 families and 69 orders, and Takhtajan (1997) no less than 589 families in 232 orders. Our wider ordinal circumscription is not because finer details of the phylogeny within the orders are as yet unclear, but because we think the classification will be more useful with a limited number of larger orders. As we develop more firmly supported phylogenies within and among orders, groups at the infraordinal and supraordinal levels can be recognized. Hence we anticipate that there will be little need to change the circumscription of the orders recognized here, except for inclusion of yet unassigned families of unknown systematic position and the transfer of misplaced families. Additional orders may have to be recognized as the phylogenetic relationships of families that are not yet placed are clarified. Discussion as to whether a widely accepted monophyletic group should be a superorder, order, suborder, or family is largely vacuous because this will always be an arbitrary decision.

Takhtajan (1997) opted in favor of "smaller, more natural families and orders, which are more coherent and better-defined, where characters are easily grasped, and which are more suitable for information retrieval and phylogenetic studies, including cladistic analyses (e.g., because it reduces polymorphic codings)." However, the size of a group has nothing to do with its "naturalness." For a smaller group, one will often be able to say more about all of its constituent members, and so the characters may be more easily grasped. However, segregates of well established monophyletic families like Rubiaceae (Gentianales) or Asteraceae (Asterales) would by Takhtajan's generalization also be more natural; by this criterion, the smaller the group, the more natural it will necessarily be, so there is no ranking criterion to be derived from "naturalness." If by "more natural" is meant "has more synapomorphies" then this, too, is incorrect; the number of synapomorphies is not connected to the size of the group or the hierarchical level at which it is recognized.

In our classification, these considerations have had little impact. The principle of monophyly in combination with the desirability of maintaining already well established and familiar entities has largely formed the ordinal classification. Monofamilial orders (and monogeneric families) are avoided as much as possible, minimizing redundancy in classification. In a few cases we have, however, recognized some monofamilial orders (Ceratophyllales, Acorales, Arecales) because these are sister groups of more than one other order. Hence, the families of these monofamilial orders cannot be included in any other order without violating monophyly.

The principle of monophyly in combination with the mandatory usage of the family category (Greuter et al., 1994) may lead to the recognition of many small families. For example, in Dipsacales, if Dipsacaceae and Valerianaceae are to be retained as families separate from Caprifoliaceae, the principle of monophyly requires the recognition also of Diervillaceae, Linnaeaceae, and Morinaceae (Backlund & K. Bremer, 1998; Backlund & Pyck, 1998). This is because each of these latter families is the sister group of more than one family so they cannot be merged with any other family without violating monophyly. Similar considerations apply at the ordinal level. Unfortunately, no absolute guidelines as to reasonable practice can be offered, but we simply observe that caution is always in order.

In other cases there are small families that may be reduced to synonymy of their sister group if the latter consists of a single family. Examples are Cabombaceae, which may be merged with Nymphaeaceae, and Kingdoniaceae, which may be merged with Circaeasteraceae (Ranunculales). Such commonly recognized families that nevertheless may be merged with their sister family are in our classification placed within square brackets below the family with which they may be merged (in Ranunculales either Fumariaceae or both Fumariaceae and Pteridophyllaceae may be merged with Papaveraceae; alternatively, either Pteridophyllaceae or both Fumariaceae and Pteridophyllaceae may be retained as distinct).

We do not attempt to thoroughly revise family circumscriptions. In general we follow recent authors and attempt to recognize as many monophyletic families as possible. It should be emphasized, however, that following additional investigation some families listed below may be shown to be nonmonophyletic; revised circumscriptions, either by merging or splitting, into monophyletic taxa are not yet possible given our current knowledge. Examples are Euphorbiaceae and Flacourtiaceae of Malpighiales (Källersjö et al., 1998) and several families of Myrtales (Conti et al., 1996; Gadek et al., 1996) and core Caryophyllales (which comprise Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Caryophyllaceae, Didiereaceae, Molluginaceae, Nyctaginaceae, Phytolaccaceae, Portulacaceae, Sarcobataceae, and Stegnospermataceae; Hershkovitz & Zimmer, 1997). Other probably non-monophyletic families that cannot yet be recircumscribed are Boraginaceae (euasterids I; Chase et al., 1993), Scrophulariaceae (Lamiales; Olmstead & Reeves, 1995), and Santalaceae (Santalales; Nickrent & Duff, 1996; Nickrent et al., 1998). Brassicaceae (Brassicales) include also the former, paraphyletic Capparaceae (Brassicaceae sensu stricto being nested inside Capparaceae; Judd et al., 1994; Rodman et al., 1996). A supposedly parallel case comprises Apiaceae and Araliaceae (Apiales), since the former have been assumed to be nested inside the latter (Plunkett et al., 1996). However, with a transfer of Hydrocotyloideae from Apiaceae to Araliaceae, it seems that two monophyletic families can be recognized, only a few genera remaining unplaced (Plunkett et al., 1997). Delimitation of Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae (Malvales) is problematical, and only Malvaceae are monophyletic (Alverson et al., 1998; Bayer et al., 1999). Here all four are treated together as a single monophyletic family, Malvaceae sensu lato (Judd & Manchester, 1997).

Our proposed classification is a modification of that conceived by Bremer et al. (1995, 1996, 1997) and since 1996 available on the Internet (Bremer et al., 1998). This classification is based on various recently published mostly molecular phylogenetic analyses (e.g., Chase et al., 1993; Chase et al., 1995; Bremer et al., 1994; Struwe et al., 1994; Nadot et al., 1995; Nickrent & Soltis, 1995; Soltis et al., 1995; Gadek et al., 1996; Gustafsson et al., 1996; Morton et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997; Anderberg et al., 1998; Backlund & B. Bremer, 1998; Bakker et al., 1998; Källersjö et al., 1998; Soltis et al., 1998; Thulin et al., 1998; further references above). The major differences are in the expansion of Alismatales (including also Araceae), Caryophyllales (including Droseraceae, Nepenthaceae, Polygonaceae, Plumbaginaceae, and several other families outside the traditional, core Caryophyllales), the recognition of a comparatively widely circumscribed Rosales (including Rhamnaceae, Urticaceae, Moraceae, and their allies), in the addition of a number of smaller orders (Ceratophyllales, Acorales, Arecales, Proteales, Garryales, Aquifoliales), and in the deletion of a few others (Aristolochiales, Nymphaeales, Bromeliales, Trochodendrales, Zygophyllales). Monocots and eudicots are not formally ranked and named because it is not yet clear at which level they should be recognized. The same problems occur with commelinoids (a phylogenetically derived subgroup of monocots) and with rosids and asterids (subgroups of eudicots), although these are commonly known as subclasses Commelinidae, Rosidae, and Asteridae, respectively.

Well supported ordinal interrelationships are shown in Figure 1. Interrelationships among the basal branches of the tree and the position of the root of the flowering plant phylogeny remain elusive. Within the eudicots there is increasing support for a large subgroup with predominantly pentamerous and isomerous flowers, the core eudicots, mainly comprising Caryophyllales, Santalales, Saxifragales, rosids, and asterids. Rosids and asterids each comprise two large subgroups, eurosids I and II and euasterids I and II, also receiving increasing support as monophyletic. These correspond to the similarly numbered rosid and asterid clades of Chase et al. (1993).

Under each of the supraordinal groups of monocots, commelinoids, core eudicots, rosids, etc., there are a number of families listed without assignment to order. These families are known to belong within the major group under which they are listed, but their ordinal position is still uncertain. Similarly, Amborellaceae, Austrobaileyaceae, Canellaceae, etc., are listed at the beginning because

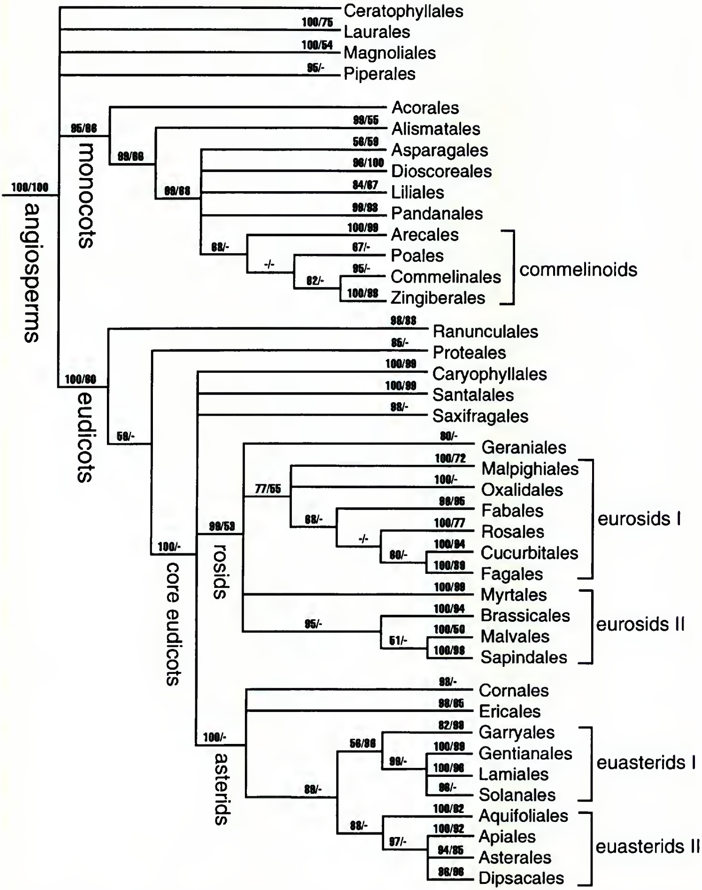

Figure 1. Phylogenetic interrelationships of the orders of flowering plants, compiled from recent cladistic analyses cited in the text. Jackknife support is given on the branches (a dash for values < 50%), first jackknife values from analysis of 545 sequences of the *rbc*L, *atp*B, and 18S rDNA genes (D. E. Soltis, M. W. Chase, P. S. Soltis, D. Albach, M. E. Mort, V. Savolainen, M. Zanis & J. S. Farris, unpublished, in prep.) and second jackknife values from analysis of 2538 *rbc*L sequences (Källersjö et al., 1998).

they belong neither in any of the phylogenetically "basal" orders at the beginning nor in the monocots or eudicots. Furthermore, families listed directly under monocots without an order are monocots but not commelinoids, and families similarly listed directly under eudicots and core eudicots are eudicots or core eudicots, respectively, but neither rosids nor asterids. At the end of the system is an additional list of families of uncertain position. Most of these are probably eudicots (including core eudicots, rosids, and asterids), but so far there are no firm data supporting their placement anywhere within the eudicots.

Literature Cited

Alverson, W. S., K. G. Karol, D. A. Baum, M. W. Chase, S. M. Swensen, R. McCourt & K. J. Sytsma. 1998. Circumscription of the Malvales and relationships to other Rosidae: Evidence from *rbc*L sequence data. Amer. J. Bot. 85: 876–877.

Anderberg, A. A., B. Ståhl & M. Källersjö. 1998. Phylogenetic interrelationships in the Primulales inferred from *rbc*L sequence data. Pl. Syst. Evol. 211: 93–102.

Backlund, A. & B. Bremer 1998. Phylogeny of the Asteridae s. str. based on *rbc*L sequences, with particular reference to the Dipsacales. Pl. Syst. Evol. 207: 225–254.

——— & K. Bremer. 1998. To be or not to be—Principles of classification and monotypic plant families. Taxon 47: 391–400.

——— & N. Pyck. 1998. Diervillaceae and Linnaeaceae, two new families of caprifolioids. Taxon 47: 657–661.

Bakker, F. T., D. D. Vassiliades, C. Morton & V. Savolainen. 1998. Phylogenetic relationships of *Biebersteinia* Stephan (Geraniaceae) inferred from *rbc*L and *atp*B sequence comparisons. Bot. J. Linn. Soc. 127: 149–158.

Bayer, C., M. F. Fay, A. Y. de Bruijn, V. Savolainen, C. M. Morton, K. Kubitzki & M. W. Chase. 1999. Support for an expanded concept of Malvaceae within a recircumscribed order Malvales: A combined analysis of plastid *atp*B and *rbc*L DNA sequences. Bot. J. Linn. Soc. [in press].

Bremer, B., R. G. Olmstead, L. Struwe & J. A. Sweere. 1994. *rbc*L sequences support exclusion of *Retzia*, *Desfontainia*, and *Nicodemia* from the Gentianales. Pl. Syst. Evol. 190: 213–230.

Bremer, K., B. Bremer & M. Thulin. 1995, 1996, 1997. Introduction to Phylogeny and Systematics of Flowering Plants. 1st, 2nd, 3rd eds. Compendium, Uppsala University, Uppsala.

———, ——— & ———. 1998. Classification of flowering plants. Internet http://www.systbot.uu.se/classification/overview.html.

Burtt, B. L. 1977. Classification above the genus, as exemplified by Gesneriaceae, with parallels from other groups. *In* K. Kubitzki (editor), Flowering plants: Evolution and classification of higher categories. Pl. Syst. Evol. Suppl. 1: 97–109.

Cantino, P. D., R. G. Olmstead & S. J. Wagstaff. 1997. A comparison of phylogenetic nomenclature with the current system: A botanical case study. Syst. Biol. 46: 313–331.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

———, D. W. Stevenson, P. Wilkin & P. J. Rudall. 1995. Monocot systematics: A combined analysis. Pp. 685–730 *in* P. J. Rudall, P. J. Cribb, D. F. Cutler & C. J. Humphries (editors), Monocotyledons: Systematics and Evolution. Royal Botanic Gardens, Kew.

Conti, E., A. Litt & K. J. Sytsma. 1996. Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbc*L sequence data. Amer. J. Bot. 83: 221–233.

Copeland, H. F. 1957. Forecast of a system of the dicotyledons. Madroño 14: 1–9.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Dahlgren, R. M. T. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147.

———, H. T. Clifford & P. F. Yeo. 1985. The Families of the Monocotyledons. Springer-Verlag, Berlin.

Davis, P. H. 1978. The moving staircase: An analysis of taxonomic rank and affinity. Notes Roy. Bot. Gard. Edinburgh 36: 325–340.

De Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. Aliso 15: 125–144.

——— & J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. Trends Ecol. Evol. 9: 27–31.

Gadek, P. A., E. S. Fernando, C. J. Quinn, S. B. Hoot, T. Terrazas, M. C. Sheahan & M. W. Chase. 1996. Sapindales: Molecular delimitation and infraordinal groups. Amer. J. Bot. 83: 802–811.

———, P. G. Wilson & C. J. Quinn. 1996. Phylogenetic reconstruction in Myrtaceae using *mat*K, with particular reference to the position of *Psiloxylon* and *Heteropyxis*. Austral. Syst. Bot. 9: 283–290.

Goldberg, A. 1986. Classification, evolution, and phylogeny of the families of dicotyledons. Smithsonian Contr. Bot. 58: 1–314.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill. 1994. International Code of Botanical Nomenclature. Regnum Veg. 131.

Gustafsson, M. H. G., A. Backlund & B. Bremer. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Hershkovitz, M. A. & E. A. Zimmer. 1997. On the evolutionary origins of the cacti. Taxon 46: 217–232.

Heywood, V. H. 1977. Principles and concepts in the classification of higher taxa. *In* K. Kubitzki (editor), Flowering plants: Evolution and classification of higher categories. Pl. Syst. Evol. Suppl. 1: 1–12.

Judd, W. S. & S. R. Manchester. 1997. Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters. Brittonia 49: 384–405.

———, R. W. Sanders & M. J. Donoghue. 1994. Angiosperm family pairs: Preliminary phylogenetic analyses. Harvard Pap. Bot. 5: 1–51.

Källersjö, M., J. S. Farris, M. W. Chase, B. Bremer, M. F. Fay, C. J. Humphries, G. Petersen, O. Seberg & K. Bremer. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbc*L DNA sequences reveals support for major clades of green plants, land plants, seed plants, and flowering plants. Pl. Syst. Evol. [in press].

Lidén, M., B. Oxelman, A. Backlund, L. Andersson, B. Bremer, R. Eriksson, R. Moberg, I. Nordal, K. Persson, M. Thulin & B. Zimmer. 1997. Charlie is our darling. Taxon 46: 735–738.

Merxmüller, H. 1977. Summary lecture. *In* K. Kubitzki (editor), Flowering plants: Evolution and classification of higher categories. Pl. Syst. Evol. Suppl. 1: 397–405.

Morton, C. M., M. W. Chase, K. A. Kron & S. M. Swensen. 1996. A molecular evaluation of the monophyly of the order Ebenales based upon *rbc*L sequence data. Syst. Bot. 21: 567–586.

Nadot, S., G. Bittar, L. Carter, R. Lacroix & B. Lejeune. 1995. A phylogenetic analysis of monocotyledons based on the chloroplast gene rps4 using parsimony and a new numerical phenetics method. Molec. Phylog. Evol. 4: 257–282.

Nickrent, D. L. & J. R. Duff. 1996. Molecular studies of parasitic plants using ribosomal RNA. Pp. 28–52 *in* M. T. Moreno, J. I. Cubero, D. Berner, D. Joel, L. J. Musselman & C. Parker (editors), Advances in Parasitic Plant Research. Junta de Andalucía, Dirección General de Investigación Agraria, Córdoba, Spain.

——— & D. E. Soltis. 1995. A comparison of angiosperm phylogenies from nuclear 18S rDNA and *rbc*L sequences. Ann. Missouri Bot. Gard. 82: 208–234.

———, J. R. Duff, A. E. Colwell, A. D. Wolfe, N. D. Young, K. E. Steiner & C. W. dePamphilis. 1998. Molecular phylogenetic and evolutionary studies of parasitic plants. Pp. 211–241 *in* D. E. Soltis, P. S. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants II: DNA Sequencing. Kluwer, Boston.

Olmstead, R. G. & P. A. Reeves. 1995. Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbc*L and *ndh*F sequences. Ann. Missouri Bot. Gard. 82: 176–193.

Plunkett, G. M., D. E. Soltis & P. S. Soltis. 1996. Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of *rbc*L sequences. Amer. J. Bot. 83: 399–415.

———, ——— & ———. 1997. Classification of the relationship between Apiaceae and Araliaceae based on *mat*K and *rbc*L sequence data. Amer. J. Bot. 84: 565–580.

Reveal, J. L. 1998. Indices nominum supragenericorum plantarum vascularium. Internet http://www.inform.umd.edu/PBIO/.WWW/supragen.html.

Rodman, J. E., K. G. Karol, R. A. Price & K. J. Sytsma. 1996. Molecules, morphology, and Dahlgren's expanded order Capparales. Syst. Bot. 21: 289–307.

Soltis, D. E. & P. S. Soltis. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: A comparison of topologies based on 18S rDNA and *rbc*L sequences. Amer. J. Bot. 84: 504–522.

———, ———, D. R. Morgan, S. M. Swensen, B. C. Mullin, J. M. Dowd & P. G. Martin. 1995. Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms. Proc. Natl. Acad. Sci., U.S.A. 92: 2647–2651.

———, ———, M. Mort, M. W. Chase, V. Savolainen, S. B. Hoot & C. M. Morton. 1998. Inferring complex phylogenies using parsimony: An empirical approach using three large DNA data sets for angiosperms. Syst. Biol. 47: 32–42.

———, ———, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, C. Shu-Miaw, L. J. Gilliespie, W. J. Kress & K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Ann. Missouri Bot. Gard. 84: 1–49.

Stevens, P. F. 1986. Evolutionary classification in botany, 1960–1985. J. Arnold Arbor. 67: 313–339.

———. 1997. How to interpret botanical classifications: Suggestions from history. Bioscience 47: 250–250.

———. 1998. What kind of classification should the practising taxonomist use to be saved? Pp. 295–319 *in* J. Dransfield, M. J. E. Coode & D. A. Simpson (editors), Plant Diversity in Malesia III. Royal Botanic Gardens, Kew.

Struwe, L., V. A. Albert & B. Bremer. 1994. Cladistics and family level classification of the Gentianales. Cladistics 10: 175–206.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

———. 1997. Diversity and Classification of Flowering Plants. Columbia Univ. Press, New York.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35–106.

———. 1992. An updated phylogenetic classification of flowering plants. Aliso 13: 365–389.

Thulin, M., B. Bremer, J. Richardson, J. Niklasson, M. F. Fay & M. W. Chase. 1998. Family relationships of the enigmatic rosid genera *Barbeya* and *Dirachma* from the Horn of Africa region. Pl. Syst. Evol. 213: 103–119.

CLASSIFICATION OF FLOWERING PLANTS

- Amborellaceae
- Austrobaileyaceae
- Canellaceae
- Chloranthaceae
- Hydnoraceae
- Illiciaceae
- Nymphaeaceae
- [+Cabombaceae]
- Rafflesiaceae
- Schisandraceae
- Trimeniaceae
- Winteraceae

Ceratophyllales Bisch.
- Ceratophyllaceae

Laurales Perleb
- Atherospermataceae
- Calycanthaceae
- Gomortegaceae
- Hernandiaceae
- Lauraceae
- Monimiaceae
- Siparunaceae

Magnoliales Bromhead
- Annonaceae
- Degeneriaceae
- Eupomatiaceae
- Himantandraceae
- Magnoliaceae
- Myristicaceae

Piperales Dumort.
- Aristolochiaceae
- Lactoridaceae
- Piperaceae
- Saururaceae

MONOCOTS
- Corsiaceae
- Japonoliriaceae
- Nartheciaceae
- Petrosaviaceae
- Triuridaceae

Acorales Reveal
- Acoraceae

Alismatales Dumort.
- Alismataceae
- Aponogetonaceae
- Araceae
- Butomaceae
- Cymodoceaceae
- Hydrocharitaceae
- Juncaginaceae
- Limnocharitaceae
- Posidoniaceae
- Potamogetonaceae
- Ruppiaceae
- Scheuchzeriaceae
- Tofieldiaceae
- Zosteraceae

Asparagales Bromhead
- Agapanthaceae
- Agavaceae
- Alliaceae
- Amaryllidaceae
- Anemarrhenaceae
- Anthericaceae
- Aphyllanthaceae
- Asparagaceae
- Asphodelaceae
- Asteliaceae
- Behniaceae
- Blandfordiaceae
- Boryaceae
- Convallariaceae
- Doryanthaceae
- Hemerocallidaceae
- Herreriaceae
- Hesperocallidaceae
- Hyacinthaceae
- Hypoxidaceae
- Iridaceae
- Ixioliriaceae
- Lanariaceae
- Laxmanniaceae
- Orchidaceae
- Tecophilaeaceae
- Themidaceae
- Xanthorrhoeaceae
- Xeronemataceae

Dioscoreales Hook. f.
- Burmanniaceae
- Dioscoreaceae
- Taccaceae
- Thismiaceae
- Trichopodaceae

Liliales Perleb
- Alstroemeriaceae
- Campynemataceae
- Colchicaceae
- Liliaceae
- Luzuriagaceae
- Melanthiaceae
- Philesiaceae
- Ripogonaceae
- Smilacaceae

CLASSIFICATION OF FLOWERING PLANTS
(cont'd.)

Pandanales Lindl.
- Cyclanthaceae
- Pandanaceae
- Stemonaceae
- Velloziaceae

COMMELINOIDS
- Abolbodaceae
- Bromeliaceae
- Dasypogonaceae
- Hanguanaceae
- Mayacaceae
- Rapateaceae

Arecales Bromhead
- Arecaceae

Commelinales Dumort.
- Commelinaceae
- Haemodoraceae
- Philydraceae
- Pontederiaceae

Poales Small
- Anarthriaceae
- Centrolepidaceae
- Cyperaceae
- Ecdeiocoleaceae
- Eriocaulaceae
- Flagellariaceae
- Hydatellaceae
- Joinvilleaceae
- Juncaceae
- Poaceae
- Prioniaceae
- Restionaceae
- Sparganiaceae
- Thurniaceae
- Typhaceae
- Xyridaceae

Zingiberales Griseb.
- Cannaceae
- Costaceae
- Heliconiaceae
- Lowiaceae
- Marantaceae
- Musaceae
- Strelitziaceae
- Zingiberaceae

EUDICOTS
- Buxaceae
- Didymelaceae
- Sabiaceae
- Trochodendraceae
- [+Tetracentraceae]

Proteales Dumort.
- Nelumbonaceae
- Platanaceae
- Proteaceae

Ranunculales Dumort.
- Berberidaceae
- Circaeasteraceae
- [+Kingdoniaceae]
- Eupteleaceae
- Lardizabalaceae
- Menispermaceae
- Papaveraceae
- [+Fumariaceae]
- [+Pteridophyllaceae]
- Ranunculaceae

CORE EUDICOTS
- Aextoxicaceae
- Berberidopsidaceae
- Dilleniaceae
- Gunneraceae
- Myrothamnaceae
- Vitaceae

Caryophyllales Perleb
- Achatocarpaceae
- Aizoaceae
- Amaranthaceae
- Ancistrocladaceae
- Asteropeiaceae
- Basellaceae
- Cactaceae
- Caryophyllaceae
- Didiereaceae
- Dioncophyllaceae
- Droseraceae
- Drosophyllaceae
- Frankeniaceae
- Molluginaceae
- Nepenthaceae
- Nyctaginaceae
- Physenaceae
- Phytolaccaceae
- Plumbaginaceae
- Polygonaceae
- Portulacaceae
- Rhabdodendraceae
- Sarcobataceae
- Simmondsiaceae
- Stegnospermataceae
- Tamaricaceae

Santalales Dumort.
- Olacaceae
- Opiliaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

- Loranthaceae
- Misodendraceae
- Santalaceae

Saxifragales Dumort.

- Altingiaceae
- Cercidiphyllaceae
- Crassulaceae
- Daphniphyllaceae
- Grossulariaceae
- Haloragaceae
- Hamamelidaceae
- Iteaceae
- Paeoniaceae
- Penthoraceae
- Pterostemonaceae
- Saxifragaceae
- Tetracarpaeaceae

ROSIDS

- Aphloiaceae
- Crossosomataceae
- Ixerbaceae
- Krameriaceae
- Picramniaceae
- Podostemaceae
- Stachyuraceae
- Staphyleaceae
- Tristichaceae
- Zygophyllaceae

Geraniales Dumort.

- Francoaceae
- Geraniaceae
- [+Hypseocharitaceae]
- Greyiaceae
- Ledocarpaceae
- Melianthaceae
- Vivianiaceae

EUROSIDS I

- Celastraceae
- Huaceae
- Parnassiaceae
- [+Lepuropetalaceae]
- Stackhousiaceae

Cucurbitales Dumort.

- Anisophylleaceae
- Begoniaceae
- Coriariaceae
- Corynocarpaceae
- Cucurbitaceae
- Datiscaceae
- Tetramelaceae

Fabales Bromhead

- Fabaceae
- Polygalaceae
- Quillajaceae
- Surianaceae

Fagales Engl.

- Betulaceae
- Casuarinaceae
- Fagaceae
- Juglandaceae
- Myricaceae
- Nothofagaceae
- Rhoipteleaceae
- Ticodendraceae

Malpighiales Mart.

- Achariaceae
- Balanopaceae
- Caryocaraceae
- Chrysobalanaceae
- Clusiaceae
- Dichapetalaceae
- Erythroxylaceae
- Euphorbiaceae
- Euphroniaceae
- Flacourtiaceae
- Goupiaceae
- Hugoniaceae
- Humiriaceae
- Irvingiaceae
- Ixonanthaceae
- Lacistemataceae
- Linaceae
- Malesherbiaceae
- Malpighiaceae
- Medusagynaceae
- Ochnaceae
- Pandaceae
- Passifloraceae
- Putranjivaceae
- Quiinaceae
- Rhizophoraceae
- Salicaceae
- Scyphostegiaceae
- Trigoniaceae
- Turneraceae
- Violaceae

Oxalidales Heintze

- Cephalotaceae
- Connaraceae
- Cunoniaceae
- Elaeocarpaceae
- Oxalidaceae
- Tremandraceae

CLASSIFICATION OF FLOWERING PLANTS
(cont'd.)

Rosales Perleb
- Barbeyaceae
- Cannabaceae
- Cecropiaceae
- Celtidaceae
- Dirachmaceae
- Elaeagnaceae
- Moraceae
- Rhamnaceae
- Rosaceae
- Ulmaceae
- Urticaceae

EUROSIDS II
- Tapisciaceae

Brassicales Bromhead
- Akaniaceae
- [+Bretschneideraceae]
- Bataceae
- Brassicaceae
- Caricaceae
- Emblingiaceae
- Gyrostemonaceae
- Koeberliniaceae
- Limnanthaceae
- Moringaceae
- Pentadiplandraceae
- Resedaceae
- Salvadoraceae
- Setchellanthaceae
- Tovariaceae
- Tropaeolaceae

Malvales Dumort.
- Bixaceae
- [+Diegodendraceae]
- Cistaceae
- Cochlospermaceae
- Dipterocarpaceae
- Malvaceae
- Muntingiaceae
- Neuradaceae
- Sarcolaenaceae
- Sphaerosepalaceae
- Thymelaeaceae

Myrtales Rchb.
- Alzateaceae
- Combretaceae
- Crypteroniaceae
- Heteropyxidaceae
- Lythraceae
- Melastomataceae
- Memecylaceae
- Myrtaceae
- Oliniaceae
- Onagraceae
- Penaeaceae
- Psiloxylaceae
- Rhynchocalycaceae
- Vochysiaceae

Sapindales Dumort.
- Anacardiaceae
- Biebersteiniaceae
- Burseraceae
- Kirkiaceae
- Meliaceae
- Nitrariaceae
- [+Peganaceae]
- Rutaceae
- Sapindaceae
- Simaroubaceae

ASTERIDS

Cornales Dumort.
- Cornaceae
- [+Nyssaceae]
- Grubbiaceae
- Hydrangeaceae
- Hydrostachyaceae
- Loasaceae

Ericales Dumort.
- Actinidiaceae
- Balsaminaceae
- Clethraceae
- Cyrillaceae
- Diapensiaceae
- Ebenaceae
- Ericaceae
- Fouquieriaceae
- Halesiaceae
- Lecythidaceae
- Marcgraviaceae
- Myrsinaceae
- Pellicieraceae
- Polemoniaceae
- Primulaceae
- Roridulaceae
- Sapotaceae
- Sarraceniaceae
- Styracaceae
- Symplocaceae
- Ternstroemiaceae
- Tetrameristaceae
- Theaceae
- Theophrastaceae

EUASTERIDS I
- Boraginaceae
- Plocospermataceae
- Vahliaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Garryales Lindl.
- Aucubaceae
- Eucommiaceae
- Garryaceae
- Oncothecaceae

Gentianales Lindl.
- Apocynaceae
- Gelsemiaceae
- Gentianaceae
- Loganiaceae
- Rubiaceae

Lamiales Bromhead
- Acanthaceae
- Avicenniaceae
- Bignoniaceae
- Buddlejaceae
- Byblidaceae
- Cyclocheilaceae
- Gesneriaceae
- Lamiaceae
- Lentibulariaceae
- Myoporaceae
- Oleaceae
- Orobanchaceae
- Paulowniaceae
- Pedaliaceae
- [+Martyniaceae]
- Phrymaceae
- Plantaginaceae
- Schlegeliaceae
- Scrophulariaceae
- Stilbaceae
- Tetrachondraceae
- Verbenaceae

Solanales Dumort.
- Convolvulaceae
- Hydroleaceae
- Montiniaceae
- Solanaceae
- Sphenocleaceae

EUASTERIDS II
- Adoxaceae
- Bruniaceae
- Carlemanniaceae
- Columelliaceae
- [+Desfontainiaceae]
- Eremosynaceae
- Escalloniaceae
- Icacinaceae
- Polyosmaceae
- Sphenostemonaceae
- Tribelaceae

Apiales Nakai
- Apiaceae
- Araliaceae
- Aralidiaceae
- Griseliniaceae
- Melanophyllaceae
- Pittosporaceae
- Torricelliaceae

Aquifoliales Senft
- Aquifoliaceae
- Helwingiaceae
- Phyllonomaceae

Asterales Lindl.
- Alseuosmiaceae
- Argophyllaceae
- Asteraceae
- Calyceraceae
- Campanulaceae
- [+Lobeliaceae]
- Carpodetaceae
- Donatiaceae
- Goodeniaceae
- Menyanthaceae
- Pentaphragmataceae
- Phellinaceae
- Rousseaceae
- Stylidiaceae

Dipsacales Dumort.
- Caprifoliaceae
- Diervillaceae
- Dipsacaceae
- Linnaeaceae
- Morinaceae
- Valerianaceae

FAMILIES OF UNCERTAIN POSITION
- Balanophoraceae
- Bonnetiaceae
- Cardiopteridaceae
- Ctenolophonaceae
- Cynomoriaceae
- Cytinaceae
- Dipentodontaceae
- Elatinaceae
- Geissolomataceae
- Hoplestigmataceae
- Kaliphoraceae
- Lepidobotryaceae
- Lissocarpaceae
- Lophopyxidaceae
- Medusandraceae
- Metteniusaceae
- Mitrastemonaceae
- Paracryphiaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Pentaphylacaceae
Peridiscaceae
Plagiopteraceae
Pottingeriaceae
Sladeniaceae
Strasburgeriaceae
Tepuianthaceae

ORDINAL SYNONYMS

Acanthales Lindl.
= Lamiales
Acerales Lindl.
= Sapindales
Actinidiales Takht. ex Reveal
= Ericales
Adoxales Nakai
- not accepted, family under euasterids II
Aesculales Bromhead
= Sapindales
Agavales Hutch.
= Asparagales
Alliales Traub
= Asparagales
Alstroemeriales Hutch.
= Liliales
Altingiales Doweld
= Saxifragales
Amaranthales Dumort.
= Caryophyllales
Amaryllidales Bromhead
= Asparagales
Ambrosiales Dumort.
= Asterales
Ammiales Small
= Apiales
Amomales Lindl.
= Zingiberales
Ancistrocladales Takht.
= Caryophyllales
Annonales Lindl.
= Magnoliales
Anthobolales Dumort.
= Santalales
Apocynales Bromhead
= Gentianales
Aponogetonales Hutch.
= Alismatales
Arales Dumort.
= Alismatales
Araliales Reveal
= Apiales
Aralidiales Takht. ex Reveal
= Apiales
Aristolochiales Dumort.
= Piperales
Asarales Horan.
= Piperales
Asclepiadales Dumort.
= Gentianales
Asteliales Dumort.
= Asparagales
Atriplicales Horan.
= Caryophyllales
Aucubales Takht.
= Garryales
Austrobaileyales Takht. ex Reveal
- not accepted, family at beginning of system
Avenales Bromhead
= Poales
Balanopales Engl.
= Malpighiales
Balanophorales Dumort.
- not accepted, family unplaced
Balsaminales Lindl.
= Ericales
Barbeyales Takht. & Reveal
= Rosales
Batales Engl.
= Brassicales
Begoniales Dumort.
= Cucurbitales
Berberidales Dumort.
= Ranunculales
Betulales Bromhead
= Fagales
Biebersteiniales Takht.
= Sapindales
Bignoniales Lindl.
= Lamiales
Bixales Lindl.
= Malvales
Boraginales Dumort.
- not accepted, family under euasterids I
Brexiales Lindl.
- not accepted, family under eurosids I
Bromeliales Dumort.
- not accepted, family under commelinoids
Bruniales Dumort.
- not accepted, family under euasterids II
Brunoniales Lindl.
= Asterales
Burmanniales Heintze
= Dioscoreales
Burserales Baskerville
= Sapindales
Butomales Hutch.
= Alismatales

Classification of Flowering Plants (cont'd.)

Buxales Takht. ex Reveal
- not accepted, family under eudicots
Byblidales Nakai ex Reveal
= Lamiales
Cactales Dumort.
= Caryophyllales
Callitrichales Dumort.
= Lamiales
Calycanthales Mart.
= Laurales
Calycerales Takht. ex Reveal
= Asterales
Campanulales Rchb.
= Asterales
Canellales Cronquist
- not accepted, family at beginning of system
Cannales Dumort.
= Zingiberales
Capparales Hutch.
= Brassicales
Caprifoliales Lindl.
= Dipsacales
Cardiopteridales Takht.
- not accepted, family under euasterids II
Carduales Small
= Asterales
Caricales L. D. Benson
= Brassicales
Cassiales Horan.
= Fabales
Casuarinales Lindl.
= Fagales
Celastrales Baskerville
- not accepted, family under eurosids I
Centrolepidales Takht.
= Poales
Cephalotales Nakai
= Oxalidales
Cercidiphyllales Hu ex Reveal
= Saxifragales
Chenopodiales Dumort.
= Caryophyllales
Chironiales Griseb.
= Gentianales
Chloranthales A. C. Sm. ex J. -F. Leroy
- not accepted, family at beginning of system
Cinchonales Lindl.
= Gentianales
Circaeasterales Takht.
= Ranunculales
Cistales Rchb.
= Malvales
Citrales Dumort.
= Sapindales
Cocosales Nakai
= Arecales
Colchicales Dumort.
= Liliales
Combretales Baskerville
= Myrtales
Connarales Takht. ex Reveal
= Cunoniales
Convolvulales Dumort.
= Solanales
Coriariales Lindl.
= Cucurbitales
Corylales Dumort.
= Fagales
Corynocarpales Takht.
= Cucurbitales
Crassulales Lindl.
= Saxifragales
Crossosomatales Takht. ex Reveal
- not accepted, family under rosids
Cunoniales Hutch.
= Oxalidales
Cyclanthales J. H. Schaffn.
= Pandanales
Cymodoceales Nakai
= Alismatales
Cynomoriales Burnett
- not accepted, family unplaced
Cyperales Hutch.
= Poales
Cytinales Dumort.
- not accepted, family unplaced
Daphnales Lindl.
= Malvales
Daphniphyllales Pulle ex Cronquist
= Saxifragales
Datiscales Dumort.
= Cucurbitales
Desfontainiales Takht.
- not accepted, family under euasterids II
Diapensiales Engl. & Gilg
= Ericales
Didymelales Takht.
- not accepted, family under eudicots
Dilleniales Hutch.
- not accepted, family under core eudicots
Dioncophyllales Takht. ex Reveal
= Caryophyllales
Diospyrales Prantl
= Ericales
Droserales Griseb.
= Caryophyllales

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Ebenales Engl.
  = Ericales
Elaeagnales Bromhead
  = Rosales
Elaeocarpales Takht.
  = Oxalidales
Elatinales Nakai
  - not accepted, family unplaced
Elodeales Nakai
  = Alismatales
Empetrales Raf.
  = Ericales
Eriocaulales Nakai
  = Poales
Eucommiales Nemejc ex Cronquist
  = Garryales
Euphorbiales Lindl.
  = Malpighiales
Eupomatiales Takht. ex Reveal
  = Magnoliales
Eupteleales Hu ex Reveal
  = Ranunculales
Euryalales H.L.Li
  - not accepted, family at beginning of system
Ficales Dumort.
  = Rosales
Flacourtiales Heintze
  = Malpighiales
Fouquieriales Takht. ex Reveal
  = Ericales
Francoales Takht.
  = Geraniales
Frangulales Wirtg.
  = Rosales
Galiales Bromhead
  = Gentianales
Geissolomatales Takht. ex Reveal
  - not accepted, family unplaced
Gesneriales Dumort.
  = Lamiales
Glaucidiales Takht. ex Reveal
  = Ranunculales
Globulariales Dumort.
  = Lamiales
Goodeniales Lindl.
  = Asterales
Greyiales Takht.
  = Geraniales
Grossulariales Lindl.
  = Saxifragales
Gunnerales Takht. ex Reveal
  - not accepted, family under core eudicots
Gyrocarpales Dumort.
  = Laurales
Gyrostemonales Takht.
  = Brassicales
Haemodorales Hutch.
  = Commelinales
Haloragales Bromhead
  = Saxifragales
Hamamelidales Griseb.
  = Saxifragales
Hanguanales R. Dahlgren ex Reveal
  = not accepted, family under commelinoids
Helleborales Nakai
  = Ranunculales
Helwingiales Takht.
  = Aquifoliales
Himantandrales Doweld & Shevyryova
  = Magnoliales
Hippuridales Pulle ex Reveal
  = Lamiales
Homaliales Bromhead
  = Malpighiales
Hortensiales Griseb.
  = Cornales
Hydatellales Cronquist
  = Poales
Hydnorales Takht. ex Reveal
  - not accepted, family at beginning of system
Hydrangeales Nakai
  = Cornales
Hydrastidales Takht.
  = Ranunculales
Hydropeltidales (Bartl.) Spenn.
  - not accepted, family Nymphaeaceae at beginning of system
Hydrostachyales Diels ex Reveal
  = Cornales
Hypericales Dumort.
  = Malpighiales
Hypoxidales Takht.
  = Asparagales
Icacinales Tiegh. ex Reveal
  - not accepted, family under euasterids II
Illiciales Hu ex Cronquist
  - not accepted, family at beginning of system
Iridales Raf.
  = Asparagales
Ixiales Lindl.
  = Asparagales
Jasminales Dumort.
  = Lamiales
Juglandales Dumort.
  = Fagales

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Julianiales Engl.
= Sapindales
Juncaginales Hutch.
= Alismatales
Juncales Dumort.
= Poales
Lacistematales Baskerville
= Malpighiales
Lactoridales Takht. ex Reveal
= Piperales
Lardizabalales Loconte
= Ranunculales
Lecythidales Cronquist
= Ericales
Leitneriales Engl.
= Sapindales
Lentibulariales Lindl.
= Lamiales
Ligustrales Bartl. ex Bisch.
= Lamiales
Limnanthales Nakai
= Brassicales
Linales Baskerville
= Malpighiales
Loasales Bessey
= Cornales
Loganiales Lindl.
= Gentianales
Lonicerales T. Liebe
= Dipsacales
Loranthales Dumort.
= Santalales
Lythrales Caruel
= Myrtales
Marathrales Dumort.
- not accepted, family Podostemaceae under rosids
Mayacales Nakai
- not accepted, family under commelinoids
Medusagynales Takht.
= Malpighiales
Medusandrales Brenan
- not accepted, family unplaced
Melanthiales R. Dahlgren ex Reveal
= Liliales
Melastomatales Oliv.
= Myrtales
Meliales Lindl.
= Sapindales
Menispermales Bromhead
= Ranunculales
Menyanthales T. Yamaz. ex Takht.
= Asterales
Metteniusales Takht.
- not accepted, family unplaced
Mitrastemonales Makino
- not accepted, family unplaced
Monimiales Dumort.
= Laurales
Moringales Nakai
= Brassicales
Myricales Engl.
= Fagales
Myristicales Thomé
= Magnoliales
Myrothamnales Nakai ex Reveal
- not accepted, family under core eudicots
Myrsinales Spenn.
= Ericales
Najadales Dumort.
= Alismatales
Narcissales Dumort.
= Asparagales
Nartheciales Reveal & Zomlefer
- not accepted, family under monocots
Nelumbonales Reveal
= Proteales
Nepenthales Dumort.
= Caryophyllales
Nolanales Lindl.
= Solanales
Nyctaginales Dumort.
= Caryophyllales
Nymphaeales Dumort.
= not accepted, family at beginning of system
Ochnales Hutch. ex Reveal
= Malpighiales
Oenotherales Bromhead
= Myrtales
Olacales Benth.
= Santalales
Oleales Lindl.
= Lamiales
Onagrales Rchb.
= Myrtales
Opuntiales Willk.
= Caryophyllales
Orchidales Raf.
= Asparagales
Paeoniales Heintze
= Saxifragales
Pandales Engl. & Gilg
= Malpighiales
Papaverales Dumort.
= Ranunculales
Paracryphiales Takht.
- not accepted, family unplaced
Paridales Dumort.
= Liliales

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Parnassiales Nakai
- not accepted, family under eurosids I
Passiflorales Dumort.
= Malpighiales
Penaeales Lindl.
= Myrtales
Petiveriales Lindl.
= Caryophyllales
Petrosaviales Takht.
- not accepted, family under monocots
Philydrales Dumort.
= Commelinales
Physenales Takht.
= Caryophyllales
Pinguiculales Dumort.
= Lamiales
Pittosporales Lindl.
= Apiales
Plantaginales Lindl.
= Lamiales
Platanales J. H. Schaffn.
= Proteales
Plumbaginales Lindl.
= Caryophyllales
Podophyllales Dumort.
= Ranunculales
Podostemales Lindl.
= not accepted, family under rosids
Polemoniales Bromhead
= Ericales
Polygalales Dumort.
= Fabales
Polygonales Dumort.
= Caryophyllales
Pontederiales Hook. f.
= Commelinales
Portulacales Dumort.
= Caryophyllales
Posidoniales Nakai
= Alismatales
Potamogetonales Dumort.
= Alismatales
Primulales Dumort.
= Ericales
Quercales Burnett
= Fagales
Rafflesiales Oliv.
- not accepted, family at beginning of system
Resedales Dumort.
= Brassicales
Restionales J. H. Schaffn.
= Poales
Rhamnales Dumort.
= Rosales
Rhinanthales Dumort.
= Lamiales
Rhizophorales Tiegh. ex Reveal
= Malpighiales
Rhodorales Horan.
= Ericales
Rhoipteleales Novák ex Reveal
= Fagales
Roridulales Nakai
= Ericales
Rubiales Dumort.
= Gentianales
Ruppiales Nakai
= Alismatales
Rutales Perleb
= Sapindales
Sabiales Takht.
= not accepted, family under eudicots
Salicales Lindl.
= Malpighiales
Salvadorales R. Dahlgren ex Reveal
= Brassicales
Samolales Dumort.
= Ericales
Samydales Dumort.
= Malpighiales
Sanguisorbales Dumort.
= Rosales
Sapotales Hook. f.
= Ericales
Sarraceniales Bromhead
= Ericales
Scheuchzeriales B. Boivin
= Alismatales
Scleranthales Dumort.
= Caryophyllales
Scrophulariales Lindl.
= Lamiales
Scyphostegiales Croizat
= Malpighiales
Sedales Rchb.
= Saxifragales
Silenales Lindl.
= Caryophyllales
Simmondsiales Reveal
= Caryophyllales
Smilacales Lindl.
= Liliales
Stellariales Dumort.
= Caryophyllales
Stylidiales Takht. ex Reveal
= Asterales
Styracales Bisch.
= Ericales
Taccales Dumort.
= Dioscoreales

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Tamales Dumort.
= Dioscoreales
Tamaricales Hutch.
= Caryophyllales
Tecophilaeales Traub ex Reveal
= Asparagales
Theales Lindl.
= Ericales
Theligonales Nakai
= Gentianales
Thymelaeales Willk.
= Malvales
Tiliales Caruel
= Malvales
Tofieldiales Reveal & Zomlefer
= Alismatales
Torricelliales Takht. ex Reveal
= Apiales
Tovariales Nakai
= Brassicales
Trilliales Takht.
= Liliales
Triuridales Hook. f.
- not accepted, family under monocots
Trochodendrales Takht. ex Cronquist
- not accepted, family under eudicots
Tropaeolales Takht. ex Reveal
= Brassicales
Turnerales Dumort.
= Malpighiales
Typhales Dumort.
= Poales
Ulmales Lindl.
= Rosales
Urticales Dumort.
= Rosales
Vacciniales Dumort.
= Ericales
Vallisneriales Nakai
= Alismatales
Velloziales R. Dahlgren ex Reveal
= Pandanales
Veratrales Dumort.
= Liliales
Verbenales Horan.
= Lamiales
Viburnales Dumort.
- not accepted, family under euasterids II
Vincales Horan.
= Gentianales
Violales Perleb
= Malpighiales
Vitales Reveal
- not accepted, family under core eudicots
Vochysiales Dumort.
= Myrtales
Winterales A. C. Sm. ex Reveal
- not accepted, family at beginning of system
Xyridales Lindl.
= Poales
Zosterales Nakai
= Alismatales
Zygophyllales Takht.
- not accepted, family under rosids

SELECTED FAMILIAL SYNONYMS

Abrophyllaceae
= Carpodetaceae
Acanthochlamydaceae
= Velloziaceae
Aceraceae
= Sapindaceae
Achradaceae
= Sapotaceae
Aegicerataceae
= Myrsinaceae
Agdestidaceae
= Phytolaccaceae
Aitoniaceae
= Meliaceae
Alangiaceae
= Cornaceae
Aloaceae
= Asphodelaceae
Alsinaceae
= Caryophyllaceae
Ambrosiaceae
= Asteraceae
Amygdalaceae
= Rosaceae
Androstachyaceae
= Euphorbiaceae
Antoniaceae
= Loganiaceae
Apodanthaceae
= Rafflesiaceae
Apostasiaceae
= Orchidaceae
Aptandraceae
= Olacaceae
Aristoteliaceae
= Elaeocarpaceae
Asclepiadaceae
= Apocynaceae
Asteranthaceae
= Lecythidaceae
Averrhoaceae
= Oxalidaceae
Avetraceae
= Dioscoreaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Balanitaceae
= Zygophyllaceae
Barbeiuaceae
= Phytolaccaceae
Barclayaceae
= Nymphaeaceae
Barringtoniaceae
= Lecythidaceae
Baueraceae
= Cunoniaceae
Baxteriaceae
= Dasypogonaceae
Bembiciaceae
= Flacourtiaceae
Berzeliaceae
= Bruniaceae
Bischofiaceae
= Euphorbiaceae
Blepharocaryaceae
= Anacardiaceae
Boerlagellaceae
= Sapotaceae
Bombacaceae
= Malvaceae
Boopidaceae
= Calyceraceae
Bretschneideraceae
= Akaniaceae
Brexiaceae
= Celastraceae
Brunelliaceae
= Cunoniaceae
Brunoniaceae
= Goodeniaceae
Bumeliaceae
= Sapotaceae
Burchardiaceae
= Colchicaceae
Byttneriaceae
= Malvaceae
Cabombaceae
= Nymphaeaceae
Caesalpiniaceae
= Fabaceae
Calectasiaceae
= Dasypogonaceae
Callitrichaceae
= Plantaginaceae
Calochortaceae
= Liliaceae
Camelliaceae
= Theaceae
Canotiaceae
= Celastraceae
Cansjeraceae
= Opiliaceae
Capparaceae
= Brassicaceae
Carduaceae
= Asteraceae
Cassythaceae
= Lauraceae
Chailletiaceae
= Dichapetalaceae
Chenopodiaceae
= Amaranthaceae
Chionographidaceae
= Melanthiaceae
Chloanthaceae
= Lamiaceae
Cichoriaceae
= Asteraceae
Cleomaceae
= Brassicaceae
Cneoraceae
= Rutaceae
Cobaeaceae
= Polemoniaceae
Compositae
= Asteraceae
Conostylidaceae
= Haemodoraceae
Cordiaceae
= Boraginaceae
Coridaceae
= Primulaceae
Corokiaceae
= Argophyllaceae
Corylaceae
= Betulaceae
Croomiaceae
= Stemonaceae
Cruciferae
= Brassicaceae
Curtisiaceae
= Cornaceae
Cuscutaceae
= Convolvulaceae
Cyananthaceae
= Campanulaceae
Cyanastraceae
= Tecophilaeaceae
Cynocrambaceae nom. illeg.
= Rubiaceae
Cyphiaceae
= Campanulaceae
Cyphocarpaceae
= Campanulaceae
Cypripediaceae
= Orchidaceae
Dactylanthaceae
= Balanophoraceae

Classification of Flowering Plants (cont'd.)

Davidiaceae
= Cornaceae
Davidsoniaceae
= Cunoniaceae
Decaisneaceae
= Lardizabalaceae
Desfontainiaceae
= Columelliaceae
Dialypetalanthaceae
= Rubiaceae
Dianellaceae
= Hemerocallidaceae
Dichondraceae
= Convolvulaceae
Diclidantheraceae
= Polygalaceae
Diegodendraceae
= Bixaceae
Dionaeaceae
= Droseraceae
Dracaenaceae
= Convallariaceae
Duabangaceae
= Lythraceae
Duckeodendraceae
= Solanaceae
Dulongiaceae nom. illeg.
= Phyllonomaceae
Dysphaniaceae
= Amaranthaceae
Ehretiaceae
= Boraginaceae
Ellisiophyllaceae
= Scrophulariaceae
Empetraceae
= Ericaceae
Epacridaceae
= Ericaceae
Eremolepidaceae
= Santalaceae
Eriospermaceae
= Convallariaceae
Erycibaceae
= Convolvulaceae
Erythropalaceae
= Olacaceae
Eucryphiaceae
= Cunoniaceae
Euryalaceae
= Nymphaeaceae
Exocarpaceae
= Santalaceae
Flindersiaceae
= Rutaceae
Foetidiaceae
= Lecythidaceae
Frangulaceae
= Rhamnaceae
Fumariaceae
= Papaveraceae
Funkiaceae
= Agavaceae
Galacaceae
= Diapensiaceae
Geitonoplesiaceae
= Hemerocallidaceae
Geniostomaceae
= Loganiaceae
Geosiridaceae
= Iridaceae
Gisekiaceae
= Phytolaccaceae
Glaucidiaceae
= Ranunculaceae
Globulariaceae
= Plantaginaceae
Goetzeaceae
= Solanaceae
Gonystylaceae
= Thymelaeaceae
Gouaniaceae
= Rhamnaceae
Gramineae
= Poaceae
Gronoviaceae
= Loasaceae
Gustaviaceae
= Lecythidaceae
Guttiferae
= Clusiaceae
Gyrocarpaceae
= Hernandiaceae
Halophilaceae
= Hydrocharitaceae
Halophytaceae
= Amaranthaceae
Hectorellaceae
= Portulacaceae
Heliotropiaceae
= Boraginaceae
Heloniadaceae
= Melanthiaceae
Helosidaceae
= Balanophoraceae
Henriqueziaceae
= Rubiaceae
Hippocastanaceae
= Sapindaceae
Hippocrateaceae
= Celastraceae
Hippuridaceae
= Plantaginaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Hortoniaceae
= Monimiaceae
Hostaceae
= Agavaceae
Humbertiaceae
= Convolvulaceae
Hydrastidaceae
= Ranunculaceae
Hydrocotylaceae
= Araliaceae
Hydropeltidaceae
= Nymphaeaceae
Hydrophyllaceae
= Boraginaceae
Hymenocardiaceae
= Euphorbiaceae
Hypecoaceae
= Papaveraceae
Hypericaceae
= Clusiaceae
Hypseocharitaceae
= Geraniaceae
Idiospermaceae
= Calycanthaceae
Illecebraceae
= Caryophyllaceae
Jasionaceae
= Campanulaceae
Jasminiaceae
= Oleaceae
Johnsoniaceae
= Hemerocallidaceae
Julianiaceae
= Anacardiaceae
Kiggelariaceae
= Flacourtiaceae
Kingdoniaceae
= Circaeasteraceae
Kirengeshomaceae
= Hydrangeaceae
Labiatae
= Lamiaceae
Langsdorffiaceae
= Balanophoraceae
Leeaceae
= Vitaceae
Leguminosae
= Fabaceae
Leitneriaceae
= Simaroubaceae
Lemnaceae
= Araceae
Lennoaceae
= Boraginaceae
Leoniaceae
= Violaceae
Lepuropetalaceae
= Parnassiaceae
Lilaeaceae
= Juncaginaceae
Limoniaceae
= Plumbaginaceae
Liriodendraceae
= Magnoliaceae
Lobeliaceae
= Campanulaceae
Lomandraceae
= Laxmanniaceae
Lophiraceae
= Ochnaceae
Lophophytaceae
= Balanophoraceae
Luxemburgiaceae
= Ochnaceae
Malaceae
= Rosaceae
Martyniaceae
= Pedaliaceae
Mastixiaceae
= Cornaceae
Medeolaceae
= Liliaceae
Meliosmaceae
= Sabiaceae
Mendonciaceae
= Acanthaceae
Mesembryanthemaceae
= Aizoaceae
Mimosaceae
= Fabaceae
Monotaceae
= Dipterocarpaceae
Monotropaceae
= Ericaceae
Mouririaceae
= Memecylaceae
Moutabeaceae
= Polygalaceae
Myriophyllaceae
= Haloragaceae
Mystropetalaceae
= Balanophoraceae
Najadaceae
= Hydrocharitaceae
Nandinaceae
= Berberidaceae
Napoleonaceae
= Lecythidaceae
Naucleaceae
= Rubiaceae
Nectaropetalaceae
= Erythroxylaceae

CLASSIFICATION OF FLOWERING PLANTS (cont'd.)

Nelsoniaceae
= Acanthaceae
Nemacladaceae
= Campanulaceae
Nesogenaceae
= Cyclocheilaceae
Nolanaceae
= Solanaceae
Nolinaceae
= Convallariaceae
Nupharaceae
= Nymphaeaceae
Nyctanthaceae
= Oleaceae
Nyssaceae
= Cornaceae
Octoknemaceae
= Olacaceae
Oftiaceae
= Scrophulariaceae
Ophiopogonaceae
= Convallariaceae
Osyridaceae
= Santalaceae
Pachysandraceae
= Buxaceae
Palmae
= Arecaceae
Papilionaceae
= Fabaceae
Peganaceae
= Nitrariaceae
Pentastemonaceae
= Stemonaceae
Peperomiaceae
= Piperaceae
Periplocaceae
= Apocynaceae
Peripterygiaceae
= Cardiopteridaceae
Petermanniaceae
= Colchicaceae
Petiveriaceae
= Phytolaccaceae
Philadelphaceae
= Hydrangeaceae
Phormiaceae
= Hemerocallidaceae
Phylicaceae
= Rhamnaceae
Picrodendraceae
= Euphorbiaceae
Pinguiculaceae
= Lentibulariaceae
Pistaciaceae
= Anacardiaceae
Pistiaceae
= Araceae
Platystemonaceae
= Papaveraceae
Plumeriaceae
= Apocynaceae
Podoaceae
= Anacardiaceae
Podophyllaceae
= Berberidaceae
Polygonanthaceae
= Anisophylleaceae
Potaliaceae
= Gentianaceae
Ptaeroxylaceae
= Rutaceae
Pteridophyllaceae
= Papaveraceae
Punicaceae
= Lythraceae
Pyrolaceae
= Ericaceae
Ranzaniaceae
= Berberidaceae
Reaumuriaceae
= Tamaricaceae
Retziaceae
= Stilbaceae
Rhinanthaceae
= Orobanchaceae
Rhodoleiaceae
= Hamamelidaceae
Rhopalocarpaceae
= Sphaerosepalaceae
Rhynchothecaceae
= Ledocarpaceae
Roxburghiaceae
= Stemonaceae
Ruscaceae
= Convallariaceae
Saccifoliaceae
= Gentianaceae
Salaciaceae
= Celastraceae
Salicorniaceae
= Amaranthaceae
Salpiglossidaceae
= Solanaceae
Sambucaceae
= Adoxaceae
Samolaceae
= Primulaceae
Saniculaceae
= Apiaceae
Sarcophytaceae
= Balanophoraceae

Classification of Flowering Plants (cont'd.)

Sarcospermataceae
= Sapotaceae
Sargentodoxaceae
= Lardizabalaceae
Saurauiaceae
= Actinidiaceae
Sauvagesiaceae
= Ochnaceae
Scaevolaceae
= Goodeniaceae
Scepaceae
= Euphorbiaceae
Schoepfiaceae
= Olacaceae
Sclerophylacaceae
= Solanaceae
Scoliopaceae
= Liliaceae
Scybaliaceae
= Balanophoraceae
Scytopetalaceae
= Lecythidaceae
Selaginaceae
= Scrophulariaceae
Sesamaceae
= Pedaliaceae
Sesuviaceae
= Aizoaceae
Simethidaceae
= Hemerocallidaceae
Siphonodontaceae
= Celastraceae
Sonneratiaceae
= Lythraceae
Spigeliaceae
= Loganiaceae
Stenomeridaceae
= Dioscoreaceae
Sterculiaceae
= Malvaceae
Stilaginaceae
= Euphorbiaceae
Strychnaceae
= Loganiaceae
Stylobasiaceae
= Surianaceae
Stylocerataceae
= Buxaceae
Symphoremataceae
= Lamiaceae
Syringaceae
= Oleaceae
Tetracentraceae
= Trochodendraceae
Tetradiclidaceae
= Peganaceae
Tetragoniaceae
= Aizoaceae
Tetrastylidiaceae
= Olacaceae
Thalassiaceae
= Hydrocharitaceae
Theligonaceae
= Rubiaceae
Thunbergiaceae
= Acanthaceae
Tiliaceae
= Malvaceae
Trapaceae
= Lythraceae
Trapellaceae
= Pedaliaceae
Tribulaceae
= Zygophyllaceae
Tricyrtidaceae
= Liliaceae
Trilliaceae
= Melanthiaceae
Triplostegiaceae
= Valerianaceae
Uapacaceae
= Euphorbiaceae
Ullucaceae
= Basellaceae
Umbelliferae
= Apiaceae
Utriculariaceae
= Lentibulariaceae
Uvulariaceae
= Colchicaceae
Vacciniaceae
= Ericaceae
Viburnaceae
= Adoxaceae
Viscaceae
= Santalaceae
Viticaceae
= Lamiaceae
Walleriaceae
= Tecophilaeaceae
Wellstediaceae
= Boraginaceae
Xanthophyllaceae
= Polygalaceae
Xerophyllaceae
= Melanthiaceae
Zannichelliaceae
= Potamogetonaceae

TAXONOMY OF THE *PAEONIA DELAVAYI* COMPLEX (PAEONIACEAE)[1]

Hong De-yuan[2], *Pan Kai-yu*[2], *and Yu Hong*[2]

ABSTRACT

The *Paeonia delavayi* complex, a group of woody peonies endemic to China, is problematic because of the lack of agreement among the taxonomic treatments of the group. Some taxonomists recognize one species with three infraspecific taxa, while others accept only two species, and yet others accept three species with two infraspecific taxa. The present paper is based on extensive field observations, population sampling, and analysis of certain characters. The results show that the complex is extremely variable both within and between populations in the number, length, and width of leaf segments and in number, size, and color of all the floral parts. This variation is continuous, and there is no correlation between the characters. Only one species, *P. delavayi*, is recognized, without infraspecific taxa. *Paeonia lutea*, *P. potaninii*, and their infraspecific names are reduced to synonymy of *P. delavayi*. Vegetative reproduction by stolons is predominant in this variable species, and the roots are thickened fusiformly. These two features probably facilitate adaptation to open and somewhat dry habitats, and allow for rapid colonization whenever plants become established. Although *P. delavayi* has been listed as endangered, it is unlikely to become extinct if wanton digging is controlled.

The *Paeonia delavayi* (Paeoniaceae) complex comprises a group of woody peonies endemic to southwestern China. It and other shrubs of the genus *Paeonia* belong to section *Moutan* DC., while the herbaceous members belong to section *Paeonia* and section *Onaepia* Lindl. Members of section *Moutan* are readily distinguished by the following key:

1a. Flowers solitary and terminal, erect.
    2a. Carpels nearly always 5, tomentose, entirely enveloped by floral disk at anthesis .... *P. suffruticosa* complex
    2b. Carpels 2–4(or 5), glabrous, enveloped by floral disk only in the lower half .... *P. decomposita* Hand.-Mazz.
1b. Flowers usually 2 or 3, both terminal and axillary, ± pendent.
    3a. Carpels nearly always solitary; petals, filaments, and stigmas always pure yellow; plants 1.5–3.5 m tall; follicles 4.7–7 × 2–3.3 cm .... *P. ludlowii* (Stern & G. Taylor) D. Y. Hong
    3b. Carpels mostly 2–5(–7); petals, filaments, and stigmas variable in color; plants < 2 m tall; follicles < 4 × 1.5 cm .... *P. delavayi* complex

Four species and numerous infraspecific taxa have been allied with *Paeonia delavayi*. The dark red-flowered *P. delavayi* Franch. and the yellow-flowered *P. lutea* Delavay ex Franch. were both based on collections from Northwest Yunnan [Lijiang (Likiang) and Eryuan, respectively] and were described on the same page (Franchet, 1886: 382). A third species, *P. potaninii* Kom., was described in 1921 based on a specimen from the Yalong Valley in West Sichuan. It has deep maroon-red flowers and was said to differ from *P. delavayi* in having narrower leaf segments, smaller flowers, paler stamen color, and in the absence of the conspicuous involucre, and from *P. lutea* in having much narrower leaf segments, smaller flowers, and deep maroon-red flowers. Stern (1931) added the yellow-flowered *P. trollioides* Stapf ex Stern, based on a specimen from Baima Shan, Deqen County, Northwest Yunnan. In addition, a number of infraspecific taxa have been described, including *P. delavayi* var. *atropurpurea* Schipcz., *P. delavayi* var. *angustiloba* Rehder & E. H. Wilson, *P. delavayi* var. *alba* Bean, and *P. delavayi* var. *lutea* f. *superba* Lemoine.

Paeonia lutea var. *ludlowii* Stern & G. Taylor, described in 1953 from Southeast Xizang (Tibet), has recently been shown by Hong (1997) to be quite different from the remaining taxa of *Paeonia lutea* in a number of characters. It is now recog-

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nized as a distinct species, *P. ludlowii* (Stern & G. Taylor) D. Y. Hong, and has been excluded from the *P. delavayi* complex under study.

Finet and Gagnepain (1904) treated *Paeonia lutea* as *P. delavayi* var. *lutea* (Delavay ex Franch.) Finet & Gagnep. In his monograph of *Paeonia*, Stern (1946) recognized in this complex three species (*P. delavayi*, *P. lutea*, and *P. potaninii*) and reduced *P. trollioides* to a variety of *P. potaninii*. Fang (1958) followed Stern (1946) in the treatment of this complex, but ignored *P. lutea* var. *ludlowii*. Wu (1984) recognized two species, *P. delavayi*, *P. delavayi* var. *angustiloba* (= *P. potaninii*) and *P. lutea*. Gong (1990) also followed Stern (1946) and recognized three with two infraspecific taxa (*P. delavayi*, *P. lutea*, *P. potaninii*, *P. potaninii* var. *trollioides*, and *P. potaninii* f. *alba*). However, Pan (1979, 1993) recognized only *P. delavayi*, with two varieties, var. *lutea* and var. *angustiloba* and ignored (Pan, 1979) *P. lutea* var. *ludlowii*. Obviously, there is a lack of agreement among the taxonomists who have studied this complex. They have variously emphasized the presence of a conspicuous involucre (*P. delavayi*), petal color (dark red or deep maroon-red in *P. delavayi* and *P. potaninii*, yellow in *P. lutea* and *P. potaninii* var. *trollioides*, white in *P. potaninii* f. *alba*), and the width of leaf segments (narrower in *P. potaninii* than in *P. delavayi* and *P. lutea*). The aim of the present paper is to present a revision of this fascinating group of woody peonies based on extensive field observations, population sampling, and analysis of certain characters.

MATERIALS AND METHODS

In order to fully understand the variation of certain characters, especially flower color, presence of an involucre, and width of leaf segments, the first author (alone or with the other two) made five trips to the distribution range of this group. The first (in 1988) and second (1993) were to the West Hill of Kunming; the third to West Sichuan (1995), including Yajiang County, the type locality of both *P. potaninii* and *P. delavayi* var. *angustiloba*; the fourth to Southeast Xizang (1996), including the type locality of *P. lutea* var. *ludlowii*; and the fifth to Northwest Yunnan (1997), including the type localities of *P. delavayi*, *P. lutea*, and *P. trollioides*. In addition to the critical examination of all morphological characters and their variation, biological features (e.g., seed set, presence or absence of cloning) were also recorded.

Eighteen populations were studied in the field by the first author (alone or with the other two), and vouchers are deposited in PE, A, CAS, K, MO, and US. The populations studied are vouchered by the following herbarium specimens (collection numbers of Hong): *H97077*, *H97078*, *H97087*, *H97095*, *H97102*, *H97103*, *H97108*, *H97112*, *H97119*, and *H97128* (from Yunnan); *H95063*, *H95070*, *H95074*, and *H97110* (from Sichuan); and *H96003*, *H96019*, *H96024*, and *H96028*. In addition, hundreds of other herbarium specimens from CPB, E, KUN, PE, WU, and XZ were studied morphologically.

Figure 1. Vegetative reproduction by stolon in the *Paeonia delavayi* complex (population *H97112*).

OBSERVATIONS AND DISCUSSION

Plants of the *Paeonia delavayi* complex are always dwarf shrubs. The tallest plants (ca. 1.8 m) were found in Yunshanping in Lijiang, Northwest Yunnan (population *H97103*), where they grew in *Picea likiangensis* forest at an altitude of ca. 3200 m. By contrast, the shortest plants (rarely reaching 1 m) were found in Ganghaizi, Lijiang (*H97095*), a population only about 20 km southeast of the first population, and grew in dry, sparse *Pinus densata*–*Quercus gilliana* forest. Many short individuals had underground woody parts, and only current-season shoots were aboveground. Plants of the other populations that we studied were intermediate between these two.

Vegetative reproduction is probably predominant in the *Paeonia delavayi* complex, and seedlings are very rarely found in the field. It is even more predominant at the northwestern and northern boundaries of the distribution range. In Yajiang County, West Sichuan, a population (*H95070*) was found near a village, where it was represented by some individuals growing by fences and on newly stabilized debris. In this population, only about 50% of the follicles were developed and, because of insect damage, only 20% had seeds. Cloning by stolons, however, was common. Based on an examination of

Figure 2. Fusiform roots and vegetative reproduction by stolon in the *Paeonia delavayi* complex (population *H97112*).

all follicles in the spring of 1996, the five populations observed in Tibet in 1995 produced no seeds. No follicles were observed in a population (temple ruins in Xituan village of the Gengzhanglungba valley, Nyingchi County, Tibet) that consisted of numerous individuals and occupied an area of about 250 m^2. This "population" probably consisted of individuals produced through cloning. Cloning was found in every population visited (Figs. 1, 2). The production of fusiform, thickened roots is characteristic of the *Paeonia delavayi* complex (Fig. 2).

Although leaves in the *Paeonia delavayi* complex are always biternate, the leaf segments are quite variable in number, length, and width. The number of segments ranged widely from 17 to 312 (Fig. 3), and seemed to differ between populations. For example, the number varied from 17 to 49 in population *H96024*, and from 68 to 312 in population *H95063*. However, the standard deviation of the variation in leaf segment number (Fig. 3) shows that these two populations were just the extremes of a wide variation that was also observed within given populations. Taking all the populations into consideration, the number of segments varied continuously in the complex.

Paeonia potaninii was described as new because it was considered to have narrower leaf segments than *P. delavayi* and *P. lutea*. However, we observed that the width of leaf segments varies greatly, and ranges from 0.4 to 2.86 cm within the complex, and from 0.76 to 1.83 cm in population *H95070*, the type locality of *P. potaninii*, which falls in the middle of the overall variation range in the complex (Fig. 4). The same situation was found for the length of leaf segments. Therefore, it is evident that *P. potaninii* is rather similar to *P. delavayi* and *P. lutea* in this regard.

Stern (1946) distinguished *Paeonia delavayi* within the complex by the presence of a conspicuous involucre immediately below the calyx. However, in the whole genus it is difficult to distinguish clearly between the bracts and sepals, and there is

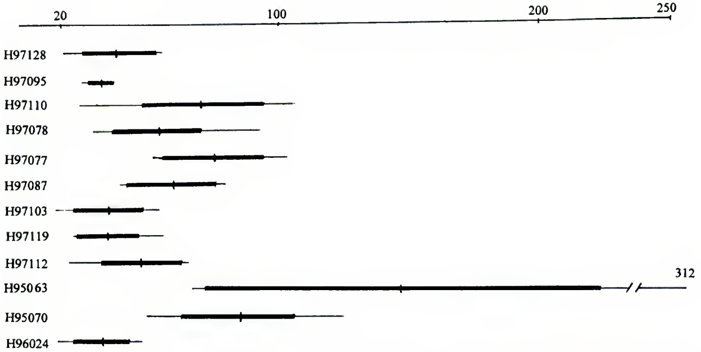

Figure 3. Variation of leaf-segment number both within and between populations in the *Paeonia delavayi* complex. Vertical line is mean, and thickened horizontal line is standard deviation. Localities of populations are: *H97128* (Zhongdian, Yunnan), *H97095* (Lijiang, Yunnan), *H97110* (Yanyuan, Sichuan), *H97078* (Chenggong, Yunnan), *H97077* (Kunming, Yunnan), *H97087* (Cang Shan, Yunnan), *H97103* (Lijiang, Yunnan), *H97119* (Deqen, Yunnan), *H97112* (Zhongdian, Yunnan), *H95063* (Dawu, Sichuan), *H95070* (Yajiang, Sichuan), and *H96024* (Bomi, Tibet).

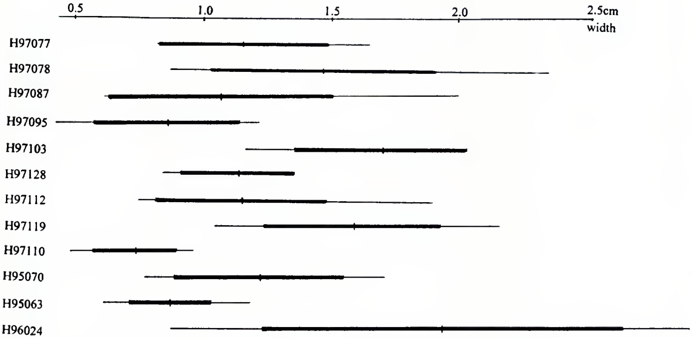

Figure 4. Variation of leaf-segment width both within and between populations in the *Paeonia delavayi* complex. Vertical line is mean, and thickened horizontal line is standard deviation. Localities of populations are: *H97077* (Kunming, Yunnan), *H97078* (Chenggong, Yunnan), *H97087* (Cang Shan, Yunnan), *H97095* (Lijiang, Yunnan), *H97103* (Lijiang, Yunnan), *H97128* (Zhongdian, Yunnan), *H97112* (Zhongdian, Yunnan), *H97119* (Deqen, Yunnan), *H97110* (Yanyuan, Sichuan), *H95070* (Yajiang, Sichuan), *H95063* (Dawu, Sichuan), and *H96024* (Bomi, Tibet).

a gradation between leaves and bracts as well. We designate the laminae that are borne some distance below the flowers as leaves, while those at the top of shoots and immediately below the calyx are bracts. Bracts, so designated, have various forms, ranging from segmented and leaflike to entire and sepal-like. The sepals have a much broader proximal part and a dark green, smaller, and narrower distal part with a mucronate or rounded apex. The total number of bracts and sepals varied greatly both within and between populations of the *Paeonia delavayi* complex. Population *H97103* (with dark red flowers) at Yunshanping, Lijiang, the type locality of *P. delavayi* (Stern, 1946), indeed had the highest number (10 or 11) of bracts and sepals forming the so-called "conspicuous involucre," while the other populations observed had fewer bracts and sepals. However, the difference was not distinct (Table 1). Population *H97095*, only about 20 km from *H97103*, was very variable in the number of both bracts and sepals, and some flowers had 10 or 11 bracts and sepals (Plate 1, vii), just as those in population *H97103*. Population *H97087* had the same total number of bracts and sepals, and its petals were pure yellow or yellow with a dark red spot at the base. Table 1 and the remarks above show clearly that there is continuous variation in the number of bracts and sepals, and no correlation between petal color and the total number of bracts and sepals. Therefore, *P. delavayi* is not distinct from the other putative taxa in the complex under study.

Variation in the number and color of floral parts involves the sepals, which vary in color both within a flower and within populations (Table 2). They are usually green, but sometimes dark red or purple (Plate 1, vii, viii; Table 2). In addition, they vary greatly in size both within and between populations, and the variation is continuous (Fig. 5). Although the population *H97103* had larger sepals than the other populations, the formation of a "conspicuous involucre" (Stern, 1946) was not unique in the complex, as alleged.

Petal color has been much emphasized in the taxonomy of the *Paeonia delavayi* complex, and was used by various authors in distinguishing *P. lutea* (yellow) from *P. delavayi* (dark red). As shown in Table 2, however, petal color is extremely variable between and within populations (Plate 1, i–vi). In populations *H97112* and *H97128*, various petal colors could be found, and a few individuals in the latter population had white petals. On the basis of the literature and our own observations, red, dark red, or dark purple-red petals occurred in the northeastern part of the distribution range, while yellow petals or yellow petals with a dark red spot at the base were found in the northwestern, western, and southern parts. For example, populations in Southwest Sichuan (Dawu, Yajiang, Muli, Yanyuan) and Northwest Yunnan (Lijiang and Ning-

Table 1. Variation of bract and sepal number in the *Paeonia delavayi* complex.

Population and locality	Petal color	Bract #	Sepal #	Total bract and sepal #	Note
H97077, West Hill, Kunming	yellow	4	3 or 4	7 or 8	no bracts segmented
H97078, Mt. Liangwang, Cheng-Gong Co.	yellow	4	3	7	no bracts segmented
H97087, Huadianba, Cang Shan, Dali	yellow	4 or 5	6	10 or 11	no bracts segmented
H97095, Ganghaizhi, Lijiang	red to dark red	2, 4, or 5	4 to 6	6 or 8–11	some flowers with 2-segmented bracts
H97103, Yunshanping, Lijiang	dark red	2 to 4	7 to 9	10 or 11	most flowers with one 3- or 4-segmented bract
H97112, Hala village, Zhongdian	yellow, orange, to dark red	1 to 3	2 to 5	3, 5, 6, or 8	no bracts segmented
H97128, Gezha Township, Zhongdian	white to red	1, 3, or 5	2 to 5	5 to 8	only one flower with one 3-segmented bract

lang), here designated as the "red region," had red petals, while those in Southeast Tibet (Nyingchi, Bomi, Zayu), Northwest Yunnan (Deqen and Gongshan), and Yunnan (Weixi, Eryuan, Dali, Chenggong, and Kunming), here designated as the "yellow region," had yellow petals with a red spot at base, pure yellow petals, and petals either yellow or yellow with a dark red spot at the base, respectively. Therefore, petal color shows a weak geographical differentiation, but it would be unwise to accord formal recognition to the populations in these two "regions" because petal color is uncorrelated with other characters and is very variable within a given "region" or population. The most pronounced petal-color variation occurred in populations *H97119* and *H97078* of the "yellow region," and some specimens with yellow flowers (e.g., *Rock 16110*, *Rock 161576*, *Kingdon-Ward 4043*, *Forrest 12565*, and *McLaren 89*, all at E) were also found within the "red region." Furthermore, petal color was extremely variable in populations such as *H97112*, *H97128*, both from Northwest Yunnan.

Petal number in the *Paeonia delavayi* complex varied enormously, and ranged from 4 to 13, but it also varied greatly within populations. For example, petals were 4–7 or 10 in population *H97119*, and 8, 10, 11, or 13 in *H97087*.

Stamen number and color were also very variable. In population *H97112* the number varied from 25 to 128. The filaments were yellow, pale red, red, or dark red, and the anthers were yellow, orange, red, or purple in populations *H97077*, *H97078*, *H97087*, *H97095*, *H97103*, *H97110*, and *H97112* (Plate 1, viii). But in the populations *H97119* and *H97128*, both filaments and anthers were yellow even in flowers with red petals. The color of the filaments and anthers was not always correlated with that of the petals, although flowers with red petals usually had red or purple filaments and anthers. We conclude that the characters of the androecium cannot be used for dividing this complex.

Unlike the nectar disk of the other woody peonies of section *Moutan*, the disk in the *Paeonia delavayi* complex is generally short and fleshy. In populations *H97112* and *H97119*, the disk secreted abundant nectar in some flowers, and it seems likely that the secretion made these flowers more scented. The disk (including teeth) varied in height from 1 to 3 mm, and in color from pale yellow or yellow to red, even within a single population (e.g., *H97112*). Therefore, the characters of the disk are of little, if any, importance taxonomically in this complex.

The gynoecium also varied greatly in the *Paeon-*

Plate 1. Variation of floral parts in the *Paeonia delavayi* complex: —i (top row, left). White flower (population *H97128*). —ii (top row, middle). Green-yellow flower (population *H97077*). —iii (top row, right). Orange flower (population *H97112*). —iv (middle row, left). Red flower (population *H97103*). —v (middle row, middle). Variation in flower color (population *H97112*). —vi (middle row, right). Variation in flower color (population *H97128*). —vii (bottom row, left). Variation in number and color of bracts and sepals (population *H97095*). —viii (bottom row, middle). Color variation of sepals, filaments, anthers, disk, and stigmas (population *H97112*). —ix (bottom row, right). Variation in number and color of carpels (population *H97095*).

Table 2. Variation of floral parts in the *Paeonia delavayi* complex.

Population	Locality	Sepal color	Petal #	Petal color	Stamen #	Filament color	Anther color	Disc color	Pistil #	Ovary color	Stigma color
H96019	Nyingchi town, Tibet	green	10	yellow with a red basal spot	ca. 110	purple-red	yellow	yellow	2 to 4	green, purple on 1 side	pale yellow
H96020	Guxiang township Bomi, Tibet	green		yellow with a red basal spot		purple-red	yellow	yellow	2 or 3	green	pale yellow
H97077	West Hill, Kunming, Yunnan	green	8 to 11	green-yellow, yellow, yellow with a purple-red basal spot	ca. 120	purple-red	yellow	yellow	2 or 3	green	pale yellow
H97078	Mt. Liangwang, Chenggong, Yunnan	green	8 or 9	green-yellow, yellow, mostly yellow with a purple-red basal spot	ca. 125	purple-red	yellow	yellow	2 or 3	green	pale yellow
H97087	Cang Shan, Dali, Yunnan	green	8, 10, 11, or 13	yellow, yellow with a pale red or purple-red basal spot	120–160	yellow, pale red, purple-red	yellow	yellow	2 to 5	green	pale yellow
H97095	Ganghaizhi, Lijiang, Yunnan	green, purple	8 to 11	red with yellow periphery, red, purple-red, dark purple-red	80 to 120	red, purple-red	red, purple-red	purple-red	2 to 4	green, purple	purple-red
H97103	Yunshanping, Lijiang, Yunnan	green with pale red base inside	10 to 13	red, dark red, with a yellow spot in center or back side	150 to 160	purple-red	purple-red	dark red	3 to 6	green	red
H97112	Hala village, 23 km W of Zhongdian town, Yunnan	green, purple-red	5 to 11	yellow, yellow with a red basal spot, orange, red, dark red	25 to 128	yellow, red, dark red	yellow, pale red, red	green-yellow, red, yellow	2 or 3	green	yellow-green, red
H97119	3 km W of Susong village, Benzilan, Deqen, Yunnan	green	4 to 7, 10	yellow, orange-yellow	ca. 110	yellow	yellow	yellow	2 to 4	green	green, yellow-green
H97128	Wengshui, 48 km N of Zhongdian, Yunnan	purple-red	5 to 8	white, yellow, yellow with a red part at base or above, red	80 to 100	yellow, red	yellow	yellow	2 to 5	green	yellow-green, yellow, red
H97110	E of Lugu Lake, Yanyuan, Sichuan	green, purple-red	5 to 7	red, purple-red	80 to 100	red	yellow	green, purple-red	2 or 3	green, purple-red	red

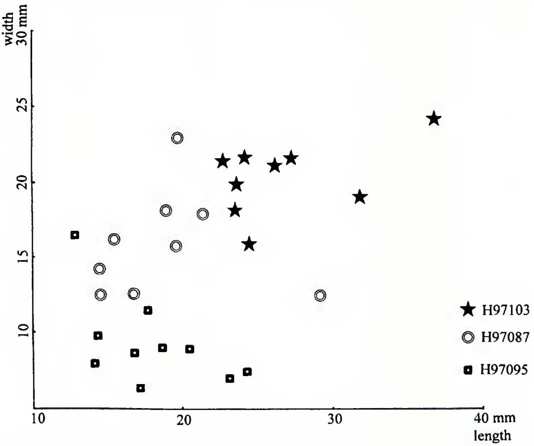

Figure 5. Variation of sepal size both within and between populations in the *Paeonia delavayi* complex. Populations *H97103* and *H97095* from Lijiang (Yunnan), and *H97087* from Cang Shan (Yunnan).

ia delavayi complex. Pistil (carpel) number was usually 2–4 in most of the populations studied, but in population *H97103* it was mostly 5 and very rarely 3, 4, or even 6, and in one collection, *Dai, Li & Tang 64–4* (CPB), it ranged from 4 to 8. This variation in pistil number was found in every population observed (Plate 1, ix; Table 2). The pistils were usually green, with a pale green, yellow, or red stigma, but some individuals in populations *H97095, H97103, H97112, H97110,* and *H97128* had entirely purple pistils (Plate 1, viii, ix). Although characters of the gynoecium are generally regarded as significant in the taxonomy of angiosperms, our observations show that they are insignificant taxonomically in this complex.

In summary, the *Paeonia delavayi* complex exhibits tremendous and continuous variation in characters of the leaves (number, length, and width of segments), bracts (number), and floral parts (color and number). Except for the very weak correlation between petal color and geography, the variation in these characters is clearly insignificant taxonomically. Therefore, none of these characters can be considered as justifying the subdivision of this complex, which we thus consider as comprising only one species, without infraspecific taxa.

TAXONOMIC TREATMENT

Paeonia delavayi Franch., Bull. Soc. Bot. France 33: 382. 1886. TYPE: China. NW Yunnan: Lijiang (Likiang), *Delavay 1142* (holotype, P; isotype, K).

Paeonia lutea Delavay ex Franch., Bull. Soc. Bot. France 33: 382. 1886. *Paeonia delavayi* var. *lutea* (Delavay ex Franch.) Finet & Gagnep., Bull. Soc. Bot. France 51: 524. 1904. TYPE: China. NW Yunnan: Eryuan County, Mt. Hea Chan Men, 25 May 1883, *Delavay s.n.* (lectotype, here designated, P; isolectotype, K).

Paeonia potaninii Kom., Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 7. 1921. TYPE: China. W Sichuan: Yajiang (Tachien-lu district in Yalung valley), *Potanin s.n.* (holotype, LE).

Paeonia trollioides Stapf ex Stern, J. Roy. Hort. Soc. 56: 77. 1931. *Paeonia potaninii* var. *trollioides* (Stapf ex Stern) Stern, Stud. *Paeonia* 50. 1946. TYPE: China. NW Yunnan: Deqen, Baima Shan, Mekong-Yangtse divide, 11,000 ft., open stony pastures, *Forrest 13195* (holotype, E).

Paeonia delavayi var. *lutea* f. *superba* Lemoine, Rev. Hort. 14: cum tab., 1906. *Paeonia lutea* var. *superba* (Lemoine) hort. ex Gard. Chron., Ser. 3. 44: 50, cum tab., 1908. TYPE: ["pl. 14 in Lemoine, Rev. Hort. 1906"].

Paeonia delavayi var. *angustiloba* Rehder & E. H. Wilson, in Sarg., Pl. Wilson. 1: 318. 1913. TYPE: China. W Sichuan: Yajiang (W of Tachien-lu, descent to Yalung river), 3000–3600 m, Oct. 1908, *Wilson 1333* (holotype, A).

Paeonia delavayi var. *atropurpurea* Schipcz., Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 47. 1921. TYPE: China. No locality given (holotype, ?LE).

Paeonia delavayi var. *alba* Bean, Trees Shrubs 3: 265. 1933. *Paeonia potaninii* f. *alba* (Bean) Stern, Stud. *Paeonia* 49. 1946. TYPE: "t. 49 in Stern, Stud. *Paeonia*, 1946" (holotype).

Shrubs 0.2–1.8 m tall, glabrous throughout. Petioles 10–15 cm long; lowermost 2 (or 3) leaves biternate, these best developed and with the most leaflets and segments, other leaves becoming smaller upward and with fewer leaflets and segments. Leaflets first divided into 3–11 primary segments, these divided again mostly to near base or lobed halfway into 2–11 secondary segments or lobes, thus each leaf with (17–)25–100(–312) segments or lobes; leaves ovate in outline, 15–30 cm long (excl. petiole), 10–22 cm wide; petiolules of middle primary divisions 5–9 cm long, petiolules of lateral primary divisions 1–3 cm long, petiolules of secondary divisions much shorter; segments or lobes linear, linear-lanceolate, entire or only occasionally dentate, 0.5–10 × 0.2–2.7 cm. Flowers 1–3 on a shoot, terminal and axillary, ± pendulous, maturing basipetally. Bracts 1–5, gradually differentiated from the upper leaves and hardly distinguished from the sepals, the outer ones 2–4-segmented, green. Sepals 2–9, green outside, green with a pink base inside, or entirely purple or purple-red, rounded or triangular-rounded, acuminate or mucronate to rounded at apex, 1.3–3.7 × 0.6–2.3 cm. Petals (4–)7–11(–13), yellow, yellow with a red or purple-red basal spot, red, dark red, or dark purple-red, sometimes white, orange, green-yellow, or yellow with red margin. Stamens 25–160; filaments yellow, pink, red, or dark purple-red; anthers yellow, pink, red, or dark purple-red. Disks short, annular or short-cylindric, 1–3 mm high, dentate, green, yellowish, yellow, red, or dark red. Carpels 2–4, very rarely 6–8; ovary usually green, sometimes purple; stigma yellow-green, yellow, red, or purple-red; ovules 7–17 per carpel. Follicles oblong-ovoid, 2–3.5 × 1–1.5 cm, brown at maturity. Seeds 1–6 in each follicle, brown-black.

Distribution. Endemic to China and restricted to Sichuan, Tibet (Xizang), and Yunnan. *Paeonia delavayi* grows at 2000–3600 m, primarily in sparse thickets or dry *Pinus* and *Quercus* woods, or rarely in grassy slopes or glades of virgin *Picea* forests (Fig. 6).

Phenology. Flowering from mid May to mid June; fruit maturing August. $2n = 10$ (Gong et al., 1991).

Additional specimens examined (all from CHINA). **SICHUAN. Batang**: Zongza Township, *Anonymous 1547* (PE), by Jinsan River, *Li & Xu 64–43* (CPB); East District, Yanrigong Township, *Li & Xu 64–38* (CPB); Zangqenrong, *Li & Xu 64–47* (CPB); Baisong Township, *Li & Xu 64–48* (CPB). **Daocheng**: Dongnyi, Gawa Township, Kasishe, *Daocheng Division 2397* (PE). **Dawu**: Mazi Township, Benglong village, *Hong, Luo & He H95063* (A, K, MO, PE, US); *Dai, Li & Tang 64–4* (CPB); Qiangning, Ochancun, *Dai, Li & Tang 64–27* (CPB). **Huidong**: Baisanpo, Paomaping, *Li, Li & Xu 64–9* (CPB). **Huili**: Xiacun, Heilaoling, *Qiu, Zhu, Deng & Shi 66–023* (CPB). **Mianning**: Jinping Shan, *Z. M. Xu 64–27* (CPB); Luning District, Xiamatou Shan, *Z. M. Xu 64–30* (CPB). **Muli**: mountains of Kopati, Diago & Muli, *Rock 16157* (E); mountains between Muli and Kulu, *Rock 24123* (E); W of Muli, Mt. Mitzuga, *Rock 16110* (E); no precise locality, *Kingdon-Ward 4043* (E); Yalientsa, in valleys, *T. T. Yü 14147* (PE); Chaiwu, *T. T. Yü 5560* (PE); Wachin, *T. T. Yü 6003* (PE); Luobo Township, near the ferry, *S. Jiang 5708* (PE); Baidiao Township, Shangjiamiwan, *Li, Xu & Tang 64–17* (CPB); Boao, *Li, Xu & Tang 64–11* (CPB); Boao, Shuzu village, *Li, Xu & Tang 64–19* (CPB), *64–20* (CPB); Zhuao Township, Aoxia village, *Li & Xu 64–26* (CPB). **Xiangcheng**: Qingda, *L. D. Sheng 64–113* (CPB). **Yajiang**: Niri Township, Bajiaolou, *Hong, Luo & He H95070* (A, K, MO, PE, US); ca. 5 km E of Yajiang Town, *Hong, Luo & He H95074* (PE); no precise locality, *Li & Xu 64–64* (CPB). **Yanbien**: Yanshi Township to Jiudao Zhuling, *Qinghai-Xizang Exped. 11458* (PE). **Yanyuan**: Zuosuo Township, by Lugu Lake, *Hong, Pan, Yu & Dai H97110* (A, CAS, K, MO, PE, US); Zuosuo Township, near Shanjiacun, *Dai, Li & Tang 64–6* (CPB); Zuosuo District, *Dai, Li & Tang 64–1*(CPB); Yantang, Dacaoxiang, Nancaowan, *Dai, Li & Tang 64–7* (CPB); Shangjiagou, *Dai, Li & Tang 64–17* (CPB); E of Yongning (Yunnan), 27°50′N, 100°56′E, *Forrest 20458* (E); Lumapu, 27°37′N, *Handel-Mazzetti 2067* (E, WU). **TIBET (Xizang). Bomi**: Guxiang Township, *Ying & Hong 39* (PE), *214* (PE), *Hong, Luo & Zhang H96024* (A, K, MO, PE, US); between Zamu & Guxiang, *Zhang & Lang 379* (PE); near Zamu, behind Army Station, *Xiao, Xia & Mi 2233* (KUN, PE); Sumzom Township, Sumzom, S of River, *Hong, Luo & Zhang H96028* (A, K, MO, PE, US). **Markam**: Cawarong, Chaila, *C. W. Wang 66335* (PE); Cawarong, Dula, *C. W. Wang 65523* (PE); Cawalong, Songta Snow Mountain, *Qinghai-Xizang Exped. 7633* (KUN, PE); E Himalayas, no precise locality, *Kingdon-Ward 5691* (E). **Nyingchi**: by Nyingchi Town, *Hong, Luo & Zhang H96019* (A, K, MO, PE, US); Gengzhang Nongba Valley, Xituan Village, Hong, *Luo & Zhang H96003* (A, K, MO, PE, US); Bayi Town, Jiaomugou, *Hong, Luo & Zhang H96004* (A, K, MO, PE, US). **Zayu**: Gujing District, *Xizang Biol. Inst. Pl. Resources Exped. 3895* (XZ), near Guyu to Cinong, *Qinghai-Xizang Exped. 73–294* (PE); Gujing District, Ni, Wang, *Cidou & Cidan 1501* (PE, XZ); no precise locality, *Ludlow & Sherriff 1376* (E). **YUNNAN. Chenggong**: Mt. Liangwan, *Hong, Pan, Yu & Dai H97078* (A, CAS, K, MO, PE, US). **Dali**: Mt. Cangshan, Huadianba, *Hong, Pan, Yu & Dai H97087* (A, CAS, K, MO, PE, US), *R. C. Ching 22954* (KUN, PE), *Sino-British Cangshan Exped. 0684* (E, KUN), Xiaohuadianba, *Q. Ling 7708* (KUN); no precise locality, *T. N. Liou 16149* (KUN, PE), *T. N. Liou 20677* (KUN, PE), *McLaren 55* (E); E flank of the Cangshan range, *Forrest 4352* (E), *6787* (E), *30998* (E); Mt. Pi-iou-se, above Tapintze, 11 June 1883, *Delavay s.n.* (P); Tali (Dali), Mt. Che-tcho-tze, 9 May 1883, *Delavay s.n.* (P); Tali (Dali), Mt. Che-tcho-tze, 10 Oct. 1883, *Delavay s.n.* (P). **Deqen**: Benzilan, 3 km W of Susong village, *Hong, Pan, Yu &*

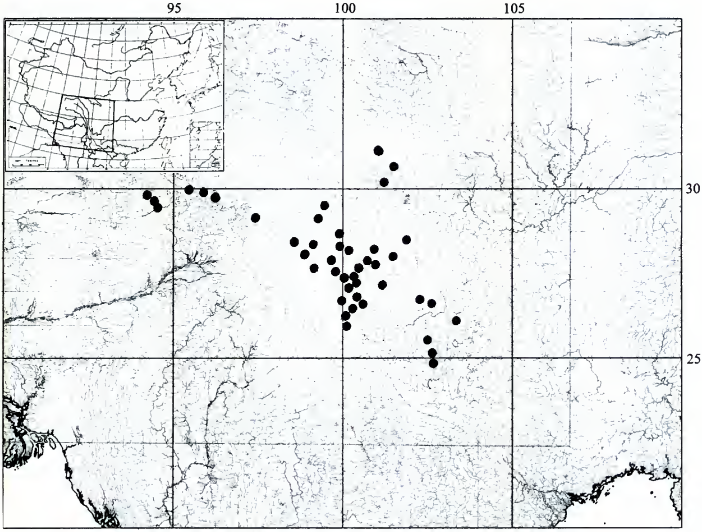

Figure 6. Distribution of *Paeonia delavayi.*

Dai H97119 (A, CAS, K, MO, PE, US); Cizhong to Yongzi, by the Lancang River, *K. M. Feng 5765* (KUN, PE); Yunling, *Nanshui Beidiao Exped. 9194* (KUN, PE); E flank of Baima Shan, Benzilan, *Qinghai-Xizang Exped. 11795* (KUN, PE); Benzilan, Yonglobu (Forest Farm), *Qinghai-Xizang Exped. 1878* (KUN, PE); Benzilan, Dongzuling, *Qinghai-Xizang Exped. 2209* (KUN, PE); no precise locality, *C. W. Wang 70211* (KUN, PE); Baima Shan, *Rock 22821* (E). **Dongchuan**: Jinniu, *D. C. Liu 0447* (CPB); Mt. Lo Shivel, *McLaren V2* (E). **Gongshan**: Suroula, *C. W. Wang 66617* (KUN, PE); Mekong-Salwin divide, 28°12′N, *Forrest 16339* (E), *Forrest 16527* (E). **Heqing**: Laugkong-Hoching divide, 26°16′N, *Forrest 10062* (E); Baiya, Sanxi, *R. C. Ching 24365* (KUN, PE); Songgui, Mt. Maer, *R. C. Ching 24191* (KUN, PE). **Jianchuan**: Xinsheng Township, Huajiaping, *P. Y. Mao 236* (KUN). **Kunming**: Shanqing temple to Shitoushan, *Liou 20677* (PE); West Hill, *Hong, Pan, Yu & Dai H97077* (A, CAS, K, MO, PE, US), *B. Y. Qiu 51019* (KUN), *B. Y. Qiu 57101* (KUN); Seventh District, Shungxiao Township, *B. Y. Qiu 51880* (KUN); Longquan District, Heping Township, *S. K. Wu 8* (KUN). **Lanping**: No. 104 Forest Farm, West Hill of Xiaoyanjing, *Hengduan Mt. Exped. 908* (PE). **Lijiang**: Yulong Snow Range, Ganghaizi, *Hong, Pan, Yu & Dai H97095* (A, CAS, K, MO, PE, US), *Qinghai-Xizang Exped. 201* (PE), *Edinburgh Bot. Gard. Exped. 85–6* (E, KUN), *R. C. Ching 20438* (KUN, PE), *Z. W. Lu 1002* (KUN), *Kingdon-Ward 238* (E); Yulong Snow Range, Muzhugou to Ganghaizi, *X. Zhou 1030* (KUN), Qingmugou to Ganghaizi, *Lijiang Bot. Gard. 100486* (KUN); Yulong Snow Range, *Yunnan Univ. Biol. Dept. Vegetation Exped. 233* (KUN), *R. C. Ching 30987* (KUN, PE); Yulong Snow Range, Yuhu, Xuesong Village, Mt. Beibazi, *R. C. Ching 30175* (KUN, PE), *K. M. Feng 21245* (KUN), E of the village, *R. C. Ching 30071* (KUN, PE); near Yuhu, Ameidiruo, *K. M. Feng 22229* (KUN); Yulong Snow Range, Wutoudi, *K. M. Feng 23029* (KUN, PE); Yulong Snow Range, Baishui, *Hong, Pan, Yu & Dai H97102* (A, CAS, K, MO, PE, US); Yulong Snow Range, Yunshanping, *Hong, Pan, Yu & Dai H97103* (A, CAS, K, MI, PE, US); Yulong Snow Range, Mahuangba to Wutoudi, *Z. H. Yang & Y. C. Cai 101777* (PE); Yulong Snow Range, Jiuzihai to Yulong Snow Range, Heishui, *J. S. Yang 4157* (KUN); Heishui River, left slope, *Lijiang Bot. Gard. 100026* (KUN); Yulong Snow Range, Mt. Gyina Loko, *Rock 24984* (E); E flank of Yulong Snow Range, *Forrest 5716* (E), *T. T. Yü 15016* (E, PE); Mt. Wenbi, *T. T. Yü 8107* (KUN, PE); northern Part, Hongshiyan, *R. C. Ching 20595* (KUN, PE); Shapingze, *T. T. Yü 5160* (KUN, PE), *T. T. Yü 5163* (KUN, PE); Sixth District, *X. L. Wang s.n.* (CPB); Zili, by the river, *R. C. Ching 22192* (KUN, PE); S of Lijiang, Sungkwe Pass between Lijiang & Heqing, *Rock 25179* (E); 22 km from Lijiang to Yongsheng, *Hong, Pan, Yu & Dai H97108* (PE). **Luquan**: Xinming Township, Laoyingya, *P. Y. Mao 939* (KUN); Emao Township, Mt. Dangan, *P. Y. Mao 01565* (KUN). **Ninglang**: Gouzuandong, *J. S. Yang 4123* (KUN); Yongning, Geao Pass, *J. S. Yang 4130* (KUN); hills around Yongning, *Forrest 12503* (E), *12565* (E); Yongning, Shize Shan, *T. T. Yü* (PE); Yongning, Wenquan Township, near Wenquan, *Dai, Li & Tang 64–2*

(CPB), Liujiashe, *Dai, Li & Tang 64–3* (CPB); *Dai, Li & Tang 64–4* (CPB); E of the Yangtze bend, 27°35′N, 100°45′E, *Kingdon-Ward 3981* (E); no precise locality, *McLaren 5* (E), *89* (E), *Kingdon-Ward 5055* (E). **Weixi**: Yezhi, by Lancang (Mekong) River, *K. M. Feng 4220* (KUN, PE); Yezi, *C. W. Wang 68199* (PE); Yangtze-Mekong divide, 29°45′N, *Handel-Mazzetti 8868* (E, WU); Pantiange District, Wucun village, *D. Y. Chen s.n.* (CPB). **Yongsheng**: Shunzhou District, Shisanzuo, *J. S. Yang 4402* (CPB). **Zhongdian**: 23 km NW of Zhongdian Town, Hala village, *Hong, Pan, Yu & Dai H97112* (A, CAS, K, MO, PE, US); 45 km N of Zhongdian Town, Gezan Township, *Hong, Pan, Yu, Dai H97128* (A, CAS, K, MO, PE, US); Wucun, Gongbi, *K. M. Feng 23561* (KUN, PE); Zhongdian to Annachang, *K. M. Feng 938* (KUN, PE); Tuguancun to Haba Xuemenkang, *Zhongdian Exped. 63–2389* (KUN, PE); Haba, Longwang Binsanba, *Zhongdian Exped. 63–2738* (KUN, PE); Huangdong, Reshuitang, *Zhongdian Exped. 63–2597* (KUN, PE); Qiaotou to Xiaozhongdian, near Hongtu xiao, *K. M. Feng 885* (KUN, PE); Haba to Xiaozhongdian, *K. M. Feng 1387* (KUN, PE); Baidi, *T. T. Yü 11389* (KUN, PE); *T. T. Yü 14915* (PE); Tuguancun, *Zhongdian Exped. 63–2375* (KUN, PE); Haba, Annazai, *Zhongdian Exped. 63–2647* (KUN, PE); Haba, near Longwanbin, *Zhongdian Exped. 1634* (KUN, PE); SE of Zhongdian Town, Jiuluo, *Zhongdian Exped. 929* (KUN, PE); no precise locality, 27°50′N, *Forrest 15162* (E); Haba Shan, N of the Yangtze loop, *Rock 24758* (E); no precise locality, 27°30′N, *Forrest 12561*(E); Chihren, *T. T. Yü 11247* (E, PE); N of Zhongdian Town, Tonwa Territory, *Rock 24717* (E).

Paeonia delavayi has the widest geographical range of any member of section *Moutan* (Fig. 6). The plants reproduce predominantly vegetatively, and cloning by stolons (Fig. 1) was commonly seen in every population visited except for population *H97103*, in *Picea likiangensis* forest in Yunshanping Lijiang, Yunnan. Vegetative reproduction is particularly prominent in West Sichuan (Dawu, Yajiang) and Southeast Tibet, where seedlings have never been found and clones often covered large areas. The roots of *P. delavayi* are always fusiformly thickened (Fig. 2). Such roots and stolons probably make the species more adapted to open, somewhat dry and disturbed habitats, and enable the species to become established very rapidly in a given population. It may also account for the scattered distribution of the species and the large number of "individuals" in a given population. *Paeonia delavayi* has been listed as an endangered species in the *China Plant Red Data Book* (Feng, 1992). On the basis of its vegetative reproduction and relatively wide distribution, however, it is reasonable to conclude that it will not become extinct if wanton digging is controlled.

Paeonia delavayi is most closely related to *P. ludlowii*, from which it is readily distinguished by having predominantly vegetative reproduction by stolons and fusiform roots, a non-caespitose habit, stems 0.2–1.8 m tall, segmented leaves with narrow and acute segments, variously colored floral parts (petals, stamens, disk, and stigmas), a 2–8-pistillate gynoecium, and small (2–3.5 × 1–1.5 cm) follicles rarely producing seeds. In contrast, *P. ludlowii* is obligately sexual, without stolons, and has slender, terete roots, a caespitose base forming a large clump with dozens of stems, stems 2–3.5 m tall, lobed leaves with short and acuminate lobes, uniformly yellow floral parts (petals, stamens, disk, and stigmas), a 1(or very rarely 2)-pistillate gynoecium, and larger (4.7–7 × 2–3.3 cm) follicles always bearing seeds. In fact, *P. delavayi* and *P. ludlowii* are better considered as members of two separate species complexes.

Literature Cited

Fang, W.-P. 1958. Notes on Chinese paeonies. Acta Phytotax. Sin. 7: 297–323.

Feng, K.-M. 1992. *Paeonia delavayi* Franch. var. *lutea* (Delavayi ex Franch.) Finet & Gagnep. Pp. 530–531 *in* L.-K. Fu & J. M. Jin (editors), China Plant Red Data Book, Vol. 1. Science Press, Beijing.

Finet, M. M. & F. Gagnepain. 1904. Contributions à la Flore de L'Asie Orientale. Bull. Soc. Bot. France 51: 524–525.

Franchet, A. 1886. Plantas yunnanensis. Bull. Soc. Bot. France 33: 358–467.

Gong, X. 1990. A Taxonomical Study of the *Paeonia delavayi* complex. Master's Thesis, Kunming Institute of Botany.

Gong, X., Z. J. Gu & Q. A. Wu. 1991. A cytological study of seven populations in *Paeonia delavayi* var. *lutea*. Acta Bot. Yunnan. 13: 402–410.

Hong, D.-Y. 1997. *Paeonia* (Paeoniaceae) in Xizang (Tibet). Novon 7: 156–161.

Pan, K.-Y. 1979. *Paeonia*. *In:* W.-T. Wang (editor), Fl. Reipubl. Popularis Sin. 27: 37–59. Science Press, Beijing.

———. 1993. Paeoniaceae. Pp. 545–546 *in* W.-T. Wang & S.-G. Wu (editors), Vascular Plants of the Hengduan Mountains. Science Press, Beijing.

Stern, F. C. 1931. Paeony species. J. Roy. Hort. Soc. 56: 71–77.

———. 1946. A Study of the Genus *Paeonia*. Royal Horticultural Society, London.

——— & G. Taylor. 1953. *Paeonia lutea* var. *ludlowii*. Bot. Mag. 169: tab. 209.

Wu, C. Y. (Editor). 1984. Index florae yunnanensis. 1: 122–123. The People's Publishing House, Kunming, China.

A CLADISTIC ANALYSIS OF SPECIES GROUPS IN *WEINMANNIA* (CUNONIACEAE) BASED ON MORPHOLOGY AND INFLORESCENCE ARCHITECTURE[1]

Jason C. Bradford[2]

Abstract

Weinmannia (Cunoniaceae) is a woody genus of about 150 species widely distributed in the tropics and the southern temperate zone. Herbarium and living specimens were examined to determine characters for a cladistic analysis to test the monophyly of the genus and its sections. A matrix of 28 taxa and 31 morphological characters was analyzed to find the most parsimonious trees. The strict consensus cladogram supports the monophyly of the genus *Weinmannia* and sections *Leiospermum*, *Weinmannia* (including sect. *Simplicifolia*), *Inspersa*, and *Spicata*, but section *Fasciculata* is paraphyletic with respect to a highly derived section *Weinmannia*. Section *Leiospermum* from the South Pacific is the sister taxon to the rest of the genus. Some of the most parsimonious trees support a monophyletic clade from Madagascar of sections *Inspersa* and *Spicata*, but this node is unresolved in the strict consensus tree. Although the deep nodes of the phylogeny are not well supported, and few evolutionary interpretations are ventured, it appears that dioecy has arisen independently at least three times in the genus. The method and theory used to analyze variation in inflorescence architecture, which emerges from the metameric construction of plants and positional homology, are emphasized. The cladistic coding of positional characters and the tracing of their evolution on the cladogram are a study in heterotopy, i.e., evolutionary change in the position of development. Heterotopic evolution in the inflorescence is common in *Weinmannia*, suggesting a role for an evolutionary-developmental process that has typically been overlooked in favor of heterochrony.

Systematic Background

Weinmannia is a genus of canopy trees and shrubs common to montane tropical and southern temperate floras. With approximately 150 species, it is the largest genus in the Cunoniaceae, a morphologically diverse family that includes 27 genera and ca. 370 species. The family has been considered a distinct, isolated lineage within the Rosidae (Dickison & Rutishauser, 1990) that is morphologically recognized by its woody habit, usually interpetiolar stipules, toothed leaves, and decussate leaf arrangement (Hufford & Dickison, 1992). A cladistic analysis using morphological and anatomical characters (Hufford & Dickison, 1992) supports the monophyly of the Cunoniaceae only when a few genera that have been treated as separate but related families are included (*Bauera*, *Brunellia*, *Eucryphia*). However, Orozco (1997) advocated splitting the family to exclude *Brunellia* and its putative Cunoniaceae relatives. *Davidsonia* may also belong in a monophyletic Cunoniaceae (Doweld, 1998). Hufford and Dickison's (1992) consensus cladogram placed *Weinmannia* in a small clade with *Cunonia* and *Pancheria*, which was nested among a large, monophyletic group of genera characterized by the presence of a stylar canal and a fused, bicarpellate ovary.

The Cunoniaceae are austral in distribution: 15 of the genera occur in Australia and Tasmania, 9 in New Guinea, 11 in the South Pacific, and

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only 5 (3 endemic) in South America. Like the Cunoniaceae in general, the present-day distribution of *Weinmannia* suggests a Gondwanaland origin (Raven & Axelrod, 1974). *Weinmannia* is widespread relative to other genera in the family, and its distribution includes the following geographic regions: Central and South America and the Caribbean islands; Madagascar, the Comores, and the Mascarenes; Malesia (the Malay Peninsula, Greater and Lesser Sundas, the Philippines, Celebes, Moluccas, New Guinea, and the Bismarck Archipelago); and the South Pacific high-elevation islands, from the Solomons and Vanuatu in the west to the Societies and Marquesas in the east, including New Caledonia and New Zealand. About half of the species occur in tropical America, a quarter are concentrated in Madagascar, and another quarter are distributed in the vast Malesian-Pacific region.

Sympatric species of *Weinmannia* are common in middle- to upper-elevation montane forests of the Andes and Madagascar (Humbert & Darne, 1965; Ríos, 1986; Kelly et al., 1994; Gentry, 1995). Species can have radically distinct life forms that correspond to local habitats. For example, at upper elevations, especially in exposed, windswept conditions, *Weinmannia* species are typically small, sometimes prostrate shrubs, whereas in eastern Madagascar some species are among the largest trees in the lowlands. *Weinmannia* is not as locally species-rich in Malesia and the Pacific, but species are often locally abundant in this region, especially in the Society Islands (Florence, 1982; Fosberg, 1992) and New Zealand (Wardle & MacRae, 1966). The genus typically has small, fragrant flowers that attract bees (Renner, 1989; Bradford, pers. obs.), and small, hairy seeds easily dispersed by wind (J. Bradford & H. C. F. Hopkins, pers. obs.).

Engler's (1928) revision of *Weinmannia* divided the genus into two sections, section *Leiospermum* and section *Euweinmannia*, based upon variation in the persistence of the calyx in fruit. Bernardi (1961, 1963b, 1964) incorporated variation in the form of the floral nectary, raceme structure, and leaf complexity to recognize six sections: section *Racemosa*, which corresponds to Engler's section *Leiospermum* and has caducous sepals, and five other sections corresponding to Engler's section *Euweinmannia*. [*Euweinmannia* is an illegal name (see Greuter et al., 1994, Article 21.3) and is no longer used.] In general, the classification of Bernardi is followed, although it is recognized that Engler's section *Leiospermum* has priority over Bernardi's section *Racemosae*. Also, Bernardi's section *Simplicifoliae* has been sunk into section *Weinmannia*. Section *Simplicifoliae* separates species with simple leaves from the compound-leaved species in section *Weinmannia* and appears to have been erected by Bernardi for taxonomic convenience. However, the number of leaflets often varies within individuals, is extremely homoplastic among species, and, therefore, has little taxonomic value at the sectional level. Previous and current classifications are compared in Table 1.

Table 1. A comparison of previous sectional classifications of *Weinmannia* vs. the one used here.

Bradford (present paper)	Bernardi (1961, 1963b, 1964)	Engler (1928)
Leiospermum	*Racemosae*	*Leiospermum*
Weinmannia	*Weinmanniae*	*Euweinmannia*
Weinmannia	*Simplicifoliae*	*Euweinmannia*
Fasciculata	*Fasciculatae*	*Euweinmannia*
Spicata	*Spicatae*	*Euweinmannia*
Inspersa	*Inspersae*	*Euweinmannia*

PURPOSE

Recent systematic studies of *Weinmannia* have identified more characters than were used by Bernardi (1961, 1963b, 1964) to circumscribe sections. Many new characters, especially from inflorescence architecture, are described here. Thirty-one qualitative characters are used in a cladistic analysis to resolve these systematic questions: (1) Is *Weinmannia* monophyletic? (2) Are the sections monophyletic? (3) How are sections related to each other? and (4) What morphological character states support each clade?

Answers to these questions may help interpret biogeographic and character-distribution patterns. For example, a dioecious to polygamodioecious breeding system is nearly ubiquitous in the Malesian section *Fasciculata*, among most species of the South Pacific section *Leiospermum*, and in the Mascarene island species of section *Weinmannia*. An understanding of whether dioecy is derived or basal within the genus and the number of times it has evolved depends upon the relationships inferred among taxa. Because most sectional delimitations are congruent with particular geographic regions (e.g., sects. *Inspersa* and *Spicata* are endemic to Madagascar and the Comores), the cladistic relationships among species groups of *Weinmannia* may inform us about area relationships among southern continents.

To understand the cladistic coding and the evolution of the inflorescence in *Weinmannia*, it is necessary to describe inflorescence characters in detail, and to discuss the methods and theory behind determinations of homology. Three points are emphasized: (1) the inflorescence is formed by the spatial arrangement of nested sets of parts, (2) the coding of inflorescence characters usually requires an assessment of positional homology (at least for this study), and (3) evolutionary change in the position of inflorescence units is a form of heterotopy.

OVERVIEW OF INFLORESCENCE ARCHITECTURE IN *WEINMANNIA*

An attempt to apply general inflorescence terminology, such as that of Briggs and Johnson (1979) and Weberling (1989), was not satisfactory. Structural definitions only approximate many inflorescence features of *Weinmannia*, or terms cannot be applied consistently among species. In a later section, I discuss why standard terminology does not work in *Weinmannia*, especially when the goal is identifying cladistic characters. But first, the terminology used here to describe *Weinmannia* inflorescences is introduced.

Following the system of Briggs and Johnson (1979), flower-bearing axes in *Weinmannia* and *Cunonia* can precisely be called "anauxotelic botrya," which includes forms of "spikes" and "pseudoracemes." To avoid these cumbersome terms in all subsequent discussion, the term "raceme" is used broadly to include any unbranched, flower-bearing axis. The terms Inflorescence Module (IM) and Total Inflorescence (TI) will refer to two other distinct levels of organization. Architectural variation in the *Weinmannia* inflorescence occurs at up to three hierarchical levels: (1) the organization of flowers along a "raceme," (2) the development of racemes in conjunction with supporting stems and buds (IM), and (3) the position these raceme-stem units occupy in relation to the main stem axis (TI).

Flowers vary in their organization along the raceme in two ways: (1) how they are initiated and (2) whether their relative positions change during axis elongation (Fig. 1). Flowers are initiated solitarily or grouped, in the axil of a bract. During elongation of the raceme axis, flowers may remain in the axil of the bract or move away from it and each other. Differences in the positional relationships among flowers give distinct forms to the raceme.

In most sections, racemes usually develop as parts of developmentally integrated units (modules) composed of internodes, nodes, meristems, and racemes. Within a species-group, raceme-stem units are organized predictably and may be repeated along the main stem axis in predictable patterns (Fig. 2). Each of these raceme-stem units will be referred to as an Inflorescence Module (IM). The term "module" has had more or less precise usage (see White, 1979; Grimes, 1992; Barlow, 1994). Here it refers to a particular level of organization, or integration of a group of metamers, to form a natural structural unit (Wagner, 1996). Of course higher and lower levels of organization, such as the raceme, are modules, but may already have useful names. The IM is at an intermediate level of organization, above the raceme but below the entire inflorescence. Within a locally dominant stem system, the structure of the racemes, the organization of racemes into an IM, and the arrangement of IMs along the main axis constitute the Total Inflorescence (TI).

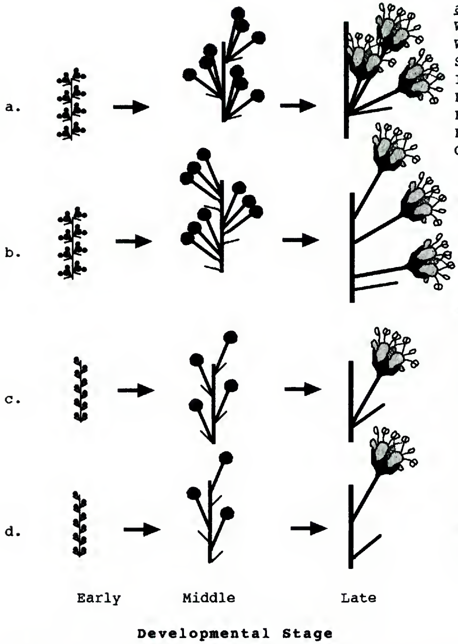
DESCRIPTION OF INFLORESCENCE ARCHITECTURES IN *WEINMANNIA*

Inflorescence architecture is taxonomically informative and may help identify an entire section, or a portion of a section, or distinguish a single species from other members of its section. Variation occurs in: (1) whether racemes develop as part of an IM or directly along the main stem axis, (2) the form of the IM, (3) the number of main stem metamers that bear racemes or IMs, and (4) the position of IMs relative to the main stem axis. There are 17 terminal taxa of *Weinmannia* in the data matrix (Appendix 4). When variation within the raceme (i.e., that shown in Fig. 1) is ignored, there are about 11 distinct inflorescence architectures among taxa, which are described below.

(A) Twelve of 18 species in section *Fasciculata* have supernumerary lateral buds that develop into lateral IMs in series at a node (e.g., *W. fraxinea*). These IMs each consist of one metamer with an opposite pair of racemes and a vegetative bud between them. The apical meristem of the main stem axis usually remains vegetative, although vegetative growth is usually suspended during reproduction. The TI is acrotonic in that the distal node of the TI usually has more IMs per series than occur at subdistal nodes (Fig. 3a).

(B) Most other members of section *Fasciculata* have similar IM morphology, but do not develop IMs in a series at a node. Also, while it is rare for IMs to form in medial positions in the *W. fraxinea* group, this is common in some other species in the section (Fig. 2b).

(C) *Weinmannia descombesiana* has a highly variable inflorescence architecture that may appear most similar to that of the *W. fraxinea* group (Fig. 3a) or other members of section *Fasciculata* (Fig. 2b).



a.
WEI-pinnata
WEI-tinctoria
SPI-comorensis
INS-venusta
FAC-fraxinea (b. form also)
FAC-pullei
FAC-clemensiae
Cunonia pulchella

b.
SPI-icacifolia
INS-madagascariensis
FAC-fraxinea (a. form also)

c.
INS-rutenbergii
LEI-serrata
LEI-affinis
LEI-sylvicola
LEI-racemosa
Cunonia-macrophylla
Cunonia-purpurea
Cunonia-aoupiniensis
Cunonia-balansae
Cunonia bullata
Cunonia-alticola

d.
SPI-bojeriana
INS-louveliana

Figure 1. The distribution of flowers along a "raceme" is determined by the number of flowers initiated in the axil of a bract and whether the flowers remain in the axil as the axis elongates: —a. Fasciculate inception + bract fidelity. —b. Fasciculate inception + floral migration. —c. Solitary inception + bract fidelity. —d. Solitary inception + floral migration. Parts not necessarily to scale and only a portion of the axis is shown. The adjoining table lists each *Weinmannia* and *Cunonia* OTU in the cladistic analysis with its raceme form. Flowers are sessile in section *Spicata* (SPI). See discussion of characters 19 and 20 (Appendix 3) and the character matrix (Appendix 4).

(D) Nearly half the species in the genus are in section *Weinmannia*, which can be recognized by its unique inflorescences. In this section, the inflorescence is limited to a pair of racemes developing from axillary buds at the most distal node of the main stem (Fig. 2c). There is no IM in this group and much variation in the suppression of leaf development at the node bearing the racemes. Within individual plants leaves may be fully developed at the raceme-bearing node or extremely reduced.

(E) About 20 species in section *Leiospermum* have a characteristic inflorescence in which the apical meristem within an IM either develops into a raceme or aborts. In many species this is fixed one way or the other [e.g., the bud almost always aborts in *W. dichotoma* (Fig. 3b)], but in several species this character varies within individual plants. Also typical of this section is that the IM may consist of sequentially arranged metamers with long internodes. The position of the IMs along the main stem is both lateral and terminal. The TI is acrotonic, with the terminal IM often developing more metamers than the laterals (Fig. 2a). Leaf development is suppressed within the IM, but generally less so at nodes proximal to the main stem when the IM consists of sequential metamers.

(F) Two species endemic to New Zealand have distinctive inflorescences. *Weinmannia sylvicola* is similar to *W. dichotoma* in that the IMs terminate with an aborted meristem, but differs in that the

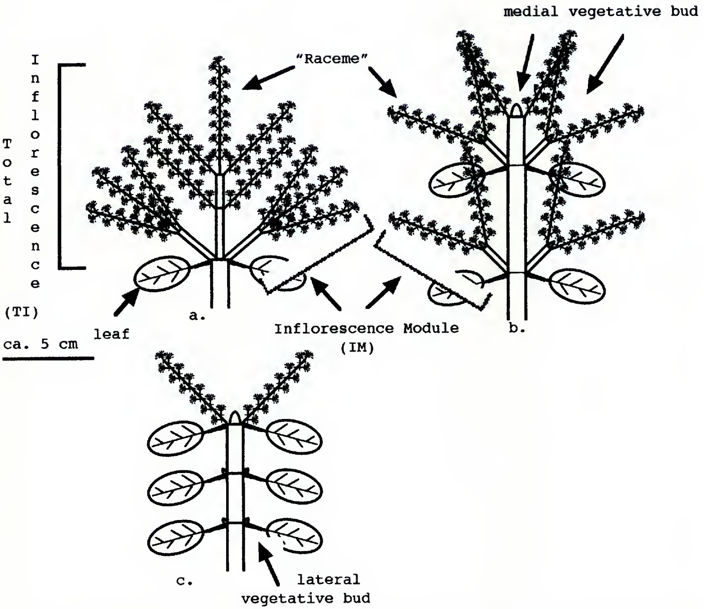


Figure 2. Diagram of inflorescence terms and examples of inflorescence architecture in *Weinmannia.* —a. Section *Leiospermum,* with IMs potentially consisting of sequential metamers, terminating with a raceme, and positioned laterally and medially. —b. Parts of sections *Inspersa, Spicata,* and *Fasciculata,* with IMs of one metamer, terminating with a vegetative bud, and borne medially and laterally at distal and subdistal nodes. —c. Section *Weinmannia,* with racemes borne laterally at vegetative nodes. See text for more complete descriptions of architectural variation within species groups, as not all patterns are shown. Actual leaves may be simple or compound. Although the figures are in two dimensions, the actual arrangement is decussate.

medial IM often produces two metamers. Also, there is usually only one lateral IM (Fig. 3c).

(G) The other New Zealand species, *Weinmannia racemosa,* is unique within section *Leiospermum* in that the IM does not terminate in a raceme or abort, but produces a vegetative bud (Fig. 9b). This is the only species within the section in which vegetative growth continues beyond the inflorescence. Furthermore, the IM is only borne in a medial position. A more detailed discussion of the inflorescence in sections *Fasciculata* and *Leiospermum* is given in Hopkins and Bradford (in Hopkins, 1998a).

(H) Most species in the two Madagascan sections, *Inspersa* and *Spicata,* have similar inflorescences. About 22 species in section *Spicata* and 5 species in section *Inspersa* have IMs consisting of one metamer with an opposite pair of racemes and a vegetative bud between them. These IMs may be positioned laterally at both distal and subdistal nodes along the main stem, as well as medially at the distal node. Racemes can also develop directly from axillary buds, but only at the most distal node of the TI (Fig. 2b).

(I) Five species in section *Spicata* (two of which, *W. comorensis* and *W. baehniana,* were placed in sect. *Leiospermum* by Bernardi, 1964) develop racemes from axillary buds along the main stem at sequential nodes (Fig. 3d).

(J) *Weinmannia rutenbergii* (not illustrated) in section *Inspersa* has extremely plastic inflorescence development. IMs may be of one or more metamers, sometimes branched but usually not, and may ter-

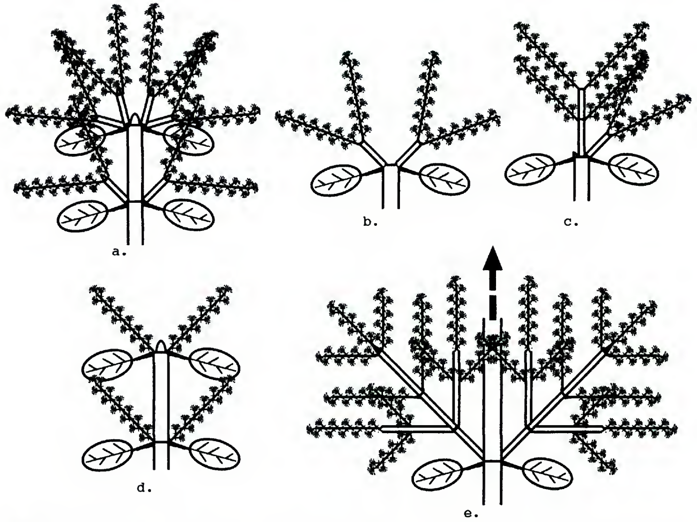


Figure 3. Examples of inflorescence architecture among *Weinmannia* species groups. —a. *W. fraxinea* (sect. *Fasciculata*). —b. *W. dichotoma* (sect. *Leiospermum*). —c. *W. sylvicola* (sect. *Leiospermum*). —d. *W. comorensis* (sect. *Spicata*). —e. *W. venusta* (sect. *Inspersa*). Note that b and c have aborted terminal meristems in the IM. See text for full descriptions.

minate in a bud or a raceme. When reproduction is prolific, IMs develop at several nodes and may vary in form within a TI. In general, larger IMs develop from lower nodes. *Weinmannia hepaticarum,* known only from the type collection, appears to be closely related to *W. rutenbergii,* but its inflorescence variability is unknown. Bernardi (1964, 1965) placed *W. rutenbergii* in section *Weinmannia.*

(K) Two species in section *Inspersa, W. venusta* and *W. sp. nov. 1,* have branched IMs that bear racemes. The length of these racemes is variable within an IM. The IM may terminate either in a raceme or in a vegetative bud. The position of IMs along the main stem may be lateral and medial. The TI is basitonic, with the largest IMs developing at lower nodes (one of the variants is shown in Fig. 3e and includes only a subdistal node of the TI). Bernardi (1964, 1965) placed *W. venusta* in section *Weinmannia.*

Most species in the closely related genus *Cunonia* have an inflorescence architecture similar to that depicted in Figure 9c, but often with IMs at two successive nodes of the TI. However, several species diverge from this pattern (see illustrations in Hoogland et al., 1997, and coding in character matrix, Appendix 4).

The photos in Plate 1 show some common forms of the inflorescence among *Weinmannia* sections. Additional color plates will be available from the World Wide Web by searching the species name in W^{3}TROPICOS at http://www.mobot.org.

The Use of Inflorescence Architecture in Cladistics

The hierarchy of inflorescence architecture and its systematic importance have been recognized in diverse groups (Venkata Rao, 1965; Mabberley, 1975; Weberling, 1977; Briggs & Johnson, 1979; Kaul & Abbe, 1984; Tucker, 1987; Weber, 1988; Weberling, 1988; Schlessman et al., 1990; Grimes, 1992; Liede & Weberling, 1995; Tortosa et al., 1996; Timonen, 1998). While many studies have proposed pathways of inflorescence evolution based on comparative morphology and development, few have used cladistic methodology to do so.

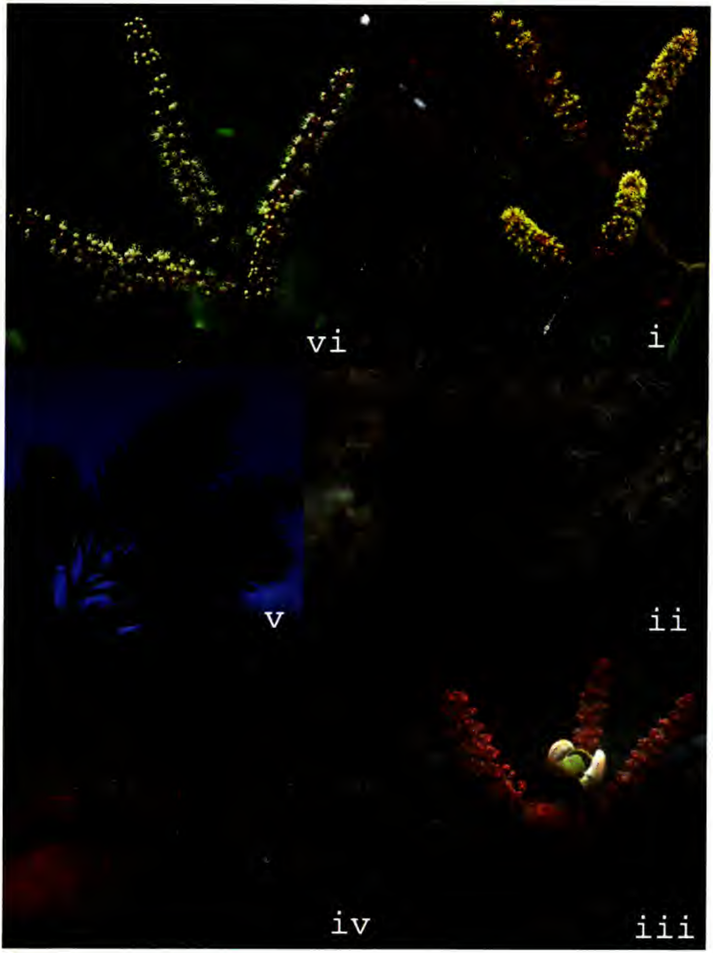


Plate 1. Photos documenting *Weinmannia* inflorescence architecture illustrated in Figures 2, 3, and 9. —i. Section *Weinmannia; W. dryadifolia* (*J. C. Bradford 160*); compare with Figure 2c. ii, iii, Section *Fasciculata.* —ii. *W. fraxinea* (*J. C. Bradford 830*); compare with Figure 3a. —iii. *W. clemensiae* (*H. F. Hopkins 5011*); compare with Figure 9c. —iv. Section *Spicata*; *W. stenostachya* (*J. C. Bradford 650*); compare with Figure 2b. v, vi, Section *Leiospermum.* —v. *W. sylvicola* (*J. C. Bradford 732*); compare with Figure 3c. —vi. *W. parviflora* (*J. C. Bradford 919*); compare with Figure 9a.

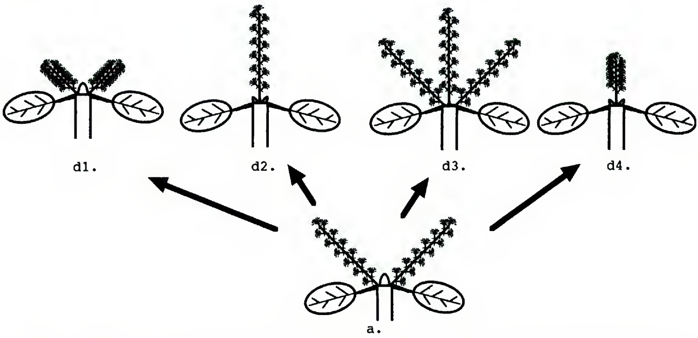


Figure 4. Morphological evolution occurs through temporal and spatial modification of development. As shown here, the ancestor (a) has racemes developing from the leaf axils. The descendants (d1–d4) are heterochronic, heterotopic, or both. —d1. Heterochronic, paedomorphic form in which the raceme axes are constricted. —d2. Heterotopic form in which the racemes develop from the terminal bud and not the axillary ones. —d3. Heterotopic form in which the racemes develop in their plesiomorphic, axillary position, and from a new position, at the terminus. —d4. Heterochronic and heterotopic form. Heterotopy is recognized by changes in the relative position of parts (d2, d3), not just quantitative shifts that are probably heterochronic (d1).

Although inflorescence architecture is diverse in many taxa, cladists may have avoided inflorescence characters because of difficulties in assessing homology. Progress came when Grimes (1992) analyzed the inflorescence of the *Pithecellobium*-complex by breaking it into nested, repeated units. Similarly, *Weinmannia* inflorescences have nested components and, in order to identify cladistic characters, the relative positions of parts within each component can be compared. Recognizing positional homology is the key to coding inflorescence characters. As a consequence of recognizing positional homologies, evolutionary changes in the positions at which parts develop, i.e., heterotopy (Haeckel, 1905; Gould, 1977; Sattler, 1988), can be inferred by tracing character transformations on the phylogeny. Therefore, this work advances a view of evolutionary development that recognizes both temporal and spatial transformation (see also Zelditch & Fink, 1996).

HETEROTOPY: DOES IT HAPPEN?

While it is well accepted that heterochrony causes the modification of form (Jong & Burtt, 1975; Gould, 1977; Raff & Wray, 1989; Kellogg, 1990; Boughton et al., 1991; McKinney & McNamara, 1991), positional changes in development have often been either ignored or considered byproducts of underlying heterochrony (see discussions in Raff, 1996; Zelditch & Fink, 1996). Heterotopic patterns are recognized by qualitative shifts in the positional relationships among parts, not just quantitative changes in relative distances among parts, which may often be due to heterochrony (Fig. 4).

For example, reproductive structures can shift from lateral to terminal positions, or from distal branches to the trunk. A possible outcome may be the evolution of monocarpy from polycarpy, or changes in how flowers are pollinated and fruit is dispersed. Distinct inflorescence modules that develop either male or female flowers are common in monoecious breeding systems [e.g., pistillate vs. staminate spikes in *Quercus* (Kaul & Abbe, 1984), and in corn]. Once male and female modules are established, they can be expressed at separate positions within the plant, which may have functional benefits.

Even though heterotopy has been mostly overlooked by evolutionary biologists, some obvious (and bizarre) examples of morphological changes in plants appear to be purely heterotopic. These include: the switch in position of leaves and lateral buds in *Utricularia* (Sattler, 1994); the positional reversal of stamens and carpels in *Lacandonia schismatica* (Martínez & Ramos, 1989); and epiphyllous inflorescences (Dickinson & Sattler, 1974, 1975).

Plant morphologists have long accepted that spatial and temporal changes in development contribute to morphological evolution. For example, heterotopy has also been called "translocation" (Leavitt, 1905) and "phylogenetic shifting" (including homeosis, Zimmermann, 1961). In discussing the "morphogenetic" basis of plant form, Sachs (1982) suggested that mutations affecting gene regulation could change the spatial and temporal expression of developmental processes to account for morphological evolution. This notion is supported by developmental-genetic studies that show how sets of genes, especially ones encoding transcription factors (Sommer et al., 1990; Yanofsky et al., 1990), act to establish the position in which an organ will form (Bradley et al., 1997; Meyerowitz, 1997). Sattler (1988) discussed how both heterochrony and heterotopy are related to homeosis. The potential for heterotopy is also embodied in Sattler's term "homotopy," referring to homology of position (Sattler, 1994).

Taken together, the data from systematists, plant morphologists, and plant molecular biologists show that heterotopy is widespread among plants. This provides the conceptual and empirical framework on which positional homologies of inflorescence architecture are here coded.

MATERIALS AND METHODS

SAMPLING METHODS

Except for recent work by H. C. F. Hopkins (1998a–c; Hopkins & Florence, 1998) in the Malesian-Pacific region, *Weinmannia* has not been revised at the species-level since Bernardi (1961, 1963b, 1964, 1965). Numerous recent collections show that many currently recognized taxa are poorly circumscribed. Sampling of specimens was done to cover the distribution of phylogenetically informative characters independently of previous species circumscriptions or determinations. For this reason, some taxa recognized as varieties of the same species by previous authors are members of different terminal taxa in this analysis. Because there will be changes in nomenclature and new species descriptions, both specific names and a set of specimens examined are listed in Appendix 1.

My goal was to examine at least one specimen of each species of *Weinmannia*. The lack of a recent treatment of Malagasy and American species made sampling more uncertain in these areas. Data come from field studies in tropical America, Madagascar, Malaysia, and the South Pacific, and examination of herbarium specimens primarily at the Laboratoire de Phanérogamie in Paris (P) and the Missouri Botanical Garden (MO). Type material was available for nearly all species from Madagascar and the Malesian-Pacific region. Several American species are known only from type specimens that were not available, but most of the characters used in this analysis were at least seen in illustrations or photos. Furthermore, the Neotropics are well represented by recent collections at MO and F, and I have collected extensively in the region. Species sampling of *Cunonia* relied on the taxonomy of R. Hoogland and his unpublished monograph of the genus at P. This study has revealed several undescribed species, each of which can be placed in an Operational Taxonomic Unit (OTU) with at least one described species.

Many inflorescence characters are coded based on developmental potential, which is fixed in some taxa but variable in others (e.g., see discussion of character 23, Appendix 3; description of *W. rutenbergii*, inflorescence J). To accurately code these taxa, groups with greater complexity and variety of inflorescence architecture, such as section *Leiospermum*, were sampled more intensively than those with less, such as section *Weinmannia*. Poorly represented species that are not known for all of their characteristics (e.g., of which fruits have never been collected) could be provisionally placed into an OTU, since an intact inflorescence with either flowers or fruits is sufficient to discriminate among the OTUs.

The observed morphological characteristics of hundreds of specimens were managed in two ways. Sketches and notes of specimens were made, and descriptive information on specimens was entered into a computerized database. The database fields were used to search for unique combinations of character states among species, and characters were reconfirmed by checking sketches and by repeated specimen examination. The OTUs in the cladistic analysis were circumscribed according to the possession of unique combinations of character states for the current character matrix. If an OTU was polymorphic for a character, it was due to polymorphism within some species of that OTU.

Identifying OTUs by unique combinations of characters could yield paraphyletic OTUs. Therefore, each ingroup OTU was studied for potential autapomorphies, which are listed in Appendix 2. Most OTUs were arguably monophyletic, but a few were not. A separate cladistic analysis was run that removed the following OTUs to see if their absence affected the tree topology: FAC-descombesiana (possible hybrid taxon), FAC-clemensiae, SPI-icacifolia, INS-madagascariensis, LEI-serrata, Cunonia-purpurea.

CHOICE OF OUTGROUPS

The character matrix and cladograms of Hufford and Dickison (1992) were used to choose outgroups. All outgroups were part of the large clade that includes *Weinmannia.* Two of them, *Caldcluvia paniculata* and *Spiraeopsis celebica,* were considered useful because they apparently lack many derived floral, inflorescence, or fruit characters that would make comparison with *Weinmannia* difficult. Within the Cunoniaceae, *Spiraeopsis* (with 6 species) has the autapomorphy of stellate pubescence on the leaves, but no obvious autapomorphies exist for the monotypic *Caldcluvia* s. str. (Hufford & Dickison, 1992). Within this data set, *Caldcluvia paniculata* is unique in possessing four stipules per node, as opposed to two stipules per node in other taxa (Dickison & Rutishauser, 1990).

In Hufford and Dickison's (1992) analysis, the position of the monotypic *Vesselowskya* was poorly resolved, but in some trees this was the sister taxon of the *Cunonia*(*Pancheria–Weinmannia*) clade and, therefore, was included here. However, their matrix had some incorrect scoring of characters in *Vesselowskya,* which has palmately compound leaves, flowers borne in racemes, and valvate sepals. These traits suggest a close relationship between *Vesselowskya* and the *Lamanonia*/*Geissois–Pseudoweinmannia* clade, rather than the *Cunonia*(*Pancheria–Weinmannia*) clade. The *Lamanonia*/*Geissois–Pseudoweinmannia* clade has two features shared with *Cunonia* and *Weinmannnia*: a racemose floral axis and a fused vascular bundle between the fruit carpels, the latter not included by Hufford and Dickison (1992). Possible autapomorphies for *Vesselowskya* are its 3-merous perianth and androecium, and its decurrent stigmas.

Ackama rosifolia was examined because this genus (with 3 species) is the only one in the Cunoniaceae other than *Weinmannia* with hairy seeds. However, for these hairs to be homologous with those of *Weinmannia* would require that *Ackama* be the sister taxon to *Weinmannia,* adding five steps to the shortest trees of Hufford and Dickison (1992). In fact, *Ackama* shares some possibly derived leaf trichome and domatium features with *Spiraeopsis.*

The monophyly of *Weinmannia* with respect to *Cunonia* was tested by treating *Cunonia* as part of the ingroup. *Pancheria* was excluded because its many derived floral and inflorescence features (Hufford & Dickison, 1992) make it difficult to recognize corresponding structures in *Weinmannia.* For example, *Pancheria* has whorled phyllotaxy, flowers arranged in spherical heads, unisexual flowers with a reduced number of parts, and an apocarpous gynoecium. In contrast, *Weinmannia* and *Cunonia* have similar floral structures and inflorescences composed of racemes. Including *Pancheria* in an analysis with *Weinmannia* and *Cunonia* would require that many characters be scored as inapplicable in *Pancheria,* and vice versa. Therefore, despite the possibility that *Pancheria* is the sister genus to *Weinmannia,* it was not useful to include it in a morphological analysis at this level.

CODING OF CHARACTERS

Because phylogenetic studies attempt to discover relationships at different hierarchical levels, characters that vary within one set of taxa may be inapplicable in other taxa (what Pleijel, 1995, termed "hierarchical dependence"). Other coding problems may arise when there is non-independence of characters due to developmental or functional coupling. For example, stem architecture may be coded separately from inflorescence architecture, although one may influence the other. The scoring of "complex characters" has generated some recent discussion (Pleijel, 1995; Wilkinson, 1995), which has recognized the different assumptions and tradeoffs in different coding methods. For example, multistate coding may reduce the problem of non-independence among characters, but may compound problems of inapplicable characters among taxa. Reductive coding (such as presence vs. absence) eliminates the problem of inapplicable characters among taxa, but may increase the frequency of non-independence among characters. Which tradeoffs or assumptions are most acceptable for a particular analysis may be difficult or impossible to know a priori.

Within this data set it was decided to adopt a moderate, consistent approach, as recommended by Hawkins et al. (1997). For features present and variable among some taxa and absent in others, the information was coded into two characters: a presence/absence character and a character denoting character-state variation for those taxa for which the character was present. Taxa for which the complex character was absent were denoted as inapplicable for variation within the character by a dash ("–") in the data matrix, and taxa for which character data were missing were denoted by a question mark ("?"). For features that may be developmentally related, the strength of this relationship was considered before establishing a character (e.g., see discussion about *W. dichotoma* for characters 3 and 27, Appendix 3). However, developmental studies have not been done, nor are the pleiotropic effects of trait evolution known.

The characters used in the cladistic analysis are discussed in Appendix 3. Several conspicuous characters that were not used also merit some discussion. Leaf characters, such as imparipinnate vs. unifoliate leaves, winged vs. unwinged leaf rachis, and entire vs. toothed margins, varied within most species-rich OTUs used here and, therefore, could not test the monophyly of sections or their relationships. Variation in leaf complexity was considered to divide the species-rich OTU of American section *Weinmannia*, but these characters were difficult to score qualitatively (see discussion about Bernardi's sect. *Simplicifoliae*) and would require the breakup of nearly all other multi-species OTUs. Another potential character that differed within the American OTU was caducous vs. persistent petals. However, this appeared related to the degree of opening of the sepals, a character more difficult to define, and not to the absence of petal abscission. Other characters that could not be defined with precision or were difficult to score for the majority of species included: variation in the thickness of the pericarp, whether the endocarp detaches in fruit, stipule shape, and leaf anatomical characters, such as whether areolation is complete, presence or absence of a hypodermis, and the degree of lignification of tertiary vascular bundles. Such characters may be found useful with more detailed anatomical, morphological, or developmental information.

CLADISTIC METHODS

Data were entered into MacClade (Maddison & Maddison, 1992), and analyses used PAUP version 3.1.1 (Swofford, 1993) run on an Apple PowerMac 7500/100. All characters were scored as unordered (nonadditive) except for "Morphology of branches" (see discussion of character 2, Appendix 3), which was treated as an ordered ("Wagner") character. No data were missing, but inapplicable entries accounted for ca. 7% of the data and were treated as "unknown" in the analysis. Polymorphisms were treated as "uncertainties," because of the way character data were partitioned in the data set. In PAUP, polymorphism is intended to represent variation among monophyletic clades (Swofford & Begle, 1993), such as between species, whereas the coding in this data set represents variation at the population level (i.e., variation within species). The heuristic-search option was implemented with 100 replicates of random-taxon addition using the TBR branch-swapping algorithm. Zero-length branches were collapsed. All shortest trees were saved, and PAUP was used to make consensus trees.

A bootstrap analysis (Felsenstein, 1985) was done with 1000 replicates, with one round of random-taxon addition for each replicate, using the heuristic-search option and TBR branch swapping. To prevent some searches from never swapping to completion, the "maxtrees" setting was held at 500 trees. Decay analyses were done by saving all trees one, and then two steps longer than the most parsimonious trees.

RESULTS

The first round of taxon addition found 192 most-parsimonious trees of 90 steps [Consistency Index (C.I.) = 0.456, Retention Index (R.I.) = 0.745], and all subsequent searches located the same island of trees. Among the outgroups, *Caldcluvia* is arbitrarily used to root the cladogram. The strict consensus tree is shown in Figure 5 and includes bootstrap values of 50% or greater and decay values. The search for trees two steps longer than parsimony could not be completed because the number of possible trees filled available memory. One of the most parsimonious trees is shown in Figures 6 and 7, and was chosen to represent the Malagasy OTUs (sects. *Spicata* + *Inspera*) as forming a monophyletic group.

When the six possibly non-monophyletic OTUs were removed, the strict consensus cladogram was less resolved than the one shown in Figure 5. Unresolved nodes included the monophyly of *Weinmannia* and the monophylies of sections *Spicata* and *Inspersa*. The node uniting sections *Fasciculata* and *Weinmannia* collapsed. The poorer resolution probably resulted from an inability to polarize character states when plesiomorphic taxa were removed, but the results were congruent with the complete matrix tree.

The monophyly of *Weinmannia* is supported with *Cunonia* as the sister taxon. One character synapomorphic for the *Weinmannia–Cunonia* clade, imbricate calyx aestivation, was expected, but other synapomorphies are homoplastic within the clade, including fused lateral stipules and medial meristem abortion. An unbranched floral axis (e.g., raceme), a fused fruit column, and IM development are synapomorphies for a *Vesselowskya* (*Weinmannia–Cunonia*) clade.

Cunonia has three distinctive apomorphies: a nectary whorl adnate to the carpel wall, circumbasal dehiscence of fruits, and a double internode on branches.

Monophyly of *Weinmannia* is supported by the

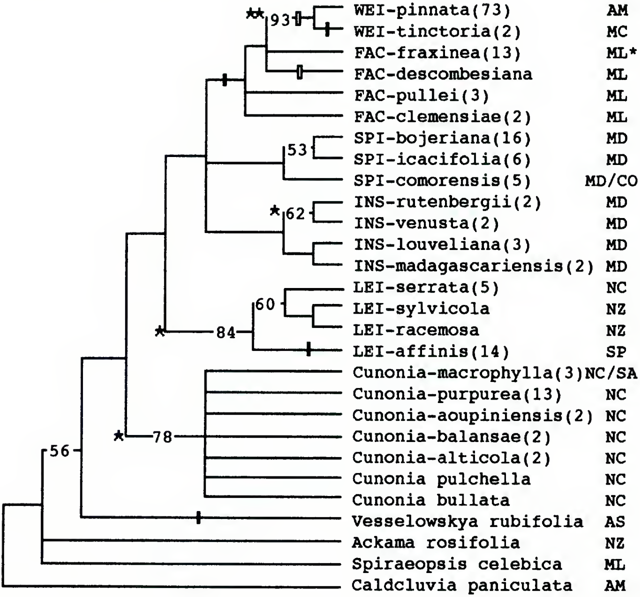


Figure 5. Strict consensus of 192 most parsimonious trees, and taxon-area cladogram. OTUs of species groups in *Weinmannia* are shown with the first three letters of their section capitalized followed by the name of one species. WEI = *Weinmannia*, FAC = *Fasciculata*, SPI = *Spicata*, INS = *Inspersa*, LEI = *Leiospermum*. The total number of species in each OTU is given in parentheses. For areas: AM = Americas, MC = Mascarenes, ML = Malesia (*with a few species in Melanesia), MD = Madagascar, CO = Comores, NC = New Caledonia, NZ = New Zealand, SP = South Pacific (Melanesia and Polynesia), AS = Australia, SA = South Africa. Numbers on branches are bootstrap values. Decay values are 1, unless indicated by a star at the node, with * = decay value of 2 and ** = decay value probably >2. As reconstructed on the cladogram, unisexual flowers have evolved from bisexual ones at least three times in *Weinmannia* (solid bars), and the reverse has happened twice (open bars).

absence of seed wings and the presence of seed hairs, even though these characters are also present in *Ackama*. Another supporting character is the development of IMs in lateral and medial positions, but this character is relatively homoplastic overall.

The first split within the *Weinmannia* clade is between the South Pacific section *Leiospermum* and the rest of the genus. Section *Leiospermum* appears to be monophyletic based upon two characters of the inflorescence architecture: sequential arrangement of metamers within the IMs, and acrotonic development of IMs in the medial position. Within this section is a group of 14 species with unisexual flowers widespread in Melanesia and Polynesia, and a clade of 7 species with bisexual flowers and a perigynous perianth found only in New Caledonia and New Zealand. The two New Zealand species are further distinguished by their inflorescences (as previously discussed).

Four unambiguous synapomorphies unite all other *Weinmannia* species: calyx persistent in fruit, fasciculate flowers, persistent floral bracts, and short IM shoots. Except for the character of fasciculate/solitary floral inception (which changes 6 times in all most parsimonious trees), these characters are not very homoplastic, as each changes only 2–3 times in all most parsimonious trees (Fig. 8). However, this clade is not supported by bootstrap or decay analyses (Fig. 5).

Relationships within this larger *Weinmannia*

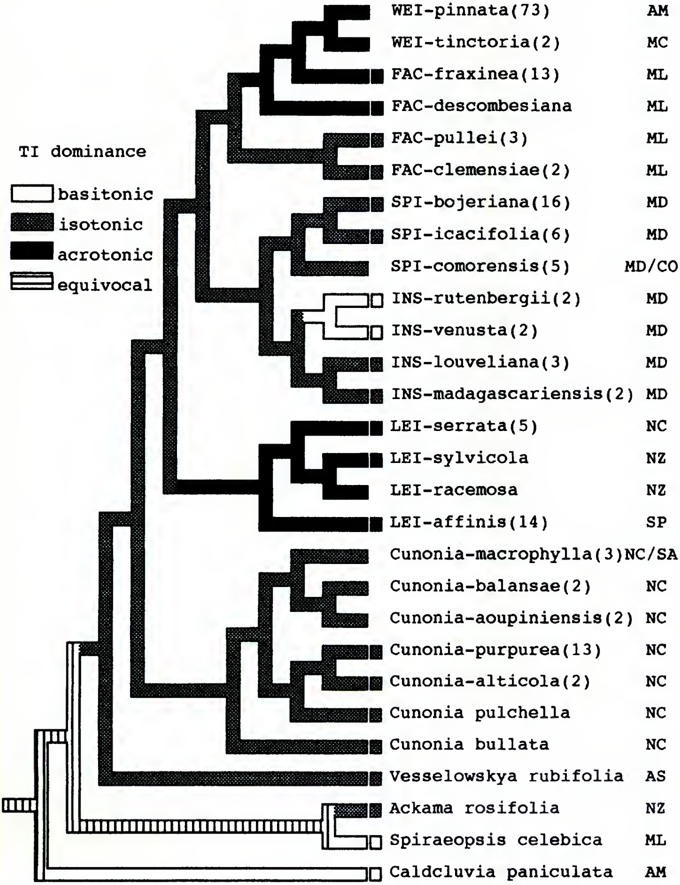


Figure 6. One of the most-parsimonious trees showing a monophyletic group from Madagascar and tracing the evolution of character 31: "TI dominance."

clade are not fully resolved. Although the monophyly of sections *Inspera* and *Spicata* is supported, the relationship of these clades to one another and to the *Weinmannia–Fasciculata* clade is uncertain. Assuming that the Malagasy sections are most closely related to one another can resolve this polytomy as shown in Figures 6 and 7. However, there are no unambiguous synapomorphies for the Malagasy clade. Section *Spicata* has only one recognized apomorphy, sessile flowers. Section *Inspera* has two apomorphies, ribbed nectaries (also present in sect. *Weinmannia* and erratically in sect. *Fas-*

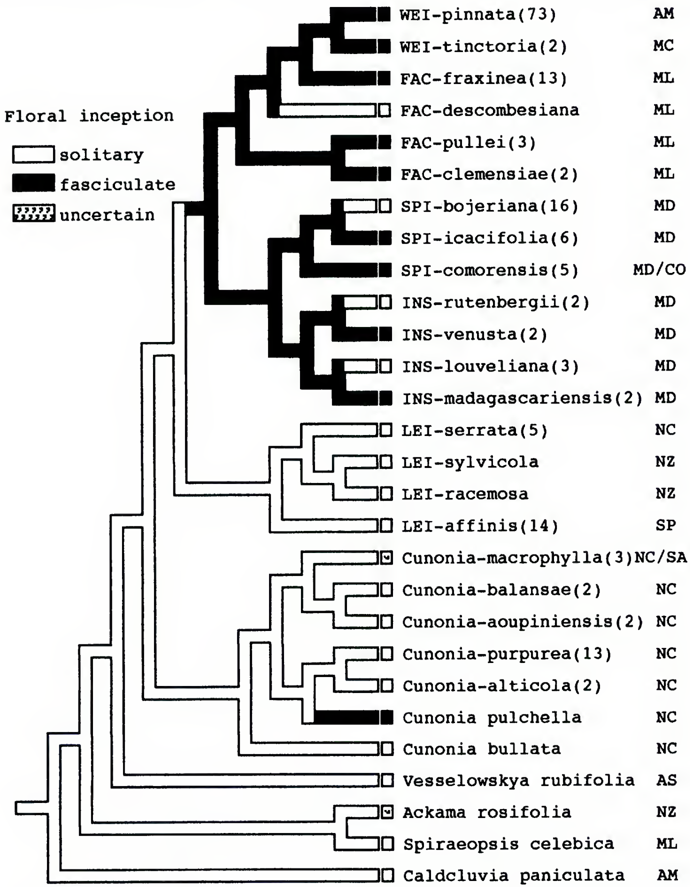


Figure 7. Floral inception (character 19) traced on one of the most-parsimonious cladograms.

ciculata) and seeds covered with dense hairs (sometimes found in sect. *Fasciculata*). In general, species-groups in Madagascar show a great diversity of characters relative to other taxa.

No most-parsimonious reconstruction supports the monophyly of section *Fasciculata*, which in this analysis is paraphyletic with respect to a highly differentiated section *Weinmannia*. These two sections are united by the absence of persistent, fused lateral stipules and the absence of a bud at the base of the axillary shoots.

The node uniting the species of section *Weinmannia*, which are disjunct between the Americas and the Mascarene Islands, is the best supported,

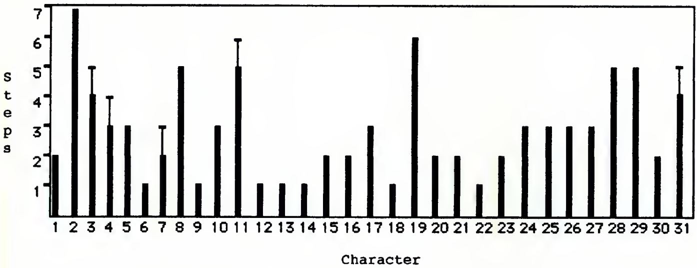


Figure 8. The number of steps (y axis) per character (x axis) calculated over all most-parsimonious trees, showing the upper bound and minimum values. Characters 24–31 represent variation in the inflorescence architecture above the level of the raceme axis (as shown in Figs. 2, 3, 9). These characters comprise 26% of the characters in the matrix (8/31), and about 29% of the total number of steps (26–27/90). When all inflorescence characters are included (characters 19–31), these values are 42% (13/31) and 44% (39–40/90), respectively, demonstrating that they do not have levels of homoplasy significantly different from traditionally used characters.

with a bootstrap support of 93% and a decay index of >2 (Fig. 5). This node has six unambiguous changes: ribbed nectaries, sparsely distributed seed hairs, reniform seed shape, absence of IM development, presence of development of racemes along the main stem axis, and only one TI metamer. Within section *Weinmannia*, the Mascarene species have two distinguishing characters: unisexual flowers formed by late suppression, and 5-merous flowers (in contrast to bisexual, 4-merous flowers in American species). As noted previously, most American species have caducous petals and may be a monophyletic sister taxon to the Mascarene clade. The American species appear monomorphic in this analysis, which relied on qualitative character variation, but are highly diversified in terms of leaf shape, distribution and form of pubescence, and size of racemes.

DISCUSSION

SYSTEMATIC IMPLICATIONS

At the generic level, this analysis supports the continued recognition of *Weinmannia* and *Cunonia* as separate genera, a distinction that has been questioned by some systematists (Cronquist, 1981: 547). However, more systematic studies within the family are needed to be more certain of cladistic relationships among genera.

Within *Weinmannia*, the sections proposed by Bernardi (1961, 1963b, 1964) appear monophyletic, with the exception of section *Fasciculata*, with some rearrangement of species indicated. Specifically, *Weinmannia descombesiana* on the one hand, and *W. comorensis* and *W. baehniana*, on the other, do not belong in section *Leiospermum*, but in sections *Fasciculata* and *Spicata*, respectively. *Weinmannia venusta* and *W. rutenbergii* do not belong in section *Weinmannia*, but in section *Inspersa* (see Appendix 1). With these rearrangements, the monophyly of sections *Leiospermum*, *Spicata*, *Inspersa*, and *Weinmannia* (including sect. *Simplicifolia*) is supported. Section *Fasciculata* is paraphyletic with respect to section *Weinmannia*, but several characters were scored as inapplicable in section *Weinmannia* (since this section lacks IM development) and may have skewed patterns within section *Fasciculata*. Furthermore, preliminary results of molecular-systematic studies (Bradford, unpublished) strongly support the monophyly of section *Fasciculata*.

The poor resolution in *Cunonia* may have been due to the selection of characters in *Weinmannia*. An analysis focusing on *Cunonia* might be more informative. Interestingly, the South African *Cunonia capensis*, the only *Cunonia* species outside of New Caledonia, shares many characters with two other species, *C. macrophylla* and *C. schinziana*. Furthermore, these three species appear very distinctive when compared to other *Cunonia* species.

UTILITY OF ARCHITECTURAL CHARACTERS FOR *WEINMANNIA* SYSTEMATICS

As judged by relative levels of homoplasy, inflorescence architecture is as informative as other sources of variation, such as vegetative, floral, and fruit characters (Fig. 8).

Parts of the cladogram rely heavily on inflorescence characters. For example, the monophyly of section *Leiospermum* is supported by inflorescence architecture alone, and section *Weinmannia* is supported by three inflorescence characters.

The inclusion of inflorescence characters has permitted the resolution of relationships within sections for the first time. This is especially true in the species-rich section *Spicata*, which can be divided into three groups largely on the basis of inflorescence differences. Inflorescence characters are also useful at the species level in section *Inspersa*. It is often easier to recognize species using qualitative differences in the inflorescence than using differences in leaves, which may be fairly similar among species and highly plastic within species.

The fact that inflorescence characters have been overlooked is illustrated by Smith (1985), who considered *W. richii* and *W. vitiensis*, both from Fiji, as fairly indistinct based upon leaves and flowers. However, at a glance one can recognize that racemes terminate the IMs of *W. vitiensis* (sect. *Leiospermum*), whereas the IMs terminate in a bud and are borne serially in *W. richii* (sect. *Fasciculata*). Although these characters have gone unnoticed, they are macroscopic, with clear patterns discernible by the naked eye and not requiring rehydration and dissection of parts, as is often necessary for flowers and fruits.

THE CONCEPT OF POSITIONAL HOMOLOGY: IMPLICATIONS AND BENEFITS

Heterotopy is the development of an organ in a different position in a descendant than where it had developed in the ancestor. This definition views the organ as primary and the position as secondary. Another perspective of heterotopy is: at a given position, a different organ develops in the descendant than that which had developed in the ancestor. This view gives primacy to positional homology, and with this perspective it may be easier to understand that an organ can develop in its plesiomorphic position and in an apomorphic position within a plant. Consideration of the homology of position has two important implications: (1) it draws attention to a broader set of characters, and (2) it may lead to more precise formulation of characters. The coding of the inflorescence using positional homology exemplifies these points.

Often, the use of inflorescence characters in systematics is vague (e.g., "inflorescence terminal or not") because the level of organization is not specified. By contrast, consider character 26, "Fate of IM terminus," which accounts for the organ (raceme, bud, or aborted meristem) that forms at a particular position, the terminus of an IM. This coding specifies topographic information in the proper hierarchic context. Because such characters are positional, patterns of heterotopy can be studied from cladograms. The mapping of character 31, "TI dominance," on the cladogram (Fig. 6) shows that TIs are generally isotonic within *Cunonia* and *Weinmannia*, but that acrotonic TIs have evolved twice (Figs. 2a, 3a) and basitonic TIs once (Fig. 3e). At the TI level, this is a *positional* change in dominance, but it is expressed by differences among IMs possibly caused by unequal *timing* of development. In other words, timing differences are among serially homologous IMs within a TI, whereas positional differences are among clades within *Weinmannia*.

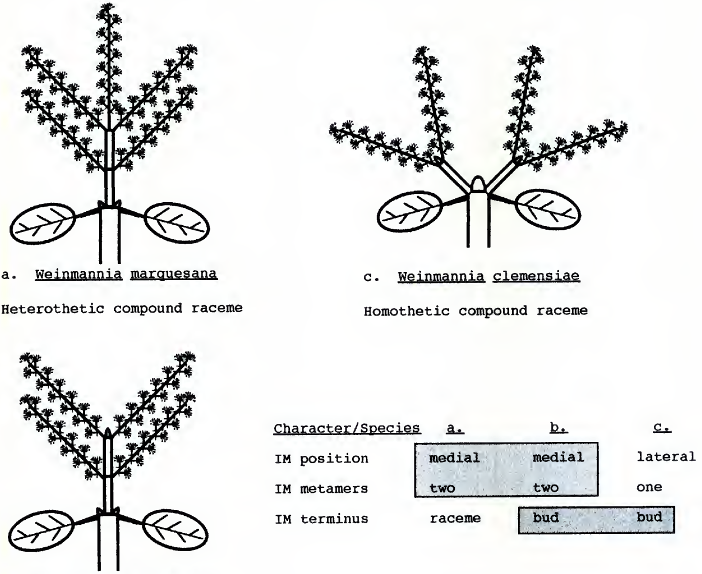
It should be stressed that nothing is being implied about the underlying molecular development of these characters. Heterotopy is only being used to describe patterns observed at the morphological level in a phylogenetic context. However, because the deep nodes of the cladograms are not well supported (Fig. 5), extensive discussion of character evolution is not warranted.

ORIGIN OF RACEMES

In the discussion of character 22 ("Flower-bearing axis: branched/unbranched") it was suggested that if fascicled flowers (character 19) were plesiomorphic in the cladogram, then the hypothesis that floral fascicles are homologous to flower-bearing short shoots would be supported. Mapping of character 19 on the cladograms does not support this hypothesis (Fig. 7). Fascicled flowers appear derived within the sister clade to section *Leiospermum*, but within this clade there are four reversals. The hypothesis is not completely rejected, however, due to the high level of homoplasy of character 19 and the lack of support for deep nodes.

INFLORESCENCE CLASSIFICATION AND CLADISTICS: SOME OBSERVATIONS AND CAUTIONS

Standard inflorescence terminology may inadequately describe cladistic characters because traditional terms frequently confound distinct characters and levels of organization. For instance, previous decriptions of inflorescence variation in *Weinmannia* (Bernardi, 1963a) recognized three forms: "racemes," "pseudoracemes," and "spikes." The first pair of terms refers to the final stage of floral position along the axis but mixes the characters "Floral inception" (character 19) and "Bract fidelity" (character 20; Fig. 1). The term "spike"



a. Weinmannia marquesana

Heterothetic compound raceme

c. Weinmannia clemensiae

Homothetic compound raceme

b. Weinmannia racemosa

Homothetic compound raceme

Character/Species	a.	b.	c.
IM position	medial	medial	lateral
IM metamers	two	two	one
IM terminus	raceme	bud	bud

Figure 9. Inflorescence typology and cladistics. Three species and their inflorescences are shown, with two labeled "homothetic compound racemes," and one "heterothetic compound raceme," following Weberling (1989). Of three characters coded using the methodology in this paper, standard terminology accounts for only one, IM terminus. That is why standard terminology classifies b and c the same, whereas this analysis suggests that a and b are most closely related.

specifies flowers borne on an unbranched axis without pedicels and is therefore unrelated to variation in the distribution of flowers along the axis that is dealt with (poorly) by the other two terms. A cladistic analysis that codified traditional terminology would therefore be comparing non-homologous parts.

As mentioned in the description of inflorescence architecture, general systems of inflorescence classification do not apply to many structures in *Weinmannia.* The various forms of the IM may loosely be termed "compound racemes" following Weberling (1989), although they do not fit the definition exactly. Standard terminology cannot be expected to describe in detail the unique aspects of a group, but details are crucial for cladistics. For example, compare the inflorescences shown in Figure 9, which are common in *W. marquesana* (Fig. 9a) and *W. racemosa* (Fig. 9b; sect. *Leiospermum*) and *W. clemensiae* (Fig. 9c; sect. *Fasciculata*). The inflorescence of *W. marquesana* can be called a "heterothetic compound raceme," and the others can be called "homothetic compound racemes." The standard terminology addresses whether the terminus of the IM produces a bud or a raceme. This fails to convey other characters important in *Weinmannia,* such as the number of IM metamers and the position the IM occupies within the TI.

It is also difficult to apply standard names to the inflorescences of some highly plastic species, such as *W. rutenbergii,* especially since variation is rampant at different levels of organization. However, by breaking down a complex structure into its parts, variation relevant to different hierarchical levels can be distinguished.

EVOLUTION OF DIOECY

The cladogram (Fig. 5) shows that bisexual flowers are plesiomorphic in *Weinmannia*. Two clearly monophyletic groups (corresponding to sects. *Weinmannia* and *Leiospermum*) have some members with bisexual and others with unisexual flowers (and which are more or less dioecious). Unisexual flowers are also most common in section *Fasciculata*, but because relationships in this portion of the tree are not well resolved, the pattern of character evolution is unclear. Minimally, unisexual flowers have arisen three times, with a possible reversal in *W. descombesiana* and in the branch of the section *Weinmannia* clade.

Weinmannia flowers are small, simply structured, and mature more or less simultaneously within an inflorescence. The pollinators of *Weinmannia* probably conform to the "generalist" category of small insects, especially bees, that Bawa (1994) and Beach (1981) suggested drove the evolution of dioecy from bisexuality. The best evidence for bee pollination of *Weinmannia* is the commercial production of honey in New Zealand (Matheson, 1991; Walsh, 1978) and Madagascar (Ralimanana, 1994).

It is noteworthy that dioecy is prevalent on islands, which has been suggested as a general trend (Baker, 1967; Baker & Cox, 1984). The only dioecious species in section *Weinmannia* occur on the Mascarene Islands, and the dioecious members of section *Leiospermum* are distributed among the smaller South Pacific islands, with bisexual species on the relatively larger islands of New Caledonia and New Zealand. In the South Pacific, dioecy is usually imperfect (e.g., "leaky dioecy" or polygamodioecy), which may promote the colonization of small, ephemeral islands (Baker & Cox, 1984).

BIOGEOGRAPHY

Weinmannia has attracted the interest of biogeographers because its distribution suggests that the genus was widespread on Gondwanaland, and its current disjunctions may have much to do with plate-tectonic processes and resultant continental vicariance (Good, 1950; Bernardi, 1963a; van Balgooy, 1971; Raven & Axelrod, 1974). However, extensive distribution among South Pacific volcanic islands shows that long-distance dispersal can also be important in this genus.

Because deep phylogeny of *Weinmannia* is not well supported, no firm conclusions about Gondwanan-area relationships can be made. However, the well-supported sister-group relationship between American and Mascarene taxa is impossible to explain without invoking dispersal, because the Mascarene Islands are of relatively recent, hot-spot volcanic origin (Patriat & Seqoufin, 1988). This disjunction can be explained by one of two general classes of hypotheses: (1) long-distance dispersal between the Americas and the Mascarenes, or (2) short-distance dispersal from a non-extant source area from Africa, Madagascar, or other, older islands in the Indian Ocean. The second hypothesis implies an historically more widespread occurrence of section *Weinmannia*, with intervening extinction.

If section *Weinmannia* is in fact a relatively young, highly derived lineage, as its current position in the cladogram suggests, then the long-distance dispersal hypothesis may be favored. However, the hypothesis of formerly widespread occurrence and short-distance dispersal gains some support from fossils. Oligocene whole-leaf fossils of either *Weinmannia* or *Cunonia* from Tasmania (Carpenter & Buchanan, 1993) look very similar to *W. trichosperma* from southern Chile.

CONCLUSIONS AND FUTURE DIRECTIONS

This cladistic study of morphological characters has identified congruent patterns of variation both within and among previous taxonomic groupings of *Weinmannia*. This helps to focus research into the origin and transformation of characters within *Weinmannia* and related genera. While good support exists for the monophyly of some sections, cladistic relationships and patterns of character evolution among sections are still poorly understood. However, molecular-systematic work will be aided by a better understanding of the disparity in morphological diversity and species richness among clades, and the overall congruence of character variation with geography.

It is likely that the methods used here to identify and cladistically code inflorescence architecture in *Weinmannia* and *Cunonia* will be useful in other taxa. This is certainly true within and among other genera of Cunoniaceae. An understanding of the nested, modular construction of plants and the potential for heterotopy in evolution may often be required to code inflorescence architecture for cladistic analysis. It is suggested that heterotopic patterns are prevalent in inflorescence evolution, and that coding of positional homologies is an effective way to infer character-state polarities of inflorescence features.

Literature Cited

Baker, H. G. 1967. Support for Baker's law—As a rule. Evolution 21: 853–56.

——— & P. A. Cox. 1984. Further thoughts on dioecism and islands. Ann. Missouri Bot. Gard. 71: 244–253.

Balgooy, M. M. J. van. 1971. Plant-geography of the Pacific. Blumea Suppl. 6: 1–222.

Barlow, P. W. 1994. From cell to system: Repetitive units of growth in the development of roots and shoots. Pp. 19–58 *in* M. Iqbal (editor), Growth Patterns in Vascular Plants. Dioscorides Press, Portland, Oregon.

Bawa, K. S. 1994. Pollinators of tropical dioecious angiosperms: A reassessment? No, not yet. Amer. J. Bot. 81: 456–460.

Beach, J. H. 1981. Pollinator foraging and the evolution of dioecy. Amer. Naturalist 118: 572–577.

Bernardi, L. 1961. Revisio generis *Weinmanniae.* Pars I: Sectio *Weinmanniae.* Candollea 17: 123–189.

———. 1963a. Considérations phytogéographiques et morphogénétiques sur le genre *Weinmannia* (Cunoniacées). Adansonia 3: 404–412.

———. 1963b. Revisio generis *Weinmanniae.* Pars II: Sectio *simplicifoliae.* Candollea 18: 285–334.

———. 1964. Revisio generis *Weinmanniae.* Pars III: Sectiones III–IV–V–VI (veteris orbis). Bot. Jahrb. Syst. 83: 126–184.

———. 1965. Cunoniacées. V. 93 *in* H. Humbert (editor), Flore de Madagascar et des Comores. Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.

Boughton, D. A., B. B. Collettte & A. R. McCune. 1991. Heterochrony in jaw morphology of needlefishes (Teleostei: Belonidae). Syst. Zool. 40: 329–354.

Bradley, D., O. Ratcliffe, C. Vincent, R. Carpenter & E. Coen. 1997. Inflorescence commitment and architecture in *Arabidopsis.* Science 275: 80–83.

Briggs, B. G. & L. Johnson. 1979. Evolution in the Myrtaceae—Evidence from inflorescence structure. Proc. Linn. Soc. New South Wales 102: 157–272.

Carpenter, R. J. & A. M. Buchanan. 1993. Oligocene leaves, fruit and flowers of the Cunoniaceae from Cethana, Tasmania. Austral. Syst. Bot. 6: 91–109.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Dickinson, T. A. & R. Sattler. 1974. Development of the epiphyllous inflorescence of *Phyllonoma integerrima* (Turcz.) Loes.: Implications for comparative morphology. Bot. J. Linn. Soc. 69: 1–13.

——— & ———. 1975. Development of the epiphyllous inflorescence of *Helwingia japonica* (Helwingiaceae). Amer. J. Bot. 62: 962–973.

Dickison, W. C. 1975. Studies on the floral anatomy of the Cunoniaceae. Amer. J. Bot. 62: 433–447.

———. 1984. Fruits and seeds of the Cunoniaceae. J. Arnold Arbor. 65: 149–190.

——— & R. Rutishauser. 1990. Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. II. Taxa without interpetiolar stipules and conclusions. Bot. Helv. 100: 75–95.

Doweld, A. B. 1998. The carpology and taxonomic relationships of *Davidsonia* (Davidsoniaceae). Edinburgh J. Bot. 55: 13–25.

Engler, A. 1928. Cunoniaceae. Pp. 229–262 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien 18a. Engelmann, Leipzig.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

Florence, J. 1982. Recherches botaniques en Polynésie Française. ORSTROM-Tahiti.

Fosberg, F. R. 1992. Vegetation of the Society Islands. Pacific Sci. 46: 232–250.

Gentry, A. H. 1995. Patterns of diversity and floristic composition in neotropical montane forests. Pp. 103–126 *in* S. P. Churchill, H. Balslev, E. Forero & J. Luteyn (editors), Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden, Bronx.

Godley, E. J. 1983. The fruit in *Ackama, Caldcluvia,* and *Weinmannia* (Cunoniaceae). New Zealand J. Bot. 21: 455–456.

Good, R. 1950. Madagascar and New Caledonia. A problem in geography. Blumea 6: 470–479.

Gould, S. J. 1977. Ontogeny and Phylogeny. The Belknap Press of Harvard Univ. Press, Cambridge.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill. 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 131.

Grimes, J. 1992. Metamerism, heterochrony and inflorescence morphology of the *Pithecellobium*-complex (Leguminosae: Mimosoideae: Ingeae). Brittonia 44: 140–159.

Haeckel, E. 1905. The Evolution of Man. Watts, London.

Hawkins, J. A., C. E. Hughes & R. W. Scotland. 1997. Primary homology assessment, characters and character states. Cladistics 13: 275–283.

Hoogland, R. D., J. Jérémie & H. C. F. Hopkins. 1997. Le genre *Cunonia* (Cunoniaceae) en Nouvelle-Calédonie. Description de cinq espèces nouvelles. Bull. Mus. Natl. Hist. Nat., B, Adansonia 19: 7–20.

Hopkins, H. C. F. 1998a. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific 1. Introduction and an account of the species of Western Malesia, the Lesser Sundas and the Moluccas. (Structure of the Inflorescence and *W. hooglandii* with J. C. Bradford). Adansonia series 3, vol. 20: 5–41.

———. 1998b. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific 2. Sulawesi and the Philippines. Adansonia series 3, vol. 20: 43–66.

———. 1998c. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific 3. New Guinea, Solomon Islands, Vanuatu and Fiji, with notes on the species of Samoa, Rarotonga, New Caledonia and New Zealand. (Vanuatu and New Caledonia with R. D. Hoogland; Fiji with J. C. Bradford). Adansonia series 3, vol. 20: 67–106.

——— & J. Florence. 1998. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific 4. The Society, Marquesas and Austral Islands. Adansonia series 3, vol. 20: 107–130.

Hufford, L. & W. C. Dickison. 1992. A phylogenetic analysis of Cunoniaceae. Syst. Bot. 17: 181–200.

Humbert, H. 1965. Description des types de végétation. Pp. 46–78 *in* H. Humbert & G. Cours Darne (editors), Notice de la carte de Madagascar. Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry, hors sérs. Vol. 6.

Jong, K. & B. L. Burtt. 1975. The evolution of morphological novelty exemplified in the growth patterns of some Gesneriaceae. New Phytol. 75: 297–311.

Kaul, R. B. & E. C. Abbe. 1984. Inflorescence architecture and evolution in the Fagaceae. J. Arnold Arbor. 65: 375–401.

Kellogg, E. A. 1990. Ontogenetic studies of florets in *Poa* (Gramineae): Allometry and heterochrony. Evolution 44: 1978–1989.

Kelly, D. L., E. V. J. Tanner, E. M. NicLughadha & V. Kapos. 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes. J. Biogeogr. 21: 421–440.

Leavitt, R. G. 1905. On translocation of characters in plants. Rhodora 7: 13–31.

Liede, S. & F. Weberling. 1995. On the inflorescence structure of Asclepiadaceae. Pl. Syst. Evol. 197: 99–109.

Mabberley, D. J. 1975. The giant Lobelias: Toxicity, inflorescence and tree-building in the Campanulaceae. New Phytol. 75: 289–295.

Maddison, W. P. & D. R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution V 3.0. Sinauer, Sunderland, Massachusetts.

Martínez, E. & C. H. Ramos. 1989. Lacandoniaceae (Triuridales): Una nueva familia de México. Ann. Missouri Bot. Gard. 76: 128–135.

Matheson, A. G. 1991. Beekeeping: Leading agricultural change in New Zealand. Bee World 72: 60–73.

McKinney, M. L. & K. J. McNamara. 1991. Heterochrony: The Evolution of Ontogeny. Plenum Press, New York.

Meyerowitz, E. M. 1997. Genetic control of cell division patterns in developing plants. Cell (Cambridge) 88: 299–308.

Orozco, C. I. 1997. Sobre la posición sistemática de *Brunellia* Ruiz & Pavon. Caldasia 19: 145–164.

Patriat, P. & J. Seqoufin. 1988. Reconstruction of the Central Indian Ocean. Tectonophysics 155: 211–234.

Pleijel, F. 1995. On character coding for phylogeny reconstruction. Cladistics 11: 309–315.

Raff, R. A. 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. Univ. Chicago Press, Chicago.

——— & G. A. Wray. 1989. Heterochrony: Developmental mechanisms and evolutionary results. J. Evol. Biol. 2: 409–434.

Ralimanana, H. 1994. Contribution à la connaissance de l'apiculture et à la melissopalynologie dans le parc national de Ranomafana. Unpublished Masters thesis, Université d'Antananarivo, Antananarivo.

Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

Renner, S. S. 1989. Floral biological observations on *Heliamphora tatei* (Sarraceniaceae) and other plants from Cerro de la Neblina in Venezuela. Pl. Syst. Evol. 163: 21–29.

Ríos, O. V. 1986. Estudios ecológicos en un relicto de bosque de *Weinmannia tomentosa* y *Drimys granadensis*. En la región de Monserrate. Perez-Arbelaezia 1: 339–356.

Sachs, T. 1982. A morphogenetic basis for plant morphology. Pp. 118–131 *in* R. Sattler (editor), Axioms and Principles of Plant Construction. Martinus Nijhoff/Dr W. Junk Publishers, The Hague.

Sattler, R. 1988. Homeosis in plants. Amer. J. Bot. 75: 1606–1617.

———. 1994. Homology, homeosis, and process morphology in plants. Pp. 424–475 *in* B. Hall (editor), Homology: The Hierarchical Basis of Comparative Biology. Academic Press, San Diego.

Schlessman, M. A., D. G. Lloyd & P. P. Lowry II. 1990. Evolution of sexual systems in New Caledonian Araliaceae. Mem. New York Bot. Gard. 55: 105–117.

Smith, A. C. 1985. Flora Vitiensis Nova: A New Flora of Fiji. 3. National Tropical Botanical Garden, Lawai, Kauai, Hawaii.

Sommer, H., J. Beltrán, P. Huijser, H. Pape, W. Lönnig, H. Saedler & Z. Schwarz-Sommer. 1990. Deficiens, a homeotic gene involved in the control of flower morphogenesis in *Antirrhinum majus*: The protein shows homology to transcription factors. E. M. B. O. J. 9: 605–613.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony V 3.1. Illinois Natural History Survey, Champaign.

——— & D. P. Begle. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1, User's Manual. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, D.C.

Timonen, T. 1998. Inflorescence structure in the sedge tribe Cariceae (Cyperaceae). Publ. Bot. Univ. Helsinki 26: 1–35.

Tortosa, R. D., L. Aagesen & G. M. Tourn. 1996. Morphological studies in the tribe Colletieae (Rhamnaceae): Analysis of architecture and inflorescences. Bot. J. Linn. Soc. 122: 353–367.

Tucker, S. C. 1987. Pseudoracemes in papilionoid legumes: Their nature, development, and variation. Bot. J. Linn. Soc. 95: 181–206.

Venkata Rao, C. 1965. Studies in the Proteaceae V. Evolution of the inflorescence. J. Indian Bot. Soc. 44: 244–271.

Wagner, G. P. 1996. Homologues, natural kinds and the evolution of modularity. Amer. Zoologist 36: 36–43.

Walsh, R. S. 1978. Nectar and Pollen Sources of New Zealand. National Beekeepers Association of New Zealand, Wellington.

Wardle, P. & A. H. MacRae. 1966. Biological flora of New Zealand. Vol. 1. *Weinmannia racemosa* Linn. F. (Cunoniaceae). Kamahi. New Zealand J. Bot. 4: 114–131.

Webb, C. J. & M. J. A. Simpson. 1991. Seed morphology in relation to taxonomy in New Zealand species of *Weinmannia*, *Ackama*, and the related South American *Caldcluvia paniculata* (Cunoniaceae). New Zealand J. Bot. 29: 451–453.

Weber, A. 1988. Development, interpretation, and phylogeny of the inflorescence of *Epithema*. Beitr. Biol. Pflanzen 63: 431–451.

Weberling, F. 1977. Beiträge zur Morphologie der Rubiaceen-Infloreszenzen. Pp. 191–209 *in* Y. Sell, F. Weberling & H. Lorenzen (editors), Morphology, Anatomy and Systematics of Higher Plants. Gustav Fischer Verlag, Stuttgart.

———. 1988. The architecture of inflorescences in the Myrtales. Ann. Missouri Bot. Gard. 75: 226–310.

———. 1989. Morphology of Flowers and Inflorescences. Cambridge Univ. Press, Cambridge.

White, J. 1979. The plant as a metapopulation. Annual Rev. Ecol. Syst. 10: 109–145.

Wilkinson, M. 1995. A comparison of two methods of character construction. Cladistics 11: 297–308.

Yanofsky, M. F., H. Ma, J. L. Bowman, G. N. Drews, K. A. Feldmann & E. M. Meyerowitz. 1990. The protein encoded by the *Arabidopsis* homeotic gene agamous resembles transcription factors. Nature 346: 35–39.

Zelditch, M. L. & W. L. Fink. 1996. Heterochrony and heterotopy: Stability and innovation in the evolution of form. Paleobiology 22: 241–254.

Zimmermann, W. 1961. Phylogenetic shifting of organs, tissues, and phases in pteridophytes. Canad. J. Bot. 39: 1547–1553.

APPENDIX 1

List of species assigned to each OTU and a selected list of specimens examined. Only the name of the first collector is given. An estimate of the number of species in each OTU includes preliminary studies of undescribed species. New species are listed and specimens are cited only if they are mentioned in the text. Types are holotypes or isotypes unless indicated otherwise. Herbaria holding specimens are given in parentheses.

Section *Weinmannia*

WEI-pinnata 73 species (in addition to the species cited below there are ca. 10 undescribed species)

Weinmannia anisophylla Standl. & L. O. Williams, *Smith P2622* (F; type), Costa Rica

Weinmannia auriculata D. Don, *Bradford 392* (MO), Venezuela; *Jørgensen 1260* (MO), Ecuador

Weinmannia auriculifera Hieron., *Cuatrecasas 6313* (F), Colombia

Weinmannia balbisiana Kunth, *Bradford 459* (MO), Venezuela

Weinmannia bangii Rusby, *Bradford 525* (MO), Bolivia; *Solomon 10683* (MO), Bolivia

Weinmannia boliviensis R. E. Fr., *Solomon 10591* (MO), Bolivia

Weinmannia bogotensis Cuatrec., *Bradford 746* (MO), Colombia; *Cuatrecasas 8005* (COL, F; type), Colombia

Weinmannia burserifolia Standl., *Bello 1338* (MO), Costa Rica; *Bradford 97* (MO), Costa Rica

Weinmannia cochensis Hieron., *Bradford 3* (MO), Ecuador; *Bradford 339* (MO), Ecuador; *Bradford 762* (MO), Colombia

Weinmannia corocoroensis P. E. Berry & J. C. Bradford, *Huber 12296* (MO), Venezuela

Weinmannia costulata Cuatrec., *Steyermark 53545* (F; type), Ecuador

Weinmannia crassifolia Ruiz & Pav., *Bradford 510* (MO), Bolivia; *Solomon 17344* (MO), Bolivia

Weinmannia cundinamarcensis Cuatrec., *Cuatrecasas 12033* (COL, F; type), Colombia

Weinmannia cymbifolia Diels, *Díaz 2654* (MO), Peru; *Llantas Quiroz 2625* (MO), Peru

Weinmannia discolor Gardner, *Davidson 5020* (MO), Bolivia; *Hatschbach 43003* (MO), Brazil

Weinmannia dryadifolia Moric., *Bradford 150* (MO), Ecuador; *Gentry 61436* (MO), Peru; *Smith 5011* (F, MO), Peru

Weinmannia ellattantha Diels, *Bradford 538* (MO), Bolivia; *Gentry 52076* (MO), Bolivia

Weinmannia elliptica Kunth, *Bradford 351* (MO), Ecuador

Weinmannia fagaroides Kunth, *Bradford 295* (MO), Ecuador

Weinmannia glabra L.f., *Breedlove 19958* (F), Mexico

Weinmannia glomerata C. Presl, *Gentry 19302* (F), Peru; *Gentry 44877* (F, MO), Peru; *Young 593* (F, MO), Peru

Weinmannia guyanensis Klotzsch ex Engl., *Delascio 11861* (MO), Venezuela; *Huber 9085* (US), Venezuela

Weinmannia haenkeana Engl., *Llatas Quiroz 1320* (F), Peru; *Smith 5039* (MO), Peru

Weinmannia humilis Engl., *Hatschbach 26323* (MO), Brazil

Weinmannia ilutepuiensis J. C. Bradford & P. E. Berry, *Liesner 23338* (MO), Venezuela; *Liesner 23413* (MO; type), Venezuela; *Maguire 33508* (US), Venezuela

Weinmannia intermedia Schltr. & Cham., *Ventura 1089* (F), Mexico

Weinmannia jelskii Szyszyl., *Gentry 80472* (MO), Ecuador; *Smith 7789* (MO), Peru

Weinmannia karsteniana Szyszyl., *Bradford 383* (MO), Venezuela

Weinmannia kunthiana D. Don, *Jaramillo Mejia 167* (F, MO), Colombia

Weinmannia latifolia C. Presl, *Cuatrecasas 23723* (F), Colombia; *Smith 7937* (MO), Peru

Weinmannia laurina Kunth, *Mori 7686* (MO), Panama

Weinmannia laxiramea Killip & A. C. Sm., *Steyermark 128321* (MO), Venezuela; *Steyermark 129882* (US), Venezuela

Weinmannia lentisifolia C. Presl, *Palacios 4128* (MO), Ecuador

Weinmannia macrophylla Kunth, *Jørgensen 92729* (MO), Ecuador

Weinmannia magnifolia Cuatrec., *Cuatrecasas 8590* (COL, F; type), Colombia; *Palacios 13415* (MO), Ecuador

Weinmannia mariquitae Szyszyl., *Bradford 208* (MO), Ecuador; *Romoleroux 253* (MO), Ecuador

Weinmannia microphylla Ruiz & Pav., *Bradford 492* (MO), Bolivia

Weinmannia multijuga Killip & A. C. Sm., *Bruijn 1296* (MO), Venezuela; *Penland 1198* (F), Ecuador

Weinmannia myrtifolia Cuatrec., *Bradford 745* (MO), Colombia; *Cuatrecasas 9451* (COL; type), Colombia

Weinmannia organensis Gardner, *Irwin 8601* (MO), Brazil

Weinmannia ovata Cav., *Bradford 541* (MO), Bolivia; *D'Arcy 13770* (MO), Peru

Weinmannia parvifoliolata Cuatrec., *Cuatrecasas 8486-A* (COL, F; type), Colombia

Weinmannia paulliniifolia Pohl ex Ser., *Pohl s.n.* (P; type), Brazil; *Sucre 6824* (MO), Brazil

Weinmannia pentaphylla Ruiz & Pav., *Gentry 43227* (MO), Peru

Weinmannia pinnata L., *Wilbur 7952* (MO), Dominica

Weinmannia platyptera Diels, *Smith 4459* (F, MO), Peru

Weinmannia polyphylla Moric. ex Ser., *Bradford 2* (MO), Ecuador; *Luteyn 5631* (F, MO), Ecuador

Weinmannia producta Moric. ex Ser., *Nuñez 7146* (MO), Peru; *Sagástegui 7766* (MO), Peru

Weinmannia pubescens Kunth, *Bradford 13* (MO), Ecuador; *Palacios 9648* (MO), Ecuador

Weinmannia reticulata Ruiz & Pav., *Bradford 296* (MO), Ecuador

Weinmannia rhoifolia Rusby, *Lectae 1989* (MO; type), Bolivia

Weinmannia rollottii Killip, *Bradford 357* (MO), Ecuador; *Bradford 747* (MO), Colombia

Weinmannia sibundoya Cuatrec., *Cuatrecasas 11624* (F; type), Colombia; *Cuatrecasas 11817* (F), Colombia; *Cuatrecasas 19308* (MO), Colombia

Weinmannia sorbifolia Kunth, *Solomon 15997* (MO), Bolivia

Weinmannia subsessiliflora Ruiz & Pav. *Schultes 5329* (COL), Colombia

Weinmannia ternata Engl., *Stein 2114* (MO), Peru; *Woytkowski 8314* (MO), Peru

Weinmannia tolimensis Cuatrec., *Cuatrecasas 20424* (MO), Colombia; *Wilson Devia 663* (MO), Colombia

Weinmannia tomentosa L.f., *Berry 175* (MO), Venezuela; *Bradford 751* (MO), Colombia; *Gentry 34725* (MO), Colombia

Weinmannia trianaea Wedd., *Cuatrecasas 11635* (COL, F), Colombia; *Cuatrecasas 8431* (COL, F), Colombia; *Vargas 438* (MO), Ecuador

Weinmannia trichocarpa Pamp., *Wurdack 704* (MO), Peru

Weinmannia trichosperma Cav., *Baum 4537* (MO), Argentina; *West 4679* (MO), Chile

Weinmannia velutina O. Schmidt, *Steyermark 104504* (F, US), Venezuela; *Steyermark 92437* (F), Venezuela

Weinmannia wercklei Standl., *Haber 2438* (MO), Costa Rica

WEI-tinctoria 2 species

Weinmannia biviniana Tul., *Badré 932* (P), Mascarenes; *Bourbon s.n.* (P), Mascarenes; *Cadet 1704* (P), Mascarenes; *Frappier 395* (P), Mascarenes; *Friedmann 2482* (P), Mascarenes

Weinmannia tinctoria Sm., *Barthe s.n.* (P), Mascarenes; *Desvaux s.n.* (P), Mascarenes; *Frappier 397* (P), Mascarenes; *Kramer 9299* (MO), Mascarenes; *Lorence 2427* (MO), Mascarenes; *Lorence 2676* (MO), Mascarenes

Section *Fasciculata*

FAC-fraxinea 13 species

Weinmannia aphanoneura Airy Shaw, *Brunig S 8785* (L), Malaysia, Sarawak; *Chew Wee-Lek 380* (L), Malaysia, Sarawak; *Clemens 29476* (L), Malaysia, Sabah; *Clemens 33076* (L), Malaysia, Sabah; *Endert 4125* (L), Indonesia, Kalimantan; *Paie S 26531* (L), Malaysia, Sarawak

Weinmannia coodei H. C. Hopkins, *Coode 6197* (L; type), Indonesia, Sulawesi

Weinmannia devogelii H. C. Hopkins, *Balgooy 3809* (L), Indonesia, Sulawesi; *de Vogel 5682* (L), Indonesia, Sulawesi; *de Vogel 5959* (L), Indonesia, Sulawesi; *de Vogel 6122* (L; type) Indonesia, Sulawesi; *Meijer 11147* (L), Indonesia, Sulawesi; *Schmid 5512* (L, P), Indonesia, Sulawesi

Weinmannia dulitensis Airy Shaw, *Hopkins 5014* (MO), Malaysia, Sabah

Weinmannia exigua A. C. Sm., *Howard 89* (BISH), Fiji; *Whitmore BSIP 995* (BSIP, L), Solomon Islands

Weinmannia fraxinea Sm. ex D. Don, *Bradford 830* (MO), Solomon Islands; *Hopkins 5004* (MO), Malaysia, Sarawak; *Hopkins 5006* (MO), Malaysia, Sarawak; *Sargent s.n.* (MO), Indonesia "Journey Round the World"; *Takeuchi 7135* (MO), Papua New Guinea

Weinmannia furfuracea H. C. Hopkins, *Balgooy 3255* (L; paratype), Indonesia, Sulawesi; *Balgooy 3464* (L; paratype), Indonesia, Sulawesi; *bb 20787* (BO; paratype), Indonesia, Sulawesi; *Rutten 2231* (BO, L; paratype), Indonesia, Seram; *Tantra 1595* (L; type), Indonesia, Sulawesi

Weinmannia hutchinsonii Merr., *Elmer 14228* (MO), Philippines; *Elmer 14918* (MO), Philippines; *Ramos BS 23494* (MO), Philippines; *Wenzel 1088* (MO), Philippines

Weinmannia luzoniensis Vidal, *Elmer 18024* (MO), Philippines; *Vanoverbergh 1253* (MO), Philippines

Weinmannia macgillivrayi Seem., *Bourdy 322* (P), Vanuatu; *Kajewski 735* (BISH, P), Vanuatu; *Schmid 3557* (P), Vanuatu; *Schmid 5083* (NOU), Vanuatu

Weinmannia negrosensis Elmer, *Ramos BS 1287* (MO), Philippines; *Wenzel 1057* (MO), Philippines

Weinmannia richii A. Gray, *Hopkins 5023* (MO), Fiji; *Degener 14379* (F, MO), Fiji; *Smith 6813* (L, P), Fiji

Weinmannia ysabelensis Perry, *Brass 3215* (BO, L; type), Solomons

FAC-descombesiana 1 species

Weinmannia descombesiana Bernardi, *bb 20870* (L), Indonesia, Sulawesi; *bb 22981* (L, P; paratype), Indonesia, Sulawesi; *bb 26643* (L), Indonesia, Sulawesi; *bb s.n.* (L), Indonesia, Sulawesi; *Eyma 3590* (L), Indonesia, Sulawesi; *Kjellberg 1618* (S; type), Indonesia, Sulawesi

FAC-pullei 3 species

Weinmannia eymaeana H. C. Hopkins, *Eyma 3578* (BO, L; type), Indonesia, Sulawesi

Weinmannia pullei Schltr., *Hoogland 6979* (BISH, BO, L), Papua New Guinea; *Hoogland 7685* (L), Papua New Guinea; *Kalkman 4859* (BO, L), Papua New Guinea; *Robbins 3056* (L), Papua New Guinea; *Veldkamp 5493* (BISH, L), Papua New Guinea; *Vink 17098* (BO, L, P), Papua New Guinea; *Frodin NGF 26964* (BISH, L), Papua New Guinea

Weinmannia urdanetensis Elmer, *Bowers 401* (L), Papua New Guinea; *Hoogland 5463* (BISH, L), Papua New Guinea; *Hoogland 7254* (L), Papua New Guinea; *Kostermans 2304* (BO, L), Indonesia, Irian Jaya; *Paijmans 1315* (L), Papua New Guinea; *Sterly 80–40* (L), Papua New Guinea; *BW 5588* (L), Indonesia, Irian Jaya; *Robbins 191* (L), Papua New Guinea; *Takeuchi 6340* (MO), Papua New Guinea; *Wade ANU 7663* (L), Papua New Guinea; *Womersley NGF 15240* (L), Papua New Guinea

FAC-clemensiae 2 species

Weinmannia clemensiae Steenis, *Beaman 9132* (L), Malaysia, Sabah; *Beaman 9837* (L), Malaysia, Sabah; *Clemens 50793* (L), Malaysia, Sabah; *Clemens 50877* (L), Malaysia, Sabah; *Hopkins 5011* (MO), Malaysia, Sabah; *Chew RSNB 4508* (L, SAN), Malaysia, Sabah; *Chew RSNB 4755* (L, SAN), Malaysia, Sabah

Weinmannia hooglandii H. C. Hopkins & J. C. Bradford, *Symington 32246* (KEP), Peninsular Malaysia; *Whitmore FRI 12582* (KEP, L, SAN; type), Peninsular Malaysia

Section *Spicata*

SPI-bojeriana 16 species (in addition to the species cited below there are 7 undescribed species)

Weinmannia bojeriana Tul., *Bojer s.n.* (P; type), Madagascar; *Bosser 13321* (P), Madagascar; *Bradford 639* (MO), Madagascar; *Decary 5010* (P), Madagascar; *Decary 5366* (P), Madagascar; *Humbert 4849* (P), Madagascar; *Malcomber 1031* (MO), Madagascar; *Perrier 6433* (P), Madagascar

Weinmannia decora Tul., *Bernardi 11961* (P), Madagascar; *Bernier 324* (P; type), Madagascar; *R.N. 3452* (P), Madagascar; *S.F. 10167* (P), Madagascar; *SF 13228* (P), Madagascar

Weinmannia eriocarpa Tul., *Baillon s.n.* (P), Madagascar; *Bojer s.n.* (P; type), Madagascar; *Decary 15104* (P), Madagascar; *Dequaire 27809* (P), Madagascar; *Hildebrandt 3562* (P), Madagascar; *Baron 1674* (P), Madagascar

Weinmannia hildebrandtii Baill. var. *arguta* Bernardi, *Bradford 642* (MO), Madagascar; *S.F. 8848* (P; type of variety), Madagascar

Weinmannia humbertiana Bernardi, *Bradford 703* (MO), Madagascar; *Humbert 23532* (P), Madagascar; *Hum-*

bert 23814 (P; type), Madagascar; *Humbert 22505* (P), Madagascar

Weinmannia humblotii Baill. var. *humblotii*, *Baron 4434* (P; type of *W. leptostachya*), Madagascar; *Humbert 12074* (P), Madagascar; *Humblot 613* (P; type), Madagascar; *Weinmannia humblotii* var. *anceps* Bernardi, *Bradford 705* (MO), Madagascar; *Perrier de la Bâthie 6421* (P), Madagascar

Weinmannia mammea Bernardi, *Louvel 191* (P; type), Madagascar; *Morat 2803* (P), Madagascar; *Humbert 24496* (P), Madagascar; *Humbert 24781* (P), Madagascar

Weinmannia sanguisugarum Bernardi, *Bernardi 11999* (P; type), Madagascar; *Humbert 3823* (P), Madagascar; *Malcomber 2363* (MO), Madagascar

Weinmannia stenostachya Baker, *Baron 3148* (P; type of *W. fraxinifolia*), Madagascar; *Baron 6406* (P; type), Madagascar; *Benoist 1345* (P), Madagascar; *Leandri 1737* (P), Madagascar; *Perrier 6422* (P), Madagascar; *S.F. 12547* (P), Madagascar; *S.F. 3* (P), Madagascar

SPI-icacifolia 6 species (in addition to the species cited below there are 4 undescribed species)

Weinmannia hildebrandtii Baill., *Cours 4792* (P), Madagascar; *Hildebrandt 3695* (P; type), Madagascar; *S.F. 5809* (P), Madagascar; *S.F. 6240* (P), Madagascar

Weinmannia icacifolia Bernardi, *Perrier de la Bâthie 15346* (P), Madagascar; *Perrier de la Bâthie 16122* (P), Madagascar; *Perrier de la Bâthie 16464* (P; type), Madagascar

SPI-comorensis 5 species (in addition to the species cited below there is 1 undescribed species)

Weinmannia baehniana Bernardi, *Perrier de la Bâthie 6431* (P), Madagascar; *R.N. 1398* (P), Madagascar; *R.N. 1837* (P), Madagascar; *S.F. 10198* (P), Madagascar

Weinmannia comorensis Tul., *Boivin s.n.* (P; type), Madagascar; *Bosser 17997* (P), Madagascar; *Boureau 68* (TEF), Madagascar; *S.F. 16591* (P), Madagascar

Weinmannia lucens Baker, *Decary 13241* (P), Madagascar; *Humbert 28744* (P), Madagascar

Weinmannia minutiflora Baker, *Baron 2542* (P; type), Madagascar; *Jardin Botanique 4710* (P), Madagascar; *S.F. 9044* (P), Madagascar

Section *Inspersa*

INS-rutenbergii

Weinmannia hepaticarum Bernardi, *Humbert 23545* (P; type), Madagascar

Weinmannia rutenbergii Engl., *Chauvet 429* (P), Madagascar; *R.N. 1786* (P), Madagascar; *SF 13518* (P), Madagascar; *SF 18382* (P), Madagascar; *SF 21468* (P), Madagascar; *Cloisel 227* (P), Madagascar

INS-venusta

Weinmannia sp. nov. 1, *R.N. 111* (MO, P), Madagascar; *Bradford 655* (MO), Madagascar; *R.N. 2853* (P), Madagascar; *S.F. 5464* (P), Madagascar; *S.F. 24061* (P), Madagascar; *Raharimalala 295* (P), Madagascar

Weinmannia venusta Bernardi, *Humbert 21944* (P; type), Madagascar; *Capuron, S.F. 27632* (P), Madagascar; *Christophe S.F. 17610* (TEF), Madagascar; *S.F. 17231* (TEF), Madagascar

INS-louveliana 3 species (in addition to the species cited below there is 1 undescribed species)

Weinmannia commersonii Bernardi, *S.F. 16718* (TEF), Madagascar; *S.F. 21528* (TEF), Madagascar; *Vegreux 42* (P), Madagascar; *Perrier de la Bâthie 14263* (P; type), Madagascar; *S.F. 10164* (P), Madagascar

Weinmannia louveliana Bernardi, *S.F. 9669* (P), Madagascar; *S.F. 5182* (P), Madagascar; *R.N. 6211* (P; type), Madagascar; *S.F. 10402* (P), Madagascar

INS-madagascariensis 2 species

Weinmannia henricorum Bernardi, *Humbert 7018* (P; type), Madagascar

Weinmannia madagascariensis DC. ex Ser., *S.F. 17814* (P), Madagascar; *Bradford 660* (MO), Madagascar; *Dumetz 535* (P), Madagascar; *S.F. 17814* (P), Madagascar; *Weinmannia madagascariensis* var. *aniba* Bernardi, *R.N. 9765* (P; type of variety *aniba*), Madagascar

Section *Leiospermum*

LEI-serrata 5 species

Weinmannia dichotoma Brongn. & Gris, *MacKee 15000* (P), New Caledonia; *MacKee 18867* (P), New Caledonia; *MacKee 31635* (P), New Caledonia; *Schmid 4135* (P), New Caledonia; *Veillon 1914* (P), New Caledonia; *Veillon 3839* (P), New Caledonia

Weinmannia monticola Däniker, *Aubréville 230* (P), New Caledonia; *Hürlimann 1875* (P), New Caledonia; *Jaffré 2707* (P), New Caledonia; *MacKee 44406* (P), New Caledonia; *McPherson 5809* (MO), New Caledonia; *Veillon 750* (P), New Caledonia

Weinmannia ouaiemensis (Guill. & Virot) Hoogland, *MacKee 18670* (P), New Caledonia; *MacKee 34088* (P), New Caledonia; *MacKee 35993* (P), New Caledonia; *MacKee 36001* (P), New Caledonia; *Schmid 3370* (P), New Caledonia; *Veillon 2273* (P), New Caledonia; *Virot 731* (P; type), New Caledonia

Weinmannia paitensis Schltr., *Bernardi 9881* (P), New Caledonia; *McPherson 3403* (MO), New Caledonia; *Schlechter 14941* (P; type), New Caledonia; *Thorne 28733* (P), New Caledonia

Weinmannia serrata Brongn. & Gris, *Balansa 2298* (P), New Caledonia; *Bernardi 12816* (P), New Caledonia; *Bradford 627* (MO), New Caledonia; *Brinon 746* (P), New Caledonia; *MacKee 35545* (P), New Caledonia; *Raynal 16608* (P), New Caledonia; *Thiebaut 22* (P), New Caledonia

LEI-sylvicola 1 species

Weinmannia sylvicola Sol. ex A. Cunn., *Bradford 912* (MO), New Zealand; *Gardner 1621* (MO), New Zealand; *Gardner 2659* (MO), New Zealand; *Gardner 5384* (MO), New Zealand; *Orchard 4048* (MO), New Zealand; *Walker 5243* (MO), New Zealand

LEI-racemosa 1 species

Weinmannia racemosa L.f., *Bradford 910* (MO), New Zealand; *Chapman CHR 258594* (MO), New Zealand; *Loh CHR 359035* (MO), New Zealand; *Gardner 169* (MO), New Zealand; *Gardner 5350* (MO), New Zealand; *Thompson 526* (MO), New Zealand; *Wood 31653* (MO), New Zealand

LEI-affinis 15 species (in addition to the species cited below there are 2 undescribed species)

Weinmannia affinis A. Gray, *Bradford 597* (MO), Fiji; *Gibbs 642* (BISH), Fiji; *Hopkins 5022* (MO), Fiji; *Seemann 200* (P), Fiji; *Smith 4905* (BISH, L, P), Fiji;

Smith 7608 (BISH, L, P, SUVA), Fiji; *U.S. Expl. Exped. US 48070* (US; type), Fiji

Weinmannia croftii H. C. Hopkins, *Clunie LAE 63017* (K, L; paratype), Papua New Guinea; *Ridsdale NGF 33981* (BISH, L; type) Papua New Guinea; *Stevens LAE 51252* (L; paratype) Papua New Guinea; *Vinas LAE 59724* (BISH, L; paratype), Papua New Guinea

Weinmannia denhamii Seem., *Aubert de la Rüe s.n.* (P), Vanuatu; *Bernardi 13258* (L, P), Vanuatu; *Morat 5897* (NOU, P), Vanuatu; *Kajewski 317* (BISH, P), Vanuatu; *MacGillivray 45* (P; isolectotype), Vanuatu

Weinmannia marquesana F. Br., *N. Hallé 2057* (P), Marquesas; *Perlman 10259* (BISH, MO, P), Marquesas; *Weinmannia marquesana* var. *myrsinites*, *Florence 9667* (MO), Marquesas

Weinmannia parviflora G. Forst., *Bradford 920* (MO), Society Islands, Tahiti; *Florence 3110* (P), Society Islands, Tahiti; *Florence 7935* (P), Society Islands; *Fosberg 62927* (BISH, P), Society Islands, Tahiti

Weinmannia purpurea Perry, *Kajewski 1738* (L; type), Papua New Guinea; *Kajewski s.n.* (L), Solomon Islands; *Mauriasi BSIP 12092* (BSIP, L), Solomons

Weinmannia raiateensis J. W. Moore, *Bradford 929* (MO), Society Islands, Raiatea; *Florence 3554* (P), Society Islands, Raiatea; *Florence 3746* (P), Society Islands, Raiatea; *Florence 3754* (P), Society Islands, Raiatea; *Florence 8945* (P), Society Islands, Raiatea; *B. H. Gagné 1457 bis* (P), Society Islands, Raiatea

Weinmannia rapensis F. Br., *Florence 6395* (MO), Rapa; *Florence 6514* (P), Rapa; *Hallé 7517* (P), Rapa; *N. Hallé 7700* (P), Rapa; *St. John 15304* (P), Rapa; *St. John 15305* (P), Rapa

Weinmannia rarotongensis Hemsl. ex Cheeseman, *Gardner 2503* (MO), Rarotonga; *MacKee 44191* (P), Rarotonga; *MacKee 44309* (MO, P), Rarotonga

Weinmannia samoensis A. Gray, *Bradford 800* (MO), Upulo, Western Samoa; *Bradford 807* (MO), Savaii, Western Samoa; *Christophersen 1943* (BISH, MO), Samoa; *U.S. Expl. Exped. US 48072* (US; type), Samoa

Weinmannia tremuloides H. C. Hopkins & Florence, *Florence 9581* (P; type), Marquesas Islands

Weinmannia vescoi Drake, *Bradford 932* (MO), Society Islands, Raitea; *Florence 8991* (P), Society Islands, Raiatea; *Morat 6990* (P), Society Islands, Raiatea; *St. John 17255* (P), Society Islands, Raiatea; *Vescoi s.n.* (P; type), Society Islands

Weinmannia vitiensis Seem., *Bryan 317* (BISH), Fiji; *Hopkins 5041* (MO), Fiji; *Seemann 199* (P; type), Fiji

Cunonia

Cunonia-macrophylla 3 species

Cunonia macrophylla Brongn. & Gris, *Bradford 607* (MO), New Caledonia; *McPherson 5387* (MO), New Caledonia; *McPherson 2277* (MO), New Caledonia

Cunonia capensis L., *Bradford 735* (MO), United States (Cultivated); *Goldblatt 1387* (MO), South Africa; *Rouske 734* (MO), South Africa; *Werdermann 2441* (MO), South Africa

Cunonia schinziana Däniker, *Däniker 506* (P; type), New Caledonia; *MacKee 17799* (P), New Caledonia; *MacKee 27546* (P), New Caledonia; *MacKee 38224* (P), New Caledonia

Cunonia-purpurea 13 species

Cunonia atrorubens Schltr., *Bradford 614* (MO), New Caledonia; *McPherson 2004* (MO), New Caledonia; *McPherson 2227* (MO), New Caledonia; *McPherson 4442* (MO), New Caledonia

Cunonia austrocaledonica Brongn. ex Guill., *Hoogland 12904* (MO), New Caledonia; *McPherson 1876* (MO), New Caledonia; *McPherson 1944* (MO), New Caledonia; *McPherson 3434* (MO), New Caledonia

Cunonia cerifera Hoogland, *McPherson 4450* (P; paratype), New Caledonia

Cunonia deplanchei Brongn. & Gris, *McPherson 4364* (MO), New Caledonia; *McPherson 6429* (MO), New Caledonia

Cunonia lenormandii Vieill. ex Brongn. & Gris, *McPherson 6418* (MO), New Caledonia

Cunonia linearisepala (Guill.) Bernardi, *McPherson 2878* (MO), New Caledonia

Cunonia nervosa Hoogland, *MacKee 15715* (P; type), New Caledonia

Cunonia pseudoverticillata Guill., *Blanchon 196* (P), New Caledonia

Cunonia pterophylla Schltr., *McPherson 2119* (MO), New Caledonia; *McPherson 4445* (MO), New Caledonia; *McPherson 2163* (MO), New Caledonia

Cunonia purpurea Brongn. & Gris, *McPherson 2082* (MO), New Caledonia; *McPherson 2637* (MO), New Caledonia; *McPherson 4396* (MO), New Caledonia

Cunonia rupicola Hoogland, *MacKee 19129* (P; type), New Caledonia

Cunonia varijuga Hoogland, *MacKee 22886* (P; type), New Caledonia

Cunonia vieillardii Brongn. & Gris, *McPherson 3998* (P), New Caledonia; *McPherson 4634* (MO), New Caledonia; *McPherson 4535* (MO), New Caledonia

Cunonia-aoupiniensis 2 species

Cunonia aoupiniensis Hoogland, *Morat 7977* (P; paratype), New Caledonia

Cunonia montana Schltr., *Bradford 609* (MO), New Caledonia; *McPherson 2930* (MO), New Caledonia; *Bernardi 12729* (MO), New Caledonia

Cunonia-balansae 2 species

Cunonia balansae Brongn. & Gris, *Bradford 617* (MO), New Caledonia; *McPherson 3313* (MO), New Caledonia; *McPherson 4127* (MO), New Caledonia; *Hoogland 12731* (MO), New Caledonia

Cunonia rotundifolia Däniker, *Jaffré 1954* (P), New Caledonia

Cunonia-alticola 2 species

Cunonia alticola Guill., *Bradford 611* (MO), New Caledonia

Cunonia bernieri Guill., *Morat 7660* (P), New Caledonia

Cunonia pulchella

Cunonia pulchella Brongn. & Gris, *Bradford 635* (MO), New Caledonia; *McPherson 4037* (MO), New Caledonia; *McPherson 6034* (MO), New Caledonia

Cunonia bullata

Cunonia bullata Brongn. & Gris, *McPherson 2241* (MO), New Caledonia

Outgroups

Ackama

Ackama rosifolia A. Cunn., *Bradford 909*, New Zealand

(MO); *Gardner 358*, New Zealand (MO); *Jessup s.n.*, New Zealand (MO#1616100); *Orchard 4040*, New Zealand (MO)

Caldcluvia

Caldcluvia paniculata D. Don, *Landrum 4476* (MO), Chile; *Morrison 17552* (MO), Chile; *Werdermann 681* (MO), Chile; *Werdermann 1855* (MO), Chile; *Zöllner 9639* (MO), Chile

Spiraeopsis

Spiraeopsis celebica Blume, *Bradford 834* (MO), Solomon Islands; *Bradford 840* (MO), Solomon Islands; *Elmer 11402* (MO), Philippines; *Elmer 14157* (MO), Philippines; *Elmer 15184* (MO), Philippines; *Wenzel 1087* (MO), Philippines

Vesselowskya

Vesselowskya rubifolia Pamp., *Boorman NSW 104729* (NSW), Australia; *Bradford 879* (MO), Australia; *Bradford 882* (MO), Australia; *Coveny 5676* (MO, NSW), Australia; *Coveny 10877* (MO, NSW), Australia; *Fraser s.n. NSW 104749* (MO, NSW), Australia; *Webb 11474* (MO), Australia

APPENDIX 2

List of possible autapomorphies for each ingroup OTU. Some assumptions of relationships were needed to hypothesize derived states. For example, comparisons of character states were made within sections, and the most generalized character state was usually considered primitive.

WEI-pinnata: caducous petals (not present in all species, see discussion)
WEI-tinctoria: unisexual flowers
SPI-bojeriana: solitary flowers, double internode of branches
SPI-icacifolia: no clear autapomorphies
SPI-comorensis: no IM
INS-rutenbergii: double internode of branches
INS-louveliana: solitary flowers
INS-madagascariensis: no clear autapomorphies
INS-venusta: IM branching
FAC-fraxinea: fixed supernumerary IMs
FAC-descombesiana: solitary flowers (has hybrid-like characteristics between sects. *Fasciculata* and *Leiospermum*)
FAC-pullei: abortion of medial meristem
FAC-clemensiae: no clear autapomorphies
LEI-serrata: no clear autapomorphies
LEI-affinis: unisexual flowers
LEI-sylvicola: IM with two internodes and terminal abortion
LEI-racemosa: no lateral IMs, IM terminus a bud
Cunonia-macrophylla: large flowers, no medial meristem abortion, racemes borne directly along main stem
Cunonia-purpurea: no clear autapomorphies
Cunonia-aoupiniensis: lateral and medial IMs
Cunonia-balansae: medial IMs only
Cunonia bullata: IM with terminal raceme
Cunonia-alticola: sessile flowers
Cunonia pulchella: fascicled flowers

APPENDIX 3

CHARACTERS USED IN THE CLADISTIC ANALYSIS.

Numbers after character states refer to the coding in the data matrix as shown in Appendix 4. The plesiomorphic condition implied by the outgroups is listed first (state 0). Illustrations for many of these characters can be found in Bernardi (1961, 1963b, 1964, 1965) and Hopkins (1998a).

Vegetative Characters

(1) Persistent, fused lateral stipules: present (0), absent (1).

Stipule pairs that enclose lateral buds may be fused at their base. Even when most of the stipule has fallen off, the fused tissue may leave a "collar" around the base of the young branches. The lateral stipules may rarely be barely fused in section *Fasciculata*, but they do not persist as "collars."

(2) Morphology of branches: basal bud absent (0), basal bud present (1), double internode present (2).

Three different branch morphologies were observed. In one, the first metamer produced by the lateral bud consists of an internode of normal length with a normal pair of leaves at the first node. In another pattern, a first internode of normal length is formed, but with buds at the base of this internode that are oriented in a plane perpendicular to the leaf axil ("basal bud" form). These basal buds appear to be homologous to axillary buds at a node. This homology becomes apparent in the third pattern of branch development. Here, the first metamer consists of a short internode without leaf development at the node, but with axillary buds produced ("double internode" form). Only the second metamer of this type of branch shows standard development of internode and leaves. This is treated as an ordered character, because the basal bud form is considered intermediate between the other conditions.

Taxa with basal buds often produce stems from them. This is especially true for section *Leiospermum*, in which the dominant medial and distal-lateral meristems are committed to reproduction. The double internode form is most pronounced in *Cunonia*.

(3) Abortion of medial meristem: absent (0), present (1).

Some groups have the tendency to abort the medial meristem. This branching pattern produces two new dominant stems, rather than a medial dominant stem plus a pair of suppressed lateral stems. Whenever this occurs as part of the branching pattern of a species it is scored as present. Only the New Caledonian species *W. dichotoma* and *W. monticola* branch this way at every node.

(4) Lateral bud formation: additional pair(s) (0), one pair only (1).

Among OTUs, the number of axillary buds formed at a node varies. In some OTUs, only a single, usually prominent bud is formed. In other groups, a large axillary bud develops along with a second, smaller bud that is positioned between the large bud and the adaxial leaf surface. Because of its small size, this bud is often difficult to see, but when the large bud develops into a lateral branch the small bud may enlarge. Usually the small bud does not develop and may fall off quickly or persist during stem thickening. In section *Fasciculata*, many species also produce additional axillary buds at a node, but with no clear dominance among buds so that the extra buds are more easily visible. The additional buds in many species of section *Fasciculata* often develop into lateral IMs to form a series of IMs at a node. This is scored by character 31.

Flower and Fruit Characters

(5) Pedicels: present (0), absent (1).

In section *Spicata* the pedicel is so short that the receptacle lies against the axis of the raceme, although it is not fused to the axis. This condition is scored as "pedicel absent." However, this character must be scored in flower, as some species develop a slender pedicel in fruit. A few species (e.g., *W. comorensis*) have a narrow, elongate receptacle that resembles a pedicel but is here considered non-homologous. See Bernardi (1964: tabs. 1–9; 1965: figs. 1–7) for illustrations.

(6) Calyx aestivation: valvate (0), imbricate (1).

Imbricate calyx aestivation is considered a synapomorphy for the *Cunonia(Pancheria–Weinmannia)* clade. Hufford and Dickison (1992) reported imbricate calyx aestivation in *Vesselowskya*, but the specimens examined for this study show valvate aestivation.

(7) Calyx persistence in fruit: present (0), absent (1).

This character is scored during fruit maturation. A score of "present" indicates that the calyx remains on mature fruits, while "absent" means that the calyx falls off during fruit maturation.

(8) Number of perianth parts: 5-merous (0), 4-merous (1), 3-merous (2).

In most OTUs the perianth tends to be either 4-merous or 5-merous, with the same number of sepals as petals. Only *Vesselowskya* has a 3-merous perianth.

(9) Free nectary disk: present (0), absent (1).

The floral receptacle bears tissue between the staminal whorl and the gynoecium, or as ribbed outgrowths at the base of the outer carpel wall. Traditionally, these tissues have been called nectaries. Whether nectar is produced has not been examined carefully, but it is likely since commercial honey is produced from *Weinmannia* flowers (Walsh, 1978; Matheson, 1991; Ralimanana, 1994). Most Cunoniaceae have free nectaries, developing unattached to the carpel wall. The nectaries of *Cunonia* are adnate to the carpel wall.

(10) Form of the nectary: segmented (0), ribbed (1), membranous (2).

Free nectaries are found in different shapes. Ribbed nectaries form a complete ring with alternating, longitudinal costae of varying thickness corresponding to the position of stamens. Membranous nectaries form an entire ring of thin tissue. Segmented nectaries do not form a continuous ring, but are composed of more or less separate, often slender parts usually positioned between the stamens.

(11) Floral sexuality: bisexual only (0), early unisexual (1), late unisexual (2), complete unisexual (3).

The sexual system of *Weinmannia* has been little studied. In most species with unisexual flowers, it appears that unisexual flowers are mostly distributed on different individuals (i.e., dioecious), but strict dioecy probably breaks down often. For example, sometimes both sexes, or bisexual and unisexual flowers, are found on the same plant (i.e., "leaky dioecy" or polygamodioecy). For this analysis, the potential to develop unisexual flowers was scored, even when bisexual flowers were known from a species. When unisexual flowers were unknown this was coded as bisexual only. See illustrations in Bernardi (1964).

There seem to be two distinct kinds of unisexual flowers in *Weinmannia*. The most common has relatively early suppression of the opposite sex, so that the carpels are very tiny in male flowers and the stamens weakly developed in female flowers. Two species of section *Weinmannia* from the Mascarene islands have flowers that are less conspicuously unisexual because sexual dimorphism is not very great. These are coded as a distinct kind of unisexual flower that is presumably caused by late suppression of the opposite sex. A third type of development is found in *Vesselowskya rubifolia*, which has extreme suppression of parts of the opposite sex so that stamens do not develop in female flowers and carpels do not develop in male flowers.

(12) Position of the perianth: hypogynous (0), perigynous (1).

Most OTUs have hypogynous flowers with a fairly broad, flat receptacle upon which the carpel is borne at the same level as the perianth. In several species of section *Leiospermum* the carpel is sunken slightly into a narrowly concave receptacle with the perianth borne above the base of the carpel. These are scored as being perigynous.

(13) Fruit dehiscence: basipetal (0), circumbasal (1).

Circumbasal fruit dehiscence occurs when a zone at the base of the carpel splits from the receptacle. Usually this results in acropetal dehiscence (i.e., the capsule opens from the bottom up) along the sutures between the carpels, but circumbasal dehiscence is a more precise description of the difference between *Cunonia* and most other Cunoniaceae. Most *Cunonia* have styles that remain connate at the base, causing acropetal fruit dehiscence. A few *Cunonia* species lack stylar fusion, and the dehiscence is non-directional along the longitudinal suture between the carpels although circumbasal dehiscence is present. When the capsule splits open from the top, dehiscence is basipetal, as in *Weinmannia* and most other capsular-fruited Cunoniaceae.

(14) Fruit column: split pair (0), fused (1).

All OTUs have fruits composed of two united carpels that dehisce along their sutures, exposing two locules full of seeds. The seeds are borne in two rows in each locule, along axile placentae (Dickison, 1975, 1984). The degree of fusion of the placentae varies, being completely fused into a single column, or fused into a pair of bundles, with each bundle composed of the opposing edges of adjacent carpels. This character is easily visible as the carpels split in the mature fruit.

Weinmannia, *Cunonia*, and *Vesselowskya* have a single central column. In many species this central column is prominent because it remains intact and upright between the separate carpels after fruit dehiscence. In other groups the column is less conspicuous because it remains partially attached to one edge of a carpel, and after fruit dehiscence only a single, short stub remains near the receptacle. *Ackama* has a pair of columns that adheres to the carpels during dehiscence. Only by examining the fruit near the receptacle can the pair of columns be seen. In contrast, *Caldcluvia* and *Spiraeopsis* have conspicuous pairs of columns that are detached from the carpel edges in fruit, but remain attached to the styles. These different patterns of fruit column morphology were illustrated by Godley (1983), although he did not notice the subtle vascular pair in *Ackama* and its underlying similarity to the columns of *Caldcluvia*.

(15) Seed wings: present (0), absent (1).

When flattened tissue extends around the seed then wings were coded as "present." Many *Weinmannia* species have a minute raphe along one side of the seed coat that may be homologous with the wings of other taxa (Dickison, 1984; Webb & Simpson, 1991). These were not coded as wings "present" because they are very small. Because minute wings occur, wings and hairs appear to be ontogenetically unrelated, and the two features were treated as separate characters, although they may serve the same function in seed dispersal.

(16) Seed hairs: absent (0), present (1).

Long, slender, unicellular outgrowths from the seed coat are found in all species of *Weinmannia* and *Ackama* (Dickison, 1984; Webb & Simpson, 1991).

(17) Distribution of hairs on seeds: sparse and widely distributed (0), comose at both ends (1), dense and widely distributed (2).

According to Dickison (1984), there are three basic patterns of hair distribution and density in *Weinmannia*. This more extensive survey largely agrees, although the distinction between the patterns is not always clear. Comose seeds have hairs concentrated at both ends in dense tufts. Otherwise, hairs are more or less evenly distributed around the seed and may be either so dense that the seed surface is obscured, or sparse, with the seed surface visible.

Many species are fixed for one of these patterns, but a few are highly variable and must be scored as polymorphic. For example, many members of section *Spicata* have comose hairs and hairs sparsely distributed on the same seed. In a few species of section *Fasciculata*, some specimens have comose seeds and other specimens have seeds with dense hairs all over the surface.

(18) Seed shape: straight (0), reniform (1).

Most seeds are straight or only slightly asymmetrical. Asymmetry is most pronounced in section *Weinmannia*, in which the seeds have a curved shape so that a line from one pole to the other would pass far from the center.

Floral Axis/Raceme Characters

(19) Floral inception: solitary (0), fasciculate (1).

Floral meristems develop in the axils of small bracts in all OTUs (Fig. 1). In some groups, a few to several floral meristems develop in each bract axil, and in others only a single floral meristem develops. The development of multiple floral meristems at a bract often results in fasciculate flowers (but see character 20 "bract fidelity"), while a solitary flower develops from a single meristem. Taxa with fasciculate inception of flowers have a large bract subtending the entire fascicle and smaller "bracteoles" subtending the individual flowers.

This character may vary within a raceme, but this variation is usually minor and occurs predictably, with solitary flowers at the very tip of the raceme and fasciculate flowers along most of the axis. A few American species of section *Weinmannia* living in extremely exposed, upland habitats have highly reduced racemes with relatively few flowers. In these species the flowers all arise solitarily. Because this feature is correlated with specialized ecology, solitary flowers within section *Weinmannia* are assumed to be a derived condition and were not scored in the matrix.

(20) Bract fidelity: present (0), absent (1).

Although flowers are initiated from bract axils, not all flowers remain in this position during the development of the raceme (Fig. 1). The elongation of the raceme axis may cause the separation from one another of flowers that were initiated at the same position. When mature flowers remain in the axil of their bract, then bract fidelity is said to be "present." When flowers move relative to the bract, due to a visible zone of elongation among the flowers, then bract fidelity is "absent."

(21) Persistence of floral bract: absent (0), present (1).

This character is scored around the time of floral maturity, such as when the anthers dehisce. Precise timing is difficult, because specimens are not collected at uniform developmental stages. If the bracts are consistently or firmly attached to the axis, not just hanging on loosely after abscision, persistence is coded as "present."

(22) Flower-bearing axis: branched (0), unbranched (1).

Vegetative branching in Cunoniaceae is almost uniformly decussate. In contrast, flower-bearing axes usually have a spiral arrangement of nodes. A distinction can be made between unbranched flower-bearing axes, which bear floral meristems only at the nodes, and branched axes, which give rise to both lateral inflorescence branches and floral meristems.

The term "raceme" is used here to denote any unbranched, flower-bearing axis. Family-level cladograms (Hufford & Dickison, 1992) imply that racemes are derived from branched flower-bearing axes. In fact, the morphology of fascicled-flowered racemes (character 19) suggests that they may be derived from branched flower-bearing axes through the suppression of lateral branching and elongation of the primary axis. For example, on occasion lateral branching is not totally suppressed in a fascicled-flowered raceme, and at the base of an axis short branches may arise. This implies that a group of fascicled flowers may be homologous to a short shoot of solitary ones, an hypothesis that also accounts for the presence of bracteoles subtending individual flowers in a fascicle. If fascicled-flowered racemes are derived from branched flower-bearing axes, then this character state (see character 19) is expected to be plesiomorphic in *Weinmannia*.

(23) Racemes arising as split pairs: present (0), absent (1).

In some taxa, raceme meristems have the tendency (i.e., this character is not always expressed) to split and form a pair of racemes from a single initial. Often, the pair of racemes is united by common rachis tissue near their base.

Inflorescence-Module (IM) Characters

(24) Development of flower-bearing axes as part of IMs: present (0), absent (1).

Species of section *Weinmannia* (Fig. 2c) and a few of section *Spicata* (Fig. 3d) have flower-bearing axes only developing directly from axillary buds along the main stem. Other taxa develop racemes as parts of an IM. IMs are recognized as distinct from vegetative metamers by such characteristics as usually shortened internodes, complete or partial suppression of leaf development, and distinct branch morphology.

(25) IM shoot: long (0), short (1).

The internodes within an IM are very short relative to vegetative internodes in most *Weinmannia* species. In sections *Leiospermum* and *Cunonia*, IM internodes are similar in length to vegetative ones.

(26) Fate of IM terminus: flower-bearing axis (0), vegetative bud (1), aborted (2).

This character accounts for what happens to the dominant apical meristem within an IM. There are three meristem fates: vegetative bud (Figs. 2b, 3a), flower-bearing axis (Figs. 2a, 3e), or aborted (Fig. 3b, c). Taxa that have vegetative buds terminating the IM often develop vegetative branches after fruiting.

(27) IM metamer development: branched (0), sequential (1), uninodal (2).

IMs may be composed of one to several metamers. In many species of *Weinmannia* and *Cunonia*, the IM is limited to a single raceme-bearing metamer (uninodal; Figs. 2b, 3a, b). Species in section *Leiospermum* and some members of section *Inspersa* have IMs with the potential to develop more than one metamer in a sequence, without branching, and with racemes at each node (sequential;

Figs. 2a, 3c). A pair of species in section *Inspersa* have racemes borne at the ends of a decussate-branched module (branched; Fig. 3e).

As mentioned previously, *Weinmannia dichotoma* and *W. monticola* have a fixed vegetative architecture in which the medial meristem at each node is aborted (Fig. 3b). This architecture is carried into the inflorescence in these species and precludes development of two medial metamers in a sequence. Here, this is regarded as a derived condition and is not included in the data matrix. Instead *W. dichotoma* and *W. monticola* have been placed in an OTU with all other New Caledonian species (*W. ouaiemensis*, *W. paitensis*, and *W. serrata*).

Total Inflorescence (TI) Characters

(28) Flower-bearing axis borne along the main stem: absent (0), present (1).

This character distinguishes whether nodes along the main stem axis bear racemes directly from axillary buds. However, direct development of racemes from axillary buds of the main stem does not preclude the development of racemes as part of an IM.

(29) Position of IM: lateral only (0), lateral and medial (1), medial only (2).

This refers to the location of IMs relative to the main axis of stem growth. Lateral IMs develop from axillary buds. A medial IM develops from medial, apical buds. This character is inapplicable when racemes only develop directly from meristems along the main stem, e.g., in section *Weinmannia* (Fig. 2c) and the *W. comorensis* group (Fig. 3d) of section *Spicata*, for which characters 24 and 28 are coded as state 1.

(30) TI formed by more than one main stem metamer: present (0), absent (1).

This character scores whether the main stem produces racemes or IMs at successive nodes. For example, this character is scored "absent" for Figure 2c and "present" for Figure 3d.

(31) TI dominance: basitonic (0), isotonic (1), acrotonic (2)

The size or proliferation of IMs or flower-bearing axes may depend on their position within the TI. Isotonic TIs have IMs or flower-bearing axes of the same size at all nodes. Basitonic TIs have larger basal, subdistal metamers, while acrotonic TIs have larger distal metamers.

Acrotonic development is manifested in two distinct ways in *Weinmannia*, but scored as the same character state: variation in the number of metamers within an IM (e.g., sect. *Leiospermum*, Fig. 2a), and variation in the number of IMs at a node in response to the position within the TI (e.g., sect. *Fasciculata*, Fig. 3a).

APPENDIX 4

Character matrix. See Appendix 1 for composition of OTUs, and Appendix 3 for discussion of characters.

OTUs/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
WEI-pinnata (73 sp)	1	0	0	0	0	1	0	1	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	-	-	-	1	-	1	-
WEI-tinctoria (2 sp)	1	0	0	0	0	1	0	0	0	1	2	0	0	1	1	1	0	1	1	0	1	1	0	1	-	-	-	1	-	1	-
SPI-bojeriana (16 sp)	0	2	1	1	1	1	0	0	0	2	0	0	0	1	1	1	0/1	0	0	1	0/1	1	1	0	1	1	2	1	1	0	1
SPI-icacifolia (6 sp)	0	1	1	1	1	1	0	0	0	2	0	0	0	1	1	1	1	0	1	1	0/1	1	1	0	1	1	2	1	1	0	1
SPI-comorensis (5 sp)	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0/1	1	1	1	-	-	-	1	-	0	-
INS-rutenbergii (2 sp)	0	2	1	1	0	1	0	0	0	1	0	0	0	1	1	1	2	0	0	0	1	1	1	0	1	0/1	0/1	0	0	0	0
INS-louveliana (3sp)	0	1	1	1	0	1	0	0	0	1	0	0	0	1	1	1	2	0	0	1	1	1	1	0	1	1	2	1	1	0	1
INS-madagascariensis (2 sp)	0	1	1	1	0	1	0	0	0	1	0	0	0	1	1	1	2	0	1	1	1	1	1	0	1	1	2	1	1	0	1
INS-venusta (2 sp)	0	1	1	1	0	1	0	0	0	1	0	0	0	1	1	1	2	0	1	0	1	1	1	0	0/1	0/1	0	0	1	0	0
FAC-fraxinea (12 sp)	1	0	0	0	0	1	0/1	1	0	0	1	0	0	1	1	1	1	0	1	0/1	0/1	1	0	0	1	1	2	0	1	0	2
FAC-descombesiana (1 sp)	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	1	2	0	1	0	2
FAC-pullei (3 sp)	1	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0/1/2	0	1	0	1	1	1	0	1	1	2	0	1	0	1
FAC-clemensiae (2 sp)	1	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0/1	0	1	0	1	1	1	0	1	1	2	0	1	0	1
LEI-serrata (5 sp)	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0/2	1	0	1	0	2
LEI-affinis (14 sp)	0	1	1	1	0	1	1	1	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	0	2
LEI-sylvicola (1 sp)	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	2	1	0	1	0	2
LEI-racemosa (1 sp)	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	1/2	1	0	2	-	-
Cunonia-macrophylla (3 sp)	0	2	0	1	0	1	1	0	1	-	0/1	0	1	1	0	0	-	0	0/1	0	0	1	1	0/1	1	1	2	1	0	1	-
Cunonia-purpurea (13 sp)	0	2	1	1	0	1	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	1	1	0	0	1	2	0	0	0	1
Cunonia-aoupiniensis (2 sp)	0	2	1	1	0	1	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	1	1	0	0	1	2	0	1	1	-
Cunonia-balansae (2 sp)	0	2	1	1	0	1	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	1	1	0	0	1	2	0	2	-	-
Cunonia bullata (1 sp)	0	2	1	1	0	1	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	1	1	0	0	0	2	0	0	0	1
Cunonia-alticola (2 sp)	0	2	1	1	1	1	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	1	1	0	0	1	2	0	0	0	1
Cunonia pulchella (1 sp)	0	2	1	1	0	1	1	0	1	-	0	0	1	1	0	0	-	0	1	0	0	1	1	0	0	1	2	0	0	0	1
Caldcluvia paniculata	1	2	0	1	0	0	1	1	0	0	0	0	0	0	0	0	-	0	0	0	1	0	-	1	-	-	-	1	-	0	0
Spiraeopsis celebica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0/1	0	0	0	-	1	-	-	-	1	-	0	1
Vesselowskya rubifolia	1	0	0	0	0	0	1	2	0	0	3	0	0	1	0	0	-	0	0	0	0/1	1	0	0	0	0/1	0	0	0	0	1
Ackama rosifolia	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	-	1	-	-	-	1	-	0	0

TAXONOMIC REVISION OF *GERANIUM* SECTIONS *BATRACHIOIDEA* AND *DIVARICATA* (GERANIACEAE)[1]

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ABSTRACT

Geranium subg. *Robertium* (Geraniaceae) comprises eight sections, of which section *Batrachioidea* and section *Divaricata* are revised here. *Geranium* sect. *Batrachioidea* consists of four species centered in Eurasia, between the Mediterranean region and the Himalaya Mountains, although they have also expanded to many temperate areas in America, South Africa, and Australia. In contrast to the current literature, we consider *G. brutium* to be a synonym of *G. molle*. We also accept *G. aequale* to include plants similar to *G. molle* but with smooth mericarps. *Geranium* sect. *Divaricata* comprises two species, one widespread between the Mediterranean region and the Himalaya Mountains and the other endemic to the Caucasus. A cladistic analysis using a data set of 15 characters showed that both sections are well supported by synapomorphic features. Conversely, no new character (other than pollen color) was found to support a relationship between them. Brief accounts are also given of chromosome number, hybrids, and diagnostic aspects of morphology. Nomenclature for all species is reviewed, 32 lectotypes are designated, and descriptions, distribution maps, and illustrations are provided.

The genus *Geranium* L. (Geraniaceae) is distributed throughout most of the world. A brief history of generic delimitation and infrageneric classification, as well as a description of the genus, can be found in Aedo (1996). *Geranium* comprises about 430 species and is divided, according to the currently accepted classification (Yeo, 1984), into three subgenera: subg. *Geranium*, subg. *Erodioidea* (Picard) Yeo, and subg. *Robertium* (Picard) Rouy. Only subgenus *Erodioidea* has been monographed recently (Aedo, 1996). *Geranium* subg. *Geranium* comprises over 380 species, grouped in at least 10 sections. Some of these sections have been revised (Davis, 1970; Carlquist & Bissing, 1976), but much more work is necessary to attain a satisfactory knowledge of subgenus *Geranium*.

Geranium sects. *Batrachioidea* W. D. J. Koch and *Divaricata* Rouy, the taxa studied here, belong to subgenus *Robertium*, which is firmly supported by both morphological and chloroplast-DNA data (Yeo, 1984; Price & Palmer, 1993). According to Yeo's (1984) sectional classification, subgenus *Robertium* comprises eight sections and 30 species. Section *Polyantha* Reiche (8 species) is endemic to the eastern Himalayas and southern China. Section *Anemonifolia* R. Knuth (2 species) also has a limited distribution, being endemic to Madeira Island. Section *Trilopha* Yeo (5 species) is restricted to mountains in tropical Africa, western Asia, and the eastern Himalayas. The distribution of the remaining five sections, *Lucida* R. Knuth, *Ruberta* Dumort., *Divaricata*, *Batrachioidea*, and *Unguiculata* (Boiss.) Reiche, is centered in the Mediterranean region and western Asia, though section *Ruberta* extends in the east to Japan, and in the south to mountains of tropical Africa.

Sections *Anemonifolia* and *Ruberta* were revised by Yeo (1973). The same author also studied most of the species of section *Polyantha* (Yeo, 1992: 192). Following upon the recent revision of *Geranium* subg. *Erodioidea* (Aedo, 1996), and in pursuit of our aim to prepare a comprehensive monograph of the genus, we here present a revision of two sections of subgenus *Robertium:* sect. *Batrachioidea* and sect. *Divaricata*.

The taxonomic problems of section *Batrachioidea* were confined to two species, *G. pyrenaicum* and *G. molle*. The variability of *G. pyrenaicum* had

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not been well studied except for Ortiz's (1989) work, which included mainly Iberian material. *Geranium molle* is a highly variable species from which the most robust forms had been segregated and named *G. brutium*. Another problem to address in this revision was the taxonomic status of some plants similar to *G. molle* but with smooth mericarps. Section *Divaricata*, comprising two non-problematic species, had not been revised since Knuth's (1912: 57, 154) monograph. Both sections could constitute a monophyletic group, as suggested by the presence of a derived character state (blue pollen). However, at present, there are no other data to confirm this hypothesis.

This revision of sections *Batrachioidea* and *Divaricata* is a first attempt to explore the phylogenetic relationships within *Geranium* subg. *Robertium*. Future work may be focused only on sections *Trilopha* and *Unguiculata*, because section *Lucida* is monotypic and non-problematic.

MATERIALS AND METHODS

This revision is based on more than 2000 herbarium specimens from the following herbaria: AK, B, BAF, BC, BISH, BM, BR, C, CAN, CAS, CHR, G, JE, H, K, L, LE, LISI, LOU, LY, M, MA, MAF, MO, MPU, MUB, NY, OXF, PAL, PH, PO, RO, and W. Furthermore, microfiche, photographs, and other data have been examined from the following additional herbaria: BREG, DS, E, GB, GFW, HAL, LD, LINN, LISU, MANCH, NAP, S, SGO, SZU, TBI, U, UPS, US, and WRSL. Unfortunately, we have had difficulties in obtaining some types on loan. The most relevant cases are those of F. Schur, A. Terracciano, and N. Terracciano. Schur's original material is spread through several herbaria. B, C, E, L, PH, and W have none of Schur's original material, while BP, BRNU, GOET, LW, MW, NA, P, and WU did not respond to our requests. Terracciano's herbarium constitutes a separate collection in NAP. However, this collection has not been available for study since World War II (fide A. Santangelo, in litt.). The dispositions of names for which no type material could be located or obtained are based on the opinions of previous authors (as indicated). Where no reliable opinion was found, these names are included in a "Dubious Names" section.

Cladistic analyses were carried out using the PAUP software package (Swofford, 1993). All characters were unweighted and unordered. Data were analyzed using the exhaustive option. Polarization of characters into plesiomorphic and apomorphic states was assessed using the standard procedure of outgroup comparison (Watrous & Wheeler, 1981). MacClade version 3.04 was used to edit the data set analyzed with PAUP (Maddison & Maddison, 1992). It was also used to map the distribution of particular character-state changes. A bootstrap analysis (Felsenstein, 1985) with 1000 replicates was conducted.

Descriptions of leaf venation in this work follow the terminology of Hickey (1973). Seeds were cut with a razor blade both longitudinally and transversely in order to reveal their internal structure. Thin hand-cut sections were taken in the micropylar third and photographed under optical microscopy. Other sections were made with a SLEE-MAINZ-MTC microtome and stained with Fasga mixture (Tolivia & Tolivia, 1987) or with Sudan red and Malachite green. For scanning electron microscopy (SEM), samples were glued to aluminum stubs, coated with 40–50 nm gold, and examined with a JEOL-TSM T330A scanning electron microscope at 20 kV.

Species-distribution maps were based primarily on exsiccatae, though for *G. albanum* literature records were also used.

RESULTS

MORPHOLOGICAL CHARACTERS

Duration and habit. Most *Geranium* species are herbaceous perennial plants with horizontal rhizomes; however, some species in subgenera *Robertium* and *Geranium* are annuals. The different annual species in the genus do not resemble one another, and they share characters with different groups of perennials. Consequently, we consider that annual species have probably been derived from perennials several times in the genus. One species of section *Divaricata* is perennial and the other is annual, while section *Batrachioidea* has one perennial and three annual species. *Geranium albanum* (sect. *Divaricata*) has a horizontal rhizome that has been codified, according to the outgroup, as plesiomorphic. *Geranium pyrenaicum* (sect. *Batrachioidea*) is also perennial, but it has a vertical, napiform rhizome. All remaining species from both sections are annuals. We consider that this could be interpreted as a linear transformation series, with horizontal to vertical rhizomes leading to annuals without rhizomes. Among the perennials, a vertical rhizome should arise from a horizontal one, and thus ought to be considered as derived. Finally, in *Geranium* annuals are usually considered derived while perennials are primitive (Yeo, 1984). Moreover, Sanderson (1991) proposed a similar multistate series for *Astragalus* (Fabaceae: Papilionoideae): 0 = perennials with well-developed

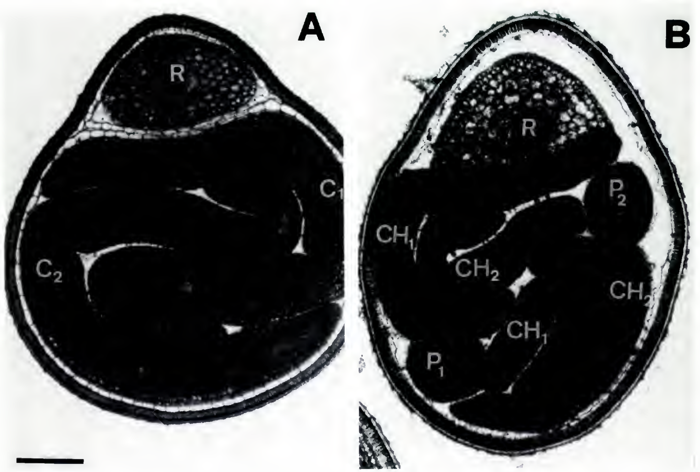

Figure 1. Optical photomicrographs of transverse sections of *Geranium* seeds showing different patterns of cotyledon folding. —A. Seeds of *Geranium pyrenaicum* subsp. *lusitanicum* (*Carreira s.n.* (MA-473325)), section *Batrachioidea*, with conduplicate cotyledons, each lying in the primary fold of the other. —B. Seeds of *G. divaricatum* (*Sánchez Mata s.n.* (MAF-118241)), section *Divaricata*, with the proximal part of cotyledons deeply cordate and cotyledon petioles longer than in section *Batrachioidea*; thus, transverse sections at the micropylar third of the seed show the cotyledons in two parts (the basal auricles of the cotyledons) and their petioles. C_1, C_2 = cotyledons; CH_1 = half of cotyledon C_1; CH_2 = half of cotyledon C_2; P_1 = petiole of cotyledon C_1; P_2 = petiole of cotyledon C_2; R = radicle. Scale bar = 300 μm.

rhizomes, 1 = short-lived perennials with poorly developed rhizomes, and 2 = annuals without rhizomes.

The aerial portion of the stem is usually erect in all species of sections *Batrachioidea* and *Divaricata*; however, the annual species of section *Batrachioidea* can also have decumbent stems.

Cotyledons. The cotyledons usually have entire margins in *Geranium*, but those of a few species are incised. *Geranium aculeolatum* Oliv., with cotyledons having two notches on each side, is the only species in subgenus *Erodioidea* without entire cotyledons (Yeo, 1990: 13). In subgenus *Geranium*, only *G. bohemicum* L. has cotyledons with a single incision on each side (Dahlgren, 1943: 137 fig. 5). Finally, in subgenus *Robertium*, the two species included in section *Divaricata* have cotyledons with a single incision on each margin. According to the outgroup, in all these cases incised cotyledons are considered as a derived condition.

The cotyledons in *Geranium* are always conduplicate, one half of each cotyledon lying in the primary fold of the opposite cotyledon (Yeo, 1990: 14). Moreover, seeds of section *Batrachioidea* show some differences from those of section *Divaricata*. In section *Divaricata*, the proximal part of the cotyledons is deeply cordate and the cotyledon petioles are longer than in section *Batrachioidea*. Consequently, transverse sections at the micropylar third of seeds of section *Divaricata* showed both the petiole and the cotyledons, the latter divided into two parts (the basal auricles). Conversely, in section *Batrachioidea*, as in most of *Geranium*, the cotyledon base is truncate and the petioles are very short (Fig. 1). These differences were not considered by Tokarski (1972), who showed a similar pattern of simply conduplicate cotyledons in these sections.

Leaves. All species in sections *Divaricata* and *Batrachioidea* have more or less deeply palmatifid leaves. Leaf outline is pentagonal in section *Divaricata*, whereas it is usually orbicular to reniform in section *Batrachioidea*. The segments can be rhombic, as in section *Divaricata*, or obdeltate, as in section *Batrachioidea.* Obdeltate segments seem to be derived, according to the outgroup (Nieto Feliner & Aedo, 1995). The number of lobes per segment varies between 7 and 15 in section *Divaricata,* and between 3 and 12 in section *Batrachioidea.* The lower cauline leaves can be either opposite or alternate in both sections. According to Davis (1970), alternate leaves should be the primitive state in *Geranium,* as well as the outgroup.

Inflorescence and branching. The inflorescence in both sections is cymose, composed of axillary, two-flowered cymules. All cymules arise along aerial stems. The most significant inflorescence feature taxonomically is the indumentum of the peduncles and pedicels. Almost all species have two types of hairs. One type comprises patent, eglandular hairs 0.7–1.8 mm long, as in *G. albanum, G. divaricatum, G. pyrenaicum* subsp. *lusitanicum, G. molle,* and *G. aequale.* This type of hair is lacking in *G. pusillum,* and usually also in *G. pyrenaicum* subsp. *pyrenaicum.* The other type of indumentum, composed of glandular or eglandular patent hairs less than 0.5 mm long, is present in all species.

Sepals. The mucro of the sepals is very short (less than 0.6 mm) in all species of both sections, except for *G. divaricatum,* in which it is ca. 1 mm long. The last-mentioned species seems to be unusual in this regard, in subgenus *Robertium,* according to Yeo's (1992) description. Long, eglandular sepal hairs are common in most species, but lacking in *G. divaricatum* and *G. pyrenaicum.*

Petals. Petals in both sections have emarginate apices, with the notch usually ca. 1 mm deep. *Geranium pyrenaicum* has more deeply emarginate (2–3 mm) petals, while its closest relative, *G. pusillum,* has shallowly emarginate petals (0.2–0.5 mm). The longest are those of the perennial species, *G. albanum* and *G. pyrenaicum.* However, the annual *G. molle* occasionally also has long petals, as discussed under that species. In section *Divaricata,* as in most other *Geranium* taxa, the petals are tapered uniformly toward the base, without any claw; however, in section *Batrachioidea,* a very short claw is evident.

Stamens and pollen. In both sections, as in the entire genus, the ten stamens are arranged in two whorls. In *G. pusillum,* the anthers of the external whorl are missing. The filaments are usually hairy on the abaxial side, as in many species of the genus. However, those of *G. molle* and *G. aequale* are glabrous abaxially, which should be interpreted as a derived character state, according to the outgroup. Another character is the presence or absence of cilia along the filament margins. All species studied have ciliate filament margins, except for *G. albanum.*

According to Stafford and Blackmore (1991: 51), pollen of *Geranium divaricatum, G. pyrenaicum, G. pusillum,* and *G. molle* belongs to the *G. molle* type, which includes most of the *Geranium* species studied by them. This type is characterized by reticulate exine ornamentation with distinctly baculate, clavate, or gemmate supratectal elements. Four groups were recognized by these authors on the basis of secondary variation in exine ornamentation. These groups showed no concordance with subgeneric or sectional classifications. Thus, *G. pusillum* and *G. pyrenaicum* were placed in the *G. robertianum* group, and *G. molle* and *G. divaricatum* in the *G. molle* group.

Blue pollen is the only feature known to be shared by sections *Divaricata* and *Batrachioidea.* The other sections of subgenus *Robertium* have yellow (sects. *Anemonifolia, Lucida, Polyantha, Ruberta,* and *Unguiculata*) or white pollen (sect. *Trilopha*) (Yeo, 1984: 13–17). All species of subgenus *Erodioidea* and most of subgenus *Geranium* have yellow pollen, though in the latter subgenus at least three species (*G. dissectum* L., *G. pratense* L., and *G. richardsonii* Fisch. & Trautv.) have blue pollen. Consequently, blue pollen is viewed most parsimoniously as derived.

Fruit. *Geranium* sects. *Divaricata* and *Batrachioidea* belong to subgenus *Robertium,* which exhibits the "carpel-projection-type" of fruit discharge (Yeo 1984). Here, the whole mericarp is actively discharged by the explosive recoiling of the awn, which remains attached to the columella. According to Yeo (1984), this discharge type is presumably derived, the *Erodium*-type discharge being the primitive condition. In section *Divaricata,* decrease in rostrum length reduces the effectiveness of the discharge mechanism. According to the outgroup, this decrease is also viewed as derived. A rostrum that tapers gradually to the remains of the stigmas is the most frequent condition in those Geraniaceae exhibiting the *Erodium*-type discharge (see discussion following the generic description). The alternative condition, a columnar rostrum abruptly narrowed at the apex, as in *G. molle* and *G. aequale,* is probably derived (Nieto Feliner & Aedo, 1995: 203).

The mericarp surface is smooth in all species of section *Batrachioidea* except *G. molle,* which has transversely wrinkled mericarps, as do the two spe-

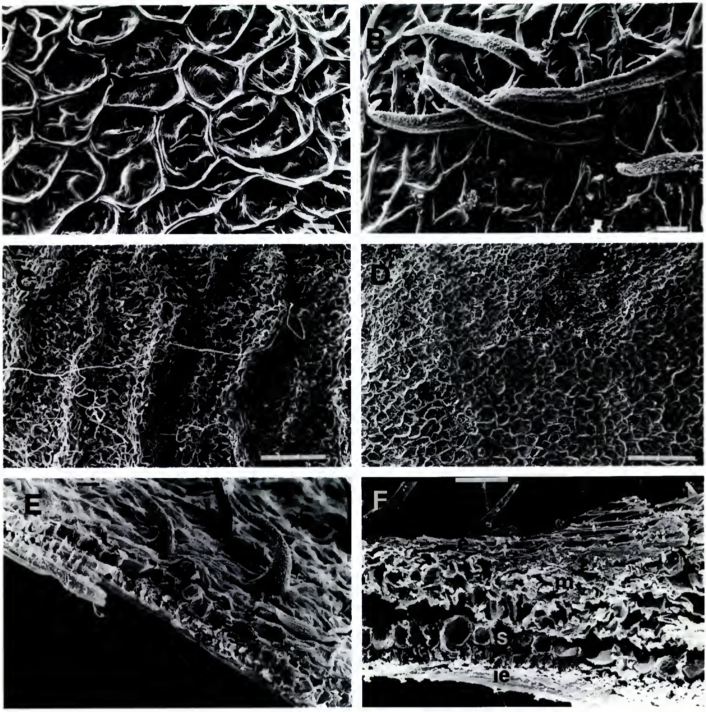

Figure 2. SEM photomicrographs of *Geranium* mericarp. A–D. Surface ornamentation in sect. *Batrachioidea.* —A. *G. pyrenaicum* subsp. *lusitanicum* (*Luceño & Vargas s.n.* (MA-407065)). —B. *G. pyrenaicum* subsp. *pyrenaicum* (*Granzow & Zaballos 365* (MA)). —C. *G. molle* (*López 590* (MA)). —D. *G. aequale* (*Airy Shaw & Nelmes s.n.* (MA-71231)). E, F. Transverse cuts of the mericarp in section *Divaricata.* —E. *G. divaricatum* (*Bernouilli s.n.* (MA-71169)). —F. *G. albanum* (*Aedo 3864* (MA)). e = exocarp, m = mesocarp, s = sclerenchyma region, ie = endocarp. Scale A, B, bar = 10 µm; C, D, bar = 100 µm; E, bar = 10 µm; F, bar = 50 µm.

cies of section *Divaricata.* According to the outgroup, transversely rugose mericarps are here interpreted as the derived condition. In both sections, the mericarps are usually covered by short hairs, but *G. pyrenaicum* exhibits two conditions: subsp. *pyrenaicum* (Fig. 2B) has hairy mericarps, while subsp. *lusitanicum* (Fig. 2A) has glabrous mericarps. The mericarp surface is also virtually glabrous in *G. molle* and *G. aequale* (Fig. 2C, 2D), with only a few cilia along the margins. According to the outgroup, glabrous mericarps are here interpreted as the derived condition.

The mericarp wall in *G. albanum* is wider and has a more well-developed mesocarp than that of the other species studied here. *Geranium divaricatum* and species in section *Batrachioidea* have relatively thin mericarps due to no or limited development of the mesocarp, with at most a single layer of cells. The mericarps of all the studied species had well-developed sclerenchyma regions with crystals (Fig. 2E, 2F). The thicker mericarp of *G. albanum* could be related to a different germination strategy in this perennial species. Several authors have reported a relationship between dormancy and the permeability of seed testas and fruit walls (Aldasoro et al., 1981; Rangaswamy & Nandakumar, 1985; Bewley & Black, 1994).

Seeds. Seeds are more or less elliptical in outline in section *Batrachioidea,* and obovate in section *Divaricata.* The seed-coat in both sections appears smooth at a magnification of 30×, but SEM shows a reticulate surface due to the prominence of the outer and the middle layer of the outer integument. The outer layer has cells with thickened walls and collapsed lumina, forming a polygonal structure. The seed-coat is usually brownish and bears scattered stomata. The cells of the inner part of the outer integument are strongly lignified and contain tannin and crystals. The next layer (the outer layer of the inner integument) is also sclerified, but the cells are not so compacted, being prismatic with undulate anticlinal walls.

In *G. albanum,* a species with thick mericarp, the testa is weaker because the cells of the outer layer of the inner integument are wider (ca. 24 μm), almost cubic, and the lignified walls are more widely separated (8–15 μm) than in the other species here studied. Conversely, *G. aequale,* with seeds only partially covered by the mericarp, has the thickest testa (Fig. 3) in sections *Batrachioidea* and *Divaricata* (ca. 41 μm, vs. 25–30 μm in the other taxa).

CHROMOSOME NUMBER

The chromosome number of all species in *Geranium* sect. *Batrachioidea* is $2n = 26$ (see Appendix 1). There has been some controversy in the case of *G. pyrenaicum* and *G. pusillum,* but Van Loon's (1984a, b) work has clarified the situation.

All chromosome counts carried out to date for *G. divaricatum* are $2n = 28$. However, for *G. albanum,* Warburg (1938: 145) reported $n = 14$ and Van Loon (1984a: 276) $2n = 20$ (see Appendix 1). Material of both species was unvouchered and collected in botanical gardens. Thus, the chromosome number in section *Divaricata* is probably $2n = 28$, but more counts should be done for *G. albanum.*

According to Van Loon (1984b: 286), the basic chromosome number in *Geranium* is $x = 14$, as in most of the perennial species of the genus. The annual taxa, with various other base numbers, probably evolved independently. In this context, the number $2n = 26$ in section *Batrachioidea* could be seen as a derived character state.

HYBRIDS

Hybridization experiments in *Geranium* subg. *Robertium* have involved species of sections *Anemonifolia, Batrachioidea, Lucida, Ruberta,* and *Unguiculata* (Van Loon, 1984c; Widler-Kiefer & Yeo, 1987). No data are available for sections *Divaricata, Polyantha,* and *Trilopha.*

In section *Batrachioidea,* three hybrids have been described: *G.* ×*oenense* (said to be *G. molle* × *G. pusillum*); *G.* ×*luganense* (said to be *G. molle* × *G. pyrenaicum*); and *G.* ×*hybridum* (said to be *G. pusillum* × *G. pyrenaicum*). According to Van Loon (1984c), intraspecific crosses were usually highly successful in this section, but the only successful interspecific cross was that involving *G. molle* and *G. brutium.* Other crosses (*G. pyrenaicum* × *G. brutium, G. pyrenaicum* × *G. molle*) also produced seeds, but the seedlings succumbed at an early stage. Thus, according to Van Loon's data, species of this section seem reproductively isolated.

Having thoroughly studied original material and/or original descriptions, we consider that *G. luganense, G. oenense,* and *G. hybridum* are probably not hybrids but synonyms of *G. molle* (the first two) or *G. pusillum.* Considering the difficulty in obtaining interspecific hybrids (Van Loon, 1984c), the only successful cross, involving *G. brutium* and *G. molle,* supports our interpretation of *G. brutium* as a synonym of *G. molle.*

DISTRIBUTION

Geranium subg. *Robertium* is distributed widely in temperate regions from Macaronesia to Japan, and sections *Trilopha* and *Ruberta* reach tropical areas of central and east Africa.

Section *Divaricata* comprises two species, with very different patterns of distribution. *Geranium albanum* is endemic to the Caucasus and northern Iran, whereas *G. divaricatum* is distributed in a wide longitudinal range between Spain and the central Himalayas. At present, neither species has been reported as introduced in other areas of the world.

The four species of *Geranium* sect. *Batrachioidea* are centered in Eurasia, between Macaronesia and the Himalayas, though all but *G. aequale* reach north Africa. They are spreading rapidly in temperate areas of North and South America, southern Africa, Australia, and Japan, where representatives of subgenus *Geranium* mainly grow. This process of colonization predominantly involves the three annual species, which occur in perturbed habitats, but also *G. pyrenaicum.*

PHYLOGENETIC RELATIONSHIPS

A cladistic analysis of *Geranium* sects. *Divaricata* and *Batrachioidea* was carried out using a data

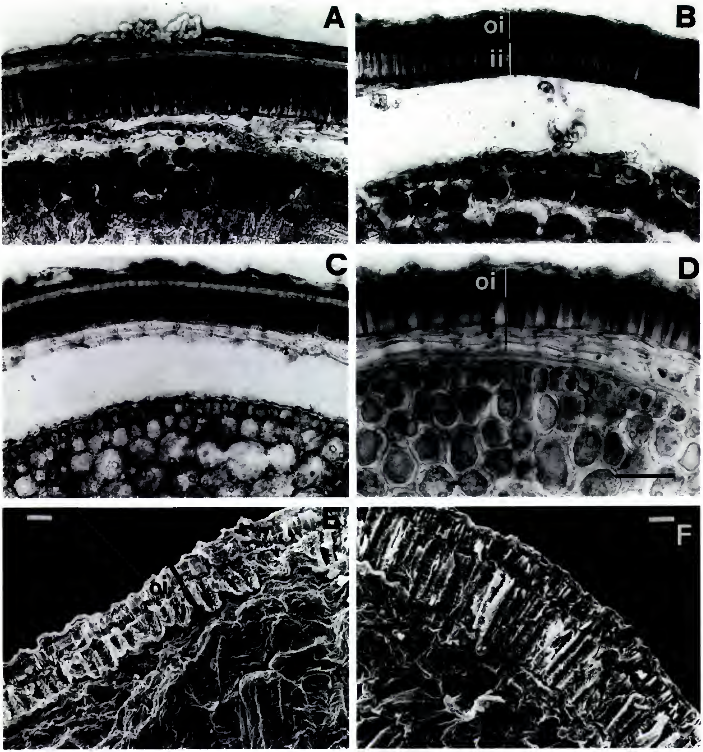

Figure 3. Optical (A–D) and SEM (E, F) photomicrographs of *Geranium* seed sections, showing the testa with the outer part of the inner integument more developed in *G. aequale* (ca. 41 μm) than the other species (25–30 μm). However, the testa cells are wider in *G. albanum* (ca. 24 μm) than in the other species (8–15 μm). —A, F. *G. aequale* (*Airy Shaw & Nelmes s.n.* (MA-71231)). —B. *G. pusillum* (*Navarro et al. 792* (MA)). —C. *G. divaricatum* (*Sánchez Mata s.n.* (MAF-118241)). —D, E. *G. albanum* (*Aedo 3864* (MA)). oi = outer integument; ii = inner integument. Scale A–D, bar = 50 μm; E, F, bar = 10 μm.

set of 15 characters (Tables 1 and 2). The species used as outgroup was *G. sylvaticum* L. This decision is supported by the results of an *rbc*L-sequence data analysis, which places the clade composed of subgenus *Erodioidea* and subgenus *Geranium* as sister to subgenus *Robertium* (Price & Palmer, 1993). We have selected *G. sylvaticum*, a member of subgenus *Geranium*, since in this species many characters of the in-group are applicable. Species of subgenus *Erodioidea* have quite different fruits, and many of the codified characters (characters 10, 11, and 12) are inapplicable (Nieto Feliner & Aedo, 1995). One most-parsimonious cladogram was obtained, with length 20, consistency index (C.I.) 80, and retention index (R.I.) 81 (Fig. 4).

Two well-supported clades were obtained in the cladogram, corresponding with sections *Divaricata* and *Batrachioidea*. In section *Divaricata*, mono-

Table 1. Data matrix used in the cladistic analysis of *Geranium* sects. *Batrachioidea* and *Divaricata* (subg. *Robertium*). Polymorphic, inapplicable, or missing data are coded as '?.' Characters 1–15 are in Table 2.

	Acronym	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
G. sylvaticum	SYL	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
G. aequale	AEQ	2	0	0	1	1	1	1	1	0	1	1	0	1	0	1
G. molle	MOL	2	0	0	1	1	1	1	1	0	1	0	0	1	0	1
G. pusillum	PUS	2	0	1	1	1	0	1	1	0	0	1	1	0	0	1
G. pyrenaicum subsp. *pyrenaicum*	PYR	1	0	1	1	1	0	1	1	0	0	1	1	0	0	1
G. pyrenaicum subsp. *lusitanicum*	LUS	1	0	1	1	1	0	1	1	0	0	1	1	1	0	1
G. albanum	ALB	0	1	1	0	0	0	1	1	1	?	0	?	0	1	?
G. divaricatum	DIV	2	1	0	0	0	0	1	1	1	?	0	0	0	1	0

phyly is supported by three synapomorphies: (a) the incised margins of the cotyledons (character 2, see Table 2); (b) the inoperative fruit-discharge mechanism (character 9); and (c) the obovate outline of the seeds (character 14). As previously described, this clade is also upheld by seedling structure. In section *Batrachioidea*, monophyly is also supported by three synapomorphies: (a) the obdeltate leaf segments (character 4); (b) the presence of a petal claw (character 5); and (c) the chromosome number $2n = 26$ (character 15).

Geranium molle and *G. aequale* constitute a

Table 2. Characters and character states used for cladistic analysis of *Geranium* sects. *Batrachioidea* and *Divaricata* (subg. *Robertium*).

Characters	Character states
1. Habit	0 = perennial with well-developed horizontal rhizome 1 = perennial with poorly developed vertical rhizome 2 = annual, without rhizome
2. Cotyledon margins	0 = entire 1 = incised
3. Basal cauline leaves	0 = alternate 1 = opposite
4. Shape of leaf segments	0 = rhombic 1 = obdeltate
5. Petal claw	0 = absent 1 = present
6. Stamen pubescence on abaxial side	0 = hairy 1 = glabrous
7. Pollen color	0 = yellow 1 = blue
8. Fruit discharge type	0 = seed-ejection-type 1 = carpel-protection-type
9. Fruit discharge mechanism	0 = operative 1 = inoperative
10. Fruit rostrum	0 = tapering gradually 1 = narrowed abruptly
11. Mericarp surface	0 = smooth 1 = transversely wrinkled
12. Mericarp with longitudinal rib	0 = absent 1 = present
13. Mericarp indument	0 = hairy 1 = glabrous
14. Seed shape	0 = elliptical 1 = obovate
15. Chromosome number	0 = $2n = 28$ 1 = $2n = 26$

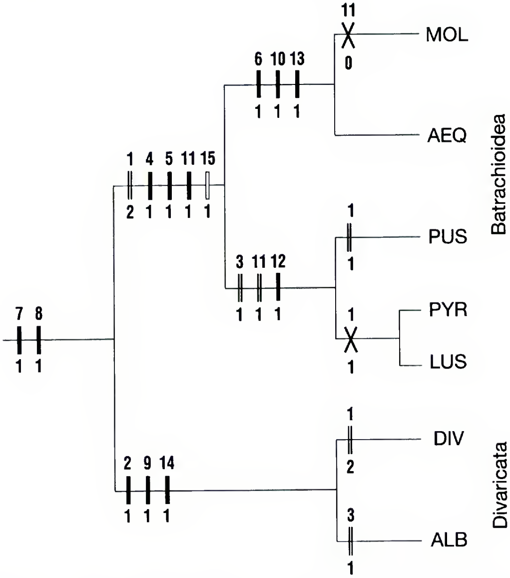

Figure 4. The most-parsimonious cladogram of *Geranium* sects. *Divaricata* and *Batrachioidea*. Solid bars are synapomorphies, open bars are synapomorphies that reverse elsewhere in the cladogram, double bars are parallelisms, and crosses are reversals (length 20, C.I. = 80, R.I. = 81). See Table 1 for acronyms.

clade within section *Batrachioidea* supported by two synapomorphies (characters 6 and 10). The clade comprising *G. pyrenaicum* subsp. *pyrenaicum*, *G. pyrenaicum* subsp. *lusitanicum*, and *G. pusillum* is supported by one synapomorphy (character 12). In this clade, *G. pusillum* appears as sister to the other two taxa.

Monophyly of a group composed of sections *Divaricata* and *Batrachioidea* is supported by only one character, pollen color. In the previously mentioned tree, character 8 (fruit-discharge type) is actually irrelevant, because it is shared by all sections in the subgenus. However, in this study it was used to support the in-group. The emarginate petal apices also seem to support monophyly of this group, but we lack sufficient data to preclude their existence in the other sections. In contrast, blue pollen seems to be a derived feature useful at this level of analysis. No other evidence was obtained about the relationships between the two sections. A comprehensive study of subgenus *Robertium* could be expected to provide more information on this matter.

TAXONOMIC TREATMENT

Geranium L., Sp. Pl. 1: 676. 1753. TYPE: *Geranium sylvaticum* L. (lectotype, designated by Hanks & Small, 1907: 4).

Annual, biennial, or perennial herbs, rarely shrubs. Leaves simple, usually palmately divided, sometimes entire or pinnately lobed, stipulate, petiolate; basal leaves usually forming a rosette; cauline leaves opposite or alternate. Inflorescence terminal or axillary, cymose, bracteate. Flowers usually paired, actinomorphic, rarely somewhat zygomorphic. Sepals 5, imbricate, obtuse to caudate at apex. Petals 5, free, frequently emarginate at apex, sometimes clawed. Stamens 10, in two whorls, the outer one opposite to and the inner one alternating with the petals, all bearing anthers or, very rarely, 5 with staminodes; filaments broad, free or united at the base. Nectaries 5, alternating with the petals. Ovary 5-locular, with 2 superposed ovules per locule, the style distinctly 5-fid. Fruit a schizocarp, long-beaked, splitting into five 1-seeded mericarps. Seed without or with very little endosperm; embryo with massive induplicate or convoluted cotydelons.

Geranium is divided into three subgenera, distinguished by their fruit-discharge mechanisms (Yeo, 1984). The "seed-ejection-type," which characterizes subgenus *Geranium*, involves a single seed actively discharged by the explosive recoiling of the awn, which remains attached to the columella together with the mericarp. A second type of discharge, the "carpel-projection-type," characterizes subgenus *Robertium*. Here, the explosive recurvature of the awn also acts as the propelling force, but in this case the whole mericarp, containing the seed, is dispersed, whereas the awn remains with the columella. Subgenus *Erodioidea* is identified by the "*Erodium*-type" of fruit discharge, in which the mericarp, including the coiled awn, is propelled over a short distance.

Geranium subg. **Robertium** (Picard) Rouy, in Rouy & Foucaud., Fl. France 4: 94. 1897. *Robertium* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 134. 1837. TYPE: *Geranium robertianum* (Greuter et al., 1994, Art. 22.5).

Annual, biennial, or perennial herbs. Leaves palmately divided to the base or more shallowly divided; cauline leaves opposite or alternate. Flowers usually actinomorphic, rarely somewhat zygomorphic. Sepals erect or patent, sometimes longitudinally carinate. Petals rounded or emarginate at apex, ± unguiculate; claw ecarinate or carinate. Stamens exserted or not; filaments glabrous to pilose; pollen yellow, blue, or white. Fruit discharge by carpel projection, each mericarp thrown off explosively with the seed in it and the awn dropping away at the moment of explosion (discharge mechanism sometimes inoperative); mericarps acute or obtuse, smooth, reticulate, ribbed or cristate. Cotyledons entire or laterally incised.

Key to the Sections of *Geranium* subg. *Robertium*

1a. Leaves divided to the base.
  2a. Glandular hairs of the inflorescence purple; more than half the length of the stamens exserted from throat of flower .... *Geranium* sect. *Anemonifolia*
  2b. Glandular hairs of the inflorescence with colorless stalks and red heads; less than half the length of the stamens exserted from throat of flower .... *Geranium* sect. *Ruberta*
1b. Leaves shallowly divided.
  3a. Fruit discharge mechanism inoperative .... *Geranium* sect. *Divaricata*
  3b. Fruit discharge mechanism operative.
    4a. Pollen blue .... *Geranium* sect. *Batrachioidea*
    4b. Pollen yellow, sometimes white.
      5a. Calyx longitudinally carinate .... *Geranium* sect. *Lucida*
      5b. Calyx not carinate.
        6a. Mericarp apex obtuse; stamens exserted .... *Geranium* sect. *Unguiculata*
        6b. Mericarp apex acute; stamens not exserted.
          7a. Plants perennial .... *Geranium* sect. *Polyantha*
          7b. Plants annual .... *Geranium* sect. *Trilopha*

Geranium sect. **Batrachioidea** W. D. J. Koch ["Batrachioides"], Syn. Fl. Germ. Helv. Ed. 1 139. 1835. *Geranium* sect. *Pyrenaica* R. Knuth, in Engl., Pflanzenr. IV.129 (Heft 53): 46, 152. 1912, nom. illeg. TYPE: *Geranium pyrenaicum* Burm. f. (designated by Yeo, 1984: 15; see Aedo & Muñoz Garmendia, 1996: 104).

Perennial or annual herbs; stems to 110 cm long, with simple or bifurcate monopodial branching, leafy, erect, decumbent or ascending, with patent eglandular and glandular hairs. Basal leaves in persistent rosettes; venation actinodromous, basal, perfect, marginal; lamina orbicular or reniform in outline, palmatifid, concolorous, hairy; segments 5–9, obdeltate, 3–12-lobed at apex; lower cauline leaves alternate or opposite; stipules lanceolate to ovate, papery, brown, pilose. Cymules solitary, arising from aerial stems; bracts lanceolate, sometimes lobed, papery, brown; peduncles present, with patent eglandular and glandular hairs; bracteoles linear to lanceolate, papery, brown; pedicels 2 per cymule, ± ascending and often curved upward after anthesis, subequal, with patent glandular or eglandular hairs; peduncle and pedicel together very often exceeding the subtending leaf. Sepals ovate, erect-patent at anthesis and erect in fruit, briefly mucronulate, marginally scarious; abaxial surface with eglandular or glandular hairs; adaxial surface glabrous, with a subapical tuft of hairs. Petals erect-patent, ± obovate, emarginate, with a very short claw, without nectar passages, ciliate at base, with sessile glands on the adaxial surface, ± purple, without a dark basal spot. Stamens 10, both whorls bearing anthers or the inner one without anthers; filaments lanceolate, expanded at base, persistent in fruit, with a conspicuous midvein, ± ciliate, usually pilose on abaxial surface, yellow with pink apex; pollen blue. Nectaries hemispherical, glabrous. Stigmas purple. Fruit of the carpel-projection-type, with discharge mechanism operative; mericarps smooth or transversely wrinkled, sometimes with a longitudinal dorsal rib but never cristate, usually covering the seed completely, without a basal beak and without a callus, glabrous or hairy; rostrum not reduced, narrowed apically or not; stigmatic remains with 5 pilose lobes. Seeds ellipsoidal, smooth, brownish or reddish, the hilum ⅕–⅙ as long as the perimeter. Cotyledons entire. Chromosome number: $n = 13$, $2n = 26$.

Distribution. Africa and Macaronesia, Europe to central Asia and the Indian subcontinent, Australia, North America, southern South America, subantarctic and north-central Pacific Islands.

The three most distinctive character states for *Geranium* sect. *Batrachioidea* are its obdeltate leaf segments, short petal claws, and chromosome number of $2n = 26$. The chromosome number is especially relevant as a derived character, as it has not been found in any other section of subgenus *Robertium.*

KEY TO THE SPECIES OF *GERANIUM* sect. *BATRACHIOIDEA*

1a. Stamens 10, the external whorl without anthers .... 3. *G. pusillum*
1b. Stamens 10, both whorls bearing anthers.
  2a. Mericarps rugose .... 2. *G. molle*
  2b. Mericarps smooth.
    3a. Plants annual; petals 3.5–4.5 mm long .... 1. *G. aequale*
    3b. Plants perennial; petals 7–11 mm long .... 4. *G. pyrenaicum*

1. **Geranium aequale** (Bab.) Aedo, Anales Jard. Bot. Madrid 55: 466. 1997. *Geranium molle* var. *aequale* Bab., Man. Brit. Bot. Ed. 2: 65. 1847. TYPE: United Kingdom. England: near Leamington [52°15′N, 1°29′W], *J. J. Murcott s.n.* (lectotype, designated by Carolin (1965), CGE not seen).

Geranium molle f. *preuschoffii* Abrom., Fl. Ost- & Westpreussen 156. 1898. TYPE: Germany. "Westpreussen, Magdebug, Pfarrgarten in Tannsee," [51°43′N, 10°43′E], *Abromeit s.n.* (no authentic material located; synonymy according to Yeo, 1984).

Annual herb to 40 cm tall; stem erect or decumbent, usually branched from the base, pilose, with long eglandular hairs 1–1.2 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 1.5–3 (–5) × 1.5–3.7(–5.8) cm, divided for 0.6–0.75 of its length, pilose, with eglandular, appressed hairs; segments 7–9, 2–4 mm wide at the base, 3(–5)-lobed at apex; lower cauline leaves alternate; petioles to 14 cm long, with patent, long eglandular hairs ca. 1 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 6–7 × 3–4 mm, ovate-lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–4 × 1.5–2 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–7 cm long, pilose, with eglandular patent hairs 1–1.7 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 1.5–3 × 1–1.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–2.2 cm long, pilose, with eglandular, patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 3–5 × 1.5–2 mm, mucronulate (with mucro 0.1–0.2 mm long), with scarious margins 0.1 mm wide, with eglandular hairs 1–2 mm long and some shorter (< 0.5 mm) eglandular and glandular ones on the abaxial side, glabrous on the adaxial side. Petals 3.5–4.5 × 2–3 mm, emarginate (with notch 1 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 3–4.5 mm long, lanceolate, glabrous except for a few ciliae on the proximal half; anthers 0.4–0.6 × 0.2–0.3 mm, purple. Gynoecium ca. 5 mm long; stigma purple. Fruit 9–12 mm long; mericarps 1.4–1.5 × 1–1.1 mm, smooth, without longitudinal rib, not covering the seed completely, glabrous on most of the surface, densely ciliate at the base; rostrum 7–10.5 mm long, with a narrowed apex 1–1.5 mm, pilose (with erect-patent eglandular hairs 0.1–0.3 mm long); stigmatic remains ca. 1–2 mm long, with 5 hairy lobes. Seeds 1.6–1.7 × 0.9–1 mm, brownish, the hilum ⅕–⅙ as long as the perimeter. Chromosome number: $2n = 26$. Figure 5.

Distribution (Fig. 6). Northern, middle, and southwestern Europe; introduced in the northeastern United States and New Zealand (North I.); cultivated fields and dry places near villages, between 0 and 200 m.

Phenology. Flowering May–August.

Representative specimens examined. NEW ZEALAND. North I., Colenso, 39°44′S, 17°4′E, 1821, *Anonymous s.n.* (K). BELGIUM. Liège, Rocherath, vallée du Tröglichtenbach, 560 m, 50°26′N, 6°18′E, *Fabri 857* (BR); Semois, 49°53′N, 4°45′E, *Vinck 422* (BR); pr. Tintomoje, route Tintomoje-Rome[?]ohomoje, 50°51′N, 5°28′E, *Wilezek 1127* (K). DENMARK. Fn[?]termglatte, 1938, *Marsen s.n.* (C). GERMANY. SW of Saxony, 51°20′N, 12°25′E, Aug. 1882, *Anonymous s.n.* (K); Samensammlung des Hamburgischen Staatsinstituts für angewandte Botanik, 53°33′N, 10°0′E, *Bredemann & Nieser 50* (K). UNITED KINGDOM. **England:** Little Sark, Channel Islands, 49°26′N,

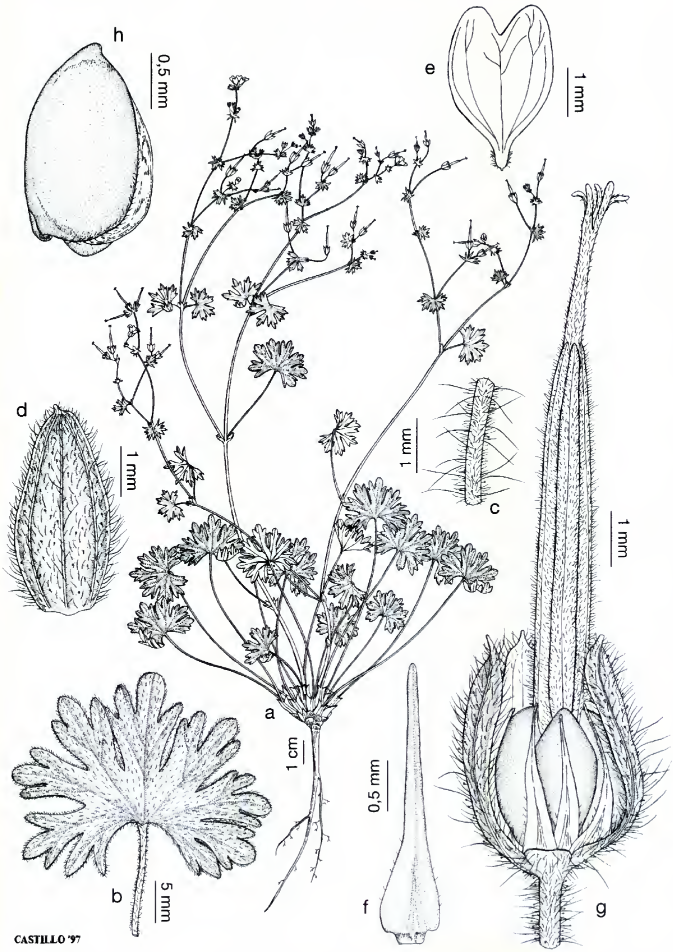

Figure 5. *Geranium aequale.* —a. Habit. —b. Leaf. —c. Peduncle. —d. Sepal. —e. Petal. —f. Stamen. —g. Fruit and sepals. —h. Mericarp. (Based on *Airy Shaw & Nelmes s.n.* (MA-71231).)

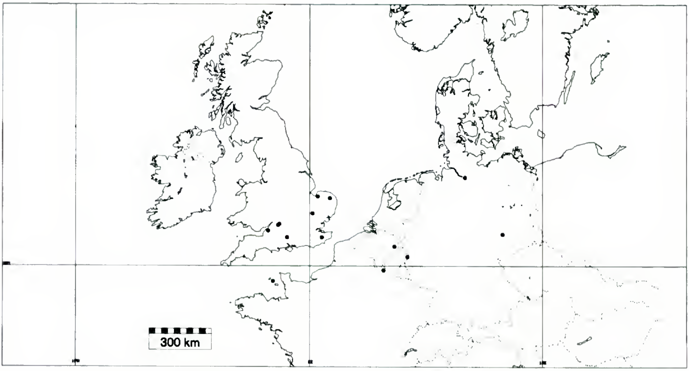

Figure 6. Natural distribution of *Geranium aequale*, based on herbarium records (also introduced in northeastern U.S.A. and New Zealand).

2°22′W, *Ballard & Gollon 228* (K); Andover, Hampshire, *Clarke 46129* (K); Norfolk, Buxton, 52°45′N, 1°18′E, 1847, *Mann s.n.* (K); W Gloucester, 34, Tarlton, Coates, m. Cirencester, 100 m, *Airy Shaw & Nelmes 45* (K, MA); W Gloucester, 34, Avonmounth Docks, 51°29′N, 2°41′W, 20 May 1933, *Sandwith s.n.* (K); West Norfolk, Appleton, 52°49′N, 0°31′W, *Hubbard 9243* (K).

U.S.A. **Massachusetts**: Wellesley, 27 May 1[?]48, *Cummings s.n.* (NY). **New Jersey**: Tom's River, 3 July 1916, *Wilson s.n.* (NY); Morris Co., above Sterlington, *Mackenzie 1261* (NY). **New York**: Long Island, Hewlett, *Bicknell 5377* (NY); Tompkins Co., lawn of East Roberts Hall, *Burnham 16985* (MO); Monroe Co., Sweden, Brockport, *Hammond 8256c* (NY). **Pennsylvania**: Lancaster, July 1894, *Bitner s.n.* (NY); Philadelphia, *Williamson s.n.* (NY); Delaware River, N of Easton, Lancaster, 4 July 1890, *Small s.n.* (NY).

Geranium aequale is close to *G. molle*, from which it is easily distinguished by its smooth, densely ciliate mericarps (those in *G. molle* are transversely wrinkled and sparsely ciliate at the base). Moreover, the mericarps of *G. aequale* do not cover the seed completely, as in *G. molle*. The seeds of *G. aequale* have a thick testa, which may compensate for the slight protection provided by the mericarp. We were not able to find any intermediates between *G. aequale* and *G. molle*.

Geranium subg. *Robertium* exhibits several different patterns of mericarp ornamentation, which are useful to differentiate the species. Thus, the absence of such ornamentation should also be of relevance. Consequently, we have decided to recognize *G. aequale* as specifically distinct from *G. molle*. *Geranium aequale* cannot be considered a variation included within the geographic range of *G. molle*, because it has a very different and smaller distribution area.

2. Geranium molle L., Sp. Pl. 682. 1753. TYPE: tab. 15 fig. 3–3a in Vaill., Bot. Paris. 1727 (lectotype, designated by Carolin, 1965: 332–333).

Geranium villosum Ten., Fl. Napol. 1: LXI. 1811–1815, nom. illeg., non Mill. (1768). *Geranium pyrenaicum* subsp. *villosum* (Ten.) Nyman, Consp. Fl. Eur. 138. 1878. *Geranium molle* subsp. *villosum* (Ten.) A. Terracc., Malpighia 4: 202. 1890. *Geranium molle* var. *villosum* (Ten.) Cout., Fl. Portugal Ed. 1: 371. 1913. TYPE: Italy. Pollino, *Tenore s.n.* (lectotype, here designated, NAP, the right-hand specimen; photocopy!).

Geranium molle var. *parvulum* Ten., Syll. Pl. Fl. Neapol. 334. 1831. *Geranium molle* [c] *parvulum* (Ten.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Calabria: Monteleone," *Tenore s.n.* (lectotype, here designated, NAP, the upper right specimen; photocopy!).

Geranium villosum var. *villosissimum* Ten., Syll. Pl. Fl. Neapol. 334. 1831. *Geranium molle* var. *arenarium* A. Terracc., Malpighia 4: 202. 1890, nom. illeg. TYPE: Italy. Monteleone, *Tenore s.n.* (lectotype, here designated, NAP, the middle specimen; photocopy!).

Geranium molle var. *album* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 129. 1837. *Geranium molle* [I] *album* (Picard) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: France. "Manchecourt, etc." (no authentic material located; synonymy according to Knuth, 1912).

Geranium abortivum De Not. ex Ces., Bibliot. Ital. Giorn. Lett. 91: 349. 1838. *Geranium molle* var. *abortivum* (De Not. ex Ces.) Nyman, Consp. Fl. Eur. 138. 1878.

TYPE: Italy. Prope Terranova in Sicilia, 1832, *Balsamo s.n.* (lectotype, here designated, RO!).

Geranium brutium Gasp., Rendiconto Accad. Sci. Soc. Borbon. Napoli 1: 49. 1842. *Geranium molle* var. *brutium* (Gasp.) K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* subsp. *brutium* (Gasp.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 53. 1913. TYPE: Italy. Calabriae, *Gasparrini s.n.* (lectotype, here designated, BM!).

Geranium leiocaulon Ledeb., Fl. Ross. 1: 470. 1842. *Geranium molle* [b] *leiocaulon* (Ledeb.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Azerbaijan. Lenkoran, *Hansen s.n.* (lectotype, here designated, H!).

Geranium stipulare Kunze, Flora 29: 698. 1846. *Geranium molle* var. *grandiflorum* Lange, in Willk. & Lange, Prodr. Fl. Hispan. 3: 528. 1878, nom. illeg., non Viv. (1824). *Geranium molle* var. *stipulare* (Kunze) Nyman, Consp. Fl. Eur. 138. 1878. *Geranium molle* f. *stipulare* (Kunze) K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* [B] *stipulare* (Kunze) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. *Geranium molle* subsp. *stipulare* (Kunze) Holmboe, Bergens Mus. Årbok 13: [6]. 1907. TYPE: Spain. In arenosis isthmi Gaditani copiose, *Kunze 537* (lectotype, here designated, K!; isolectotypes, BM!, W!).

Geranium molle var. *macropetalum* Boiss., Fl. Orient. 1: 882. 1867. *Geranium macropetalum* (Boiss.) Posp., Fl. Oesterr. Küstenl. 2: 30. 1898. *Geranium molle* subvar. *macropetalum* (Boiss.) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1703. 1924. TYPE: Greece. Prope Mazeïca, Arcadia, *Heldreich 3404* (lectotype, here designated, G!).

Geranium molle var. *annuum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1877. *Geranium molle* f. *annuum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. *Geranium molle* [I] *annuum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Austria. "Auf Rasenplätzen im Augarten, Oktober, November 1872," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium molle var. *subperenne* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1877. *Geranium molle* [II] *subperenne* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. *Geranium molle* f. *subperenne* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. TYPE: Czech Republic. "Bei Brünn die gewöhnliche Form, Mai–Juni," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium oenense Borbás ex Hallier, in W. D. J. Koch, Syn. Deut. Schweiz. Fl. Ed. 3, 1: 454. 1891. TYPE: Austria. Innsbruck, Hall, 1890, *Murr s.n.* (lectotype, here designated, W!, the left-hand flowering specimen; isolectotypes, K!, W!).

Geranium molle var. *caespitosum* N. Terracc., Nuov. Giorn. Bot. Ital. n.s., 14: 138. 1907. *Geranium molle* [b] *caespitosum* (N. Terracc.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Pisterola," *N. Terracciano s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium molle subsp. *sinjaricum* Al-Shehbaz & Al-Khakani, Candollea 38: 353. 1983. TYPE: Iraq. Sinjar Mt., Gulley of Dair Aasy, *Al-Shehbaz, Al-Mayah & Sharifi s.n.* (holotype, BUH-30568 not seen).

Annual herb to 45 cm tall; stem erect or decumbent, usually branched from the base, pilose, with long eglandular hairs 1–1.7 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 0.9–4 × 0.9–5.2 cm, divided for 0.5–0.75 of its length, pilose, with eglandular appressed hairs; segments 7–9, 1.5–5 mm wide at the base, usually 3(–4)-lobed at apex; lower cauline leaves alternate; petioles to 14 cm long, with patent, long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 6–9 × 1.5–4 mm, ovate-lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–3 × 1.3–1.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.5–8 cm long, pilose, with eglandular patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 1–2 × 0.5–1.2 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 0.5–1.5 cm long, pilose, with eglandular patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals (1–)2.5–5.5(–6) × (0.9–)1.2–2.1(–2.5) mm, mucronulate (with mucro 0.1–0.2 mm long), with scarious margins 0.1–0.2 mm wide, with eglandular hairs 1–1.5 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals (3–)4.5–8.5 (–10.5) × (1.5–)2–5(–7) mm, emarginate (with notch 1–2.5 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 4–5 mm long, lanceolate, glabrous except for few cilia on the proximal half; anthers 0.7–1.5 × 0.3–0.5 mm, purple. Gynoecium 5–6 mm long; stigma purple. Fruit 8–14 mm long; mericarps 1.8–2.1 × 1.2–1.4 mm, transversely wrinkled, without longitudinal rib, covering the seed completely, glabrous on the surface, with a few ciliae at the base; rostrum 6–11 mm long, with a narrowed apex 1–3 mm, pilose (with erect-patent eglandular hairs ca. 0.3 mm long); stigmatic remains ca. 1–2 mm long, with 5 pilose lobes. Seeds 1.4–1.8 × 1–1.2 mm, brownish, the hilum 1/6 as long as the perimeter. Chromosome number: $n = 13$; $2n = 26$. Figure 7. *Additional illustrations.* Cavanilles (1787: tab. 83 fig. 3); Reichenbach (1841–1842: tab. 191); Ross-Craig (1952: pl. 34); Tokarski (1972: 66, pl. 22).

Distribution (Fig. 8). Africa and Macaronesia, Australia, New Zealand, Europe; to western Asia and to the Indian subcontinent, North America, South America, subantarctic and north-central Pa-

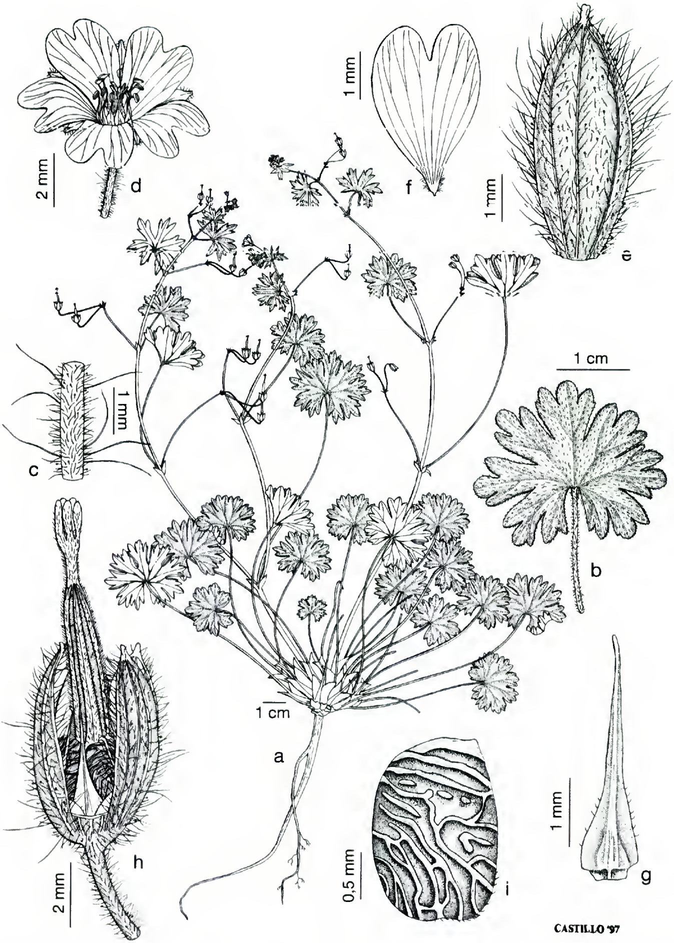

Figure 7. *Geranium molle.* —a. Habit. —b. Leaf. —c. Peduncle. —d. Flower. —e. Sepal. —f. Petal. —g. Stamen. —h. Fruit and sepals. —i. Mericarp. (Based on *Rigual s.n.* (MA-371877).)

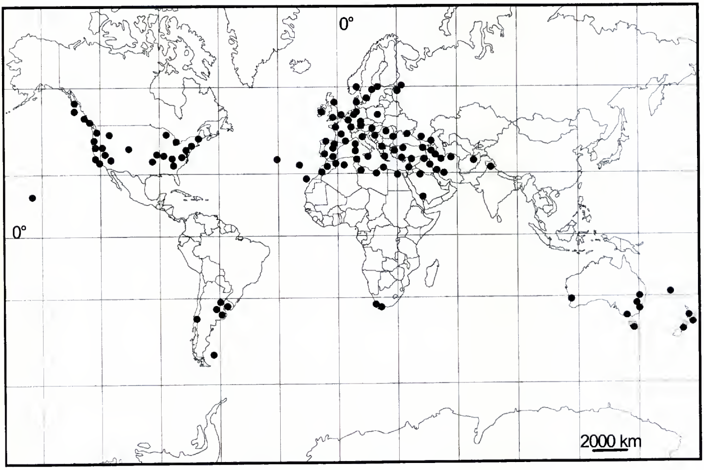

Figure 8. Distribution of *Geranium molle*, based on herbarium records.

cific Islands; also reported from Japan (Knuth, 1912: 58); cultivated and waste places, open habitats, dunes, dry grassland, or roadsides, between 0 and 1400 m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 635, map 1269).

Phenology. Flowering February–August (October–January in Southern Hemisphere).

Representative specimens examined. ALGERIA. Arrew, *Munby s.n.* (K); Cherchell, 36°36′N, 2°12′E, 8 Mar. 1962, *Charpin s.n.* (G). EGYPT. Quarry Bourg el Arab, *Simpson 3277* (K); Gedeirat, East Sinai, Mar. 1950, *Meinertzhagen s.n.* (BM). LIBYA. Bughailan, *Guichard 317* (BM). MOROCCO. 2 km SW of El Jadida, roadside by coast, 10 m, *Lambert 47A* (BM). SOUTH AFRICA. Cape Peninsula, *Salter 6855* (K). TUNISIA. Ain Sebaa to Jebbara beach, E of Tabarka, *Davis 57759* (BM).

AUSTRALIA. Lord Howe I., 0.4 km N of Pine Trees, 10 m, *Johnson & Rodd 1210* (K). **New South Wales:** 6.5 mi. E of Scone towards Moonan Flat, 150 m, *Coveny 2384* (K). **Queensland:** Ballandean, from property of F. W. Coll, Darling Downs district, 19 Oct. 1956, *Clark s.n.* (K). **Tasmania:** embankment of R. Mersey, Devonport, 28 Oct. 1943, *Curtis s.n.* (K). **Victoria:** Port Lonsdale, *Jones 18* (K). **Western Australia:** Perth, *Howard 324* (K); Subiaco, *Morrison 19095* (K). NEW ZEALAND. North I., Mypres Bush, 1861, *Lindsay s.n.* (K); South I., Christchurch, 43°3′S, 172°3′E, *Healy 71/300* (AK).

AFGHANISTAN. "Afghanistan," 20 Apr. 1915, *Anonymous s.n.* (K). ALBANIA. Bertiscus, Alpes boreales albanicae, in monte Lumbardska Planina, pr. Pec, 700 m, *Rechinger f. & Scheffer 624* (K). AUSTRIA. Tyrol sept., Innsbruck, *Kerner s.n.* (K). BELGIUM. Alleur, 50°41′N, 5°30′E, 20 June 1895, *Polchet s.n.* (BR). CYPRUS. Agios Philon, nr. Rizohanpzo, *Davis 2209* (K). CZECH REPUBLIC. Doksy, Bohemia bor., 270 m, 5 July 1980, *Hadinec et al. s.n.* (G). DENMARK. Brabrand W of Aarhus, 22 May 1968, *Nielsen s.n.* (MA-204309). FINLAND. Alandia, Lemland, in insula Slätholm, 9 June 1907, *Florström s.n.* (K). FRANCE. Corcega, Aitony valley, near Evisa, 21 Apr. 1928, *Edwards s.n.* (BM); Andresselles, Pas de Calais, *Coutrez 3816* (MA). GEORGIA. Abchasia, Suchumi, *Markovicz 2942* (G). GERMANY. Bad.-Württ., Mindelsee, Unterberger am See, 6 May 1980, *Anonymous s.n.* (B). GREECE. Cholomondos mountains, Chalchidiki peninsula, 5 May 1931, *Chick 29a* (K); Corfu, Feb. 1862, *Mill s.n.* (K). INDIA. Chamba, 32°N, 76°E, *Clarke 23581* (K). IRAN. 15 km from Masiri to Basht, 700 m, *Davis & Bokhari 55856* (K). ISRAEL. Ghor, 4 km S Dair Alla, Al-Masri Triangular, *Al-Eisawi 1724* (BM). ITALY. Calabria, Reggio, supra Bagnara, 1000 m, 29 Apr. 1920, *Anonymous s.n.* (K); Sardinia, Lido San Giovanni, along the coastal road from Alghero to Fertillia, *Dunford 22* (BM); Sicilia, Palermo, *Todaro 1122* (K). LEBANON. Beirout, *Post s.n.* (K). NETHERLANDS. Friescheveen, *Bloemberger 1391* (L). NORWAY. Tisler, en af Slvolóerne, 25 May 1865, *Collet s.n.* (K). POLAND. Varsoviae, *Fuckel s.n.* (BM). PORTUGAL. Matosinhos, Esposade, 13 Mar. 1977, *Alexandre & Serra s.n.* (MA-484473); Madeira, S. Seb. up the valley, *Lowe 139* (K); Azores, Fayal, 1865, *Godman s.n.* (K). ROMANIA. Dobrogea, N von Costinesti, am Bahndamm, 30 m, 14 May 1976, *Krendl s.n.* (BM). RUSSIA. North Caucasus, Dagestan, Tarkitan u Machackaln, 42°53′N, 47°33′E, *Kuvaev 1–7* (LE); Russia Northwest: Lublinskoj gub., 60°19′N, 29°55′E, 18 May 1907, *Ganesin s.n.* (W). SAUDI ARABIA. Jabal Aja nr. Hail off the

Jaharah road, *Collenette 8585* (K). SPAIN. Mon, San Martín de Oscos, 570 m, 29TPH6993, *Aedo et al. A226* (MA); Baleares, Alcudia, 1899, *Gandoger s.n.* (W); Canary Is., Canaria, San Matheo, Apr. 1846, *Bourgeau s.n.* (K). SWEDEN. Smolandia, 57°0′N, 15°0′E, *N. J. Andersson s.n.* (MA-99920). SWITZERLAND. Lausanne, Aug. 1879, *Favrat & Barbey s.n.* (K). TURKEY. A1 Edirne, 8 km W of Edirne, 100 m, *Davis 41972* (K). UKRAINE. Krym, Gornaja Grjada mezdu m. Aija S. Rezerv, Sevastopolja, 44°28′N, 34°8′E, *Cvelev et al. 366* (LE). UNITED KINGDOM. **Scotland:** Braemar, *Croall 411* (K). YUGOSLAVIA. **Serbia:** Jablanica, 29 Apr. 1914, *Malý s.n.* (K).

CANADA. **British Columbia**: Cadborough Bay, Vancouver Island, *Whiting & Stewart 431* (K). U.S.A. **Arkansas**: Marion Co., Buffalo State Park, ca. 15 mi. SE Yellville, *D'Arcy & Porter 4426* (MO). **California**: Mendocino Co., 2 mi. N Point Arena between Coast Highway and beach, 15 m, *True 4222* (CAS). **Georgia**: Oconee Co., 3 mi. ESE of Farmington, *Duncan 29037* (NY). **Hawaii**: Hamakua, Upper Paauhau, 1500 m, *Hosaka 2203* (BISH). **Idaho**: Idaho Co., Clearwater River Canyon between Syringa and Orofino, ca. 5 mi. downstream of Syringa, *Henderson & Cholewa 6486* (NY). **Maryland**: Prince George Co., Beltsville, *Hill 16730* (NY). **Massachusetts**: Nantucket Island, Siasconset, *Mackeever 991* (BM). **Missouri**: McDonald Co., 1.5 mi. S of Goodam, T23N, R32W S 19, roadside park on W side of Hwy. 71, *Summers 2944* (MO). **New Jersey**: Camden, 11 June 1876, *Parker s.n.* (NY). **New York**: Long Island, Hunter's Point, 19 May 1880, *Brown s.n.* (NY). **North Carolina**: Avery Co., entrance to Grandfather Mountain on US 221, 1400 m, *Boufford & Wood 23898* (MO). **Ohio**: Painesville, 4 June 1886, *Werner s.n.* (NY). **Oklahoma**: 4.3 mi. SE of Eagletown, *Goodman 8336* (G). **Oregon**: Baker Co., old campground along Pine Creek, below North Pine Creek, between Halfway and Homestead, *Cronquist 6543* (NY). **Pennsylvania**: Chester Co., Brookfield, July 1817, *Canby s.n.* (NY). **Tennessee**: Blount Co., Mt. Nebo, Walland, *Thomas 71177* (NY). **Utah**: Utah Co., Provo Bench near Pleasant View, Utah Ditchbank, 1500 m, *Harrison 7543* (MO). **Virginia**: Isle of Wight Co., Fort Boykin, 5 May 1991, *Grimm s.n.* (BM). **Washington**: King Co., 1 mi. N Snoqualmie Falls on the road between Falls City and Snoqualmie, Cascade Mountains, 250 m, *Anderson 2138* (MO). **West Virginia**: Pendleton Co., Pike Gap rd., 0.5 mi. SE jct. of St. Rt. 28 at Circleville, *Cusick 28120* (NY). **Wisconsin**: Olga, 10 June 1905, *Engberg s.n.* (NY).

ARGENTINA. **Entre Ríos**: Gualeguay, Estancia San Ambrosio, 33°10′S, 59°14′W, *Burkart 18088* (NY). CHILE. **Concepción**: región de Bíobio, La Posada, 17 km S Concepción, 36°51′S, 73°3′W, *Rechinger 63095* (W). FALKLAND IS. Byron Sound, West Falkland I., 7 Feb. 1912, *Vallentin s.n.* (K). URUGUAY. **Montevideo**: Cerro, 50 m, *Herter 1312b* (MO).

Geranium molle is a very distinctive species, easily identified by its transversely wrinkled mericarp, glabrous on the surface and sparsely ciliate at the base. It grows naturally almost throughout Europe, in the circum-Mediterranean area, Macaronesia, and central and western Asia. The eastern limit in Europe is not well known, because of the scarcity of herbarium material. In Asia, this species reaches the western Himalayas to 76°E in India. It has been introduced in many temperate areas of North America, South America, southern Africa, and Australia.

Geranium molle shares some derived character states with *G. aequale*, such as glabrous stamen filaments, an abruptly tapered fruit rostrum, and glabrous mericarp surface, supporting their close phylogenetic relationship.

A number of minor morphological variants of *G. molle* have been recognized in the literature, of which the most notable seems to be *G. brutium*. According to Webb and Ferguson (1968: 198), this is an eastern Mediterranean species similar to *G. molle* but frequently perennial (*G. molle* was considered annual by these authors), with the lowermost inflorescence leaves shorter than the peduncle or slightly exceeding it (as opposed to considerably longer in *G. molle*) and with petals 6–11 mm long (3–7 mm long in *G. molle*). Davis (1967: 460) and Persson (1987: 547) considered *G. brutium* as a subspecies of *G. molle*, whereas Pignatti (1982: 10) preferred specific rank. All of these authors used the above-mentioned characters to recognize *G. brutium*.

All the studied material identified (by several authors) as *G. brutium* is clearly annual, though variable in stature and robustness. This was already pointed out by Boissier (1867: 880, 882). *Geranium molle* subsp. *sinjaricum*, described by Al-Shehbaz et al. (1983: 353) from Iraq, was said to be perennial. Unfortunately, we were not able to examine any original material on which this name was based, but all specimens studied from Iraq were annuals. The ratio between the length of the lowest inflorescence leaf and the peduncle varies considerably in *G. molle*, but independently of plant robustness and petal length. This suggests that *G. brutium* has been distinguished from *G. molle* only because of its longer petals. However, some plants with long petals can be found throughout the geographic range of *G. molle*, even in populations with mainly short petals. According to Yeo (pers. comm.) and our own observations, the earliest flowers usually exhibit the longest petals, with petal length diminishing as the season progresses. Moreover, the type specimen of *G. brutium* has petals 7.8 mm long, not far from the *G. molle* values. Consequently, the forms with long petals are here not accorded taxonomic recognition.

Sometimes it is possible to find depauperate plants of *G. molle* (up to 5 cm high), fertile but with the leaves not fully developed. Some such specimens [e.g., *Florström s.n.* (K) from Finland, or *Davis & Bokhari 55856* (K) from Iran] have leaves with undivided lobes. However, no other character state is associated with this size reduction, which suggests that this form also does not deserve taxonomic recognition.

3. Geranium pusillum L., Syst. Nat. Ed. 10: 1144. 1759 [May–June]. *Geranium parviflorum* Curtis, Fl. Londin. 4(43): tab. 46. 1782, nom. illeg. *Geranium parviflorum* Chevall., Fl. Gén. Env. Paris Ed. 1, 2: 802. 1828, nom. illeg. TYPE: "Habitat in Anglia, Galia" [according to L., Sp. Pl. Ed. 2: 957. 1763] (lectotype, here designated, LINN-858.86; microfiche!).

Geranium humile Cav., Diss. 4: 202, tab. 83 fig. 2. 1787. *Geranium pusillum* var. *humile* (Cav.) Steud., Nomencl. Bot. 1: 365. 1821. *Geranium parviflorum* var. *humile* (Cav.) Chevall., Fl. Gén. Env. Paris Ed. 1, 2: 803. 1828. TYPE: locality and collector unknown, specimen annotated in Cavanilles's hand as "*humile*" (lectotype, here designated, MA-475736!).

Geranium dubium Chaix, Pl. Vap. 23. 1785. TYPE: France. "Circà pagos frequens" [in agro vapincense, Gap], *Chaix s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium delicatulum Ten. & Guss., in Ten., Fl. Napol. 5: XII, 84. 1835–1836. *Geranium pusillum* subsp. *delicatulum* (Ten. & Guss.) A. Terracc., Malphigia 4: 212. 1890. TYPE: Italy. Majella, *Tenore s.n.* (lectotype, here designated, NAP; photocopy!).

Geranium pusillum var. *elatum* Picard, in Mém. Soc. Agric. Boulogne-sur-Mer 1: 133. 1837. TYPE: France. "Dans les terres fortes et les endroits herbeux," *Picard s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium circinatum Kanitz ["*circinatnm*"], Linnaea 32: 570. 1863. *Geranium pusillum* [B] *circinatum* (Kanitz) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Hungary. "Habitat ad Varasdinum et in valle Vilena draga monte Croatiae," *Kanitz s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pusillum var. *axilliflorum* Schur, Enum. Pl. Transsilv. 137. 1866. *Geranium pusillum* f. *axilliflorum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [β] *axilliflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913. TYPE: Romania. "Auf Sandboden am Zibinfluss bei Neppendorf. Jul.," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pseudopusillum Schur, Oesterr. Bot. Z. 18: 317. 1868. *Geranium pusillum* [II] *pseudopusillum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "Auf unbehauten steinig-sandigen Aeckern und Plätzen, unweit des Landgutes vor der Favoriten-Linie. Anfang Mai 1867," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pusillum var. *albiflorum* Schur, Verh. Naturf. Vereins Brünn 15: 163. 1876. *Geranium pusillum* [1] *albiflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913. TYPE: Austria. "In Obstgärten bei Hermannstadt, eine Schattenform, Mai 1850," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pusillum var. *gracillimum* Schur, Verh. Naturf. Vereins Brünn 15: 162. 1876. *Geranium pusillum* f. *gracillimum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [1] *gracillimum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Czech Republic. "Auf der Spitalswiese bei Brünn truppweise, Juni 1872," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pusillum var. *majus-grandifolium* Schur, Verh. Naturf. Vereins Brünn 15: 162. 1876. *Geranium pusillum* [2] *majus-grandifolium* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "In der Au an der Schwarzawa bei Komein nächst Brünn, July 1870," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pusillum var. *rigidum* Schur, Verh. Naturf. Vereins Brünn 15: 163. 1876. *Geranium pusillum* f. *rigidum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [2] *rigidum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "Auf steinig-sandigem Boden vor der Favoritenlinie in der Nähe des Landgntes bei Wien, Mai 1867," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium ×*hybridum* Hausskn., Mitt. Geogr. Ges. (Thüringen) Jena 3: 278. 1884, nom illeg., non L. (1767). TYPE: Germany. Ilmviaduktes bei Weimar, *Hausknecht s.n.* (lectotype, here designated, JE!).

Geranium pusillum var. *condensatum* Druce, Bot. Soc. Exch. Club Brit. Isles 5: 17. 1917. TYPE: United Kingdom. England: The Haven, Muddiford, Hants., 27 July 1916, *Green s.n.* (lectotype, here designated, OXF!).

Geranium pusillum var. *tenuilobum* Sennen, Pl. Espagne 1927, no. 6058. 1928, in sched. TYPE: France. Cerdagne: Angoustrine [42°29′N, 1°56′E], 7 July 1927, *Sennen s.n.* (lectotype, here designated, BC-825290!; isolectotypes, BM!, MA-71059!, MA-71060!, MA-470864!, W!).

Annual herb to 50 cm tall; stem erect or decumbent, usually branched from the base, pilose, with short glandular and eglandular patent hairs (< 0.3 mm long). Basal leaves in a persistent rosette; lamina 1.5–3.8 × 1.5–4.8 cm, divided for 0.3–0.75 of its length, pilose, with eglandular, appressed hairs; segments 7, 2–4 mm wide at the base, 3–5-lobed at apex; lower cauline leaves opposite; petioles to 12 cm long, with short (< 0.3 mm) eglandular and glandular patent hairs; stipules 2–4 × 1–1.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–4 × 1–1.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.5–3.2 cm long, pilose, with short (< 0.3 mm) glandular and eglandular patent hairs; bracteoles 1.5–2 × 0.5 mm, linear-lanceolate; pedicels 0.6–1.6 cm long, pilose, with short (< 0.3 mm) glandular and eglandular patent hairs. Sepals 3–4.5 × 1.5–2 mm, mucronulate (with mucro 0.1 mm long), with scarious margins ca. 0.1 mm wide, with eglandular hairs ca. 1 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 2–3 × 1–1.5 mm, emarginate (with notch 0.2–0.5 mm deep), with short claw, pale purple. Stamens 10, the inner whorl with filaments 1.2–1.5 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half; anthers 0.3 × 0.2 mm, purple; external whorl with filaments 1 mm long, almost glabrous, lacking anthers. Gynoecium ca. 3 mm long; stigma light purple. Fruit 9–11 mm long; mericarps 1.7–1.9 × 1–1.1 mm, smooth, with a longitudinal rib, covering the seed completely, pilose, with appressed-eglandular hairs to 0.2 mm long, with a few ciliae at the base; rostrum 7–9 mm long, obtuse at apex, pilose (with erect-patent, eglandular and glandular hairs ca. 0.2 mm long); stigmatic remains 0.5–0.7 mm long, with 5 pilose lobes. Seeds 1.7–1.8 × 1–1.1 mm, reddish; hilum $\frac{1}{6}$ as long as the perimeter. Chromosome number: $2n = 26$. Figure 9. *Additional illustrations.* Curtis (1782: tab. 46) [sub *G. parviflorum*]; Reichenbach (1841–1842: tab. 190 fig. 4877); Gams (1924: 1703 fig. 1641); Ross-Craig (1952: pl. 35); Tokarski (1972: 68, pl. 28).

Distribution (Fig. 10). Europe to central Asia and the Indian subcontinent, North Africa, and North America; also reported from Bermuda (Britton & Brown, 1913: 429) and Uruguay (Hetter, 1954); cultivated and waste places, open habitats, rocky slopes, and dry grassland, between 0 and 1900(–2500) m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 635, map 1270).

Phenology. Flowering March–September (December–January in Southern Hemisphere).

Representative specimens examined. MOROCCO. Refugio de Taffert, Atlas Medio, 33°38′N, 4°09′W, 1950 m, *Aedo 4144* (MA).

NEW ZEALAND. Wellington Harbour, 41°18′S, 174°47′E, 2 Apr. 1941, *Healy s.n.* (CHR); Burwood Hospital, Christchurch, 43°30′S, 172°42′E, *Healy 70.188* (CHR).

AFGHANISTAN. Mazari-I Sharif, N Afghanistan, faucibus fluvii Balkh supra Aq Kupruk, 700 m, 36°5′N, 66°52′E, *Rechinger 16298* (W). ARMENIA. Gdzi[?]rakaia, Such[?]ch, 9 July 1966, *Anonymous s.n.* (G). AUSTRIA. Austria superior, pr. Wildberg ad Lentiam urbem, 6 Sep. 1884, *Topiz s.n.* (BC-12605). BELARUS. Prov. Minsk, S Khojn Mozyr., 52°4′N, 29°12′E, 1905, *Bordzilowski s.n.* (LE). BELGIUM. Aarschot, 50°59′N, 4°50′E, 5 Sep. 1940, *Michelis s.n.* (BR). BOSNIA AND HERZEGOVINA. Sarajevo, *Gilliat-Smith 3321* (K). BULGARIA. Planities Thraciae, pr. Karlovo, 28 May 1975, *Petrova s.n.* (MA-209947). CYPRUS. Pagum Prodromo, *Kotschy 704* (K). CZECH REPUBLIC. Moravia australis, Uhersky Ostroh, 6 June 1949, *Podpera s.n.* (K). DENMARK. Saltholm, 55°38′N, 12°46′E, *Hansen 46* (C). ESTONIA. Wormsö, Hullo, 6 Aug. 1924, *Grontved s.n.* (C). FINLAND. Kyrkbackece, Nagu, 18 June 1912, *Dahl s.n.* (MA-71056). FRANCE. Alençon, Orne, 48°26′N, 0°05′E, 25 June 1889, *Beaudouin s.n.* (MA-71055). GERMANY. Bayern, Oberbayern, Gräfelfing bei München, auf Brachäckern, 28 June 1902, *Dihm s.n.* (MA-360452). GREECE. Pisoderion, 1000 m, *Alston & Sandwith 684* (K). HUNGARY. Evdely, 12 June 1912, *Bark s.n.* (K). IRAN. Ardebil-Astara, 1300 m, *Bowles Schol. Bot. Exp. 2313* (K). IRAQ. Pught Ashan, 15 km NE of Rania, 36°15′N, 44°53′E, 1150 m, *Rawi 23906* (K). IRELAND. Dublin, July 1903, *Meade s.n.* (K). ITALY. Aprutium, montis Magellae, valle Orfenta, 41°38′N, 14°00′E, 200 m, July 1908, *Guadagno s.n.* (K). JAMMU-KASHMIR. Kashmir, *East India Company 323* (W). KAZAKSTAN. Almatinsk u., pr. Almati, 43°3′N, 76°56′E, *Pavlova 32* (LE). NETHERLANDS. Friesland, Harich, 52°54′N, 5°34′E, 4 July 1972, *Slim s.n.* (L). NORWAY. Holmsbo, 59°54′N, 12°06′E, 29 June 1869, *Collet s.n.* (K). PAKISTAN. Chitral, Drosh, 35°52′N, 71°58′E, *Toppin 91* (K). POLAND. Cracovia, pr. Zabierzów, ad vicum Modlniczka Mala versus, 27 Apr. 1974, *Sztyler & Tacik s.n.* (MA-252530). PORTUGAL. Francoso, *Sampaio 1909* (MA). ROMANIA. Oltenia, distr. Dolj, 120 m, 9 May 1931, *D. Cîrtu & M. Cîrtu s.n.* (MA-252531). RUSSIA. North Caucasus, ad fl. Terek, Ossetia, Balta, *Brotherus 216* (BM); Russia Central, Briansk, Pogar, in valle fluv. sudest prope Markovsk, 52°35′N, 33°15′E, 8 June 1980, *Skvortsov s.n.* (M); Russia North, Pskovsk gub., Opochetskij, st. Novgorodki, 57°3′N, 28°35′E, *Kuznetsova 461* (LE); Russia Northwest, prope urb. Pskow, 57°50′N, 28°20′E, *Andrejew 1608* (G). SPAIN. Lérida, Alto Arán, Bagergue, 1465 m, 31TCH2736, *Aedo 2273* (MA). SWEDEN. Gästrikland, Gävle, 60°40′N, 17°10′W, *Nannfeldt 17173* (K). SWITZERLAND. Disentis beim Kloster, 1160 m, 46°43′N, 8°51′E, 19 May 1920, *Bühler s.n.* (BC-12603). SYRIA. Kessab, 35°56′N, 35°59′E, *Pabot 194* (G). TURKEY. Elmoli, 1200 m, *Tengevall 364* (K). TURKMENISTAN. Ashabad, 37°58′N, 58°24′E, *Litwinow 1144* (G). UKRAINE. Kiew, Belaja Tserkov, 20 Aug. 1966, *Skvortsov s.n.* (M); Krym, Severnoe Chernomovskoe poberezhe, 45°34′N, 32°52′E, *Pobedimova 189* (LE). UNITED KINGDOM. **England:** Aylexford, Kent, Aug. 1902, *Gregor s.n.* (MA-170873). UZBEKISTAN. Tian-shan, montes Keksuiski khrebet, in vicinitati pagi Brichmulla, 1900 m, 41°37′N, 70°5′E, 11 July 1973, *Vasák s.n.* (G).

CANADA. **Alberta**: Banff, 51°10′N, 115°34′W, *Sanson 1028* (NY). **British Columbia**: Agarriz, 20 May 1889, *Macoun s.n.* (NY). **Manitoba**: Brandon, 49°50′N, 99°57′W, *Stevenson 788* (CAN). **Ontario**: Bruce Co., Crane Lake, 45°10′N, 81°24′W, *Soper et al. 13637* (CAN). U.S.A. **Arkansas**: Carroll Co., Elk Ranch, *Palmer 39459* (NY). **California**: Santa Cruz Co., Boulder Creek, 200 m, *Hesse 1118* (CAS). **Colorado**: St. Lupton, *Johnston 555* (MO). **Delaware**: Brandywine, Aug. 1863, *Canby s.n.* (NY). **Hawaii**: Maunakea, 2000 m, *Faurie 856* (BISH). **Idaho**: Moscow, 46°43′N, 116°59′W, *Werner 13599* (NY). **Illinois**: Alton, along the track of the Illinois Terminal Railroad, E of Piasa Street, 38°53′N, 90°11′W, 100 m, *Muehlenbach 4336* (MO). **Indiana**: St. Joseph Co., E side of Wolverton bog, along Road 23, 7 mi. SW of South end, *Friesner 20440* (MO). **Kansas**: Ellsworth Co., Kanopolis Reservoir, N Shore St. Park, *Brooks 17145* (NY). **Kentucky**: Boyle Co., Bellevue Cemetery, N Danville, *Cusick 30297* (NY). **Maryland**: Bladensburg, 38°56′N, 76°56′W, June 1879, *Chickering s.n.* (NY). **Massachusetts**: Martha's Vineyard, Edgartown, *MacKeever 445* (NY). **Michi-**

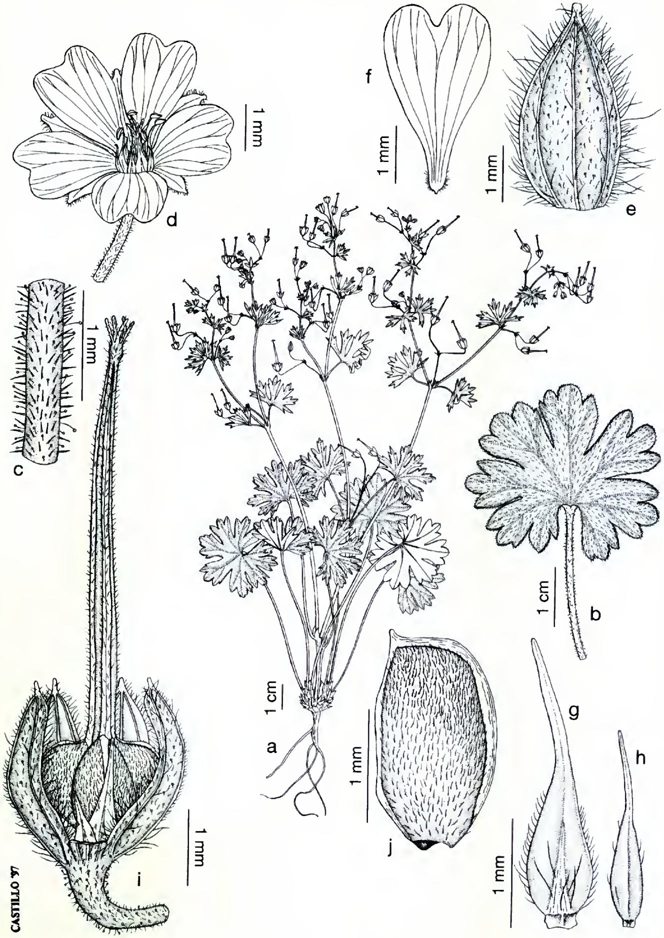

Figure 9. *Geranium pusillum.* —a. Habit. —b. Leaf. —c. Peduncle. —d. Flower. —e. Sepal. —f. Petal. —g, h. Stamens. —i. Fruit and sepals. —j. Mericarp. (a–d, i, j based on *Anttila s.n.* (MA-180451); e–h based on *Aedo 2371* (MA).)

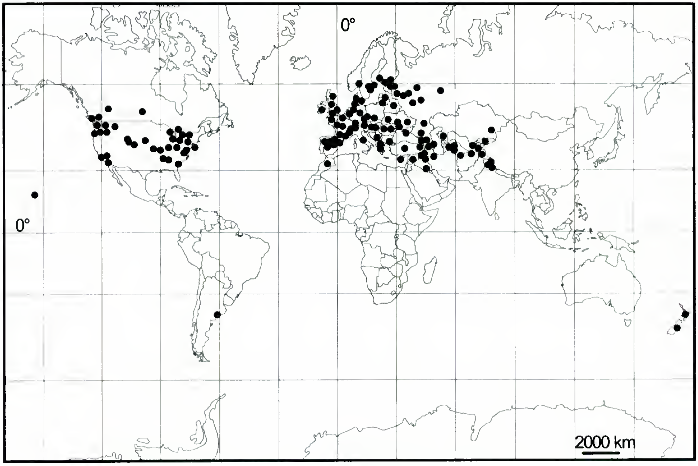

Figure 10. Distribution of *Geranium pusillum*, based on herbarium records.

gan: Flint, *Clarke s.n.* (NY). **Missouri**: Noel, *Bush 5727* (NY). **Montana**: Flathead Mission, 47°55′N, 114°5′W, Sep. 1899, *Blankinship s.n.* (NY). **Nebraska**: Minden, 10 June 1931, *Hapeman s.n.* (MO). **New Jersey**: Camden, *Parker s.n.* (NY). **New York**: Albany, 16 June 1882, *Dudley s.n.* (CAS). **Ohio**: Euclid, 41°34′N, 81°33′W, *Scair s.n.* (NY). **Oregon**: Wallowa Co., Imnaha canyon, *Peck 17528* (NY). **Pennsylvania**: Allegheny Co., 1869, *Porter s.n.* (NY). **South Dakota**: pr. Brookings, 44°18′N, 96°47′W, 26 July 1893, *Williams s.n.* (CAS). **Tennessee**: Davison Co., Belle Meade area, *Kral 50321* (MO). **Utah**: Bidolph's garden on road to Green Canyon, *Shaw 36* (NY). **Virginia**: Smyth Co., Laurel Creek, North Fork of the Holston River Valley, 700 m, 22 June 1892, *Britton et al. s.n.* (NY). **Washington**: Asotin Co., 10 mi. S of Asotin, on bluffs along W side of Snake R., *Hitchcock & Muhlick 21801* (NY). **West Virginia**: Smyth Co., Fork Holston river, near Broad Ford, 750 m, 20 June 1892, *Small s.n.* (MO). **Wyoming**: Laramie Expt. Farm, 41°18′N, 105°35′W, *Nelson 2038* (CAS).

ARGENTINA. Campo La Susana, 10 km de Peralta, 38°03′N, 61°40′W, 320 m, *Huidobro 1160* (NY).

Geranium pusillum has only five anther-bearing stamens, which is the best character to identify this species. It has been frequently confused with *G. pyrenaicum*, a closely related perennial species with ten anther-bearing stamens. It is also often confused with *G. rotundifolium*, another widespread annual species. However, *G. rotundifolium*, a member of subgenus *Geranium*, has typical seed-ejection fruits, reticulate seeds, and ten anther-bearing stamens.

Geranium pusillum is indigenous in the Eurasian portion of its range. The eastern limit of *G. pusillum* in Europe is not well known, because of the scarcity of herbarium material. In Asia, this species reaches the western Himalayas to 75°E in Jammu-Kashmir. *Geranium pusillum* has been introduced to many temperate areas of North America, South America, and Australia.

A search of the Linnaean Herbaria has yielded three sheets potentially related to the protologue of *G. pusillum*: LINN-858.85, LINN-858.86, and S-282.19. LINN-858.85 is not a suitable choice, because it represents *Geranium molle*. S-282.19 was annotated only by Linnaeus's son, hence is not relevant. Consequently, we prefer to select LINN-858.86, annotated by Linnaeus himself, as lectotype.

The name *G. pusillum* has often been attributed to "Burm. f., Spec. Bot. Geran. 1759"; however, that work was published on 17 August, about two months after the Linnaean protologue.

4. **Geranium pyrenaicum** Burm. f., Spec. Bot. Geran. 27. 1759. TYPE: "Habitat in Pyrenaeis" (authentic specimens in G, lectotype not designated; see discussion below).

Perennial herb with short vertical napiform rhizome; stem 15–70(–110) cm tall, erect, usually branched from the base, pilose, with long eglandular hairs 1–1.4 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 2.8–6.2 × 2.5–7.5 cm, divided for 0.5–0.6 of its length, pilose, with eglandular, appressed hairs; segments 5–7, 4–8 mm wide at the base, (3–)7–10(–12)-lobed at apex; lower cauline leaves opposite; petioles to 25 cm long, with patent, long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 3–9 × 1–3.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 4–7 × 1.5–2.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–3.8 cm long, pilose, with eglandular, patent hairs 1–1.3 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 2.5–5 × 0.5–0.8 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–3 cm long, pilose, with short (< 0.5 mm) glandular and eglandular hairs and sometimes with eglandular patent hairs 0.7–1.3 mm long. Sepals 3.5–5 × 1.6–2.5 mm, ovate, mucronulate (with mucro 0.2–0.3 mm long), with scarious margins ca. 0.1 mm wide, with short (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 7–11 × 5–6.5 mm, emarginate (with notch 2–3 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 4–5 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half; anthers 1–1.2 × 0.5–0.7 mm, purple. Gynoecium 4–4.5 mm long; stigma purple. Fruit 18–20 mm long; mericarps 2.4–3.1 × 1.1–1.4 mm, smooth, with a longitudinal rib, covering the seed completely, pilose, with appressed-eglandular hairs ca. 0.1 mm long or glabrous, not ciliate at the base; rostrum 10–15 mm long, obtuse at apex, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 1.5–1.8 mm long, with 5 pilose lobes. Seeds 2.2–2.7 × 1.2–1.4 mm, brownish; hilum ⅕–⅙ long.

Geranium pyrenaicum is the only perennial species in section *Batrachioidea*. *Geranium pusillum* seems to be the closest relative of *G. pyrenaicum.* The mericarps of *G. pyrenaicum* are quite similar to those of *G. pusillum*: smooth, with appressed-eglandular hairs (except for subsp. *lusitanicum*), but slightly smaller. Moreover, *G. pyrenaicum* and *G. pusillum* share one derived character state: the presence of a dorsal, longitudinal rib on the mericarp.

Geranium pyrenaicum grows naturally in almost all of Europe, the Caucasus, Asia Minor, northern Iran, and northwest Africa. It has been introduced in some temperate areas of northeastern North America, and probably in northern Europe.

Among the great number of morphological variants formally described under *Geranium pyrenaicum,* only that here segregated as subspecies *lusitanicum* seems of some importance.

According to F. Jacquemoud (in litt.), two sheets of *G. pyrenaicum* are kept in the Burman herbarium at G. However, neither can be related unequivocally to the protologue because of the lack of dates, locality, and other relevant information.

KEY TO THE SUBSPECIES OF *GERANIUM PYRENAICUM*

1a. Mericarps pilose; pedicels with hairs shorter than 0.1 mm .... 4a. *G. pyrenaicum* subsp. *pyrenaicum*
1b. Mericarps glabrous; pedicels usually with hairs (0.5–)0.7–1.3 mm long .... 4b *G. pyrenaicum* subsp. *lusitanicum*

4a. **Geranium pyrenaicum** subsp. **pyrenaicum**

Geranium perenne Huds., Fl. Angl. Ed. 1: 265. 1762. TYPE: England. "Habitat in pratis montanis. Ad ripam fluvii inter Bingley et Kighley in agro Eboracensis; prope Enfield, et inter Hyde-Park et Little-Chelsea," collector unknown (lectotype, here designated, LINN-858.80; microfiche!).

Geranium umbrosum Waldst. & Kit., Descr. Icon. Pl. Hung. 2: 131, tab. 124. 1803–1805. *Geranium pyrenaicum* var. *umbrosum* (Waldst. & Kit.) DC., Prodr. 1: 643. 1824. *Geranium pyrenaicum* subvar. *umbrosum* (Waldst. & Kit.) Nyman, Consp. Fl. Eur. 137. 1878. *Geranium pyrenaicum* [b] *umbrosum* (Waldst. & Kit.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Hungary. *Kitaibel s.n.* (lectotype, here designated, BM!).

Geranium pyrenaicum var. *pumilum* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 131. 1837. TYPE: France. "à Abbeville, sur le versant du rempart, du côté du champs de Foire, et à la porte St.-Gilles, dans les fortifications; à Amiens, sur le rempart, auprès du Jardin des Plantes, et dans le jardin même, sur le petit rideau qui se trouve au-devant de la salle des Démonstrations," *Picard s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium minae Tineo, Pl. Rar. Sicil. 25. 1846. *Geranium pyrenaicum* var. *minae* (Tineo) Nyman ["Minaae"], Consp. Fl. Eur. 138. 1878. TYPE: Italy. Minà, *Tineo 514* (lectotype, here designated, PAL!, the left-hand specimen).

Geranium pyrenaicum var. *subvillosum* Schur, Enum. Pl. Transsilv. 137. 1866. TYPE: Romania. "In den Weinbergen bei Hammersdorf. Jun," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum var. *albiflorum* Schur, Oesterr. Bot. Z. 18: 316. 1868. *Geranium pyrenaicum* [1] *albiflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Austria. "Wächst auf schattigen Rasenplätzen in Wäldern und Obstgärden, häufig ist sie im Garten des k.k. Theresianums, wo ich nur diese beobachtet habe," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum var. [β] *pilosum* Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg, sér. 7, 15: 275. 1869. TYPE: Georgia. "15–22 Sept. . . . in m. Bai Gora alt. 1140–900 hex.," *Owerin s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium rhaeticum Brügger, Jahresber. Naturf. Ges. Graubündens 39: 56. 1885. TYPE: Switzerland. Chur, Lürlibad, *Brügger s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum subsp. *australe* A. Terracc., Malpighia 4: 209. 1890. TYPE: Italy. Palermo alla Pizzuta, *Todaro 638* (lectotype, here designated, K!).

Geranium pyrenaicum var. *gracilescens* A. Terracc., Malpighia 4: 211. 1890. *Geranium pyrenaicum* [*b*] *gracilescens* (A. Terracc.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Italy. "D'Abruzzo e degli alti monti romani, e qui e là sino in Basilicata," *Terracciano s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum var. *patulivillosum* Hausskn. & Bornm. ex Bornm., Mitth. Thüring. Bot. Vereins 20: 10. 1904–1905. TYPE: Turkey. Pontus australis, Amasia, mte. Lokman, 9 May 1890, *Bornmüller 1974* (lectotype, here designated, JE!).

Geranium crinitum N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. Pisterola, *N. Terracciano s.n.* (lectotype, here designated, NAP; photocopy!).

Geranium pyrenaicum [2] *grandiflorum* Schur ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Romania. *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum [3] *parviflorum* Schur ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Romania. *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

Geranium pyrenaicum var. *malvaceum* Beauverd, Bull. Murith. Soc. Valais. Sci. Nat. 42: 183. 1925. TYPE: Switzerland. Bourg-St-Pierre, *Beauverd s.n.* (lectotype, here designated, G!, the specimen on the lower part).

Geranium pyrenaicum var. *longepedicellatum* Sennen, Pl. Espagne 1926, no. 5688. 1927, in sched. TYPE: Spain. Cerdagne: Llivia, Estavar, les Escaldes, *Sennen s.n.* (lectotype, here designated, BC-12495!; isolectotypes, BM!, MA-71633!, MA-471335!, W!).

Geranium pyrenaicum f. *pallidum* Gilmour & Stearn, J. Bot. 70, Suppl.: 6. 1932. TYPE: England. Hab. Hills Road, near Strangeways Research Hospital, Cambridge, *Gilmour & Stearn s.n.* (lectotype, here designated, K!; isolectotype, W!).

Geranium pyrenaicum var. *turolense* Sennen, Diagn. Nouv. 262. 1936. TYPE: Spain. Teruel, *León s.n.*, Pl. Espagne no. 9773 (lectotype, here designated, BC-88765!).

Geranium elbursense Gilli, Repert. Spec. Nov. Regni Veg. 46: 44. 1939. TYPE: Iran. Demawend, alm ober Rehne, 2640 m, 22 July 1936, *Gilli s.n.* (lectotype, here designated, W!).

Stem (15–)25–50(–70) cm tall. Pedicels 1–3 cm long, pilose, with glandular and eglandular hairs shorter than 0.1 mm, usually without long eglandular hairs. Mericarps 2.4–3.1 mm long, pilose. Chromosome number: $n = 13$; $2n = 26$. Figure 11a–g. *Additional illustrations.* Cavanilles (1787: tab. 79 fig. 2); Reichenbach (1841–1842: tab. 192); Ross-Craig (1952: pl. 33); Tokarski (1972: 69, pl. 30).

Distribution (Fig. 12). Europe, North Africa, the Caucasus, western Asia, and North America; also reported from Chile (Marticorena & Quezada, 1985: 47); waste places, field margins, and forest margins, between 0 and 2650 m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 634, map 1268).

Phenology. Flowering May–September.

Representative specimens examined. MOROCCO. 71 km S Marrakech, 2 km below Oukaimeden, 2520 m, 31°12′N, 7°50′W, *Jury et al. 9004* (BM).

ALBANIA. M. Parmu, Alpes alb. sept., distr. Scutari, *Baldaci 257* (BM). ARMENIA. Pr. oz. Sevan, 40°33′N, 44°57′E, *Avetisian et al. s.n.* (MA-252462). AUSTRIA. In pratis agri Vindobonensis, *Kerner s.n.* (K). BELGIUM. Caestert, 23 May 1950, *Bakhuizen s.n.* (K). BULGARIA. Rila pr. Samokov, 42°8′N, 23°33′E, *Petrova & Kozuharov 838* (MA). CZECH REPUBLIC. Moravia SW, Dacice, pago Police haud procul ab opp. Jemnice, 450 m, *Unar 1537* (MA). DENMARK. Stautrup near Aarhus, 56°10′N, 10°13′E, *Nielsen & Pedersen 429* (MA). FINLAND. Aloa, 1878, *Hollmén s.n.* (MA-71628). FRANCE. Aveyron, St. Paul des-Fonts, cultivé de gr. orig. d'Igny (Seine-et-O.), May 1905, *Coste s.n.* (BC-825302). GERMANY. Bavaria, pr. Bamberg, 380 m, May 1907, *Harz s.n.* (BM). GREECE. Bordag, 20 km NW Drama, Macedonia, 1000 m, *Stainton 7704* (K). HUNGARY. Erdely, Brafsó, 18 May 1898, *Kuel s.n.* (BC-12504). IRAN. Fao project Camp, 1520 m, 36°0′N, 53°0′E, *Fishwick 8* (K). IRELAND. Dublin, *Gamble 20055* (K). ITALY. Lucania, M. Sacro, 1700 m, July 1907, *Guadagno s.n.* (MA-71635); Sicilia, Madonie, *Citarda 331* (LY); Madonie mts., well above Isnello towards Piano Battaglia on slopes Pzo Antenna Grande, 1000 m, 26 May 1972, *Stace & Cotton s.n.* (BM); Messina, Nebrodie Mountains, mt. Soro, 1710 m, 37°56′N, 14°41′E, *Akeroyd et al. 3744* (BM); Palermo, ca. 45 km S of Cefalù, SE of Rifugia Marini, 1600 m, *Davis & Sutton 63866* (BM); in silvaticis montosis Madonie, 1882, *Citarda s.n.* (K); m. Pizzuta, 1300 m, 7 June 1907, *Lacaita s.n.* (BM). NETHERLANDS. Culemborg, 51°57′N, 5°14′E, 5 June 1938, *Van Soest s.n.* (L). NORWAY. Akershus amt, *Werenskiold 15298* (C). POLAND. Dittmannsdorf, pr. Waldenburg in Silesia, 50°46′N, 16°17′E, 400 m, 17 June 1884, *Felsmann s.n.* (BC-12492). ROMANIA. Transylvania, *Schur 756* (K). RUSSIA. North Caucasus, Terek prov., 43°28′N, 44°11′E, 8 June 1911, *Busch s.n.* (W). SPAIN. Potes, bajada hacia Sotres, *Castroviejo et al. 4131EV* (MA). SWEDEN. Uppsala, 59°55′N, 17°38′E, *N. J. Andersson s.n.* (MA-99906). SWITZERLAND. Bern, *Thring H965.34* (K). SYRIA. Gifi el Hajar, June 1822, *Ehrenberg s.n.* (K). TURKEY. A4 Ilgaz Daglari, Karasu Valley, Gulmezler, S of Kastamonu, 1780 m, *Cheese 1751* (K). UKRAINE. Krym, Bisetka Vetrov, 15 km NNE of Yalta, 1250 m, *Chater 140* (BM). UNITED KINGDOM. **England:** Bakewell, NW Derbyshire, *Bailey 277* (K). YUGOSLAVIA. **Montenegro:** Crna Gora, Zablzak, lower

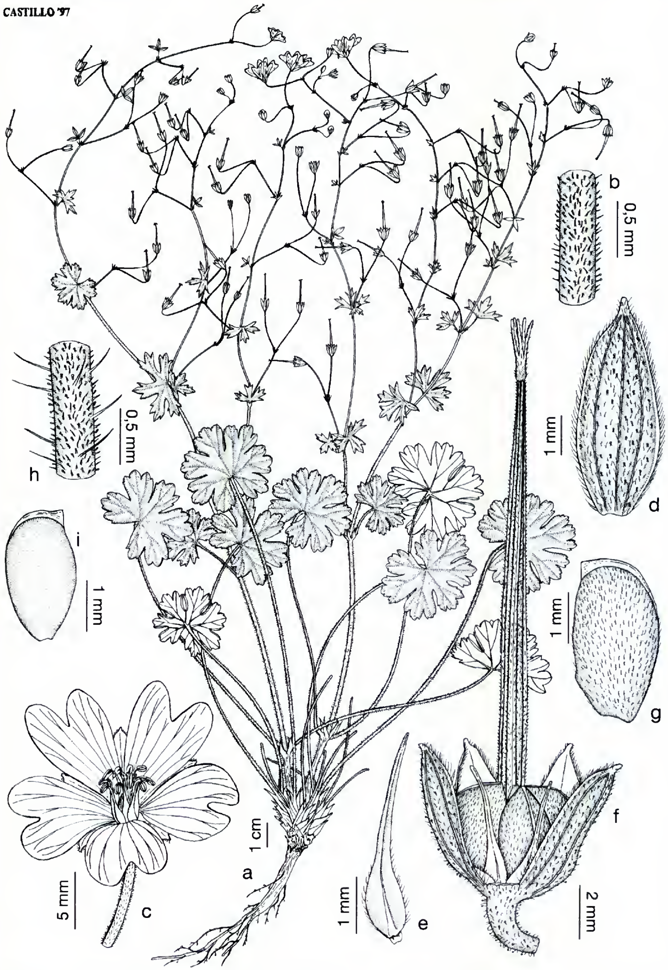

Figure 11. a–g. *Geranium pyrenaicum* subsp. *pyrenaicum.* —a. Habit. —b. Pedicel. —c. Flower. —d. Sepal. —e. Stamen. —f. Fruit and sepals. —g. Mericarp. h, i. *Geranium pyrenaicum* subsp. *lusitanicum.* —h. Pedicel. —i. Mericarp. (a, b, d–g based on *Aedo 2084* (MA); c based on *Aedo et al. CN340* (MA); h, i based on *Losa s.n.* (MA-71620).)

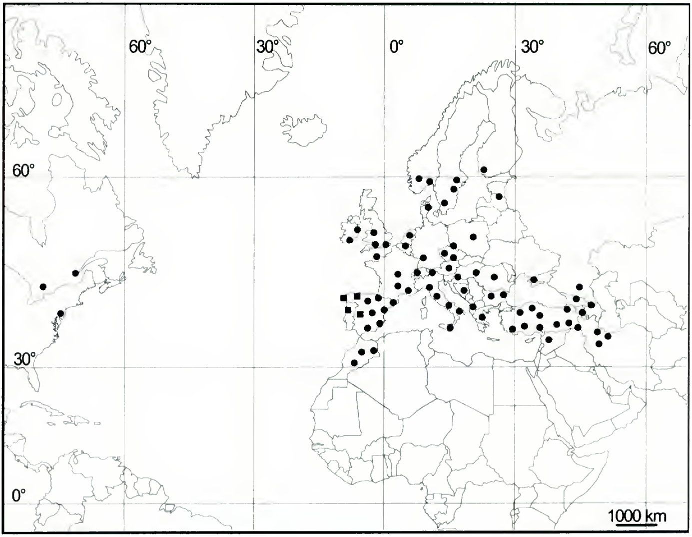

Figure 12. Distribution of *Geranium pyrenaicum* subsp. *pyrenaicum* (dots) and subsp. *lusitanicum* (squares), based on herbarium records.

slopes of Savin Kuk, above Crno Jezero, 1750 m, *Gardner 2441* (BM).

CANADA. **Ontario:** Grey Co., W of Beaverdale, 44°24′N, 80°38′W, *Whiting 1666* (CAN). **Québec:** Sillery, cimetière St-Patrice, 46°46′N, 71°15′W, *Bernard B84–53* (CAN). U.S.A. **New York:** Bronx Co., New York Botanical Garden, Bronx Park, *Gilly 426* (NY).

4b. Geranium pyrenaicum subsp. **lusitanicum** (Samp.) S. Ortiz, Anales Jard. Bot. Madrid 47: 244. 1990. *Geranium pyrenaicum* raça *lusitanicum* Samp., Man. Fl. Port. 273. 1911. *Geranium lusitanicum* (Samp.) Samp. ex J. M. M. Lopes, Bol. Soc. Brot. ser. 2, 5: 245. 1928. *Geranium pyrenaicum* var. *lusitanicum* (Samp.) Samp., Fl. Port. Ed. 2: 331. 1947. TYPE: Portugal. Castro Laboreiro, July 1903, *Sampaio s.n.* (lectotype, here designated, PO-4606!).

Geranium pyrenaicum var. *majus* Pau ex Merino, Fl. Galicia 1: 283. 1905. TYPE: Spain. ad Rivas Pequeñas, *Merino 305* (lectotype, here designated, LOU!).

Stem (23–)40–75(–110) cm tall. Pedicels 1–2.5 mm long, pilose, with glandular and eglandular hairs shorter than 0.1 mm and usually also with long eglandular hairs (0.5–)0.7–1.3 mm. Mericarps 2.4–2.6 mm long, glabrous. Chromosome number: $2n = 26$. Figure 11h, i. *Additional illustration.* Ortiz (1989: 242 fig. 1).

Distribution (Fig. 12). Spain and Portugal; waste places, field margins, and forest margins between 0 and 2000 m. *Additional map.* Ortiz (1989: 244 fig. 3).

Phenology. Flowering June–July.

Representative specimens examined. PORTUGAL. Bragança, Paramio, Zeibe, 28 July 1971, *Dias Pereira s.n.* (LISI); Caldas do Gerez, June 1887, *Murray s.n.* (K); Campea, 3 Aug. 1961, *Rozeira et al. s.n.* (PO-15435); Castelo de Vide, June 1908, *Sampaio s.n.* (PO-4609); Fafe, Armil, 8 May 1943, *Barros s.n.* (PO-30979); Macedo de Cavaleiros, 23 Apr. 1943, *Rozeira & Castro s.n.* (MA-191371); Mata do Fundao, June 1906, *Tavares s.n.* (PO-4607); Meda, dentro do Castelo, 5 Oct. 1976, *Costa s.n.* (PO-45102); Mogadouro a Azinhoso, Qta. da Nogueira, *Barbosa & García 6754* (LISI); Moimenta da Beira, Vila da Rua, beira da Ribeira, 26 June 1977, *Costa s.n.* (PO-28436); Póvoa de Lanhoso, Quintal de S. Geus, May 1908, *Sampaio s.n.* (PO-4608); Sabugal, Quadrazais, junto ao rio Côa na reserva, 2 June 1988, *Ladero & Lousa s.n.* (LISI); Serra da Estrela, Fonte Paulo Martius, *Rozeira s.n.* (PO-15434);

Tabuaço, Vale da Figueira, *Barbosa & García 8083* (LISI); Vinhais, Tuizelo, 28 May 1972, *Marcos & Almeida s.n.* (LISI); Castro Laboreiro, Povoaçao, June 1903, *Sampaio s.n.* (PO-4606). SPAIN. Ávila, El Arenal, 1300 m, 12 Aug. 1986, *Luceño & Vargas s.n.* (MA-407065); Vizcaya, Gorbea, *Guinea 4020* (MA); Burgos, La Revilla, Carazo, 1400 m, 30TVM6949, 6 July 1979, *Pons & Susana s.n.* (MA-414207); Cáceres, Baños de Montemayor, 17 May 1944, *Caballero s.n.* (MA-71194); León, Los Apóstoles, La Guiana, 42°30'N, 6°36'W, 26 June 1984, *Fernández Alonso et al. s.n.* (MA-518975); La Rioja, Arnedillo, Peñalmonte, 1100 m, 14 Oct. 1972, *Segura Zubizarreta s.n.* (MA-359912); Lugo, 13 June 1979, *Carreira s.n.* (MA-493007); Madrid, El Escorial, 16 June 1907, *Rodríguez s.n.* (MA-341882); Asturias, Belmonte, Faedo, 685 m, *Aedo 3700* (MA); Palencia, Dehesa de Montejo, valle de Tosande, 1350 m, *Monasterio 1341* (MA); Salamanca, Castañar de las Honfrías, Linares del Río Frío, 15 June 1974, *Castroviejo s.n.* (MA-324277); Segovia, Altos del puerto de la Quesera, 1340 m, 24 June 1973, *Gómez et al. s.n.* (MA-323972); Soria, Cañón del río Lobos, 7 June 1980, *Buades s.n.* (MA-571625); Álava, Ichine, mt. Gorbea, *Guinea 4019* (MA); Zamora, Rivadelago, barranco del Fornillo, June 1945, *Losa s.n.* (MA-71620).

Geranium pyrenaicum subsp. *lusitanicum* comprises plants from northwestern Spain and Portugal with glabrous mericarps and long, patent, eglandular hairs on the peduncles and pedicels. In this area, all specimens examined exhibit these features. However, eastward, in the eastern portion of the Cantabrian range and in the Iberian range, where the two subspecies occur sympatrically, the indumentum of the peduncles and pedicels is variable. This was pointed out by Ortiz (1989: 243), who proposed subspecific rank for these entities. The rank of subspecies is here used according to Du Rietz (1930), for allopatric taxa merging morphologically where they come into contact. Lidén (1986) described subspecies as "taxa believed to be allopatrically evolved from a common ancestor, not sufficiently different to be recognized as species, i.e. resulting from primary speciation at an early stage." This could be the case in *G. pyrenaicum*, considering its geographical distribution and weak morphological divergence.

We consider occasional specimens with glabrous mericarps from within the geographic range of *G. pyrenaicum* subsp. *pyrenaicum* to be discordant elements representing minor variation of no taxonomic relevance. However, if such individuals were confirmed as more common, the status of subsp. *lusitanicum* would have to be reconsidered.

Geranium sect. **Divaricata** Rouy, in Rouy & Foucaud, Fl. France 4: 88. 1897. TYPE: *G. divaricatum* Ehrh.

Perennial or annual herbs; stems to 60 cm long, with simple or bifurcate monopodial branching, leafy, erect, with patent eglandular and glandular hairs. Basal leaves in persistent or deciduous rosettes; venation actinodromous, basal, perfect, marginal; lamina pentagonal in outline, palmatifid, concolorous, hairy; segments 5–7, rhombic, 7–15-lobed at apex. Cauline leaves opposite or alternate; stipules lanceolate, sometimes lobed, papery, brown, pilose. Cymules solitary, arising from aerial stems; bracts lanceolate, papery, brown; peduncles present, with patent glandular and eglandular hairs; bracteoles linear-lanceolate, sometimes lobed, papery, brown; pedicels 2 per cymule, ± ascending and often curved upward after anthesis, subequal, with patent glandular and eglandular hairs; peduncle and pedicel together very often exceeding the subtending leaf. Sepals ovate, erect-patent at anthesis and erect in fruit, briefly mucronulate, marginally scarious; abaxial surface with eglandular or glandular hairs; adaxial surface glabrous, with a subapical tuft of hairs. Petals erect-patent, ± obovate, emarginate, without claw, without nectar passages, ciliate at base, with sessile glands on the adaxial surface, ± purple, without a dark basal spot. Stamens 10, both whorls bearing anthers; filaments lanceolate, expanded at base, persistent in fruit, with a conspicuous midvein, sometimes ciliate, pilose on abaxial surface, pale pink; pollen blue. Nectaries hemispherical, glabrous. Stigmas pink-purple. Fruit of the carpel-projection-type, with discharge mechanism inoperative; mericarps transversely wrinkled, sometimes cristate, covering the seed completely, without a basal beak and without a callus, hairy; rostrum reduced, obtuse at apex; stigmatic remains with 5 pilose lobes. Seeds obovoid, smooth, brownish, the hilum 1/6 as long as the perimeter. Cotyledons laterally incised. Chromosome number: $2n = 20?$, 28.

Distribution. Southwestern Europe to central Asia and China.

The most distinctive feature of *Geranium* sect. *Divaricata* is the inoperative fruit-discharge mechanism. Other characters states, such as the incised margin of the cotyledons and the obovate seed outline, also support this section as a natural entity.

KEY TO THE SPECIES OF *GERANIUM* sect. *DIVARICATA*

1a. Plants perennial; mericarps with a longitudinal crest .... 5. *G. albanum*
1b. Plants annual; mericarps without a longitudinal crest .... 6. *G. divaricatum*

5. **Geranium albanum** M. Bieb., Fl. Taur.-Caucas. 2: 137. 1808. TYPE: Georgia. "Ex Albaniâ ibericâ, Wakiri" [Bakir district, pr. Signakh, 41°37'N, 45°54'E], *Steven s.n.* (lectotype, here designated, LE, photo!).

Geranium cristatum Steven, Mém. Soc. Imp. Naturalistes Moscou 4: 50, tab. 5. 1813. TYPE: Georgia. Jucharibasch [pr. Soudour], *Steven s.n.* (lectotype, here designated, H!).

Perennial herbs with rootstock ca. 6–8 mm diam., branched, with fusiform-swollen roots and remains of stipules and petioles at apex; stem 40–60 cm tall, erect, usually branched from the base, pilose, with long eglandular hairs 1–2 mm long, and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a deciduous rosette; lamina 2.3–5.2 × 3–4.5 cm, divided for 0.65–0.75 of its length, pilose, with eglandular, appressed hairs; segments 4–7 mm wide at the base, 7–9-lobed in distal half; petioles to 11 cm long, with patent long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; cauline leaves opposite; stipules 4–6 × 2–3 mm, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 3–4 × 1.5–2 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–4.8 cm long, pilose, with eglandular, patent hairs ca. 1 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 3–4 × 0.5–1 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–4 cm long, pilose, with eglandular patent hairs 1–1.5 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 6–9 × 2.5–3 mm, mucronulate (with mucro 0.3–0.6 mm long), with scarious margins 0.1–0.2 mm wide, with eglandular hairs 1–1.3 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 12–14 × 8–9 mm, emarginate (with notch ca. 1 mm deep), bright purple. Stamen filaments 5–6 mm long, with spreading glandular hairs and a tuft of eglandular hairs at the base on the abaxial side, without ciliae; anthers 1.5–1.6 × 0.8–0.9 mm, purple. Gynoecium 6–7 mm long; stigma pink-purple. Fruit 15–17 mm long; mericarps 6–7 × 3–3.5 mm, with 3–4 transverse ribs and a longitudinal crest, pilose, with appressed-eglandular hairs up to 0.5 mm long, not ciliate at the base; rostrum 9–10 mm long, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 1–2 mm long, with 5 pilose lobes. Seeds 2.8–3 × 1.8–1.9 mm; hilum ⅕ as long as the perimeter. Chromosome number: $n = 14$; $2n = 20$?. Figure 13. *Additional illustrations.* Karjagin (1955: 39 tab. 2); Grossheim (1962: 11 tab. 1 fig. 3); Tokarski (1972: 59, pl. 1).

Distribution (Fig. 14). Northern Iran and Caucasus; meadows, stony places, and forest margins, between 100 and 2600 m. *Additional maps.* Grossheim (1962, map no. 4); Meusel et al. (1978: 263).

Phenology. Flowering June–August.

Representative specimens examined. AZERBAIJAN. Lankoran, 38°45′N, 48°50′E, 1836, *Hohenacker s.n.* (BM, M, W); Elisabethpol, Schuscha, pr. Chan-Kendy, 39°17′N, 46°23′E, June 1900, *Fedossejew s.n.* (LE). GEORGIA. Georg. Cauc., m. Wilnser, 1838, *Kalm s.n.* (G); in dumosis circa Telav, Kachetia, 41°55′N, 45°29′E, 20 June 1918, *Pastuchov s.n.* (K, W); Transcaucasia, Georgia Orient., Steppa Shiraki, m. Schavi-mta, 41°42′N, 46°15′E, 600 m, 8 May 1940, *Sachokia s.n.* (MA-575069); pr. Sihuscha Georg. Cauc., 1838, *Hohenacker s.n.* (K, M). IRAN. 59 km S of Shahi, 1500 m, 36°27′N, 52°51′E, *Furse 2979* (K, W); Ardabil-Astara, 1200 m, 38°24′N, 48°52′E, *Bowles Scholarship Bot. Exped. 2312* (K); East Azerbaijan, W side of Hasi Amir Pass, on Russian border, 28 km NE of Ardabil, 1600 m, *Grant 16229* (W); Gilan, around the village Damash-E of Rudbar, 1700 m, 36°48′N, 49°23′E, *Ala 17143G* (W); Gilan, in collibus 10–20 km W Astara, ad viam versus Heyran ducentem, 500 m, 38°22′N, 48°38′E, *Rechinger 39902* (B, G, W); Gorgan, 37°00′N, 54°30′E, *Sharif 545* (W); Gozlu, Mazenderan, *Koelz 16221* (W); Guilan, *Lindsay 741* (BM, K, W); Mazanderan, Haraz valley, Karehsang, 100 m, 36°18′N, 52°0′E, *Wendelbo 584* (W); Ostan 1, Hassankif, 1070 m, 36°29′N, 51°9′E, *F. Schmid 6636* (G); Ostan 2, Dimelo, sommet du versant caspien, peu en dessous de la crête, 2600 m, *F. Schmid 5986* (G, W); Ostan 2, entre Amol et Siavicheh, 1800 m, 36°28′N, 52°21′E, *F. Schmid 5853* (G, W); Persia borealis, in dumetis prope Rascht, 37°16′N, 49°35′E, *J. Bornmüller & A. Bornmüller 6507* (BM, G, K, W); Persia borealis, Elburz, Pole-Zangulé, *Gauba 1553* (B); Persia borealis, Elburz, Kandaran, 1900 m, 36°16′N, 49°42′E, *Gauba 1453* (B); prov. Talysh et Korabach, m. Kohenaker, 38°29′N, 48°27′E, 1838, *Kalm s.n.* (G). RUSSIA. North Caucasus, Dagestan, pr. urb. Derbent, 130 m, 42°3′N, 48°17′E, *Alexeenko 7437* (LE); distr. Kurinskij, pr. st. Diviczi, 41°35′N, 47°45′E, *Alexeenko 7428* (LE).

Geranium albanum is a perennial species endemic to northern Iran and the Caucasus. It has a singular mericarp, with a very thick wall and a well-developed dorsal crest. Features shared with *G. divaricatum* are the inoperative discharge mechanism and the ribbed mericarp.

The chromosome number in this species is not fully clarified. Warburg (1938: 145) and Van Loon (1984a: 276) have given different numbers, with only that of the first author concording with data for *G. divaricatum.*

6. **Geranium divaricatum** Ehrh., Beitr. Naturk. 7: 164. 1792. *Geranium winterlii* Roth ["winterli"], Catal. Bot. 2: 78. 1800, nom. illeg. TYPE: Hungary. *Ehrhart Plant. Select. 69* (lectotype, here designated, M!).

Geranium divaricatum var. *ambiguum* Rochel ex Schult., Oestr. Fl. Ed. 2, 2: 285. 1814. *Geranium divaricatum*

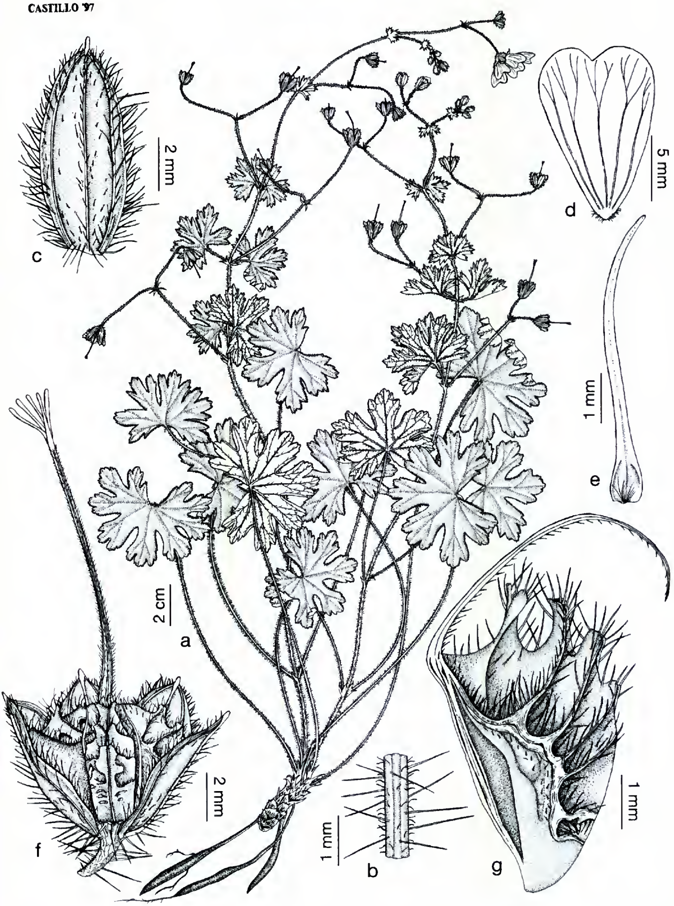

Figure 13. *Geranium albanum.* —a. Habit. —b. Peduncle. —c. Sepal. —d. Petal. —e. Stamen. —f. Fruit and sepals. —g. Mericarp. (a–e based on *Kalm s.n.* (G); f, g based on *Schmid 6636* (G).)

[B] *ambiguum* (Rochel ex Schult.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 51. 1913. TYPE: Cultivated, *Rochel 292* (lectotype, here designated, M!; isolectotype, W!).

Annual herb 20–50 cm tall; stem erect, usually branched from the base, pilose, with long eglandular hairs 1–3 mm long and short glandular and

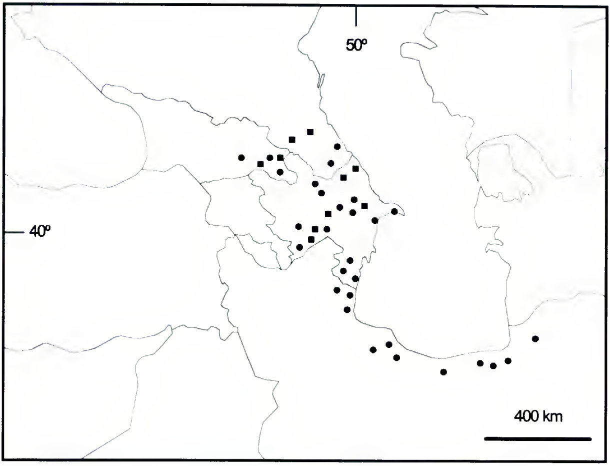

Figure 14. Distribution of *Geranium albanum* (longitude = 50°E; latitude = 40°N). Dots correspond to herbarium records, and squares indicate literature records from Grossheim (1962).

eglandular hairs < 0.5 mm long. Basal leaves in a ± persistent rosette; lamina 2.5–7 × 3.1–7.9 cm, divided for 0.65–0.85 of its length, pilose, with glandular and eglandular, appressed hairs; segments 4–9 mm wide at the base, 7–12(–15)-lobed in distal half; petioles to 15 cm long, with patent long eglandular hairs 1–2.8 mm long and short glandular and eglandular hairs < 0.5 mm long; cauline leaves alternate; stipules 4–7 × 1–2 mm, pilose with glandular and eglandular hairs on abaxial surface, glabrous adaxially. Bracts 4–5 × 1.5–2 mm, linear-lanceolate, sometimes lobed, pilose with glandular and eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.6–3.5 cm long, pilose, with eglandular patent hairs 1–3.5 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 3–4 × 0.5–1 mm, pilose with glandular and eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–2.8 cm long, pilose, with eglandular patent hairs 1–2.5 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 4–4.5 × 1.8–2 mm, mucronulate (with mucro ca. 1 mm long), with scarious margins ca. 0.1 mm wide, with short (< 0.8 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 4.5–6.5 × 2.5–3 mm, emarginate (with notch ca. 1 mm deep), bright purple. Stamen filaments 1–2.5 mm long, pilose on the abaxial side, ciliate on the proximal half; anthers 0.4–0.6 × 0.3–0.4 mm, purple. Gynoecium 3–3.5 mm long; stigma purple. Fruit 7–11 mm long; mericarps 2.8–3.5 × 2–1.8 mm, with 3–4 transverse ribs, without a longitudinal rib or crest, pilose, with appressed-eglandular hairs up to 0.5 mm long, not ciliate at the base; rostrum 5–8 mm long, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 0.5–1 mm long, with 5 pilose lobes. Seeds 2.4–2.6 × 1.3–1.4 mm; hilum 1/6 as long as the perimeter. Chromosome number: $2n = 28$. Figure 15. *Additional illustrations.* Reichenbach (1841–1842: tab. 188 fig. 4873); Gams (1924: 1695, fig. 1637e–h); Tokarski (1972: 63, pl. 13).

Distribution (Fig. 16). Europe to central Asia, China, and the Indian subcontinent; waste places, meadows, stony dry slopes, field margins, and shady wood borders, between 0 and 2100 m.

Phenology. Flowering March–September.

Representative specimens examined. AFGHANISTAN. Farkhar-Tal, Takhar, 1250 m, 36°34′N, 69°51′E, *Podlech 10484* (M). ARMENIA. Ararat, montes Gegamski khrebet, in vicinitate ruinarum pagi Akhkeng, 2100 m, 39°47′N,

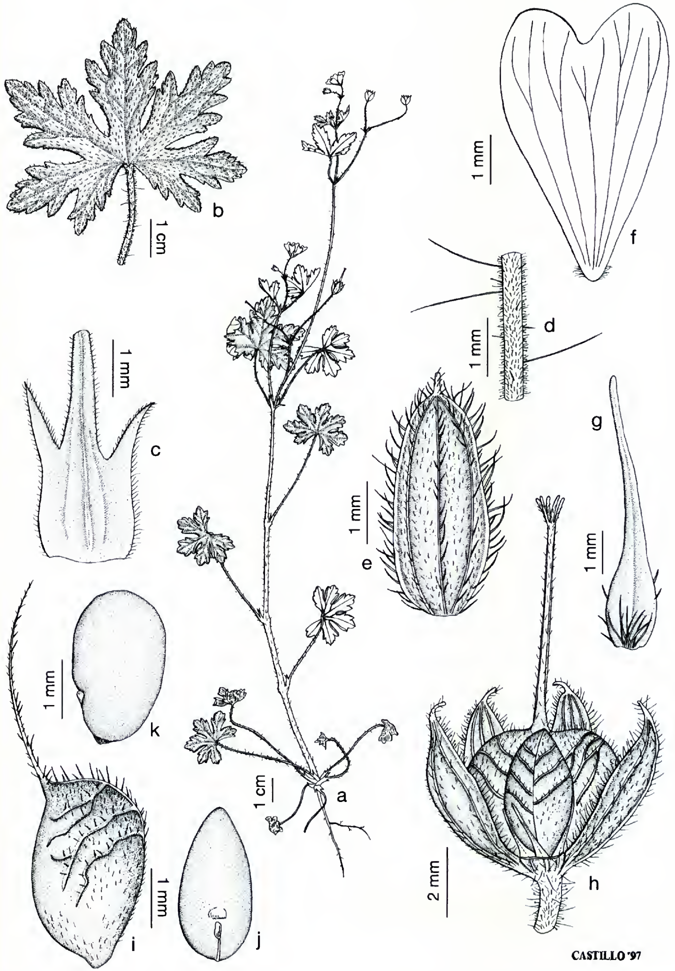

Figure 15. *Geranium divaricatum.* —a. Habit. —b. Leaf. —c. Stipule. —d. Peduncle. —e. Sepal. —f. Petal. —g. Stamen. —h. Fruit and sepals. —i. Mericarp. —j, k. Seeds. (a, c–g based on *Popov & Vvedensky s.n.* (MA-71170); b based on *Fritzsche s.n.* (BC-825281); h–k based on *Koch 46/348* (MA).)

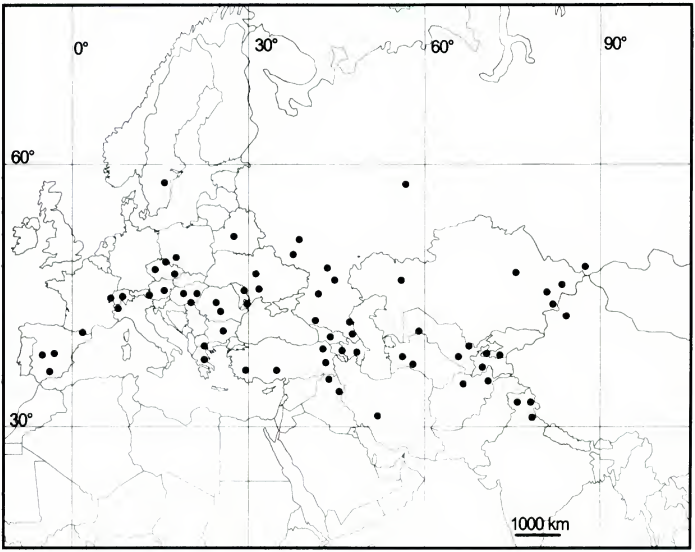

Figure 16. Distribution of *Geranium divaricatum*, based on herbarium records.

44°46′E, 10 July 1975, *Vasák s.n.* (B). AUSTRIA. Lienz, Tirolis, 46°15′N, 12°50′E, 19 May 1869, *Gander s.n.* (K). BELARUS. Minsk, Khojni, Mozyrskago, 53°54′N, 27°34′E, 1902, *Bordzilowski s.n.* (LE). BULGARIA. In graminosis ad Sofia, June 1924, *Stefanoff s.n.* (BM). CHINA. **Xinjiang**: Songarei, *Schrenk s.n.* (G); Tian-schan, Aktasch in montibus Karshan-tau, 43°0′N, 84°0′E, 15 May 1928, *Popov & Vvedensky s.n.* (MA-71170). FRANCE. Cerdagne, vallée de Carol à Porta, 1500 m, 13 Aug. 1916, *Sennen s.n.* (MA-155028). GERMANY. Pr. Francfort-sur-l'Oder, 52°20′N, 14°32′E, 27 June 1847, *Buek s.n.* (K). GREECE. Macedonia, Pisoderion, 1200 m, *Alston & Sandwith 970* (K). HUNGARY. Pest, in dumetis insula Cspel, 19 June 1900, *Degen s.n.* (G). INDIA. Chamba, W Himalaya, 2000 m, 32°N, 76°E, *Watt 2067* (K); Gaon, Bashahr, NW Himalaya, *Lace 882* (K). IRAN. Noa-kuh, Nawa, nr. Karend, W of Kermanshah, 2000 m, 31°28′N, 54°54′E, *Furse 1892* (K). IRAQ. Jebel Sinjar, Mosul liwa, 1000 m, *Gillet 11134* (K). ITALY. Oulx, ad saepes secundum viam quae est inter Borgata superiore di Oulx et S. Marco, Torino, 1200 m, 45°02′N, 6°50′E, 25 June 1906, *Ferrari & Vallino s.n.* (K). JAMMU-KASHMIR. Preslang near Pahlgam, Kashmir, 43°1′N, 75°25′E, *Stewart 21676* (K). KAZAKSTAN. Turkestania, Wernoje, 43°17′N, 68°16′E, 24 Sep. 1876, *Kuschakewitz s.n.* (K). KYRGYZSTAN. Turkestania, prov. Fergana, distr. Osch. pr. Gulcza, 40°21′N, 73°26′E, 30 May 1900, Tranzschel s.n. (LE). POLAND. Breslau, 51°5′N, 17°0′E, June 1860, *Uechtriz s.n.* (W). ROMANIA. Oltenia, Dolj, pr. Tîmburesti, 70 m, 9 May 1971, *D. Cîrtu & M. Cîrtu s.n.* (MA-252485). RUSSIA. North Caucasus, Dschmagat-Tal nordöstlich Teberda, 43°28′N, 41°46′E, *Stohr 9* (B); Russia Central, Kursk, Bielgorod, 50°38′N, 36°36′E, 5 June 1900, *Sukaczew s.n.* (LE); Russia East, Bashkiria Autonomous SSR, Zilairskij rajon, Userganskaya, 54°N, 56°E, *Grebner 241* (LE); Russia South, Saratov, Sarepta, 48°31′N, 44°29′E, 1 June 1894, *Becker s.n.* (M). SLOVAKIA. In mte. Zobor, Nitriam, 48°21′N, 18°7′E, 1836, *Láng s.n.* (K). SPAIN. Granada, Sierra Nevada, loc. dumetes inter Cerro Trevenque et Aquilones de Dilar, 1800 m, *Porta & Rigo 104* (K). SWEDEN. Sodermanland, Nacka, 4 Sep. 1915, *Vestergren s.n.* (W). SWITZERLAND. Cantou des Grisons, Engadine, ruine Steinsberg Ardez, 1490 m, 22 July 1933, *Huber s.n.* (BC-79174). TADZHIKISTAN. Pendjhakent, 1000 m, 39°29′N, 67°37′E, 23 May 1892, *Komarov s.n.* (LE). TURKEY. Babadagh Dobrudscha, bei Cucarova, 36°32′N, 29°10′E, *Sintenis 524* (K). TURKMENISTAN. Ashabad, in angustiis Karanky, 37°58′N, 58°24′E, *Litwinow 1129* (G). UKRAINE. Charkov pr. Walki, 50°0′N, 36°15′E, *Lindeman s.n.* (W). UZBEKISTAN. Pr. Tashkent, 41°16′N, 69°13′E, *Kuschakewitz s.n.* (K).

The most distinctive feature of this annual species is the transversely ribbed mericarp, which has thin walls and no longitudinal crest.

The eastern limit of *Geranium divaricatum* in

Europe is not well established, because it is quite difficult to obtain material from Russian herbaria. In Asia, this species reaches the Chinese Xinjian (84°E) and the western Himalayas to 76°E. It is known from Sweden by only one collection, which could be an introduction; the nearest locality is in Germany, almost 1000 km southward.

DUBIOUS NAMES

Geranium brutium [b] *micranthum* N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. "Pisterola a Signa sopra Vallesega," *N. Terracciano s.n.* (no authentic material located). = *G. molle?*

Geranium ×*luganense* Chenevard, Bull. Herb. Boissier sér. 2, 3: 427. 1903. TYPE: Switzerland. "Crocefisso, Mt S. Giorgio," *Chenevard s.n.* (no authentic material located). = *G. molle?*

Geranium molle f. *candidum* Beck, Fl. Nieder-Österreich. 563. 1892. TYPE: Austria. "Auf bebauten und wüsten Stellen, unter Buschwerk hie und da um Wien und bis gegen Baden, bei Laxenburg, Hainburg, Melk, Schenkenbrunn, Retz. V–IX," *Beck s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *grandiflorum* Viv. ["*grandiflora*"], Fl. Libyc. Spec. 39. 1824. TYPE: Libya. "H. in totâ Cyrenaicâ," *Viviani s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *grandiflorum* Vis., Fl. Dalmat. 3: 212. 1851, nom. illeg., non Viv. (1824). TYPE: Italy. "Hab in agris, cultis et ruderatis circa Zara, Sebenico, Traù, Spalato, Ragusa, var. praecipue in saxosis ad Scagliari prope Cattaro et in Montenegro," *Visiani s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *grandiflorum* Lojac., Malpighia 20: 194. 1906, nom. illeg., non Viv. (1824). TYPE: Italy. "In herbidis Palermo. Herb. Pan.!," *Lojacono s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *minus* Chevall. ["*miuus*"], Fl. Gén. Env. Paris Ed. 1, 2: 802. 1828. TYPE: France. "Commun dans les bois et les décombres," *Chevallier s.n.* (no authentic material located). = *G. molle?*

Geranium molle subsp. *pollinense* A. Terracc., Malpighia 4: 198. 1890. *Geranium pollinense* N. Terracc. ex A. Terracc., Malpighia 4: 198. 1890. TYPE: Italy. "Del monte Pollino alle Neviere ed all'Affircata," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *suaveolens* Boenn. ex Rchb., Fl. Germ. Excurs. 778. 1832. *Geranium pusillum* f. *suaveolens* (Boenn. ex Rchb.) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. *Geranium molle* [1] *suaveolens* (Boenn. ex Rchb.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Germany. "Auf bebautem Boden, Schutt, an Mauern, Planken" (no authentic material located). = *G. molle?*

Geranium molle f. *pinguis* K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* [B] *pinguis* (K. Malý) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Yugoslavia. "Novibazar: kljeznicatal zwischen Prijepolje und Jabuka (Weisbach)," *Weisbach s.n.* (no authentic material located). = *G. molle?*

Geranium molle var. *montanum* A. Terrac. ex N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 123. 1913. TYPE: Italy. "Acquanera," *N. Terracciano s.n.* (no authentic material located). = *G. molle?*

Geranium molle [II] *tenuisecta* A. Terracc. ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Nei colli sino a che sui monti. . .," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

Geranium molle [I] *triviale* A. Terracc. ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Porto d'Anzio," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

Geranium punctatum Kanitz, Linnaea 32: 569. 1863, nom. illeg., non Andrews (1799). TYPE: Hungary. "Habitat inter frutices Syrmii, unde a Wolny pro G. umbroso missum," *Kanitz s.n.* (no authentic material located). = *G. molle?*

Geranium pusillum var. *exsertum* Peterm., Fl. Lips. Excurs. 512. 1838. TYPE: Germany. ". . . ad praedium Pfaffendorf, ad pagos Leutzsch, Anger, Reudnitz, ad oppidum Delitzsch etc.," *Petermann s.n.* (no authentic material located). = *G. pusillum?*

Geranium pusillum var. *luxurians* A. Terracc., Malphigia 4: 206. 1890. TYPE: Italy. ". . . che ho qui di Carlsbaad e dell'Alpe Gebbo (1165 m) in val Cairasca (Ossola) Frizzi!," *A. Terracciano s.n.* (no authentic material located). = *G. pusillum?*

Geranium pusillum f. *subcalvum* Casp. ex Abrom., Fl. Ost- & Westpreussen 154. 1898. TYPE: Germany. "Westpreussen, Fl. zw. Kamin u. Obkaser Mühle, Abhang am Mochelsee (Km. 70)," *Abromeit s.n.* (no authentic material located). = *G. pusillum?*

Geranium pusillum var. *villosum* F. Saut., Oesterr. Bot. Z. 49: 402. 1899. *Geranium pusillum* [?] *villosum* (F. Saut.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Italy. "Bozen: an Weinbergsmauern in St. Johann, Guntschna, St. Magdalena, bei Caslar," *Sauter s.n.* (no authentic material located). = *G. pusillum?*

Geranium pyrenaicum var. *depilatum* Sommier & Levier, Trudy Imp. S.-Peterburgsk. Bot. Sada 16: 102. 1900. *Geranium depilatum* (Sommier & Levier) Grossh., in Grossh. & Schischk., Sched. Herb. Pl. Or. Exsicc. 14: 36. 1928. TYPE: Georgia. "Rekom, fl. fr. (Lojka)," *Lojka s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

Geranium pyrenaicum var. *leiocarpum* Guss. ex Lojac., Malpighia 20: 195. 1906. TYPE: Italy. "Lojac. exsicc. pl. Pizzuta. Herb. Pan.!," *Lojacono s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

Geranium pyrenaicum var. *montanum* A. Terracc., Malpighia 4: 208. 1890. TYPE: Italy. "Monte Pollino all'Afforcata N. Terracciano!, sommità del Coccorello in Abruzzo Cherici! Velino Sanguinetti!," *N. Terracciano s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

Geranium pyrenaicum var. *mutilum* Beck, Fl. Nieder-Österreich. 563. 1892. *Geranium pyrenaicum* [4] *mutilum* (Beck) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Austria. "Bei Hütteldorf, Laxemburg," *Beck s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

Geranium pyrenaicum [b] *murense* N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. "S. Vito vecchio, e nei pressi del Piscone di Pisterola," *N. Terracciano s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

Excluded Names

Geranium bifidum Ehrenb. ex R. Knuth, in Engl., Pflanzenr. IV.129 (Heft 53): 152. 1912, nom. nud., pro syn.

Geranium calabrum Ten., nom. nud., in sched. (NAP: photocopy!).

Geranium divaricatum var. *tenuisectum* Sennen, Pl. Espagne 1916, no. 2575 (1916), nom. nud., in sched. (BC-825282).

Geranium molle subf. *abortiva* (De Not. ex Ces.) A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle f. *albiflorum* R. Uechtr., Jahresber. Schles. Ges. Vaterl. Cult. 60: 254. 1883, nom. nud.

Geranium molle var. *caucasicum* Regel ex Woronow, in Kusn., N. Busch & Fomin, Fl. Cauc. Crit. 7(3): 66. 1909, nom. nud., pro syn.

Geranium molle var. *diffusum* Ten. ex A. Terracc., Malpighia 4: 202. 1890, nom. nud.

Geranium molle var. *elatum* Ten. ex A. Terracc., Malpighia 4: 202. 1890, nom. nud.

Geranium molle f. *glabrata* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle var. *graecum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

Geranium molle var. *lucanum* Gasp. ex Nyman, Consp. Fl. Eur. 138. 1878, nom. nud., pro syn.

Geranium molle var. *maioriflorum* Borbás, Oesterr. Bot. Z. 40: 382. 1890, nom. nud.

Geranium molle var. *maritimum* Lojac., Malpighia 20: 194. 1906, nom. nud., pro syn.

Geranium molle var. *montanum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

Geranium molle subsp. *normale* A. Terracc., Malpighia 4: 202. 1890; nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium molle f. *pygmaea* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle f. *sepincola* A. Terracc., Malpighia 4: 200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle f. *tenuisecta* A. Terracc., Malpighia 4: 199–200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle f. *trivialis* A. Terracc., Malpighia 4: 199–200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle [a] *triviale* A. Terracc. ex Gortani & M. Gortani, Fl. Friulana 2: 300. 1906, nom. nud.

Geranium molle var. *typicum* Posp., Fl. Oesterr. Küstenl. 2: 31. 1898, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium molle f. *villosissima* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium molle var. *vulcanicum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

Geranium multiflorum Lang ex Schur, Oesterr. Bot. Z. 18: 317. 1868, nom. nud., pro syn.

Geranium novum Winterl, Index Hort. Bot. Univ. Hung., fig. 2. 1788, nom. inval. (see Greuter et al., 1994, Art. 23.6).

Geranium pseudovillosum Schur ["*pseudo-villosum*"], Enum. Pl. Transsilv. 921. 1866, nom. nud., pro syn.

Geranium pusillum var. *albiflorum* Opiz, Seznam 47. 1852, nom. nud.

Geranium pusillum var. *album* Lindm., Bot. Soc. Exch. Club Brit. Isles 7: 766. 1925, nom. nud.

Geranium pusillum f. *major* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pusillum f. *minor* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pusillum [α] *genuinum* Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium pusillum subf. *humifusa* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pusillum f. *humile* Bueck ex Prahl, Krit. Fl. Schlesw.-Holst. Ed. 1 2: 37. 1889, nom. nud., pro syn.

Geranium pusillum subsp. *normale* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium pyrenaicum f. *algeriensis* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pyrenaicum var. *diffusum* Ten. ex A. Terracc., Malpighia 4: 211. 1890, nom. nud., pro syn.

Geranium pyrenaicum var. *grandiflorum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1876, nom. nud.

Geranium pyrenaicum var. *heterotrichum* Sennen, nom. nud., in sched. (PH!).

Geranium pyrenaicum f. *maior* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pyrenaicum f. *minor* A. Terracc., Malpighia 4: 208. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pyrenaicum subsp. *normale* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium pyrenaicum var. *parviflorum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1876, nom. nud.

Geranium pyrenaicum f. *sicula* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

Geranium pyrenaicum var. *typicum* Woronow, in Kusn., N. Busch & Fomin, Fl. Cauc. Crit. 3(7): 56. 1908, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium pyrenaicum [a] *typicum* Woronow ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913, nom. inval. (see Greuter et al., 1994, Art. 24.3).

Geranium pyrenaicum var. *velutinum* Buhse, Aufzähl. Transkauk. 48. 1860, nom. nud.

Geranium subdivaricatum Schur, Verh. Naturf. Vereins Brünn 15: 160. 1877, nom. inval. (see Greuter et al., 1994, Art. 34.1).

Geranium villosum f. *albiflorum* Sennen, Pl. Espagne, no. 2994. 1917, nom. nud., in sched. (BM!, W!).

Geranium villosum var. *gracile* Sennen, Pl. Espagne, no. 2994. 1917, nom. nud., in sched. (BM!, W!).

Literature Cited

Aedo, C. 1996. Revision of *Geranium* subgenus *Erodioidea* (Geraniaceae). Syst. Bot. Monogr. 49: 1–104.

——— & F. Muñoz Garmendia. 1996. Some notes on the sectional nomenclature of *Geranium* (Geraniaceae). Taxon 45: 104–106.

Aldasoro, J. J., Á. Matilla & G. Nicolás. 1981. Effect of ABA, fusicoccin and thiourea on germination and K^+ and glucose uptake in chick-pea seeds at different temperatures. Physiol. Pl. (Copenhagen) 53: 139–145.

Al-Shehbaz, I. A., M. K. Al-Khakani & A.-R. A. Al-Mayah. 1983. New or noteworthy taxa for the flora of Iraq. Candollea 38: 349–358.

Alves, M. C. & M. T. Leitão. 1976. Contribuçao para o conhecimento citotaxonomico des Spermatophyta de Portugal XIII. Bol. Soc. Brot. ser. 2, 50: 231–245.

Arohonka, T. 1982. Chromosome counts of vascular plants of the island Seili in Nauvo, SW Finland. Ann. Univ. Fenn. Åbo., A 3: 1–12.

Baltisberger, M. 1991. Cytological investigations of some Greek plants. Fl. Medit. 1: 157–173.

Bewley, J. D. & M. Black. 1994. Seeds. Physiology of Development and Germination, ed. 2. Plenum Press, New York.

Böcher, T. W. & K. Larsen. 1958. Experimental and cytological studies on plant species. IV. Further studies in short-lived herbs. Biol. Skr. 10(2): 1–24.

Boissier, É. 1867. Flora orientalis, Vol. 1. H. Georg, Basel, Genève and Lyon.

Britton, N. L. & H. A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada, ed. 2. Dover Publications, New York.

Buttler, K. P. 1989. Chromosomenzahlen von Gefässpflanzen aus Hessen, 4. Hess. Florist. Briefe 38: 11–14.

Carlquist, S. & D. R. Bissing. 1976. Leaf anatomy of Hawaiian geraniums in relation to ecology and taxonomy. Biotropica 8: 248–259.

Carolin, R. C. 1965. The genus *Geranium* L. in the south western Pacific area. Proc. Linn. Soc. New South Wales ser. 2, 89: 326–361, pl. VI–VII.

Cavanilles, A. J. 1787. Monadelphiae classis dissertationes decem. Quarta dissertatio botanica. F. A. Didot, Paris.

Chatterjee, A. & A. K. Sharma. 1970. Chromosome study in Geraniales. Nucleus (Calcutta) 13: 179–200.

Curtis, W. 1782. Flora Londinensis, Vol. 6. W. Curtis, London.

Dahlgren, K. V. 1943. Svedjenävan (*Geranium bohemicum*) och brandnävan (*Geranium lanuginosum*). Svensk Bot. Tidskr. 37: 127–160.

Davis, P. H. 1967. *Geranium* L. *In:* P. H. Davis, J. Cullen & J. E. Coode, Flora of Turkey 2: 451–474. Univ. Press, Edinburgh.

———. 1970. *Geranium* sect. *Tuberosa*, revision and evolutionary interpretation. Israel J. Bot. 19: 91–113.

Dersch, G. 1974. Über einige Chromosomenzählungen an mitteleuropäischen Blütenpflanzen. Philippia 2: 75–82.

Du Rietz, G. E. 1930. The fundamental units of biological taxonomy. Svensk Bot. Tidskr. 24: 333–429.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

Fernández Casas, J., S. Pajarón & M. L. Rodríguez Pascual. 1978. Números cromosómicos para la flora española. 60–65. Lagascalia 8: 109–112.

Franzén, R. & L.-Å. Gustavsson. 1983. Chromosome numbers in flowering plants from the high mountains of Sterea Ellas, Greece. Willdenowia 13: 101–106.

Fritsch, R. M. 1973. IOPB chromosome number reports XLI. Taxon 22: 460–461.

Gadella, Th. W. J. & E. Kliphuis. 1966. Chromosome numbers of flowering plants in the Netherlands II. Proc. Kon. Ned. Akad. Wetensch. C 69: 541–556.

Galland, N. 1988. Recherche sur l'origine de la flore orophile du Maroc: Étude caryologique et cytogeographique. Trav. Inst. Sci. Univ. Mohammed V, Sér. Bot. 35: 1–168.

Gams, H. 1924. *Geranium* L. *In:* G. Hegi. Illustrierte Flora von Mittel-Europa 4(3): 1668–1716. J. F. Lehmann, Munich.

Gauger, W. 1937. Ergebnisse einer zytologischen Untersuchung der Familie der Geraniaceae. I. Planta 26: 529–531.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill. 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 131: 1–389.

Grossheim, A. A. 1962. Flora Kavkaza ed. 2, Vol. 6. Acad. Sci. Moscow, Moscow-Leningrad.

Hanks, L. T. & J. K. Small. 1907. Geraniaceae. *In:* N. L. Britton & L. M. Underwood, North American Flora, Vol. 25: 3–24. New York Botanical Garden, New York.

Heitz, E. 1926. Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Grösse und Form im Pflanzenreich I. Z. Bot. 18: 625–681.

Hetter, G. 1954. Flora Ilustrada del Uruguay. G. Hetter, Basel.

Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–33.

Hill, L. M. 1989. IOPB chromosome data 1. Int. Organ. Pl. Biosyst. Newslett. 13: 17–19.

Hultén, E. & M. Fries. 1986. Atlas of North European Vascular Plants, Vol. 2. Koeltz Scientific Books, Königstein.

Jankun, A., J. Małecka, R. Izmaiłwow, H. Weisło, R. Czapik & K. Musiał (Editors). 1996. Further studies in chromosome numbers of Polish angiosperms Part XXV. Acta Biol. Cracov., Ser. Bot. 38: 9–27.

Karjagin, I. I. 1955. Flora Azerbajdžana, Vol. 6. AN Azerbajdžanskoj SSR Press, Baku.

Knuth, R. 1912. Geraniaceae. *In:* A. Engler, Das Planzenreich IV.129 (Heft 53): 1–631. Wilhelm Engelmann, Leipzig.

Lidén, M. 1986. Synopsis of Fumarioideae (Papaveraceae) with a monograph of the tribe Fumarieae. Opera Bot. 88: 1–133.

Löve, Á. & E. Kjellqvist. 1974. Cytotaxonomy of Spanish plants. IV. Dicotyledons: Caesalpinaceae–Asteraceae. Lagascalia 4: 153–211.

——— & D. Löve. 1945. Cyto-taxonomical studies on boreal plants. III. Some new chromosome numbers of Scandinavian plants. Ark. Bot. 31A: 1–22.

——— & ———. 1956. Cytotaxonomical conspectus of the Icelandic flora. Acta Horti Gothob. 20: 65–291.

Maddison, W. P. & D. R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution. Version 3.0. Sinauer Associates, Sunderland, Massachusetts.

Májovský, J. (Editor). 1974. Index of chromosome numbers of Slovakian flora. Part 4. Acta Fac. Rerum Nat. Univ. Comenianae, Bot. 23: 1–23.

——— (Editor). 1978. Index of chromosome numbers of Slovakian flora (Part 6). Acta Fac. Rerum Nat. Univ. Comenianae, Bot. 27: 1–42.

Marticorena, C. & M. Quezada. 1985. Catálogo de la flora vascular de Chile. Gayana, Bot. 42: 1–157.

Meusel, H., E. Jäger, S. Rauschert & E. Weinert. 1978.

Vergleichende Chorologie der zentraleuropäischen Flora -Karten-, Vol. 2. G. Fischer, Jena.

Mizianty, M., Z. Mirek & L. Frey. 1983. Chromosome numbers of Polish vascular plants (Part 4). Acta Soc. Bot. Poloniae 52: 205–214.

Mulligan, G. A. 1959. Chromosome numbers of Canadian weeds. II. Canad. J. Bot. 37: 81–92.

Natarajan, G. 1978. IOPB chromosome number reports LXII. Taxon 27: 526–531.

Nieto Feliner, G. & C. Aedo. 1995. A cladistic analysis of *Geranium* subgen. *Erodioidea* (Picard) Yeo (Geraniaceae). Bot. J. Linn. Soc. 119: 195–212.

Ortiz, S. 1989. Caracterización taxonómica de las poblaciones ibérico-occidentales de *Geranium pyrenaicum* Burm. fil. (Geraniaceae). Anales Jard. Bot. Madrid 47: 242–244.

Persson, J. 1987. *Geranium* L. *In:* A. Strid, Mountain Flora of Greece 1: 538–549. Cambridge Univ. Press, Cambridge, London, New York, New Rochelle, Melbourne & Sydney.

Pignatti, S. 1982. Flora d'Italia. Edagricole, Bologna.

Pólya, L. 1950. Chromosome numbers of Hungarian plants II. Ann. Biol. Univ. Debrecen. 1: 46–56.

Price, R. A. & J. D. Palmer. 1993. Phylogenetic relationships of the Geraniaceae and Geraniales from *rbcL* sequence comparisons. Ann. Missouri Bot. Gard. 80: 661–671.

Rangaswamy, N. S. & L. Nandakumar. 1985. Correlative studies on seed coat structure, chemical composition, and impermeability in the legume *Rhynchosia minima*. Bot. Gaz. 146: 501–509.

Reichenbach, H. G. L. 1841–1842. Icones Florae Germanicae et Helveticae, Vol. 5. F. Hofmeister, Leipzig.

Ross-Craig, S. 1952. Drawings of British Plants, Part VI. G. Bell & Sons, London.

Sanderson, M. J. 1991. Phylogenetic relationships within North American *Astragalus* L. (Fabaceae). Syst. Bot. 16: 414–430.

Semerenko, L. V. 1985. Chromosome numbers in some species of flowering plants of Byelorussian flora. Bot. Zhurn. (Moscow & Leningrad) 70: 992–994. [In Russian.]

Shaw, R. J. 1952. A cytotaxonomic study of the genus *Geranium* in the Wasatch region of Idaho and Utah. Madroño 11: 297–304.

Skalińska, M., J. Jankum & H. Weisło (Editors). 1976. Further studies in chromosome numbers of Polish angiosperms. Eleventh contribution. Acta Biol. Cracov., Ser. Bot. 19: 107–148.

———, E. Pogan & R. Czapik (Editors). 1978. Further studies in chromosome numbers of Polish angiosperms. Twelfth contribution. Acta Biol. Cracov., Ser. Bot. 21: 31–63.

Stafford, P. J. & S. Blackmore. 1991. Geraniaceae *In:* W. Punt & S. Blackmore, The Northwest European Pollen Flora 6: 49–78. Elsevier, Amsterdam, London, New York, and Tokyo.

Strid, A. 1980. Chromosome number reports LXIX. Taxon 29: 709–711.

——— & R. Franzén. 1981. IOPB chromosome number reports LXXIII. Taxon 30: 829–842.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Tischler, G. 1934. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins, mit Ausblicken auf andere Florengebiete. Bot. Jahrb. Syst. 67: 1–36.

Tokarski, M. 1972. Morphological and taxonomical analysis of the fruits and seeds of the European and Caucasian species of the genus *Geranium* L. Monogr. Bot. 36.

Tolivia, D. & J. Tolivia. 1987. Fasga: A new polychromatic method for simultaneous and differential staining of plant tissues. J. Microscopy 148: 113–117.

Van Loon, J. C. 1984a. Chromosome numbers in *Geranium* from Europe, I. The perennial species. Proc. Kon. Ned. Akad. Wetensch. C 87: 263–277.

———. 1984b. Chromosome numbers in *Geranium* from Europe, II. The annual species. Proc. Kon. Ned. Akad. Wetensch. C 87: 279–296.

———. 1984c. Hybridization experiments in *Geranium*. Genetica 65: 167–171.

——— & A. K. Van Setten. 1982. IOPB chromosome number reports LXXVI. Taxon 31: 589–592.

———, T. W. J. Gadella & E. Kliphuis. 1971. Cytological studies in some flowering plants from southern France. Acta Bot. Neerl. 20: 157–166.

Warburg, E. F. 1938. Taxonomy and relationship in the Geraniales in the light of their cytology. New Phytol. 37: 130–159.

Watrous, L. E. & Q. L. Wheeler. 1981. The outgroup comparison method of character analysis. Syst. Zool. 30: 1–11.

Webb, D. A. & J. K. Ferguson. 1968. *Geranium* L. *In:* T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb, Flora Europaea 2: 193–199. Cambridge Univ. Press, Cambridge.

Widler-Kiefer, H. & P. F. Yeo. 1987. Fertility relationships of *Geranium* (Geraniaceae): Sects. *Ruberta*, *Anemonifolia*, *Lucida* and *Unguiculata*. Pl. Syst. Evol. 155: 283–306.

Yeo, P. F. 1973. The biology and systematics of *Geranium*, sections *Anemonifolia* Knuth and *Ruberta* Dum. Bot. J. Linn. Soc. 67: 285–346.

———. 1984. Fruit-discharge-type in *Geranium* (*Geraniaceae*): Its use in classification and its evolutionary implications. Bot. J. Linn. Soc. 89: 1–36.

———. 1990. The classification of Geraniaceae. *In:* P. Vorster, Proceedings of the International Geraniaceae Symposium. Univ. Stellenbosch, Stellenbosch, South Africa.

———. 1992. A revision of *Geranium* L. in south-west China. Edinburgh J. Bot. 49: 123–211.

APPENDIX 1

Chromosome numbers of *Geranium* sects. *Batrachioidea* and *Divaricata*.

Geranium sect. *Batrachioidea*

G. aequale, $2n = 26$ (Gauger, 1937: 529).

G. molle, $n = 13$ (Warburg, 1938: 142); $2n = 26$ (Gauger, 1937: 529; Warburg, 1938: 142; Löve & Löve, 1956: 209; Böcher & Larsen, 1958: 19; Mulligan, 1959: 83; Gadella & Kliphuis, 1966: 548; Löve & Kjellqvist, 1974: 163; Alves & Leitão, 1976: 233; Skalińska et al., 1976: 120; Natarajan, 1978: 529; Májovský, 1978: 25; Franzén & Gustavsson, 1983: 104; Van Loon, 1984b: 295; Hill, 1989: 18).

G. pusillum, $2n = 26$ (Gauger, 1937: 529; Löve & Löve, 1945: 11; Pólya, 1950: 51; Shaw, 1952: 299; Löve & Löve, 1956: 209; Gadella & Kliphuis, 1966: 548; Fritsch, 1973: 460; Májovský, 1974: 10; Alves & Leitão, 1976:

233; Skalińska et al., 1976: 121; Fernández Casas et al., 1978: 109; Arohonka, 1982: 5; Van Loon, 1984b: 295; Buttler, 1989: 13); $2n = 34?$ (Warburg, 1938: 142).
G. pyrenaicum subsp. *pyrenaicum*, $n = 11$–12 (Heitz, 1926: 642, 678; Tischler, 1934: 10); $n = 13$ (Galland, 1988: 144); $2n = 20$ (Chatterjee & Sharma, 1970: 183); $2n = 26$ (Gauger, 1937: 530; Májovský, 1974: 11; Skalińska et al., 1978: 42; Strid, 1980: 710; Strid & Franzén, 1981: 836; Van Loon & Van Setten, 1982: 591; Van Loon, 1984a: 277; Semerenko, 1985: 993; Galland, 1988: 144; Baltisberger, 1991: 167); $2n = 28?$ (Warburg, 1938: 151; Van Loon et al., 1971: 159; Mizianty et al., 1983: 208).
G. pyrenaicum subsp. *lusitanicum*, $2n = 26$ (Alves & Leitão, 1976: 232; Van Loon, 1984a: 277).

Geranium sect. *Divaricata*

G. albanum, $n = 14$ (Warburg, 1938: 145); $2n = 20$ (Van Loon, 1984a: 276).
G. divaricatum, $2n = 28$ (Májovský, 1974: 10; Dersch, 1974: 77; Van Loon, 1984b: 294; Jankun et al., 1996: 12).

INDEX TO SCIENTIFIC NAMES

Accepted names are in roman type; the main entry for each is in **boldface.** Synonyms are in *italics.*

REVISIÓN Y ANÁLISIS CLADÍSTICO DE *STEINCHISMA* (POACEAE: PANICOIDEAE: PANICEAE)[1]

Fernando O. Zuloaga[2], *Osvaldo Morrone*[2], *Andrea S. Vega*[2] *y Liliana M. Giussani*[2]

RESUMEN

En el presente tratamiento se realiza una revisión de las especies del género *Steinchisma* Raf. (Poaceae), perteneciente a la tribu Paniceae de la subfamilia Panicoideae. Se estudiaron seis especies de este género, incluyendo el análisis exomorfológico, anatómico y cladístico de las mismas. El género *Steinchisma* se caracteriza por incluir especies perennes, que habitan en lugares abiertos, en campos o bordes de ríos y arroyos; las plantas poseen lígulas membranáceas, láminas lanceoladas a filiformes, inflorescencias laxas y difusas a contraidas, con espiguillas solitarias dispuestas sobre pedicelos usualmente cortos; las espiguillas son ancha a largamente elipsoides, glabras, con la gluma inferior ⅓ a ½ del largo de la espiguilla, gluma superior y lemma inferior subiguales, pálea inferior tan larga como el antecio superior y más o menos ensanchada a la madurez, flor inferior presente, con tres estambres, a neutra; antecio superior crustáceo, y un número básico de cromosomas de $x = 10$. Desde el punto de vista histofoliar, el género posee una anatomía intermedia entre las especies Kranz y non-Kranz. Se discuten, por medio de un análisis cladístico, la monofilia del género y su relación con subgéneros de *Panicum*, como así también con géneros afines de la tribu Paniceae. Se incluye una clave de las especies analizadas, una descripción anatómica del género, fotografías de antecio superior de dos especies, descripciones morfológicas, ilustraciones y mapas de distribución de los diferentes taxones. Se realiza una nueva combinación, *S. stenophylla* (Hack.) Zuloaga & Morrone.

ABSTRACT

The genus *Steinchisma* Raf. (Poaceae: Panicoideae: Paniceae) is revised. Six species are treated in this work, in which exomorphological and anatomical characters are analyzed cladistically. *Steinchisma* comprises perennial species that grow in open areas or near borders of rivers and streams. The plants possess membranous ligules, leaves lanceolate to filiform, inflorescences lax and diffuse to contracted, with spikelets solitary on short or long pedicels; ellipsoid spikelets, glabrous, with the lower glume ⅓ to ½ the length of the spikelet, upper glume and lower lemma subequal, lower palea as long as the upper anthecium, expanded at maturity, lower flower present, with three stamens, or absent; indurate upper anthecium; and a basic chromosome number of $x = 10$. A similar anatomical pattern, intermediate between Kranz and non-Kranz species, was found in all species. A cladistic analysis of *Steinchisma* was conducted in order to test its monophyly, and relationships with the subgenera of *Panicum*. A key to the species is provided, as well as an anatomical description of the genus and photomicrographs of two species; morphological descriptions, illustrations, and distribution maps are presented for all six species of *Steinchisma*. A new combination is made, *Steinchisma stenophylla* (Hack.) Zuloaga & Morrone.

Steinchisma fue establecido como género por Rafinesque en el año 1830, sobre la base de *Panicum hians* Elliott. Nash (1903) distinguió a *Steinchisma* de *Panicum* por poseer pálea inferior expandida a la madurez de la espiguilla. Hitchcock y Chase (1910, 1915), Pilger (1931, 1940) y Hsu (1965) consideraron especies de *Steinchisma* dentro de la sección *Laxa* (Hitchc. & Chase) Pilg. de *Panicum*. Brown (1977) consideró a *Steinchisma* a nivel genérico, distinguiéndolo de *Panicum* por incluir especies con inflorescencias laxas a contraidas, sin espiguillas dispuestas en racimos unilaterales, con antecio superior verrugoso en toda su superficie, siendo, de acuerdo a este autor, la mayoría de sus especies intermedias entre las Kranz y las non-Kranz, y mencionó que *S. cuprea* (Hitchc. & Chase) W. V. Br. (= *Panicum cupreum* Hitchc. & Chase) pudiera ser una especie C_3. Brown transfirió *P. decipiens* Nees ex Trin, *P. cupreum* y *P. exiguiflorum* Griseb. al género *Steinchisma*. Bouton et al. (1981) estudiaron la vía fotosintética de varias especies de *Steinchisma* (bajo *Panicum*), y señalaron la afinidad de las mismas con especies de la sección *Laxa* de *Panicum*, incluyendo caracteres exomorfológicos y

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el número básico de cromosomas. Renvoize (1982) estableció el género *Plagiantha*, al cual distinguió de *Panicum* por poseer espiguillas dispuestas oblícuamente en los pedicelos y lemma inferior membranácea; no relacionó este género con *Steinchisma*. Gould y Shaw (1983) trataron a *Steinchisma* a nivel genérico, mencionando como caracteres diferenciales la pálea inferior expandida y el antecio superior con papilas verrugosas en toda su superficie. Brown et al. (1985) produjeron híbridos artificiales entre especies de *Steinchisma*, como *S. spathellosa* (Döll) Renvoize (bajo *P. spathellosum* Döll) y *S. hians* (Elliott) Nash (bajo *P. hians*), con especies de la sección *Laxa*. Clayton y Renvoize (1986) revalidaron *Steinchisma*, separándolo de *Panicum* por la pálea expandida a la madurez de las espiguillas. Renvoize (1987) transfirió *Panicum spathellosum* a *Steinchisma*.

Zuloaga (1987a) ubicó a *Steinchisma* como un subgénero de *Panicum*, caracterizándolo por incluir especies con inflorescencias laxas, espiguillas glabras, con gluma inferior 3-nervia, ⅓ a ½ del largo de la espiguilla, gluma superior y lemma inferior 5-nervia, pálea inferior expandida a la madurez y antecio superior con papilas verrugosas en toda su superficie. Un criterio similar adoptó Webster (1988), quien mencionó que no existen suficientes diferencias para distinguir a *Steinchisma* como un género independiente, aunque indicó que el análisis de especies sudamericanas podría justificar esta separación. Posteriormente, Zuloaga et al. (1993), al realizar un estudio fenético de las especies americanas de *Panicum*, trataron a *Steinchisma* como subgénero, estableciendo relaciones entre éste y el subgénero tipo. Estos autores indicaron que *Steinchisma* comparte ciertos caracteres con el subgénero tipo, como mesofilo compacto, células del mesofilo radiadas y células tipo "empalizada" ausentes en el mesofilo. A la vez, Zuloaga et al. (1993) también relacionaron a *Steinchisma* con secciones del subgénero non-Kranz *Phanopyrum* (Raf.) Pilg., en particular con aquellas que incluyen especies con número básico de cromosomas $x = 10$, una similar nerviación de las brácteas de la espiguilla y rango de variación de isótopos de carbono.

Watson y Dallwitz (1992) trataron a *Steinchisma* con cuatro especies, a nivel de género, señalando no obstante que su posición taxonómica es arbitraria, pudiendo incluirse también como un subgénero de *Panicum*. Caracterizaron al mismo por tener inflorescencias laxas, con pálea inferior endurecida y expandida a la madurez y antecio superior endurecido. *Plagiantha* fue separado por estos autores por comprender una especie anual, non-Kranz, con espiguillas comprimidas dorsiventralmente, lemma inferior biaquillada, 4-nervia y pálea inferior endurecida y expandida a la madurez.

En la presente contribución se ha efectuado un análisis exomorfológico e histofoliar de las especies de *Steinchisma*. Con estos datos, sumados a la información citológica, se llevó a cabo un análisis cladístico, a fin de poner a prueba la monofilia de este taxón, y discutir su ubicación dentro de la tribu Paniceae en relación con los subgéneros de *Panicum* y otros géneros de la tribu. A partir de este análisis cladístico se establecen las relaciones filogenéticas de las especies del género.

MATERIALES Y MÉTODOS

ESTUDIO HISTOFOLIAR

Se obtuvieron cortes transversales y epidermis a la altura del tercio medio de la penúltima lámina de la innovación fértil. Se utilizó material proveniente de ejemplares de herbario, previamente tratado con Contrad 70 (Schmid & Turner, 1977) durante 24 a 48 hs a 20°C, o material fresco fijado en FAA. Los cortes transversales se hicieron a mano alzada, previo tratamiento con HF al 5% durante 24 hs. Para la obtención de las epidermis, se siguió el método de Metcalfe (1960). Los cortes fueron coloreados con azul de metileno al 1% y con safranina al 1% en alcohol 80° o con safranina-alcian blue y montados en gelatina-glicerina. Para la observación de las células clorenquimáticas, se realizaron macerados siguiendo el método de Jeffrey (Sass, 1940).

Para la identificación de los cuerpos de sílice y células suberosas, se utilizó respectivamente fenol líquido (Metcalfe, 1960) y Sudán III (Sass, 1940). La determinación de los plástidos de almidón, y su distribución, se realizó mediante unas gotas de solución iodo-iodurada (Sass, 1940). Para las descripciones histofoliares, se adoptó la terminología propuesta por Ellis (1976, 1979). Las observaciones anatómicas fueron hechas con un microscopio fotónico Wild M20 con cámara de dibujo. Las disecciones fueron estudiadas con un microscopio estereoscópico Wild M5 con cámara de dibujo. Las fotomicrografías fueron tomadas con un equipo automático Nikon FXA, con cámara fotográfica DX-DB2 35 mm, y la película utilizada Kodak T-MAX de 100 ASA. Para la obtención de fotomicrografías de epidermis abaxiales de la lemma y pálea del antecio superior, se empleó un microscopio electrónico de barrido Jeol JSM-25 SII, perteneciente

Tabla 1. Lista de los caracteres y estados de los caracteres usados en el análisis cladístico.

1. Duración: 0 = anual; 1 = perenne
2. Rizomas largamente hojosos: 0 = ausentes; 1 = presentes
3. Láminas: 0 = planas; 1 = filiformes
4. Inflorescencias: 0 = laxas; 1 = contraidas
5. Ramificaciones: 0 = unilaterales; 1 = no unilaterales
6. Ejes de las ramificaciones: 0 = espiguillas no agrupadas sobre las ramas; 1 = espiguillas agrupadas en la porción distal de las ramas
7. Espiguillas dispuestas: 0 = oblicuas; 1 = no oblicuas
8. Gluma superior: 0 = ⅓–¼ del largo de la espiguilla; 1 = ¾–$^{1}/_{1}$ del largo de la espiguilla
9. Desarrollo de la pálea inferior a la madurez: 0 = nulo; 1 = expandida apicalmente; 2 = expandida lateralmente
10. Textura de la lemma inferior: 0 = papirácea; 1 = herbácea
11. Nerviación de la lemma inferior: 0 = 3-nervia; 1 = 2–4-nervia; 2 = 5–11-nervia
12. Flor inferior: 0 = neutra; 1 = estaminada
13. Textura del antecio superior: 0 = sin papilas simples; 1 = con papilas simples en el apice; 2 = con papilas simples en toda la superficie
14. Textura del antecio superior: 0 = sin papilas verrugosas; 1 = con papilas verrugosas en toda la superficie
15. Color del antecio superior: 0 = castaño; 1 = pajizo
16. Androceo de la flor superior—número de estambres funcionales: 0 = 3; 1 = 2; 2 = 0
17. Células fusoides: 0 = presentes; 1 = ausentes
18. Número de células clorenquimáticas entre haces: 0 = 2–3; 1 = 5–7; 2 = más de 7
19. Mesofilo: 0 = laxo; 1 = compacto
20. Vaina parenquimática: 0 = sin cloroplastos; 1 = con cloroplastos no especializados; 2 = con cloroplastos especializados
21. Valor promedio ^{13}C: 0 = −9 a −12‰; 1 = −20 a −30‰
22. Número cromosómico básico: 0 = x = 10; 1 = x = 9

a la Facultad de Odontología (Universidad Nacional de Buenos Aires, Argentina).

ESTUDIO EXOMORFOLÓGICO

El mismo fue realizado sobre la base de materiales pertenecientes a los siguientes herbarios: B, BA, BAA, BLA, CEN, CEPEC, COL, CORD, CTES, F, G, GH, IAN, IBGE, K, LIL, LP, LPB, M, MEXU, MO, MY, NY, P, PORT, R, RB, S, SI, SP, UB, USM, UTMC, US, VEN, W. Dentro del material examinado de cada especie, sólo se citan ejemplares representativos de cada país; una lista completa de los especímenes numerados estudiados, se encuentra ordenada alfabéticamente por coleccionista al final del texto. Con un asterisco (*) se señalan los ejemplares empleados en el estudio histofoliar y con dos asteriscos (**) aquellos especímenes utilizados en el análisis de la lemma y pálea superior: *Chase 10847***, *Davidse 31539**, *Ekman 6064**, *7400**, *Harley et al. 19384***, *Hitchcock 23356*,***, *Joergensen 2439**, *León 18579***, *Liesner & Holst 21288**, *Pringle 3449***, *Reeder & Reeder 4466***, *Steinbach 2654**, *Zuloaga et al. 2330**, *3108**, ***, *3161**, *3214**, *3244**, *3305**, ***, *Zuloaga & Deginani 462**, *Zuloaga & Morrone 3012**, *3074**, *4660**, *4706**.

ANÁLISIS CLADÍSTICO

Para el análisis filogenético se emplearon 22 caracteres exomorfológicos (vegetativos y reproductivos), histofoliares y citológicos, los que fueron analizados sobre la base de material de herbario (ver Apéndice 1) y completados con datos bibliográficos. Seis de éstos (9, 11, 13, 16, 18, 20) son caracteres multiestados y fueron tratados como no aditivos (no ordenados). La lista de los caracteres y la codificación de sus estados se muestran en la Tabla 1. La Tabla 2 contiene la matriz de datos (especies por caracteres).

El análisis cladístico fue llevado a cabo utilizando la opción de enumeración implícita (ie*) del programa Hennig86 versión 1.5 (Farris, 1988) y MSWAP+ del programa NONA versión 1.6 (Goloboff, 1993). Para el análisis de la distribución de los caracteres en los cladogramas, obtenidos a partir de las rutinas del Hennig86, y la generación de los mismos, se empleó el programa CLADOS (Nixon, 1993). NONA fue usado también para calcular el "Bremer support" (Bremer, 1988, 1994). Fue utilizado para determinar en los árboles subóptimos cuántos pasos adicionales eran necesarios para colapsar un nodo.

Taxones del grupo interno. El género *Panicum* es el centro de un complejo de taxones dentro de

Tabla 2. Matriz de datos utilizada para el análisis de *Steinchisma*; entre corchetes "[]" se indican binomios polimórficos, con ? los estados de caracteres no codificables.

					11	11111111222
	1	2	3	4	5678901	23456789012
Otachyrium	1	0	[01]	[01]	1100200	11000120011
Panicum subg. *Panicum*	[01]	[01]	0	0	1111012	[01]1010101201
Panicum secc. *Laxa*	1	0	0	0	0111010	[01]2010020010
Plagiantha	0	0	0	0	1101211	10110120010
Steinchisma cuprea	1	0	0	1	1111210	00111111110
Steinchisma decipiens	1	1	0	1	1111110	00111111110
Steinchisma exiguiflora	1	0	1	0	1011210	0011111111?
Steinchisma hians	1	0	0	0	1011210	00111111110
Steinchisma spathellosa	1	1	0	0	1111110	10112111110
Steinchisma stenophylla	1	1	1	0	1111110	10110111110

la tribu Paniceae (Hsu, 1965; Clayton & Renvoize, 1986). *Panicum* posee una amplia distribución con cerca de 500 especies que habitan en regiones templadas a tropicales en ambos hemisferios (Clayton & Renvoize, 1986). Hasta el presente no se han llevado a cabo estudios filogenéticos de *Panicum*, taxón con presencia de un notable polimorfismo, estando este género dividido en varios subgéneros, o secciones, los que podrían ser considerados géneros diferentes (Crims, 1991). Este marcado polimorfismo podría indicar que *Panicum* no es monofilético, y posiblemente no podrían ser usados caracteres para definir el género. En el presente análisis se incluyeron, para poner a prueba la monofilia de *Steinchisma*, subunidades monofiléticas del género *Panicum* como taxones terminales siguiendo el criterio de Nixon y Davis (1991). Dichas subunidades corresponden al subgénero *Panicum* y la sección *Laxa* del subgénero *Phanopyrum*, de *Panicum*, y al género monotípico *Plagiantha*. Las especies de *Steinchisma* fueron incluidas como taxones terminales a fin de reconocer el patrón filogenético del género.

Zuloaga et al. (1993) realizaron un análisis fenético estableciendo las relaciones entre los subgéneros de *Panicum*. Estos autores señalaron que *Panicum* subgénero *Panicum* es un grupo homogéneo claramente separado del resto de los subgéneros. Este subgénero se asemeja a *Steinchisma* por caracteres anatómicos del mesofilo y la vaina externa de los haces vasculares. El subgenéro *Panicum* incluye aproximadamente 100 especies, habiéndose analizado, en el presente estudio, 26 especies. Este subgénero posee cinco secciones (Zuloaga, 1987a), pero la clasificación infragenérica no ha sido examinada en este trabajo.

Brown et al. (1985), Zuloaga (1987a), Webster (1988) y Zuloaga et al. (1993) relacionaron asimismo a *Steinchisma* con *Panicum* sección *Laxa* por caracteres de la espiguilla, como el largo de la gluma inferior, la nerviación de las brácteas y la presencia ocasional en *P. laxum* Sw. de una pálea inferior expandida y papilas verrugosas en la superficie del antecio superior. Zuloaga et al. (1992) revisaron la sección *Laxa* e incluyeron en la misma 13 especies, que comparten los siguientes caracteres: lígula membranácea, espiguillas dispuestas unilateralmente, con la gluma inferior 1–3-nervia, gluma superior y lemma inferior 5(–7)-nervias, antecio superior con papilas simples regularmente distribuidas en toda su superficie, un número básico de cromosomas $x = 10$, y por incluir especies non-Kranz, con células fusoides en el mesofilo. De esta sección se revisaron cinco especies.

Plagiantha es exomorfológicamente similar a *Steinchisma*; ambos géneros poseen la pálea inferior expandida a la madurez, papilas verrugosas sobre la superficie del antecio superior y un número básico de cromosomas de $x = 10$. *Plagiantha* difiere por incluir plantas anuales, con espiguillas oblicuas sobre los pedicelos, con la lemma inferior 2–4-nervia, deprimida en su porción central; es además un género non-Kranz. La única especie de *Plagiantha* fue examinada en este trabajo.

Taxón del grupo externo. Clayton y Renvoize (1986), en su esquema de relaciones dentro de la tribu Paniceae, presentaron a *Otachyrium* Nees como el grupo hermano de *Steinchisma* y *Plagiantha*, por la presencia de la pálea inferior expandida. Consecuentemente, este género es utilizado como grupo externo en el presente análisis, siguiendo el criterio de Nixon y Carpenter (1993). *Otachyrium* es un grupo monofilético, definido por poseer la gluma inferior y superior subiguales, cortas, ⅓–¼ del largo de la espiguilla, dejando al descubierto el dorso del antecio superior, siendo este castaño oscuro a la madurez (Sendulsky & Soderstrom, 1984).

RESULTADOS

MORFOLOGÍA Y CARACTERES TAXONÓMICOS

Hábito. El género incluye especies perennes, cespitosas a largamente rizomatosas (en el último caso en *S. decipiens*, *S. spathellosa* y *S. stenophylla*), con cañas decumbentes hacia la base a erectas. Los entrenudos son cilíndricos, huecos y glabros, mientras que los nudos son comprimidos y glabros. Las lígulas son membranáceas en la base y cortamente ciliadas en el ápice. Las láminas van desde planas a filiformes, en este último caso en *S. exiguiflora* y *S. stenophylla*.

Inflorescencias. Las inflorescencias son laxas a contraidas. Inflorescencias laxas se presentan en *S. exiguiflora*, *S. hians*, *S. spathellosa* y *S. stenophylla*; las ramificaciones son divergentes del raquis, hallándose, en *S. exiguiflora* y *S. hians*, los ejes desnudos en la base, con las espiguillas aproximadas hacia la porción superior. *Steinchisma cuprea* y *S. decipiens* poseen inflorescencias contraidas, con ejes cortos aproximados al eje principal.

Las espiguillas se encuentran, en todas las especies, dispuestas en pares en ramificaciones no unilaterales.

Espiguillas. Las espiguillas son bifloras, dorsiventralmente comprimidas, glabras, con una flor inferior estaminada a neutra y una flor superior perfecta. La gluma inferior es típicamente 3-nervia, variando en longitud desde ⅓ a ½ del largo de la espiguilla. La gluma superior es 3–5-nervia, obtusa y no cubriendo el ápice del antecio superior; la lemma inferior es 5-nervia, aguda, incluyendo una pálea inferior endurecida y expandida a la madurez, con las alas escabrosas a cortamente pilosas; sobresale a lo ancho de la espiguilla en *S. hians*, *S. exiguiflora* y *S. cuprea*, mientras que sobresale a lo largo en *S. decipiens*, *S. spathellosa* y *S. stenophylla;* la flor inferior puede ser neutra a estaminada. El antecio superior es ovoide, cartilaginoso, pajizo, glabro y cubierto de papilas verrugosas en toda su superficie.

Flor. Es importante resaltar la variación presente en el androceo en las diferentes especies de *Steinchisma*. El flósculo inferior es neutro en *S. cuprea*, *S. decipiens*, *S. exiguiflora* y *S. hians*, y estaminado en *S. spathellosa* y *S. stenophylla*. Por otra parte, el flósculo superior posee androceo con dos estambres en las primeras cuatro especies antes citadas, tres estaminodios en *S. spathellosa* y tres estambres desarrollados en *S. stenophylla*. En todos los casos se observan dos estilos y dos estigmas plumosos, y dos lodículas truncadas y conduplicadas.

Vega (1996) citó la presencia, como carácter único, en *S. spathellosa*, de flor inferior estaminada y flor superior pistilada, describiendo a la especie como la única diclino-monoica dentro de *Panicum*. En el resto de las especies de *Steinchisma* se halla andromonoecia en *S. stenophylla*, con flor inferior estaminada y flor superior perfecta, mientras que en los cuatro taxones restantes son monoclinos, con la flor inferior neutra y la superior perfecta, siendo este caso similar al que ocurre en *Panicum elephantipes* Nees ex Trin. (Urbani, 1990).

Textura y Ornamentación del Antecio Superior (Fig. 1). En todas las especies del subgénero se hallan papilas verrugosas, dispuestas regularmente, sobre la superficie de la lemma y pálea superior; un carácter similar se presenta en *Plagiantha tenella* Renvoize. Papilas similares se han hallado hacia el ápice de la pálea superior en especies del subgénero *Panicum* (Zuloaga, 1987a, b; Zuloaga & Morrone, 1996) y en ejemplares aislados de *Panicum laxum*, perteneciente a la sección *Laxa* (Zuloaga et al., 1992).

ANATOMÍA FOLIAR

Caracteres histofoliares en corte transversal (Fig. 2). *Transcorte*: lámina en transcorte en forma de "V" abierta, con un ángulo menor o mayor de 90° entre ambas láminas; zonas costales e intercostales adaxiales y abaxiales manifiestas, con aspecto moniliforme; zonas costales opuestas a los haces vasculares de primer y segundo orden, de 114–156 µm de espesor; zonas intercostales no asociadas a haces vasculares, de 52–109 µm de espesor.

Haz vascular medio: formado por un haz vascular de primer orden solitario (en *S. decipiens*, *S. hians*, *S. exiguiflora* y *S. stenophylla*), asociado a dos haces vasculares de segundo orden, en *S. cuprea*, o bien asociado, en *S. spathellosa*, a dos haces vasculares de primer y segundo orden con una proyección abaxial y adaxial formada por extensiones de células parenquimáticas de mayor diámetro que el de las células de la vaina parenquimática.

Distribución de los haces vasculares: haces vasculares de primer y segundo orden equidistantes de ambas epidermis o levemente desplazados hacia la epidermis abaxial; haces vasculares de primer orden contiguos separados por (1–)3–5 haces vasculares de segundo orden.

Estructura de los haces vasculares: haces vascu-

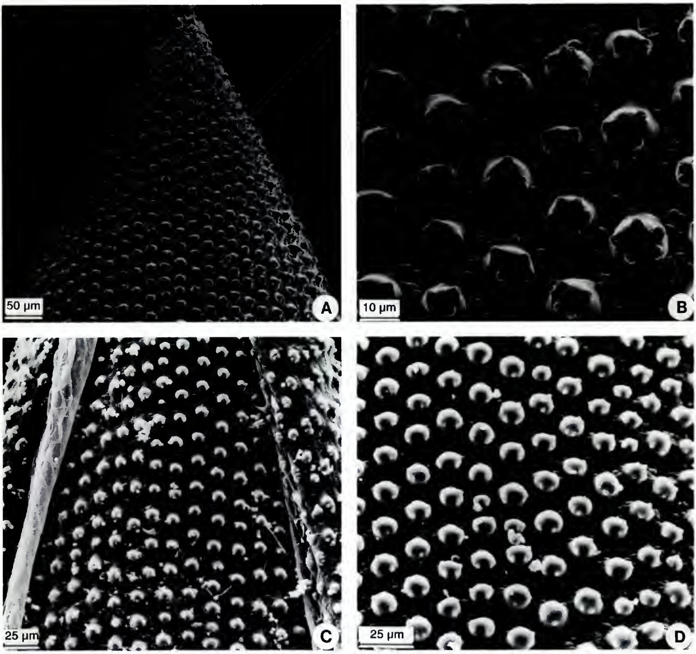

Figura 1. Fotomicrografías MEB de antecios superiores de especies de *Steinchisma*. A, B. *Steinchisma cuprea* (*Pringle 3449*, US). —A. Apice de la lemma, con papilas verrugosas. —B. Detalle de A, con papilas verrugosas. C, D. *Steinchisma hians* (*Chase 10847*, US). —C. Porción media de la pálea y borde de la lemma, con papilas verrugosas. —D. Detalle de la lemma, con papilas verrugosas.

lares de primer orden trabados, de contorno elíptico, metaxilema formado por dos vasos de contorno poligonal a circular y diámetro mayor que el de las células de la vaina parenquimática con las que se encuentra en contacto; laguna protoxilemática presente; vaina mestomática contínua; vaina parenquimática discontínua, interrumpida por el esclerénquima hacia la cara abaxial; haces vasculares de segundo orden trabados, de contorno elíptico o circular, con floema y xilema distinguibles.

Vainas de los haces vasculares: haces vasculares de primer y segundo orden rodeados por la vaina mestomática y la vaina parenquimática; vaina mestomática contínua, células de paredes engrosadas y lumen pequeño, las paredes radiales derechas y las tangenciales arqueadas; vaina mestomática de los haces vasculares de primer orden formada por 18–26 células, 10–13 en los de segundo orden; vaina parenquimática de los haces vasculares de primer orden formada por 9–11 células, 6–7 en los de segundo orden, con cloroplastos de posición centrípeta.

Esclerénquima: pobremente desarrollado, de posición subepidérmica, discontínuo, formando grupos densos de fibras asociados a los haces vasculares y al margen de la lámina.

Mesofilo: células clorenquimáticas nodulares, de disposición compacta y radiada alrededor de los haces vasculares; 5–7 células clorenquimáticas (52–156 µm) entre haces vasculares contiguos; "arm cells," células fusoides y células distintivas Kranz ausentes.

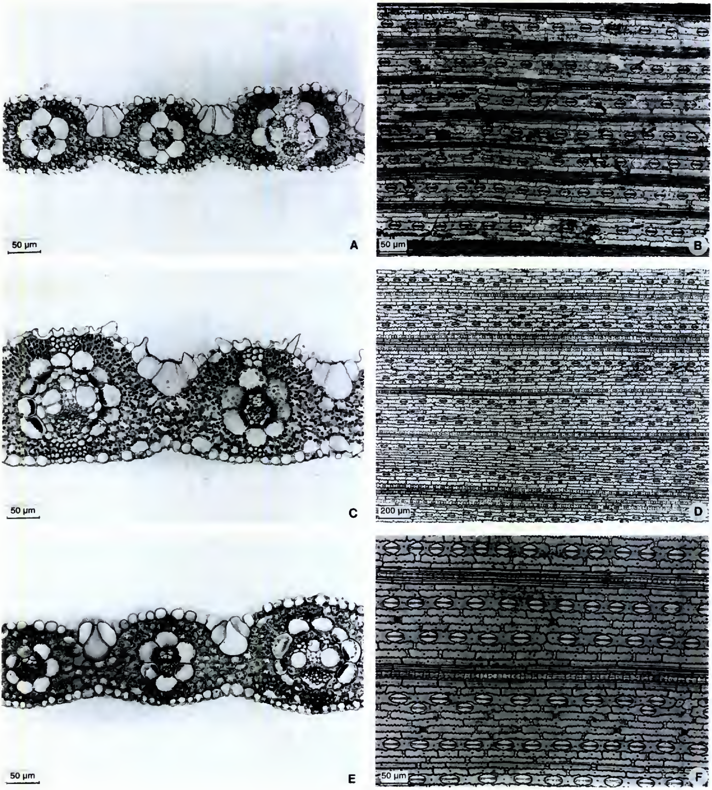

Figura 2. Anatomía foliar en corte transversal y epidermis de especies de *Steinchisma*. A, B. *Steinchisma hians* (*Zuloaga 3108*, SI). —A. Transcorte de una porción de la lámina, con haces vasculares de primer y segundo orden, células parenquimáticas de la vaina con cloroplastos de posición centrípeta. —B. Epidermis abaxial. —C, D. *Steinchisma decipiens* (*Zuloaga 3214*, SI). —C. Transcorte de una porción de la lámina, con haces vasculares de primer y segundo orden. —D. Epidermis abaxial. E, F. *Steinchisma spathellosa*. —E. Transcorte de una porción de la lámina, con haces vasculares de primer y segundo orden (*Zuloaga 3161*, SI). —F. Epidermis abaxial (*Zuloaga 3074*, SI).

Células epidérmicas adaxiales: células buliformes presentes en las zonas intercostales, en forma de abanico, en grupos de 4–6 células, siendo la célula central de mayor tamaño que las laterales, no asociadas a parénquima incoloro; epidermis formada por células papilosas, con aguijones, ganchos y micropelos bicelulares; macropelos presentes, con un cojín basal de células epidérmicas sobreelevadas (en *S. cuprea* y *S. exiguiflora*), o ausentes en las restantes especies.

Células epidérmicas abaxiales: epidermis abaxial formada por células de paredes arqueadas, no papilosas, con ganchos, aguijones y micropelos bicelulares; macropelos y células buliformes ausentes.

Epidermis abaxial en vista paradermal (Fig.

Tabla 3. Números cromosómicos en especies del género *Steinchisma.*

Especie	Número cromosómico	Referencias bibliográficas
Steinchisma cuprea	$2n = 20$	en etiqueta del ejemplar *Reeder & Reeder 4466*
Steinchisma decipiens	$n = 10$	Dubcovsky & Zuloaga, 1991
	$2n = 20$	Bouton et al., 1981; Dubcovsky & Zuloaga, 1991
Steinchisma hians	$n = 10$	Pohl & Davidse, 1971
	$2n = 18$	Brown, 1948
	$2n = 20$	Parodi, 1946; Brown, 1951; Núñez, 1952; Gould, 1968; Davidse & Pohl, 1972; Bouton et al., 1981; Dubcovsky & Zuloaga, 1991
Steinchisma spathellosa	$2n = 60$	Bouton et al., 1981; Dubcovsky & Zuloaga, 1991
Steinchisma stenophylla	$n = 10$	Morrone et al., 1995

2). *Zonación*: zonas costales e intercostales distinguibles. ***Células largas intercostales***: rectangulares, más de tres veces más largas que anchas, de paredes anticlinales longitudinales moderada a profundamente onduladas, las periclinales derechas a oblicuas, no papilosas. ***Células cortas intercostales***: solitarias, entre células largas. *Aparatos estomáticos*: tipo "panicoide," de 31–35 × 24.7–26 μm, dispuestos en 1–4 hileras longitudinales en las zonas intercostales y separados entre si por 1(–3) células largas interestomáticas; células suberosas o pares sílico-suberosos aislados; células subsidiarias triangulares o en forma de domo. *Aguijones* y *Ganchos* ausentes o presentes en las zonas costales y/o intercostales. *Micropelos*: bicelulares, de 65–88 μm de largo, presentes en las zonas intercostales entre células largas; célula distal generalmente caediza, de paredes delgadas y ápice agudo; célula basal persistente, de paredes levemente engrosadas. *Macropelos*: ausentes. *Cuerpos silíceos costales*: halteriformes, longitudinalmente alargados, asociados a células suberosas formando hileras longitudinales contínuas. *Cuerpos silíceos intercostales*: ausentes.

Epidermis adaxial en vista paradermal: presenta células largas con papilas anchas, una por célula, de posición distal y sin paredes engrosadas. *Aparatos estomáticos* dispuestos en 2–3 hileras longitudinales en las zonas intercostales. *Aguijones, ganchos* y *micropelos bicelulares* frecuentes, similares a los presentes en la epidermis abaxial. *Macropelos unicelulares* con cojín basal de células epidérmicas sobreelevadas.

DISCUSIÓN

El género *Steinchisma* se caracteriza por incluir especies intermedias entre las especies Kranz y non-Kranz. Anatómicamente, las especies son Kranz pero tienen un número menor de organelas en la vaina parenquimática externa (Brown et al., 1985); las organelas son de posición centrípeta en la vaina. Además, las vainas vasculares se encuentran a una distancia mayor que la presente en las especies Kranz: el número de células del mesofilo varía entre 5 y 7, siendo de 2 a 4 en los taxones Kranz, y usualmente de más de 7 en las especies non-Kranz (Ellis, 1988). El patrón fisiológico es intermedio entre las plantas Kranz y non-Kranz (Brown & Brown, 1975; Kanai & Kashiwagi, 1975; Ku & Edwards, 1978; Ku & Kanai, 1976; Morgan & Brown, 1979; Brown et al., 1985; Oguro et al., 1985); no obstante, todas las especies poseen un valor de isótopos de carbono (^{13}C) correspondiente al rango de los taxones C_3, el que varía entre −22 y −38‰; el valor varía entre −9 y −18‰ en los taxones C_4 (Brown, 1977). Esta variación se presenta pues la materia orgánica de las especies C_3 es mucho más baja en contenido de ^{13}C; esto se debe a la acción no discriminatoria de la enzima ribulosa difosfato carboxilasa en las especies C_3.

Brown (1977) publicó los siguientes recuentos de isótopos de carbono para especies de *Steinchisma*: *S. cuprea*: ^{13}C −26.9‰; *S. decipiens*: ^{13}C −26.7‰; *S. exiguiflora*: ^{13}C −28.1‰, *S. hians* ^{13}C −26‰. Para *S. spathellosa* se registró un valor de ^{13}C −27.1‰ (R. H. Brown, com. pers.), siendo el mismo de ^{13}C −27.5‰ en *S. stenophylla* (R. H. Brown, com. pers.). Para *Plagiantha tenella* existe un recuento de ^{13}C de −29.09‰ (R. H. Brown, com. pers.).

NÚMEROS CROMOSÓMICOS

Steinchisma posee un número cromosómico básico de $x = 10$, de acuerdo a los recuentos realizados hasta el momento (Tabla 3).

El género se caracteriza por incluir especies diploides, con excepción de *S. spathellosa*, única especie hexaploide de *Steinchisma.*

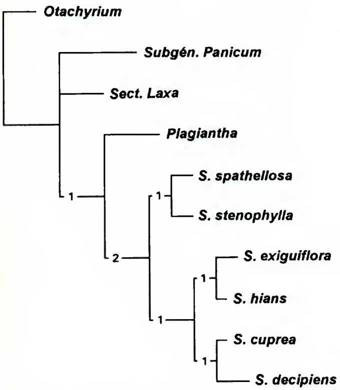

Figura 3. Cladograma de consenso estricto obtenido a partir de 2 cladogramas igualmente cortos. Los números indicados sobre las ramas corresponden a los valores del "Bremer support."

ANÁLISIS CLADÍSTICO

Los patrones filogenéticos obtenidos, a partir de los datos de la matriz (Tabla 2), fueron similares. Se obtuvieron dos árboles igualmente parsimoniosos con una longitud de 34 pasos, un índice de consistencia de 0.82 y un índice de retención de 0.76. Al excluir las autapomorfías de los taxones terminales (caracteres 5, 8, 10, 15, 17, 21), el índice de consistencia es de 0.78. El árbol de consenso estricto de los cladogramas (Fig. 3) define a *Steinchisma* como un grupo monofilético y a *Plagiantha* como su grupo hermano. Los dos cladogramas originales difieren en la posición de *Panicum* subgénero *Panicum* y de la sección *Laxa*. En uno de ellos (Fig. 4A), la sección *Laxa* es el grupo hermano del clado que une *Steinchisma* con *Plagiantha*, y *Panicum* es el grupo hermano del resto. En el otro cladograma (Fig. 4B), ambos taxones, secciones *Laxa* y *Panicum*, forman un clado monofilético, sustentado por poseer pálea inferior hialina o ausente (9).

Al calcular el "Bremer support" para los cladogramas (Bremer, 1988, 1994), y luego de varias horas de cómputos, se obtuvieron 12,941 árboles, para 15 pasos adicionales de largo. Los resultados se muestran en el árbol de consenso estricto, donde el clado *Steinchisma* necesita dos pasos adicionales para colapsar el nodo. Las restantes ramas del árbol de consenso tienen un soporte igual a uno. El bajo valor soporte de las ramas es típico para los análisis basados en un conjunto de datos morfológicos (Karis, 1995).

El presente análisis soporta la hipótesis que considera a *Steinchisma* como un grupo monofilético sustentado por dos sinapomorfías: el número de células clorenquimáticas entre haces vasculares (18) y la presencia de cloroplastos en la vaina parenquimática (20). Estos caracteres estan correlacionados con el tipo anatómico y fisiológico C_3/C_4. En el cladograma de la Figura 4A, el clado formado por *S. spathellosa* y *S. stenophylla* es basal dentro del género, y está sustentado por la presencia de largos rizomas hojosos y cundidores (2). Estas especies crecen preferentemente en cursos de aguas turbulentas, en orillas de arroyos y ríos, entre las piedras. *Steinchisma spathellosa* presenta la novedad de poseer estaminodios en la flor superior (16). Un segundo clado está constituido por *S. exiguiflora-S. decipiens*, sustentado por dos sinapomorfías: flor inferior neutra (12) y flor superior con dos estambres (16). *Steinchisma exiguiflora* y *S. hians* forman, asimismo, un clado por tener espiguillas distribuidas en la porción superior de las ramas (6). El clado *S. cuprea* y *S. decipiens* posee inflorescencias contraidas (4). En el segundo cladograma (Fig. 4B), *Steinchisma* presenta la misma topología; estos cladogramas difieren en la evolución del carácter 9.

En ambos cladogramas se observa que *Plagiantha* se comporta como el grupo hermano de *Steinchisma*, en una posición inclusiva entre este último taxón y *Panicum* más la sección *Laxa*, sustentando este hecho la hipótesis que excluye a *Steinchisma* de *Panicum*. Si bien el resultado de este análisis también podría llevar a la inclusión de *Plagiantha* y *Steinchisma* dentro de *Panicum*, se considera que este último género es polifilético y la inclusión de *Plagiantha* y *Steinchisma* harían al mismo aún más heterogéneo.

La evolución de la flor en Poaceae ha sido sujeta a numerosas investigaciones (Arber, 1934; Clifford, 1961; Anton & Connor, 1995). En la tribu Paniceae las espiguillas son bifloras, con una flor superior perfecta, con un pistilo y tres estambres, y una flor inferior estaminada, con tres estambres (Clayton & Renvoize, 1986). En el presente análisis se observa el siguiente patrón en el sistema floral de *Steinchisma*: la condición andromonoica es primitiva, y a partir de la misma deriva la condición diclinomonoica, presente en *S. spathellosa*; en esta especie, por reducción de los estambres de la flor superior, se halla una flor superior pistilada y una flor inferior estaminada. A la vez, en el clado *S. exiguiflorum-S. decipiens* se presenta la condición monoica, la que sería derivada por reducción de la

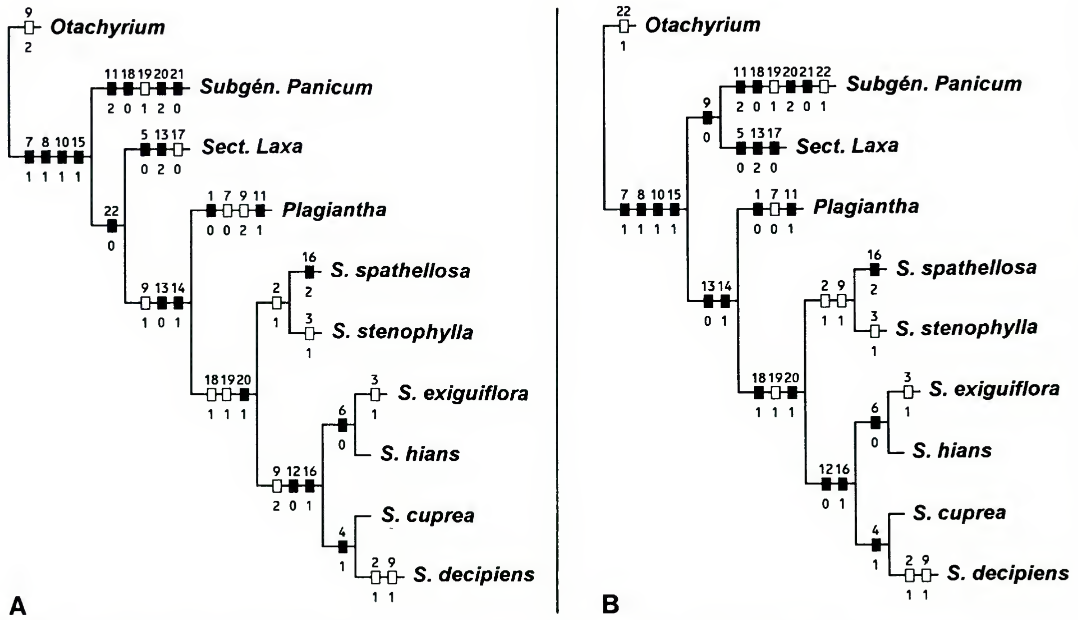

Figura 4A, B. Cladogramas igualmente parsimoniosos obtenidos a partir de la matriz de caracteres (Tabla 2). Los caracteres indicados con barras negras señalan sinapomorfías, las barras vacías homoplasias. L (longitud): 34; IR (índice de retención): 0.76; IC (índice de consistencia): 0.82.

flor estaminada inferior, que es neutra, permaneciendo la flor superior perfecta. Cabe destacar que esta flor superior, en el clado antes mencionado, posee dos estambres de posición lateral, siendo el frontal ausente. Este carácter ha sido citado como excepcional dentro de la tribu Paniceae (Simon & Weiller, 1995).

DISTRIBUCIÓN Y ECOLOGÍA

Las especies de *Steinchisma* se distribuyen desde Estados Unidos de América hasta la Argentina. *Steinchisma hians* es la especie que posee una mayor distribución, hallándose en los Estados Unidos de América, México, Guatemala, Honduras, Nicaragua y América del Sur, desde Colombia hasta Argentina. *Steinchisma cuprea* es una especie endémica de México, donde crece en campos entre los 2100 y 2600 m s.m. Por otra parte, *S. exiguiflora* se halla únicamente en las islas del Caribe, desde las Bahamas hasta Jamaica y Haití. *Steinchisma decipiens, S. stenophylla* y *S. spathellosa* son exclusivas de América del Sur; *S. spathellosa* tiene una distribución restringida, encontrándose a lo largo de cursos de agua desde Santa Catarina, en Brasil, hasta la provincia de Buenos Aires en la Argentina. *Steinchisma stenophylla* es una especie que crece en bordes de arroyos y ríos de la Guyana Venezolana, y diversas áreas del cerrado en Brasil, encontrándose en Bahia, Minas Gerais y Pará. Finalmente, *S. decipiens* también crece en bordes de ríos y arroyos, desde el nordeste de Brasil hasta Bolivia, Paraguay, Uruguay y Argentina; se ha hallado ocasionalmente en Colombia y Venezuela.

Es interesante destacar que, de acuerdo al resultado del análisis cladístico, los clados resultantes dentro del género, formados por *S. spathellosa* + *S. stenophylla, S. decipiens* + *S. cuprea,* y *S. hians* + *S. exiguiflora,* poseen una distribución alopátrica, de acuerdo a lo antes expuesto y lo que se observa en las Figuras 5 y 6.

TRATAMIENTO TAXONÓMICO

Steinchisma Raf., Bull. Bot., Geneva 1: 220. 1830. *Panicum* subg. *Steinchisma* (Raf.) Zuloaga, en Soderstrom et al., Grass Syst. Evol. 300. 1987. TIPO: *Steinchisma hians* (Elliott) Nash [= *Panicum hians* Elliott].

Inflorescencias laxas a contraidas, con espiguillas congestas en las ramificaciones. Espiguillas glabras, con gluma inferior 3-nervia, ⅓ a ½ del largo de la espiguilla. Gluma superior y lemma inferior 3–5(–7)-nervias. Pálea inferior conspicua, expandida a la madurez a lo ancho y/o a lo largo de la espiguilla; flor inferior estaminada o neutra. Antecio superior ovoide a elipsoide, con papilas verrugosas dispuestas regularmente en hileras longitudinales, con aguijones hacia el ápice de la lemma o sin los mismos. Plantas cespitosas, corta a largamente rizomatosas, a largamente rizomatosas, con lígulas membranáceas, cortamente ciliadas a laciniadas, láminas lanceoladas a filiformes, planas.

Género con 6 especies americanas, distribuidas desde los Estados Unidos de América hasta la Argentina. Habitan comúnmente en lugares húmedos y abiertos, en bordes de arroyos, pantanos o zonas inundables, desde el nivel del mar hasta los 2600 m de elevación.

CLAVE PARA DIFERENCIAR LAS ESPECIES DE *STEINCHISMA*

1a. Inflorescencia contraida, espiciforme, con ramificaciones de segundo orden adpresas al eje principal y espiguillas cubriendo desde la base los ejes de las ramificaciones.

 2a. Espiguillas de 2.6–3.2 mm de largo, con pálea inferior sobresaliendo a lo ancho a la madurez; plantas cespitosas, con cañas erectas; México .... *S. cuprea*

 2b. Espiguillas de 1.8–2.4(–2.8) mm de largo, con pálea inferior no sobresaliendo a lo ancho a la madurez; plantas largamente rizomatosas, con cañas decumbentes; Colombia a Argentina .... *S. decipiens*

1b. Inflorescencia laxa, con ramificaciones de segundo orden distantes entre si y divergentes del raquis; eje de las ramificaciones desnudo hacia la porción basal.

 3a. Espiguillas de 1.2–1.4 mm de largo; islas del Caribe .... *S. exiguiflora*

 3b. Espiguillas de (1.7–)2.4–3.6 mm de largo; Estados Unidos de América a la Argentina.

  4a. Plantas con cañas rígidas, manifiestamente ramificadas en los nudos basales y medios; inflorescencias axilares presentes; láminas filiformes, de 0.2–0.5(–2) mm de ancho; flor superior con tres estambres .... *S. stenophylla*

  4b. Plantas con cañas herbáceas, no rígidas, no ramificadas en los nudos basales y medios; inflorescencias axilares ausentes; láminas lanceoladas, de 2–10 mm de ancho; flor superior con dos estambres o tres estaminodios.

   5a. Plantas de 15–60 cm de alto, cortamente rizomatosas; espiguillas de (1.7–)2.2–2.6 mm de largo, con pálea inferior sobresaliendo a lo ancho de la espiguilla; flor inferior neutra; flor superior con dos estambres .... *S. hians*

   5b. Plantas de 60–120 cm de alto, largamente rizomatosas; espiguilla de 3–3.6 mm de largo, con pálea inferior no sobresaliendo a lo ancho de la espiguilla; flor inferior estaminada; flor superior con tres estaminodios .... *S. spathellosa*

Figura 5. Distribución de *Steinchisma cuprea*, *S. decipiens*, *S. exiguiflora*, *S. spathellosa* y *S. stenophylla*.

Figura 6. Distribución de *Steinchisma hians.*

1. **Steinchisma cuprea** (Hitchc. & Chase) W. V. Br., Mem. Torrey Bot. Club 23: 20. 1977. *Panicum cupreum* Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 120, fig. 113. 1910. *Panicum hians* var. *purpurascens* Scribn., Proc. Acad. Nat. Sci. Philadelphia 1891: 296. 1891. TIPO: México. México: Flor de María, wet hollows of plains, *Pringle 3449* (holótipo, US-80756!).

Plantas perennes, cespitosas, cortamente rizomatosas, con *cañas* de 20–60 cm de alto, erectas, simples, paucinodes; entrenudos cilíndricos, huecos, glabros, pajizos a violáceos; nudos comprimidos, castaños, glabros. *Vainas* estriadas, aquilladas, las basales más largas que los entrenudos, las superiores más cortas, glabras, los bordes membranáceos. *Lígulas* de ca. 0.6 mm de largo, membranáceas, cortamente ciliadas en la porción superior; cuello glabro. *Láminas* de 8–25 × 0.2–0.4 cm, linear-lanceoladas, con los bordes involutos, de base redondeada y ápice subulado, pilosa en la cara adaxial, con pelos largos, delgados, cara abaxial glabra o esparcidamente pilosa hacia la base. *Inflorescencias* terminales largamente exertas; pedúnculo de 17–20 cm de largo; cilíndrico, glabro, panojas de 4–13 × 1–2 cm, contraidas; *eje principal* anguloso, escabriúsculo; pulvínulos glabros; ramificaciones de primer orden alternas, las inferiores de 2–7 cm de largo, contraidas a ocasionalmente algo divergentes, el resto ascendentes, distanciadas entre si, adpresas al eje principal; ejes de las ramificaciones y pedicelos triquetros, escabriúsculos; espiguillas sobre ejes de tercer orden hacia la porción superior de las ramas. *Espiguillas* de 2.6–3.2 × 0.8–1 mm, largamente elipsoides, glabras, pajizas a violáceas a la madurez; gluma superior y lemma inferior subiguales o la gluma superior ligeramente menor y no cubriendo el ápice del antecio superior. *Gluma inferior* de 1–1.4 mm de largo, ⅓ a menos de ½ del largo de la espiguilla, ovada, aguda, 3-nervia. *Gluma superior* de 2.5–3.1 mm de largo, aguda, 5-nervia. *Lemma inferior* de 2.5–3.1 mm de largo, glumiforme, 5-nervia. *Pálea inferior* de 2.5–3 × 1 mm, elíptica, expandida y ensanchada a la madurez, rígida, pajiza o con tintes violáceos, glabra, los bordes escabriúsculos; flor inferior neutra. *Antecio superior* de 2.4 × 1 mm, ovoide, pajizo o con tintes violáceos, plano-convexo, glabro, con papilas verrugosas distribuidas regularmente en toda su superficie; lemma apiculada, hialina en el ápice; lodículas 2, de 0.2 mm de largo, conduplicadas, truncadas; estambres 2, anteras de 0.8–1.2 mm de largo. *Cariopsis* de 1.5 × 0.6 mm, largamente elipsoide, castaño, hilo oblongo; embrión menos de ½ del largo de la cariopsis.

Distribución y ecología. México, en los estados de Durango, Jalisco, México, Puebla, Querétaro, Veracruz y Zacatecas, sobre suelos húmedos; común a orillas de lagunas y ríos. Se encuentra entre los 2100 y 2600 m s.m.

Material representativo citado. MÉXICO. **Durango:** near El Salto Los Angeles, small stream road between Durango and Mazatlán, *Beetle M-7708* (MO); 3 mi. E of El Salto, 8400 ft., *Reeder & Reeder 4466* (US). **Jalisco:** 25 mi. S of Guadalajara, *Reeder 2330* (US). **México:** Toluca, 9000 ft., *Leavenworth & Leavenworth 1925* (US). **Puebla:** Laguna San Baltasar, 2140 m, *Nicolás 217, 5879* (P, US), *s.n.* (MEXU); Paso de Arcediano, *Oliva 58* (US); San Fernando, Orte de Puebla, 2300 m, *Boege 2543* (MEXU). **Querétaro:** cerca de San Bartolo, 8 km al E de Amealco, sobre la carretera a Aculco, 2600 m, *Rzedowski 48632* (MEXU). **Veracruz:** near El Puerto, above Acultzingo, 7650 ft., *Sharp 44753* (MEXU). **Zacatecas:** 38 km al W de Jalpa, sobre la carretera a Tlaltenango, 30 km del entronque con la carretera Jalpa–Juchipila, 2550 m, *Rzedowski & McVaugh 1024* (US).

Steinchisma cuprea, especie endémica de México, comparte con *S. decipiens*, especie de América del Sur, inflorescencias contraidas, con las ramas adpresas al eje principal; se diferencia de esta especie por incluir plantas cespitosas, con espiguillas de mayor tamaño, con la pálea inferior expandida a lo ancho a la madurez. A su vez, se distingue de *S. hians*, especie de amplia distribución, por incluir esta última plantas con inflorescencias laxas, abiertas, y espiguillas menores, hasta de 2.6 mm de largo.

2. **Steinchisma decipiens** (Nees ex Trin.) W. V. Br., Mem. Torrey Bot. Club 23: 20. 1977. *Panicum decipiens* Nees ex Trin., Gram. Panic. 227. 1826. TIPO: Brasil. Minas Gerais: in humidis arenosis pr. Agua Quenti, *Langsdorff s.n.* (holótipo, LE!; isótipos, B!, US-974489!, US-2903516!; foto del holótipo, K!). Figura 7.

Panicum decipiens Nees en Mart., Fl. Bras. Enum. Pl. 2(1): 193. 1829, nom. illeg, non Nees ex Trin. (1826). TIPO: Brasil. Minas Gerais: "habitat in deserto Minarum versus Paranan, ubi ad Lagoam formozam itur," *Martius s.n.* (holótipo, M!; isótipo, US-2903515!).

Planta perenne, largamente rizomatosa, con rizomas hojosos; *cañas* de 15–70 cm de alto, erectas, geniculadas y arraigadas o no en los nudos inferiores, paucinodes, simples; entrenudos cilindricos a comprimidos, huecos, glabros; nudos glabros, blanquecinos a violáceos. *Vainas* de 2–8 cm de largo, comprimidas, esparcidamente pilosas a glabras, papiráceas, verdosas a violáceas, de bordes hialinos, los superiores cortamente ciliados. *Lígulas* de 0.2–0.4 mm de largo, membranáceas, cortamente ciliadas en la porción superior; cuello blanquecino, glabro. *Láminas* de 5–25 × 0.4–0.7 cm, linear-lanceoladas, con los bordes involutos, de base angosta y ápice acuminado, verde oscuras; nervio medio conspicuo a inconspicuo; cara adaxial con pelos tuberculados caducos; cara abaxial pilosa a glabra. *Inflorescencias* corta a largamente pedunculadas; pedúnculo hasta de 40 cm de largo; panojas, de 6–13 × 0.5–2 cm, contraidas, espiciformes, con ramificaciones de segundo orden adpresas al eje principal, la inferior algo distanciada y divergente; *eje principal* anguloso, liso, glabro; ramificaciones alternas; pulvínulos glabros; espiguillas en pares o solitarias sobre ramificaciones cortas de tercer orden; pedicelos claviformes, escabriúsculos. *Espiguillas* de 1.8–2.4(–2.8) × 0.6 mm, largamente elipsoides, glabras, verdosas a violáceas. *Gluma inferior* de 1.2–2 mm de largo, ⅓ a ½ del largo de la espiguilla, de ápice obtuso a acuminado, 3-nervia, los nervios anastomosados hacia el ápice. *Gluma superior* de 1.5–2(–2.3) mm de largo, de ápice obtuso a agudo, dejando al descubierto la porción superior del antecio, 5-nervia. *Lemma inferior* de 1.8–2.3(–3) mm de largo, lanceolada, 3–5-nervia, glumiforme. *Pálea inferior* de 1.8–2.4(–2.8) × 0.6 mm, lanceolada; quillas escabriúsculas; flor inferior neutra. *Antecio superior* de 1.6–2.2(–2.6) × 0.5–0.6 mm, largamente ovoide, glabro, blanquecino o con tintes violáceos hacia el ápice, acuminado; lodículas 2, de 0.3 mm de largo, conduplicadas, truncadas; estambres 2; anteras de 0.2–0.4 mm de largo. *Cariopsis* largamente obovoide, castaño, de 1.3

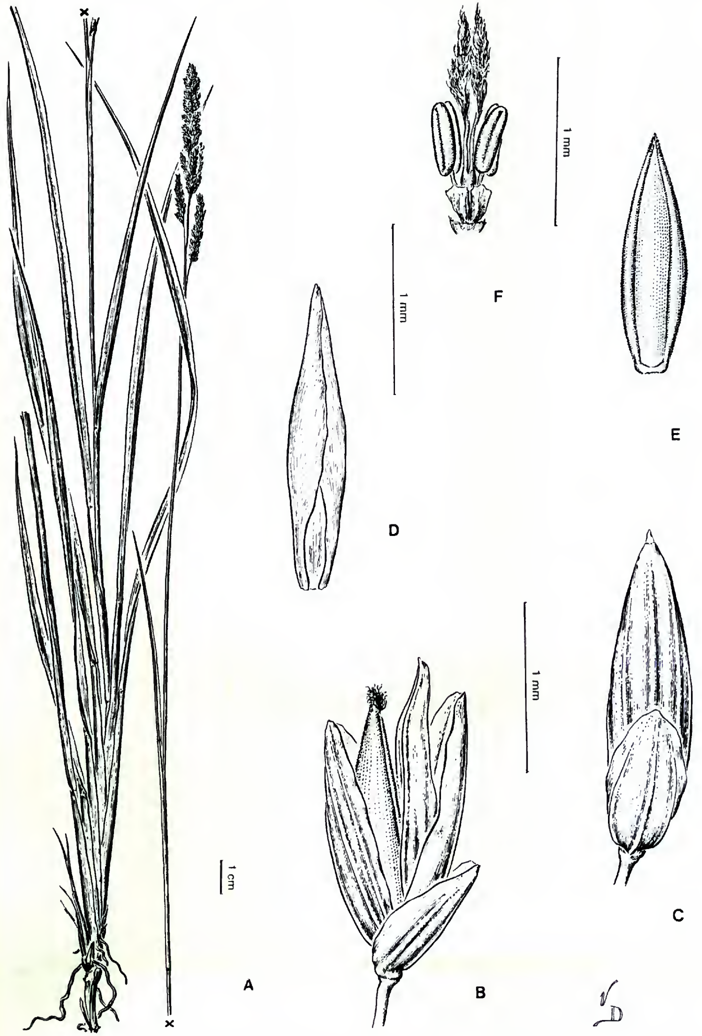

Figura 7. *Steinchisma decipiens* (*Joly 1805*, SP). —A. Hábito. —B. Espiguilla, vista lateral. —C. Espiguilla vista del lado de la gluma inferior. —D. Pálea inferior, vista ventral de la pálea inferior con dos alas. —E. Antecio superior visto del lado de la pálea. —F. Flor superior con dos lodículas, dos estambres y dos estigmas.

× 0.6 mm; hilo oblongo; embrión ½ del largo de la cariopsis.

Distribución y ecología. Especie sudamericana, hallándose desde Colombia y el norte del Brasil hasta Paraguay, Uruguay, Bolivia y la Argentina. Habita en suelos húmedos en bordes de pantanos o lagunas o a lo largo de cursos de agua sobre suelos arenosos. Se encuentra desde el nivel del mar hasta aproximadamente los 1600 m s.m.

Material representativo citado. ARGENTINA. **Corrientes:** de Ituzaingó a Villa Olivari, *Zuloaga et al. 3305* (SI). **Misiones:** camino de Apóstoles a Azara, *Zuloaga & Deginani 544* (SI, US). **Salta:** Alemanía, *Venturi 9932* (MO, US). **Tucumán:** Los Chamicos, *Venturi 2785* (LIL, SI). BOLIVIA. **Santa Cruz:** Terebinto, *Steinbach 2654* (SI). BRASIL. **Bahia:** 19.5 km SE of town of Morro do Chapéu, on the BA 052 road to Mundo Novo by the Rio Ferro Doido, *Harley et al. 19384* (CEPEC, K, MO, P, US); 25 km WNW of the Vila do Rio de Contas, middle NE slopes of the Pico das Almas, *Harley et al. 19647* (CEPEC, K, MO, P, US). **Distrito Federal:** Reserva Ecologica do IBGE, Corrego Roncador, *Silva 436* (SI). **Goiás:** 6 km S of Cristalina, *Irwin et al. 9751* (F, K, MO, NY, SP, UB, US). **Mato Grosso do Sul:** between Campo Grande and Dourados, 400 m, *Chase 10925* (RB, US). **Minas Gerais:** 45 km SE of Belo Horizonte, Serra do Itabirito, *Irwin et al. 19571* (F, NY, UB, US); 35 km S of Gouvea, km 243 on MG 259, *Anderson et al. 35147* (F, MO, NY, SP, UB); Serra do Cipó, 1220 m, *Anderson et al. 36395* (MO, NY, UB, US). **Paraná:** 10 km NW of Palmas, *Smith et al. 15626* (NY, P, RB, SI, US). **Rio Grande do Sul:** São Leopoldo, *Dutra 422* (SI); Torres, *Valls et al. 2326* (CEN). **Santa Catarina:** Mun. Agua Doce, 10 km S of Horizonte, *Smith & Klein 15584* (K, MO, P, RB, US). **São Paulo:** Fazenda Campininha, just N of rio Moji-Guaçu, ca. 8.5 km NNE of Padua Sales, *Eiten & Eiten 2667* (MO, SP, UB, US). COLOMBIA. **Meta:** 20 km SE of Villavicencio, 480 m, *Alston 7578* (COL, US). **Norte de Santander:** Abrego, *García & Cabrales 2* (COL). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, *Hahn 2533* (MO); Sierra de Amambay, *Hassler 10110* (G, K, LIL, NY, P, US). **Central:** in regione lacus Ipacaray, *Hassler 12347* (G, US). **Concepción:** zwischen Río Apa und Río Aquidaban, *Fiebrig 4507* (G, K, US). **Cordillera:** Cordillera de Altos, *Hassler 3658* (G). **Guairá:** Villa Rica, Balansa 60 (G, K, P). **Paraguarí:** Parque Nacional Ybycuí, *Zardini et al. 9038* (SI). URUGUAY. **Rocha:** Palmares de Castillos, 25 km N of Castillos, *Bartlett 21348* (SI). **Tacuarembó:** camino a Rivera, 32 km de Tacuarembó, *Cabrera & Zuloaga 32427* (SI). VENEZUELA. **Bolívar:** Hato Divina Pastora, Gran Sabana, *Tamayo 2901* (US, VEN).

Exomorfológicamente, esta especie es afín a *S. spathellosa*, con la que comparte la presencia de largos rizomas en la base. Ambos taxones son frecuentes en bordes de cursos de agua. *Steinchisma spathellosa* se distingue por incluir plantas de mayor tamaño, con inflorescencias laxas con espiguillas de 3–3.6 mm de largo; las espiguillas llevan en la flor superior tres estaminodios (en lugar de los dos estambres desarrollados que están presentes en *S. decipiens*).

Steinchisma decipiens es común en cerrados del Brasil, donde se extiende desde Bahia hasta Rio Grande do Sul, llegando hasta Paraguay y el nordeste de Argentina. Por el contrario, se ha hallado esporádicamente en Venezuela, Colombia y el noroeste de la Argentina.

3. **Steinchisma exiguiflora** (Griseb.) W. V. Br., Mem. Torrey Bot. Club 23: 20. 1977. *Panicum exiguiflorum* Griseb., Cat. Pl. Cuba 234. 1866. *Panicum minutiflorum* A. Rich., en Sagra, Hist. Fis. Cuba, Bot. 11: 305. 1850, nom. illeg., non (P. Beauv.) Raspail (1825). TIPO: Cuba: sin localidad, *de la Sagra s.n.* (holótipo, P!).

Panicum laxum var. *variegatum* Griseb., Cat. Pl. Cuba: 233. 1866. TIPO: Cuba: sin localidad, *Wright 3450* (holótipo, GOET? no visto; isótipos, G!, MO-2095470!, NY!, P!, US-80733!, -974211!).
Panicum tricolor Hack., Oesterr. Bot. Z. 51: 370. 1901. TIPO: Bahamas. Fortune Island, inter frutices, *Eggers 3978* (holótipo, W!).

Planta perenne, cespitosa, cortamente rizomatosa; cañas de (7–)40–60 cm de alto, erectas, ocasionalmente decumbentes, simples o ramificadas; entrenudos de 1–3(–8) cm de largo, cilíndricos, glabros; nudos pajizos, comprimidos, glabros. *Vainas* de 2–4 cm de largo, estriadas, ciliadas hacia los bordes superiores, glabras en el resto de la superficie. *Lígulas* de 0.3 mm de largo, membranáceo-ciliadas, hialinas, cuello pajizo, glabro. *Láminas* de 3–4.5(–10) × 0.1–0.5 cm, lineares a filiformes, involutas, pilosas en la cara adaxial, glabras en la cara abaxial, de ápice subulado, los bordes lisos. *Inflorescencia* exerta; pedúnculo de (2–)10 cm de largo, cilíndrico, glabro; panoja de (2–)5–8 × (1–)2–7 cm, laxa, ocasionalmente contraida; eje principal anguloso, glabro; ramificaciones primarias alternas, distantes y divergentes del eje principal; pulvínulos glabros; raquis de las ramificaciones de 0.5–3.5 cm de largo, glabras, lisas; pedicelos de 0.1–0.4 cm de largo, solitarios, claviformes, glabros. *Espiguillas* de 1.2–1.4 × 0.6–0.8 mm, elipsoides, glabras, pajizas a verdosas o con tintes violáceos. *Gluma inferior* de 0.5–0.6 mm de largo, ½ del largo de la espiguilla, 3-nervia, aguda, glabra. *Gluma superior* de 0.8–1 mm de largo, más corta que la lemma inferior y dejando al descubierto el ápice del antecio superior, 3-nervia, obtusa. *Lemma inferior* de 1–1.2 mm de largo, 3-nervia, aguda. *Pálea inferior* de 1.2 × 0.6 mm, elíptica, ensanchada a la madurez, llegando hasta 1.4 mm de ancho, papirácea, glabra, los bordes escabrosos; flor inferior neutra. *Antecio superior* de 1.2 × 0.5 mm, ovoide, papiloso, glabro; flor superior perfecta; lodículas 2, truncadas, conduplicadas; estambres 2; anteras de 0.4 mm de largo; estigmas plumosos. *Cariopsis* de 0.8 × 0.4 mm, largamente elipsoide, castaña; hilo oblongo; embrión menos de ½ del largo de la cariopsis.

Distribución y ecología. Especie exclusiva de las islas del Caribe, hallándose desde las Bahamas hasta Haití; se encuentra en sabanas húmedas, llegando desde el nivel del mar hasta 400 m de elevación.

Material representativo citado. BAHAMA ISLANDS. Acklin Island, near Snug Corner, *Correll & Proctor 48888* (MO, NY, US); Great Inagua, about 1 mi. E of Matthew Town, *Correll 41685* (NY). CUBA. 12 km E of Baragua, *Hitchcock 23356* (US). **Habana:** Guanabacoa, *Hitchcock 23241* (US); foot of Jiquima hill, Madruga, *León 14690* (US). **Isla de la Juventud:** Siguaena, *Britton et al. 15381* (MO, NY, P, US); San Pedro and vicinity, *Britton & Wilson 14699* (NY, US); at the road between Santa Ana and Rosalía, *Ekman 12259* (G). **Oriente:** Bayate, banks of Río Canto, *Ekman 2443* (US); Holguín, foot of Cerro de Fraile, *Ekman 7580* (NY, US); Bayate, Sabana Miranda, *Ekman 6064* (US). **Pinar del Río:** savannas near Laguna de Asiento Viejo, between Guane and Remates, *Killip 32314* (US); 13 km S of Pinar del Río, *Hitchock 23278* (US); Sabana de San Julián, S of Guane, *León & Roca 7008* (US); Laguna de Piedras, SW of Artemisa, *León 18579* (US); Santa Cruz de los Pinos, Finca Mamey, *Ekman s.n., Amer. Gr. Hb. 702* (G, NY, US, W). **Villa Clara:** 3 km E of Santa Clara, *Howard 4343* (NY, US); Sabana de Manacas, *León 9277* (NY, US); sin localidad, *Wright 756* (G, MO), *3450* (W). REPÚBLICA DOMINICANA. **Santo Domingo:** vicinity of Ciudad Trujillo, *Allard 14276* (US). HAITÍ. Massif du Nord, Gros-Morne, M. Bellance, *Ekman 4916* (US). JAMAICA. **Clarendon:** 0.8 mi. by road E of Toll Gate, *Proctor 37804* (MO).

Davidse (1994) sinonimizó *S. exiguiflora* (*Panicum exiguiflorum*) con *S. hians* (*P. hians*), sin establecer cual fue el criterio que llevó a esta determinación. Sin embargo, la especie se distingue de *S. hians* por tener hojas lineares a filiformes y espiguillas de 1.2–1.4 mm de largo. Se separa de *S. stenophylla*, taxón suramericano que también posee láminas filiformes, por incluir esta última especie plantas de mayor porte, de 30–120 cm de alto, con láminas hasta de 30 cm de largo y espiguillas de 2.4–3.2 mm de largo, con la flor inferior estaminada y superior perfecta con tres estambres.

4. **Steinchisma hians** (Elliott) Nash, en Small, Fl. S.E. U.S. 105. 1903. *Panicum hians* Elliott, Sketch Bot. S. Carolina 1: 118. 1816. TIPO: Estados Unidos de América. Virginia: "in pinetis humidis" (holótipo, CHARL no visto; isótipo y foto del holótipo, US-80696!). Figura 8.

Panicum milioides Nees ex Trin., Gram. Panic. 225. 1826. *Panicum milioides* Nees en Mart., Fl. Bras. Enum. Pl. 2(1): 175. 1829. TIPO: Brasil. "Juazeiro et Oeiras, Bahia and Piauhy," *Martius s.n.* (lectótipo, aquí designado, LE-TRIN!; isolectótipos, M!, US).

Panicum megapotamicum Spreng., Syst. Veg. 4(2): 34. 1827. TIPO: Brasil. Rio Grande do Sul: sin localidad, *Sellow s.n.* (holótipo, B!; isótipo, US-2830915!).

Panicum oblongiflorum Desv., Opusc. Sci. Phys. Nat. 89. 1831–1833. TIPO: Estados Unidos de América. "Habitat in Carolina," *sin colector, s.n.* (holótipo, P!).

Panicum jejunum Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 2: 103. 1836. TIPO: Estados Unidos de América. "Louisiana," *sin colector, s.n.* (holótipo, LE-TRIN!).

Panicum hians var. *pallescens* Döll, en Mart., Fl. Bras. 2(2): 240. 1877. TIPO: Brasil. Minas Gerais: Lagoa Santa, *Warming s.n.* (? no visto).

Panicum milioides var. *filifolium* R. A. Palacios, en Burkart, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 6(2): 302. 1969. TIPO: Argentina. Entre Ríos: Dpto. La Paz, ruta 126, km 53, *Burkart 21073* (holótipo, SI!).

Planta perenne, cespitosa, cortamente rizomatosa, con *cañas* de 15–60 cm de alto geniculadas y arraigadas hacia la base, luego erguidas, simples a ramificadas en los nudos inferiores y ramificadas o no en los nudos superiores; entrenudos de 2–10 cm de largo, comprimidos, huecos, glabros; nudos glabros, oscuros, comprimidos. *Vainas* de 1.6–8 cm de largo, estriadas, esparcidamente híspidas a glabras, un borde pestañoso, el restante membranáceo. *Lígulas* de 0.4–0.8 mm de largo, membranáceas, cortamente ciliadas en la porción superior; cuello glabro, de color castaño claro. *Láminas* de 4.5–20 × 0.2–0.5 cm, linear-lanceoladas, planas o con los bordes involutos, de base angostada y ápice largamente atenuado, pilosa hacia la base en la cara adaxial y los bordes inferiores, el resto de la superficie glabra. *Inflorescencias* terminales exertas; pedúnculo de 4–15 cm de largo, cilíndrico, glabro; panojas de 5–20(–25) × 4–10 cm, laxas, difusas, con ramificaciones de segundo orden alternas, divergentes y distanciadas entre si; eje de las ramificaciones desnudos en la porción basal; ramificaciones de tercer orden cortas, con espiguillas apareadas o solitarias sobre pedicelos cortos; *eje principal* anguloso, escabriúsculo; pulvínulos castaño-claros, esparcidamente pilosos a glabros; eje de las ramificaciones escabroso; pedicelos de 0.7–2 mm de largo, claviformes, escabriúsculos. *Espiguillas* de (1.7–)2.2–2.6 × 0.6–0.9 mm, largamente elipsoides, biconvexas, glabras, verdosas o con tintes violáceos. *Gluma inferior* de 0.8–1.2 mm de largo, ovada, ⅓ del largo de la espiguilla, 3(–5)-nervia; nervio medio escabriúsculo, el ápice agudo. *Gluma superior* de 1.6–1.8 mm de largo, generalmente más corta que el antecio superior, 5(–7)-nervia, el nervio medio escabriúsculo. *Lemma inferior* de 1.8–2.5 mm de largo, glumiforme, 5(–7)-nervia.

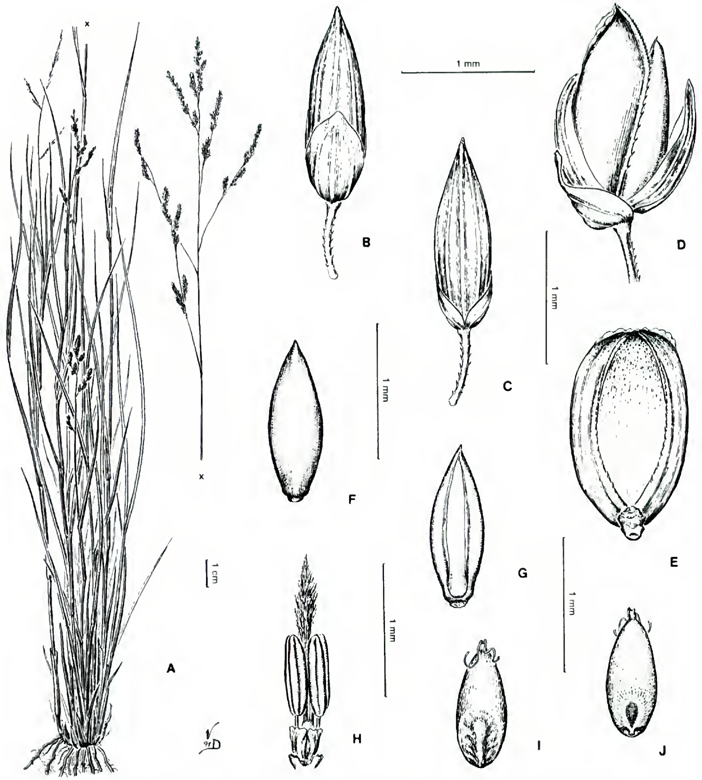

Figura 8. *Steinchisma hians* (A–C, *Hassler 123*, SI; D–I, *Burkart 17513*, SI). —A. Hábito. —B. Espiguilla vista del lado de la gluma inferior. —C. Espiguilla vista del lado de la gluma superior. —D. Espiguilla, vista lateral. —E. Pálea inferior madura. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea. —H. Flor superior con dos lodículas, dos estambres y dos estigmas. —I. Cariopsis, vista escutelar. —J. Cariopsis, vista hilar.

Pálea inferior de 2–2.5 × 0.7–1.2 mm, oblonga, papirácea, sobresaliendo a lo largo y ancho de la espiguilla a la madurez; alas manifiestas, cortamente escabriúsculas en los márgenes; flor inferior neutra. *Antecio superior* de 1.7–2.1 × 0.4–0.6 mm, largamente ovoide, pajizo, papiloso, con aguijones en el ápice de la lemma, el resto de la superficie glabra, de ápice agudo a acuminado; lodículas 2, ca. 0.2 mm de largo, conduplicadas; estambres 2; anteras de 0.4–0.6 mm de largo. *Cariopsis* de 1.1–1.2 × 0.4–0.5 mm, largamente ovoide, castaña, hilo oblongo; embrión poco menor de la mitad del largo de la cariopsis.

Distribución y ecología. Se halla en Estados Unidos de América, México, Centroamérica, Colombia, Brasil, Bolivia, Paraguay, Uruguay y la Argentina. Crece en lugares abiertos y húmedos desde el nivel del mar hasta los 2600 m s.m.

Material representativo citado. ESTADOS UNIDOS DE AMÉRICA. **Florida:** Jupiter, *Curtiss 5534* (P). **Georgia:** along Ogeechee Creek, near Oliver, *Curtiss 6836* (P). **Texas:** Dallas, *Reverchon 1680* (P). GUATEMALA. **Huehuetenango:** 3 km S of Huehuetenango, 1800 m, *Williams et al. 22091* (F, G, US). **Jalapa:** vicinity of Jalapa, 1360 m, *Standley 76607* (F, US). HONDURAS. **Morazán:** 10 km by road S of La Venta, 870 m, *Pohl & Davidse 12017* (F, MO). MÉXICO. **Chiapas:** 9 km S of Comitán on Mexican Highway 190, 1585 m, *Breedlove & Davidse 54947* (MO). **Guanajuato:** Santa Cruz de Juventino Rosas rumbo a Guanajuato, oak forest, *Beetle M-7323* (MO). **Jalisco:** 1 km adelante del crucero de Arandas, carretera Tepatitlán–Pegueros, 1780 m, *Guzmán et al. 956* (MEXU). **Michoacán:** vicinity of Morelia, N of Loma del Zapote, 1950 m, *Arsène 5657* (MEXU, MO, US). NICARAGUA. **Estelí:** Mesas Moropotente, 13°14′N, 86°16′W, 1100–1300 m, *Davidse et al. 30617* (MO).

ARGENTINA. **Buenos Aires:** Pdo. La Plata, Elizalde, *Cabrera 7417* (MO, SI, US). **Chaco:** Dpto. Bermejo, Las Palmas, *Joergensen 2439* (MO, SI). **Córdoba:** San Teodoro, *Stuckert 21459* (G), *21494* (G). **Corrientes:** Dpto. Berón de Astrada, 46 km W de Itá Ibaté, Valencia, *Ahumada 417* (CTES, F, MO, SI); Ruta Nac. 40, 6 km S entrada a Garruchos, *Zuloaga et al. 3108* (SI). **Distrito Federal:** Barrancas al sur, *Venturi 160* (G). **Entre Ríos:** Dpto. Federación, Arroyo Mandisoví Chico y ruta 14, *Bacigalupo et al. 779* (SI). **Formosa:** Dpto. Formosa: ruta 11 vieja, al N de Arroyo Francesa Cué, *Guaglianone et al. 261* (SI, US). **Jujuy:** Quebrada de Tiraxi, camino a Tiraxi, *Zuloaga & Morrone 3012* (MO, SI). **Misiones:** Dpto. Apóstoles, San José, Escuela Agrotécnica Pascual Gentilini, *Cabrera et al. 28516* (SI), *29066* (SI). **Salta:** Dpto. Anta, La Lagunita, *Morello & Cuezzo 375* (LIL). **Santa Fe:** Dpto. Las Colonias, próximo a Cavour, *Pensiero 1297* (MO). **Santiago del Estero:** Dpto. Belgrano, 10 km de Bandera a Pinto, *Cristóbal 47* (CTES). **Tucumán:** Dpto. Leales, Chañar Pozo, *Venturi 480* (BAA, LIL, US), *1635* (BAA, LIL, US). BOLIVIA. **Beni:** Espíritu, *Beck 5314* (LPB, SI, US), *5017* (LPB). **Tarija:** Guerra Huaico, 16 km SW de Tarija, *Coro 1373* (LPB). BRASIL. **Bahia:** Alagoinhas, *Chase 8118* (MO, NY, US). **Goiás:** entre Brasilia y Niquêlandia, *Pires et al. 9676* (UB). **Mato Grosso do Sul:** Campo Grande, *Chase 10847* (IAN, RB, US). **Minas Gerais:** Serra do Curral, SE of Belo Horizonte, 1000 m, *Chase 8969* (US). **Paraná:** 8 km NE of the Paraná-Santa Catarina border at the Rio Negro, 820 m, *Davidse et al. 11035* (MO, NY). **Piauí:** Mun. Uruçuí, ca. 11 km SW of Uruçuí, bank of Rio Uruçuí-Preto, *Eiten & Eiten 4522* (NY, US). **Rio Grande do Sul:** 60 km W of Passo Fundo along Hwy. BR-285 to Vacaria, at intersection of highway with the Rio Ligeiro, 800 m, *Davidse et al. 11157A* (MO). **Santa Catarina:** 19 km al S de Abelardo Luz, *Smith & Klein 11518* (NY, US). COLOMBIA. **Cundinamarca:** Finca San Rafael, 2600 m, *García Barriga 10773* (US). **Valle:** Cartago, Santa Ana de los Caballeros, 950 m, *Cuatrecasas 23035* (F, US). PARAGUAY. **Alto Paraguay:** Puerto Casado, *Hartley 118* (US). **Alto Paraná:** Irala, *Montes 11054* (US). **Amambay:** Sierra de Amambay, *Hassler 10783* (G, K, NY, P, US). **Boquerón:** Puerto Casado, *Hartley 118* (US); Ruta Trans Chaco, 8 km SE de Mariscal Estigarribia, *Schinini & Palacios 25780* (MO). **Central:** Asunción, *Balansa 59* (G, K, P, US); lago Ipacaray, *Hassler 12433* (G, NY); Itá Enramada, riberas del Río Paraguay, *Schinini 6294* (NY). **Concepción:** entre el Río Apa y el Río Aquidabán, *Fiebrig 4776* (F), *5093* (F, G). **Cordillera:** San Bernardino, *Hassler 123* (G, SI). **Guairá:** Villa Rica, *Joergensen 3543* (BAF, F, MO, NY, SI, US). **Paraguarí:** Paraguarí, *Lindman A1887* (P). **Presidente Hayes:** Chacoí, 25°12′S, 57°38′W, *Schinini 26706* (MO), *26764* (MO). **San Pedro:** Alto Paraguay, Colonia Primavera, *Woolston G.66* (NY, SI), *G.49* (NY), *G.80* (NY), *G.105* (NY). URUGUAY. **Artigas:** Bella Unión, *Herter s.n.* (US); vicinity of Artigas, *Beetle & Rosengurtt 1029* (MO). **Cerro Largo:** Río Negro y Arroyo Palleros, cerca de Melo, *Rosengurtt 263* (US). **Durazno:** Río Yí, *Herter 548* (MO, US). **Florida:** costa del Río Santa Lucía, *Lombardo 3050* (US). **San José:** monte de Santa Lucía, I-1926, *Lombardo s.n.* (US). **Soriano:** Juan Jackson, *Gallinal et al. B-244* (US). **Tacuarembó:** Pozo, Hondo, 6 km de Tambores, *Cabrera & Zuloaga 32356* (SI).

Steinchisma hians es la especie con más amplia distribución y variabilidad dentro del género; es un elemento frecuente en campos húmedos desde Estados Unidos de América hasta la Argentina, caracterizándose, junto con *S. cuprea* y *S. exiguiflora*, por tener la pálea inferior conspicuamente expandida a lo ancho a la madurez de la espiguilla. Se distingue de *S. cuprea* por sus panojas laxas, difusas, y de *S. exiguiflora* por el mayor tamaño de plantas, inflorescencias y espiguillas.

5. **Steinchisma spathellosa** (Döll) Renvoize, Kew Bull. 42: 921. 1987. *Panicum spathellosum* Döll, en Mart., Fl. Bras. 2(2): 241. 1877. TIPO: Brasil: sin localidad, *Sellow s.n.* (holótipo, B!; isótipos, BAA!, K!, US-81127!). Figura 9.

Panicum schenckii Hack., Osterr. Bot. Z. 51: 426. 1901. TIPO: Brasil. Santa Catarina: Itajaí, prope Blumenau, *Schenck 579* (holótipo, W!; isótipos, BAA!; US!).

Panicum turfosum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 1. 1921.TIPO: Paraguay. Alto Paraná: Alto Paraná, 1909/1910, *Fiebrig 6471* (holótipo, M!; isótipos, BAA!, G!, K!, LIL!, SI!, US-81159!).

Planta perenne, herbácea, largamente rizomatosa, con rizomas hojosos; *cañas* de 60–120 cm de alto radicantes y ramificadas en los nudos inferiores, luego erguidas; entrenudos de 3.5–20 cm de largo, glabros, comprimidos, huecos; nudos glabros, comprimidos, violáceos. *Vainas* de 5–14 cm de largo, mayores o menores que los entrenudos, glabras, verdosas a violáceas, con los bordes membranáceos, pestañosos en su parte superior. *Lígulas* de 0.4–0.7 mm de largo, membranáceas, cortamente laciniadas o ciliadas en la parte superior, con pelos por detrás en la base de la lámina; cuello glabro, pajizo. *Láminas* de 13–35 × 0.3–1 cm, linear-lanceoladas, planas o con los bordes involutos, de base angostada, el ápice largamente atenuado, pilosas hacia la base de la cara adaxial, glabras en el resto de la superficie, los bordes lisos. *Inflorescencias* terminales exertas, pedúnculos de 10–30 cm de largo,

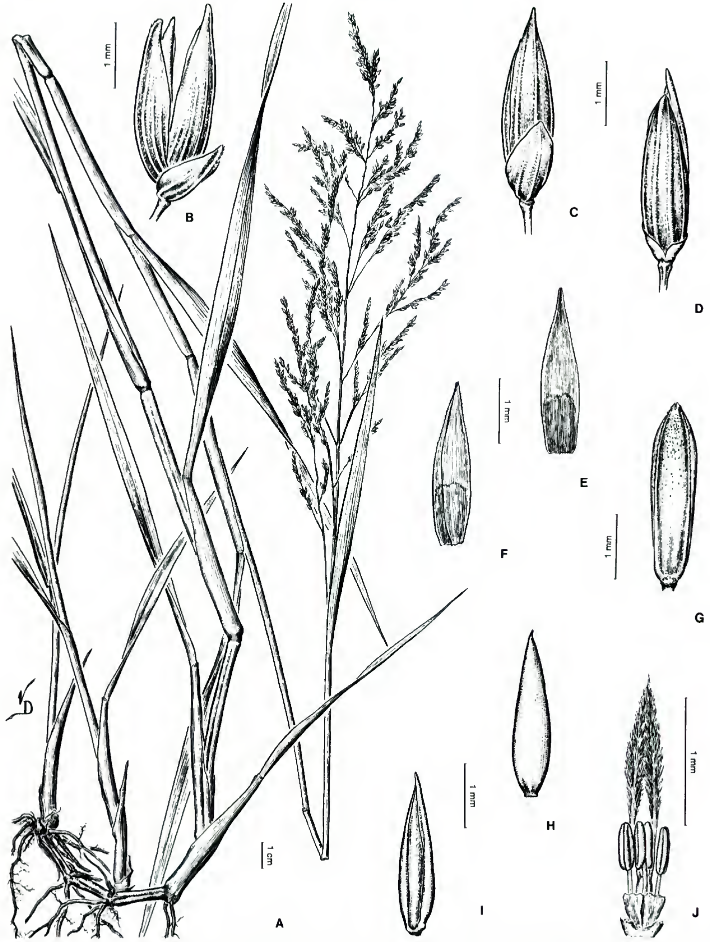

Figura 9. *Steinchisma spathellosa* (*Hicken & Rojas 5450*, SI). —A. Hábito. —B. Espiguilla, vista lateral. —C. Espiguilla vista del lado de la gluma inferior. —D. Espiguilla vista del lado de la gluma superior. —E. Pálea inferior, vista dorsal, encerrando 3 estambres. —F. Pálea inferior, vista ventral, encerrando 3 estambres. —G. Pálea inferior madura. —H. Antecio superior visto del lado de la lemma. —I. Antecio superior visto del lado de la pálea. —J. Flor superior con dos lodículas, tres estaminodios y dos estigmas.

cilíndricos, glabros; panojas de 10–28 × 2–15 cm, laxas, difusas a contraidas; ramificaciones de segundo orden divergentes del raquis, alternas u subopuestas, lisas, onduladas, las de tercer orden cortas, con espiguillas apretadas sobre los ejes; *eje principal* escabroso, anguloso, pulvínulos glabros; pedicelos de 0.4–2 mm de largo escabriúsculos a glabros, claviformes. *Espiguillas* de 3–3.6 × 0.7–0.9 mm, largamente elipsoides, glabras, verdosas o con tintes violáceos. *Gluma inferior* de 1.2–1.6 mm de largo, ovada, ⅓ del largo de la espiguilla, de ápice obtuso, 1–3-nervia, el nervio medio escabroso hacia la porción superior. *Gluma superior* de 2.2–2.8 mm de largo, llegando o no a cubrir al antecio superior, 3–5-nervia; nervio medio escabroso. *Lemma inferior* de 2.8–3.3 mm de largo, 3–5-nervia, de ápice agudo. *Pálea inferior* de 2.5–3.3 × 0.6–0.8 mm, papirácea, con alas manifiestas, no sobresaliendo a lo ancho a la madurez, los bordes cortamente ciliados a glabros, el ápice obtuso; flor inferior estaminada; anteras 3, de 1.2–2 mm de largo, anaranjadas; lodículas 2. *Antecio superior* de 2.5–3 × 0.6–0.7 mm, largamente ovoide, glabro, membranáceo, blanquecino, papiloso, de apice agudo; lemma 3-nervia; lodículas 2, conduplicadas; estaminodios 3, de 0.4–0.6 mm de largo. *Cariopsis* de 1.6–1.8 × 0.7 mm, elipsoide, castaña; hilo oblongo; embrión menos de la mitad del largo de la cariopsis.

Distribución y ecología. Brasil, Paraguay y la Argentina, llegando hasta la provincia de Buenos Aires. Habita en forma de densas matas en bordes de arroyos y ríos, en suelos rocosos, desde el nivel del mar hasta aproximadamente 1000 m s.m.

Material representativo citado. ARGENTINA. **Buenos Aires:** Pdo. Berisso, Isla Santiago, *Cabrera 3368* (G, SI, SP). **Distrito Federal:** Palermo, *Hicken s.n.* (SI-13493). **Entre Ríos:** Salto Grande, *Renvoize et al. 2965* (MO, SI); Dpto. Uruguay, ruta 14, N de Concepción del Uruguay, *Troncoso et al. 2396* (SI). **Misiones:** De Apóstoles a Concepción de la Sierra, Arroyo Las Tunas, *Zuloaga et al. 3244** (MO, SI); Jardín América, *Zuloaga & Deginani 462* (LP, MO, SI); Dpto. Montecarlo, Puerto Piray, *Renvoize et al. 3191* (K, MO, NY, SI). BRASIL. **Paraná:** Mun. São Jorge do Oeste, Rio Iguaçú, Salto Osorio, *Hatschbach 20555* (K). **Rio Grande do Sul:** Pelotas, *Costa Sacco 363* (US). **Santa Catarina:** above Ibirama, *Smith et al. 7600* (K, NY, RB); Fazenda Campo São Vicente, 24 km W of Campo Eré, *Smith & Klein 13841* (NY, R, SI). PARAGUAY. **Alto Paraná:** Arala, *Montes 9896* (LIL). **Cordillera:** Piribebuy, Salto Piraretá, *Degen 1369* (MO). **Paraguarí:** Salto Piraretá, *Sparre & Vervoorst 508* (LIL); Salto Cristal, *Hahn 2611* (PY, SI).

En esta especie se observa una reducción en el tamaño de las plantas en su límite austral de distribución. Es así que los ejemplares de Entre Ríos y Buenos Aires son más pequeños, con inflorescencias algo más contraídas. Vega (1996) indicó que existe una particular reducción de las estructuras florales de *S. spathellosa*; esta autora describió a la especie como diclino monoica, señalando que existe una reducción de la fertilidad masculina en las flores superiores de cada espiguilla, conservándose tres estaminodios en forma vestigial.

6. **Steinchisma stenophylla** (Hack.) Zuloaga & Morrone, comb. nov. Basionym: *Panicum stenophyllum* Hack., Oesterr. Bot. Z. 51: 371. 1901. TIPO: Brasil. Goiás: Paranana, 28 Mayo 1895, *Glaziou 22534* (holótipo, W!; isótipos, G!, K!, P!). Figura 10.

Panicum goyazense Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. TIPO: Brasil. Goiás: sin localidad, *Gardner 4067* (holótipo, B!; isótipos, BAA!, K!, US-80683!, foto del holótipo, US-80683!).

Plantas perennes, cortamente rizomatosas, con *cañas* de 30–120 cm de alto, erectas, decumbentes a geniculadas y marcadamente ramificadas en los nudos medios y basales, multinodes, entrenudos hasta de 15 cm de largo, cilíndricos, rígidos, glabros, huecos; nudos glabros. *Vainas* hasta de 11 cm de largo, estriadas, más cortas que los entrenudos, pajizas, persistentes sobre los entrenudos basales, glabras, un borde membranáceo, el restante cortamente pestañoso a glabro. *Lígulas* de 0.4–0.7 mm de largo, membranáceas, cortamente laciniadas en la porción superior; cuello glabro. *Láminas* de 9–16(–30) cm × 0.2–0.5 mm (con los bordes involutos), hasta 2 mm de ancho cuando abierta, angostada hacia la base, el ápice largamente subulado, aquilladas; cara adaxial densa a esparcidamente pilosa, con pelos largos blanquecinos, más densos hacia la región basal, a glabra; cara abaxial glabra. *Inflorescencias* largamente exertas; pedúnculo de 10–23 cm de largo, cilíndrico, glabro; panojas de 2–15 × 2–10 cm; *eje principal* anguloso, escabriúsculo; pulvínulos glabros; ramificaciones de primer orden divergentes, ocasionalmente adpresas, desnudas hacia la base, alternas y distanciadas entre si; ejes de las ramificaciones y pedicelos triquetros, escabriúsculos; espiguillas sobre ejes de segundo orden hacia la porción superior de las ramas; panojas axilares presentes, similares a la panoja terminal. *Espiguillas* de 2.4–3.2 × 0.5–0.8 mm, largamente elipsoides, biconvexas, glabras, verdosas o con tintes violáceos; gluma superior y lemma inferior subiguales, o la gluma superior menor que la lemma inferior, dejando al descubierto el ápice del antecio superior. *Gluma inferior* de 1–1.2 mm de largo, ⅓ o poco más del largo de la espiguilla, ovada, aguda a obtusa, 3-

Figura 10. *Steinchisma stenophylla* (*Zuloaga & Morrone 4660*, SI). —A. Hábito. —B. Detalle de la región ligular. —C. Espiguilla vista del lado de la gluma inferior. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla, vista lateral. —F. Pálea inferior madura, vista dorsal. —G. Pálea inferior madura, vista ventral. —H. Antecio superior visto del lado de la lemma. —I. Antecio superior visto del lado de la pálea. —J. Pálea superior con tres estambres. —K. Cariopsis, vista escutelar. —L. Cariopsis, vista hilar.

nervia. *Gluma superior* de 2.2–3 mm de largo, ⅕ del largo de la lemma inferior, 5-nervia, obtusa. *Lemma inferior* de 2.2–3 mm de largo, 3–5-nervia. *Pálea inferior* de 2.2–2.8 × 0.6–0.8 mm, expandida a la madurez y sobresaliendo a lo largo de la espiguilla, papirácea y con márgenes escabrosos; flor inferior estaminada; estambres 3; anteras de 1–1.6 mm de largo, lodículas 2, conduplicadas. *Antecio superior* de 2.2–2.8 × 0.6 mm, largamente ovoide, cartilaginoso, pajizo, verrucoso, finamente escabroso en el ápice; lodículas 2, ca. 0.5 mm de largo, conduplicadas; estambres 3; anteras de 1.2–1.4 mm de largo. *Cariopsis* de 1.3 × 0.5 mm, de contorno oblonga; hilo oblongo; embrión menos de ½ del largo de la cariopsis.

Distribución y ecología. Se halla en Venezuela, en el departamento de Amazonas, y en Brasil, en cerrados en los estados de Bahia, Minas Gerais y Pará. Crece en márgenes arenosos y rocosos de orillas de ríos y arroyos; llega desde 200 m hasta los 1250 m s.m.

Material representativo citado. BRASIL. **Bahia:** Serra do Rio de Contas, about 2 km N of the town of Rio de Contas in flood plain of the Rio Brumado, 980 m, *Harley et al. 15498* (P); Serra da Agua de Rega, Rio Riachao, ca. 27 km N of Seabra, road to Agua de Rega, 1000 m, *Irwin et al. 31028* (MO). **Minas Gerais:** Rio das Pedras, *Glaziou 20110* (P); ca. 18 km W of Grão Mogol, 950 m, *Irwin et al. 23589* (MO, US); Cardeal Mota, Fazenda Monjolos, 19°15'N, 43°40'W, *Zuloaga & Morrone 4660* (MO, SI); rodovia de Cardeal Mota a Conceiçao do Mato Dentro, BR-010, Serra do Cipó, km 117, Córrego Vitalino, 19°20'N, 43°30'W, 1320 m, *Zuloaga & Morrone 4706* (MO, SI). **Pará:** Caripi, *Spruce 63* (M, W), *76* (P). VENEZUELA. **Amazonas:** vicinity of Rio Coro-Coro, near Airport of Yutaje, 250 m, 5°35'N, 66°10'W, *Liesner et al. 10956* (MO, NY, VEN), sand island in Caño Asisa, *Cowan & Wurdack 31556* (NY, US); Caño Yutaje, Serrania Yutaje, 1250 m, *Maguire 32509* (NY, US); Río Orinoco, Río Cumucunuma, Culebra rapids, *Maguire et al. 30350* (NY, US, VEN); Dpto. Atures, Río Coro-Coro, W of Serranía Yutaje, 6 km N of settlement of Yutaje, 5°41'N, 66°07'W, 320 m, *Liesner & Holst 21288* (MO, SI); Dpto. Atabapo, Caño Negro, río arriba desde la confluencia con el Río Cunucunuma, 200 m, *Steyermark et al. 126266* (MO, NY, VEN); Dpto. Atures, Río Coro-Coro, W of Serranía de Yutaje, 3 km N of settlement of Yutaje, 200 m, 5°38'N, 66°07'W, *Holst & Liesner 3094* (MO, SI, VEN).

Steinchisma stenophylla es una especie afín a *S. spathellosa*, de la cual se distingue por sus láminas filiformes, espiguillas menores y por tener flor superior perfecta, con tres estambres desarrollados. Esta especie posee una distribución disyunta, hallándose en cerrados de Brasil y en la Guayana venezolana.

Literatura Citada

Anton, A. M. & H. E. Connor. 1995. Floral biology and reproduction in *Poa* (Poeae: Gramineae). Austral. J. Bot. 43: 577–599.

Arber, A. 1934. The Gramineae. Cambridge Univ. Press, Cambridge.

Bouton, J. H., R. H. Brown, J. K. Bolton & R. Campagnoli. 1981. Photosynthesis of grass species differing in carbon dioxide fixation pathways. Pl. Physiol. (Lancaster) 67: 433–437.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brown, R. H. & W. V. Brown. 1975. Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. Crop Sci. (Madison) 15: 681–685.

———, J. H. Bouton, P. T. Evans, H. E. Malter & L. L. Rigsby. 1985. Photosynthesis, morphology, leaf anatomy, and cytogenetics of hybrids between C_3 and C_3/C_4 *Panicum* species. Pl. Physiol. (Lancaster) 77: 653–658.

Brown, W. V. 1948. A cytological study in the Gramineae. Amer. J. Bot. 35: 382–395.

———. 1951. Chromosome numbers of some Texas grasses. Bull. Torrey Bot. Club 78: 292–299.

———. 1977. The Kranz syndrome and its subtypes in grass systematics. Mem. Torrey Bot. Club 23: 1–97.

Clayton, W. D. & S. A. Renvoize. 1986. Genera graminum. Kew Bull., Additional Ser. 13: 1–389.

Clifford, H. T. 1961. Floral evolution in the family Gramineae. Evolution 15: 455–460.

Davidse, G. 1994. *Panicum*. Pp. 302–318 *en* G. Davidse, M. Sousa S. & A. O. Chater (editores), Flora Mesoamericana, Vol. 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, México, D.F.; Missouri Botanical Garden, St. Louis; The Natural History Museum, London.

——— & R. W. Pohl. 1972. Chromosome numbers and notes on some Central American grasses. Canad. J. Bot. 50: 1441–1452.

Dubcovsky, J. & F. O. Zuloaga. 1991. Números cromosómicos de especies sudamericanas de *Panicum* (Poaceae: Paniceae). Bol. Soc. Argent. Bot. 27: 201–206.

Ellis, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. Bothalia 12: 65–109.

———. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–671.

———. 1988. Leaf anatomy and systematics of *Panicum* (Poaceae: Panicoideae) in southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 129–156.

Farris. J. S. 1988. Hennig86. Reference, version 1.5. J. S. Farris, Port Jefferson Station, New York.

Goloboff, P. 1993. NONA vesión 1.6, Programa y documentación distribuida por el autor. Tucumán, Argentina.

Gould, F. W. 1968. Chromosome numbers of Texas grasses. Canad. J. Bot. 46: 1315–1325.

——— & R. B. Shaw. 1983. Grass Systematics, 2nd. ed. Texas A & M Univ. Press, College Station.

Hitchcock, A. S. & A. Chase. 1910. The North American species of *Panicum*. Contr. U.S. Natl. Herb. 15: 1–396.

———. 1915. Tropical North American species of *Panicum*. Contr. U.S. Natl. Herb. 17: 459–539.

Hsu, C. C. 1965. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 9: 43–150.

Kanai, R & M. Kashiwagi. 1975. *Panicum milioides*, a gramineae plant having Kranz leaf anatomy without C_4-photosynthesis. Pl. Cell Physiol. 16: 669–679.

Karis, P. O. 1995. Cladistics of the subtribe Ambrosiinae (Asteraceae). Syst. Bot. 20: 40–54.

Ku, M. S. B. & G. E. Edwards. 1978. Photosynthetic efficiency of *Panicum hians* and *Panicum milioides* in relation to C_3 and C_4 plants. Pl. Cell Physiol. 19: 665–675.

——— & R. Kanai. 1976. Distribution of enzymes related to C_3 and C_4 pathways of photosynthesis between mesophyll and bundle sheath cells of *Panicum hians* and *Panicum milioides*. Pl. Cell Physiol. 64: 257–262.

Metcalfe, C. R. 1960. Anatomy of Monocotyledons. I. Gramineae. Oxford Univ. Press, Oxford.

Morgan, J. A. & R. H. Brown. 1979. Photosynthesis in grass species differing in carbon dioxide fixation pathways. Pl. Physiol. (Lancaster) 64: 257–262.

Morrone, O., J. H. Hunziker, F. O. Zuloaga & A. Escobar. 1995. Números cromosómicos en Paniceae sudamericanas (Poaceae: Panicoideae). Darwiniana 33: 53–60.

Nash, G. V. 1903. Poaceae. Pp. 49–161 *en* J. K. Small (editor), Flora of the Southeastern United States. New York.

Nixon, K. C. 1993. Clados, versión 1.38 [32 bit] beta version. Programa de computación distribuido por el autor.

——— & J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7: 233–241.

——— & J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413–426.

Núñez, O. 1952. Investigaciones cariosistemáticas en las gramíneas argentinas de la tribu Paniceae. Revista Fac. Agron. Univ. Nac. La Plata 28: 229–255.

Oguro, H., K. Hinata & S. Tsunoda. 1985. Comparative anatomy and morphology of leaves between C_3 and C_4 species in *Panicum*. Ann. Bot. (Oxford) 55: 859–869.

Parodi, L. R. 1946. Gramíneas bonariensis. Clave para la determinación de los géneros y enumeración de las especies, 4 ed. Acme Agency, Buenos Aires.

Pilger, R. 1931. Bemerkungen zu *Panicum* und verwandten Gattungen. Notizbl. Bot. Gart. Berlin-Dahlem 11: 240–245.

———. 1940. Gramineae. III: Unterfamilie Panicoideae. *En* A. Engler & K. Prantl (editores), Die natürlichen Pflanzenfamilien, Ed. 2, 14e: 1–208. Engelmann, Leipzig.

Pohl, R. W. & G. Davidse. 1971. Chromosome numbers of Costa Rican grasses. Brittonia 23: 293–324.

Renvoize, S. A. 1982. A new genus and several new species of grasses from Bahia (Brazil). Kew Bull. 37: 323–333.

———. 1987. New grasses from Paraná, Brazil. Kew Bull. 42: 921–925.

Sass, J. E. 1940. Elements of Botanical Microtechnique. McGraw Hill, New York and London.

Schmid, R. & D. Turner. 1977. Contrad 70, an effective softener of herbarium material for anatomical study. Taxon 26: 551–556.

Sendulsky, T. & T. R. Soderstrom. 1984. Revision of the South American genus *Otachyrium* (Poaceae: Panicoideae). Smithsonian Contr. Bot. 57: 1–24.

Simon, B. K. & C. M. Weiller. 1995. *Fasciculochloa*, a new grass genus (Poaceae: Paniceae) from south-eastern Queensland. Austrobaileya 4: 369–379.

Urbani, M. 1990. Citología y método de reproducción de *Panicum elephantipes* (Gramineae). Bol. Soc. Argent. Bot. 26: 205–208.

Vega, A. S. 1996. Biología reproductiva de *Panicum spathellosum* (Poaceae: Panicoideae: Paniceae). Darwiniana 34: 199–211.

Watson, L. & M. J. Dallwitz. 1992. The Grass Genera of the World. CAB International/Univ. Press, Cambridge.

Webster, R. D. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). Syst. Bot. 13: 576–609.

Zuloaga, F. O. 1987a. Systematics of the New World species of *Panicum* (Poaceae: Paniceae). Pp. 287–306 *en* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editores), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

———. 1987b. A revision of *Panicum* subgenus *Panicum* section *Rudgeana* (Poaceae: Paniceae). Ann. Missouri Bot. Gard. 74: 463–478.

——— & O. Morrone. 1996. Revisión de las especies americanas de *Panicum* subgénero *Panicum* sección *Panicum* (Poaceae: Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 83: 200–280.

———, R. P. Ellis & O. Morrone. 1992. A revision of *Panicum* subgenus *Phanopyrum* section *Laxa* (Poaceae: Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 79: 770–818.

———, J. Dubcovsky & O. Morrone. 1993. Infrageneric phenetic relations in genus *Panicum* (Poaceae: Panicoideae: Paniceae): A numerical analysis. Canad. J. Bot. 71: 1312–1327.

Indice de colecciones numeradas. Cada especimen es citado por el apellido del primer colector en el caso en que otros coleccionistas participen de la colección.

1. *Steinchisma cuprea* (Hitchc. & Chase) W. V. Br.
2. *Steinchisma decipiens* (Nees ex Trin.) W. V. Br.
3. *Steinchisma exiguiflora* (Griseb.) W. V. Br.
4. *Steinchisma hians* (Elliott) Nash
5. *Steinchisma spathellosa* (Döll) Renvoize
6. *Steinchisma stenophylla* (Hack.) Zuloaga & Morrone

Abrell 52 (5); Aguilar 746 (4), 999 (4); Ahumada, O. 417 (4), 785 (4), 1151 (4), 1453 (4), 1493 (4), 2023 (4), 2274 (4), 2752 (4), 3201 (4); Allard, S. T. 14276 (3); Allem, A. 1306 (4), 1825 (4), 1861 (4), 1914 (4); Alonso, J. 37 (4); Alston, A. H. G. 7578 (2); Amaral, A. 1086 (6); Anderson, W. R. 1142 (4), 35147 (2), 36395 (2); Araujo 359 (4); Arbo, M. M. 986 (4); Arsène, Bro. 5657 (4).

Bacigalupo, N. M. 565 (5), 646 (4), 779 (4), 965 (4); Balansa, B. 59 (4), 60 (2); Balegno 579 (4); Bazzi, R. 307 (4), 421 (4); Bartlett, H. H. 21328, 21348 (2); Beck, S. G. 3221 (4), 5314 (4), 5017 (4); Beetle, A. 1029 (4), 1439 (4), 1959 (4), 7323 (4), 7708 (1); Bertoni, M. 2290 (5), 4629 (5); Black, G. A. 2152b (2), 51-10985 (2), 51-11069 (2); Boege 2543 (1); Boelcke, O. 1483 (4); Brace, L. J. K. 4164 (3), 4380 (3); Breedlove, D. E. 54947 (4); Britton, N. L. 6432 (3), 14699 (3), 15381 (3); Brown, R. H. 109 (5); Burkart. A. E. 26 (5), 271 (5), 285 (5), 1721 (5), 3349 (4), 3924 (5), 5016 (4), 12760 (4), 12953 (5), 14063 (4), 15040 (5), 17513 (4), 18584 (4), 20173 (4), 20296 (4), 21597 (4), 22877 (4), 24090b (4); Burman, A. G. 87 (2), 645 (2).

Cabrera, A. L. 3368 (5), 5392 (4), 7417 (4), 26569 (4), 27321 (4), 28161 (4), 28368 (4), 28516 (4), 28629 (4), 29066 (4), 32356 (4), 28631 (5), 28634 (2), 28666 (5), 28934 (5), 29472 (5), 32427 (2); Cano 1846 (4); Chase, A. 8068 (4), 8073 (4), 8118 (4), 8591 (2), 8634 (2), 8727 (2), 8969 (4), 9105 (6), 9417 (2), 10279 ½ (2), 10283 (2), 10286 (2), 10332 (2), 10501 (2), 10847 (4), 10854 (2), 10925 (2), 10941 (4), 10990 (4), 11242 (2), 11759 (2), 11815 (6); Clayton, D. W. 4284 (2), 4473 (4); Coro 1373 (4); Correll, D. S. 48888 (3), 41685 (3); Corte 1026 (4); Costa Sacco, A. 363 (5); Cowan, R. S. 31556 (6); Cristóbal, C. 47 (4); Cuatrecasas, J. 23035 (4); Curtiss, A. H. 5534, 6836 (4); Cutler, D. 2005 (2).

Davidse, G. 10597 (2), 10613 (2), 11035 (4), 11157A (4), 30617 (4), 31539 (4); Degen, R. 1369 (5); Dombrowski, L. T. D. 443 (2); Dusén, P. 279a (2), 3658 (2), 13230 (2), 17571 (2); Dutra, J. 422 (2).

Eiten, G. 1973 (2), 2667 (2), 4522 (4), 4773 (4), 4776 (4), 5093 (4); Ekman, E. L. 572 (3), 573 (3), 639 (5), 2443 (3), 4916 (3), 6064 (3), 7400 (3), 7580 (3), 12259 (3), Amer. Gr. Hb. 702 (3).

Fiebrig, K. 4507 (2), 5403 (5); Filgueiras, T. S. 2078 (2), 2169 (2), 3014 (2).

Galli, I. 242 (4); Gallinal B-244 (4); García Barriga, H. 10773 (4), 15552 (4); García 2 (2); Gautier 4 (4); Glaziou, A. F. 15620 (2), 16619 (2), 17639 (2), 20110 (6), 22535 (2); Guaglianone, E. R. 261 (4), 1170 (5); Guzmán 956 (4).

Hahn, W. J. 2533 (2), 2611 (5); Harley, R. 15498 (6), 15803 (2), 19384 (2), 19647 (2); Hartley 118 (4); Hassler, E. 123 (4), 2694 (4), 3658 (2), 10110 (2), 10783 (4), 11643 (4), 11907 (2), 12347 (2), 12433 (4); Hatschbach, G. 2875 (2), 4321 (2), 12888 (2), 15169 (5), 15238 (2), 20555 (5), 22820 (2), 32995 (2), 33573 (2); Herter, W. 548 (4); Hicken, C. M. 5450 (5); Hitchcock, A. S. 179 (3), 23241 (3), 23278 (3), 23356 (3); Holst, B. 3094 (6); Howard 4343 (3); Huber, O. 4322 (6).

Ibarrola, A. 361 (4); Idinael 597 (4); Imaguire 1207 (2); Irwin, H. S. 9751 (2), 12591 (2), 19571 (2), 23589 (6), 25628 (2), 31028 (6).

Job, M. M. 757 (4); Joergensen, P. 2439 (4), 3543 (4); Joly, A. B. 1805 (2).

Killip, E. P. 32314 (3), 43980 (3); Klein, R. M. 3593 (2), 5900 (2), 10282 (2), 11875 (5); Koninck, de 121 (4); Krapovickas, A. 23652 (4), 24553 (4), 24666 (2), 25716 (5); Kurtz, F. 4766 (4).

Leavenworth, M. C. 1925 (1); León, Bro. 911 (3), 5608 (3), 6377 (3), 6654 (3), 7008 (3), 9277 (3), 14690 (3), 18579 (3), 20249 (3); Liesner, R. 10956 (6), 17513 (6), 21288 (6); Lillo, M. 3921 (4); Lindman, C. A. M. A1887 (4); Lombardo, A. 3050 (4); Lorentz, P. G. 615 (4); Lossen, W. 298 (4); Luna 883 (3).

Macedo, A. 4552, 5223 (2); Maguire, B. 30350 (6), 32509 (6); Martínez Crovetto, R. 4351 (4), 4835 (4); Mattos, J. 12810 (2); Meyer, T. 364 (4), 5439 (2); Molina 10057 (4); Monetti 1745 (4); Montes, J. E. 612 (4), 3305 (4), 3346 (4), 9896 (5), 11054 (4), 15268 (4), 15325 (4); Morel, I. 707 (4), 2128 (4); Morello, J. 375 (4); Morrone, O. 444 (2); Morton 2996 (3); Múlgura, M. E. 356 (4).

Nash, G. V. 213 (4), 1331 (3), 1450 (3); Nicolás, Bro. 217 (1), 5879 (1); Nicora, E. G. 2604 (4), 2670 (4), 3043 (4), 4659 (4), 17694 (4); Niederlein, G. 2069 (2).

Oliva 58 (1).

Parodi, L. R. 3943 (4), 5648 (2); Pedersen, T. M. 1297 (4), 1374 (4), 7092 (2), 10240 (4); Pereira 6730 (4); Pflanz, C. 4016 (4); Pickel, D. B. 5198 (2); Pinto, P. 279 (4); Pires, J. M. 9676 (4); Pohl, R. W. 12017 (4), 12162 (4), 12165 (4); Praderi 536 (4); Prance, G. T. P24905 (6); Proctor, G. R. 37804 (3); Puiggari, J. I. 3245 (2).

Quarín, C. 1335 (4), 2085 (4), 2667 (4), 3460 (5).

Rambo, B. 35143 (4), 37387 (2), 41186 (4); Ramírez 27 (4); Rana 9 (4); Reeder, J. R. 2330 (1), 4466 (1); Reitz, R. 6157 (2), 6959 (5), 7888 (2), 11955 (4); Renvoize, S. A. 2965 (5), 2967 (4), 3033 (5), 3151 (2), 3191 (5), 3629 (4); Reverchon, J. 1680 (4); Rodríguez 74 (4), 378 (5); Rojas, T. 113 (4), 9148 (2); Romanz 204 (2); Rosengurtt, B. B-263 (4), B-5379 (4), B-5505 (4); Rúgolo, Z. E. 1106 (2); Rzedowski, J. 1024 (1), 48632 (1).

Schinini, A. 6294 (4), 7434 (2), 8323 (2), 12796 (4), 12818 (4), 13177 (2), 25780 (4), 26706 (4), 26764 (4); Schulz, A. G. 3845, 5779, 10310 (4), 14847 (4), 15768 (4), 17462 (4); Schwacke, C. A. W. 13790 (2); Schwarz 5116 (4), 6751 (4), 7675 (4), 10726 (5); Schwindt 914 (4); Sendulsky, T. 146 (2), 418b (2), 1883 (2); Sergues 2566 (3); Scipione 264 (4); Shafer 10742 (3); Sharp 44753 (1); Silva, T. 263 (6), 436 (2); Skvortzov, B. 64 (2); Smith, L. B. 7600 (5), 8294 (2), 9643 (4), 9947 (4), 10928 (4), 11518 (4), 11934 (4), 12594 (5), 13064 (4), 13841 (5), 13985 (2), 15489 (2), 15626 (2), 15584 (2), 16048 (2), 16145 (4); Sparre, B. 508 (5), 1120 (2); Spruce, R. 63 (6), 76 (6); St. Hilaire, A. 416 (2); Standley, P. C. 4784 (4), 4785 (4), 24028 (4), 24089 (4), 26636a (4), 76607 (4); Steinbach, J. 2654 (2); Steyermark, J. 32077 (4), 48148 (4), 126198 (6), 126266 (6); Stuckert, T. 16812 (4), 18736 (4), 21459 (4), 21494 (4); Swallen, J. R. 3849 (5), 7098 (4), 7164 (2), 7613 (4), 7726 (2), 8870 (2), 10760 (4).

Tamayo, F. 2901 (2), 3209 ½ (2); Tedone 4889 (4); Tracy, S. M. 9075 (3); Tressens, S. G. 939 (2), 2848 (4); Triana, J. J. 319 (4); Troncoso, N. S. 2728 (4), 2755 (4), 3412 (4).

Ule, E. 1961 (2).

Valla, J. J. 63 (4); Valls, J. F. 1721 (4), 2326 (2), 4761 (2), 4769 (2); Venturi, S. 160 (4), 480 (4), 1635 (4), 2629 (2), 2727 (2), 2785 (2), 4348 (2), 9932 (2).

Williams, T. A. 22091 (4); Woolston, L. G.66 (4), G.49 (4), G.80 (4), G.105 (4); Wright, C. 756 (3), 3450 (3).

Zardini, E. M. 7443 (5), 9038 (2); Zuloaga, F. O. 130 (4), 425 (2), 462 (5), 544 (2), 1985 (4), 2330 (4), 3012 (4), 3074 (5), 3094 (2), 3095 (2), 3108 (4), 3161 (5), 3214 (2), 3244 (5), 3305 (2), 3314 (4), 3617 (4), 4179 (4), 4660 (6), 4706 (6).

APÉNDICE I. LISTA DE MATERIAL ANALIZADO PARA EL ESTUDIO CLADÍSTICO.

Panicum subgénero *Panicum* sección *Panicum*

P. bergii. ARGENTINA. **Buenos Aires:** *Krapovickas 2906* (MO, SI). **Chaco:** *Renvoize et al. 3583* (MO, SI). BOLIVIA. **La Paz:** *Beck & Haase 9921* (K). *P. capillare.* CANADA. **Nova Scotia:** *Fernald & Long 19754* (US). ESTADOS UNIDOS DE AMÉRICA. **Arizona:** *Kearney & Peebles 12868* (US). *P. capillarioides.* ESTADOS UNIDOS DE AMÉRICA. **Texas:** *Tharp 43066* (MO). MÉXICO. **Nuevo León:** *Hitchcock 5547* (US). **San Luis Potosí:** *Rzdewosky 4618* (US). *P. hallii.* ESTADOS UNIDOS DE AMÉRICA. **Arizona:** *Hitchcock 3706 (US); Griffiths & Thornber* 238 (US). MÉXICO. **Aguascalientes:** *Atrupo 1723* (MEXU). *P. hirsutum.* BELICE. **Cayo: Croat 23483** (MO). COSTA RICA. **Heredia:** *Hammel 11795* (MO). CUBA. **Cienfuegos:** *Jack 6295* (NY, US). **Habana:** *León 14181* (MO, US). *P. hispidifolium.* COLOMBIA. **Magdalena:** *Smith 2152* (F, G, GH, K, MO, NY, P, US). COSTA RICA. **Guanacaste:** *Pohl & Davidse 11291* (F, MEXU). HONDURAS. **Cortés:** *Nelson et al. 5621* (MO). *P. lepidulum.* GUATEMALA. *Hitchcock 9014* (US). MÉXICO. **Aguascalientes:** *Reeder & Reeder 3814* (US). **Hidalgo:** *Moore Jr. 4218* (GH, US). *P. miliaceum.* ESTADOS UNIDOS DE AMÉRICA. **California:** *Ahart 6168* (MO). **North Dakota:** *Seiler 3825* (MO). GUAYANA FRANCESA. *Feuillet 4442* (US). HONDURAS. **Morazán:** *Rodríguez 3512* (US).

Panicum subgénero *Panicum* sección *Dichotomiflora*

P. aquaticum. BRASIL. *Davidse et al. 12034* (MO). MÉXICO. **Quintana Roó:** *Sousa 11207* (MEXU). *P. bartowense.* BAHAMAS. **Grand Bahama:** *Correll & Popenoe 46671* (MO). *P. dichotomiflorum.* VENEZUELA. **Anzoátegui:** *Burkart 17289* (SI). **Apure:** *Borsotti 66* (US). *P. elephantipes.* ARGENTINA. **Buenos Aires:** *Zuloaga 3084* (SI). BRASIL. **Mato Grosso:** *Rondon s.n.* (SI). *P. sublaeve.* EL SALVADOR. **La Libertad:** *Pohl 12774* (MO). MÉXICO. **Chiapas:** *Breedlove & Davidse 54548* (MO). *P. vaseyanum.* MÉXICO. **Aguas Calientes:** *Hitchcock 7491* (US), *7485* (US).

Panicum subgénero *Panicum* sección *Rudgeana*

P. campestre. BRASIL. **Mato Grosso:** *Chase 10790* (RB). **São Paulo:** *Lofgren 212* (RB). *P. cayennense.* COLOMBIA. **Cauca:** *Lehmann 5268* (US), *5269* (US). MÉXICO. **Campeche:** *Reeder & Reeder 6111* (MEXU). GUATEMALA. **Izabal:** *Le Doux et al. 106* (NY). *P. cervicatum.* VENEZUELA. **Amazonas:** *Huber 862* (MO), *1351* (MO). *P. ligulare.* BRASIL. **Distrito Federal:** *Filgueiras 1261* (SI). *P. rudgei.* COSTA RICA. **Puntarenas:** *Zamora et al. 1184* (MO). VENEZUELA. **Amazonas:** *Maguire 29424* (NY), *Cowan 31486* (US).

Panicum subgénero *Panicum* sección *Urvilleana*

P. chloroleucum. ARGENTINA. **Catamarca:** *Cabrera et al. 32443* (SI). **Jujuy:** *Cabrera et al. 31731* (SI). *P. racemosum.* ARGENTINA. **Buenos Aires:** *Cabrera 5535* (SI); *Zuloaga 3360* (SI). *P. urvilleanum.* ARGENTINA. **Buenos Aires:** *Cabrera 6620* (SI). **Mendoza:** *Boelcke et al. 15797* (SI).

Panicum subgénero *Panicum* sección *Virgata*

P. amarum. ESTADOS UNIDOS DE AMÉRICA. **Alabama:** *Deramus 726* (MO). MÉXICO. **Campeche:** *Saver et al. 3350* (US). *P. glabripes.* ARGENTINA. **Corrientes:** *Tressens et al. 414* (SI). BRASIL. **Paraná:** *Jonsson 1124a* (SI). *P. tricholaenoides.* ARGENTINA. **Chaco:** *Joergensen 2430* (MO). **Corrientes:** *Schinini 16095* (SI). *P. virgatum.* MÉXICO. **Chiapas:** *Purpus 9199* (MO). **Quintana Roó:** *Durán & Espejel 551* (MEXU).

Panicum subgénero *Phanopyrum* sección *Laxa*

P. hylaeicum. GUATEMALA. **Alta Verapaz:** *von Tuerckheim 1254* (US). HONDURAS. **Comayagua:** *Williams & Williams 18435* (US). MÉXICO. **Chiapas:** *Breedlove & Davidse 54040* (MO, US). *P. laxum.* ARGENTINA. **Buenos Aires:** *Parodi 4662b* (BAA). BOLIVIA. **Beni:** *Beck 3228* (SI). BRASIL. **Acre:** *Croat & Rosas 62653* (SI). *P. pilosum.* ARGENTINA. **Corrientes:** *Krapovickas et al. 24307* (CTES, SI). BRASIL. **Amapá:** *Rabelo et al. 3319* (MO); Curuçá Ore Body, *Cowan 38177* (NY). COSTA RICA. **Alajuela:** *Pohl & Davidse 11254* (US). *P. polygonatum.* BOLIVIA. **Cochabamba:** *Steinbach 484* (MO, NY), *Cárdenas 700* (US). BRASIL. **Acre:** *Prance et al. 7703* (M, MO, P). COLOMBIA. **Amazonas:** *Black & Schultes 46–122* (US). **Antioquia:** *Gutiérrez & Barkley 17C172* (LIL, SI, US). *P. stevensianum.* BRASIL. **Pernambuco:** *Chase 7717* (US). COLOMBIA. **Casanare:** *Blydenstein s.n.* (SI, US). CUBA. **Habana:** *Ekman 11516, 13093* (US).

Plagiantha tenella. BRASIL. **Bahia:** *Harley et al. 16769* (K), *Pinto 127/80* (US); *Zuloaga et al. 4773* (IBGE, MO, SI), *Zuloaga et al. 4775* (SI), *Zuloaga et al. 4808* (SI), *4813* (SI).

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- ☐ One paragraph per basionym is used as follows: *Taxon* author, literature citation, type citation, e.g., *Pleurothyrium amplifolium* (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P).
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This volume of the ANNALS of the Missouri Botanical Garden has been set in APS Bodoni. The text is set in 9 point type while the figure legends and literature cited sections are set in 8 point type.

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