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THE "ANTARCTIC" FLORA: RESEARCHES OF CHARLES DARWIN AND JOSEPH HOOKER

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One of the most intriguing patterns in plant geography is the floristic affinity among the cool temperate floras of the southern hemisphere. Although separated by a vast expanse of ocean and a continental ice sheet, southern South America, New Zealand, Australia, Tasmania, and the scattered islands of the south Atlantic and Indian Oceans display a remarkable number of identical or vicarious species. These amphiantarctic disjuncts have been the subject of several reviews (Skottsberg, 1960; Wace, 1965; Moore, 1972). Recent analyses of the problem take into account the former proximity of Australia, New Zealand, and South America prior to their separation from the Antarctic continent (Moore, 1972; Raven and Axelrod, 1974). However, prior to the general acceptance of continental drift in the 1960's, most biogeographers assumed that the relative positions of the southern land masses had remained constant. This assumption led to the emergence of two opposing schools of thought concerning the origin of the amphiantarctic disjunctions. One school favored former land connections and the other transoceanic dispersal (Wace, 1965).

This study is an attempt to reconstruct the origins of the land-bridge vs. long distance dispersal debate which characterized the study of amphiantarctic disjunctions for over a century. It is actually a reconstruction of the ideas put forth by two men: Joseph Hooker and Charles Darwin. The former, destined to become the foremost British botanist of his day, was the first to recognize and define an "Antarctic" flora. The latter, by his own estimation a "botanical ignoramus," laid the foundation for a revolution in biogeography.

Both Darwin and Hooker devoted considerable attention to plant geography. Their researches concerning the origin of the "Antarctic" flora present an interesting case study. They approached the problem with essentially the same set of facts. They differed in their interpretations of the origin of the southern hemisphere disjunctions as a result of differences in the theoretical assumptions upon which their interpretations were based. These assumptions, as well as their consequences, merit close attention.

Between 1844 and 1860, Hooker published three volumes on the botany of the southern hemisphere: *Flora Antarctica* (1844–47), *Flora Novae-Zelandiae* (1852–55), and *Flora Tasmaniae* (1855–60). The works were collectively titled *The Botany of the Antarctic Voyage of H. M. Discovery Ships Erebus and Terror in the Years 1839–1843* (Hooker, 1844–60). The expedition, captained by Sir James Ross, was launched with the intent of locating the south magnetic pole and exploring the poorly-known Antarctic seas. Joseph Hooker, age 22 at departure, held a berth as Assistant Surgeon and Botanist.

In christening the first volume *Flora Antarctica,* Hooker was apparently unaware that the icebound lands the *Erebus* and *Terror* had visited were the northern extremities of a buried continent. As defined by Hooker, the "Antarctic" flora included the vegetation of Tierra del Fuego and the poorly-known islands scattered across the south Atlantic and south Indian Ocean. Included among these were the Falkland Islands, Palmer's Land, the South Shetlands, South Georgia, Tristan d'Acunha, and Kerguelen's Land (Kerguelen Island).

On the basis of shared and closely related taxa, Hooker considered the plants of these southern islands an extension of the flora of southernmost South America. Thus Tierra del Fuego contained a flora "... characterizing isolated groups of islands extending for 5000 miles to the eastward of its own position." Moreover, these islands were all "... situated in latitudes and under circumstances eminently unfavorable to the migration of species ..." (Hooker, 1844–47, II, p. 211).

This extension of the Fuegian flora covered an astounding range in latitude. Kerguelen Island lay midway between the tip of Africa and Australia, yet sustained a flora which was clearly more closely allied to distant South America. In including Kerguelen Island within the "Antarctic" flora, Hooker was constrained "... to follow the law of botanical affinity in preference to that of geographical position" (Hooker, 1844–47, II, p. 210).

During the preparation of *Flora Novae-Zelandiae* and *Flora Tasmaniae* it became apparent that many "Antarctic" plants also occurred in the mountains of New Zealand, Australia, and Tasmania. Moreover, these lands exhibited strong floristic affinities with southern South America which did not involve the strictly "Antarctic" taxa. Hooker and Darwin were originally attracted to the problem posed by the "Antarctic" flora, but eventually extended their researches to take into account the other southern disjuncts as well.

Motives

What induced Darwin and Hooker to devote so much attention to the subject of geographical distribution? One important motive for both men was simply fascination with the subject. Hooker recalled an incident from his childhood which occurred following a hiking excursion with his father: "I built up by a heap of stones a representation of one of the mountains I had ascended, and stuck upon it specimens of the mosses I had collected on it, at heights relative to those at which I had gathered them. This was the dawn of my love for geographical botany" (Huxley, 1918, v. 1, p. 5).

Darwin made the following comment while preparing the chapter on geographical distribution for his intended magnum opus, *Natural Selection:* "I have lately been especially attending to Geograph. Distrib., & a most splendid sport it is,—a grand game of chess with the world for a Board" (Stauffer, 1975, p. 528).

Geography was not however simply an enjoyable pastime. Hooker's definition of geography encompassed a host of topics. He included within it not only the distribution and migration of species, but problems concerning their origin, variation, and ecological tolerances as well. Hooker considered plant geography a steppingstone, enabling him to confront a variety of problems.

Darwin's interest in biogeography was prompted by a more immediate motive: the preservation of his "species theory" against critical attack. In 1844, the same year that the first numbers of Hooker's *Flora Antarctica* appeared, Darwin completed the manuscript of an expanded version of his 1842 "species sketch." The 1844 sketch (Darwin and Wallace, 1958) outlined most of the important points made public 15 years later with the publication of the *Origin of Species.* It articulated many of the geographical themes presented in the *Origin,* including the importance of barriers, the migration of plants during the glacial epoch, and the significance of long distance dispersal in the origin of plant disjunctions. It also included a reference to the possible origin of Hooker's "Antarctic" flora. From this early date, Darwin realized that anomalous cases of geographical distribution constituted one of the strongest arguments against his theory. If one accepted natural selection, he was forced to reject the notion of polytopic origins of species. If the evidence of plant geography was overwhelmingly in favor of multiple creations, and there were many who felt it was, his theory would be crippled. For this reason, he turned his attention to geographical problems from an early date and devoted two chapters to the subject in the *Origin.*

A working relationship

It is not always easy to separate the personal friendship from the professional relationship in the correspondence between Darwin and Hooker, nor is it realistic. Within a single page, their letters pass from a discussion of variation twenty years ahead of its time, to a request for a recipe for crab soup. Their professional and personal relationships combined to form a working relationship. This relationship is richly documented in three works: *Life and Letters of Charles Darwin* (F. Darwin, 1888), *More Letters of Charles Darwin* (F. Darwin and Seward, 1903), and *Life and Letters of Sir J. D. Hooker* (Huxley, 1918, see especially v. 1, p. 486–503). The ultimate source of reference rests in the Cambridge University Library, where the majority of the original correspondence between Darwin and Hooker is preserved. Taken together, the published and unpublished letters tell a fascinating story. It is no exaggeration to assert that the birth of the modern approach to plant geography is documented in the correspondence between these two men.

Their first letters were exchanged in 1843. Darwin had returned from the *Beagle* voyage seven years earlier. He had already constructed a predictive model of geographic distribution based on his still private evolutionary theories. Now he was in need of facts to test his theory, facts coupled with informed criticism. Joseph Hooker was in a position to provide both.

Hooker on the other hand was dissatisfied with the laws of distribution as then understood and was looking for a more critical approach to the subject based on well-defined assumptions. His interaction with Darwin stimulated his own theoretical speculations and contributed to his emergence as a first-rate geographer in his own right. Darwin was always full of questions, many of them seemingly irrelevant to a non-evolutionist, but they were never boring. In reply to a letter from Darwin which posed questions concerning the ranges of species belonging to widespread genera, Hooker wrote "Your queries & remarks have opened a wide field for research and investigation, for which I am truly obliged. These are all subjects which I ought to have attended to, without requiring to be reminded of them by a more industrious Naturalist" (unpublished letter; April 5, 1844; Darwin Papers, v. 100, folios 12–13; University Library, Cambridge).

Darwin profited no less than Hooker. The latter willingly served as both a sounding board and a botanical encyclopedia over a forty-year period. Reminiscing, Hooker recalled the routine of his visits to Darwin's home at Down: "It was an established rule that he everyday pumped me, as he called it, for half an hour or so after breakfast in his study, when he first brought out a heap of slips with questions botanical, geographical, &c., for me to answer, and concluded by telling me of the progress he had made in his own work, asking my opinion on various points" (F. Darwin, 1888, v. 2, p. 27).

The synergistic nature of the Darwin-Hooker relationship is apparent in their work on the "Antarctic" flora. Darwin had an endless string of questions. Hooker supplied a corresponding stream of facts. Both were intrigued by the inexplicable gaps in the "Antarctic" flora, gaps consisting of thousands of miles of ocean and howling westerly winds. As they continued to study the problem and to consider the flora in the light of their other researches, both began to formulate explanations of how such a distribution could have arisen. The synergism stimulated both men's powers of reasoning, but in this case the paths of reasoning diverged.

Assumptions

In order to understand the Darwin-Hooker conflict concerning the origin of the "Antarctic" flora, it is necessary to examine the theoretical position from which each man approached the problem. Several differences, as well as similarities, can be identified among their initial premises.

They agreed on two important points. First, both rejected polytopic origins of species. Darwin's commitment to this principle has already been mentioned. Hooker accepted single centers of creation even before he embraced the theory of evolution. His reasons are stated in the introductory essay to *Flora Novae-Zelandiae.*

Second, both were opposed to catastrophic explanations of past geological events, such as world-wide deluges. They were however willing to admit gradual changes in the surface of the earth and its climates over geological time. In this they acknowledged their debt to the geologist Charles Lyell.

Because they shared the above beliefs, many of their interpretations of geographic patterns ran parallel. However, they disagreed on three important issues: the mutability of species, the efficacy of long distance dispersal, and the relative weight given to geological vs. botanical evidence in substantiating the existence of former land connections. These points will be examined individually.

Darwin believed that new species evolved from previously existing species. Until 1858, when he read the drafts for the *Origin of Species,* Hooker assumed the opposite stance: species were immutable. He read and criticized Darwin's 1844 species sketch in 1844 or 1846 (conflicting evidence, unpublished research) but this essay failed to alter his opinion. In the introductory essay to *Flora Tasmaniae* (1859) he reversed his position and declared himself an evolutionist, but prior to this time he argued from the premise that species varied but did not give rise to new species.

From the first, Darwin and Hooker disagreed over the ability of plants to migrate by long distance dispersal. Hooker acknowledged its importance in the dispersal of fungi, mosses, and ferns, but he was unwilling to extend this ability to higher plants. An exception is his discussion of the Galapagos flora (Hooker, 1851), whose 120 non-endemic species had arrived, he assumed, via winds, ocean currents, bird and human transport. The Galapagos are located, however, only 500 miles west of the American mainland.

It should be remembered that during Ross's Antarctic expedition, Hooker spent many months traversing the southern seas which separated the scattered outposts of the "Antarctic" flora. As a result he had a great appreciation of the problems and distances involved in oceanic dispersal and his rejection of the likelihood of sea-transport should not be taken lightly.

Darwin was no stranger to the southern seas, but he held an entirely different attitude. He was never able to fully understand Hooker's bias against transoceanic dispersal. "I cannot make out why you would prefer a continental transmission, as I think you do, to carriage by sea. I should have thought you would have been pleased at as many means of transmission as possible" (F. Darwin, 1888, v. 2, p. 59). Darwin felt their inability to agree on the necessity of land connections stemmed from their ignorance concerning the actual dispersal abilities of plants. Consequently, he began compiling as much information on the subject as possible.

Their final point of departure reflected a difference in their scientific backgrounds. Darwin, who had been devoted to geology during the *Beagle* voyage, was generally opposed to the practice of postulating former land connections to explain floristic affinities. He was willing to admit such connections only when plausible geological evidence was available. Hooker on the contrary proposed the existence of connecting land masses when the botanical evidence seemed to require them. He was less discriminating in his evaluation of the geological evidence. This discrepancy, coupled with their opposing views concerning transoceanic dispersal, was at the heart of their disagreement over the origins of the "Antarctic" flora. It was also the one subject in their correspondence where dissension twice spilled over into indignation.

Darwin refers to these incidents in his autobiography. "He [Hooker] once sent me an almost savage letter from a cause which will appear ludicrously small to an outsider, viz. because I maintained for a time the silly notion that our coal plants lived in shallow water in the sea . . . On another occasion he was almost equally indignant because I rejected with scorn the notion that a continent had formerly extended between Australia and S. America" (Barlow, 1958, p. 105–06).

The coal-plant episode is revealing. Darwin believed that the geological difficulties surrounding the origin of coal seams were considerable. However, they could be greatly reduced by assuming that the upright plants of *Sigillaria,* associated with the seams, had grown under water. He became enthusiastic about the aquatic origin of coal after reading an article by Binney (1844 or 1848), which supported the idea.

While Darwin was engaged in this casual speculation, Hooker was working on a systematic treatment of the fossil flora associated with the coal seams (Hooker, 1848). He was familiar with *Sigillaria* and was horrified by Darwin's suggestion that it was aquatic. Replying to an angry letter from Hooker, Darwin clarified his position: "The foundation of my letter, and what is my deliberate opinion, though I dare say you will think it absurd, is that I would rather trust, *caeteris paribus,* pure geological evidence than either zoological or botanical evidence . . . I think the basis of pure geological reasoning is simpler . . . than a basis drawn from the difficult subject of affinities and of structure in relation to habits" (F. Darwin, 1888, v. 1, p. 358).

This attitude was not shared by Hooker. He could not deny the importance of geological evidence, but he could de-emphasize it. He laid greater stress on the botanical facts. This is illustrated in his response to a paper by Edward Forbes (1846) on the origins of the British flora and fauna.

In *Flora Novae-Zelandiae,* Hooker cites Forbes' work as a logical predecessor of his own views on the origins of the New Zealand flora. Forbes recognized five geographical elements in the British fauna and flora and sought to explain their presence by a series of overland migrations from neighboring continents. Among his five groups, the most puzzling consisted of a score of plants in western Ireland. These species were closely allied to the flora of the Iberian peninsula. To explain their presence in Britain, Forbes postulated an Atlantic continent extending past the Azores, connecting western Ireland with northern Spain. As further evidence, he cited a great belt of gulfweed extending between 15° and 45° north latitude, which he believed indicated the former coastline of the sunken continent.

Forbes' continent drew a strong reaction from Darwin. A decade later he referred to Forbes as the "head sinner" among the proponents of land extensions (F. Darwin, 1888, v. 2, p. 73). In a letter to Charles Lyell, explaining his reasons for opposing continental extensions, Darwin again passed judgement: "I cannot avoid thinking that Forbes' 'Atlantis' was an ill-service to science, as checking a close study of the means of dissemination" (F. Darwin, 1888, v. 2, p. 78).

Hooker apparently accepted Forbes' Atlantis at first, but then retreated after conducting his own examination of the botanical evidence. In a letter to Darwin, he wrote "I have been more coolly analysing the bearings of the Forbes botanical question lately, and with the distressing result, that I fear I must haul out of all participation with him. You will think me unstable as water, and I must blame myself for speaking too much without thinking. It is not from a reconsideration of *his* facts and arguments that my faith is weakened, but from an independent examination of the Flora of the N. Atlantic Isles and W. U. Kingdom . . ." (Huxley, 1918, v. 1, p. 444).

Both men rejected Forbes' north Atlantic continent, but their reasons for rejecting it reflected their different biases. Darwin was opposed on geological grounds, Hooker on botanical. However, the specter of a sunken Atlantis was destined to surface once again. This time Hooker would be the architect, shifting the scene of controversy from the northern to the southern seas.

Interpretation of the "Antarctic" flora

Having explained Darwin's and Hooker's stands on the pertinent theoretical issues, one can observe the manifestations of these premises in their individual interpretations of the "Antarctic" flora. Both men based their interpretations on essentially the same material: taxonomic and distributional data compiled by Hooker. These were available to Darwin informally through correspondence and conversation, and formally in the published *Botany of the Antarctic Voyage.*

Hooker's theory is presented briefly in *Flora Antarctica,* then elaborated in *Flora Novae-Zelandiae.* In the earlier work, he made the following observation regarding Fuegia, Kerguelen Island, and the scattered islands in between: "Throughout this position of the world, the land exhibits a manifest tendency eastward, from the extreme south of the American continent; for there are no fewer than 5 detached groups of islands between Fuegia and Kerguelen's Land . . ." (Hooker, 1844–47, II, p. 211). To Hooker, this "manifest tendency" suggested the existence of a former east-west mountain chain, now submerged beneath the sea, ". . . of which Prince Edward Island, Marion, and the Crozets are the exposed peaks" (Hooker, 1844–47, II, p. 220). He acknowledged the legendary force of the westerly winds south of 45°, but did not believe that winds were effective in transporting the seeds of higher plants over such distances. In short, Hooker adopted a connect-the-archipelagos approach to account for the overland exchange of plants between Fuegia, Kerguelen Island, and all points in between.

In *Flora Novae-Zelandiae* Hooker uncovered equally remarkable affinities between New Zealand and South America and reported the presence of many "Antarctic" species in the mountains of New Zealand. He defined elements of the Chilean, Australian, Pacific, and Antarctic floras in New Zealand. To account for their presence, he found it necessary to deal with the problem of former land connections in greater detail. Following Forbes' philosophy, he concluded that land connections must have existed between New Zealand and all of these areas in the past. These connections need not have been simultaneous, nor continuous for that matter: ". . . an intermediate land . . . may have existed between New Zealand and Chile when neither of these countries was as yet above water" (Hooker, 1852–55, I, p. xxiii).

To explain the presence of several "Antarctic" plants in New Zealand, Hooker postulated a former large continent connecting the Antarctic islands. The presence of this continental land mass where ocean now exists would ". . . under certain circumstances render New Zealand as cold as Britain during the glacial epoch" (Hooker, 1852–55, I, p. xxiii). This would have permitted the "Antarctic" plants to migrate to New Zealand, where the cooling of the lowlands should have been sufficient to permit their survival. When this southern continent sank beneath the sea, the climate would have ameliorated. The "Antarctic" species in New Zealand would have been forced to climb the mountainsides to avoid the warming of the lowland. In this fashion the present limitation of the "Antarctic" species to the mountains of New Zealand and their migration across the presently inhospitable lowlands was explained.

In *Flora Novae-Zelandiae* Hooker admitted ". . . there was nothing in the shape of evidence by which my speculation [in *Flora Antarctica*] could be supported." Ironically, he then thanked Lyell and Darwin ". . . for the facts that could alone have given countenance to such a hypothesis, the one [Lyell] showing that the necessary time and elevations and depressions of land need not be denied; and the other [Darwin] that such risings and sinkings are in active progress over large portions of the continents and islands of the southern hemisphere" (Hooker, 1852–55, I, p. xxi-xxii).

Darwin must have winced upon seeing his *Journal of a Naturalist* and his works on coral and volcanic islands used as evidence in favor of Hooker's continent. He must have been equally discomfited by Hooker's broad interpretation of Lyell's *Principles of Geology,* which seemed to give license to unrestrained bridge-building: "It follows from what is there shown, that a change in the relative positions of land and sea has occurred to such an extent since the creation of still existing species, that we have no right to assume that the plants and animals of two given areas, however isolated by ocean, may not have migrated over pre-existing land between them" (Hooker, 1852–55, I, p. xxii).

Darwin praised *Flora Antarctica* and *Flora Novae-Zelandiae,* but he was unable to "gulp down" Hooker's continent. A brief reference to the "Antarctic" flora, included in his 1844 species sketch, is of interest as an indication that he favored long distance dispersal over land connections to explain the "Antarctic" flora from an early date: ". . . the present most singularly close similarity in the vegetation of the lowlands of Kerguelen's Land and of Tierra del Fuego (Hooker), though so far apart, may perhaps be explained by the dissemination of seeds during this same cold period, by means of icebergs . . ." (Darwin and Wallace, 1958, p. 182).

Fifteen years later, in the *Origin of Species,* his opinion was relatively unchanged: ". . . as far as regards the occurrence of identical species at points so enormously remote as Kerguelen Land, New Zealand, and Fuegia, I believe that towards the close of the Glacial period, icebergs, as suggested by Lyell, have been largely concerned in their dispersal" (Darwin, 1859, p. 381). Darwin admitted that vicarious species constituted a problem by his theory, since he did not believe that sufficient time had passed since the Glacial period for them to have undergone sufficient modification. He then proposed a more radical theory, but one still consistent with his assumptions, to explain the vicariads:

> The facts seem to me to indicate that peculiar and very distinct species have migrated in radiating lines from some common centre; and I am inclined to look in the southern, as in the northern hemisphere, to a former and warmer period, when the Antarctic lands, now covered with ice, supported a highly peculiar flora. I suspect that before this flora was exterminated by the glacial epoch, a few forms were widely dispersed to various points . . . (Darwin, 1859, p. 381–82)

Darwin and Hooker each presented explanations, therefore, which were consistent with their assumptions. Hooker postulated a network of land-bridges and a sunken continent to explain the present day affinity among the southern floras. He was convinced that overland communication was necessary to permit the required migrations. Darwin realized the necessity for some "common centre" of dispersal, but minimized the geological difficulties by assuming that extant lands were a suitable base, granted changes in climate and considerable overseas transport.

"Representative" species

Darwin and Hooker were led to different interpretations concerning the migration of the "Antarctic" flora because they adopted different assumptions. These assumptions determined their relative success in dealing with other issues as well. One such issue was the problem of "representative" species. Darwin and Hooker used this term to indicate species, occupying separate regions, which were closely similar but not identical. "Representative" species are currently referred to as vicariads or species pairs. Darwin believed that such closely allied species arose from modification of a single species. "This theory implies a communication of some kind between the areas occupied by the representative species at some former period . . . as distinctly as does the theory of single centres of creation in regard to the same species when found at distant and separated points" (Stauffer, 1975, p. 577).

Prior to his acceptance of the mutability of species, Hooker was on unstable ground when dealing with this subject. He frequently used vicarious species to indicate floristic affinities, but his theoretical justification for doing this was never stated. There is nothing in his assumptions necessitating the inference that vicarious species imply communication. It would have been equally logical to maintain that the members of species pairs were created individually in their respective countries and just happened to show affinities to species in other lands. Their occurrence in anomalous clusters required no explanation.

While this would have been logically consistent, it would have been rather unsatisfying. Hooker intuitively understood that the more than 200 species he listed as "representative" among the floras of South America, Tasmania and Australia, and New Zealand betrayed ". . . a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones . . ." (Hooker, 1852–55, I, p. xxxvi).

Nonetheless, one searches the pages of *Flora Antarctica* and *Flora Novae-Zelandiae* in vain for an explanation of vicarious species corresponding to Darwin's, but based on the assumption of immutable species. One deeply buried passage, however, reveals an attempt by Hooker to support his intuition with concrete evidence. Credit for uncovering the passage goes to Darwin.

Darwin's copy of *Flora Antarctica* presently resides in the Cambridge University Library. Attached to the book is a sheet of paper bearing the watermark "E. Towgood, 1856." The paper bears an index, written in Darwin's script, identifying the pages he wished to refer back to. The 1856 watermark suggests that the index was compiled while Darwin was collecting materials for the chapter on geographical distribution for his "big species book," *Natural Selection,* written during that year. Next to the number '276' is the following notation: "on representative & identical species going together." Page 276 of the text is well into the taxonomic treatment, but it includes several paragraphs of discussion sandwiched among the Myrtaceae.

Hooker was comparing the manner in which the similarity between the South American and Australasian floras increases with increasing latitude:

> I would cite the Floras of Chile, between 40° and 45°, containing many of the features of New Zealand and Australian Botany, though few or no [identical] species are common to both; whilst Fuegia and the countries between 50° and 56°, contain far more representatives of south New Zealand and Tasmanian plants, and a very considerable proportion of [identical] species found in those countries. (Hooker, 1844–47, II, p. 276)

In other words, Hooker observed that an increase in the number of identical species, which he considered as indisputable evidence of communication, was accompanied by an increase in the number of vicarious species. This correlation is as close as Hooker comes to proving that vicariads signify former communication.

A somewhat more candid confession of Hooker's inability to explain the presence of species pairs is found in his essay on the Galapagos, read in 1846. He declares that the occurrence of so many species clearly allied to South American forms and the presence of allied species on the different islands is ". . . a mystery which it is my object to portray, but not to explain" (Hooker, 1851, p. 259).

Darwin and Hooker were the first, but not the last, to debate the importance of land connections in the origin of southern hemisphere disjunctions. As with many later investigators, their ignorance of continental drift was a handicap. They were unaware that the board upon which they played their "grand game of chess" bore a pattern of constantly shifting squares. Nonetheless, their early researches concerning the origins of the "Antarctic" flora should not be forgotten. They illustrate the birth of a classic problem in phytogeography and the origin of a controversy which persisted well into the twentieth century. In 1858, Darwin wrote to Hooker: "When we are dead and gone, what a noble subject will be Geographical Distribution" (F. Darwin and Seward, 1903, v. 1, p. 117). More than a century later, we can still appreciate their efforts to hasten the progress of that complex subject.

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ECTOPOPTERYS, A NEW GENUS OF MALPIGHIACEAE FROM COLOMBIA AND PERU

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In the course of a study of the tropical rain forest in the valley of the Río Anorí in northern Colombia, Dr. Djaja D. Soejarto has found a fascinating plant that is not assignable to any described genus of Malpighiaceae. Search of major herbaria has turned up two additional collections from Peru. This plant is described here as a new genus and species, and its possible affinities are discussed.

Ectopopterys soejartoi W. R. Anderson, gen. et sp. nov. Figurae 1 et 2.

Liana lignosa, usque 25 m scandens, ramis sericeis mox glabratis. Folia decussata; lamina foliorum majorum 7–12 cm longa, 3.0–5.3 cm lata, elliptica, basi cuneata, margine plana vel paulo revoluta, apice acuminata vel cuspidata, primum sericea permox glabrata vel subtus sparsissime sericea, subtus plerumque serie aliquot (usque 10) glandularum parvarum prope marginem vel usque 5 mm infra marginem instructa, nervis lateralibus utrinque 5–7 et reticulo utrinque in sicco prominulis; petiolus 6–9 mm longus, sparsim sericeus vel glabratus, eglandulosus vel prope apicem 2 glandulis parvis instructus; stipulae 0.5–1.0 mm longae, triangulares, interpetiolares ramulo portatae, liberae vel connatae, demum deciduae. Inflorescentia sericea demum glabrescens, axillaris et terminalis, paniculata, ramulis ultimis 4–12-floris, floribus decussatis in pseudoracemo vel corymbo 6-floro vel umbella 4-flora, bracteis 2.0–2.5 mm longis, 0.6–1.2 mm latis, linguiformibus, patentibus vel ± revolutis, plerumque eglandulosis, persistentibus vel demum deciduis, pedunculo 4–8 mm longo, apice bibracteolato, in fructu incrassato, bracteolis bracteis similibus plerumque brevioribus. Pedicellus 8–12 mm longus, sericeus demum glabratus, in fructu incrassatus. Alabastrum sphaeroideum, petalo extimo exposito (i.e. sepalis non tecto) in alabastro accrescenti. Sepala 5, omnia eglandulosa, 3 mm longa lataque, rotundata, abaxialiter sparsim sericea praecipue in centro, margine ciliolata, adaxialiter glabra, imbricata, sub anthesi valde reflexa. Petala 5, lutea, glabra, 4 lateralia patentia vel reflexa, limbo 8.0–9.5 mm longo latoque, circulari, margine eroso-dentato, 2 antero-lateralibus profunde concavis, 2 postero-lateralibus planis vel parum concavis, ungue 2.0–3.0 mm longo, apice non constricto; petalum posticum erectum vel limbo reflexo, limbo 8.0–9.0 mm longo, 7.0–8.5 mm lato, obovato, distaliter paulo trilobato, margine basi integro incrassatoque aliter eroso-dentato, corrugato, ungue 2.5–3.5 mm longo, apice valde constricto. Stamina 10, valde inaequalia sed omnia fertilia; filamenta glabra, basi 0.5–1.0 mm connata, recta distaliter parum reflexa, 5 sepalis opposita 1.5–2.0 mm longa, 5 petalis opposita 1.0–1.5 mm longa; antherae loculis apice basique fasciculis pilorum instructis, 5 sepalis oppositae introrsae, loculis 1.4–1.8 mm longis, connectivis pyriformibus glandulosis loculos 0.8–1.1 mm superantibus, 3 petalo postico et petalis antero-lateralibus oppositae introrsae, loculis 1.5–1.8 mm longis, connectivis globosis glandulosis loculos non superantibus, 2 petalis postero-lateralibus oppositae latrorsae, loculis 0.8 mm longis, connectivis exiguis non glandulosis, subnullis; pollen 33–42 μm diametro, colporatum, colpis non omnibus parallelis, oribus non omnibus aequatoriis. Ovarium ex 3 carpellis uniovulatis connatis constans, 1 carpello antico,

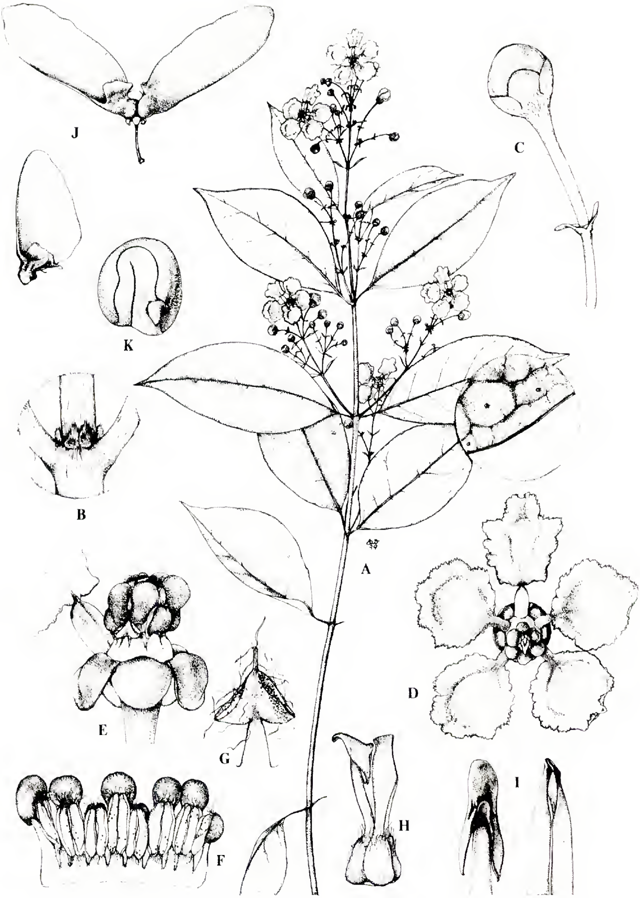

FIG. 1. *Ectopopterys soejartoi,* drawn from the type by Karin Douthit. A, flowering branch × 0.5, the circle × 5; B, stipules × 5; C, flower bud × 2.5; D, flower × 2; E, androecium *in situ,* lateral petals removed, base of flag petal left for orientation, × 5; F, androecium opened out, adaxial view, with stamen opposite flag petal at far right, the 2 reduced anthers hidden by larger neighbors, × 6; G, reduced stamen opposite postero-lateral petal × 15; H, gynoecium, side view, anterior style to left, × 7.5; I, styles, adaxial views, anterior on left, posterior 2 on right, × 15; J, samaras, the lower one with a third small wing, × 0.5; K, embryo × 2.5.

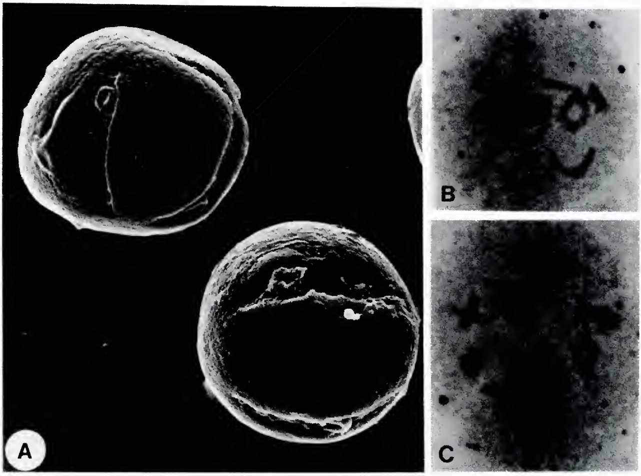

FIG. 2. *Ectopopterys soejartoi.* A, SEM of unacetolyzed pollen, *Soejarto 4488,* X 1285; B and C, meiosis I in pollen mother cells, n = 8, *Soejarto 4416,* X 1500.

2 posticis, ca. 1.3 mm altum, sericeum; styli 3, basi sericei distaliter glabri; stylus anticus ca. 2.9 mm longus, stigmate interno, dorsaliter apice unco 0.8 mm longo et utrinque foliolis triangularibus pendentibus 0.9 mm longis instructus; 2 styli postici 2.5 mm longi, a lateribus complanati, apice truncati et connati vel cohaerentes, stigmatibus internis. Fructus ex 3 samaris (vel saepius abortu 2–1) in toro trigono portatis constans; samara matura glabrata vel sparsim sericea, 45–65 mm longa, pleurumque 2 alis valde inaequalibus instructa; ala principalis 36–55 mm longa, 17–25 mm lata, alam dorsalem in *Heteropteryge* simulans, i.e. ut videtur dorsalis, margine abaxiali ("inferiore") incrassata et adaxiali tenui, ± falcata, re vero probabiliter lateralis, versus dorsum luxata; ala minor triangularis vel trapezoidea vel cristiformis, 3–14 mm alta (i.e. e nuce projecta), 9–18 mm lata, re vero probabiliter dorsalis sed versus laterem luxata; ala tertia raro evoluta, triangularis, usque 6 mm alta et 5 mm lata, in latere nucis ala principali remoto portata; nux 7–12 mm longa (e toro ad alam), apice 8–12 mm diametro, cylindrica vel truncato-turbinata, in sicco nervis longitudinalis prominentibus striata. Embryo sphaeroideus, cotyledonibus crassis, laevibus, replicatis, subaequalibus vel exteriore parum majore. Chromosomatum numerus (in typo numeratus): n=8.

Type. Anorí river bank, tropical rain forest, between Providencia and Alhibe, Antioquia, Colombia, elev. 400–800 m, 20–25 February 1976 flr/frt, *Djaja D. Soejarto et al. 4416* (holotype MICH, isotype HUA).

Paratypes. COLOMBIA. Antioquia, Municipio de Anorí, Corregimiento de Providencia, Valle del Río Anorí, elev. 400–900 m: Buenos Aires, advanced secondary forest, 20 Oct 1972 flr, *Soejarto 3399* (MICH); entre Dos Bocas y Anorí, advanced secondary forest, 12 Dec 1972 frt, *Soejarto 3617* (MICH, MO); Buenos Aires, forest above the road to Anorí, about 4 km from Providencia, 26 Apr–3 May 1973 flr/frt, *Soejarto et al. 4011* (COL, HUA); remnants of forest, Quebrada La Tirana, just above its confluence with Anorí river, 20–25 Feb 1976 flr, *Soejarto et al. 4488* (HUA, MICH); forest of Buenos Aires, trail side, 20–25 Feb 1976 flr, *Soejarto et al. 4512* (HUA, MICH). PERU. Loreto: edge of forest, Yurimaguas, lower Río Huallaga, elev. 155–210 m, 22 Oct 1929 flr/frt, *Ll. Williams 3872* (F); rainforest on lower north slopes of Cerros Campanquiz at Pongo de Manseriche, right bank of Río Marañón, elev. 300–550 m, 12–21 Oct 1962 flr, *Wurdack 2356* (US).

This plant is notable for its eglandular, strongly reflexed sepals, its androecium with two anthers greatly reduced and the others bearing large glandular connectives, and its strongly heteromorphic styles, with the anterior stigmaphylloid and the posterior two truncate and coherent at the apex. The chromosome number (n=8) is also interesting, being new for the family. It is probably reduced from n=10, the common and apparently basic number for most samaroid genera for which counts have been made. Most peculiar of all is the samara, which superficially resembles that of *Heteropterys.* It usually bears two wings, one short, the other long and thickened on the abaxial edge as in *Heteropterys.* Rarely, a small third wing is present on the side of the nut. The form and disposition of these wings strongly suggest to me that the principal wing is actually one of the lateral wings that has become enlarged and shifted into a functionally dorsal position, while the other lateral wing has been suppressed. This interpretation is strengthened by the fact that in the very rare cases of development of a third wing, it develops on the side of the nut away from the large wing, not beside it. A third possibility is that the two wings usually developed represent two lateral wings unequally developed. The position of the third wing when it develops, and the absence of any sort of crest or midvein between the two usual wings, argue against this interpretation.

I really do not know where this plant's affinities lie. If my interpretation of the samara is correct, it is not close to *Heteropterys.* Even if I am wrong and the principal wing is truly dorsal, this species still does not belong in *Heteropterys,* since its sepals, anthers, and styles are quite unlike anything found in that genus. If the principal wing is actually lateral in origin, the obvious place to seek relatives is among the mascagnioid genera, such as *Mascagnia* and *Tetrapterys.* No species of either has an androecium or gynoecium like those of *Ectopopterys,* nor of course such a fruit. However, it is not very difficult to imagine a samara like that of *Mascagnia psilophylla* giving rise to that of *Ectopopterys.* A third possible relative is *Stigmaphyllon.* This suggestion is not based on the samara, because even if the principal wing is truly dorsal it is thickened on the wrong edge and bent the wrong way for *Stigmaphyllon.* The inflorescences of the two genera are also quite different, although it is possible that the dichasium of congested racemes found in *Stigmaphyllon* was ultimately derived from an ancestor with terminal panicles. However, the anterior style of *Ectopopterys* is identical to that of some species of *Stigmaphyllon,* and such a style is found in no other genus. The tufts of hairs on the anthers are also similar in species of both groups, and the strongly heteromorphic anthers with some of the connectives enlarged suggest a common ancestry, although the specific anthers reduced were ultimately different in the two lines. These characters suggest that generic relationships in the samara-bearing Malpighiaceae are more complex than the traditional "dorsal vs. lateral" taxonomy allows. In fact, too great reliance on characters of the fruit has probably obscured relationships in some cases, and in the future we must consider other aspects of the plants and be alert for parallel and, as in *Ectopopterys,* convergent origin of similar structures in lines that are not very closely related.

The disjunct distribution of this species is further support for the Nechí refuge, which is discussed in my paper on *Dicella* in Colombia (Acta Amazônica 5(3): 279–283. 1975). *Ectopopterys soejartoi* should eventually be found in Amazonian Colombia and westernmost Brazil.

The name *Ectopopterys* comes from the Greek words *ektopos* (displaced) and *pterys* (wing). It reflects my belief that the apparently dorsal wing of the samara is a displaced lateral wing. The epithet *soejartoi* honors Dr. Djaja D. Soejarto, collector of the type. I am most grateful to Dr. Soejarto for returning to the type locality and collecting preserved buds, flowers, and fruits for me, which made the description and illustration much easier to prepare.

ACKNOWLEDGMENTS

Field work to collect material of *Ectopopterys soejartoi* in Antioquia was funded, in part, by a grant from the Colombian COLCIENCIAS No. Co. 002-1-14-74 to D. D. Soejarto.

Contr. Univ. Mich. Herb. 14:17–23. 1980.

NOTES ON *MASCAGNIA* IN SOUTH AMERICA

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The genus *Mascagnia* is one of the most diverse in the Malpighiaceae. One repeated trend in this group is the reduction or loss of the lateral wings of the samara. Two South American species in which this has occurred are described here as new; in both cases, the closest relative is an undoubted *Mascagnia* with large lateral wings on the samara. The third species treated here is one of the many rare plants endemic to the area of Rio de Janeiro. Study of specimens from Leningrad reveals that the plant originally described in flower as *Banisteria riedeliana* Regel is conspecific with *Mascagnia metallicolor* Niedenzu, which was based on fruiting material.

Mascagnia aptera Anderson, sp. nov. Fig. 1.

Suffrutex scandens, ramis gracilibus (usque 4 mm diametro) sero glabratis, ramulis velutinis, pilis sessilibus vel subsessilibus, bifurcatis brachiis ± rectis, erectis, saepe inaequalibus. Foliorum lamina 2.8–5.8 cm longa, 1.8–5.0 cm lata, late elliptica vel suborbicularis, basi cordata, margine revoluta, apice rotundata apiculataque, coriacea, supra rugosa et velutina pilis sessilibus, bifurcatis, brachiis rectis erectisque, subtus dense albo-lanata pilis sessilibus, brachiis longis, mollibus, subrectis vel tortis, appressis vel parum patentibus, subtus utrinque 3–4 glandulas planas immersas in serie 0.5–3.5 mm ab margine distanti gerens, costa, utrinque 5–6 nervis lateralibus, et venis tertiariis parallelis supra impressis, subtus prominentibus; petiolus 2–5 mm longus, velutinus, basi vel supra basim biglandulifer; stipulae 0.4 mm longae, anguste triangulares, rubrae, abaxialiter velutinae, adaxialiter glabrae, ramulo inter petiolos portatae. Folia sub racemis distalibus minoria. Racemi axillares, 2.0–3.5 cm longi, velutini, pedunculo inflorescentiae 6–15 mm longo, floribus 6–14 confertis, bracteis 1–2 (–3) mm longis, anguste triangularibus vel linearibus, velutinis, eglandulosis vel duabus proximalibus basaliter biglanduliferis, pedunculo florifero 4.0–5.5 mm longo, velutino, parum sub apice 2 bracteolas suboppositas gerenti, bracteolis velutinis, inaequalibus, minore 1.0–1.5 mm longa, recta, angustissime lineari vel subulata, eglandulosa, majore 1.5–2.0 mm longa, falcata, uno latere laminari et glandulam magnam gerenti, altero lineari eglanduloso. Pedicellus 2.5–4.5 mm longus (fructu usque 5.5 mm), piloso-sericeus, apice parum tumidus. Sepala libera, late ovata vel triangularia, apice obtusa vel rotundata, glandulas 0.5–1.0 mm superantia, appressa, abaxialiter laxe piloso-sericea, adaxialiter glabra, anticum eglandulosum, 4 lateralia biglandulifera, glandulis ca 2 mm longis, obovatis. Petala rubo-rosea, glabra, dorsaliter alulata alula 0.4 mm lata (alula petali postici minus prominenti); petala 4 lateralia patentia vel reflexa, ungue 1.0–1.2 mm longo, limbo 4.8–5.0 mm longo, 3.0–3.5 mm lato, late elliptico vel orbiculari, margine eroso vel denticulato, concavo vel convexo; petalum posticum erectum, ungue 1.5 mm longo, limbo 5.5 mm longo, 3.0 mm lato, oblongo, margine proximaliter denticulato, distaliter fimbriato, plano vel corrugato. Staminum 10 filamenta glabra, fere libera (basi brevissime connata), 5 interiora (sepalis opposita) 2.5 mm longa, 5 exteriora (petalis opposita) 2.1 mm longa, recta vel distaliter parum reflexa; antherae glabrae, subaequales, 1.3–1.5 mm longae, loculis 4 linearibus aequalibus pendulis, 5 petalis oppositae apice

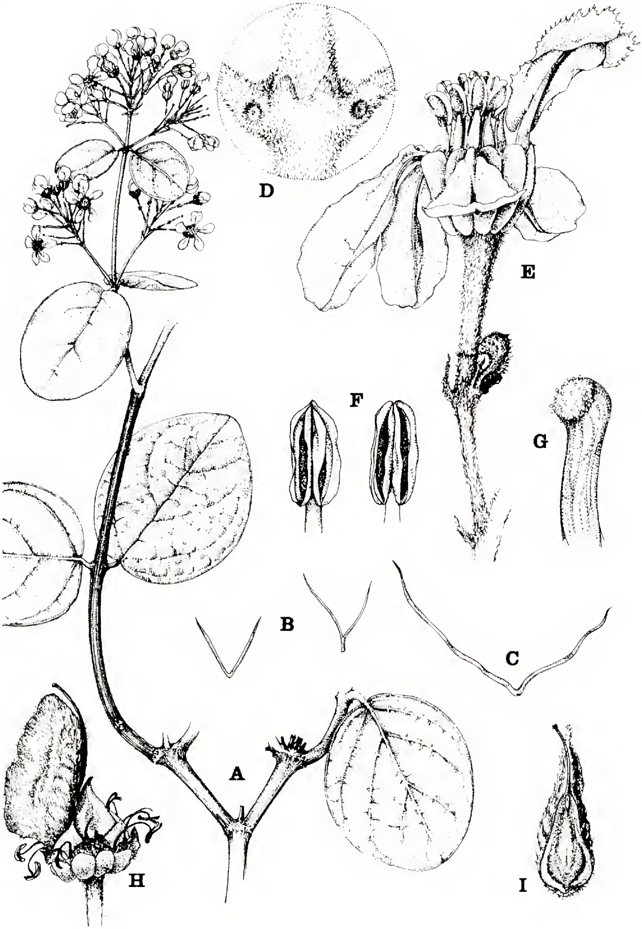

FIG. 1. *Mascagnia aptera,* drawn from the type by Karin Douthit. A, flowering branch X 0.7; B, hairs from adaxial surface of leaf X 50; C, hair from abaxial surface of leaf X 50; D, node with stipules and petiolar glands X 7; E, flower X 7; F, anthers, left opposite petal, right opposite sepal, X 17.5; G, stigma X 42; H, fruit with 2 samaras removed to show pyramidal torus X 5.6; I, samara, ventral view, X 5.6.

brevi-apiculatae. Ovarium sphaeroideum, 1.2 mm altum, 1.3 mm diametro, laxe piloso-sericeum; styli 3, ± aequales, 2.5 mm longi, graciles, glabri, parum patulo-arcuati, antheras superantes, apice interne stigmatiferi et dorsaliter rotundati. Fructus albo-tomentosus vel pilosus, ex 3 (vel abortu 2–1) "samaris" alulatis in toro pyramidali 1.2–1.7 mm alto portatis constans. Samarae nux 3.5–4.0 mm longa, 2 mm diametro, obpyriformis, lateribus nervosis, areola ventrali ovata ca 3.5 mm alta; alae laterales nullae, utrinque in nervo crasso longitudinali reductae; ala dorsalis 0.5–1.5 mm lata, ex basi nucis super apicem ad basim styli persistentis extensa, membranacea, integra vel repanda.

BRAZIL. Mato Grosso: Road Buriti to Cuiabá, rocky escarpment of Chapada dos Guimarães, amongst sandstone rocks, elev. 720 m, 22 Oct 1973 flr/imm frt, *G. T. Prance, E. Lleras, & D. F. Coelho 19274* (INPA, holotype; MICH, isotype).

The fruits of *Mascagnia aptera* have completely lost the lateral wings that are the most important diagnostic character of the genus *Mascagnia.* Nevertheless, in all other respects this species is typical of the genus; in fact, it is very similar to *Mascagnia cordifolia* (Adr. Jussieu) Grisebach. They are easily distinguished in fruit, because each samara of *M. cordifolia* is 2–3 cm in diameter with well-developed lateral wings. Flowering specimens of the two species can be distinguished on the following bases: *M. cordifolia* is a vigorous twining vine, often climbing to 2 m or more; *M. aptera* was described by the collectors as a "scandent subshrub," and the specimens give the impression of a twiggy plant that may have largely abandoned the climbing habit, as is not uncommon in open rocky places like the Chapada dos Guimarães. The largest leaves of *M. cordifolia* are usually larger (7–10 cm long, 6–10 cm wide) and less coriaceous than in *M. aptera.* The leaves are velutinous on both sides in *M. cordifolia,* whereas in *M. aptera* they are velutinous on the adaxial side and woolly on the abaxial side. The stipules are larger and more prominent in *M. cordifolia* than in *M. aptera. Mascagnia aptera* is probably a local endemic derived from *M. cordifolia* with one major adaptive change and accumulated minor vegetative differences.

Mascagnia mirabilis Anderson, sp. nov. Fig. 2.

Liana lignosa, ramis glabris fistulosis 8 mm diametro. Foliorum lamina 21.0–22.5 cm longa, 11.5–13.5 cm lata, late ovata, basi obtusa, apice abrupte breviacuminata, utrinque glabra, eglandulosa, nervis lateralibus utrinque 8–9 subtus supraque prominentibus, venis tertiariis ± scalariformibus prominulis; petiolus 32–36 mm longus, glaber, 6 mm sub apice biglandulosus, glandulis 3 mm longis; stipulae non visae. Inflorescentia axillaris, panicula decomposita 28 cm longa et 26 cm diametro, tomentosa vel subvelutina, floribus in verticillis 4-floris portatis, bracteis 0.7–1.5 mm longis latisque, triangularibus, eglandulosis, abaxialiter tomentosis, adaxialiter glabris, persistentibus, pedunculo 3–8 mm longo, subvelutino, bracteolis ca 0.8 mm longis latisque, ovatis, abaxialiter tomentosis, adaxialiter glabris, 1 bracteola 1 glandulam magnam excentricam gerenti, apice pedunculi portatis, persistentibus. Pedicellus 3–6 mm longus (–8 mm in fructu), apice tumidus ca 3.5 mm diametro, subsericeus. Sepala omnia 2 glandulis circularibus 1.5–2.0 mm diametro munita (minoribus in sepalo antico), 1.5–2.0 mm longa ultra glandulas, 2.0–2.6 mm lata, late rotundata, abaxialiter sericea, adaxialiter glabra, per anthesin appressa. Petala lutea, glabra, exposita in alabastro accrescenti, 4 lateralia patentia vel reflexa, limbo 4.5 mm longo, 5.0–6.0 mm lato, transverse late elliptico, subintegro vel denticulato et eglanduloso vel in 2 posterioribus basi aliquot glandulis parvis et sessilibus munito, ungue 1.8–2.3 mm longo; petalum posticum erectum, limbo 5.5–6.5 mm longo, 6.0–7.0 mm lato, glanduloso-fimbriato toto circuitu vel apice eglanduloso-fimbriato, ungue 3.0–3.5 mm longo. Filamenta glabra, libera vel basi brevissime connata, 5 petalis opposita 2.0–2.4 mm longa, recta et ± erecta, 5 sepalis

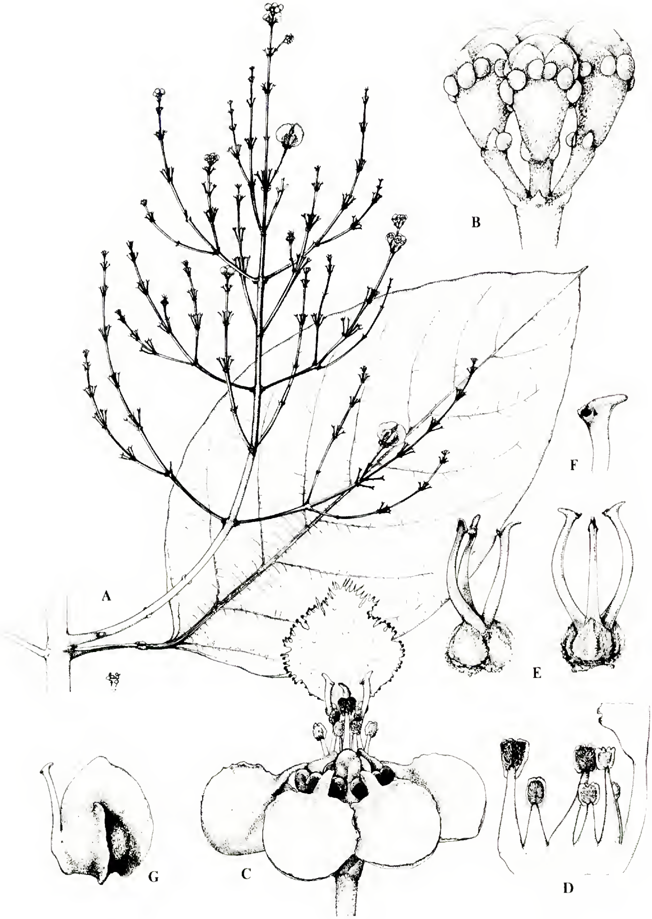

FIG. 2. *Mascagnia mirabilis,* drawn from the type by Karin Douthit. A, inflorescence and leaf X 0.5; B, umbel of 4 flower buds X 3.5; C, flower X 3.5; D, portion of androecium, opened out, with base of posterior petal for orientation, the stamen to left opposite anterior sepal, X 5; E, gynoecia, left a side view with anterior style to right, right an anterior view with anterior style in center, X 5; F, apex of style X 10; G, samara X 2.5.

opposita 3.3–3.5 mm longa, 2 sepalis antico-lateralibus opposita versus petalum posticum inclinata, 3 cetera recta et erecta; antherae glabrae, 0.9–1.6 mm longae, ea petalo postico opposita minima, ea sepalo antico opposita maxima. Ovarium 1.5 mm altum, sericeum; styli glabri, apice dorsaliter longe uncinati unco 0.3–0.5 mm longo, anticus 3.7–4.3 mm longus, rectus et erectus, 2 postici 4.5–5.0 mm longi, sigmoidei et versus petalum posticum inclinati. Samara paulo immatura sericea, nuce 4–6 mm diametro, alis lateralibus reductis 1–2 mm latis, distinctis apice basique, integris, ala dorsali 3–4 mm lata, 8–10 mm alta, apice producta et nucem amplectenti.

PERU. San Martín: liana in open thickets, road from Puente Colombia to Shapaja, along Río Mayo, elev. 280 m, 30 Apr 1976 flr/imm frt, *T. Plowman 6019* (MICH, holotype).

This species is most closely related to *Mascagnia macrophylla* Rusby, which is known only from two Bolivian collections. Both species belong in a group including *M. hippocrateoides* (Tr. & Pl.) Nied. and *M. platyrachis* (Tr. & Pl.) Cuatr., of Colombia and Ecuador, and *M. hiraea* (Gaertn.) F. & R. of Jamaica. Like *M. macrophylla, M. mirabilis* has very large, glabrous leaves with long glabrous petioles. They are both notable for their whorls of four flowers along the ultimate axes of the inflorescence. However, the samara of *M. macrophylla* has large, membranous lateral wings, ca 3 cm wide and 5 cm high, whereas in *M. mirabilis* the lateral wings are reduced to rudimentary winglets 1–2 mm wide and the dorsal wing has become dominant. This situation is analogous to that in *M. aptera* and *M. cordifolia,* except that *M. mirabilis* and *M. macrophylla* are otherwise almost identical, while *M. aptera* differs from *M. cordifolia* in vegetative characters as well as characters of the fruit. Note that Cuatrecasas (Webbia 13(2): 374. 1958) justified recognizing *M. platyrachis* on the basis of a similar but less extreme reduction of the wings of the samara.

Mascagnia macrophylla Rusby (Mem. New York Bot. Gard. 7: 272. 1927) was typified by two collections, *Cárdenas 1943* (flr, NY!) and *Cárdenas 2044* (frt, NY! MICH!). The NY sheet of *Cárdenas 2044* is here designated lectotype.

Mascagnia mirabilis is known only from the type. It is named for its extraordinary fruit and inflorescence.

Mascagnia riedeliana (Regel) Anderson, comb. nov. Fig. 3.
Banisteria riedeliana Regel, Ind. Sem. Hort. Bot. Petropol. 17. 1855.
Mascagnia metallicolor Niedenzu, Arb. Bot. Inst. Lyc. 3: 20. 1908.

Woody vine; youngest stems sericeous, without lenticels; older stems glabrate, fissured and punctate, with both elongated and punctiform lenticels. Lamina of the larger leaves 9.5–18.5 cm long, 4.5–8.0 cm wide, elliptical or somewhat ovate, cuneate to rounded at the base, flat at the margin, acute or more commonly gradually to abruptly acuminate at the apex, sericeous to soon or eventually glabrate above, densely and persistently metallo-sericeous below, eglandular or, frequently on the same branch, bearing several small marginal glands on the proximal half, the reticulum prominent on both sides; petiole 8–14 mm long, sericeous to glabrate, eglandular or occasionally bearing 1–2 small glands near the apex; stipules 0.4–1.0 mm long, triangular, borne on stem near base of petiole. Inflorescence a sericeous, usually compound, axillary or terminal panicle containing deciduous bracts, the flowers ultimately borne decussate in pseudoracemes 1–4 cm long of 6–20 flowers; floriferous bracts 1.5–2.5 mm long, narrowly triangular, eglandular, persistent in fruit; peduncle 1.7–3.5 mm long; bracteoles 0.5–1.0 mm long, triangular, eglandular, borne at the apex of the peduncle, persistent. Pedicel 3–6 mm long (–8 mm in fruit), sericeous. Sepals leaving the outer petal exposed during enlargement of the bud, 2.0–2.5 mm long, 1.6–2.0 mm wide, appressed in

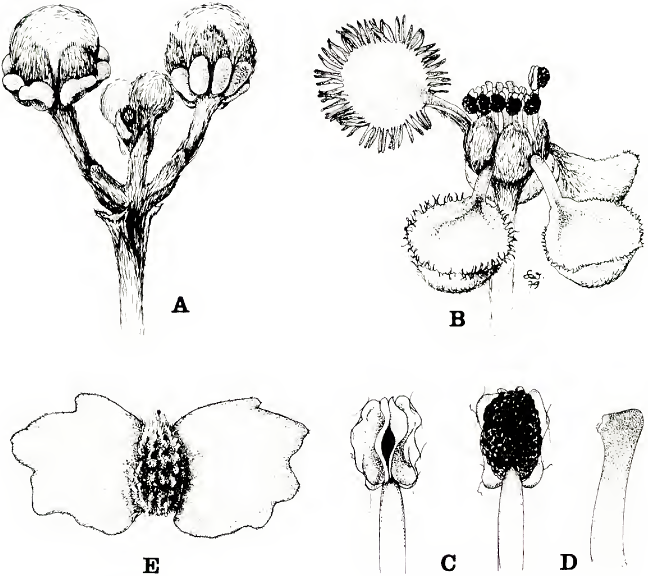

FIG. 3. *Mascagnia riedeliana.* A, ultimate branch of inflorescence × 5.6; B, flower × 5.6; C, anthers × 16; D, stigma × 16; E, samara, dorsal view, × 1.6. Drawn by Karin Douthit, A from the holotype, B-D from another cultivated collection from LE, E from *Angeli 263.*

anthesis, broadly rounded at the apex, abaxially densely sericeous except the membranous margin, adaxially glabrous, all eglandular or the lateral 4 biglandular with the glands 1.5–2.3 mm long and free and revolute at the apex or all around the margin. Petals very densely golden- or silvery-sericeous abaxially on claw and limb except toward margin, the lateral 4 reflexed, with the claw 2.0 mm long and the limb 3.5–5.0 mm long, 4.0–5.0 mm wide, ± deeply concave (especially the anterior 2), dentate (the anterior 2) to fimbriate (the posterior 2); posterior petal ± erect, with the claw 2.0–2.5 mm long and the limb 4.5–5.5 mm long, 4.5–5.0 mm wide, flat or slightly concave, glandular-fimbriate all around the margin, the fimbriae ca 1 mm long. Filaments 2.0–3.5 mm long, longest opposite the anterior sepal, shortest opposite the posterior petal, abaxially sericeous on the proximal 1/2, adaxially glabrous, straight, connate up to 1 mm; anthers 1.0–1.3 mm long, bearing a few spreading hairs on the locules, the connective black, glandular, swollen but not exceeding the locules. Ovary 1.3 mm high, sericeous; styles 2.0–2.4 mm long, subequal, glabrous, diverging at the base, laterally flattened, dorsally rounded or truncate or slightly apiculate at the apex, with internal stigmas. Samara with the nut 5–7 mm wide and 9 mm high, tomentose, bearing between the 2 lateral wings ca. 5 parallel ± dissected winglets 1.0–2.5 mm wide; lateral wings discrete, 11–15 mm wide, ca. 15 mm high, erose and often with irregular shallow lobing, loosely sericeous; ventral areole linear, 7–8 mm long, 1.5 mm wide.

Type. Cultivated in Hort. Petropol. from seeds sent by Riedel from Rio de Janeiro, Brazil (holotype LE!).

BRAZIL. Rio de Janeiro: Estr. da Vista Chinesa, próximo à Est. Biol., May frt, *Angeli 263* (MICH); Jard. Bot. cult., Feb flr, *J. Kuhlmann* [RB 47963] (RB); Copacabana, *Riedel 80* in 1832 (GH, LE, W).

Leningrad has an extensive series of specimens of this species, several apparently collected by Riedel in Rio de Janeiro, the rest cultivated in the Petersburg Botanical Garden. All are sterile or in flower, which is peculiar since Riedel sent seeds, according to Regel's protologue. Identifying one of the Leningrad sheets as Regel's holotype turns out to be surprisingly easy, because Regel described the sepals as bearing glands and only one sheet at LE has glanduliferous sepals. It is also the only sheet labeled "Banisteria Riedeliana H. Petrop.," which matches the protologue, and the only sheet annotated "v. v. Rgl." [vidi vivam Regel]. I do not know whether or not the label was written by Regel.

Regel described the petals as four and the stamens as eight. They are actually five and ten, respectively, in all specimens seen, including the type.

Mascagnia riedeliana belongs in the group of species that includes *M. chlorocarpa* (Adr. Jussieu) Grisebach, *M. polycarpa* Brandegee, and the plant described as *Diplopterys microcarpa* Sandwith, which will be transferred to *Mascagnia* in my paper on the Malpighiaceae of the Guayana Highland (Memoirs N. Y. B. G., in press).

Niedenzu based his description of this species in Das Pflanzenreich, under *Banisteria riedeliana,* on *Peckolt 266* from Cantagalo. That plant is not referable to this species. It seems to be an undescribed species, for which the proper genus is not obvious. It will be treated in a future paper.

Contr. Univ. Mich. Herb. 14:25–52. 1980.

A GUIDE TO THE IDENTIFICATION OF MEXICAN SPHAGNA

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Sphagnum is a minor element in the Mexican moss flora. Only ten species have been found in the country, only one of them endemic. Phytogeographic probabilities are that at least half a dozen others of broad distribution and nearby occurrence can be expected to occur there. It is reasonable to expect some additional species to show up as disjuncts from the Coastal Plain of southeastern United States, possibly from the Southern Appalachian Mountains, and a few others from Antillean and Andean floras. The moss flora of Mexico is incompletely known, and the *Sphagnum* flora especially needs careful attention. Few bryologists have collected intensively in Mexico, and still fewer have known *Sphagnum* well enough to collect with discrimination.

The genus is taxonomically difficult, yet with basic understanding and some experience one can recognize most species with ease, owing to fairly obvious differences in size, color, and form, as well as habitat preference. A readable explanation of the characters useful in taxonomy is to be found in Blomquist's illustrated account of the peatmosses of the southeastern United States (Jour. Elisha Mitchell Sci. Soc. 54: 1–21. 1938). The microscopic characters basic to critical determination are best observed on staining. Any water-soluble stain can be used. A saturated solution of Gentian (or Crystal) Violet gives especially good contrast.

Andrews' revision of the North American *Sphagna*, published in the *North American Flora* in 1913, includes most of the species known from Mexico. His keys and descriptions are excellent, but his concept of species is cautious and conservative to a fault. Warnstorf's *Sphagnologia Universalis*, published in *Das Pflanzenreich* in 1911, is also useful, even though species are narrowly defined. Rigid definitions of species are scarcely possible, or desirable, but further study of the tropical *Sphagna* should result in a more meaningful taxonomy than Andrews' lumping and Warnstorf's splitting have offered.

The unique features of the peatmosses justify treatment at the level of class, as the Sphagnopsida. The class consists of a single genus, *Sphagnum* L., and something less than 200 species. The genus is especially well represented in the North, in glaciated areas of impeded drainage. Many of the species of broad northern distribution range disjunctively southward into the tropical highlands, but a good many species are completely tropical in range. It is curious that the majority of the *Sphagna* of Mexico, tropical in position, are disjuncts from the North.

The following treatment is based on an accumulation of Mexican records in various North American herbaria noted over a period of 30 years and more, especially in the herbaria of the University of Michigan, University of Tennessee, New York Botanical Garden, U. S. National Museum, and Field Museum. Because this is intended as an aid in identification rather than a scholarly monograph, little attempt is made to cite specimens and precise localities. Collections have been too spotty and too incomplete to make such citations meaningful. Habitat information, gleaned from Mexican specimens, is presented with apology as it is scarcely informative as to ecological preferences or requirements and scarcely useful in evaluating species as ecologically meaningful taxa.

SPHAGNUM L.

Slender to moderately robust mosses of wet habitats, sometimes submerged but more often growing above water level in carpets, cushions, or hummocks. Protonema a small, flat thallus producing 1 or rarely 2 leafy gametophores, proliferating secondary thalli at the ends of filamentous outgrowths from the margins; rhizoids few, at base of the gametophore (and lacking after early stages of growth), with oblique cross walls. Stems of indeterminate apical growth, erect (or in aquatic species weak and spreading), repeatedly forked, consisting of a central core of thin-walled parenchyma enveloped by a pigmented wood cylinder (scleroderm) of thick-walled prosenchyma which is surrounded by a cortex (hyaloderm) of 1 or more layers of large, empty, hyaline, thin-walled cells which are sometimes spirally fibrillose and, if so, usually porose on the outer surface, or efibrillose and generally lacking pores. Branches determinate in growth, in fascicles spirally disposed around the stem and crowded at the stem tip in a head-like tuft (capitulum), some branches spreading and others, of more slender construction, pendent and often corticating the stem. Branch cortex usually in 1 layer, consisting of large, empty, hyaline cells which may be spirally fibrillose and generally porose or lacking fibrils with some cells differentiated as retort cells, larger and porose at the tip of a short, protruding neck, rarely all cells uniform and porose. Branch leaves spirally inserted in a 2/5 phyllotaxy, consisting of linear green cells (chlorocysts) in a network enclosing large, empty, hyaline, rhomboidal cells (hyalocysts) reinforced within by annular fibrils and perforated by rounded to elliptic pores on 1 or both surfaces (or very rarely lacking fibrils and/or pores), commonly bordered by about 2–3 rows of linear cells, sometimes by 1 row of elongate cells apparently digested away at the outer margin as a resorption furrow. Stem leaves less crowded, usually differentiated in size and shape, the hyaline cells sometimes subdivided, typically with a lesser development of pores and fibrils, often extensively resorbed on 1 or both surfaces resulting in a wrinkling as membrane pleats or in rounded thin spots or large, irregular membrane gaps. Dioicous or monoicous; antheridial branches catkin-like, with leaves not much differentiated but commonly crowded and often highly colored, single or in fascicles of 2–3, the antheridia globose, long-stalked, borne singly at the side of each leaf of the catkin; perichaetial branches short, 1–2 or more per fascicle, bearing at the apex 1–5 narrowly flask-shaped archegonia, the perichaetial leaves large, broadly lingulate, sheathing the sporophyte until its maturity. Sporophyte consisting of a sessile capsule and a massive foot embedded in the tip of the perichaetial branch which elongates as a pseudopodium to elevate the mature capsule beyond the perichaetium; capsules globose, becoming cylindric to urceolate when dry and empty, reddish to dark-brown or black, without annulus or peristome; operculum flat or nearly so; wall of several layers of cells, without intercellular spaces, usually, in the lower half of the urn or nearly throughout, with a large number of somewhat sunken pseudostomata (consisting of paired guard cells but no pore); endothecium giving rise to a dome-like columella surrounded and overarched by sporogenous tissue derived from the inner layer of the amphithecium (and from the endothecium where the sporogenous tissue overarches the columella). Spores large (ca. 18–42 μm), tetrahedral, triradiate-ridged, nearly smooth to finely papillose-roughened, explosively discharged as the capsule shrinks on drying. Calyptra a very delicate, hyaline membrane becoming irregularly ruptured at maturity of the capsule.

1. Branches club-shaped, with cortical cells nestled together because of funnel-like bases. 3. *S. portoricense*
1. Branches not club-shaped, with cortical cells plane at base.
   2. Branches stout and tumid, with cortical cells spirally fibrillose; branch leaves broadly ovate to suborbicular, cucullate-concave at a broadly obtuse apex, roughened at back of the apex and denticulate-bordered because of resorption.

3. Plants normally reddish; cells of stem cortex with 1 or sometimes 2–4 pores on the outer surface; green cells of branch leaves in section elliptic, central, and entirely included. 1. *S. magellanicum*

3. Plants pale-green, yellowish, or yellow-brown; cells of stem cortex normally with numerous pores, (1)2–7(11); green cells of branch leaves in section narrowly triangular, with the base exposed on the inner surface. 2. *S. palustre*

2. Branches slender; cortical cells lacking fibrils; branch leaves narrower, generally oblong-ovate to lanceolate, concave but not cucullate, narrowly to broadly truncate, not roughened at back of the apex, with 1–3 or more rows of linear cells at the margins and generally entire (or, in *S. strictum*, denticulate-bordered because of marginal resorption).

4. Cortical cells of branches uniform, uniporose at upper ends; stem leaves much smaller than branch leaves; branch leaves concave but not usually involute-tapered, broadly truncate, denticulate-bordered by a resorption furrow. 4. *S. strictum*

4. Cortical cells of branches of 2 kinds, some large and porose at their protruding upper ends, others smaller and lacking pores; stem leaves generally half as long as the branch leaves or longer; branch leaves (at least when moist) involute-tapered to a narrowly truncate tip, bordered by linear cells in 2 or more rows, entire, without a marginal resorption furrow.

5. Branch leaves abruptly narrowed from a broad erect base to a squarrose limb; hyaline cells of branch leaves usually faintly papillose on inner surfaces adjacent to green cells. 5. *S. squarrosum*

5. Branch leaves gradually tapered, sometimes spreading to the tips when dry but scarcely squarrose; hyaline cells of branch leaves not papillose.

6. Hyaline cells of branch leaves, especially on the outer surface, with pores numerous and crowded in commissural rows (generally resembling a string of beads). 8. *S. subsecundum* var. *rufescens*

6. Hyaline cells with pores fewer, not crowded in commissural rows.

7. Plants pale-green to yellowish or brownish; cortical cells of stems not porose; green cells of branch leaves in section triangular to ± trapezoidal, exposed exclusively or more broadly on the outer surface.

8. Young pendent branches appearing to be in pairs; branch leaves when dry with spreading tips and wavy margins. 7. *S. recurvum*

8. Young pendent branches not in pairs; branch leaves not particularly spreading or wavy when dry.

9. Retort cells of branch cortex with long-spreading necks. 6. *S. tenellum*

9. Retort cells less markedly differentiated. 9. *S. richardsianum*

7. Plants pinkish to reddish (or, when shaded, green but with some parts red-tinged); cells of stem cortex often uniporose; green cells of branch leaves in section triangular to trapezoidal with broader or exclusive exposure on the inner surface or narrowly lenticular with equal exposure on both surfaces.

10. Plants very soft, loosely tufted, and laxly foliate; branch leaves broadly concave, broadly oblong-ovate or elliptic, shortly involute-concave at the apex; hyaline cells of branch leaves on the outer surface normally with pores only near the leaf tips and very few, minute, and inconspicuous; green cells of branch leaves lenticular or truncately elliptic to narrowly rectangular in section, with equal exposure on both surfaces. 11. *S. meridense*

10. Plants less soft, compact, densely foliate; branch leaves oblong-lanceolate, slenderly involute-pointed; hyaline cells on the outer surface with pores throughout the leaf, numerous, small but conspicuous, at ends and corners, and often near the commissures as well; green cells in section triangular to trapezoidal and exposed exclusively or more broadly on the inner surface. 10. *S. sparsum*

Section Sphagnum

Cortical cells of stem nearly always reinforced on the inner surface with delicate spiral fibrils and generally porose at the outer surface. Stem leaves lingulate, fringed. Branch cortex usually spirally fibrillose, generally 1-porose. Branches stout and tumid; branch leaves broadly ovate to suborbicular, cucullate-concave, rough at back of the apex because of resorption of hyaline cells and narrowly denticulate-bordered because of marginal resorption; pores on the outer surface of hyaline cells large, elliptic, at ends and corners, commonly in 2's or 3's at adjacent corners.

1. **Sphagnum magellanicum** Brid. – Plants stout, pink, red, or purplish (or, rarely, in shaded conditions, green), in compact cushions or hummocks. Wood cylinder of stem red; cortical cells in 3–4 layers, short-rectangular, thin-walled, delicately spirally fibrillose, with 1 or occasionally 2–4 large, rounded to elliptic pores. Stem leaves ± flat, oblong-lingulate, rounded at the apex, finely fringed at the margins; hyaline cells not divided, with fibrils none or only near the leaf apex, largely resorbed on the outer surface or sometimes on both surfaces. Branches relatively short, stout and tumid, in fascicles of 4–5 (2 spreading); cortical cells in 1 layer, short-rectangular, delicately fibrillose, the outer walls not porose or sometimes with 1 large, rounded pore at the upper end. Branch leaves imbricate or rarely somewhat spreading at the tip, ca. 2 mm long, broadly ovate, deeply cucullate-concave, denticulate and bordered by a single row of linear cells resorbed at their outer margins to form a furrow, rough at back of the apex because of resorption; hyaline cells plane or nearly so on both surfaces, fibrillose, on the outer surface with 2–5(10), large, elliptic pores (or occasionally pseudopores) at ends and corners and along the commissures, usually in groups of 3 at adjacent corners, fewer and passing into membrane gaps toward the leaf apex, on the inner surface with few (0–5) elliptic pores or pseudopores at corners and along the commissures in upper and lateral regions of the leaf, varying in size, often with 1 large, rounded to elliptic pore at the upper end; green cells in section small, elliptic, central, included. Dioicous. Spores 22–27 μm, obscurely roughened or nearly smooth. – Fig. A.

Not known to occur in Mexico but almost surely present on the highest peaks, as it occurs in Guatemala and rather commonly at higher elevations in other parts of Latin America, in compact cushions or hummocks in open, springy places. Common and widespread in Europe, northern Asia, and North America from Alaska to Greenland and south to California in the West and the Gulf of Mexico in the East; Bermuda; West Indies; Central America; northern South America to Tierra del Fuego; Falkland Islands; New Zealand.

The plants are stout and, at least when growing in the sun, reddish. The branch leaves are broad, cucullate-concave, rough at back of the apex, and narrowly denticulate-bordered owing to marginal resorption. The cortical cells of stems and branches are fibrillose. The branch leaves have hyaline cells nearly flat on both surfaces, and their green cells in section appear to be elliptic and entirely included.

In northern South America and few West Indian localities is another reddish member of the section *Sphagnum*, *S. alegrense* Warnst. It also has green cells of the branch leaves central and included, but the inner surfaces of hyaline cells, where they lie adjacent to green cells, are covered with very fine vermiform ridges which are demonstrable, with some difficulty, in longitudinal sections and in cross-sections appear as irregular, bumpy papillae. The cortical cells lack fibrils.

2. **Sphagnum palustre** L. – Plants robust, pale-green to yellowish or yellowish-brown, in cushions or carpets. Wood cylinder of stem brown; cortical cells in 3–4 layers, short-rectangular, thin-walled, delicately spiral-fibrillose, the outer cells with numerous, irregularly rounded pores, (1)2–7(11). Stem leaves ± flat, long-lingulate, rounded at the apex, finely fringed at the margins; hyaline cells not divided, frequently with membrane pleats and traces of fibrils, the outer surface largely resorbed or with fibrils and pores in addition to a large membrane gap, the inner surface fibrillose, non-porose. Branches stout and tumid, in fascicles of 4–5 (2 spreading); cortical cells in 1 layer, delicately fibrillose, frequently with a single, large pore. Branch leaves imbricate to spreading at the tips, broadly ovate, cucullate-concave, denticulate-bordered by 1 row of linear cells resorbed at their outer margins and forming a furrow, rough at back of the apex because of

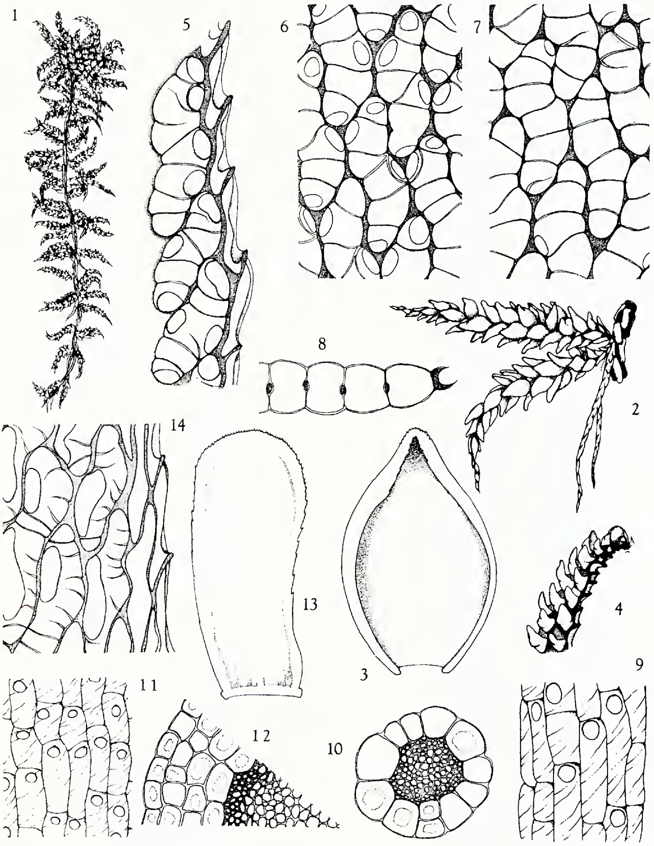

FIG. A. *Sphagnum magellanicum.* 1. Habit, X 1. 2. Fascicle of branches, X 3. 3. Branch leaf, X 27. 4. Resorption at back of the apex of a branch leaf, X 400. 5. Resorption at the margin of a branch leaf (as a resorption furrow), X 400. 6. Upper cells of branch leaf, outer surface, X 400. 7. Upper cells of branch leaf, inner surface, X 400. 8. Cross-section of branch leaf showing marginal resorption furrow, X 400. 9. Branch cortex, X 117. 10. Branch in cross-section, X 117. 11. Stem cortex, X 117. 12. Portion of stem in cross-section, X 117. 13. Stem leaf, X 27. 14. Upper cells of stem leaf, at margin, inner surface, X 400.

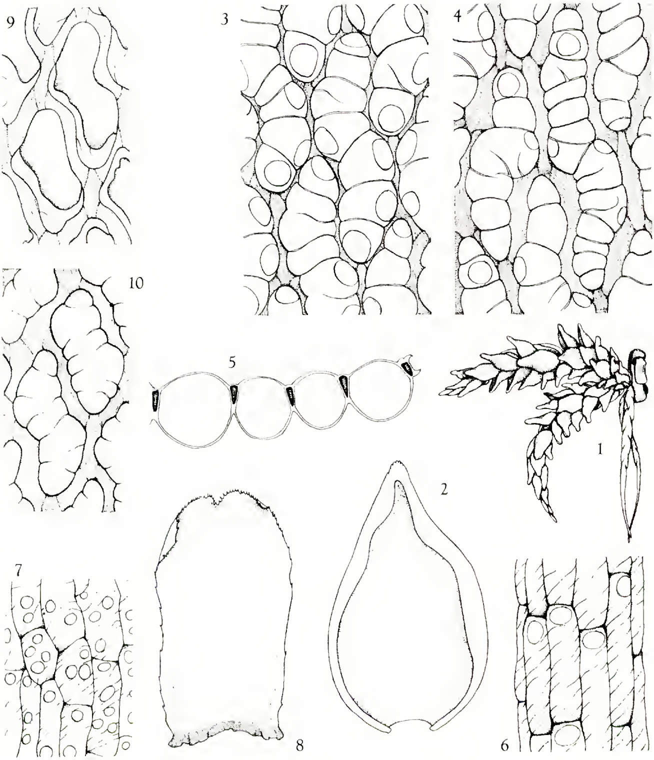

FIG. B. *Sphagnum palustre.* 1. Fascicle of branches, X 3. 2. Branch leaf, X 27. 3. Upper cells of branch leaf, outer surface, X 200. 4. Upper cells of branch leaf, inner surface, X 200. 5. Cross-section of branch leaf, X 200. 6. Branch cortex, X 117. 7. Stem cortex, X 117. 8. Stem leaf, X 27. 9. Upper cells of stem leaf, outer surface, X 400. 10. Upper cells of stem leaf, inner surface, X 400.

resorption; hyaline cells fibrillose, somewhat convex on the inner surface, more so on the outer surface which has large, rounded to elliptic end and corner pores, mostly in 2's and 3's at adjoining corners, and large, elliptic, ringed pores along the commissures, 3–7 above and sometimes as many as 10–13 below (sometimes especially numerous and ± rounded toward the basal margins), passing into single, large membrane gaps at the leaf apex, on the inner surface with pores none or few, elliptic to rounded in corners and often with a few large, rounded, unringed pores ± in the middle of cells, more numerous (2–8) near the leaf margins; green cells in section narrowly isosceles-triangular (or rarely ±

trapezoidal), exposed on the inner surface. Dioicous. Spores 24–29 μm, finely roughened or nearly smooth. – Fig. B.

In cushions or carpets in wet depressions or on seepage banks in shaded places at 6200 to 6800 ft. altitude. Eastern Mexico–Hidalgo (Apulco; Zacualtipán); Veracruz (Huayacocotla). Europe and Asia; Hawaii; British Columbia to California; Newfoundland to Wisconsin and south to the Gulf of Mexico; Jamaica. Records from South America, New Zealand, Australia, and Fiji need confirmation. Many of the South American records can be referred to a large, lax form of *S. perichaetiale.*

Sphagnum palustre tends to be yellowish or brownish. It has broad leaves hooded and roughened at the apex and denticulate along a marginal resorption furrow. The cortical cells of stems and branches are spirally fibrillose, and the cells of the stem cortex have numerous pores (sometimes as many as 11). The green cells of branch leaves, as seen in section, are narrowly triangular, with the base exposed on the inner surface.

Sphagnum imbricatum Hornsch. *ex* Russ. (Fig. C), similar in appearance to *S. palustre,* has been found in British Honduras. (A Guatemalan record, based on *Steyermark 49912,* can be referred to *S. subsecundum* var. *rufescens.*) The branch leaves in section

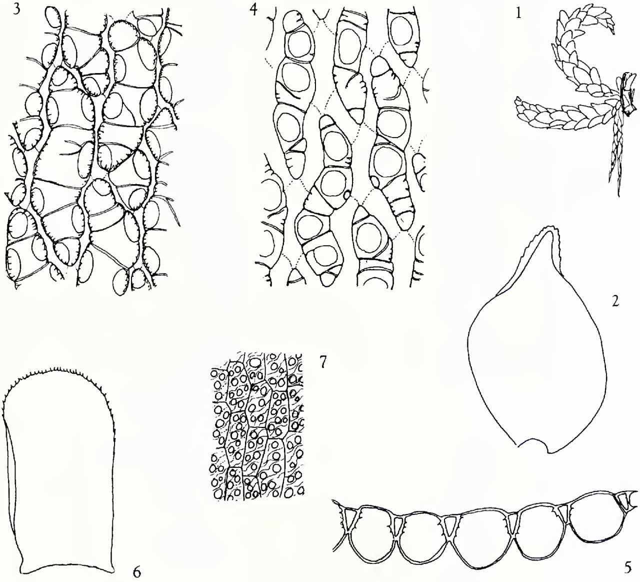

FIG. C. *Sphagnum imbricatum.* 1. Fascicle of branches, X 3. 2. Branch leaf, X 27. 3. Upper cells of branch leaf, outer surface, X 400. 4. Upper cells of branch leaf, inner surface, X 400. 5. Cross-section of branch leaf, X 400. 6. Stem leaf, X 27. 7. Stem cortex, X 117.

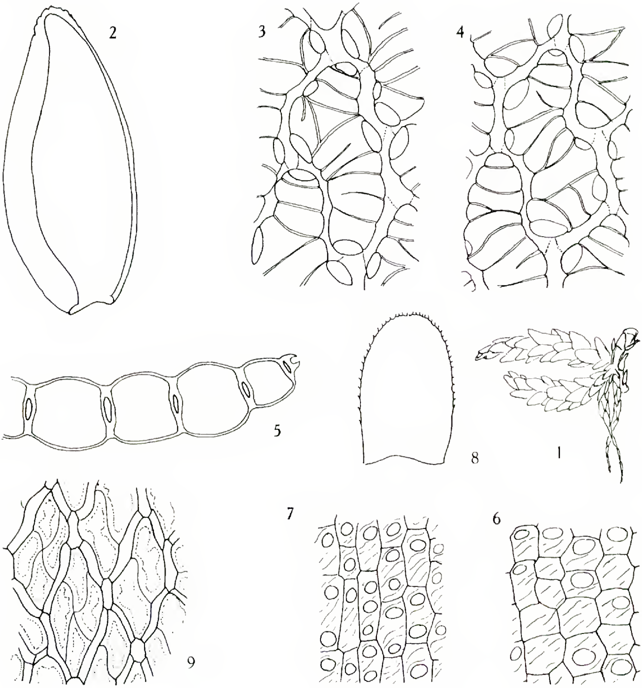

FIG. D. *Sphagnum perichaetiale.* 1. Fascicle of branches, X 3. 2. Branch leaf, X 27. 3. Upper cells of branch leaf, outer surface, X 400. 4. Upper cells of branch leaf, inner surface, X 400. 5. Cross-section of branch leaf, X 400. 6. Branch cortex, X 117. 7. Stem cortex, X 117. 8. Stem leaf, X 27. 9. Upper cells of stem leaf, X 400.

show green cells equilateral-triangular, with exposure on the inner surface and adjoining walls of hyaline cells ornamented by comb-like ridges. The "comb fibrils" may be coarse and conspicuous or variously reduced (perhaps even lacking).

Sphagnum perichaetiale Hampe (Fig. D), known from the Greater Antilles, northern South America, and British Honduras (as well as the Coastal Plain of the eastern United States), is likely to be found in Mexico. Usually the plants are small and compact, with stem and branch leaves much alike in size, shape, and structure, but larger plants of loose habit may have stem and branch leaves clearly differentiated. The branch leaves have on the outer surface of hyaline cells elliptic corner pores that are generally unperforated and easily overlooked. The green cells of the branch leaves are exceedingly variable in section; they are most often narrowly rectangular, but they can be especially narrow and even lenticular and exposed on both surfaces because of thickened end walls or narrowly triangular and exposed on the inner surface. The plants are generally tinged with yellow, orange, pinkish-orange, or rarely red.

Eddy (Bull. Brit. Mus. Nat. Hist. 5: 357–445. 1977) showed that the name *S. erythrocalyx* Hampe *ex* C. M., which Andrews used in place of *S. perichaetiale,* belongs to a species with branch leaf sections similar to those of *S. magellanicum* (with green cells central and included), except for papillae on the inner walls of hyaline cells where they lie adjacent to green cells. *S. erythrocalyx* is a Brazilian species. *S. alegrense* Warnst., which was described on the basis of Brazilian material, is somewhat similar, but its hyaline cells have fine worm-like ridges along the commissures and therefore appear to be sparsely and irregularly papillose in section.

3. **Sphagnum portoricense** Hampe – Plants robust, dark, greasy-green above and brown below or yellow-brown throughout (generally yellow to brown throughout when dry), in extensive carpets. Wood cylinder of stem brown; cortical cells in 3–4 layers, irregularly quadrilateral, sometimes wider than long, thin-walled, delicately fibrillose, those at the surface with 1–6 irregularly rounded pores. Stem leaves lingulate, with a broad, finely meshed, hyaline fringe at the sides and around the broad apex; hyaline cells often 1–2-divided, about as wide as long near the leaf tip, narrower below, on the outer surface almost entirely resorbed, on the inner surface often showing small pores and traces of fibrils, especially near the leaf apex. Branches in fascicles of 4–5 (2 spreading), stout, tumid, club-shaped; cortical cells in 1 layer, increasing in size toward the branch tip, nested together by a funnel-shaped base ending in a pore, delicately fibrillose, the inner wall corrugated by dense cross-fibrils (the outer surface without pores). Branch leaves closely imbricate, dimorphous: leaves at the base of branches smaller than those toward the branch tips, cucullate-concave, broadly cordate-ovate, hyaline-fringed; hyaline cells nearly plane on the inner surface, strongly convex on the outer, on the outer surface almost entirely resorbed in the upper part of the leaf, in the lower part with 7–10 large, elliptic pores at corners and along commissures, on the inner surface with about 4 small, elliptic pores at the corners in the upper part of the leaf, those in the lateral regions more numerous, larger, and rounded; leaves of the upper part of branches much larger, denticulate along a resorption furrow, not hyaline-fringed, with hyaline cells resorbed on the outer surface only in a few apical cells; green cells in section equilateral-triangular, exposed on the inner surface (or rarely ± trapezoidal with narrow exposure on the outer surface), the inner walls of hyaline cells where they abut the green cells usually beset with fringe fibrils (sometimes evident only at leaf bases). Apparently dioicous. Spores 22–29 µm, finely roughened. – Fig. E.

On wet soil at 3800 ft. altitude; Mexico–Puebla (Villa Juárez). In tropical America on wet banks in mountains but in the Coastal Plain of eastern North America submerged in shallow water of pools and drainage ditches and extending upward above water level at the margins, sometimes also in swampy places submerged during part of the year. Along the coast from Maine and New York to Florida and Mississippi; Puerto Rico and Guadeloupe; Venezuela.

Sphagnum portoricense is recognized in the field by dark-green, wet-shiny, stout, club-shaped branches. The cortical cells of the branches are funnel-like and nested together; they lack pores at the surface; and their inner walls are densely corrugate-fibrillose. The leaves of the upper part of the branches are denticulate-bordered by a resorption furrow; those toward the branch bases are hyaline-fringed, as in the stem leaves. The green cells of branch leaves are broadly triangular in section, and the commissures of hyaline cells are normally covered by fringe fibrils.

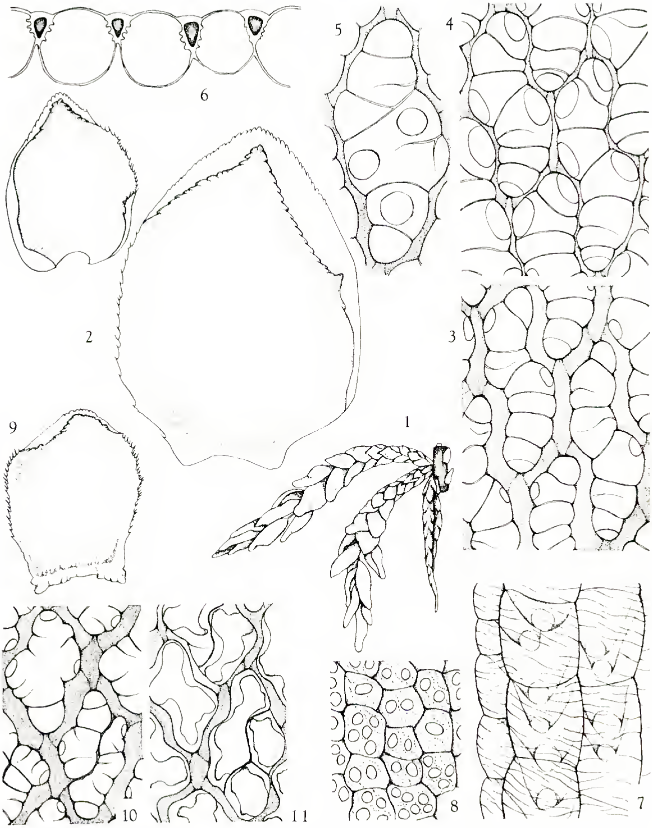

FIG. E. *Sphagnum portoricense.* 1. Fascicle of branches, X 3. 2. Branch leaves, X 27. 3. Upper cells of branch leaf, inner surface, X 400. 4. Upper cells of branch leaf, outer surface, X 400. 5. Upper cells of branch leaf, near margin, inner surface, X 400. 6. Cross-section of branch leaf, X 400. 7. Branch cortex, X 117. 8. Stem cortex, X 117. 9. Stem leaf, X 27. 10. Upper cells of stem leaf, inner surface, X 400. 11. Upper cells of stem leaf, outer surface, X 400.

Section Rigida

Cortical cells of stems and branches without fibrils, those of stems without pores, those of branches uniformly 1-porose at the upper ends. Stem leaves very small, lingulate to deltoid, scarcely bordered; hyaline cells not divided, without pores or fibrils. Branch leaves often squarrose-spreading, broadly ovate to elliptic, broadly truncate, concave because of inrolled margins, smooth at back of the apex, narrowly denticulate-bordered because of marginal resorption.

4. **Sphagnum strictum** Sull. (syn. *S. mexicanum* Mitt.). – Plants yellowish, generally in low, dense mats or small cushions. Wood cylinder of stem yellow-green; cortical cells in 1–3 layers, short-rectangular, thin-walled, without pores or fibrils. Stem leaves very small, bluntly deltoid, scarcely bordered; hyaline cells not divided, without fibrils or pores, sometimes with membrane pleats at the leaf apex, each cell on the inner surface with an irregular membrane gap which near the leaf apex occupies nearly the entire cell. Branches usually in fascicles of 5 (2 spreading); cortical cells in 1 layer, without fibrils, each ending in an apical pore. Branch leaves squarrose, ovate, involute-concave, and ending in a broadly truncate, toothed apex, ± denticulate along a marginal resorption furrow toward the leaf tip, smooth at back of the apex; hyaline cells distinctly convex on the inner surface, slightly so on the outer, fibrillose, on the outer surface toward the leaf apex with 2–6 large, rounded to rounded-elliptic, distinct but not ringed pores along the commissures, up to 12 or 16, more nearly elliptic, and more distinctly ringed below, on the inner surface with few (2–4), somewhat smaller, elliptic, strongly ringed pores in the corners and occasionally along the commissures, often in 2's and 3's at adjacent corners; green cells in section to narrowly triangular ± trapezoidal, exposed on both surfaces or only on the outer, the inner walls of hyaline cells where they abut the green cells usually faintly papillose. Dioicous. Spores 31–39 μm, finely roughened or nearly smooth. – Fig. F.

In seepage on roadbanks at about 3000 to 4000 ft. altitude (but in the Coastal Plain of southeastern United States on sandy soil in open, grassy places). Mexico–Hidalgo (Tenango de Doria); Oaxaca (*sine loco,* type of *S. mexicanum*). Andrews (Bryol. 16: 23. 1913) reported that a specimen at the Copenhagen Botanical Garden, designated as "Mexico, *Liebmann,* Musci 10," was wrongly named by Schimper as *S. squarrosum.* Northwestern and central Europe; Newfoundland to Florida and Louisiana, primarily in the Coastal Plain; Santo Domingo and Guadeloupe; Venezuela and Ecuador. The type of *S. mexicanum* and material from Guadeloupe and Santo Domingo were referred by Eddy to the ssp. *pappeanum* (C. M.) Eddy, otherwise known from Africa and Malaysia. The subspecies is said to differ slightly in anatomical detail and somewhat more robust stature (which in Africa grades into the ssp. *strictum*).

The plants form low and usually compact cushions or small mats. The stem leaves are much smaller than the branch leaves. The cells of the branch cortex are uniformly porose at slightly protruding upper ends. The spreading to squarrose branch leaves are broadly truncate, with margins denticulate-bordered above because of resorption. Very fine papillae are usually present on the inner walls of hyaline cells where they adjoin the green cells.

Sphagnum strictum differs from the widespread *S. compactum* Lam. & DC most notably in the absence of pseudopores in the hyaline cells of branch leaves and in the exposure of green cells on the outer surface. *S. compactum* has green cells central and included. It has been found in Guatemala in an alpine meadow at 3100–3150 m altitude; the specimen, *Steyermark 49918,* was referred by Bartram to *S. magellanicum.* Widespread in the Northern Hemisphere, it has also been found in northern South America.

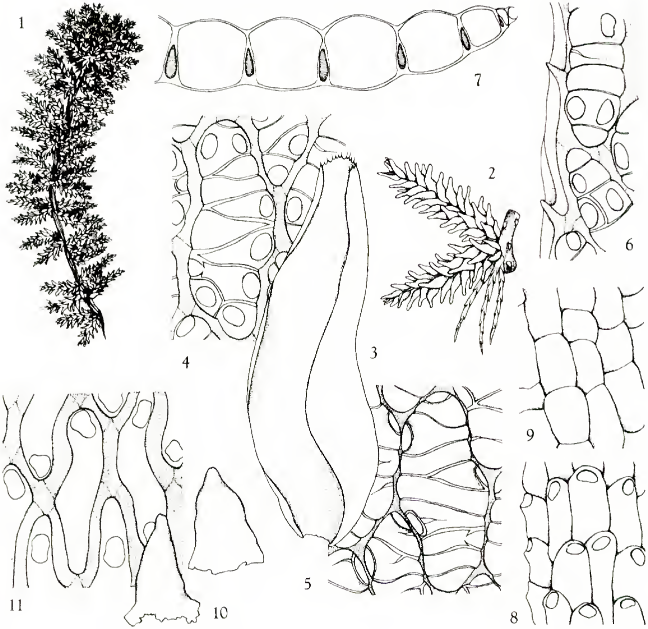

FIG. F. *Sphagnum strictum*. 1. Habit, X 1. 2. Fascicle of branches, X 3. 3. Branch leaf, X 27. 4. Upper cells of branch leaf, outer surface, X 400. 5. Upper cells of branch leaf, inner surface, X 400. 6. Upper cells of branch leaf and marginal resorption furrow, X 400. 7. Cross-section of branch leaf, X 300. 8. Branch cortex, X 117. 9. Stem cortex, X 117. 10. Stem leaves, X 27. 11. Upper cells of stem leaf, inner surface, X 400.

Section Squarrosa

Terminal bud large. Cortical cells of stem without fibrils, sometimes with a single pore or pore-like thin spot at the upper end. Stem leaves elliptic, perforate to slightly fringed at the broad apex; hyaline cells undivided, without fibrils, on the outer surface mostly resorbed, on the inner surface resorbed only in the apical portion of the leaf. Cortical cells of branches without fibrils, some enlarged with a single pore terminating an apical projection. Branch leaves generally spreading- to squarrose-tipped at least when dry, ovate-hastate to ovate-lanceolate, narrowly truncate, involute-concave, entire at the margins and narrowly bordered by several rows of linear cells; hyaline cells on the outer surface with large, rounded to rounded-elliptic pores, on the inner surface with large, elliptic pores with distinct or ringed margins; green cells exposed exclusively or more broadly on the outer surface, with the adjacent walls of hyaline cells faintly papillose.

5. **Sphagnum squarrosum** Crome – Relatively robust plants in loose, pale-green to yellowish carpets. Terminal bud large. Wood cylinder green to red-brown; cortical cells of stem in 2–3 layers, short-rectangular, without fibrils or pores. Stem leaves only slightly concave, relatively large, oblong-lingulate, perforate or slightly fringed at a rounded apex, not or indistinctly bordered; hyaline cells mostly undivided and without fibrils, on the outer surface almost entirely resorbed, on the inner surface with membrane pleats, only at the leaf apex with membrane gaps. Branches in fascicles of 5 (2 spreading); cortical cells in 1–2 layers, without fibrils, the retort cells with inconspicuous necks. Branch leaves squarrose from an erect base, ca. 2–2.5 mm long, broadened from the base upward and abruptly narrowed at the middle to an involute-concave acumen, toothed across a narrowly truncate apex, bordered by 2–3 rows of linear cells; hyaline cells somewhat convex on both surfaces (somewhat more so on the inner), often faintly papillose on the inside where they adjoin green cells, fibrillose, on the outer surface in the upper portion of the leaf with 1–3 rounded to rounded-elliptic, non-ringed pores at ends and corners, in the lower median region with 10 or more large pores in 1–2 rows, on the inner surface with 4–7 large, rounded-elliptic, ringed pores at ends and along commissures; green cells in section triangular or trapezoidal, exposed exclusively or more broadly on the outer surface. Monoicous. Spores 17–27 μm, smooth or nearly so to finely papillose. – Fig. G.

The Mexican habitat is unknown. In temperate regions, the plants characteristically grow in base-rich woodland habitats, in wet depressions in *Thuja* swamps, for example. In boreal and arctic latitudes, the species grows in willow thickets or in open, calcareous fens. In montane situations, it occurs on wet rock ledges. The sole collection from Mexico, in the herbarium of the Field Museum of Natural History, was made by Harde Le Sueur in Chihuahua, in the Chupie Lake area (near Chuhuichupa, municipio de Madera, at 7500 ft. altitude, on August 25, 1937. – Norton Miller provided me with information on the locality of Chupie Lake. His information came from data on Le Sueur's collections assembled by I. M. Johnston and preserved at the Arnold Arboretum). Widespread in Europe, south at least to Romania and the Armenian SSR; China and Japan; Greenland to Alaska and southward to Arizona, Colorado, Iowa, and the Great Lakes region and in the mountains to North Carolina and Tennessee. Reported from India, Korea, eastern Siberia, and New Zealand.

Sphagnum squarrosum, when well developed, can be recognized at a glance by its large size and conspicuously squarrose branch leaves. Other features of note include a large terminal bud, extensive resorption on both surfaces at the broad apex of stem leaves, and abruptly acuminate branch leaves with hyaline cells having ringed pores on the inner surface.

Section Cuspidata

Plants mainly in depressions, sometimes submerged, often yellowish to brownish. Cortical cells of stems often poorly differentiated, without pores or fibrils. Stem leaves extensively resorbed on the inner surface (and in some species on both surfaces across the apex or down the middle of the leaf resulting in laceration). Cortical cells of branches not fibrillose, some of them enlarged, apically porose, and retort-shaped. Branch leaves involute-concave, especially when moist, ± flattened out and often wavy at the margins when dry, ovate to lanceolate, narrowly truncate, entire-margined and narrowly bordered by linear cells; hyaline cells convex on the inner surface, variously porose on 1 or both surfaces; green cells with exclusive or broader exposure on the outer surfaces.

6. **Sphagnum tenellum** Ehrh. *ex* Hoffm. – Plants small, soft, delicate, in loose, pale, green, yellowish-green, or brownish carpets. Branches of the capitulum somewhat curved. Stems brown; wood cylinder yellow-green; cortical cells moderately enlarged and thin-walled in 2–3 layers, short-rectangular, without fibrils or pores. Stem leaves much like branch leaves, 1.3–1.4 mm long, oblong-elliptic, concave and seemingly broadly acute because of incurved upper margins, with a narrow border which is not or only slightly

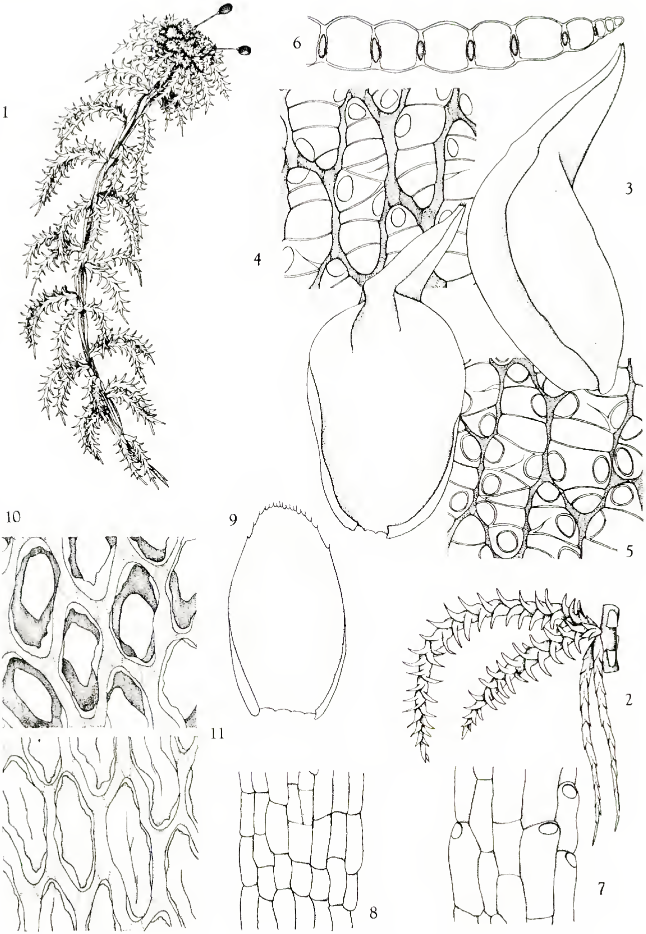

FIG. G. *Sphagnum squarrosum.* 1. Habit, × 1. 2. Fascicle of branches, × 3. 3. Branch leaves, × 27. 4. Upper cells of branch leaf, outer surface, × 400. 5. Upper cells of branch leaf, inner surface, × 400. 6. Cross-section of branch leaf, × 400. 7. Branch cortex, × 117. 8. Stem cortex, × 117. 9. Stem leaf, × 27. 10. Upper cells of stem leaf, near apex, showing resorption on both surfaces, × 400. 11. Upper median cells of stem leaf, inner surface, × 400.

broadened at base; hyaline cells narrow below, broader toward the leaf apex, not divided (or occasional cells 1-divided), fibrillose in the upper 1/2 or nearly to the base, on the outer surface with 1–4 small, ringed pores at ends and corners, on the inner surface with 1–2 large, non-ringed pores at ends or corners or ± large membrane gaps, especially toward the sides of the leaf apex. Branches in fascicles of 3–5 (1–3 spreading); cortical cells in 1 layer, without fibrils, the retort cells with very conspicuous necks. Branch

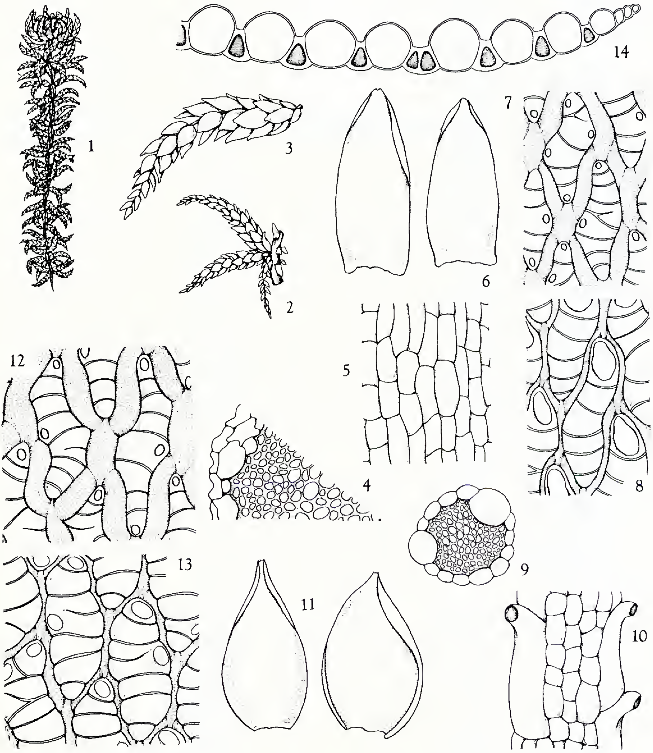

FIG. H. *Sphagnum tenellum.* 1. Habit, X 1. 2. Fascicle of branches, X 3. 3. Spreading branch, X 7. 4. Portion of stem in cross-section, X 117. 5. Stem cortex, X 117. 6. Stem leaves, X 27. 7. Upper cells of stem leaf, outer surface, X 400. 8. Upper cells of stem leaf, inner surface, X 400. 9. Branch in cross-section, X 117. 10. Retort cells of branch cortex, X 117. 11. Branch leaves, X 27. 12. Upper cells of branch leaf outer surface, X 400. 13. Upper cells of branch leaf, inner surface, X 400.

leaves not crowded, loosely spreading or somewhat incurved to subsecund, concave, ca. 1.3 mm long, oblong-ovate to elliptic, appearing broadly acute when dry but shortly involute-pointed when moist, toothed at the apex, bordered by 2–3 rows of narrow cells; hyaline cells very convex on the inner surface but only slightly so on the outer, fibrillose, on the outer surface with 2–4 small, round, ringed pores at ends and corners, on the inner surface with 2–3 large, round, non-ringed pores; green cells in section broadly triangular or sometimes trapezoidal with a broader exposure on the outer surface. Dioicous. Spores 27–31 μm, very finely roughened or nearly smooth. – Fig. H.

In seepage from springs or on wet banks of streams at 6200 to 9800 ft. altitude (sometimes growing with *Breutelia* and *Rhacocarpus*). Eastern Mexico–Oaxaca (Sierra Juárez; Llano de las Flores). Northern and Central Europe; Japan; southeastern Alaska and British Columbia; Greenland; Newfoundland to northern Ontario and south to New York, New Jersey, and the mountains of North Carolina; Brazil and Ecuador.

The small, delicate plants grow in loose, pale carpets. The well-spaced, broad leaves are rather flat when dry, but not wavy-margined. The stem and branch leaves are similar in shape and structure, and the retort cells of the branch cortex are remarkably long-necked.

7. **Sphagnum recurvum** P.-Beauv. (syn. *S. pulchricoma* C. M.) – Plants usually moderately robust, in bright-green to yellow-brown carpets. Capitulum often conspicuously 5-radiate; young pendent branches as seen between the arms of the capitulum appearing to be paired; leaves of young spreading branches noticeably spiral-ranked when moist; tip of stem and base of spreading branches sometimes flushed with red; apical bud not noticeable. Wood cylinder of stem yellow-green; cortical cells poorly differentiated in 1 layer, long-rectangular, without fibrils or pores. Stem leaves flat, 0.7–1.3 mm long, usually somewhat longer than broad, ± lingulate or less commonly broadly triangular, moderately erose across a broadly rounded or truncate, flat apex, the border of linear cells broader at base but not abruptly widened or sharply differentiated; hyaline cells not divided, without pores or fibrils (or rarely ± fibrillose above), mostly resorbed on the inner surface toward the apex. Branches in fascicles of 5 (with 2–3 spreading); cortical cells in 1 layer, without fibrils, the retort cells with inconspicuous necks. Branch leaves ± flattened out, recurved at the tips, and wavy at the margins when dry, lanceolate, involute-concave, and erect, with incurved margins when moist, 1.3–1.4 mm long, bordered by 2–4 rows of linear cells, entire except across the narrow, truncate apex; hyaline cells nearly plane on the outer surface, slightly convex on the inner, fibrillose, on the outer surface with a moderately large and rather conspicuous round pore at the upper end and near the apex of the leaf with a few small, ringed pores in corners and along commissures, on the inner surface with 3–7 rather large, round, unringed pores at corners and near the commissures (usually evident only on strong staining); green cells in section isosceles-triangular, with the base exposed on the outer surface, the apex of the triangle usually reaching the inner surface. Dioicous. Spores 24–27 μm, finely roughened to nearly smooth. – Fig. I.

In relatively base-rich depressions in open or shaded peatlands. Eastern Mexico–Veracruz (Huayacocotla). Widely distributed in boreal and temperate latitudes in Europe and North America (and probably across northern Asia as well); across Canada to Alaska and south to California in the West; throughout eastern United States, though more common northward; Cuba; northern South America.

Sphagnum recurvum tends to develop yellow to yellow-brown tinges, although shade forms can be a bright-green. The capitulum can be conspicuously 5-radiate. Between the rays the young pendent branches appear to be paired. A pink flush is common at the base of spreading branches and near the tip of the stem. The branch leaves, at

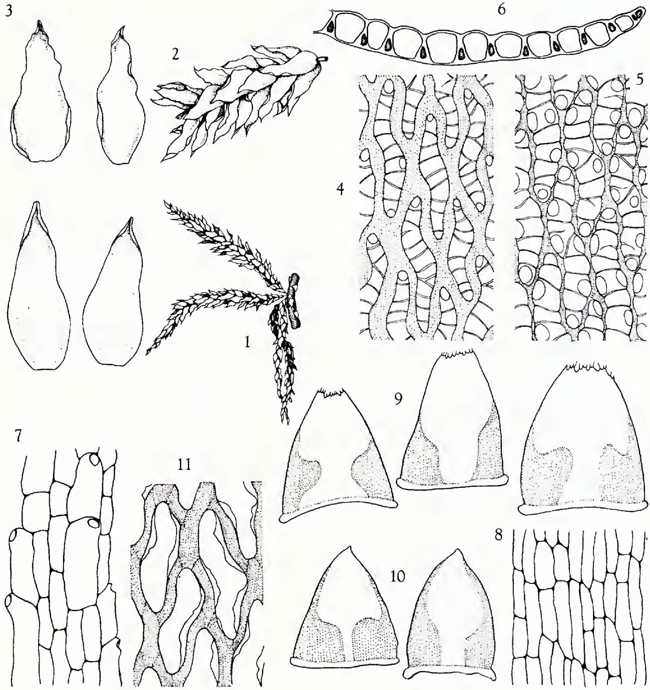

FIG. I. *Sphagnum recurvum.* 1. Fascicle of branches, dry, X 3. 2. Spreading branch, dry, X 10. 3. Branch leaves, dry (above), moist (below), X 27. 4. Upper cells of branch leaf, outer surface, X 400. 5. Upper cells of branch leaf, inner surface, X 400. 6. Cross-section of branch leaf, X 400. 7. Branch cortex, X 117. 8. Stem cortex, X 117. 9. Stem leaves (var. *recurvum*), X 27. 10. Stem leaves (var. *brevifolium*), X 27. 11. Upper cells of stem leaf, inner surface, X 400.

least on young spreading branches of the capitulum, are noticeably spiral-seriate when moist. On drying the branch leaves are relatively flat, with spreading or recurved tips and wavy margins. The hyaline cells of branch leaves have few pores on the outer surface, but a rather small, rounded pore at the upper ends of cells is rather conspicuously window-like; on the inner surface are numerous rounded pores with thin margins, noticeable on strong staining. The stem leaves are broadly lingulate and somewhat erose at a broad, truncate or more or less rounded apex.

The var. *recurvum* (Fig. I 1–9) includes *S. pulchricoma* in synonymy. Other names for the same form include *S. flexuosum* Dozy & Molk. and *S. amblyphyllum* (Russ.) Zick.

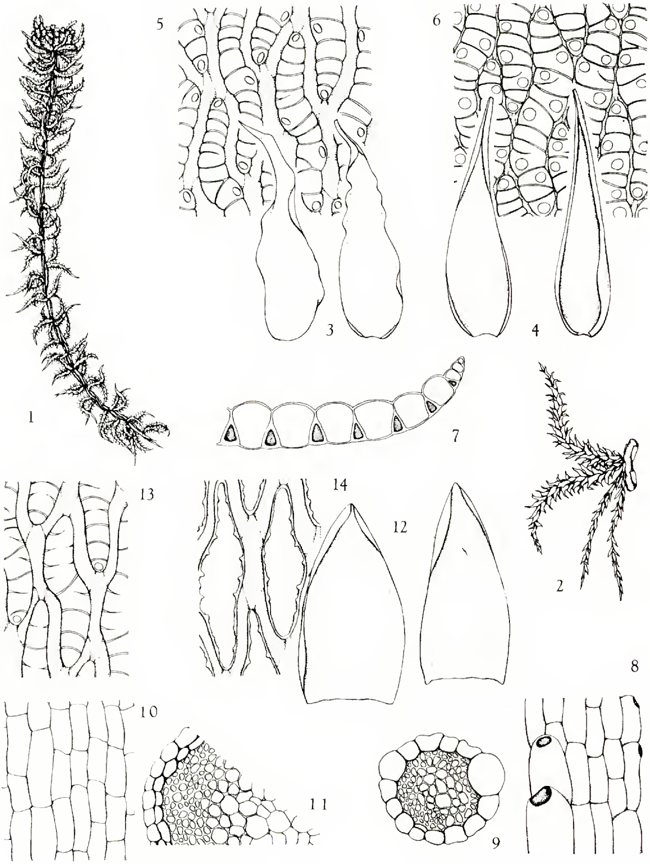

FIG. J. *Sphagnum sancto-josephense.* 1. Habit, × 1. 2. Fascicle of branches, × 3. 3. Branch leaves, dry, × 27. 4. Branch leaves, moist, × 27. 5. Upper cells of branch leaf, outer surface, × 400. 6. Upper cells of branch leaf, inner surface, × 400. 7. Cross-section of branch leaf, × 400. 8. Branch cortex, × 117. 9. Branch in cross-section, × 117. 10. Stem cortex, × 117. 11. Portion of stem in cross-section, × 117. 12. Stem leaves, × 27. 13. Upper cells of stem leaf, outer surface, × 400. 14. Upper cells of stem leaf, inner surface, × 400.

What American authors have generally considered the typical expression of *S. recurvum* has stem leaves acute to concave-apiculate and entire at the apex (Fig. I 10). It can be called the var. *brevifolium* (Lindb. *ex* Braithw.) Warnst. It has been called *S. fallax* (Klinggr.) Klinggr., *S. mucronatum* (Russ.) Zick., and *S. apiculatum* H. Lindb. *in* Bauer.

Sphagnum sancto-josephense Crum & Crosby (Fig. J), described from Costa Rica and widespread, perhaps common, in northern South America, much resembles *S. recurvum.* It has oblong, concave-acute stem leaves with hyaline cells fibrillose on the outer surface toward the apex; the inner surface is largely resorbed, but stumps of fibrils may be seen at the margins of the uppermost cells.

Sphagnum cuspidatum var. *serrulatum* (Schlieph.) Schlieph. (syn. *S. trinitense* C. M.), widely distributed in coastal regions of eastern North America, the West Indies, and northern South America, has been found in Honduras. An aquatic, it has leaves somewhat flattened out and wavy when dry. The branch leaves are long and narrow, and at the branch tips especially long-subulate and, when dry, loosely flexuose; the margins (especially in elongate leaves at branch tips) are serrulate toward the apex and sometimes well below it. The variety (Fig. K 7–8) is, in most of its structural features, much like the var. *cuspidatum* (Fig. K 1–6), but it is rather more robust and tends to have hyaline cells of stem leaves once-divided, whereas those of the var. *cuspidatum* are undivided.

Section Subsecunda

Plants in small tufts or cushions, in wet depressions, often tinged with orange. Cortical cells of stems not fibrillose, sometimes 1-porose at the upper end. Stem leaves rather small but sometimes larger than branch leaves and sometimes similar to them in shape and structure, narrowly bordered by linear cells, the border not conspicuously widened at base; hyaline cells sometimes divided, usually fibrillose and porose at least near the apex, sometimes nearly throughout, with numerous commissural pores on 1 or both surfaces. Cortical cells of branches not fibrillose, some of them large, apically porose, and retort-shaped. Branches often curved (especially in the capitulum). Branch leaves often ± secund, ovate-lanceolate to ovate or elliptic, narrowly truncate, involute-concave, entire-margined and narrowly bordered by linear cells; hyaline cells on the outer surface usually with many ringed, elliptic pores crowded along the commissures, on the inner surface with pores none to numerous; green cells with exposure ± equal, greater on the outer surface, or (rarely) greater on the inner surface.

8. **Sphagnum subsecundum** Nees *ex* Sturm, *sensu lato* – Plants rather small to fairly robust, green or more often yellow-brown to orange. Branches of capitula often curved. Stems usually brown; wood cylinder yellow-green to brown; cortical cells in 1–4 layers, subquadrate to short-rectangular, thin-walled, without fibrils or pores, or sometimes with cracks, rounded membrane thinnings, or actual pores at upper ends. Stem leaves much shorter than branch leaves or to varying degrees larger and resembling branch leaves in size, shape, and structure, concave, deltoid to oblong-lingulate or elliptic, rounded at the apex, with a narrow border which is not much broadened at base; hyaline cells not at all or commonly divided, in more isophyllous forms with pores and fibrils on both surfaces, sometimes nearly throughout, the pores often crowded in rows along the commissures, in other forms with fibrils and pores only at the extreme apex, sometimes without fibrils but with membrane pleats, on the inner surface with irregular gaps in cells of the immediate apex, with membrane pleats below, sometimes porose. Branches in fascicles of 2–6 (2–3 spreading); cortical cells in 1 layer, without fibrils, the retort cells with inconspicuous necks. Branch leaves often subsecund, oblong-ovate to suborbicular, involute-tapered, toothed at the narrow apex, bordered by 2–3 rows of narrow cells; hyaline cells slightly convex on both surfaces, sometimes slightly more so on the inner, fibrillose, on the outer surface with pores usually 10–20 or more, small, elliptic, ringed,

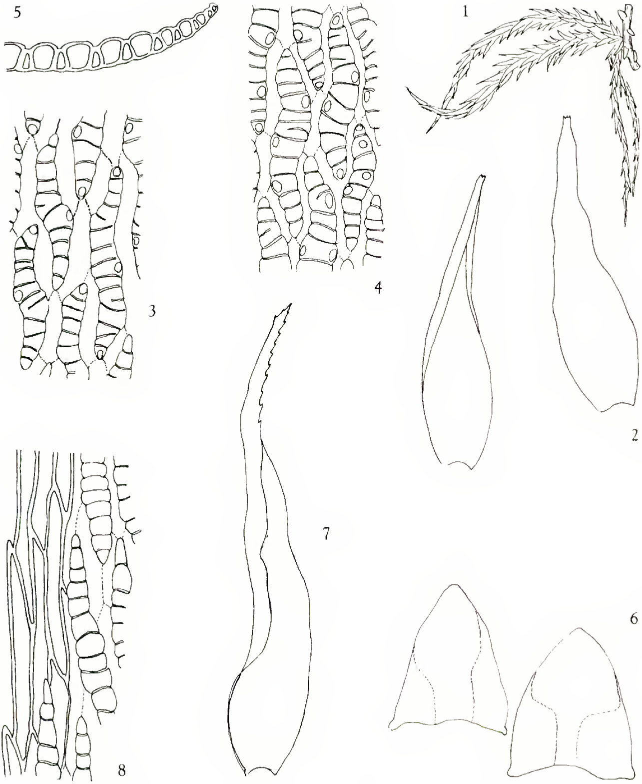

FIG. K. *Sphagnum cuspidatum* var. *cuspidatum*. 1. Fascicle of branches, X 3. 2. Branch leaves, X 27. 3. Upper cells of branch leaf, outer surface, X 400. 4. Upper cells of branch leaf, inner surface, X 400. 5. Cross-section of branch leaf, X 400. 6. Stem leaves, X 27. Var. *serrulatum*. 7. Branch leaf, X 27. 8. Margin of upper part of branch leaf, X 400.

often arranged along the commissures like a string of beads, sometimes with pseudopores and occasional compound pores (2–3 minute pores enclosed in a ring), on the inner surface with pores none or few, small, and rounded, in the angles or quite numerous along the commissures; green cells in section truncately elliptic and equally exposed on both surfaces or variously trapezoidal with broader exposure on the outer surface. Dioicous. Spores 22–24 μm, smooth.

Var. *rufescens* (Nees, Hörnsch. & Sturm) Hub. (syn. *S. flavicans* Warnst.) – Stem cortex in 1 layer (sometimes rather irregularly so). Stem leaves oblong-ovate to lingulate, 1.3–2.5 mm long; hyaline cells often divided, fibrillose and porose in the upper 1/3–1/2 or nearly throughout, with many pores along the commissures on both surfaces, or occasionally few or none on the inner surface. Branch leaves 1.5–2.2 mm long; hyaline cells on the outer surface with many pores crowded along the commissures, on the inner surface with pores and pseudopores in continuous or interrupted rows along the commissures, occasionally few or none. – Fig. M 3–4.

In small cushions on wet banks at 8000 to 9000 ft. altitude. Eastern Mexico–Chiapas (between San Cristobal de las Casas and Tenejapa); Oaxaca (W of Oaxaca, type of *S. flavicans*); Veracruz (Huayacocotla). Widespread in Europe; California; Newfoundland to Wisconsin, south to Florida and Texas; Guatemala (reported by Bartram as *S. subsecundum, Sharp 4968,* and *S. imbricatum, Steyermark 49912*); British Honduras.

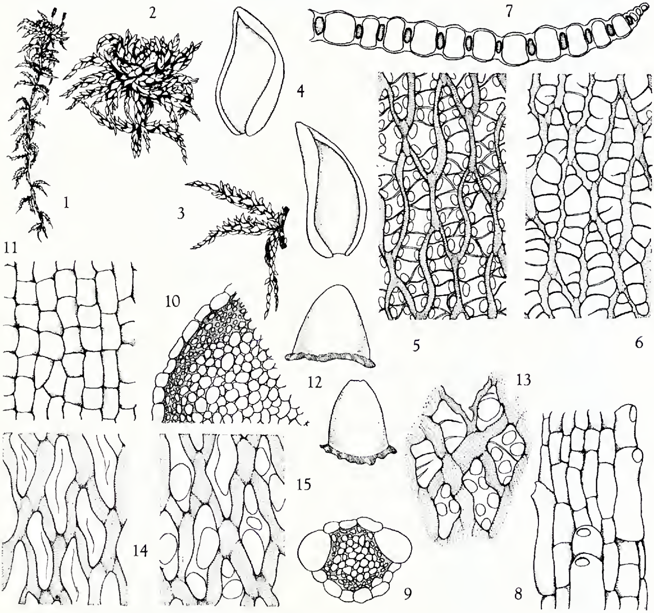

FIG. L. *Sphagnum subsecundum* var. *subsecundum.* 1. Habit, X 1. 2. Capitulum, X 3. 3. Fascicle of branches, X 3. 4. Branch leaves, X 27. 5. Upper cells of branch leaf, outer surface, X 400. 6. Upper cells of branch leaf, inner surface, X 400. 7. Cross-section of branch leaf, X 400. 8. Branch cortex, X 117. 9. Branch in cross-section, X 117. 10. Portion of stem in cross-section, X 117. 11. Stem cortex, X 117. 12. Stem leaf, X 400. 13. Cells at apex of stem leaf, outer surface, X 400. 14. Upper median cells of stem leaf, outer surface, X 400. 15. Upper median cells of stem leaf, inner surface, X 400.

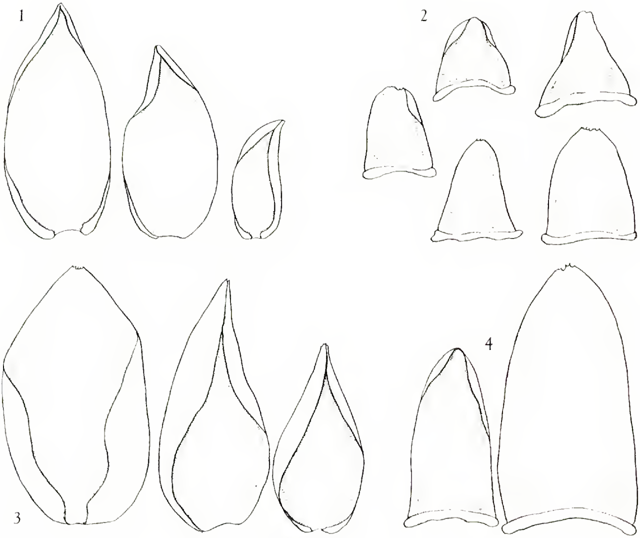

FIG. M. *Sphagnum subsecundum* varieties. 1. Branch and 2. stem leaves of var. *subsecundum*, X 27. 3. Branch and 4. stem leaves of var. *rufescens*, X 27.

Sphagnum subsecundum is a complex of intergrading forms that must be viewed with suspicious conservatism, although some of the many names that have fallen into its synonymy need recognition at some taxonomic level, not necessarily specific. The var. *subsecundum* (Fig. L, M 1–2) causes little trouble: The stem cortex consists of one layer of cells; the stem leaves are smaller than the branch leaves, deltoid to oblong, and more or less fibrillose and/or porose at the extreme tip. The wide-ranging and exceedingly variable var. *rufescens* (Fig. M 3–4) has cells of the stem cortex essentially one-layered (but sometimes, most irregularly and indistinctly, more or less two-layered); the stem leaves are half as long as the branch leaves or even longer, oblong-lingulate, and porose and fibrillose in the upper third to half or more; the pores are especially numerous on the outer surface of stem leaves, where they occur in commissural rows, but they are usually few or lacking on the inner surface.

9. **Sphagnum richardsianum** Crum – Plants small, soft, pale-green or yellowish, sometimes orange-brown above. Cortical cells of stems moderately differentiated in 2 layers, short-rectangular, without pores or fibrils. Stem and branch leaves similar: Stem leaves somewhat concave, 1.6–2.2 mm long, ovate-elliptic, broadly rounded to truncate at the apex, bordered by 2–3 rows of linear cells, entire except for coarse dentations across the apex; hyaline cells fibrillose throughout, not or rarely 1-divided, on the outer surface near the leaf apex with 3–6 very small, rounded, unringed pores, mostly at

corners, and often few to numerous, sometimes crowded pseudopores at the commissures, in the lower part of the leaf with 1–4 small, rounded pores at or near the corners and no pseudopores, on the inner surface near the apex with a few small, rounded, unringed pores or pseudopores at the corners and elsewhere along the commissures, in the lower portions with 1–5 small, rounded-elliptic pores mainly at the corners, very numerous along the commissures at the basal margins of the leaf. Branches in fascicles of 3 (2 ± spreading); cortical cells in 1 layer, without fibrils, the retort cells with inconspicuous necks. Branch leaves deeply concave when moist, less so when dry, erect or erect-spreading, not at all secund, 1.5–2 mm long, ovate, bordered by 2–3 rows of linear cells, dentate across the broad though concave apex; hyaline cells bulging on both surfaces,

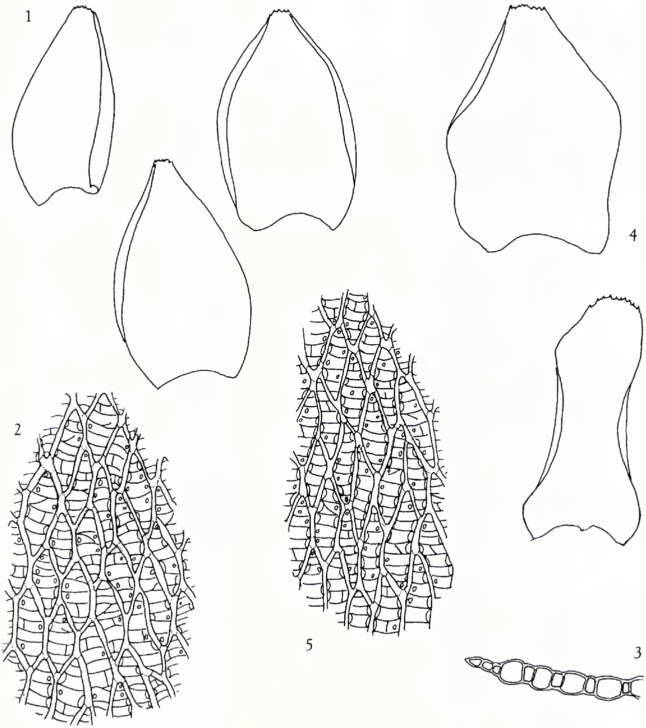

FIG. N. *Sphagnum richardsianum*. 1. Branch leaves, X 22. 2. Upper cells of branch leaf, outer surface, X 260. 3. Cross-section of branch leaf, X 260. 4. Stem leaves, X 22. 5. Upper cells of stem leaf, outer surface, X 260.

fibrillose throughout, undivided or in some leaves occasional cells repeatedly divided lengthwise, on the outer surface near the apex with 1–7 small, rounded-elliptic, ± ringed pores at the corners or scattered along the commissures, also with numerous pseudopores, on the inner surface with pores very few, small, and rounded, or more often none, with some pseudopores; in section green cells truncately elliptic or rectangular, broadly and equally exposed on both surfaces or with a slightly broader exposure on the outer surface. – Fig. N.

Oaxaca, in a cloud forest on Highway 175 on the east side of Sierra Juárez between Oaxaca and Tuxtepec; Guatemala (Baja Verapaz, *Sharp 5143,* CU, as *S. subsecundum*).

The stem and branch leaves are essentially isomorphous. The stem leaves are broadly ovate-elliptic, somewhat concave, and broadly truncate or more or less rounded at a dentate apex; the margins are bordered by linear cells; the hyaline cells are fibrillose throughout; the pores are few and very small, but in the upper part of the leaf, on the outer surface, pseudopores may be quite numerous and sometimes crowded in commissural rows. The branch leaves are somewhat smaller, ovate, and deeply concave; concavity obscures the fact that the apex is broad; the hyaline cells generally have rather few pseudopores even near the apex (although they are sometimes rather numerous).

An orange-brown pigmentation, more or less equal exposure of green cells of branch leaves, and the occurrence of pseudopores in something of a beaded arrangement make placement in the Subsecunda reasonable, although resemblances to *S. fitzgeraldii* Ren. *ex* Lesq. & James, in the Cuspidata, are rather disturbing.

Section Acutifolia

Plants often reddish, generally compactly tufted in cushions or hummocks. Cortical cells of stem without fibrils, sometimes 1-porose. Stem leaves about as long as branch leaves, nearly flat to ± concave, oblong-lingulate to ovate, rounded-obtuse to involute-pointed, bordered by linear cells, the border sometimes abruptly broadened at the base; hyaline cells often divided once to several times, without fibrils and pores and with membrane pleats on the outer surface or fibrillose with pores or gaps on the outer surface, in either case generally largely resorbed on the inner surface. Cortical cells of branches without fibrils, some of them large, apically porose, and retort-shaped. Branch leaves involute-concave, ovate-lanceolate, narrowly truncate, entire-margined and narrowly bordered by linear cells (very rarely with marginal resorption); hyaline cells strongly convex on the outer surface, fibrillose, on the outer surface with ringed and elliptic (or rarely rounded) pores at corners and along the commissures, usually rather numerous, on the inner surface with pores more rounded and thin-margined; green cells with exclusive or broader exposure on the inner surface.

10. **Sphagnum sparsum** Hampe – Plants rather slender, in low, compact mats, pinkish or yellowish-green. Capitula dense, rounded. Wood cylinder of stem yellowish-pink; cortical cells in 4 layers, short-rectangular, thin-walled, without fibrils, the outer cells generally porose at the upper ends. Stem leaves oblong or oblong-ovate, somewhat concave at the broadly acute and slightly erose apex, the border narrow above, slightly broadened at the base, the median basal cells somewhat enlarged in a triangular area; hyaline cells commonly 1(2)-divided, ± fibrillose in the upper 1/3–1/2, occasionally throughout, on the outer surface with membrane pleats and sometimes a few, scattered, rounded membrane gaps, on the inner surface largely resorbed or sometimes with 1 to several large, rounded membrane gaps or pores in commissural rows. Branches in fascicles of 4 (2 spreading). Branch cortex in 1 layer, without fibrils, the retort cells with rather conspicuous necks. Branch leaves crowded, not noticeably ranked, sometimes slightly secund, broadly oblong-lanceolate, narrowly involute-pointed, toothed across the narrow

apex, bordered by a few rows of linear cells; hyaline cells decidedly convex on the outer surface, only slightly so on the inner, on the outer surface with pores numerous, at the leaf tip very small, elliptic, strongly ringed, becoming larger and less ringed below, in ends and corners (often in 3's at adjacent corners) and occasionally along the commissures, on the inner surface with pores none or few, occasionally with 1–2 rather large, rounded gaps (of nearly cell width) in ends and corners toward the leaf tip; green cells in section broadly triangular, with the base exposed on the inner surface. Apparently dioicous. Spores ca. 22 μm, smooth or nearly so. – Fig. O.

On wet, shaded banks and cliffs at 6000 to 10,000 ft. altitude. Eastern and southern Mexico–Chiapas (Liquidambar; Montebello; Mapastepec); Oaxaca (Sierra Juárez; Zacatepec; Llano de las Flores; Chinantla); Puebla (Honey Station). Guatemala, Costa Rica, and northern South America.

Having the compact appearance of *S. capillifolium* (Ehrh.) Hedw. (a common species of circumpolar range), *S. sparsum* has cells of the stem cortex uniformly porose. The stem leaves are involute-pointed, and their hyaline cells, more or less fibrillose, are rather consistently 1–2-divided and have membrane pleats on the outer surface. The branch leaves are crowded-imbricate and rather slenderly involute-acuminate. The green cells of the branch leaves are broadly exposed on the inner surface; and the hyaline cells, on their outer surfaces, have numerous, rather small, elliptic, strongly ringed pores.

11. **Sphagnum meridense** (Hampe) C. M. (syn. *S. platycladum* C. M.) – Plants tall and loosely tufted in very soft, deep mounds, pale whitish-green to pink. Wood cylinder of stem yellowish to pinkish; cortical cells in 2–3 layers, rectangular, thin-walled, without fibrils or pores or, more frequently, with some cells porose at their upper ends. Stem leaves 1.5–2 mm long, oblong-ovate or oblong-triangular, concave and broadly acute at

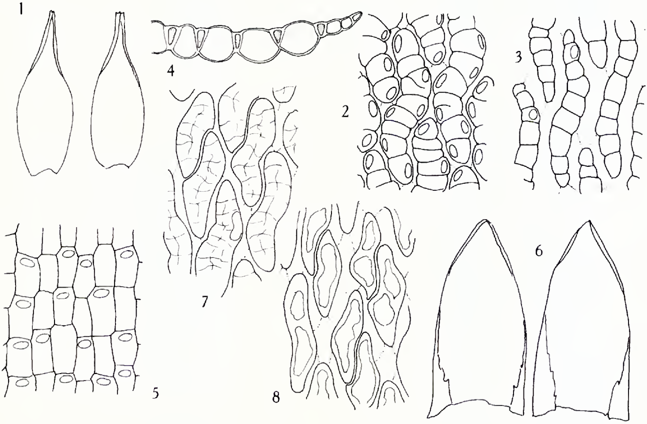

FIG. O. *Sphagnum sparsum.* 1. Branch leaves, × 27. 2. Upper median cells of branch leaves, outer surface, × 400. 3. Upper median cells of branch leaves, inner surface, × 400. 4. Cross-section of branch leaf, × 400. 5. Stem cortex, × 400. 6. Stem leaves, × 27. 7. Upper cells of stem leaf, outer surface, × 400. 8. Upper cells of stem leaf, inner surface, × 400.

the apex, the border rather strong above, not or slightly broadened at base; hyaline cells not or rarely 1-divided above, sometimes divided toward the base, usually without fibrils and pores but exceedingly variable, on the outer surface often with membrane pleats but no pores or membrane gaps, sometimes ± fibrillose near the apex, on the inner surface without pores or gaps, or sometimes with 1–5 irregularly rounded membrane gaps (often as broad as the cells) or 6–12 large, rounded or rounded-elliptic, unringed commissural pores. Branches in fascicles of 5–6 (2–3 spreading). Branch cortex in 1 layer, without fibrils, the retort cells with only slightly protruding necks. Branch leaves soft, rather widely spaced, loosely erect-spreading, deeply but broadly concave, 1.3–2 mm long, broadly oblong-ovate or elliptic, gradually narrowed to a short, involute-concave tip (more concave, narrower, and more abruptly short-pointed when moist), toothed across a narrowly truncate apex, bordered by 1–3 rows of linear cells (with no resorption furrow); hyaline cells slightly convex on the inner surface, somewhat more so on the outer,

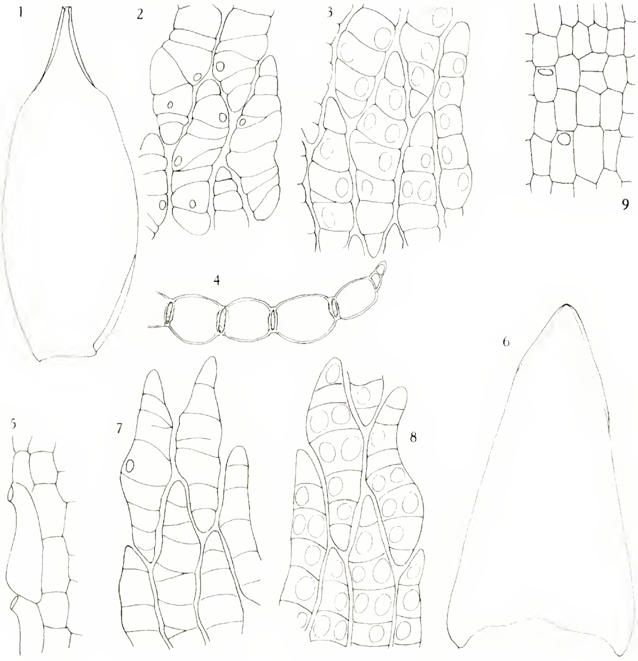

FIG. P. *Sphagnum meridense*. 1. Branch leaf, moist, × 23. 2. Apical cells of branch leaf, outer surface, × 364. 3. Upper median cells of branch leaf, inner surface, × 364. 4. Cross-section of branch leaf, at margin, × 364. 5. Branch cortex, × 364. 6. Stem leaf, × 23. 7. Upper median cells of stem leaf, outer surface, × 364. 8. Upper median cells of stem leaf, inner surface, × 364. 9. Stem cortex, × 364.

on the outer surface often with membrane pleats near the leaf apex, pores usually lacking except for a few, very small and inconspicuous, rounded to elliptic, ringed pores near the leaf tip, at ends and corners, sometimes in the middle (3–6, rarely 8, or sometimes none), very rarely with a scattered few larger, elliptic corner pores in median and lower portions of the leaf, on the inner surface with pores usually numerous, 4–8 per cell (rarely only 1–3), rather large, rounded, distinct but not ringed, at ends and corners, sometimes also at the commissures; green cells in section lenticular to fusiform, equally exposed because of thickened ends. Dioicous. Spores 20–24 μm, very minutely papillose. – Fig. P.

On moist banks of trails, sometimes on rock faces in forests at altitudes of 5500 to 10,000 ft. Mexico–Chiapas (Liquidambar; Mapastepec; Montebello); Guerrero (Cerro Teotepec); Hidalgo (Apulco; Tenango de Doria); Oaxaca (Sierra Juárez; Llano de las Flores; La Esperanza; Cerro de Fentila); Puebla (Atoluca; Cuetzalen; Honey Station; Teziutlán); Veracruz (between Teziutlán and Tlapacoyán). Guatemala and Costa Rica; northern South America; Greater Antilles.

Sphagnum meridense is a beautiful moss, very soft and pale, often attractively pink. The softness results from wide-spaced and erect-spreading leaves. The branch leaves are broadly concave, more or less elliptic, and shortly involute-pointed. The hyaline cells of the branch leaves are mainly without pores on the outer surface, except for a few, very small, and very inconspicuous ones in a few uppermost cells; on the inner surface the pores are numerous, rounded, and relatively large. The stem leaves show a remarkable variation. Usually both pores and fibrils are lacking, but sometimes fibrils are present, especially on the inner surface where they may be associated with membrane gaps or few to numerous large, rounded to elliptic commissural pores (as shown in Fig. P, 8). The cortex of the stem is sometimes lacking in pores, but more commonly some, many, or perhaps even all of the cells are porose.

The species is remarkably similar in appearance and structural detail to *S. limbatum* Mitt. (syn. *S. antillarum* Besch.), a species not known from Mexico but widespread elsewhere in tropical America. *S. limbatum* has cells of the stem cortex mostly porose; stem leaves with numerous ringed, elliptic commissural pores on the outer surface of hyaline cells and rounded commissural gaps on the inner surface; branch leaves with numerous narrowly elliptic corner pores on the outer surface of hyaline cells–throughout the leaves–and rather noticeably in 2's or 3's at adjacent corners; and green cells narrowly truncate-elliptic or lenticular with equal exposure on both surfaces. The elliptic pores on the outer surface of branch leaves (and throughout their length) and the pores or pore-like gaps on both surfaces of the stem leaves provide the best distinctions from *S. meridense.* The crowded, imbricate, and narrowly involute branch leaves, coupled with the triangular sectional view of its green cells, serve to separate *S. sparsum* from both *S. limbatum* and *S. meridense.*

In Guatemala, *Sphagnum meridense* is used in Christmas decoration. It is called *colchon de niño,* owing to a belief that the Christ Child was bedded in that soft and colorful moss. (It is also called *ush*–a name suitably descriptive of spongy softness regardless of the language!)

Andrews' report of *S. meridense* from Florida (in the *North American Flora,* 1913, without locality data) appears to be based on a specimen from Austin's herbarium (NY) of uncertain origin. It is labeled "*S. acutifolium* nr. *tenerum,* Closter, New Jersey" [Austin's home], but it has a penciled query after the locality which Andrews assumed Austin himself had made. Andrews (Ann. Bryol. 6: 4. 1933; Bryol. 61: 275. 1958) recognized the species as a tropical one, having nothing to do with *S. tenerum* Sull. & Lesq. *ex* Sull. or *S. acutifolium* "var." *tenerum* Aust. *ex* Warnst. (Hedwigia 29: 194. 1890, *nom. nud. in syn.*), a name that resulted from a misinterpretation of Austin's determination (as near, not var. *tenerum*). Andrews assumed that the specimen came from some place farther south, perhaps Florida where Austin had collected, but since the species is montane in its distribution in tropical America, it is not likely to occur in Florida's lowlands. Other more recent records of *S. meridense* from Florida are based on misdeterminations of *S. magellanicum* and *S. tenerum.*

ACKNOWLEDGMENTS

Many of the illustrations were made by Constance Butley and copied by myself or by Sara Long. The pictures of *S. sancto-josephense,* slightly altered from those published in *The Bryologist,* are reproduced here by permission. I am grateful for support from a National Science Foundation Grant BMS 73-0748.

Contr. Univ. Mich. Herb. 14:53–56. 1980.

COMMENTS ON *SPHAGNUM HENRYENSE*

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Sphagnum henryense, described by Warnstorf in 1900, has remained to this day unknown or, at best, confused with other look-alike species. The original collection was made in 1898 near the seacoast at Cape Henry, Princess Anne Co., Virginia, by Thomas H. Kearney. In 1911 Warnstorf added to the species a var. *bartlettii* from McDuffie Co., Georgia. Although the variety has been completely ignored, and with good reason, it appears to have been included in Andrews' concept and in the range of distribution that he gave, in 1913, as Delaware, Virginia, Georgia, and Louisiana. In 1938 Andrews characterized the species as strictly oceanic, known from a few coastal localities from Delaware to Louisiana. Blomquist, that same year, mentioned that *Sphagnum henryense* had been found only in the Coastal Plain of the Southeast, but in 1963, in Ruth Breen's *Mosses of Florida,* his statement of range included Nova Scotia and southward along the Coastal Plain to Florida and Louisiana and Cuba. Andrus, in 1974, gave reference to upland localities in New York and Pennsylvania and extended the range along the coast as far west as Texas.

I have not seen material from Texas, but I have seen specimens from coastal areas of New York, New Jersey, Delaware, Maryland, North and South Carolina, Georgia, Florida, and Louisiana. A collection from Hot Spring Co., Arkansas (at 240 ft. elev., Elmore Community, Malvern, *D. Demaree 45318,* in herb. Redfearn), was presumably from the Mississippi Embayment area, a lowland area in effect no more than a northward extension of the Coastal Plain. The species is unquestionably rare and localized in the Coastal Plain, but not limited to it. I have seen a few upland collections, from Magnolia, Massachusetts; Schenectady Co., New York; and Iredell Co., North Carolina. Iredell County is in the North Carolina Piedmont. Lewis Anderson has told me of a collection made in the mountains of North Carolina, in Jackson County (*Anderson 8271,* DUKE). I have not seen the specimen, but a "prominent ridge network" on the commissures of branch leaf hyaline cells makes the identification certain. I can confirm the occurrence in Nova Scotia (in shade, spruce-fir woods near Pond Cove, Brier Island, *W. B. Schofield 1827,* September 30, 1951, DUKE) and Cuba (in a wet place, 700 m. alt., near the headwaters of Arroyo Guayabo, Sierra de Nipe, Oriente province, *Bros. León, Marie-Victorin, Clemente & Alain 19774,* April 4, 1941, DUKE).

The range of *Sphagnum henryense* is like that of many rare plants of the youthful Coastal Plain but also occurring disjunctively in the uplands, especially in areas of known antiquity, in many instances in the mountains of the Southeast, and also in the mountains of tropical America. *Sphagna* of similar distributions and presumably similar phytogeographic histories include *S. pylaesii, S. cyclophyllum, S. tenellum,* and *S. perichaetiale.* The occurrence of *S. henryense* in Cuba makes a discovery elsewhere in tropical America likely.

In the field *Sphagnum henryense* greatly resembles *S. palustre, S. papillosum,* and *S. imbricatum.* All those species grow together, even intermingled, in the Coastal Plain of North Carolina. Microscopically they are easily distinguished. The special features of *Sphagnum henryense* include the following:

1. The green cells of branch leaves are isosceles-triangular in cross-section, with exposure on the inner surface.
2. The inner walls of hyaline cells of branch leaves where they lie adjacent to green cells are often covered by a network of vermiform ridges. The network, not very prominent at best and sometimes lacking, is most easily observed in longitudinal sections of the leaf base. In cross-sections the ridges give the semblance of very low, blunt papillae.
3. In the lower third to half of the branch leaves the pores on the outer surface of hyaline cells are very numerous (16–26 per cell); they are large, rounded, irregularly arranged in commissural rows or more or less scattered, and often enclosed in sigmoid or loop-like fibrils. In the upper part of the leaf (below the area of extensive resorption), the pores are 5–14 per cell, rather large, and rounded-elliptic.
4. The hyaline cells of the stem leaves are undivided. Most commonly they are short and show considerable resorption on their outer surfaces (resulting in 1, 2 or sometimes 3 large membrane gaps per cell). Hemi-isophyllous expressions, such as the so-called var. *bartlettii,* have much longer, hyaline cells with numerous large, rounded pores on the outer surface.

Sphagnum henryense was not well characterized in Andrews' revision of the North American species of peatmosses, in 1913. His statement that the inner surfaces of the hyaline cells where they overlie the chlorophyll cells are "beset with a net-work of prominently projecting ridges, especially in the lower part of the leaf" suggests a resemblance to the conspicuously developed comb fibrils of *S. imbricatum.* The pores on the outer surface of the hyaline cells at the base of branch leaves are rather numerous in *S. imbricatum* (11–17 per cell in the middle of the base), and they are rather large, more or less rounded, and often enclosed in looplike or S-shaped fibrils. In the upper part of the leaf, below a large area of extensive resorption, the pores on the outer surface are 2–5 or 7 per cell, elliptic along the commissures but rounded and rather conspicuously grouped in 2's and 3's at adjoining angles. The green cells, as viewed in section, are equilaterally triangular. (The comb fibrils are often very conspicuous, but they are sometimes visible only near the leaf insertion; they are sometimes very poorly developed or even lacking in the so-called var. *affine* Ren. & Card.). The hyaline cells of stem leaves are consistently once-divided.

Sphagnum palustre normally has relatively few pores on the outer surface of hyaline cells throughout the branch leaves, although in some specimens toward the basal margins the pores may be as many as 10 to 13 per cell. They tend to be elliptic or rounded-elliptic, noticeably commisural in arrangement, and only rarely enclosed in loops or S's. More commonly, in the basal part of the leaf the pores are rather few and distinctly elliptic at the commissures but more rounded and noticeably larger at the ends and corners. In the upper part of the leaves, below the area of extensive resorption resulting in membrane gaps, the pores are 2–7 per cell and elliptic, with those at ends and corners rather conspicuously in 2's and 3's as one expects in the section *Sphagnum;* the grouping of corner pores is less conspicuous in *S. henryense* where the commissural pores are larger and more nearly rounded and therefore less differentiated from those of ends and corners. *Sphagnum palustre* has no comb fibrils or ridge reticulum on the commissures of hyaline cells of branch leaves, and it has undivided hyaline cells of stem leaves (as in *S. henryense*).

Sphagnum henryense Warnst., Hedwigia 39: 107. 1900.

S. henryense var. ∝ *Bartlettii* Warnst., Sphagn. Univ. 445. 1911.

Plants robust, in deep cushions or hummocks, pale-green or brown. Wood cylinder of stem brown; cortical cells in 3 layers, ± square or short-rectangular, fibrillose, the outer cells with (1)4–6(9) rounded pores. Stem leaves large, lingulate, rounded at the apex, finely fringed all around; hyaline cells not divided, not at all fibrillose or porose, or with a varying development of fibrils on both surfaces and pores on the outer, sometimes greatly resorbed on the outer surface with 1–3 or more large membrane gaps below and almost complete resorption near the apex, but sometimes with large membrane gaps only at the apex and/or upper median region and numerous large, rounded or rounded-elliptic pores, mostly along the commissures, in the side regions, across the lower 2/3 of the leaf, or nearly throughout, on the inner surface often with membrane pleats but no membrane gaps. Branches stout, in fascicles of 4–5, 2 spreading; cortical cells in 1 layer, conspicuously fibrillose, with 1–2 large, rounded pores. Branch leaves spreading, broadly ovate, concave-cucullate, roughened at back of the apex because of resorption, denticulate along a single row of apparently linear cells owing to marginal resorption (appearing as a furrow in section); hyaline cells rhomboidal, 6–8:1 at the leaf base, becoming shorter toward the apex, fibrillose, plane or nearly so on the inner surface, slightly to moderately convex on

FIG. A. *Sphagnum henryense.* 1. Fascicle of branches, X 2.5 2. Branch leaf, X 24. 3. Branch leaf in cross-section, X 350. 4. Upper cells of branch leaf, outer surface, X 350. 5. Upper cells of branch leaf, inner surface, X 350. 6. Basal cells of branch leaf, outer surface, X 350. 7. Branch cortex, X 103. 8. Stem cortex, X 103. 9. Stem leaf, X 24. 10. Upper median cells of stem leaf, X 350.

the outer, on the outer surface with 4–14 large, rounded-elliptic pores along the commissures above, with the apical pore similar to others or somewhat larger, and about 16–26 large, rounded pores in 2 or rarely 3–4 irregular rows in lower cells; on the inner surface with a few ringed pores in the corners in the upper part of the leaf and large, rounded pores in the middle of cells in the side regions, in a marginal row of cells sometimes as many as 12 in 2 rows, occasionally one or a few large, rounded pores in the leaf middle also; green cells in section narrowly or sometimes nearly equilaterally triangular with the base exposed on the inner surface and the sides somewhat convex, the lumen also triangular, the adjacent walls of hyaline cells with an irregular network of fine ridges, especially noticeable at the leaf base, usually very faint, sometimes fairly conspicuous, evident in cross-section as minute and irregular papillae. Apparently dioicous; antheridia not seen; perichaetial leaves large, oblong-ovate, the cells of upper and marginal portions dimorphous, porose and fibrillose, those toward the base uniformly narrow. Pseudostomata very numerous. Spores 24 μ, very finely papillose-roughened. – Fig. A.

In loose carpets and low cushions on peaty humus in wooded or shrubby swamps, at the edge of ponds or along streams, rarely submerged, along the coast in *Chamaecyparis* swamps, pocosins, and gum-cypress swamps, in distinctly acid habitats southward but in the northern part of its range apparently in minerotrophic habitats (as indicated, on labels, by an apparent association with alders and *Sphagnum teres* at the margins of *Chamaedaphne* mats or in *Chamaecyparis* "carrs"). Occurring interruptedly along the coast from Nova Scotia to Florida and westward to Louisiana and Arkansas; also in uplands in Massachusetts, New York, and North Carolina; Cuba.

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I appreciate the help of Lewis Anderson, who showed me populations of *Sphagnum henryense* in numerous North Carolina localities, shared with me records of unusual interest, and gave me a better understanding of the variability of this species and others needlessly confused with it. I am grateful to the National Science Foundation for support under grant BMS 73-0748. I am grateful for the opportunity of examining specimens in the herbaria of Duke University, the University of Tennessee, Cornell University, DePauw University, the Field Museum of Natural History, the Smithsonian Institution, the New York Botanical Garden, and the National Museum of Canada, as well as private herbaria of Winona Welch and Paul Redfearn.

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CARLOWRIGHTIA MCVAUGHII: A POLYMORPHIC SPECIES FROM SOUTHWESTERN MEXICO

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Carlowrightia (Acanthaceae) is a relatively small genus of shrubs and perennial subshrubs which range from the southwestern United States into northern Costa Rica. During my study of this genus, it became apparent that several collections from southwestern Mexico represented an undescribed and highly variable species.

Carlowrightia mcvaughii T. F. Daniel, sp. nov. Figs. 1–2.

Planta suffruticosa, usque ad 1 m alta. Caules glabri vel pubescentes. Folia petiolata vel subsessilia; petioli (0.5–) 1–4 mm longi; laminae ovatae vel cordiformes, (20–) 30–70 mm longae, (7–) 15–40 mm latae, 1.3–2.8-plo longiorae quam latiorae. Inflorescentia thyrsiformis usque ad 30 cm longa; thyrsus saepe glandulosus. Flores pedicellis 0.5–4 (–7) mm longis. Calyx quinquelobus, (4–) 5–7 (–10) mm longus. Corolla alba, pallide rosea, vel pallide purpurea, 13–16 mm longa. Capsula glabra, 10–13 mm longa. Semina ovalia, 4.8–5.5 longa, 3.5–4.2 mm lata; testa granulata, tuberculata.

Erect to spreading suffrutescent perennial to 1 m tall, arising from a stout to tortuous woody caudex to 15 mm in diameter or a woody rhizome to 8 mm in diameter. Numerous woody roots originating from the caudex. Older stems woody, glabrate. Younger stems green or purplish, ridge-angled to quadrate (to terete) below, terete to multistriate above, essentially glabrous to variously pubescent, frequently with a strigillose-pubescent understory, the trichomes eglandular, erect to retrorse, 0.05–0.2 mm long, and a strigose overstory of infrequent to dense, flexuous trichomes to 1.5 mm long, or with one layer of pubescence greatly elaborated with respect to the other. Lower internodes (20–) 60–90 mm long, upper internodes 35–60 mm long. Leaves ascendant, petiolate to subsessile. Petioles (0.5–) 1–4 mm long, pubescent like younger stems. Laminas ovate to cordiform, (acute) truncate to subcordate to cordate at base, acuminate to acute at apex, (20–) 30–70 mm long, (7–) 15–40 mm wide, 1.3–2.8 times longer than wide, reduced acropetally into lanceolate to linear-subulate bracts, 2–12 mm long, 0.5–3.5 mm wide; margins entire, flat, strigose-ciliate, the trichomes bent, 0.5–1.5 mm long; laminar surfaces minutely puberulent to densely strigose; several orders of venation evident on both surfaces. Inflorescence a terminal, leafy thyrse to 30 cm long; thyrse axis either glabrous, strigose-pubescent with eglandular, retrorse to erect trichomes, 0.05–0.5 mm long, or strigose-pubescent with an overstory of scattered to dense, capitate glands, 0.3–0.8 mm long. Flowers in lateral dichasia to 10 cm long, pedicellate from the axil of 2 bractlets, the pedicels 0.5–4 (–7) mm long. Bractlets of the dichasia 1.5–16 mm long, 0.3–5 cm wide, the lowermost lanceolate, the uppermost linear-subulate. Calyx deeply 5-lobed, (4–) 5–7 (–11) mm long, pubescent like inflorescence axis; tube 0.5–2 mm long; lobes subulate, 3.5–8 (–9.5) mm long. Corolla bilabiate, whitish to light pink or light purple with 2 faint, rose-colored lines on the upper lip, 13–16 mm long, strigillose on outer surface; tube 3.5–4 mm long, 1.5–2 mm in diameter; upper lip spatulate, 9–11.5 mm long, 2–3 mm wide, entire at apex; lower lip 10–12.5 mm long, trilobate, the lobes obovate-elliptical, 7–8.5 mm long, 2–3 mm wide. Stamens 8–8.5

FIG. 1. *Carlowrightia mcvaughii,* drawn from the type by Karin Douthit. a–b, habit × 0.5; c, calyx × 5; d, open capsule × 3.5; e, seed × 5; f, disc and ovary × 10; g, style apex and stigma × 50; h, corolla with upper lip removed, showing insertion of stamens × 3; i, anther × 10.

mm long; filaments becoming distinct from the corolla just below the lobes on the lower lip, 7–7.5 mm long, glabrous or pubescent especially near the base, the trichomes 0.1–0.2 mm long; thecae parallel, subequally inserted on filament, 1.5–2 mm long. Disc 0.7–0.8 mm long. Ovary glabrous; style terminal, 10–14 mm long, glabrous or pubescent especially near the base, the trichomes 0.1–0.4 mm long; stigma terminal on style, capitate to minutely bilobed, the lobes to 0.2 mm long. Capsules stipitate, 10–13 mm long, glabrous, scabridulous; stipe 3–5 mm long; head elliptical, laterally compressed, 7–8 mm long, including a terminal beak to 1 mm long; retinacula 2 mm long. Seeds usually 2 per capsule, white or turning black when mature, oval, laterally compressed, obliquely notched at chalazal end, 4.8–5.5 mm long, 3.5–4.2 mm wide; testa granulate, tuberculate; margins dentate.

Type: MEXICO. Jalisco: Precipitous S-facing mountainsides 4 miles NNE of Talpa de Allende, elev. 1450–1500 m, 12–13 Oct 1960 flr & frt. *McVaugh 20105* (MICH, holotype).

Flowering: August through November and probably sporadically during other months as well. Fruiting occurs simultaneously.

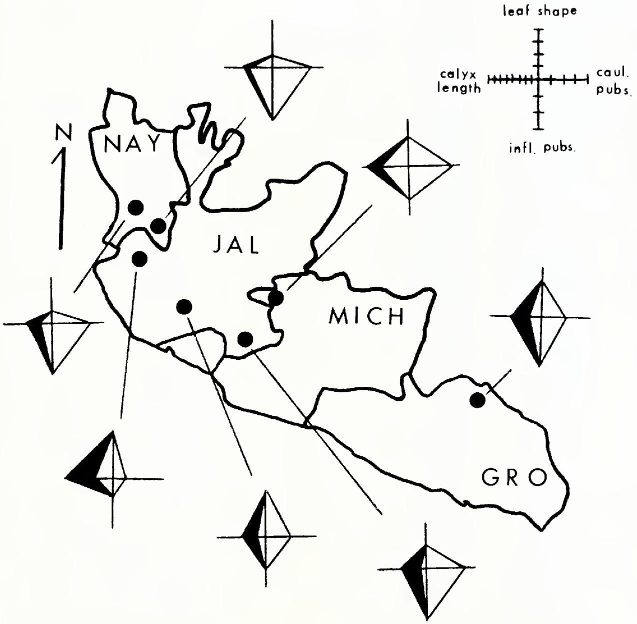

FIG. 2. Distribution and variation of *Carlowrightia mcvaughii*. See text for explanation.

Distribution and habitat: *Carlowrightia mcvaughii* is known to occur from southern Nayarit southeastward along the western escarpment of the Sierra Madre Occidental in Jalisco and eastward into Michoacán and Guerrero. The species is found sporadically to abundantly on wooded slopes in the sandy or clay loams of the oak forest zone at elevations of 1100 to 2000 meters.

Although *Carlowrightia* is primarily a genus of arid and semiarid associations, *C. mcvaughii* appears to be a mesophyte. It differs from other species in the genus by the combination of its large, ovate to cordiform leaves, well-developed and leafy thyrses, long calyces, white to light pink or purple corollas, and oval, tuberculate seeds. With respect to certain features, specimens of *C. mcvaughii* illustrate a high degree of variation. Figure 2 shows the variation of character states (in each case proceeding from the center of the axis to its periphery) encountered in seven specimens of *C. mcvaughii* with respect to the following characters: range of calyx length (4–11 mm), leaf shape (ovate, ovate to subcordiform, subcordiform to cordiform, cordiform), cauline pubescence (glabrous, understory pubescence with little or no overstory pubescence, understory and overstory pubescence, overstory pubescence with little or no understory pubescence), and inflorescence pubescence (glabrous, eglandular-pubescent, glandular-pubescent). Vesture is the most conspicuous variable with respect to *C. mcvaughii.* In addition to the variation shown on the polygons, the styles and filaments may be glabrous, partially pubescent, or entirely pubescent. The pubescence of these structures, however, is often variable from flower to flower on the same plant.

Despite the polymorphism exhibited by *C. mcvaughii,* no intraspecific taxa are recognized since the variation cannot be correlated geographically, ecologically, or altitudinally. Indeed the variability of *C. mcvaughii* is similar to that found in certain other species of the genus.

Additional specimens: Nayarit: Mountains 9 mi N of Compostela, elev. 1000–1200 m, 27 Aug 1957, *McVaugh 16456* (MICH); mountains 10 mi SE of Ahuacatlán, on road to Barranca del Oro, elev. 1100–1300 m, 11–12 Aug 1959, *Feddema 401* (MICH). Jalisco: Precipitous slopes, eastern foothills of the Sierra del Halo, ca 11–12 km W of Jilotlán de los Dolores, elev. 1300 m, 21 Nov 1970, *McVaugh 24583* (MICH); 13 km S de El Chante, mpio. Autlán, sobre el camino al Aserradero Tecopatlán, elev. 1450 m, 25 Aug 1976, *Rzedowski & McVaugh 1304* (ENCB, MICH). Michoacán: Cerro Santa María, 8–10 km SW of Jiquilpan and ca 5 km NE of Quitupan, elev. ca 2000 m, 8–9 Aug 1959, *Feddema 173* (MICH). Guerrero: Taxco, 21 Jul 1932, *Abbott 290* (GH); Taxco, 31 Aug 1932, *Abbott 369* (GH).

This species is named in honor of Dr. Rogers McVaugh, who recognized it as undescribed several years ago.

Contr. Univ. Mich. Herb. 14:61–67. 1980.

THE GENUS *JUSTICIA* (ACANTHACEAE) IN THE CHIHUAHUAN DESERT

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Justicia L. is the largest and most complex genus of Acanthaceae, containing 300 to 400 species. Although numerous segregate genera have been recognized, the current trend is to include *Dianthera* L., *Beleperone* Nees, *Jacobinia* Nees ex Moric., *Drejerella* Lindau, and others within the limits of *Justicia* (Gibson 1972, Durkee 1978). The genus is widely distributed in the tropics and subtropics of both hemispheres and occurs to a lesser extent in temperate areas. In the Chihuahuan Desert, *Justicia* may be distinguished from other Acanthaceae by the combination of two stamens with unequally inserted thecae of different sizes, the lower theca with a short spur, and the ampliate corolla tube. Although Standley (1926) does not list any species of *Justicia* from the Chihuahuan Desert Region of north-central Mexico, as defined by Henrickson and Straw 1976, four species, two of them described here, are now known to occur there. An additional species is known only from the arid regions of western Texas and the Chihuahuan Desert of southeastern New Mexico. These five rarely collected species comprise an unusual assemblage of linear-leaved, wispy subshrubs with ephemeral flowers. They can be distinguished by the following key:

1. Corolla 6.5–15 mm long; thecae more or less parallel to the filament, 0.5–1.3 mm long; spur on lower theca 0.2 mm long; seeds flat.
    2. Bractlets 10–19 mm long; calyx 5-lobed, 7–19 mm long, the lobes glandular; corolla 11–15 mm long, the outer surface glabrous. 1. *J. coahuilana*
    2. Bractlets 2.5–9 mm long; calyx 4-lobed, 2–4 mm long, the lobes eglandular; corolla 6.5–10.5 mm long, the outer surface pubescent.
        3. Young stems more or less evenly strigillose, the trichomes recurved-appressed: leaves pubescent.
            4. Leaves linear-subulate, 0.7–1.5 mm wide; corolla 6.5–7.5 mm long; lower theca 0.8–1 mm long. 2. *J. henricksonii*
            4. Leaves linear to oblanceolate, 1.5–4 mm wide; corolla 8.5–10.5 mm long; lower theca 1–1.3 mm long. 3. *J. wrightii*
        3. Young stems strigillose in two vertical, often decussate lines, the trichomes recurved; leaves glabrous. 4. *J. warnockii*
1. Corolla 15–20 mm long; thecae perpendicular or oblique to the filament, 1.9–2.8 mm long; spur on lower theca 0.5–1 mm long; seeds globose. 5. *J. linearis*

1. **Justicia coahuilana** T. F. Daniel, sp. nov. Figs. 1–2.

Planta suffruticosa, usque ad 3.5 dm alta. Caules juniores striati, glabri. Folia sessilia, linearia vel oblanceolata, 10–30 mm longa, 1–2 mm lata. Flores pedunculati, solitarii in axillis foliorum. Pedunculi 5–13 mm longi. Bracteolae 10–19 mm longae. Calyx quinquelobus 7–19 mm longus, extus glandulosus. Corolla glabra, 11–15 mm longa. Capsula 9–10 mm longa. Semina 3–3.5 mm diametro.

Erect to spreading, ± flimsy, suffrutescent perennial to 3.5 dm tall, arising from a woody base to 6 mm in diameter. Older stems whitish-grey or brown, ± striate, glabrous. Younger stems striate, the ridges brownish, the grooves greenish, glabrous. Leaves sessile, strongly ascendant, linear to narrowly oblanceolate, 10–30 mm long, 1–2 mm wide, 8–25 times longer than wide, acute at apex, the margins flat, glabrous. Flowers solitary in leaf axils, sessile between 2 bractlets at apex of a peduncle 5–13 mm long. Bractlets linear, 10–19 mm long, 0.5–0.8 mm wide, glabrous or with orangish, capitate glands along the upper 1/3, the glands 0.1–0.2 mm long. Calyx deeply 5-lobed, 7–19 mm long, glabrous below, glandular like the bractlets on the upper 1/2; tube 0.3–0.8 mm long; lobes linear-subulate, 6.5–18.5 mm long. Corolla bilabiate, 11–15 mm long, glabrous on outer surface; tube 5–7 mm long; lips 7–8 mm long. Stamens 4 mm long; filaments 3.5 mm long, glabrous; thecae ± parallel to filament, the upper theca 0.8 mm long, the lower theca 1 mm long including a spur 0.2 mm long. Style 7–8 mm long, glabrous; stigma ± capitate to minutely bilobed, the lobes 0.2 mm long. Capsules stipitate, 9–10 mm long, glabrous; stipe 3–3.5 mm long; head elliptical, laterally compressed, 6–7 mm long including a terminal beak to 1 mm long, 3–4 mm wide; retinacula 1.5 mm long. Seeds 4 (or fewer by abortion) per capsule, round, flat, obliquely notched at chalazal end, 3–3.5 mm in diameter; testa smooth and glabrous on one side, smooth to muriculate and pubescent on the other, the trichomes appressed to erect, 0.1 mm long; margin recurved, fringed with minute capitate glandular trichomes 0.1 mm long.

Type: MEXICO. Coahuila: Mouth of canyon, 4 miles W of Cuatro Ciénegas, 24–26 Aug 1938 flr & frt, *Johnston 7162* (GH, holotype).

Paratype: MEXICO. Coahuila: Rocky slopes of canyon, 4 miles W of Cuatro Ciénegas, 2800 ft, 26 Aug 1938, *Shreve 8465* (ARIZ).

This species is known only from a canyon west of Cuatro Ciénegas in central Coahuila. According to D. J. Pinkava (pers. comm.), the Cuatro Ciénegas Basin and the surrounding mountains are extremely rich in species, the area being one of the richest in the Chihuahuan Desert Region.

2. **Justicia henricksonii** T. F. Daniel, sp. nov. Figs. 1–2.

Planta suffruticosa, usque ad 3 dm alta. Caules juniores striati, pubescentes. Folia sessilia, linearia-subulata, 7–20 mm longa, 0.7–1.5 mm lata. Flores solitarii, sessiles in axillis foliorum vel brevipedunculati apicibus ramorum. Bracteolae 4–9 mm longae. Calyx quadrilobus 3–3.5 mm longus, extus eglandulosus. Corolla strigillosa, 6.5–7.5 mm longa. Capsula 7–7.5 mm longa. Semina 2.5–3 mm longa, 2.5 mm lata.

Erect, basally branched, wispy, suffrutescent perennial to 3 dm tall, arising from a stout or gnarled woody caudex to 15 mm in diameter. Older stems whitish-grey, striate to terete, glabrate. Younger stems green, striate, ± evenly and sparsely strigillose, the trichomes eglandular, recurved-appressed, 0.1–0.2 mm long. Leaves sessile, horizontal to ascendant, linear-subulate, 7–20 mm long, 0.7–1.5 mm wide, 10–27 times longer than wide, acute at the apex, the margins flat, pubescent like the young stems although frequently more densely so. Flowers solitary, sessile in leaf axils or short-pedunculate at branch apices, subtended by 2 bractlets. Peduncles 1–2 mm long. Bractlets linear-subulate, (2.5–) 4–9 mm long, 0.5–0.9 mm wide, pubescent like the leaves or more densely so. Calyx deeply 4-lobed, 3–3.5 mm long, pubescent like the bractlets; tube 0.5–1 mm long; lobes subulate, 2–3 mm long. Corolla pinkish, bilabiate, 6.5–7.5 mm long, strigillose on outer surface, the trichomes 0.2–0.3 mm long; tube 3.5–4 mm long; upper lip emarginate, 2.5–3 mm long, lower lip trilobate, 2.5–3 mm long, the lobes 1.5–2 mm long, 1.5–2 mm wide, the central lobe larger than the outer lobes. Stamens 3 mm long; filaments 2.5 mm long, glabrous; thecae ± parallel to filament, the upper theca 0.5–0.7 mm long, the lower theca 0.8–1 mm long, including a spur 0.2 mm long. Style 2.5–4 mm long, strigillose at base; stigma ± capitate to minutely bilobed, the lobes 0.2 mm long. Capsules stipitate, 7–7.5 mm long, glabrous to sparsely strigillose below, strigillose on beak, the trichomes 0.2–0.3 mm long; stipe 2–2.5 mm long; head elliptical,

FIG. 1. *Justicia coahuilana* and *J. henricksonii,* a–d, *J. coahuilana* (from holotype): a) habit, X 0.5; b) leaf, X 3; c) opened capsule with one seed and persistent calyx, X 4; d) sepal tip, X 5. e–i, *J. henricksonii* (from holotype): e) habit, X 0.5; f) leaf, X 3.5; g) capsule and persistent calyx, X 3.5; h) sepal tip, X 11.5; i) opened capsule with three seeds, X 3.

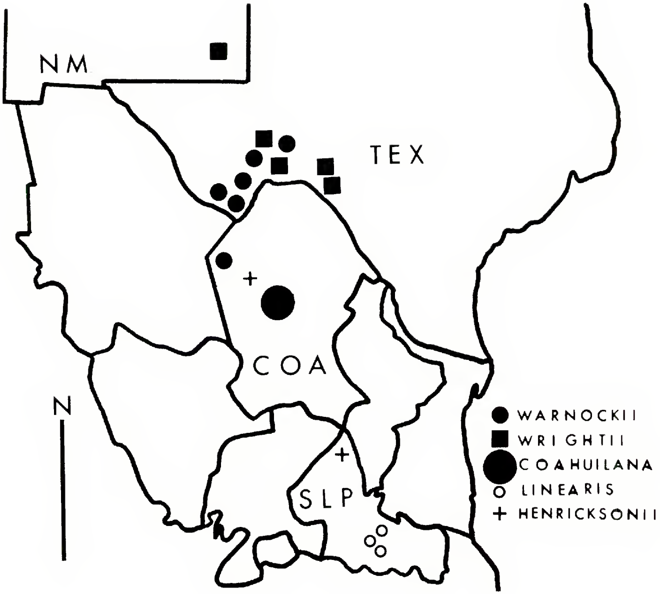

FIG. 2. Distribution of the species of *Justicia* in the Chihuahuan Desert and adjacent areas.

laterally compressed, 4.5–5 mm long including a terminal beak 0.5–0.8 mm long, 4 mm wide; retinacula 1.3–1.5 mm long. Seeds 4 (or fewer by abortion) per capsule, round to obcordiform, flat, obliquely notched at chalazal end, 2.5–3 mm long, 2.5 mm wide; testa muriculate, floccose; margin flat to somewhat recurved, fringed with glandular trichomes 0.2–0.3 mm long.

Type: MEXICO. Coahuila: Road from Puerto del Caballo easterly, 16 km across the broad valley to the low hills at Tanque Jerico, ca. Lat. 27° 34′ N, valley floor, one colony on silty barreal, 22–23 Aug 1941 flr & frt, *Johnston 8324* (GH, holotype; F, GH, isotypes).

Paratype: MEXICO. San Luis Potosí: 24 miles S of Salado, in shade of bushes, 5550 ft, 22 Aug 1940, *Shreve & Tinkham 9631* (GH).

Justicia henricksonii appears to be most closely related to *J. wrightii* of the United States, from which it differs by its more robust habit, less densely strigillose stems, narrower leaves, smaller corollas, and shorter thecae. Shreve and Tinkham's fruiting specimen from San Luis Potosí is a flimsier, more open plant with somewhat longer leaves and internodes than the type material from Coahuila. However, in these characters there is considerable overlap with Johnston's specimens and in all other characters this plant is indistinguishable from *J. henricksonii.* The label data on Shreve and Tinkham's specimen note that the plant grew "in shade of bushes," and this specimen is therefore regarded as a shade form of *J. henricksonii.*

This species is named in honor of Dr. James Henrickson, a student of the Acanthaceae of the Chihuahuan Desert Region who has given me considerable assistance during my study of the Acanthaceae of Mexico.

3. **Justicia wrightii** A. Gray, Syn. Fl. N. Am. 2: 329. 1878.

Ecbolium wrightii (A. Gray) O. Ktze., Rev. Gen. 2: 981. 1891. Type: Texas: Val Verde Co.: Western Texas to El Paso, New Mexico, calcareous hills on the San Felipe, May–Oct 1849, *Wright 445* (GH, holotype; US, isotype).

Erect, basally branched, suffrutescent perennial, 8–15 cm tall, arising from a stout, woody caudex to 7 mm in diameter. Older stems whitish-grey or brown, striate, glabrate. Younger stems striate, the ridges frequently brownish, the grooves green, ± evenly strigillose, the trichomes eglandular, recurved-appressed, 0.1–0.2 mm long. Leaves sessile, ascendant, linear to oblanceolate, (5–) 10–15 mm long, 1.5–4 mm wide, 2.8–8.6 times longer than wide, usually reduced in size acropetally, acute to rounded at apex, the margins flat, pubescent like the young stems. Flowers solitary, sessile in leaf axils, subtended by 2 bractlets. Bractlets linear-subulate, 2.5–6 cm long, 0.5–0.7 mm wide, pubescent like the leaves. Calyx deeply 4-lobed, 2.5–3.8 mm long, pubescent like the leaves; tube 0.4–0.5 mm long; lobes subulate, 2–3.3 mm long. Corolla purplish, bilabiate, 8.5–10.5 mm long; tube 4.5–5 mm long; upper lip emarginate, 4.5–6 mm long, 2.8–3 mm wide at base; lower lip trilobate, 4–5.5 mm long, the lobes 3–4 mm long, 1.5–3.5 mm wide, the central lobe larger than the outer lobes. Stamens 3–5 mm long; filaments 2–3.5 mm long, glabrous; thecae ± parallel to filament, the upper theca 0.6–0.9 mm long, sparsely strigillose, the lower theca 1–1.3 mm long including a spur 0.2 mm long. Style 4.5–6 mm long, sparsely strigillose near base; stigma ± capitate, 0.2–0.3 mm long. Capsules stipitate, 8 mm long, glabrous or with a few scattered trichomes at apex; stipe 2 mm long; head elliptical, laterally compressed, 6 mm long including a terminal beak 0.8–1 mm long, 3.7–4 mm wide. Seeds not seen, reported as oval to elliptic, 2.5 mm long, 3 mm wide, mucronate, puberulent (Wasshausen 1966).

Additional specimen examined: U.S.A. New Mexico: Eddy Co.: Carlsbad, 9 Jun 1958, *McKechnie 29* (MO).

Justicia wrightii is reported to be endemic to the western edge of the Edwards Plateau in Texas (Correll and Johnston 1970), and this report extends its range into the Chihuahuan Desert of southeastern New Mexico (Fig. 2). The only other *Justicia* known from this part of the Chihuahuan Desert is *J. warnockii,* which may be expected to occur in New Mexico as well. Both species are sufficiently rare to be listed as threatened species in Texas (Ayensu and DeFilipps 1978).

4. **Justicia warnockii** Turner, Field & Lab. 19: 100. 1951. Type: Texas: Brewster Co.: Limestone slope one third way up Old Blue, Glass Mountains, 2 Jun 1941, *Warnock W325* (TEX, holotype; DS, F, GH, NCU, NY, PH, SRSC, UC, UCLA, isotypes).

Erect, basally branched, broom-like to globose suffrutescent perennial to 40 cm tall, arising from a stout, woody caudex, 5–15 (–25) mm in diameter. Older stems whitish-grey, striate to terete, glabrate. Younger stems green, striate, strigillose (rarely only slightly so) in 2 vertical, often decussate lines, the trichomes eglandular, recurved, 0.05–0.2 mm long. Leaves sessile, strongly ascendant, linear to narrowly oblanceolate (to obspatulate near base of plant), 2.5–20 mm long, 0.4–1.3 (–2) mm wide, 6–18 times longer than wide, acute at apex, the margins flat to somewhat revolute, glabrous. Flowers solitary, sessile in leaf axils or sessile in the axils of reduced leaves or bracts along the upper portion of the stem, forming a spicate axis to 8 cm long, each flower subtended by 2 bractlets. Bractlets linear-subulate to filiform, 2.5–4.5 mm long, 0.2–0.4 mm wide, glabrous. Calyx deeply 4-lobed, (2–) 3–4 mm long, strigillose, especially near base; tube 0.3–0.5 mm long; lobes subulate, (1.5–) 2.5–3.5 mm long. Corolla lavender with purplish markings in throat, bilabiate, 7–10 mm long, strigillose on outer surface; tube 4.5–5 mm long; upper lip emarginate, 4–5 mm long, 1.3–2.2 mm wide at base, lower lip 6 mm long, trilobate, the lobes 2–3 mm long, 1.2–3 mm wide, the central lobe larger than the outer lobes. Stamens 3.5 mm long; filaments 2–3 mm long, glabrous; thecae ± parallel to filament, the upper theca 0.5–0.6 mm long, the lower theca 0.7–0.8 mm long including a spur 0.2 mm long. Style 5–7 mm long, glabrous; stigma ± capitate, 0.2 mm long. Capsules stipitate, 6.5–8 mm long, glabrous; stipe 2–3.2 mm long; head elliptical, laterally compressed, 4.5–5 mm long including a terminal beak 0.5–0.8 mm long, 2.5–3 mm wide; retinacula 1–1.8 mm long. Seeds 4 (or fewer by abortion) per capsule, round to oval, flat, obliquely notched at chalazal end, 2–2.5 mm long, 2–2.5 mm wide; testa granulate, glabrous (or glandular); margin flat to recurved, fringed with capitate glandular trichomes 0.1 mm long.

Additional specimens examined: U.S.A. Texas: Brewster Co.: Reagan Canyon, 1800 ft, 24 Dec 1946, *Warnock & Hinckley 3742* (NY); limestone slopes of Reagan Canyon, 3 miles from the Rio Grande, 24 Dec. 1946, *Hinckley & Warnock 461097* (TEX, UC); Crockett Co.: Rocky limestone bluff of Pecos River, above its junction with Independence Creek, 6 Jul 1949, *Webster 492* (MICH); Pecos Co.: Rocky limestone slopes, main canyon on NE side of Sierra Madera, about 25 miles S of Fort Stockton, 26 May 1949, *McVaugh 10654* (DS, DUKE, ENCB, MICH, MO, NY, PH, UC); mesa margins, 17 Jul 1943, *Tharp 43-854* (NY, PH, UC). MEXICO. Coahuila: Calcareous eastern foothills of the Sierra de las Cruces, Picacho de San José, rocky N ridge, 17 Aug 1941, *Johnston 8205* (F, GH); about 15 miles below Picacho del Centinela in limestone soil, 24 Aug 1953, *Warnock 11536* (MICH).

This species is reported to be endemic to the Trans-Pecos region of western Texas (Correll and Johnston 1970). This report extends its known range into the Chihuahuan Desert of western Coahuila (Fig. 2). Turner (1951) noted the unique vegetative aspect of *J. warnockii* and its similarity to *Carlowrightia linearifolia* A. Gray. Indeed most collections are annotated as the latter species. Fertile material of *J. warnockii* may be distinguished from *C. linearifolia* by the obliquely attached thecae, the lower theca with a spur, and by the retinacula which are inserted at different heights in each locule of the capsule. Vegetatively, *C. linearifolia* is a tall (to 1 m), openly-branched shrub with evenly puberulent stems and leaves. In contrast, *J. warnockii* is a low (to 4 dm), broom-like subshrub with strigillose stems, the trichomes being disposed in two vertical lines, and glabrous leaves.

5. **Justicia linearis** Rob. & Greenm., Amer. J. Sci. 50: 161. 1895. Type: Mexico. San Luis Potosí: Dry hills, Las Tablas, 5 Aug 1891, *Pringle 5038* (GH).

Erect to decumbent subshrub to shrub to 4 dm tall. Older stems whitish-grey, irregularly fissured, glabrate below, canescent above. Younger stems green, striate, strigillose-canescent, the trichomes evenly distributed, straight to recurved, 0.3–0.5 mm long. Leaves sessile, mostly crowded at nodes of new growth, strongly ascendant, linear to filiform, 7–40 mm long, 0.5–2 mm wide, 10–30 times longer than wide, acute at apex, the margins revolute, pubescent like the young stems although the trichomes are frequently shorter, the older leaves whitish-grey, persistent. Flowers solitary, sessile in leaf axils, subtended by 2 bractlets. Bractlets linear-subulate, 6–9 mm long, 0.7–1 mm wide, pubescent like the leaves, the margins conspicuously ciliate. Calyx deeply 5-lobed, 8–11 mm long, pubescent like the bractlets; tube 1–2 mm long; lobes subequal, linear-subulate, 6–10 mm long. Corolla white on outside, lobes maroon-purple within, bilabiate, 15–20 mm long, strigillose on outer surface; tube 10–11 mm long, upper lip entire to emarginate, 5.5–6.5 mm long, 4.5–5 mm wide at base, with a prominent rugula within; lower lip 5–9 mm long, trilobate, the lobes 3–5 mm long, 2–4 mm wide, the central lobe larger than the outer lobes. Stamens 8–8.5 mm long; filaments 6.5–7 mm long, glabrous; thecae perpendicular or oblique to filament, the upper theca 1.9–2.1 mm long including a basal spur 0.05–0.3 mm long, the lower theca 2–2.8 mm long including a basal spur 0.5–1 mm long. Style 12 mm long, glabrous above, pubescent along lower half, the trichomes ascending, 0.2–0.4 mm long; stigma capitate to bilobed, the lobes 0.2–0.3 mm long. Capsules stipitate, 11–15 mm long, pubescent, the trichomes 0.3–0.4 mm long; stipe 4–8 mm long; head elliptical, not laterally compressed, 7–8 mm long including a terminal beak 0.5–0.8 mm long, 4.5–5 mm wide; retinacula 2 mm long. Seeds 4 (or fewer by abortion) per capsule, globose, 3 mm in diameter, testa smooth, with an understory of appressed trichomes 0.05 mm long, and an overstory of scattered, flexuous trichomes 0.2–0.3 mm long.

Additional specimens examined: MEXICO. San Luis Potosí: San Francisco, 20 km al NE de Rioverde, 1000 m, llano con vegetación de mezquital, 14 Sep 1954, *Rzedowski 5141* (MO); ± 5 km al SE de San Francisco, Mpio. de Rioverde, ± 1000 m, terrenos aluviales con vegetación de mezquital, 21 Jan 1957, *Rzedowski 8653* (MICH); open plains near San Francisco, 800–1200 m, 14–15 Sep 1954, *Sohns 1259* (US); Las Tablas, rocky hill, 1000–1100 m, 9–10 Aug 1934, *Pennell 18033* (GH, US); 47.5 road miles E of El Huizache (at Hwy. 57) on Hwy. 80 to Cd. del Maiz, 23.1 miles W of Cd. del Maiz, in gypsum flats, 1200 m, 24 Sep 1978, *Henrickson & Lee 17574* (MICH).

This species is found in the southernmost part of the Chihuahuan Desert in central San Luis Potosí and in the semi-arid associations in the vicinity of San Francisco in the southeastern part of the state (Fig. 2). The four preceding species appear to form a closely related group from which *J. linearis* differs in several important characters. In addition to its larger corolla, thecae, and thecal spurs, the thecae of *J. linearis* are more perpendicular than parallel to the filament, and the seeds are globose rather than flat.

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TWO NEW CUCURBITACEAE FROM MEXICO

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University of Michigan

Among Cucurbitaceae collected in Mexico by various University of Michigan expeditions are two apparently undescribed plants from the Pacific lowlands, one a species of *Sechiopsis,* the other a species allied to members of the genus *Sicydium,* but different in having a more specialized androecial structure, and variant in other characters. These two entities are described here, one as a new species, the other as a new genus and species.

Sechiopsis tetraptera Dieterle, sp. nov. Fig. 1.

S. triquetrae (Ser.) Naud. affinis, a qua fructibus barbatis acuminatisque et inflorescentia staminata laxa differt.

Herba scandens 2–10 m longa. Radix grosse fibrosa. Caules sat graciles sulcati plus minusve pubescentes vel glabrati internodiis 9–24 cm longis. Cirrhi plerumque 4-partiti. Foliorum lamina membranacea simplex ambitu late ovata, suborbicularis, vel reniformis usque ad 14 cm longa palmatim 3(–5)-lobata lobis basilaribus subauriculatis utrinque plus minusve scabridula hispidulaque subtus densius sinu basilari rectangulari; petiolus 1–3(–7) cm longus. Flores sat parvi viridulo-flavi viridinervi. Florum staminatorum inflorescentia paniculata ramulis paucis 5–23 cm longa glanduloso-puberula. Flos staminatus: pedicellus tenuis 10–21 mm longus; hypanthium cupuliforme 2.5–4 mm longum infime nectariis saccatis 10; sepala 5 subulata 0.3–1 mm longa; corollae lobi late triangulares 3.5–4 mm longi basin breviter connati; filamentorum columna tenuis 1.5 mm longa; antherarum capitulum truncate obpyriforme; thecae 5 triplicatae; pollinis granum 10-colpatum echinatum ca 55 μ diametro. Inflorescentia pistillata: florum fasciculus pedunculatus, pedunculo communi tenui 11–16 mm longo glanduloso-puberulento. Flos pistillatus flore staminato minoris; pedicellus tenuis 0.3–1.5 mm longus dense puberulentus; ovarium anguste ovato-attenuatum alatum rostratum inter alas dense lanatum; hypanthium cupuliforme 1.3–2.2 mm longum nectariorum saccatorum destitutum; sepala 4 (interdum 3) dentiformia vel subulata 0.3–0.6 mm longa; corollae lobi 4(3 si sepala 3) late triangulares 1.2–2.6 mm longi; stylus 1 tenuis 2.5–3.1 mm longus, glaber; stigmata 3 dilatata recurvata. Fructus siccus 1.5–2.5 cm longus indehiscens unilocularis quadrialatus (interdum trialatus) longe acuminatus inter alas albo-barbatus. Semen solitarium pendente laeve anguste ovoideum leviter compressum 7 mm longum 2.3 mm latum 1.4 mm crassum.

TYPE: MEXICO. JALISCO: Along the main highway from Guadalajara to Autlán and Barra de Navidad, about 19 km from Melaque, 8–9 Nov 1971, *Dieterle 4124* (MICH, holotype).

Additional representative specimens: JALISCO: Vicinity of Barra de Navidad, 23 Sep 1969, *Dieterle 3524;* along the highway between Barra de Navidad and Chamela, 10–12 Nov 1971, *Dieterle 4131, 4152, 4155A, 4159;* UNAM Biological Field Station, 7–8 km southeast of Chamela, 12 Feb 1975, *H. & M. Gentry 23537;* coastal plain near the highway to Autlán, 4 miles north of Bahía Navidad, 8 Nov 1960, *McVaugh 20829;* steep forested hills 2–6 km southeast of La Manzanilla, above Bahía Tenacatita on the new road to Melaque, 9 Dec 1970, *McVaugh 25043;* "Centro de Investigación

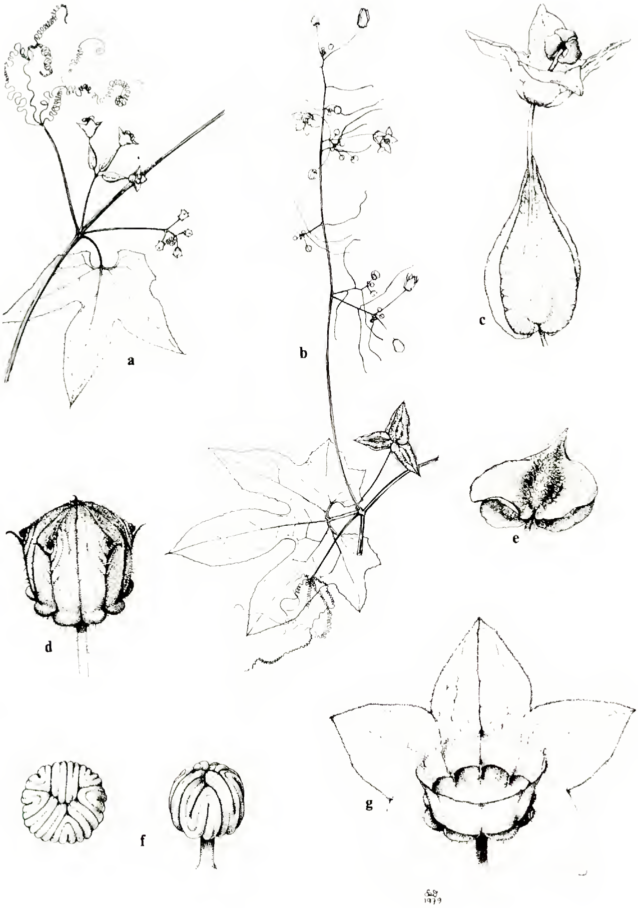

FIG. 1. *Sechiopsis tetraptera,* drawn from the type by Karin Douthit. a, node with pistillate inflorescence X 1; b, node with staminate inflorescence and fruit cluster X 0.5; c, pistillate flower X 5; d, staminate bud X 10; e, basal aspect of tilted fruit X 2.5; f, apical and lateral views of androecial head X 7.5; g, staminate flower with androecium removed X 5, semidiagrammatic.

y Experimentación de la UNAM," 8 km east of Chamela, 8–10 Dec 1970, *McVaugh 25086;* vicinity of Estación Biologica, UNAM, 3 km southeast of Chamela, 13–14 Feb 1975, *McVaugh 26258;* stream-valley crossing the highway to Autlán, 9 miles north of the road-junction at the west end of Bahía de Navidad, 12–13 Dec 1959, *McVaugh & Koelz 1744.* COLIMA: About 29 km east of Manzanillo, along route to Armeria, 25 Sep 1969, *Dieterle 3533;* along highway from Manzanillo to Colima, 12–13 Nov 1971, *Dieterle 4162, 4165.*

The genus *Sechiopsis* now includes two species, separable as follows:

S. triquetra (Ser.) Naud.: fruits ovoid, mostly 3-winged or -angled, the wings rounded at apex, the faces between wings finely and densely short-hispid to glabrous (never white-wooly); fruit clusters pedicellate and umbellate on short peduncles; staminate flowers in sessile or short-branched clusters along erect rachises, the inflorescences glabrous or nearly so; uplands, ca 600 m or higher.

S. tetraptera Dieterle: fruits long-acuminate, mostly 4-winged, the wings attenuate at apex, each face between wings adorned with a white-wooly stripe; fruit clusters nearly sessile at the tips of slender, drooping peduncles; staminate flowers loosely paniculate, the panicles 1–3-branched, glandular-pubescent; lowlands, sea level to ca 500 m.

Chalema Dieterle, gen. nov. [*Zanonieae - Sicydiinae* Pax] ex affinitate *Sicydii* Schlechtendal a qua staminibus connatis fructibus siccis et habitu monoecio differt.

Herba annua monoecia; radices fibrosae; folia simplicia cordata membranacea; cirrhi apice bifidi; flores pentameri minuti, masculis feminisque in paniculis parvis simul dispositis; corolla alba rotata usque ad basim 5-partita; staminum filamenta in columnam connata; connectiva non producta; antherarum loculi 5 ellipsoidei rimis unicis horizontalibus dehiscentes; pollinis granum prolatum striatum tricolporatum; floris pistillati calyx et corolla eis floris staminati similes; styli 3 liberi; fructus parvulus subglobosus monospermus siccus indehiscens; semen sphaericum pendente testa crustacea.

Species nominis generis typica: *Chalema synanthera* Dieterle.

Chalema synanthera Dieterle, sp. nov. Fig. 2.

Herba gracilis scandens aliquantum puberula vel glanduloso-puberula ubique; caules 1–3 m longi graciles striati parce ramosi; cirrhi longi subtiles; foliorum laminae membranaceae acuminatae 4–5(–5.5) cm latae; petioli graciles striati 1.5–3(–4) cm longi; paniculae parvae petiolis propinquis breviores vel vix longiores; flores circa 1.5–2 mm diametro; flores staminati floribus pistillatis circa 10-plo numerosiores; flos staminatus: pedicellus gracilis attenuatus inarticulatus ebracteatus 1.3–2.8 mm longus, hypanthium disciforme viride glabrum (0.4–)0.5–0.6 mm diametro, sepala ovata virella plus minusve villosula 0.3–0.4 mm longa, petala ovato-lanceolata alba vel albido-viridia 0.7–0.8 mm longa intus villosula vel marginibus villosulis, filamentorum columna viridis glabra gracilis (0.2–)0.25(–0.3) mm longa, antherarum capitulum 0.3 mm latum connectivis glabris, pollinis granum prolatum circa 30 μ longum 16 μ latum; flos pistillatus: ovarium ovoideum 0.7 mm longum plus minusve hispidulosum, styli graciles lineares vel uncinati; fructus 3–3.5 mm diametro pericarpio tenue puberulus et plus minusve hispidulus paulim rostratus floris vestigiis longe persistentibus; semen ca 3 mm diametro paulim rostratum testa verrucosa.

TYPE: MEXICO. MICHOACÁN: 11–13 km WSW of Apatzingán, along road to Dos Aguas and Aguililla, elev. ca 300 m, low hill with volcanic rocks and debris; thickly overgrown with shrubs, 5–9 Sep 1972, *Dieterle 4307* (MICH, holotype).

Distribution. Mexico (Jalisco and Michoacán). Known to me only from the type and one other collection: *McVaugh 25095,* 8 km E of Chamela, Jalisco, lowland forest of *Cordia, Caesalpinia, Thouinidium,* elev. 30–50 m, 8–10 Dec 1970.

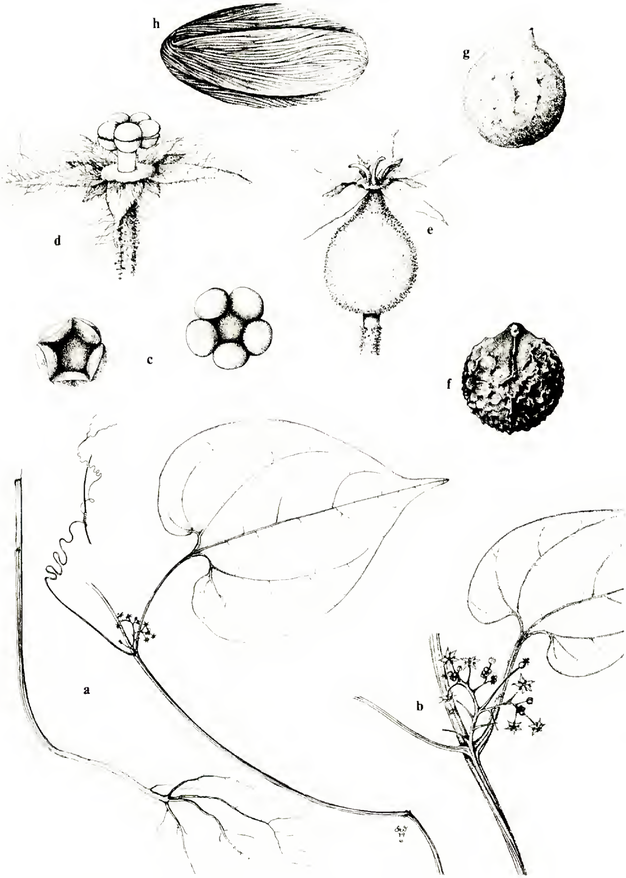

FIG. 2. *Chalema synanthera*, drawn from the type by Karin Douthit. a, root and fertile node × 1; b, fertile node × 2.5; c, anther sacs after and before dehiscence × 35; d, staminate flower × 25; e, pistillate flower with one sepal removed × 25; f, seed × 6; g, fruit × 6; h, pollen grain × 1500.

This species is the only representative of the subfamily *Zanonioideae* C. Jeffrey in Western Mexico. Its androecial structure, consisting of a central column of united filaments bearing a horizontal ring of anther sacs at its apex, is a primary character distinguishing it from members of the genus *Sicydium,* in which the androecium consists of three separate stamens, two double and one single. Its features of monoecy and annual habit are not found in any other known *Zanonioideae.* The genuineness of these attributes may therefore be doubted. However, the monoecious condition, evident in specimens taken from widely separated localities on dates months apart in the season, can hardly be dismissed as abnormal, and it is difficult to concede that these small fibrous-rooted vines may be perennial through the long and severe dry-season occurring yearly in their habitat. None of the material at hand, 25 sheets, includes vines that appear to be unisexual, or roots of a type other than fibrous.

Etymology: the generic name is an anagram of Chamela, a town near which the new species is reported to be frequent; the specific epithet alludes to the plant's androecial structure.

Contr. Univ. Mich. Herb. 14:75–82. 1980.

ADDITIONS TO THE HYPOGEOUS MYCOFLORA OF THE CANARY ISLANDS AND MADEIRA

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Mycological investigations in Macaronesia (Canary Islands, Madeira, Cape Verde Islands, Azores) have produced few records of hypogeous fungi. Of the Basidiomycotina, only *Hymenogaster vulgaris* Tul. var. *madeirensis* Torrend has been reported from Madeira (Torrend 1912). Reported collections from the Canaries include *Hydnangium carneum* Wallr. in Dietr. (Calonge and Demoulin 1975, Eckblad 1975), *Rhizopogon luteolus* Fr. em. Tul. (Calonge and Demoulin 1975, Eckblad 1975), and *Rhizopogon vulgaris* (Vitt.) M. Lange (Calonge and Demoulin 1975). *Hymenogaster maurus* Maire is the only hypogeous basidiomycete reported from the Azores (Dennis et al. 1977). No hypogeous Ascomycotina or Endogonaceae have been reported from Macaronesia.

Nearly all of the hypogeous fungi described herein were collected during an expedition to Madeira and the islands of Tenerife, Gomera, and Hierro in the Canary Islands archipelago during December 1976 and January 1977. The steep topography of these islands, decreased precipitation from west to east, and both endemic and exotic mycorrhizal hosts combine to create an amazing variety of potential habitats for hypogeous fungi.

The Canarian vascular plant flora totals some 1,750 species of which 550 are endemic (Bramwell and Bramwell 1974). The dense native evergreen hardwood forest is dominated by presumed endomycorrhizal hosts: *Laurus azorica* (Seub.) Franco, *Apollonias barbujana* (Cav.) Bornm., *Ocotea foetens* (Aiton) Benth., and *Persea indica* (L.) Spreng. The native ectomycorrhizal *Pinus canariensis* Chr. Sm. ex DC. forest is an open, savanna-like formation resembling the ponderosa pine forest in central Oregon. In addition to the native forests, stands of exotic *Picea, Pinus,* and *Eucalyptus* have been introduced in reforestation (Kunkel 1976).

The native evergreen hardwood forest of Madeira is similar to that of the Canaries with exotic *Pinus, Eucalyptus,* and *Pseudotsuga menziesii* (Mirb.) Franco also introduced for timber production and regulation of the island's water economy.

Only new records of hypogeous fungi for Macaronesia are fully described here. Hypogeous fungi were collected by raking away the humus and then a few cm into the mineral soil. After specimens were dried in repeated changes of activated silica gel, freehand sections mounted in 3% KOH, lactophenol-cotton blue, or Melzer's reagent were used for observation of microscopic features. Colors of sporocarps were determined by use of the ISCC-NBS color charts (Kelly and Judd 1965). Collections are deposited in the herbaria of Cornell University (CUP), Oregon State University (OSC), and Universidad de La Laguna, Tenerife, Canary Islands (LAG).

ZYGOMYCOTINA

1. **Endogone flammicorona** Trappe & Gerdemann, Trans. Br. Mycol. Soc. 59: 403–407. 1972.

Material examined: MADEIRA: leg. Korf et al. MM1509 (CUP, OSC).
Habitat and season: hypogeous under *Pseudotsuga menziesii* in January.

Sporocarps up to 7 X 3 mm, globose to subglobose, pale orange yellow to brownish orange. *Zygospores* 45–55 X 57–63 μm, globose to ellipsoid or obovoid, deep yellow; spore wall up to 4 μm thick. Spores enclosed in a hyphal mantle, up to 11 μm thick, hyphae encircling spore in a spiral manner; in cross section thickened lateral walls of two adjacent hyphae coalesce to form pointed, flame-shaped projections from the spore.

Gerdemann and Trappe (1974) have described this species in detail and give its distribution as widespread but infrequent in North America and Europe. Fassi and Palenzona (1969) have demonstrated it to form ectomycorrhizae with Pinaceae; it may have been introduced with *Pseudotsuga menziesii.*

2. **Glomus fasciculatus** (Thaxter) Gerdemann & Trappe, Mycol. Mem. No. 5, p. 51–53. 1974.

Material examined: CANARY ISLANDS: TENERIFE, leg. Korf et al. MM1247 (CUP, OSC). *MADEIRA:* leg. Korf et al. MM1571 (CUP, OSC).

Habitat and season: on soil under *Eucalyptus* sp. and *Cupressus* sp. in January.

Sporocarps up to 4 X 2 mm, flattened, tuberculate, light orange yellow. Peridium lacking. *Gleba* light orange yellow. *Chlamydospores* 55–73 X 53–70 μm, subglobose, smooth, light yellow; spore wall up to 7 μm thick.

Gerdemann and Trappe (1974) have described this species and its distribution as North America, Europe, and Australia, and indicate that it is probably associated with most of the endomycorrhizal hosts where it occurs.

3. **Glomus macrocarpus** Tul., Giorn. Bot. Ital. I, 2: 63. 1845 var. **macrocarpus.**

Material examined: CANARY ISLANDS: GOMERA, leg. Korf et al. MM1369, MM1370 (CUP, OSC).

Habitat and season: in mixed forests under *Ilex canariensis* Poir. in January.

Sporocarps up to 8 X 6 mm, irregularly globose, containing a considerable proportion of soil in the lower portion, light orange yellow as dried, exterior covered with soil particles. Peridium thin. *Gleba* light orange yellow. *Chlamydospores* 148–222 X 136–171 μm, globose to subglobose, smooth, yellow brown; spore wall up to 17 μm thick.

Gerdemann and Trappe (1974) indicate this species is widely distributed over much of the world, associated with a wide variety of endomycorrhizal hosts.

4. **Glomus microcarpus** Tul., Giorn. Bot. Ital. I, 2: 63. 1845.

Material examined: MADEIRA: leg. Korf et al. MM1500 (CUP, OSC).

Habitat and season: in leaf mold in mixed *Laurus* spp. forest in January.

Sporocarps up to 5 X 2 mm, irregularly globose, white to pale orange yellow as dried. Peridium thin. *Gleba* moderate yellow. *Chlamydospores* 33–40 X 30–39 μm, globose to subglobose, smooth, light yellow; spore wall up to 5 μm thick.

Reported from Europe, North America, and Tasmania (Gerdemann and Trappe 1974).

ASCOMYCOTINA

5. **Geopora clausa** (Tul.) Burdsall, Mycologia 60: 507. 1968 ssp. **clausa** f. **clausa.**

Material examined: CANARY ISLANDS: GOMERA, Gro-Gulden 75/73 (CUP).

Habitat and season: hypogeous in a *Pinus canariensis* - *Erica* stand during January, elevation ca. 1350 m.

Ascocarps 7 X 4 mm as dried, subglobose, attached by a basal tuft of brown mycelium; outer surface grayish brown, verrucose, the warts pyramidal, 0.5 mm broad at base; excipular hairs abundant over lower surface, superficial, 10–11 μm broad, thick-walled (1–4 μm thick), septate, smooth-walled, flexuous, yellowish brown, simple or branched, arising from outer cells of outer ectal excipulum, terminating in an obtuse tip; interior surface smooth, white. *Spores* (23–) 24–26 (–28) X (15–) 17–20 μm, broadly ellipsoid, mean length-width ratio 1.4, smooth, hyaline, uniserially arranged in asci. *Asci* in a hymenium among paraphyses, 170–250 X 15–20 μm, cylindrical, long-tapered below the basal spore to a croziered base ± 5 μm broad, hyaline, thin-walled, 8-spored, operculate, not bluing in Melzer's reagent. *Paraphyses* 150–250 X 3–5 μm, filiform, terminal cell swollen to 5–8 μm broad, hyaline, thin-walled, septate. *Outer ectal excipulum* 20–50 μm thick, textra angularis, cells 18–45 X 20–25 μm, walls 2–5 μm thick, dark yellowish brown, lighter in interior cells. *Inner ectal excipulum* 200–900 μm thick, textura intricata, of hyaline, thin-walled, 5–7 μm broad hyphae becoming inflated to 20–25 μm, appearing pseudoparenchymatous in some areas.

Burdsall (1968) cites collections of this species from France, Italy, and Portugal. This form differs from *Geopora clausa* f. *ellipsospora* in having broadly ellipsoid (L/W = 1.4) rather than ellipsoid spores (L/W = 1.7–1.8) and in having abundant excipular hairs.

6. **Geopora clausa** (Tul.) Burdsall ssp. **clausa** f. **ellipsospora** Burdsall, Mycologia 60: 511. 1968.

Material examined: CANARY ISLANDS: HIERRO, leg. Korf et al. MM1432, MM1433 (CUP, OSC).

Habitat and season: hypogeous to partly emergent under *Pinus* sp. in January.

Ascocarps up to 35 X 20 mm, irregularly lobed, attached by a basal tuft of brown mycelium; outer surface grayish brown to pale orange yellow, verrucose, the warts pyramidal, 0.5 mm broad at base; excipular hairs scarce; interior surface smooth, white. *Spores* (20–) 22–24 X 12–14 (–15) μm, ellipsoid, mean length-width ratio 1.7–1.8, smooth, hyaline, uniserially arranged in asci. *Asci* in a hymenium among paraphyses, 130–200 X 15–17 μm, cylindrical, long-tapered below the basal spore to a croziered base ± 5 μm broad, hyaline, thin-walled, 8-spored, operculate, not bluing in Melzer's reagent. *Paraphyses* 150–200 X 5–8 μm, filiform, terminal cell swollen to 8–12 μm, hyaline, thin-walled, septate. *Outer ectal excipulum* 25–40 μm thick, textura angularis, cells 20–40 X 20–25 μm, walls 2–4 μm thick, dark yellowish brown, lighter in interior cells. *Inner ectal excipulum* 200–400 μm thick, textura intricata, of hyaline, thin-walled, 5–7 μm broad, periclinal hyphae becoming inflated to 20–25 μm, appearing pseudoparenchymatous in some areas.

Burdsall (1968) has described this species in detail from material collected in Portugal under *Pinus*. The Canary Islands collections differ from his description in having larger paraphysis tips and sparse rather than abundant excipular hairs.

7. **Terfezia olbiensis** (Tul.) Tul., Fungi Hypogaei, p. 176. 1851.

Material examined: CANARY ISLANDS: TENERIFE, leg. Korf et al. MM330 (CUP, OSC), MM1325 (CUP, OSC, LAG), Wildpret and Eckblad MM1133 (CUP, OSC). *HIERRO,* leg. Korf et al. MM1434 (CUP, OSC), MM1440 (CUP, OSC, LAG).

Habitat and season: hypogeous under *Pinus* sp. from January to April.

Ascocarps up to 30 X 19 mm, subglobose to reniform, attached by a basal tuft of hyphae emerging from a short (2 X 3 mm), pulvinate, sterile base; surface minutely pubescent, light orange, grading to gray where exposed. *Gleba* composed of brown pockets of fertile tissue separated by white tramal veins, pockets 2 mm in diam;

consistency extremely hard as dried. Odor not recorded. *Spores* 14–17 X 12–16 μm excluding ornamentation, subglobose, hyaline in youth, becoming brownish yellow at maturity; in youth, with spines 1.5 X 0.25 μm, not joined by lines, by maturity the spines 1–2 X 1 μm broad at base and joined by short lines between 2 or 3 spines. *Asci* 65–70 X 54–61 μm, obovoid, broadly ellipsoidal, or irregular due to mutual pressure, hyaline, not bluing in Melzer's reagent, 8-spored, thick-walled in youth, becoming thin-walled at maturity, immature asci orange in Melzer's reagent. *Trama* of interwoven, hyaline, thick-walled (0.8 μm) hyphae 6–8 μm in diam, cells becoming inflated to 19 μm. Hyphae of fertile pockets hyaline, thin-walled, elongated to spherical cells 8–24 μm in diam. *Outer ectal excipulum* 160–185 μm thick, of periclinal, thick-walled (1 μm), 7–19 μm broad hyphae which become progressively more inflated toward gleba. *Inner ectal excipulum* 340–420 μm thick, differentiated as smaller, thick-walled, less pigmented cells, becoming inflated to 35 μm in diam and ± isodiametric.

The spore color and ornamentation of the Canary Islands collections suggest that *Terfezia olbiensis* and the closely related species *T. leptoderma* (Tul.) Tul. may represent different developmental stages of the same species. *T. olbiensis* is characterized by having spherical, echinulate, non-reticulate, slightly colored spores, 13–16 μm in diam (Tulasne and Tulasne 1851). *T. leptoderma* is described as having spherical, echinulate, partly reticulate, slightly colored spores, 16–19 μm in diam (Tulasne and Tulasne 1851). Spores within the same sporocarp from the Canary Islands show a progression from hyaline spores with separate spines through brownish yellow spores with short lines joining 2 or 3 spines.

BASIDIOMYCOTINA

8. **Hydnangium carneum** Wallr. in Dietr., Flor. Boruss. VII, p. 465. 1839.

Material examined: CANARY ISLANDS: TENERIFE, leg. Korf et al. MM1246, MM1251 (CUP, OSC, LAG), MM1285 (CUP, OSC), MM1303 (CUP). *HIERRO*, leg. Korf et al. MM1437, MM1439 (CUP, OSC, LAG). *MADEIRA:* leg. Korf et al. MM1543 (CUP, OSC).

Habitat and season: on soil under *Eucalyptus* sp. during December and January.

Previously reported from Tenerife under *Eucalyptus* (Calonge and Demoulin 1975) and widely distributed worldwide.

9. **Hymenogaster maurus** Maire, Bull. Soc. Hist. Nat. Afr. Nord 22: 18. 1931.

Material examined: CANARY ISLANDS: TENERIFE, leg. Korf et al. MM1286, MM1287 (CUP, OSC, LAG). *MADEIRA:* leg. Korf et al. MM1555 (CUP, OSC, LAG).

Habitat and season: hypogeous under *Viburnum tinus* L. ssp. *rigidum* (Vent.) P. Silva in a stand with *Prunus lusitanica* L. overstory and in a mixed stand of *Pinus, Eucalyptus*, and *Mimosa* spp. during December and January.

Basidiocarps up to 21 X 14 mm, subglobose to irregularly lobed, no obvious rhizomorphs; peridium tomentose, with adherent debris, white with pallid yellow stains, finally pale yellow. *Gleba* strong reddish brown; locules labyrinthiform, 0.1 to 0.5 mm broad; consistency spongy. Odor farinaceous. Chemical reactions of fresh peridium: KOH, pink; Melzer's reagent negative. *Spores* 16–19 (–22) X 8–9 μm including ornamentation, ellipsoid to citriform, yellowish brown, immature dextrinoid; with embedded rods 0.8–1.5 μm tall at medial axis, shorter toward apex, joined by incomplete lines on spore surface, apex papillate. *Basidia* in a hymenium with basidioles, 23–25 X ± 10 μm, cylindrical, hyaline, thin-walled, 2-spored; sterigmata conical, up to 4 X 4 μm. *Basidioles* 23–25 X 8–9 μm, cylindrical, hyaline, thin-walled. *Subhymenium* of hyaline, thin-walled, spherical cells 5–7 μm in diam. *Tramal plates* 70–80 μm wide, trama 30–35 μm wide, of subparallel, hyaline, thin-walled hyphae 4–5 μm in diam. No clamp connections observed. *Peridial epicutis* 30–40 μm thick, of loosely interwoven, subhyaline, thin-walled hyphae 5–10 μm in diam with clamp connections. *Subcutis* 120–130 μm thick, of loosely interwoven to periclinal, hyaline, thin-walled hyphae 4–6 μm in diam; no clamp connections observed.

Previously reported from southern France, the Azores (Dennis et al. 1977), Algeria and Morocco (Malencon 1975). All of the reported collections were made in *Eucalyptus* stands, although the Tenerife collections appeared to be associated with *Viburnum* in a stand with only a few, widely scattered *Eucalyptus*.

10. Phlebogaster laurisylvicola Fogel, gen. et sp. nov. Figs. 1–5.

Fructificationes subglobosae vel lobatae, candidae deinde luteae. Peridium in crassitie varians. Gleba areis ravis fecundis, venis albis sterilibus separatis; loculis vacuis, sphaericis, ± 0.2 mm in diam. Trama gelatinosa. Basidia cylindracea vel obpyriforma, in euhymeniis ordinata. Sporae 6–8 X 5 μm, oblongae, apicibus obtusis, brunneae, verrucosae. Holotypus: Canary Islands, Tenerife, leg. R. P. Korf, R. Fogel, G. L. Hennebert, L. M. Kohn MM1289 (CUP).

Etymology: Greek, phlebo- (vein), gaster (stomach). Latin, laurisylvicola (a dweller in the laurel forest).

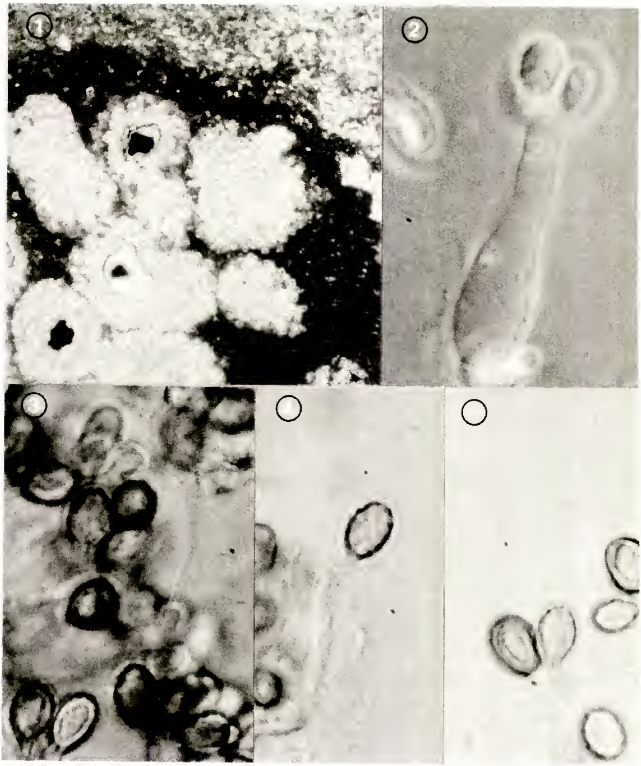
Material examined: CANARY ISLANDS: TENERIFE, Fuente de las Pulgas, Las Yedras, under *Laurus azorica,* 30 December 1976, leg. R. P. Korf, R. Fogel, G. L. Hennebert, L. M. Kohn MM1289 (Holotypus: CUP), leg. Korf et al. MM1290 (CUP, OSC).

Habitat and season: hypogeous under *Laurus azorica* in December.

Basidiocarps up to 10 X 6 mm, subglobose to lobed, attached by several basal rhizomorphs ± 0.25 mm in diam; peridium 0.5 mm thick fresh, white, quickly staining yellow when exposed, then very deep red, drying yellowish white with strong pink stains, minutely tomentose with adhering debris. *Gleba* composed of grayish olive clusters of fertile locules separated by white sterile veins; locules empty, spherical to slightly elongate, ± 0.2 mm broad; consistency firm, sectioning easily after drying. Odor and macrochemical tests on the peridium not recorded. *Spores* oblong, apices obtuse, 6–8 X 5 μm including the ornamentation, brown in mass (KOH), hyaline to moderate greenish yellow singly, nonamyloid, strongly cyanophilic when immature; walls 0.4 to 1 μm thick, two-layered: the inner layer verrucose, the warts largest toward the apex, 0.4 μm or less high, rounded, connected by faint lines, outer layer smooth; sterigmal appendage central, straight, hyaline, 1.5–2 X 1.6 μm, appearing flanged under phase contrast. *Basidia* cylindrical to obpyriform, 22–40 X 4–5 (–8) μm, 4-spored, thin-walled, hyaline, in a euhymenium; sterigmata straight to slightly curved, 2 X 1.5 μm. Basidioles not observed. *Trama* 20–37 μm wide, of hyaline, thin-walled, gelatinous, (2–) 5–9 μm broad, interwoven hyphae. *Peridium* variable in thickness: apex 120–155 μm thick, of periclinal, thin-walled hyphae 1.5–3 μm in diam, lacking obscuring pigment; at base 770 μm thick, two-layered, the epicutis 80–120 μm thick, of hyaline, thin-walled, periclinal hyphae 3–5 μm in diam; subcutis 500–650 μm thick, of randomly oriented, thin-walled, hyaline hyphae 6–9 μm in diam.

A few thick-walled (1.5 μm) hyaline hyphae 9–11 μm in diam and thick-walled spherocysts up to 62 X 39 μm are present in the subcutis. These thick-walled elements may be homologous to the nodose hyphae in *Protubera majacuja* Moell. (Imai and Kawamura 1958) or they may be hyphae of another fungus.

The greenish yellow, oblong spores, cartilaginous gleba, and lack of peridial sutures place *Phlebogaster* in the Hysterangiaceae. The sporocarps are subglobose to lobed and lack the prolonged, tapered, sterile base and raised ridges attaching the gleba to the peridium characteristic of *Phallogaster.* The greenish yellow spores and absence of a percurrent columella differentiate *Phlebogaster* and *Rhopalogaster.* The sectored gleba



FIGS. 1–5. *Phlebogaster laurisylvicola* (MM1289, CUP). 1. Section of the gleba and subcutis showing the locules and gelatinous hyphae completely enclosing the gleba. A portion of a large sterile vein is shown in the lower right-hand corner, X 160 (interference contrast). 2. Obpyriform basidium bearing immature spores, X 1600 (interference contrast). 3. Section of the hymenium showing the small, oblong basidiospores with verrucose ornamentation, X 1600. 4. Upper focus of basidiospore still attached to the basidium. A faint reticulate pattern is evident, X 1600. 5. Basidiospore in median section. The spore wall is two-layered: the outer layer is smooth and the inner layer ornamented, X 1600.

separates *Phlebogaster* from *Hysterangium.* The small, ornamented spores may also be distinctive, although Malençon (1975) has described similar spore ornamentation, except for the very faint reticulation, in *Hysterangium cistophilum* (Tul.) Zeller & Dodge and in *H. rickenii* Soehner.

11. **Rhizopogon rubescens** (Tul.) Tul., Giorn. Bot. Ital. I, 2: 58. 1844.

Material examined: MADEIRA: leg. Korf et al. MM1514, MM1518, MM1544, MM1570, MM1608, MM1609, MM1610 (CUP, OSC).

Habitat and season: hypogeous under *Pinus* spp. during January.

Smith and Zeller (1966) have been followed in retaining *R. rubescens* as distinct from *R. roseolus* (Corda) Fr. due to the pronounced yellow color of the peridium in the Madeira collections. *R. rubescens* has been collected in Europe and North America under *Pinus.*

12. **Rhizopogon subareolatus** Smith in Smith and Zeller, Mem. N. Y. Bot. Gard. 14: 81. 1966.

Material examined: MADEIRA: leg. Korf et al. MM1501, MM1502, MM1508 (CUP, OSC), MM1611 (CUP).

Habitat and season: hypogeous under *Pseudotsuga menziesii* in January.

Basidiocarps up to 29 X 19 mm, subglobose, attached by appressed basal rhizomorphs, concolorous with peridium; outer surface scabrous with grayish brown aerolate patches, ± 0.1 mm broad; peridium thin, light yellowish brown, flushing pink on exposure, dark red in cross section when bruised. *Gleba* moderate yellowish brown; locules labyrinthiform, 0.25–0.5 mm broad as dried; consistency firm. Odor not noted. Chemical reactions of peridium: KOH, green; $FeSO_4$ plus ethanol, dark green. *Spores* 6–7 X 2.5–3 μm, ellipsoid, thin-walled, pseudoseptate, hyaline singly, light brown in mass in Melzer's reagent. *Basidia* 15–20 X 4–6 μm, subcylindric, hyaline, thin-walled, 8-spored. Paraphyses 2–3 celled, terminal cell clavate or obclavate, 10–20 X 7–10 μm, hyaline, thin-walled. *Trama* 25–30 μm wide, of loosely interwoven, hyaline, gelatinous, 4–5 μm broad hyphae, simple septate. *Subhymenium* of hyaline, thin-walled, ± globose, 5–8 μm in diam cells. *Epicutis* 50–100 μm thick, of brown, thick-walled, simple-septate, loosely interwoven, 5–7 μm broad hyphae, apex of terminal cells rounded. *Subcutis* 50–70 μm thick, of periclinal, appressed, thin-walled, hyaline, 4–5 μm broad hyphae. Black granules in water or Melzer's solution scattered throughout the trama just below the subcutis, dissolving in KOH to produce a diffuse green pigment in the subcutis and adjacent locules. No clamp connections noted.

R. subareolatus is collected under *Pseudotsuga menziesii* in California, Oregon, and Washington. Presumably, it was introduced to Madeira with *P. menziesii,* but we were unable to determine the source and whether seed or seedlings had been imported.

13. **Rhizopogon vulgaris** (Vitt.) M. Lange sensu Smith in Smith and Zeller, Mem. N. Y. Bot. Gard. 14: 136. 1966.

Material examined: CANARY ISLANDS: TENERIFE, leg. Korf et al. MM1235, MM1236, MM1237, MM1238, MM1239, MM1240, MM1241, MM1248, MM1249, MM1250 (CUP, OSC, LAG). *HIERRO,* leg. Korf et al. MM1431, MM1435, MM1438 (CUP, OSC, LAG), MM1436, MM1442 (CUP, OSC).

Habitat and season: hypogeous to emergent under *Pinus canariensis* during December and January.

This species has previously been reported from Tenerife (Calonge and Demoulin 1975) and is widely distributed in Europe and North America.

ACKNOWLEDGMENTS

The author is grateful to Dr. Richard P. Korf of Cornell University for the opportunity to collect hypogeous fungi in Marcaronesia. The field work was supported by National Science Foundation Grant DEB 75-23557 to Korf. Special thanks to Dr. James M. Trappe, U.S.D.A., Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory for assistance in identifying *Rhizopogon subareolatus* and for help with the Latin diagnosis.

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Contr. Univ. Mich. Herb. 14:83–84. 1980.

A *STRYPHNODENDRON* NEW TO THE AMAZONIAN FLORA

Elêna Maria Occhioni Martins[1]

Study of collections of *Stryphnodendron* (Leguminosae) from western Amazonia has revealed the existence of an undescribed species, which is described and illustrated here. This raises to 11 the number of species of *Stryphnodendron* known from Amazonia.

Stryphnodendron foreroi Martins, sp. nov. Fig. 1.

Arbor 7–15 m alta, ramulis juvenilibus tenuibus ferrugineo-tomentosis; folia 10–17 cm longa, petiolo ferrugineo-tomentoso 4.5–5 cm longo, 1–1.5 cm supra basin glandula verruciformi munito, glandula 1–2 mm alta, rhachis cylindrica ferrugineo-tomentosa, infra 1–2 paria distalia pinnarum glandulis munita; pinnae 7–9-jugae alternae vel subopposítae, tomentosae 5–7 (–9) cm longae, infra 1–2 paria distalia foliolorum glandulis minutis munitae; foliola 5–11-juga alterna, ovato-oblonga ultima valde obovata, 0.7–1.1 cm longa, 0.3–0.6 cm lata, apice obtusa vel breviter mucronata, basi truncata vel inaequalia, supra puberula, subtus dense pubescentia, basi unilateraliter barbata, petiolulo brevi; spicae 1–3 axillares, pedunculis ferrugineo-tomentosis, 1–1.5 cm longis, rhachis pubescens 5–8 cm longa, calyx campanulatus leviter pubescens 1 mm longus; corolla glabra laciniis 5 lanceolatis, 3–4 mm longis; stamina 10 libera, filamentis filiformibus 6–7 mm longis, antheris elongatis minutis glandula decidua munitis; ovarium paullo stipitatum elongatum, glabrum 2 mm longum, stylo filiformi 2 mm longo; alabastra ellipsoidea 2 mm longa; legumen leviter curvatum subturgidum, pubescens, (10–) 12–13 cm longum, 1–1.5 cm latum.

BRAZIL. Terr. Rondônia: Track from Mutumparaná to Rio Madeira, 30 Nov 1968, fl, *G. T. Prance et al. 8955* (MG, holotype; F, NY, S, US, isotypes); road to Cassiterite Mine in Serra dos Tres Irmãos, N bank of Rio Madeira, 8 km above Abunã, fr, *Prance et al. 5623* (INPA, NY); km 220-223 Madeira-Mamoré railroad near Abunã, fr, *Prance et al. 6004* (F, MG, NY). Amazônas: Municipality of Humaitá, road Humaitá to Lábrea km 44, fl, *Prance et al. 3465* (F, GH, MG, NY, S). BOLIVIA. Pando: W bank of Rio Madeira, 2 km above Abunã, fr, *Prance et al. 6243* (F, GH, MG, NY, S).

This is a well-marked species, clearly differing from its closest relative, *Stryphnodendron guianense* (Aublet) Bentham ssp. *guianense,* in the pubescence, number, and size of its pinnae and leaflets. I name it in honor of Dr. Enrique Forero, of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, in gratitude for his constant encouragement and cooperation.

SUMARIO

O presente trabalho consiste na classificação de nova entidade de *Stryphnodendron* de occorrência no Floresta Amazônica. Com esta espécie eleva-se a 11 o número de espécies desta região.

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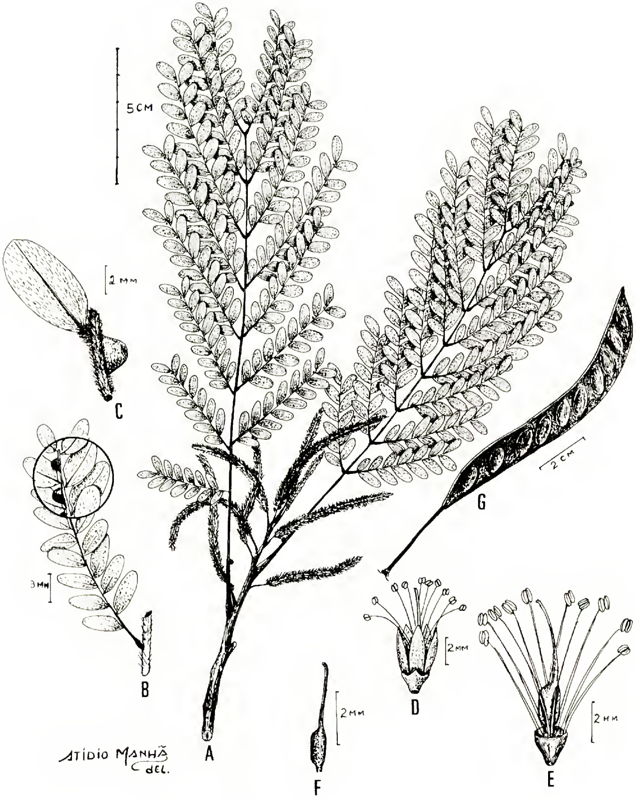

FIG. 1. *Stryphnodendron foreroi,* drawn from the type. A, flowering branch; B, pinna with glands enlarged; C, leaflet, gland, and pubescence; D, flower; E, flower with calyx and corolla removed; F, ovary; G, fruit.

Contr. Univ. Mich. Herb. 14:85–97. 1980.

EIGHT NEW SPECIES OF *IPOMOEA* AND *QUAMOCLIT* FROM MEXICO

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As part of the results of studies in the genus *Ipomoea* and related genera of Mexico and Central America, I propose the following eight new species, seven in *Ipomoea* and one in *Quamoclit.*

Ipomoea teotitlanica McPherson, sp. nov. Fig. 1.

Ab aliis speciebus arboreis combinatione caulium tomentosorum cum foliis orbiculatis supra pubescentibus infra tomentosis, sepalis 11–16 mm longis in pagina abaxiali pubescentibus in pagina adaxiali interdum pubescentibus, corollis glabris distinguenda.

"Small trees with gray trunks" (collector's notes). Young stems somewhat ridged, densely tomentose with soft, curled hairs about 0.5 mm long; older stems more strongly ridged to much roughened, glabrescent. Leaf blades (immature?) round in outline, 3–4 cm in diameter, obtuse at the apex, cordate at the base, bearing 7–8 lateral veins on each side of the midrib, pubescent on the upper surface with very slender, more or less appressed hairs 0.3–1.0 mm long, much more densely pubescent on the lower surface (which is completely obscured) with similar hairs; petioles 0.8–1.5 cm long, densely tomentose like the stem. Inflorescences axillary or terminal, each cyme consisting of 1 flower, these reduced cymes borne on shortened, leafless, tomentose branches up to 5 mm long. Peduncles about 1 mm long, tomentose. Bracts broadly ovate, 1–1.5 mm long, 1 mm wide, tomentose on the abaxial surface and centrally on the adaxial surface, caducous. Pedicels 10–15 mm long, ridged, slightly thickened distally, tomentose and glabrescent. Sepals elliptical to broadly ovate, subequal, 11–16 mm long, 7–10 mm wide, obtuse at the apex, coriaceous, at least the outer sepals tomentose over the abaxial surface and partially so on the adaxial surface, the curled hairs up to about 0.7 mm long. Corolla funnelform, 5.5–6.5 cm long, about 4 cm in diameter across the limb, "light clear yellow" (collector's notes), glabrous, twisted in bud. Stamens included, 2.8–3.8 cm long, the anthers 8 mm long, the basal hairs up to 1 mm long. Style about 4.5 cm long, the stigmas 2, globose, about 1.5 mm in diameter. Capsule unknown.

OAXACA: Tambor, about 17 miles west of San Antonio, District of Teotitlán, limestone canyon, 25 Nov 1967, *H. S. Gentry 22475* (GH, holotype).

Amongst the other Mexican tree species, *Ipomoea teotitlanica* is probably most nearly related to *I. murucoides,* which it resembles in leaf pubescence, sepal pubescence and texture, and in the tendency of the sepals to lack hairs on the adaxial surface.

Ipomoea praecox McPherson & Meacham, sp. nov. Fig. 2.

Ab aliis speciebus volubilibus pariter corollis maxime pubescentibus gaudentibus combinatione anthesis praecicis cum inflorescentils aggregatis et floribus rufis distinguenda.

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[1] Present address: Missouri Botanical Garden, St. Louis, Missouri.

FIG. 1. *Ipomoea teotitlanica,* drawn from the type by Jan McCarthy. Flowering branch X 0.6; opened flower X 1.

FIG. 2. *Ipomoea praecox,* drawn from the type by Jan McCarthy. Flowering branch × 0.8; flower × 2.

Woody vine 1–2 m long. Young stems smooth, pubescent with soft hairs about 0.5 mm long; older stems ridged and roughened, partially glabrescent. Leaves absent during flowering, unknown. Inflorescences axillary or terminal, each cyme consisting of 1–2 flowers, these reduced cymes clustered in groups of up to 27 flowers on reduced, densely pubescent branches 1–2 cm long. Peduncles 1–2 mm long, pubescent. Bracts lanceolate, 3–5 mm long, about 1 mm wide, pubescent. Pedicels 4–8 mm long, slender, densely pubescent. Sepals elliptical to ovate, equal, 7–8.5 mm long, 4–5 mm wide, broadly obtuse at the apex, subcoriaceous, reddish, abaxially pubescent, the hairs about 0.5 mm long and often forming a small tuft at the apex of the sepal. Corolla salverform, the tube 3.5–4 cm long, 0.5–0.7 cm in diameter at the base of the limb, the lobes of the limb 5–10 mm long, obtuse at the apex; corolla purple-red, abaxially pubescent except at the very base with hairs 0.5–0.9 mm long, not twisted in bud. Stamens slightly exserted, 3–4 cm long, the anthers 3 mm long. Style about 3.5 cm long, the stigmas 2, globose, about 0.75 mm in diameter. Capsules unknown.

OAXACA: Limestone hillside southwest of Sola de Vega, near 16°29′ N, 96°58′ W, elev. ca 1700 m, 5 Dec 1962, *Moran 10095* (UC, holotype).

This species belongs to a group of which *Ipomoea jalapa* is typical.

Ipomoea pruinosa McPherson, sp. nov. Fig. 3.

Ab aliis speciebus volubilibus pariter corollis maxime pubescentibus gaudentibus combinatione anthesis praecicis cum inflorescentiis aggregatis et floribus albis distinguenda.

Woody vine 3–5 m long. Young stems smooth, tomentose, the hairs soft, curled, 0.1–0.25 mm long; older stems somewhat roughened, glabrescent, revealing a finely granular, waxy coating, which in turn is often absent from the oldest stems. Leaves absent during flowering and fruiting, unknown. Inflorescences axillary and terminal, each cyme consisting of 1–4 flowers, these cymes gathered in groups of up to 10 flowers at the ends of often angular branches. Peduncles 1.5–6 mm long, tomentose. Bracts caducous, unknown. Pedicels 2–9 mm long, grooved, thickened distally, tomentose. Sepals ovate, subequal (the outermost 4–6 mm long, 3–4 mm wide, the innermost 5–7.5 mm long, 5–6.5 mm wide), obtuse or obtuse-mucronate at the apex, often somewhat asymmetrical, often ridged, coriaceous with thinner, often reddish margins, tomentose abaxially and occasionally adaxially. Corolla more or less funnelform, 6.5–9 cm long, 1–1.5 cm in diameter at the base of the limb, 4.5–7 cm in diameter across the limb, white with pale red interplical areas, tomentose over the entire surface excepting the plical areas and the basal 5–10 mm, twisted in bud (sometimes only slightly so). Stamens included, 3–4.5 cm long, the anthers 8–10 mm long, the basal hairs about 0.75 mm long. Style 3.5–4.5 cm long, the basal 1–4 mm persistent in fruit, the stigmas 2, globose, about 1 mm in diameter. Capsules (immature) 2-locular, 4-valved, the valves 12–15 mm long, the seeds (immature) 4, pubescent along the dorsal margins, the hairs soft, at least 5 mm long.

GUERRERO: Deciduous forest, rocky hills 3–5 km on road from Casa Verde to Xochipala, with *Bursera, Cordia, Haematoxylum, Pseudosmodingium,* about 35 km north-northwest of Chilpancingo, elev 1000–1150 m, 2 Feb 1965, *McVaugh 22192* (MICH, holotype).

This species, like *Ipomoea praecox,* belongs to a group of which *I. jalapa* is typical.

Ipomoea pseudoracemosa McPherson, sp. nov. Fig. 4.

Ab aliis speciebus volubilibus pariter sepalis concavis coriaceis et corolla recta (non torta) in aestivatione gaudentibus combinatione anthesis praecicis cum cymis unifloris aggregatis distinguenda.

FIG. 3. *Ipomoea pruinosa*, drawn from the type by Jan McCarthy. Flowering and fruiting branches X 1.2.

FIG. 4. *Ipomoea pseudoracemosa,* drawn from the type by Jan McCarthy. Flowering branch × 1.1; fruiting cluster × 0.9; seed × 3.

Woody vine 2–5 m long. Young stems smooth or somewhat roughened, glabrous or pubescent, the hairs 0.3–0.6 mm long, straight or curled, usually appressed, the basal cell slightly swollen; older stems ridged and roughened, often glabrescent. Leaves absent during flowering and fruiting, unknown. Inflorescences axillary or terminal, each cyme consisting of 1 flower, these reduced cymes borne in groups of 2–10 flowers on shortened, occasionally branched, tomentose shoots 2–30 mm long, the leaves of these reduced stems represented by caducous, triangular, tomentose bracts up to 4 mm long, 1.5 mm wide. Peduncles 0.5–4 mm long, tomentose, sometimes glabrescent. Bracts triangular, 1.5–2.5 mm long, 1–1.7 mm wide, glabrous adaxially, glabrous or distally pubescent abaxially, caducous. Pedicels 5–17 mm long, ridged, slightly thickened distally, glabrous. Sepals round to somewhat flattened in outline, unequal (the outermost 2.5–4 mm long, 3–4 mm wide, the innermost 4.5–6.5 mm long, 5–7 mm wide), broadly obtuse or shallowly emarginate at the apex (sometimes mucronate), concave, coriaceous over those portions exposed in bud, thinner and often reddish on the margins and over those portions shielded in bud, glabrous throughout or sparsely pubescent near the apex of the abaxial surface, the hairs straight or curled, up to 0.5 mm long. Corolla funnelform, 5–7 cm long, 3.5–6 cm in diameter across the limb, white, the tube and interplical regions greenish or pale reddish abaxially, glabrous, not twisted in bud. Stamens included, 1.8–3.5 cm long, the anthers 4–6 mm long, the basal hairs up to 1 mm long. Style 3–4 cm long, the stigmas 2, globose, about 1 mm in diameter. Capsule 2-locular, 4-valved, the valves 12–13 mm long, the seeds 4, pilose on the dorsal margins with hairs 7–9 mm long.

JALISCO: Dry brush-covered mountainsides 6.5 miles northeast of Autlán, near highway pass, with *Bursera, Heliocarpus, Acacia,* elev. 925 m, 24 Nov 1959, *McVaugh & Koelz 1037* (MICH, holotype); steep mountainsides now becoming leafless, 2 miles north of San Cristóbal de la Barranca, tropical deciduous forest, with *Acacia, Alvaradoa, Bauhinia,* elev. 950 m, 11 Nov 1962, *McVaugh 22141* (MICH); steep rocky hills near the mines north of Bolaños, east of the Río de Bolaños, in disturbed deciduous forest dominated by *Croton alamosanus, Acacia farnesiana,* and arborescent *Ipomoea,* elev. ca 1000 m, 18–19 Jan 1975, *McVaugh 25852* (MICH).

NAYARIT: Mountains 10 miles southeast of Ahuacatlán, on the road to Barranca del Oro and Amatlán, precipitous rocky south-facing slopes, elev. 1100–1300 m, 17–18 Nov 1959, *McVaugh & Koelz 728* (MICH).

This species belongs to a large group of which *Ipomoea microsticta* and *I. tuxtlensis* are typical. Species of this group can be readily recognized by their concave, coriaceous sepals, their corollas not twisted in bud, and their seeds long-pubescent on the dorsal margins only.

Ipomoea noctulifolia McPherson, sp. nov. Fig. 5.

Ab aliis speciebus foliis bilobis et late dentatis facile distinguenda.

Prostrate trailing vine up to 2 m long from a woody, irregular rootstalk. Stems up to 3 mm in diameter, ridged, coarsely pubescent, the hairs straight, stiff, mostly ascending, 0.5–1.5 mm long from a conspicuously swollen basal cell. Leaf blades round to somewhat flattened in general outline, truncate or cordate at the base, prominently bilobed, the midrib 1.5–10 mm long, extending into the short, acute leaf apex, the lobes 0.8–3 cm long, 0.8–2.2 cm wide, each bearing 4–6 veins and, along the distal margin, 2–5 broad teeth, the upper surface glabrous or sparsely coarse-pubescent, the lower surface sparsely coarse-pubescent at least along the midrib and on proximal portions of the main veins; petioles 0.6–1.8 cm long, coarsely pubescent. Inflorescences axillary, 1-flowered. Peduncles 1–22 mm long, wrinkled, coarsely pubescent, occasionally partly fused with the petiole of the subtending leaf, often distally thickened and bearing supernumerary bracts (remnants of a cymose inflorescence). Bracts ovate, about 1 mm

FIG. 5. *Ipomoea noctulifolia,* drawn from the type by Jan McCarthy. Rootstalk X 0.8; flowering branch (corollas still expanding) X 0.7; fruiting branch X 0.7; opened flower X 1; calyx X 3; seeds X 2.5.

long, 1 mm wide, carinate, glabrous. Pedicels 2–15 mm long, ridged, usually thickened distally, coarsely pubescent. Sepals ovate to elliptical, unequal (the outermost 2.0–4.0 mm long, 1–3 mm wide, the innermost 5.5–8.5 mm long, 3–4.5 mm wide), obtuse or obtuse-mucronate (rarely acute) at the apex, often somewhat asymmetrical, smooth to somewhat roughened and ridged, subcoriaceous with thinner margins, glabrous. Corolla funnelform, 5–7 cm long, 3–4 cm in diameter across the limb, purplish-red, sometimes white near the base of the tube and on the interplical areas, glabrous, twisted in bud.

Stamens included, 1.0–2.0 cm long, the anthers 3–3.5 mm long, the basal hairs about 0.75 mm long. Style 2.6–2.8 cm long, the stigmas 2, globose, 1 mm in diameter. Capsule 2-locular, 4-valved, the valves 7–10 mm long, the seeds 4, covered with soft hairs up to 0.75 mm long.

JALISCO: Gently sloping pastured hills near km 647, ca 5 road-miles south-west of Santa Cruz de las Flores, elev. 1550 m, 24 Aug 1957, *McVaugh 16308* (MICH, holotype); mountains north of Autlán, 3–5 miles above Mina San Francisco (Cia. Minera de Autlán), tropical deciduous forest zone with *Bursera, Ceiba, Ipomoea, Triumfetta,* elev. 1500–1650 m, 5 Oct 1960, *McVaugh 19931* (MICH); dry, shrub-covered slopes 9 miles south of Autlán toward La Resolana, 13 Aug 1949, *Wilbur & Wilbur 2309* (MICH).

This species belongs to a group of which *Ipomoea purga* is typical.

FIG. 6. *Ipomoea mcvaughii,* drawn from the type by Jan McCarthy. Flowering branch X 0.9; opened corolla X 1; calyces X 1.5.

Ipomoea mcvaughii McPherson, sp. nov. Fig. 6.

Ab aliis speciebus inflorescentiis aggregatis et subtentis foliis viridibus bracteis similibus distinguenda.

Woody vine. Young stems smooth, glabrous; older stems ridged, glabrous. Leaves various, the blades ovate, entire, typically 5–13 cm long, 3–8 cm wide, acuminate at the apex, cordate at the base, bearing 6–8 large veins on either side of the midrib, glabrous throughout or pubescent along the margin with stiff hairs up to 0.5 mm long; petioles 0.5–7 cm long, glabrous; first leaf, and sometimes the second, of each branch usually much smaller than adjacent leaves, sessile or subsessile (the petioles 0–2 mm long); leaves subtending flowers separated by short internodes (0–1.0 cm long), their blades 1.5–5 cm long, 1–3 cm wide, their petioles 0.5–4 mm long. Inflorescences axillary, each cyme consisting of 1–3 flowers, these cymes clustered in groups of 4–8 flowers at the ends of branches. Peduncles 0.5–1 mm long, glabrous. Bracts ovate to lanceolate, 1.5–3 mm long, about 0.75 mm wide, carinate, glabrous. Pedicels 3.5–4 mm long, ridged, thickened distally, glabrous. Sepals elliptical or obovate, unequal (the outermost 6.5–9 mm long, 2–2.5 mm wide, the innermost 11–13 mm long, 4.5–5.5 mm wide), acute or obtuse-mucronate at the apex, often somewhat asymmetrical, subcoriaceous, glabrous or more typically pubescent along the margin, the hairs up to 0.5 mm long. Corollas more or less funnelform, 5–7.5 cm long, 1–1.5 cm in diameter at the base of the limb, 3–4 cm in diameter across the limb, pink with paler throat and interplical regions and white base, glabrous, twisted in bud. Stamens included, 3.5–4.5 cm long, the anthers 3–3.5 mm long, the basal hairs about 1 mm long, Style 4.5–5 cm long, the stigmas 2, globose, about 1 mm in diameter. Capsule unknown.

OAXACA: Steep slopes in pine forests, 5–6 km northeast of Putla, road to Tlaxiaco, elev. 850 m, 6 Feb 1965, *McVaugh 22268* (MICH, holotype).

This species, like *Ipomoea noctulifolia,* belongs to a group of which *I. purga* is typical, and is most nearly related to *I. bracteata* and *I. suffulta,* which also have inflorescences subtended by modified leaves.

Ipomoea perpartita McPherson, sp. nov. Fig. 7.

Ab aliis speciebus pariter foliis palmatis gaudentibus combinatione foliorum lobis etiam centralibus in lobis minoribus denuo furcatis cum segmentis ultimis foliorum linearibus distinguenda.

Woody vine 2–3 m long. Young stems smooth, glabrous; older stems ridged, glabrous. Leaf blades round to somewhat flattened in general outline, 1–3 cm long, 2–3 cm wide, deeply palmately 5–7 lobed (the basal two lobes on one side of the leaf sometimes shortly joined proximally), the lobes themselves 1–1.5 cm long, 0.4–1.5 cm wide, each consisting of 3–9 linear segments 1–8 mm long, 0.3–0.6 mm wide, glabrous, and arranged more or less pinnately along the lobe axis; petioles 0.2–1.2 cm long, glabrous; pseudostipules, apparently the reduced leaves of tiny, axillary branches, sometimes present. Inflorescences axillary, each cyme consisting of 1–3 (–probably more) flowers. Primary peduncles 20–55 mm long, glabrous; secondary (more distal) peduncles 4–5 cm long, glabrous. Bracts ovate-lanceolate to elliptical, 1.5–3.0 mm long, 1–1.5 mm wide, acute or obtuse-mucronate at the apex, carinate, glabrous. Pedicels 8–12 mm long, ridged, usually thickened distally and often markedly thicker than the peduncle, glabrous. Sepals ovate-lanceolate to elliptical, unequal (the outermost 3.5–5.5 mm long, 2–2.5 mm wide, the innermost 6–7.5 mm long, 2–2.5 mm wide), acute to obtuse-mucronate (the mucro up to 0.5 mm long) at the apex, carinate and often basally roughened, subcoriaceous with thinner, often white margins, glabrous. Corolla funnelform, 3–4 cm long, 2.5 cm in diameter across the limb, "white, purple in the tube, the 5 radiate lines violet outside" (collector's notes), glabrous, twisted in bud. Stamens included, 1.3–1.9

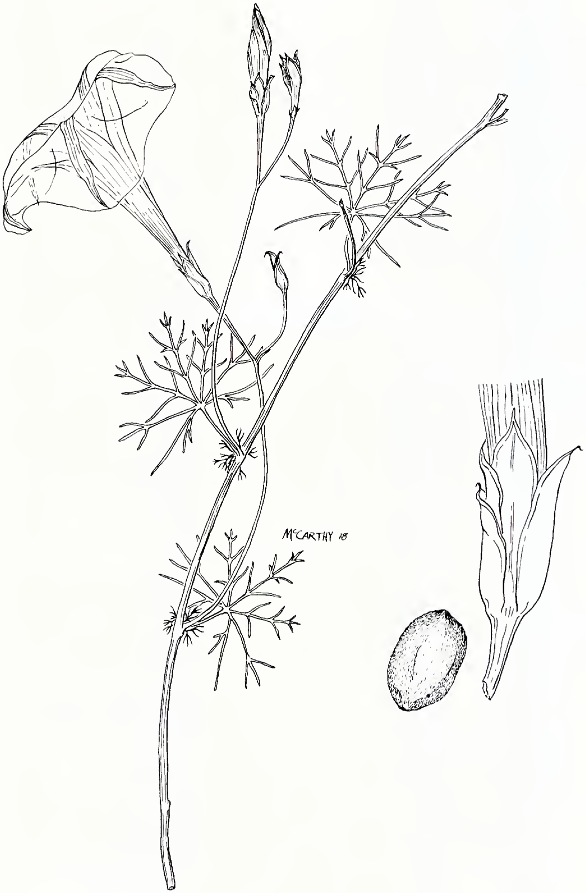

FIG. 7. *Ipomoea perpartita*, drawn from the type by Jan McCarthy. Flowering branch × 1.5; calyx and seed × 6.

FIG. 8. *Quamoclit fissifolia*, drawn from the type by Jan McCarthy. Flowering branch × 0.8; fruit and seed × 2.

cm long, the anthers 1–1.5 mm long, the basal hairs up to 0.5 mm long. Style about 3.5 cm long, the stigmas 2, globose, about 0.75 mm in diameter. Capsules 2-locular, 4-valved, the valves 6–7 mm long, the seeds 4, pubescent over the entire surface with hairs about 0.1 mm long.

JALISCO: Steep mountainsides 3–10 km generally east on the road to Mina del Cuale, from the junction 5 km northwest of El Tuito, Mpio. de Cabo Corrientes, pink-oak forest on decomposed granitic soils, with *Podocarpus,* oaks, and other deciduous trees in rocky stream valleys, elev. 850–1150 m, 16–19 Feb 1975, *McVaugh 26371* (MICH, holotype).

This species is obviously related to the long-recognized group of which *Ipomoea costellata* is typical.

Quamoclit fissifolia McPherson, sp. nov. Fig. 8.

Ab aliis speciebus combinatione foliorum profunde divisorum cum pedunculis longis et inflorescentiis multifloris distinguenda.

Woody vine 4–6 m long, up to 1 cm thick at the base. Young stems smooth, glabrous; older stems ridged and wrinkled, glabrous. Leaves scattered along the stem or clustered on reduced branches as short as 1.3 mm; blades orbicular to oval in outline, 2–14 cm long, 2–14 cm wide, deeply palmately lobed (the sinuses extending to within 1.3–7.5 mm of the petiole apex), cordate at the base, the lobes (5–) 7–9 in number (the two basal lobes each bearing a smaller lateral lobe), entire, linear to narrowly ovate-lanceolate, 2–9 cm long, 0.1–1.4 cm wide with 7–10 lateral veins on each side of the central vein, glabrous; petioles 2.8–10.2 cm long, glabrous. Inflorescences erect, axillary, each cyme consisting of (5–) 10–40 flowers, the cymes modified so that the flowers (excepting the one terminating the primary peduncle) are borne on two rachises which arise from the apex of the primary peduncle and each of which resembles a scorpioid cyme. Primary peduncles 20–50 cm long, glabrous, the more distal peduncles 0.3–1.2 cm long, glabrous. Bracts triangular, subopposite, carinate, glabrous, unequal, that subtending the rachis 1–1.5 mm long excluding the awn (1–3.5 mm long), that subtending the pedicel 0.5–1.5 mm long including the mucro. Pedicels (28–) 30–45 mm long, grooved, slender, glabrous. Sepals round to somewhat flattened in outline, unequal, subterminally awned (the outermost 2.5–3.5 mm long excluding the stout 1–3 mm long awn, 2–3 mm wide, the innermost 4.5–6 mm long excluding the 2–5 mm long awn, 5–8 mm wide), obtuse or more usually deeply and often asymmetrically emarginate at the apex, concave, carinate, subcoriaceous with thinner, sometimes reddish margins, glabrous. Corolla more or less funnelform but the tube curved and the corolla thus zygomorphic, the tube 2.5–3 cm long, 1.5–2.0 cm in diameter at the base of the limb, 2.5–3.5 cm in diameter across the limb, the lobes of the limb 0.9–1.2 cm long, 0.7–1.1 cm wide, their margins 1–2 mm wide, markedly thinner than the central region, the corolla "dark bronzy red to green with faint red tinge" (collector's notes), glabrous, not twisted in bud. Stamens exserted, curved over the corolla mouth, 5–7 cm long, the anthers 6.5–8 mm long, the filaments glabrous. Style 5.5–7 cm long, the basal 2–3 mm persistent in fruit, the stigma 2-lobed, about 1.5 mm in diameter. Capsule 4-locular, 4-valved, the valves 8–10 mm long, the seeds 2–4, covered with extremely short appressed hairs.

MICHOACAN: Steep hillsides among shrubs and small trees, 15–16 km southeast of Aserradero Dos Aguas and nearly west of Aguililla, on tumbled and eroded sharp-toothed limestone rocks, elev. 1400–1450 m, 25–26 Nov 1970, *McVaugh 24694* (MICH, holotype).

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I wish to express my thanks to Jan McCarthy for drawing the plates.

Contr. Univ. Mich. Herb. 14:99–140. 1980.

BOTANICAL RESULTS OF THE SESSÉ & MOCIÑO EXPEDITION (1787–1803)

II. The *Icones Florae Mexicanae*

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The first part of this study of the botanical results of the Sessé & Mociño expedition, a summary of the excursions and travels of the members of the Spanish *Expedición Real de Botánica,* appeared in 1977 (Contr. Univ. Michigan Herb. 11: 97–195). This second part aims to provide documentation for approximately 460 of the paintings, the numbered series called *Icones Florae Mexicanae,* that were made by the artists of the expedition during the early years of the work in Mexico. The paintings made in this early period, from late in the year 1787 until about April 1791, have a special botanical importance because (unlike those painted in later years in widely separated parts of the New World) they were all painted in a limited region in Mexico, they were numbered serially, and the numbers (at least most of them) were cited in the posthumous works of Sessé & Mociño, *Plantae Novae Hispaniae* and *Flora Mexicana.* More than 100 of them are identifiable with existing paintings that are the holotypes (or occasionally lectotypes or paratypes) of the names of taxa described between 1813 and about 1850 by A. P. de Candolle and others. Of these about half represent species described again as new in the *Plantae Novae Hispaniae* or the *Flora Mexicana.* About 60 additional new species described in the same works are recognizable from the paintings representing the *Icones,* and many more can be assigned to a definite genus or tentatively to a species from the paintings alone. Some few, mostly not yet fully studied, serve to identify names that still have nomenclatural priority in spite of the century that elapsed between the time when they were proposed and when they were published. When any numbered plate is cited in association with a particular species and an identifiable locality, it is usually possible after examination of the painting and after study of the relevant texts to identify the plant described by Sessé & Mociño even in the absence of authentic herbarium specimens. For Mexican botanists especially this may be a matter of some moment.

The published floras of Sessé & Mociño (for a description of which see McVaugh, 1977), even though they were delayed a century in publication, are of much more than historical interest. They contain carefully prepared descriptions of some hundreds of new species, and many additional data relative to geographical distributions, habitats, uses, and vernacular names of these species, and hundreds of other species that were not thought to be new. The problem is largely one of precise identification of the species that were named and described. Some of the species are so characterized as to be unmistakable, but the great majority can be identified only tentatively in terms of currently accepted taxa, at least from the descriptions alone. Comparison with herbarium material is useful in a somewhat limited number of cases. In the original herbarium of Sessé & Mociño (at MA), and in the many specimens in European herbaria that were collected by Sessé & Mociño and distributed as duplicates by Pavón, locality-data seldom (in fact, rarely) appear on the labels. It is therefore very helpful to be able to tie an identifiable named and numbered painting to a description and a cited locality (sometimes in addition, of course, to an actual herbarium specimen bearing the same name).

For example, the name *Silene mexicana* was published in *Plantae Novae Hispaniae* in 1888, with type-locality San Angel (now a suburb of Mexico City), and the citation of "Fl. Mex. Ic. 82." The name had already been published, and attributed to Mociño & Sessé, by Otth in de Candolle's *Prodromus* in 1824. In the *Prodromus* the name was based entirely on a painting [no. 56] in the de Candolle collection at Geneva, and the type-locality was given only as "Mexico." There is no original specimen under the name of *Silene mexicana* in the Sessé & Mociño herbarium, and as far as I know none exists elsewhere. The painting, however (the type of *S. mexicana* Otth), proves to be not a copy (see discussion later on in this paper) but an original, a "duplicate" made in Mexico by the original artist and presented by Mociño to de Candolle, bearing the number "82" as well as the Sessé & Mociño name in contemporary lettering. The plant depicted is readily identifiable as *Silene laciniata* Cav., and there seems no reasonable doubt that *Silene mexicana* Otth and *S. mexicana* Sessé & Moc. are the same species, nor that the type-locality for both was in fact San Angel, as stated in *Plantae Novae Hispaniae.*

In this instance as in many others it is probable, if not conclusively demonstrable, that when one of the numbered plates is associated in *Plantae Novae Hispaniae* or *Flora Mexicana* with a particular locality, that the painting was made at the locality in question. Whether or not this is true in every instance, the association of plate and locality provides a useful starting point for further inquiry. The artists of the Expedition customarily worked from fresh material whenever some interesting or spectacular plant new to the botanists was first met with in the field. There is some evidence (see below) that paintings of some species were discarded in favor of new ones made from better material (or perhaps because the original painting was thought to be too crudely done). Because of the relatively long time needed to make each painting, however, and the consequent pressure on the artists to keep up with the botanists, there seem to have been relatively few paintings done over.

I cannot explain why formal numbering of the *icones* seems to have ceased after the completion of the field-season of 1791. It is true that after the "Third Excursion" the Expedition never again travelled as a unit. Mociño went to Nootka, and later went without Sessé to the Atlantic slope of Mexico and eventually to Central America. Sessé worked alone or with Castillo or Senseve in Puebla and Veracruz, in the State of Mexico, and later in the West Indies. Possibly it was not thought to be appropriate to combine the paintings from outlying areas into the same list with those from New Spain. Perhaps the lack of contacts between the field-parties made it impossible for Mociño to work with the plates of all the artists as he had done in the beginning. It may have been simply that neither Mociño nor Sessé could take the time for such details unless special pressure was applied as it had been in 1791.

In any event it was not until after the completion of all work in the New World that a reorganization of the herbarium and the collection of paintings was attempted. Apparently this reorganization was begun after the Expedition returned to Spain; in the archive at Madrid (MA) is a manuscript (4^a División, núm. 6), in which each species in the herbarium is assigned a number, and plate-numbers are assigned according to the new system. The number of species is much larger than that listed in *Plantae Novae Hispaniae* or in *Flora Mexicana.* In the genus *Convolvulus,* for example, 47 numbered and 8 unnumbered species are listed, including several that have never been published; the plate numbers listed for *Convolvulus* are 149–158, inclusive. In the *Plantae Novae Hispaniae* and the *Flora Mexicana* together the number of species in this genus is less than 35; the plate numbers are 49, 194, 197, 201, 210, and 405. Probably the new scheme was never completed, as the new numbers appear on relatively few specimens in the herbarium, and the new plate-numbers as far as I know were never used except that the first seven appeared in *Flora Mexicana.* Of that work the first 8 pages of the manuscript (through *Alpinia bicalyculata*) are in Mociño's hand, and evidently are intended as the beginning of a new work like the *Plantae Novae Hispaniae.* The numbers cited for species of

Amomum, Costus, Maranta and *Alpinia* [e.g. "Ic. 1; Herb. 1"] correspond exactly to the numbers of the new system that was written down in manuscript form accompanying a list of the entire herbarium from New Spain but was never applied except to these species:

Herb. 1, Ic. 1	Amomum zingiber	Fl. Mex. ed. 2.	1.
Herb. 2, Ic. 2	Amomum trispicatum	l.c.	
Herb. 3, Ic. 3	Amomum bimaculatum	l.c.	2
Herb. 4, Ic. 4	Costus spicatus	l.c.	2
Herb. 5	Maranta arundinacea	l.c.	2
Herb. 6	Maranta Galanga	l.c.	2
Herb. 7, Ic. 6	Alpinia racemosa	l.c.	3
Ic. 7	Alpinia bicalyculata	l.c.	3

A few numbers cited in the *Flora Mexicana* (e.g. 805, *Hibiscus mutabilis* Fl. Mex. ed. 2. 160, and 884, *Senecio canicida* Fl. Mex. ed. 2. 185) probably refer to herbarium serial numbers rather than to plates, although in the text each number is preceded by the word "Ic." As often in the herbarium itself, the juxtaposition of the "Ic." and the number probably merely meant that a plate [Icon] existed, and that the species-number in the herbarium was 805, or 884.

The origins of more than 800 of the existing un-numbered paintings remain in doubt; specialists will perhaps find it possible to identify them by association with the localities known to have been visited by Sessé & Mociño (McVaugh, 1977), but will have to consider each one as a special case. No general treatise on these is possible unless to some one person or group with an extraordinarily detailed knowledge of the floras of all of Central America, the Caribbean, Mexico, and the Pacific Coast from California northward.

Introduction

There is no more romantic story in botanical history than that of the paintings that were made by the artists of the Royal Botanical Expedition, and hardly any that has been told more often. A. P. de Candolle first related it at length in his *Mèmoires* (1862); how Mociño, discouraged and aging, exiled from Spain, brought the priceless collection of more than 1300 plates to Montpellier and confided them to de Candolle; how the latter made use of them in the early volumes of the *Systema* and the *Prodromus;* how Mociño, finally permitted to return to Spain and wishing to carry with him the only tangible result of the long expedition to Mexico, asked for the return of most of the paintings; how de Candolle, by this time settled in Geneva, enlisted the aid of more than a hundred artists, and had more than a thousand of the plates copied in ten days and thereby saved them for posterity. The tragic end of Mociño, and that of the plates, are less well documented, but it is known that Mociño died in Barcelona in 1820. The original paintings never reached Madrid, and have been lost to the botanical community for the last 160 years, presumably in Barcelona. Colmeiro (1858, p. 186) says that after Mociño's death they came improperly into the hands of someone, perhaps Mociño's doctor, and that a relative of that person had them in Barcelona "before the year 1846." Rickett (1947, p. 78) does not repeat this story, saying merely that Mociño lodged for a time in Barcelona in the house of Don Jacobo Villa Urrutia. Altamirano ("1897") says that in 1898 he met Sr. Felipe Esteva, who as a child had seen the paintings when his father had them; his grandfather had been the doctor who received them from Mociño. They had ultimately passed to his uncle, Lic. D. Manuel Planos y Casals, and it was the opinion of Sr. Esteva that his uncle had probably given them to some public institution. Altamirano received conflicting stories about the final disposition of the paintings, and never succeeded in finding them.

Botanically speaking, the paintings in the de Candolle collection are of paramount importance because they have been the object of much study and many published comments since de Candolle and Mociño together began to organize them. About 279 of them are in fact the holotypes of names published by A. P. de Candolle and his contemporaries (A. de Candolle, 1874). The original set, even if it could now be located, would be of lesser botanical interest, even though presumably of greater artistic value than the existing copies.

From the beginning of the Botanical Expedition it was planned to include artists as an integral part of the group. As soon as possible after the formal "incorporation" of the expedition on 4 August 1787, the Director (Sessé) appointed two young Mexican artists that had been recommended to him (McVaugh, 1977). Atanasio Echeverría, less than 18 years of age when he joined the expedition, was thought to be the more talented, but the other, Vicente de la Cerda, eventually proved to be a draftsman and colorist of more than average competence. From 1788 until the virtual cessation of botanical activity about ten years later, one or both of these artists accompanied each major field-excursion and made paintings of plants and animals under the direction of the naturalists. Wilson (1970, p. lviii) says that another artist, Francisco Lindo, "worked with the Royal Scientific Expedition in New Spain," but I have not seen his name mentioned elsewhere.[1]

When Cavanilles first saw the plants and other materials brought back to Spain by Sessé in 1804, he wrote to Sir J. E. Smith (6 Apr 1804) that probably about 4000 species were represented, "dont la plus grande partie est dessiné a merveille. Quelle cantite [sic] des genres nouveaux! Nous pouvons deja dire Voicy l'embarras des richesses." When de Candolle's friend Duméril visited Madrid in 1805 he wrote of his visit, after having seen, as he said, more than 600 paintings, "Ces dessins sont pour la plupart magnifiques et semblables à ceux de Redouté."

From the beginning of the Expedition, the artists seem to have painted about one species out of every three encountered and described. Presumably they were directed to those that were found in the best condition for showing flowering and fruiting structures, or that for one reason or another were thought to be the most interesting. No attempt was made (and indeed it seems no attempt could have been made) to make the paintings in any kind of systematic sequence, but merely in the order in which good specimens became available.

The situation was alluded to somewhat cryptically by Mociño in the preface to the *Plantae Novae Hispaniae:* From the fact that plants of the first classes are represented in the series in greater numbers than those of the later classes, it is easy to understand that we inspected these [the later ones] first and the others afterward.[2]

Copyists and duplicate paintings

There is ample evidence that many or most of the plates made by the artists were ultimately represented by two or more copies, made in the field at the same time as the original, or somewhat later after the field-parties had returned to base. There are many references in the notes and letters of Sessé and Mociño and others, to this work of making duplicates of paintings already executed. In at least one known instance, one set of duplicates was reserved for the King; presumably a complete set was kept for the purposes of eventual publication; and sometimes additional sets seem to have been available for the use of Expedition members and for Cervantes at the Botanical Garden. When

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[1] In the following discussion I have not attempted to digress and discuss the zoological work of the artists; numerous examples of this work are known, and various references to these may be found in the works of Wilson (1962, 1970), and Arias (1968).

[2] "Et quoniam iconum ipsarum series ita inordinatim exprimitur, ut priorum classium plantae majore plerumque quam subsequentium numero notentur; id eo factum fuisse quod has priores illas vero posteriores inspeximus, facile est ad inteligendum."

Sessé sent the manuscript of *Plantae Novae Hispaniae* to the King, via the Viceroy, he asked that Cervantes be allowed to keep a set of the paintings ["reteniendo en su poder del duplicado de Dibujos"] before the second set was forwarded to Spain (see below, p. 110). Mociño, as is well known, presented about 300 duplicates to A. P. de Candolle when he returned to Spain with the original set of paintings. Wilson (1970, p. xlviii) states that when Echeverría returned to Mexico from the Nootka trip in 1793, he "apparently placed his original sketches in the hands of fellow artists at the Academy of San Carlos for multiple reproduction"; she lists 16 artists including Cerda and Francisco Lindo, who were engaged in this activity. Sometimes the duplicates were exact copies (presumably as in the case of Echeverría's drawings mentioned above); sometimes extra flower-parts or fruits or dissections of flowers were sketched in; in at least one instance the same plant was shown unwilted in one plate and wilted in another; one would suppose this was done by the same artist under field-conditions!

Presumably the original set of paintings, and the duplicates, were kept together in some kind of order by the botanists until the Expedition returned to Spain. There seems to have been no general record preserved; we do not know how many paintings were made, or how many copies. It may have been that no general record or index was ever made, but only lists including those paintings made in one particular year or on one particular "Excursion." What we do know about the extent of the collection and the sources of the paintings may be summarized as follows:

1. In the Instituto Botánico 'A. J. Cavanilles,' Madrid (MA), is a series of about 110 plates representing the duplicates resulting from the "Third Excursion" of 1790–91, these having been sent for Royal inspection (McVaugh, 1977, p. 112). None of these is represented by an original in the de Candolle collection (see below); it may be supposed that when Mociño presented the other duplicates to de Candolle, he was not able to include any from the "Third Excursion" because the only available set had already been sent to Spain in 1791. It may be noted that when Mociño returned to Spain in 1803, these particular drawings were not available to him; along with the manuscript of *Plantae Novae Hispaniae* they had been lost, and it was not until 1813 that they came into the hands of Lagasca (McVaugh, 1977, p. 112).

When Altamirano visited the Madrid Botanical Garden in 1898, he obtained copies of a large number of manuscripts that he supposed to be those of Mociño, and also about 110 "foto-calcas de todos los dibujos del mismo señor representando plantas mexicanas que encontré en el archivo" (cf. Altamirano "1897"). These photo-copies were made by a process involving transmitted light, resulting in a reversed image (a negative) on paper. The copies were studied by José Ramírez and described by him (Ramírez, 1899, 1903). Also in the Madrid archive is a numbered list of the same paintings (from 1 to 104); the list is in Mociño's hand, providing supporting evidence that these plates are the same ones that were sent from Guadalajara in 1791.

2. Of the paintings and sketches made by Echeverría on the Nootka Expedition in 1792, several sets are known. The originals seem to have been taken by the artist himself to Cuba in 1795, that he might complete certain unfinished details (McVaugh, 1977, p. 137). The fate of this first set is unknown to me. There are some copies in the de Candolle collection, and presumably the originals were among those carried by Mociño on his last trip to Barcelona. Other sets exist in the Archivo del Ministerio de Asuntos Exteriores, Madrid, and in the Revillagigedo Papers, Vol. 29 (Wilson, 1970, p. xlviii). According to Wilson the extant drawings are all contemporary copies, made by artists employed in Mexico for that purpose. Five of the drawings of plants from the Nootka Expedition are reproduced from AMAE ms. 146 by Arias (1968) and by Wilson (1970, *pl. 19–23*). The total number of paintings of plants made by Echeverría in 1792 is unknown; the total number of plant-species studied during the same period (Mociño's estimate) was about 200 (Wilson 1970, p. 83).

3. In the Museo de Ciencias Naturales, and the Instituto Botánico (MA), Madrid, are contemporary lists of paintings that were made during the early years of the Expedition's stay in Mexico. The principal lists are as follows:

Index plantarum quae iconibus demonstrantur. Litera N. novas indicat. Published in full by Arias (1968, pp. 387–388). A list of 187 paintings made during the "First Excursion," i.e. during the work in the vicinity of México, 1787–1788.

Index iconum rariores omnes, novasque vegetabilium stirpes ab Expeditione Botanica Novae Hispaniae in secunda excursione detectas repressentatum. A list of the paintings made in 1789, arranged by Linnaean classes, published in full by Arias (1968, pp. 376–378). A list with essentially the same title, arranged in numerical order (nos. 190–392, with some numbers missing and some numbers below 190 included) is in the archive at MA.

Rariora Novae Hispaniae vegetabilia in tertia excursione botanica iconibus repraesentata. A list of the paintings made in 1790–1791, arranged by Linnaean classes, published in full by Arias (1968, pp. 388–390) under the above title and (pp. 385–386) under the title *Icones Tertiae Excursionis.* Both these lists are credited to the Museo de Ciencias Naturales. A list with the longer title, arranged in numerical order (new numbers from 394 to 460, and about 55 numbers filling in gaps in the two earlier series), is in the archive at MA.

An untitled list of the numbers from 1–416, in Mociño's hand, evidently intended to represent an interim arrangement, is in the archive at MA.

Of the paintings made in the West Indies, on Mociño's trip to Central America, on the Nootka Expedition, and in Mexico after 1791, no lists have come to light, and there is no evidence that any of these were ever numbered or listed.

4. The de Candolle collection at the Conservatoire Botanique, Genève.

The history of the collection now at Geneva, and of Mociño's relationship with A. P. de Candolle, was first told by de Candolle himself (1862, pp. 219–221, 288–291), and has appeared more recently in several versions, including that of Rickett (1947). The interested reader may consult those works for details. In brief, when Mociño fled to France in 1812 with his manuscripts and paintings, he took with him not only the primary set of paintings that had been prepared to accompany the new *Flora Mexicana,* but also all the duplicates that were in the collection. When he left to return to Spain in 1817, he presented to de Candolle all the "duplicates" (to the number of about 309), and de Candolle arranged to have copies made in Geneva of all those for which there were no duplicates. Mociño's set of the plates having been lost, there remains at Geneva an essentially complete set of the paintings made by the Botanical Expedition, with one exception. De Candolle (1862) noted that when he was arranging to have the collection copied, he put aside the paintings of about 200 well known species, considering these to be of minor interest. Probably several species for which plates were cited in the works of Sessé & Mociño, but for which no plates are now known (e.g. *Tropaeolum majus, Caesalpinia pulcherrima, Psidium guajava, Parkinsonia aculeata, Corchorus siliquosus,* and *Zea mays*), were represented by paintings in the collection carried by Mociño to Barcelona.

The copies made at Geneva vary greatly in quality. This is not surprising, considering the haste with which they were done (all in about 10 days) and the number of artists (more than 100) that took part in the work. Some of the artists (e.g. Node-Vêran and Heyland)[1] were well known either then or later for their fine botanical drawings. Others

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[1] Toussaint-François Node was born at Marsillargues (Hérault), France, where he was baptized on November 1, 1773. He removed to Montpellier before 1800, and eventually became the artist ("dessinateur") at the Jardin des Plantes of that city, where he worked under the direction of A. P. de Candolle until the latter moved to Geneva. Node continued as staff artist at the garden for the rest of his life, assembling there a collection of more than 900 watercolor paintings of plants ("magnifiques aquarelles sur beau velin pour lesquelles on ne sait ce qu'on doit admirer le plus de la scrupuleuse

were students, or friends and acquaintances of de Candolle, notable for their willingness to cooperate in an emergency rather than for any genuine artistic talent.

The duplicates presented by Mociño also vary in quality. Some are merely preliminary sketches marked by Sessé or by Mociño, "Copiar" or "Copiado"; many others were unnamed and unnumbered and probably were never classified; about 225 are identifiable with certainty as belonging to the numbered *Icones Florae Mexicanae.* Fewer than half of the plates from the "First Excursion" (Ic. Fl. Mex. 1–187) are represented by duplicates (i.e. original paintings); more than two-thirds of those from the "Second Excursion" (i.e. from the series 190–392) are present. The "Third Excursion" is represented by copies only (i.e. those made in Geneva). The inference is clear that Mociño had no extras, having sent the principal set of duplicates to Madrid in 1791 (see above, p. 103).

The original plates are usually recognizable by the conspicuous watermarks. In addition to the chain-lines, at least a third of the plates have the mark J KOOL or JAN KOOL, with a fleur-de-lys above the letters. About the same number are marked IV. Some few have the chain-lines only. An occasional plate is marked CATALVNYA, or with a bird over JP, or with a crown and swords over JP RV. The common marks (J KOOL and IV) occur frequently among the *Icones Florae Mexicanae* without any order that I can determine. The name Jan Kool is apparently Dutch, and this follows from an item in one of the inventories of equipment sent from Cádiz to Mexico in 1787: Papel de Holanda p[ara] los Dibujos de Plantas y Animales seis resmas (AGH 527^1: 15). Presumably this represented about 3000 sheets of paper, which should have been ample supply for a time.

The plates obtained by de Candolle from Mociño, together with the copies made in Geneva, were arranged by de Candolle in one systematic series irrespective of the quality of the plate or its supposed geographic origin. De Candolle supposed that all or nearly all the plates were based on Mexican plants, although he knew that some of them (e.g. *Rubus nutkanus*) were not. He numbered the entire series soon after the arrangement was complete, perhaps early in 1817. Each plate bears a pencilled number in his hand, usually at the upper right. The numbers begin with no. 1, *Ranunculus dichotomus,* and end with the grasses (nos. 1302–1337). The numbers were seldom cited in publication by de Candolle and his contemporaries even when the plates formed the bases for new species.

The "copies" that make up more than three-fourths of the collection usually bear but the one number, that assigned by de Candolle himself. In a few instances only, the copyist carried over a number from the original painting, but so few of the copies bear any number at all that we do not know if the original plates from Central America, the West Indies, and the Atlantic lowlands of Mexico, were consistently numbered in the first place. It seems unlikely that they were, as after the return of Sessé from Cuba in 1798,

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exécution du dessin jusque dans ses moindres détails ou de l'exactitude et de la fraicheur des differentes couleurs."). He died March 7, 1852, in Montpellier.

The origin of the name Node-Véran is not certainly known. The artist's family name was Node. It is said that on the occasion of his birth, his father signed the name "Node *dit* Véran"; he himself used the name sometimes in this way, but on his death-certificate it is written merely as Node. For most of the above information I am indebted to Dr. Louis Dulieu, then of Montpellier, who in 1963 sent me a most informative account based on his own research on the life and work of Node-Véran.

Heyland, whose real name was Jean Cristophe Kumpfler, was born at Frankfurt-am-Main in 1792. As a child he came to live in Geneva with an uncle named Heyland. "A la fin de 1816," at the time when artists in Geneva were being recruited to copy Mociño's plates, Heyland did 16 of these copies so well that he was encouraged by A. P. de Candolle to continue as an artist. He became one of the leading botanical artists in Europe. He executed most of the plates in the publications of de Candolle from 1817 to 1841, and worked also for Delessert, Boissier, and Webb. In 1849 he accepted a post as artist attached to the garden of the Archduke Reynier, Viceroy of Lombardy, near Milan, and was there about 10 years, then returned to Geneva where he lived until August 29, 1866. (A. de Candolle, in Act. Soc. Helvet. Sci. Nat. 1866: 274–279. ?1867.)

and the return of Mociño from Guatemala in 1799, there seems to have been amazingly little botanical work done in Mexico before the return of the Expedition to Spain.

Probably, however, some sort of temporary field-numbers were assigned to the plates as they were made on the later excursions. A few originals in the de Candolle collection, all apparently made during one of the later years of the Expedition, are labelled by Sessé so as to suggest that they form part of an incomplete series:

DC plate	38	Marked by Sessé:	"Tab. 4," "fol. 157" and "Viola."
	96		"Tab. 8," and "fol. 99."
	1160		"Tab. 22," and "fol. 10."
	453		"Tab. 33."

Of the approximately 309 originals in the de Candolle collection, about 52 are not numbered in any way except with the general serial number assigned by de Candolle. Each of the other originals bears either one of the numbers of the *Icones Florae Mexicanae* (usually in the hand of Mociño in one of the upper corners of the sheet), or what appear to be remnants of an earlier numbering system (mostly in one of the lower corners of the frame surrounding the picture), or both (see p. 108).

The plates at Geneva are arranged in thirteen looseleaf folio volumes. The first volume includes an index to all the plates under the names by which they were known to de Candolle, or under which they were received from Mociño; there is also an index to all the artists who took part in the copying of the plates, and which plates were copied by each one; there is a copy of the printed text of the *Calques des Dessins* (A. de Candolle, 1874), and a lengthy handwritten introduction by Alphonse de Candolle. The remainder of Volume 1 is taken up by 39 pages of plates, separately numbered with Roman numerals I–XXXIX and so cited in the text of the *Calques des Dessins* and in the present paper. Each plate includes one or more sketches in outline, these copied by the artist Node-Véran from the original colored plates, and usually consisting of details of flowers or fruits or both, sometimes with leaves and other flower parts. The total number of such sketches is about 184; each was photographed separately by Macbride (Field Museum negatives 30257–30440, inclusive). Most of the sketches, naturally enough, merely duplicate drawings that are represented as well or better in other plates in the collection, but some of them have assumed the importance of types because the complete paintings, the actual types of de Candolle and others, have been lost.

Although the plates in the collection are numbered from 1 to 1337, the number now extant is probably about a hundred less than this. Alphonse de Candolle made an inventory of the set in 1873, before the publication of the *Calques des Dessins,* and made notations (in the index to the first volume, and elsewhere) on the ones that were missing at that time. Some others have apparently disappeared since 1873, and a few that were missing then have reappeared. Some of the disappearances have presumably been incidental to the use of the collection; that is, some of the plates have probably been misplaced in the herbarium or the library, or loaned and forgotten. The most rapid attrition seems to have been in the early days of the collection, when plates pertaining to certain plant-families were loaned for study or were copied for publication and were never returned to the collection. I do not know why this should have been, unless in some way the plates were damaged or destroyed in the process of publication, or simply that the originals were thought not worth keeping after the publication of a good copy.

All the plates relating to Solanaceae seem to have been kept by Félix Dunal, who took part with de Candolle and Mociño in the original arrangement of the collection when it was first brought to Montpellier. Some of the species of *Solanum* published by Dunal in the third volume of Poiret's *Supplément* to Lamarck's *Encyclopédie* (1813) were in fact the first published species based directly on Mociño's plates. As there are no Solanaceae listed in the index to the de Candolle collection, it may be supposed that these plates were never returned to de Candolle and so never formed a part of his permanent collection. Dunal seems also to have borrowed, but never returned, de Candolle plates 7–9, pertaining to the Annonaceae; these were reproduced as plates 2, 25, and 28 of Dunal's monograph of that family (1817), but the original paintings are still missing.

Other authors, including de Candolle himself, made similar inroads on the collection. All the plates on Cactaceae (about 18 in number), have been missing at least since 1873, but most of them were reproduced with suitable acknowledgment in de Candolle's review of the Cacti in 1829. Plates representing the five species of "Elaterium" described by Seringe in the *Prodromus* in 1828 are now represented only by sketches in plate XXXVIII, although it seems from the original descriptions that the complete paintings were seen by Seringe. Colladon, in his *Histoire . . . des Casses* (1816), acknowledges the receipt from Mociño, in 1815, of 5 plates representing new species of *Cassia.* The plates are not in the de Candolle collection, and perhaps were never included in it. Other gaps in the collection doubtless exist.

The paintings in the collection at Geneva seem to have come from all the regions visited by the members of the Botanical Expedition. The nucleus of the collection is formed by the plates of known geographical origin in the highlands of southern and southwestern Mexico, namely those plates that can be identified with the *Icones Florae Mexicanae.* With this one large exception, no great number of plates can be certainly identified as from any particular region. The most that can be said is that any plate not identifiable with the *Icones Florae Mexicanae* may have been painted (or copied from an original that was painted) in British Columbia or California; almost anywhere in central or southern Mexico as far southeast as Tabasco and Chiapas; in Central America along a route extending from Oaxaca, Mexico, to the Gulf of Nicoya; in western Cuba particularly near Havana; or almost anywhere in the coastal districts of Puerto Rico.

In 1874 Alphonse de Candolle distributed his *Calques des Dessins de la Flore du Mexique, de Mocino et Sessé qui ont servis de types d'espèces dans le Systema ou le Prodromus.* This work consisted of sets of tracings of the 279 plates supposed to have served as types of names of genera or species (or in some instances varieties), together with a printed text in which were listed the number assigned to each plate by de Candolle, the nature of each plate (i.e. whether an "original," a colored copy or merely a sketch), and a brief reference to the name and place of publication in de Candolle's *Systema* or the *Prodromus.* Ten sets were offered for sale, to the directors of the principal botanical museums. No tracings were made of plates that had already been published in various *Mémoires* by A. P. de Candolle and others; in fact as noted above some of these were missing at the time the tracings were being made.

Similarly omitted from the *Calques des Dessins* were at least the following original plates that are identifiable as types, and at the same time represent the numbered *Icones Florae Mexicanae:*

Ic. Fl. Mex.	*DC. plate*	*Type of*
28	897	Tournefortia hernandesii Dun. ex DC. in DC. Prodr. 9: 529. 1845.
37	856	Ipomoea emetica Choisy in DC. Prodr. 9: 376. 1845.
93	306	Cerasus capollin DC. ex Ser. in DC. Prodr. 2: 539. 1825.
97	46	Helianthemum obcordatum Dun. in DC. Prodr. 1: 284. 1824.
199	196	Icica ? serrata DC. in DC. Prodr. 2: 77. 1825.
280	93	Riedleia corymbosa DC. in DC. Prodr. 1: 491. 1824.
320	146	Cissus tuberosa DC. in DC. Prodr. 1: 629. 1824.
335	119	Triumfetta oxyphylla DC. in DC. Prodr. 1: 508. 1824.
341	320	Cuphea coccinea DC. in DC. Prodr. 3: 85. 1828.
347	117	Triumfetta polyandra DC. in DC. Prodr. 1: 508. 1824.
368	219	Coulteria mexicana DC. in DC. Prodr. 2: 481. 1825.
376	87	Malvaviscus ? flavidus DC. in DC. Prodr. 1: 446. 1824.

A photographic record of most of the above plates, and others, in addition to the sketches mentioned above, was made for the Field Museum by J. Francis Macbride. These "Field Museum Negatives" have been widely known and used in publication in recent decades.

Numbering of the *Icones Florae Mexicanae*

At the very beginning of the Botanical Expedition, a numbered series of *Icones Florae Mexicanae* was envisioned, to accompany the flora that was planned. Botanists and artists worked rapidly during the first year in Mexico. Early in May, 1788, it was noted that there were already 200 plants in the herbarium, and paintings of a like number of species (AGH 462^{1}: 7). Probably the actual number of paintings was not quite so large, as the total number that eventually resulted from the "First Excursion" (that is, the sum of the exploration near Mexico in 1787–1788), was only 187.

As often neither artists nor botanists knew the identity of the plant that was being painted, the paintings were customarily assigned serial numbers in the order in which they were finished. Only after the completion of the work of the first field-season did it seem desirable to make an arrangement of the collection on systematic principles, and to assign new numbers to the paintings.

I have not found any complete record of the numbers first assigned to the paintings made near Mexico City in the early months of the Expedition, but some clues to these numbers may be found in documents at Madrid (MA, 4^{a} Div., núms. 7–8). In one of Sessé's notebooks of this early period, headed "Singenesia"; that is, Compositae, about 80 species from near Mexico City are described. About 19 plates are cited, including numbers ranging from 8 to 174; these numbers evidently represent those of the earliest enumeration. The number 61, for example, was recorded for *Solidago sinuata;* on the manuscript of the notebook this number has been crossed out and 163 written in; the latter is the number assigned to this painting in the newer series called *Icones Florae Mexicanae,* continued through 1791. The number 172 appears in Sessé's notebook under the name *Eupatorium triangulare;* through an oversight, apparently on the part of Mociño, this same number was cited in the *Plantae Novae Hispaniae,* even though in the renumbering this plate has become *Ic. Fl. Mex. 148.*

The primary evidence connecting this earliest numbering system with that of the *Icones Florae Mexicanae* may be found on some of the original paintings in the de Candolle collection. Almost all the paintings made by the artists of the *Expedición Botánica* in the first years are identifiable by the formal style in which they are done. The usual practice was to mark out a rectangular frame of a predetermined size (usually about 16 X 22 cm.; sometimes 18.5 X 27.5–29.5 cm.), then to fit the plant to the frame regardless of its original size, shape or habit. About 50 of the originals at Geneva bear a pencilled number near the corner of the frame (usually inside the frame, at the lower left, but sometimes in other positions). These numbers range from 1 to 170, and I suppose them to represent remnants of the original numbering system. Six of the numbers, listed in the table below, correspond to those cited in Sessé's notebook for the same plates, thus affording a credible clue to the meaning of the entries on the plates at Geneva:

Number as listed by Sessé	Name as listed by Sessé	DC. plate number and name	Added number
8	Ageratum febrifugum	551 Stevia? febrifuga	8
12	At[h]anasia	675 [Tridax?]	12
81	Eupatorium? commune	520 Porophyllum linaria	81
121	Melampodium pinnatifidum	630 Melampodium sessiliflorum	121
135	Eriocephalus Artemisiaefolius?	703^{g} Eriocephalus arthemisifolius	135
139	Bupt[h]almum heliantoides	699 Buphthalmum procumbens	139

Presumably the numbers on these plates were assigned in the order of completion, as they were to paintings made in later years. In the renumbering of the plates from the First Excursion, as described below, the order was changed to conform to the Linnaean system. The renumbered list of 187 paintings, as published by Arias (see above, p. 104) is preserved in the Museo de Ciencias Naturales, Madrid. At the Instituto Botánico (MA) there is an incomplete copy of the same list, beginning with no. 49. This latter list is apparently in Sessé's hand, and includes numerous changes from, and additions to, the list published by Arias. The final list, in order by Linnaean classes, served as a foundation to which were added the plates made on the Second and Third Excursions. These later lists were eventually put into systematic arrangement, as shown in the versions published by Arias (see above), but the plates were never renumbered; the numbers cited in *Plantae Novae Hispaniae* and *Flora Mexicana* were essentially those assigned in 1789 and 1790–91, respectively.

Because the *Expedición Botánica* travelled slowly and with relative difficulty, and set up various headquarters at places that now seem very close together in the vicinity of Mexico City, it is probable that most of their botanizing, and most of the work of the artists, were done fairly close to headquarters, rather than along the routes between settlements. No more than 12 localities (including México) were mentioned in connection with the *icones* made during the first field season; the presumption is that as a general thing the paintings were made at the same localities, when the plants were discovered and studied:

Nochiztlan [= Xochitlán]
Ayacapiztla
Cuernavaca
San Angel
Amecameca
Eremus P. P. Carmelitarum
Mexico
Coyoacán
Tepelpa
San Agustín
Ixtapalapa
Santa María de los Remedios

Some species are not mentioned in the published texts in connection with a specific locality; for these a general statement may be made, e.g. "in calidiore America," "in Nova Hispania," "in calidis Novae Hispaniae regionibus," or merely "ubique." About a third of the species are located thus vaguely.

Mociño seems to have been responsible, at least after 1789, for the assignment of the plate-numbers; if the work was not formally delegated to him, he was in any event much involved in it. At the Instituto Botánico (MA) there is a list in his handwriting of all the paintings made during the "Second Excursion" (that to Acapulco, in the summer of 1789); a similar list for the "Third Excursion" (that to Guadalajara, 1790–1791); a list of plates sent to Madrid in 1791 (i.e. essentially the same plates as those listed for the Third Excursion but with a different series of numbers [1–104]; a list including most of the plates from the First and Second Excursions but omitting those of the Third; and a list of plates 1–416, inclusive.

In devising an arrangement for the inclusive *Icones Florae Mexicanae,* Mociño seems to have left unchanged the numbers assigned (presumably by Sessé) to the first 187 plates, and added the plates obtained in the next two years, including approximately 180 from the expedition of 1789, and about 100 from that of 1790–1791.

In the early summer of 1791, after the completion of three years' field work, the numbering of the plates posed a problem. Logic demanded that they be numbered consecutively according to the Linnaean system, the arrangement already effected for the plates painted the first year. As a practical matter, the plates from the second and third "Excursions" had been numbered first in the order in which they were painted, that is, as plants in suitable condition had been encountered in the field. The expectation was that at the conclusion of the work of the Expedition, the whole would be reorganized into one systematic series; as Mociño wrote in the preface to *Plantae Novae Hispaniae,* "coeterum opere confecto, aliter omnino iconum numerus exprimendus est." The assignment of temporary numbers to all the plates available in 1791 seems to have been an expedient, necessary for the time, but by no means final. The task seems to have been done hastily, under the pressure of finishing the manuscript of the *Plantae Novae Hispaniae* in Guadalajara in the summer of 1791 so it could be returned to the Viceroy as evidence of accomplishment before the Expedition went on westward.

The known circumstances concerning the completion of the manuscript, and the way it came to be transmitted through the Viceroy to the Court of Spain, all point toward the conclusion that it was finished under pressure. As the Expedition was preparing to leave Guadalajara for Tepic, on July 22, 1791, Sessé wrote to the Viceroy (Revillagigedo), announcing the shipment of two volumes of manuscript "en folio" and a number of paintings ["dibujos"]. The manuscript, of course, was that of the *Plantae Novae Hispaniae,* as discussed previously by various authors (cf. Contr. Univ. Michigan Herb. 11: 112–113, 1977). Many of the deficiencies in that work, as Mociño himself wrote, may be attributed to "the difficulties imposed by travel."

The intention was to include an account of all the species that had been studied during the first three years of the Expedition, and this in fact seems to have been what was done. The number of species that were included (1383 according to Sessé), agrees well enough with existing lists of those of which specimens had been collected, to confirm the idea that the authors treated most of the plants that they regarded as interesting or significant. In the manuscript, exactly as in the version that was ultimately printed, the species were arranged in one series according to Linnaean Classes. The localities that were cited include not only those from near Mexico (1787–1788), but those visited on the trip to Acapulco (1789), and those from the trip of 1790–1791, up to as late as April of 1791, after the Expedition reached Guadalajara.

It seems clear that when the *expedicionarios* left México in May, 1790, they carried with them their unfinished manuscripts pertaining to the years 1787–89, lists of the paintings from those years if not copies of the paintings themselves, and at least enough of the available literature to enable them to identify new plants as they encountered them. Descriptions of and comments on species already studied were probably carried on individual sheets of paper (as so many are still to be found in the archive at MA). Because the entire text of *Plantae Novae Hispaniae* is in one continuous manuscript all in Mociño's hand, and including many species that were studied up to and including April, 1791, it follows that he completed all the work of arrangement and final copying between about the first of April, when the Expedition reached Guadalajara, and the latter part of July.

Returning to the numbering of the *icones,* it may be supposed that Mociño, as suggested above, provided the temporary plate-numbers assigned in 1789 and 1790–91 as a necessary expedient. It was evidently his intention to cite all the plates but in fact nos. 447–460, although assigned in the usual manner, were not included in the final draft. References to the *Icones* appear to have been added to the manuscript by Mociño after the completion of the rest of the text (often in a different ink), each written under the trivial name in the margin, thus:

pulcherrima Ic. 192	Iusticia folliis ovatis, . . .

In the printed version quite a different arrangement was used; the listing of each *icon* follows immediately after the character and the cited synonyms, if any, and for typographical reasons it is often difficult to separate the reference to the *icon* from the rest of the literature citation:

Pulcherrima. Justicia foliis ovatis, . . . Suppl. 81. Ic. 192.

Although, if my surmise is correct, the plates numbered from 190 to 460 were not renumbered because of the need to complete the manuscript, some attempt was nevertheless made to fill gaps in the earliest series, that of 1787–88. Inspection of the text of *Plantae Novae Hispaniae* shows that there were 18 plates (out of the series 1–187) for which the published localities were not those visited during the "First Excursion" of 1787–88, but visited either in 1789 or during the trip of 1790–91. The plates and localities in question are as follows:

Plate number	Locality cited	Plate number	Locality cited
4	Mazatlán, [Gro.]	38	Apatzingán
12	Santa Rosa, [Gto.]	40	Coahuayana
13	Pátzcuaro, [Mich.]	97	Santa Rosa
22	Coahuayana, [Mich.]	105	Puruándiro
24	Puruándiro, [Mich.]	130	Xorullo, [Mich.]
27	Apatzingán, [Mich.]	132	Apatzingán
32	Chilpancingo, [Gro.]	137	Chilapa, [Gro.]
33	Huango, [Mich.]	161	Michoacán, hot places
34	Apatzingán	172	Mazatlán

Some of the numbers (12, 13, 132) may have been omitted in the original enumeration; they are not cited in Arias' published list of nos. 1–187. The new or renumbered plates are inserted in the systematic sequence in approximately the right places (e.g. nos. 38 and 40, *Echites undulata* and *Varronia bullata,* are associated with other Pentandria, viz. *Cordia, Ipomoea, Cestrum,* and *Plumeria*). My assumption is that if there were gaps in the original enumeration (for whatever reason), the numbers were assigned to new plates; if the plates already numbered were lost or damaged or were considered inacceptable or inferior, they were replaced by new plates.

Gaps seem to have been filled similarly in the series of plates from 190–392, and in that from 394–460. In the former series about 25 are cited as from localities not visited in 1789; all but two of these localities were visited in the journeys of 1790–91, making it easy to suppose that earlier plates were replaced whenever better new plates were available for the same or different species. About 8 plates in the last series (394–460) are similarly cited from what seem to be the wrong localities for that particular year. I cannot explain this unless it was an attempt to fit some previously unnumbered plates into some semblance of order in the new series. The numbering of the later plates from the last series (the "Third Excursion") suggests that someone (presumably Mociño) kept the systematic order in mind as numbers were assigned plates that had accumulated. For example, the plates from 413 to 440 (except 415) are approximately in the order in which they appear in *Plantae Novae Hispaniae.* The numbers from 441 to 460 may well have been assigned in haste after the arrival of the Expedition at Guadalajara. They represent a miscellaneous assemblage; only 5 of them were cited in *Plantae Novae Hispaniae,* presumably because of lack of time in which to attend to all the necessary details. Four of the names and one of the numbers were ultimately cited in *Flora Mexicana,* and six (both names and numbers) are apparently unpublished to this day.

In summary, the numbers assigned to the *Icones Florae Mexicanae* are neither in strictly systematic order nor in chronological order, but mixed in a way that represents a compromise between the wishes of the authors and practical necessity. References to localities in the published works of Sessé & Mociño appear to be reasonably trustworthy; i.e. most of the plates in the series 1–187 (unless otherwise specified) were probably painted in the region of Mexico City; those from 190–392 along a transect from Cuernavaca to Acapulco, and those from 394–460 from along the route from Querétaro to Coahuayana or from there to Guadalajara. When gaps in the numbering series were filled, apparently they were usually filled with new plates from new localities. For example, no. 300 does not appear in lists of the paintings made during the Second

Excursion (i.e. nos. 190–392), but only in the final list, and in publication, where it is assigned the name *Quassia amara* and the locality is given as Coahuayana. The identity of the plant depicted is readily ascertained by inspection of the plate, and there seems no reason to doubt the correctness of the locality cited, as this plant may still be found in abundance in the region of Coahuayana.

Identification of the *Icones*

In making identifications of names published by Sessé & Mociño, it must always be remembered that the *Plantae Novae Hispaniae* and the *Flora Mexicana* are not ordinary floristic works in which most statements can be accepted at face value without verification. The posthumous works of Sessé & Mociño were not really ready for publication. The manuscript of *Plantae Novae Hispaniae* was presented as a formal report and was therefore organized into the semblance of a flora, but because of the haste with which it was prepared there could have been very little careful checking for accuracy of details. There are omissions, misspellings and, notable in the present context, a regrettable lack of care in the assignment of plate-numbers and the citation of such numbers in the manuscript. To compound the difficulty, the editors of the printed version often omitted the plate-numbers completely or cited the wrong numbers. The manuscript of *Flora Mexicana* is more frustrating because it is hardly more than a collection of field-notes and field-descriptions, similar to those that made up the *Plantae Novae Hispaniae* but including preliminary drafts, names that were assigned before the authors had studied the plants completely, taxa that should have been reported in *Plantae Novae Hispaniae* but were not, taxa that were published in *Plantae Novae Hispaniae* under another name, descriptions without any accompanying locality data or without an accompanying binomial. In short, both the manuscripts and the works that were printed from them are full of errors, and anyone who studies them must make due allowance for this.

Descriptions in both works are carefully drawn, for the most part. The authors were good observers and of more than average botanical competence (a case in point is their identification of *Anemopsis californica* with *Saururus cernuus*). Often, however, they confused two or more species under the same name. At the beginning of their work in Mexico they were slow to accept the fact that some of the species were new to science. Later they described many new species, but one gets the impression that they never fully realized the richness of the flora of the New World; if they found a new species of *Physalis* near Mexico City, it must have seemed unlikely to them that they would find ten more species in the Pacific lowlands between Coahuayana and Tepic. Probably like most of their contemporaries they were relatively unaware of the importance of variation in populations and in species. This surely must have influenced their approach to the preparation of a *Flora:* Once a species had been described, it was not necessary to look at it carefully again. This approach, and a similar approach to the illustrations for the *Flora,* makes for difficulties when one tries to understand them today. Like the descriptions, the *icones* were prepared *ad hoc,* that is, whenever a plant presented itself in suitable condition. For example, a description and illustration may have been prepared, in 1787 or 1788, for a plant found near Mexico City. If for some reason the illustration was incomplete or unsatisfactory, it may have been replaced by another one (assigned the same number) made years later, in the Pacific lowlands on the other side of Mexico, with the assumption that it applied to the original species. When the description of a high-montane plant is published, with the citation of an illustration of a lowland plant, and a locality that applies to neither, in order to indicate a wide range for the species (e.g. "in temperatis et calidis N. H. montibus"), it may be quite impossible to equate a name published by Sessé & Mociño with any one species. In attempting to identify such names, botanists should examine each case in terms of specimens named in the Sessé &

Mociño herbaria, the account in the protologue, and the identity of the plant depicted in the plate. In a gratifying proportion of the cases there is reasonable agreement. In many instances, however, especially when herbarium material is lacking, it is difficult to reconcile the protologue with the plate.

The identifications reported below are primarily from specimens named to correspond with the names applied to the plates, and from inspection of the plates themselves. They do not represent typifications of the names of the species proposed as new by Sessé & Mociño, although if one or both of the above agree sufficiently with the protologue in any individual case, they may aid in typification.

It is not feasible to document fully here the identifications of all the herbarium specimens that bear on the identities of the *Icones.* Contemporary identifications in the Sessé & Mociño herbarium include those made by the collectors themselves, and some by Lagasca. Modern identifications are chiefly those that were made by Paul C. Standley and others during the time the entire herbarium was on loan from Madrid to the Field Museum (McVaugh, 1977, pp. 101–102).

When the material arrived in Chicago in May, 1936, Standley finished the work of sorting within a few months, and began the task of identification. Much of this he undertook himself, but of certain critical families he sent all the specimens to specialists. All the Acanthaceae were sent to E. C. Leonard; Boraginaceae to I. M. Johnston; Gramineae to J. R. Swallen; *Senecio* to J. M. Greenman; Pteridophyta to W. R. Maxon; Labiatae to Carl Epling; *Smilax, Hybanthus* and *Viburnum* to C. V. Morton; Orchidaceae to Oakes Ames and Charles Schweinfurth; Piperaceae to William Trelease; Passifloraceae and Urticaceae to E. P. Killip; Bromeliaceae to Lyman B. Smith; Asclepiadaceae and Apocynaceae to R. E. Woodson, Jr. Some other special groups were named for Standley during the first years the collection was in Chicago: S. F. Blake and E. E. Sherff studied some of the Compositae; B. A. Krukoff named *Erythrina;* I myself was privileged to study some of the Campanulaceae and Euphorbiaceae soon after 1940. By the spring of 1942 Standley had named "a good proportion of the collection" (Letter to C. V. Morton, May 27; Williams, 1963, pp. 12–13), but he said "I have myself just about lost interest in the collection, largely perhaps because I see no likelihood of having to return it soon to Madrid! Perhaps some day I shall get around to finishing the report on it."

In 1958, when Dr. Theodor Just and his colleagues at the Field Museum began a concerted effort to complete the identifications, there were representatives of about 80 families of flowering plants remaining unnamed. A few groups were almost untouched (e.g. Burseraceae, 34 sheets; Cactaceae, 11; Capparaceae, 55; Commelinaceae, 27; Cucurbitaceae, 59; Dioscoreaceae, 37; Iridaceae, 31; Liliaceae, 20; Lythraceae, 65). There remained also a series of residues in various families, evidently representing species and genera that Standley had put aside for later study after naming the rest of the specimens in the family in question. The largest such residues were in Compositae (about 80), Cyperaceae (27), Euphorbiaceae (about 75), Leguminosae (about 115), and Rosaceae (30). Early in the summer of 1964, just before the last of the herbarium was returned to Madrid, the naming was completed except for that of the few fragmentary or otherwise undeterminable specimens that inevitably turned up. It is a pleasure to acknowledge here again the help of the many specialists who took part in this task, colleagues without whom the task could never have been satisfactorily completed:

Ames, Oakes*	Orchidaceae
Bacigalupi, Rimo	Compositae
Barkley, F. A.	various
Barneby, Rupert C.	Leguminosae
Benson, Lyman	Ranunculus
Blake, Sidney Fay*	Compositae Polygalaceae
Bravo H., Helia	Cactaceae
Clausen, Robert T.	Crassulaceae
Constance, Lincoln	Umbelliferae

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*Deceased.

Constance, Lincoln	Hydrophyllaceae Compositae
Correll, Donovan S.	Solanum
Cowan, Richard S.	Leguminosae
Cristóbal, Carmen L.	Sterculiaceae
Cronquist, Arthur	Compositae
Cuatrecasas, José	Theobroma Malpighiaceae
DeJong, D. C. D.	Achaetogeron
Dressler, Robert L.	Pedilanthus
Duke, James A.	Drymaria
Epling, Carl C.*	Labiatae
Ewan, Joseph	Delphinium
Graham, Shirley A.	Cuphea
Grant, Verne	Polemoniaceae
Greenman, J. M.*	Senecio
Hermann, F. J.	Juncaceae Cyperaceae
Hodgdon, Albion R.*	Cistaceae
Howard, Richard A.	Coccoloba
Iltis, Hugh H.	Capparaceae Liliaceae
Irwin, Howard S.	Cassia
Jackson, R. C.	Iva
Johnston, Ivan M.*	Boraginaceae
Johnston, Marshall C.	Compositae Rhamnaceae
Kearney, Thomas H.*	Malvaceae
Killip, E. P.*	Urticaceae Passifloraceae Bomarea
Kobuski, Clarence E.*	Theaceae
Krukoff, B. A.	Erythrina
Kuijt, Job	Dendrophthora
Leonard, E. C.*	Acanthaceae
Lundell, C. L.	Celastraceae Myrsinaceae
Mathias, M. E.	Umbelliferae
Matuda, Eizi*	Commelinaceae
Maxon, William R.*	Pteridophyta
Meyer, F. G.	Valerianaceae
Miranda, Faustino*	various
Moldenke, Harold N.	Verbenaceae Eriocaulaceae
Moore, H. E., Jr.	Palmae Geranium
Morley, Thomas	Mouriri
Morton, Conrad V.*	Hybanthus Smilax Viburnum Solanaceae
Munz, P. A.*	Onagraceae
Ogden, Eugene C.	Potamogeton
Ownbey, Marion*	Liliaceae
Perry, Lily M.	Verbena
Philcox, David	Buchnera
Pippen, Richard W.	Cacalia
Rock, Howard F. L.*	Helenium
Rogers, David J.	Manihot
Rollins, Reed C.	Cruciferae
Roon, Adrianus C. de	Marcgraviaceae
Rudd, Velva E.	Leguminosae
Sandwith, N. Y.*	Bignoniaceae
Schubert, Bernice G.	Desmodium Dioscorea Begonia
Schweinfurth, Chas.*	Orchidaceae
Senn, Harold A.	Crotalaria
Sherff, Earl Edward*	Compositae
Smith, Albert C.	Hippocrateaceae Araliaceae
Smith, Lyman B.	Bromeliaceae Begonia
Stern, Kingsley R.	Dicentra
Straw, Richard M.	Penstemon
Svenson, Henry K.	Cyperaceae
Swallen, Jason R.	Gramineae
Thompson, Henry J.	Loasaceae
Trelease, William*	Piperaceae
Turner, Billie L.	Compositae
Webster, Grady L.	Phyllanthus
Wilbur, Robert L.	Cistaceae
Williams, Louis O.	Orchidaceae Melastomataceae
Wood, Carroll E., Jr.	Tephrosia
Woodson, Robert E.*	Asclepiadaceae Apocynaceae
Wurdack, John J.	Melastomataceae

Table 1. Icones Florae Mexicanae, nos. 1–460

The numbered icones are arranged below in numerical order, with the following included for each number as far as possible:

1. Name as published or used by Sessé & Mociño. Names thought to have been newly published by these authors are so designated, e.g. *Justicia exilis* Sessé & Moc. Names taken by them from earlier authors, as indicated by citation of literature, references to localities cited by earlier authors, and adoption of the diagnostic "character" more or less verbatim, are included with the names of such earlier authors in brackets, e.g. *Boerhaavia diffusa* [L.?]. Names applied by Sessé & Mociño to individual *icones* but never published by them are in quotation marks, e.g. "Clitoria mariana," "Salvia spicata N." The "N." in names like the last one means "new"; it was commonly added by Sessé & Mociño to names of what they supposed to be new species. It appears 83 times in the

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*Deceased.

list of plates 1–187, with the explanation in the heading written by Sessé: "Index plantarum quae iconibus demonstrantur. Litera N novas indicat."

2. In the columns to the right of the name, the pages on which the published names appeared in both editions of *Plantae Novae Hispaniae,* with citation of the plate-number in question. When a name was published and the number cited in *Flora Mexicana* but not in *Plantae Novae Hispaniae,* the appropriate pages are cited with the letters FM. When the page-number is given in square brackets, the plate-number was omitted from the printed text, but was cited in the manuscript from which the text was made. (Approximately 54 numbers were thus omitted in publication.) When the page-number in the chart is followed by a hyphen, e.g. 8-, the plate-number was mentioned neither in the manuscript nor in the printed text, but was mentioned in one of the lists cited above on page 104.

3. In the column to the right of the page-numbers, the paintings sent to Spain from Guadalajara in 1791, now in the archive at MA. These were numbered and listed by Mociño and are cited under his numbers, thus, "M52."

4. In the column immediately to the left of the list of modern names, the numbers assigned to plates of the de Candolle collection, as far as these can be identified with the numbers of the *Icones Florae Mexicanae.* In de Candolle's numbering system the asterisk was an integral part of some numbers. Unless otherwise specified the de Candolle plates are original paintings bearing the corresponding numbers of the *Icones,* or the names as published (or otherwise used) by Sessé & Mociño, or both number and name. A few original paintings with neither name nor number are mentioned specifically below.

Plates other than those described above are identified by the addition of superscript letters as follows:

^{c}A copied plate, bearing neither the name published by Sessé & Mociño nor the original plate-number.

^{cn}A copy annotated (not by Mociño) with the name published by Sessé & Mociño, or the original plate-number, or both.

^{cdc}A plate, whether an original or a copy, that was seen by A. P. de Candolle or one of his contemporaries, but was missing when A. de Candolle took inventory in 1873, or missing in 1963. When the plate-number is unknown, it is cited as "DC-."

5. In the right-hand column, modern names derived from herbarium specimens, from the *Icones,* or from inspection of the printed texts of Sessé & Mociño's works. These names are followed by superscript numbers as follows:

^{1}Identification directly from the numbered plate, either that in the de Candolle collection or that at Madrid. The plant thought to be depicted in the plate is identified thus, e.g., "Salvia patens Cav.^{1}" An exception is made for the approximately 110 plates that are the holotypes of names published by de Candolle and others; these are identified merely by the addition of the words "(Type)," "(Paratype)," or "(Lectotype)." I have confirmed most of the identifications of plates that are reported here, following many earlier opinions by the de Candolles, Bentham, Asa Gray, A. Richard and others, and more modern opinions expressed by specialists in certain groups. A valuable contribution was made by José Ramírez (1903), who listed 90 plates from the collection at Madrid, identified them as far as possible with plates in the de Candolle collection, and provided modern names.

^{2}Identification from specimens in the Sessé & Mociño herbarium. Almost without exception the specimens so identified bear contemporary names identical with those published or used by Sessé & Mociño, or synonyms of such names. When specimens so named in the herbarium represent different species, both are reported. Modern names arrived at in this way are reported thus, e.g., "Tagetes lucida Cav.^{2}"

^{3}Identifications from the descriptions in *Plantae Novae Hispaniae* and *Flora Mexicana.* These are reported thus, e.g., "Zea mays L.^{3}"

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex.		Madrid plate no.	de Candolle plate no.	Identification
		Ed. 1	Ed. 2			
1	Boerhaavia diffusa [L.?]	[1]	[1]		1086•[cn]	Boerhaavia caribea Jacq.[2]
2	Justicia exilis Sessé & Moc.	4	4		1056[c]	Pseuderanthemum cf. cuspidatum (Nees) Radlk.[1]
3	Justicia superba Sessé & Moc.	3	3		1044	?Anisacanthus tulensis Greenm.[1]; A. insignis A. Gray[2]
4	Justicia papilionacea Sessé & Moc.	4	4		1064	Tetramerium hispidum Nees[2]
5	Justicia lutea Sessé & Moc.	[3]	[3]		1068	Barleria micans Nees[1,2]
6	Justicia sexangularis [L.?]	4-	4-		1042	Dicliptera peduncularis Nees[2]
7	Salvia aegyptiaca [L.] (see also no. 456)	7	6		987	Salvia laevis Benth.[1]
8	Salvia stricta Sessé & Moc.	9	8		986	?Salvia lavanduloides H.B.K.[1]; S. elongata H.B.K.[2]
9	"Salvia spicata N."	[Unpublished]			999	Salvia hispanica L.[2]; S. lavanduloides H.B.K.[2]
10	Salvia palafoxiana Sessé & Moc.	8-	8-		1000	Salvia involucrata Cav.[1,2]
11†	Salvia grandiflora Sessé & Moc.	8	7		1001,1002	Salvia fulgens Cav.[2]; S. gesneraeflora Lindl. & Paxt.[2]
12	Salvia glutinosa [L.]	7	7	M68		Salvia patens Cav.[1]
12	Salvia hirsuta Sessé & Moc.	FM7	FM7			Salvia amarissima Ort.[2]
13	Salvia patzquarensis Sessé & Moc.	9	8	M10	992[c]	Salvia clinopodioides H.B.K.[2]
14	Verbena lapulacea [L.]	6	6			Priva lappulacea (L.) Pers.[2]; P. mexicana (L.) Pers.[2]
15	"Verbena laciniata N."	[Unpublished]				Verbena ciliata Benth.[2]
16	Verbena scabrella Sessé & Moc.	6	6		955	Buchnera obliqua Benth.[2]
17	Morea graminea Sessé & Moc.	11-	11-		1237	Nemastylis tenuis (Herb.) Baker[2]
18	Ixia mexicana Sessé & Moc.	11	10		1236	Sisyrinchium sp.[1]
19	Commelina erecta [L.]	[11]	[11]			Commelina coelestis Willd.[2]
20	Commelina graminifolia Sessé & Moc.	[12]	[11]		1290[cn]	Commelina coelestis Willd.[2]; C. dianthifolia DC.[1,2]
21	Commelina communis [L.]	11	11			Commelina diffusa Burm. f.[2]
22	Dianthera sexangularis Sessé & Moc.	5	5	M s.n.		Dicliptera resupinata (Vahl) Juss.[1]; D. peduncularis Nees[2]
23	Hedyotis ["Hedyptis"] mexicana Sessé & Moc.	15	14		DC-[cdc]	Bouvardia jacquinii H.B.K.[1]; B. ternifolia (Cav.) Schlecht.[3]
24	Verbena grandiflora Sessé & Moc.	6	6	M7	1030[c]	Verbena amoena Paxt.[1,2]
25	Mirabilis jalapa [L.]	[19]	[18]			?Mirabilis jalapa L.[3]
26	Mirabilis triandria Sessé & Moc.	19-	18-		? 1081[cn]	Mirabilis microchlamydea Standl.[2]
26	Ixora uniflora Sessé & Moc.	16	15	M43		Bouvardia longiflora (Cav.) H.B.K.[1]

27	Krameria ixina [L.]	18	17			Krameria cuspidata Presl[2]
28	Tournefortia suffruticosa [L.]	[31]	[30]		897	Tournefortia hernandesii Dun. ex DC. (Type); T. mutabilis Vent.
29	Heliotropium mexicanum Sessé & Moc.	20	19		1174^{cn}	Lithospermum strictum Lehm.[2]
30	Lithospermum virginianum [L.]	20	19	M63	900†	Lasiarrhenum strigosum (H.B.K.) Johnst.[1]
31	Buddleia americana [L.]	15	14	M67	?941^{c}	Buddleia cordata H.B.K.[2]
32	Allionia incarnata [L.]	[14]	[13]	M78	1075^{c}	Allionia incarnata L.[2]
33	Lisianthus pauciflorus Sessé & Moc.	24	23	M73	812^{c}	Spigelia scabrella Benth.[1,2]
34	Cordia gerascanthus [L.]	[30]	[28]	M33		Cordia sp.[1]
35	Ipomoea hastata [L.]	27	25		855	Convolvulus incanus Vahl[2]
36	Cordia sebestena [L.]	30	28	M95	877^{c}	?Cordia seleriana Fern.[1,2]
37	Ipomoea sagittata Sessé & Moc.	27	25		856	Ipomoea emetica Choisy (Type)
38	Echites undulata Sessé & Moc.	28	26	M38	802^{c}	?Tabernaemontana sp.[1]
39	Ipomoea tuberosa [L.]	26	25		857	Pharbitis heterophylla (Ort.) Choisy[1]
40	Varronia bullata [L.]	[30]	[28]	M s.n.		Cordia stellata Greenm.[2]
41	Cestrum nocturnum [L.]	32	30		911	?Cestrum leucocarpum Dun.[1]
42	Cestrum tomentosum [L.f.]	[33]	[31]		912	Cestrum benthamii Miers[1]
43	Plumeria alba [L.]	29	27		759	Plumeria rubra L.[1,2]
44	Cerbera thevetia [L.]	32	30		792	Thevetia peruviana (Pers.) K. Schum.[2]
45	Tabernaemontana laurifolia [L.]	29	27	M s.n.	800^{c}	?Tabernaemontana amygdalifolia Jacq.[2]
46	Solanum mexicanum Sessé & Moc.	[35]	[33]			Solanum sp.‡
47	Solanum virginianum [L.]	35	33			?Solanum heterodoxum Dun.[2]
48	Physalis pubescens [L.]	35	33		916	Physalis coztomatl Dun. (Type)
49	Convolvulus arboreus Sessé & Moc.	23	22		850	Ipomoea murucoides Roem. & Schult.[2]; I. intrapilosa Rose[2]
50	Chiococca axillaris Sessé & Moc.	36	34		481	Symphoricarpos microphyllus H.B.K.[2]; Margaris nudiflora DC. (Type).
51	Ceanothus americanus [L.]	38	36		?176*★	Ceanothus coeruleus Lag.[2]
52	"Claytonia scapifera"	[Unpublished]				Unknown
53	Stapelia herbacea Sessé & Mos.	41	39		?769^{cdc}	?Matelea sp.[3]
54	Apocynum mexicanum Sessé & Moc.	42	39			Sarcostemma bicolor Decne.[2]
55	Asclepias filiformis [L.f.]	[43]	[41]		?780^{c}	Asclepias linaria Cav.[2]

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†No. 11 was also used for Ic. 290, q.v.

†This is assumed to be the plate listed as no. 30 among those painted near Mexico City in 1787–88. Ic. 30 is also listed among the paintings of 1790–91; this is evidently Mociño's no. 63 in the collection at MA, labelled *Lithospermum virginianum.* DC. plate 904, the type of *Macromeria viridiflora* DC., is a copy based on Mociño's original of the same painting.

‡Not *Solanum mexicanum* Dunal, which was also based on a Sessé & Mociño plate, but a tuberous-rooted herb more like *S. mozinianum* Dunal.

★An original painting, but without name or number as used by Sessé & Mociño.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
56	Gentiana coerulea Sessé & Moc.	[44]	[41]		805	Gentiana spathacea H.B.K.[2]
57	"Gomphrena diffusa"	[Unpublished]			?1093[cn]	Gomphrena decumbens Jacq.[2]
58	Anthericum ossifragum [L.]	FM96-	FM88-			Anthericum, cf. aurantiacum Baker ex Hemsl.[2]
59†	"Anthericum minimum N."	[Unpublished]			1258	Anthericum sp.[1]; Hypoxis sp.[3]
60†	"Anthericum serotinum"	[Unpublished]			1259	Hypoxis sp.[1]
61	Pancratium illiricum [L.]	52	49			Crinum erubescens Soland.[2]
62	Tradescantia coapatli Sessé & Moc.	50	47			Unknown
63	Amaryllis formosissima	52	49			Sprekelia formosissima (L.) Herb.[2]
64	"Tillandsia parasiticum"	[Unpublished]				Unknown
65	Loranthus americanus [L.]	50	47		449	Psittacanthus calyculatus (DC.) G. Don[1]
66	"Lilium variegatum" (or "superbum")	[Unpublished]				Unknown
67	"Bulbocodium stellatum N."	[Unpublished]			1265	Milla biflora Cav.[1]
68†	Polianthes tuberosa [L.]	54-	50-			Unknown
69	Polianthes americana Sessé & Moc.	54	50		1266	Polianthes geminiflora (Ll. & Lex.) Rose[1,2]
70	"Fritillaria n.sp."	[Unpublished]			1269	Calochortus sp.[1]
71	Agave americana [L.]	53	49			Agave sp.[3]
72	Tropaeolum majus [L.]	56	52			Unknown
73	Tropaeolum peregrinum [L.?]	[56]	[52]			Unknown
74	Epilobium palustre [L.]	56	52		379	Epilobium mexicanum Ser. (Type)
75	Gaura hexandra Sessé & Moc.	56	52			Gaura tripetala Cav.[2]
76	Gaura spicata Sessé & Moc.	56	52		?373[c]	Gaura bracteata Ser. (Type)
77	"Clethra integrifolia N."	[Unpublished]			731	Clethra mexicana DC. (Paratype)
78	Jussieua repens [L.]	70	65		369[cn]	Jussiaea repens L.[2]
79	Poinciana pulcherrima [L.]	65	61			Caesalpinia pulcherrima (L.) Sw.[2]
80	Poinciana elatior Sessé & Moc.	66	61		218	Caesalpinia exostemma DC. (Type)
81	Melastoma aspera [L.]	70	66		341	Tibouchina mexicana (D. Don) Cogn.[2]
82	Silene mexicana Sessé & Moc.	72	68		56	Silene laciniata Cav.; S. mexicana Otth (Type)
83	"Arenaria pentaginia N."	[Unpublished]			55	Spergula arenarioides Ser. (Type); ?Arenaria lanuginosa (Michx.) Rohrb.[1]
84	Oxalis violacea [L.]	75	70			Oxalis (Ionoxalis) sp.[3]
85	Oxalis stricta [L.]	[75] ‡	[70] ‡		151	Oxalis verticillata DC. (Type)
86	Oxalis flabelliformis Sessé & Moc.	75	70		149	Oxalis hernandesii DC. (Lectotype)
87	Sedum spicatum Sessé & Moc.	75	70		416[cdc]	Echeveria coccinea (Cav.) DC.[1]
88	Lythrum album Sessé & Moc.	78	73		319	Cuphea tricolor DC. (Type)
89	Lythrum vulnerarium Sessé & Moc.	78	73			Cuphea aequipetala Cav.[2]; ?Cuphea sp.[3]
90	Ginora americana [Jacq.]	78	73		326	Heimia syphilitica DC. (Type)

91	Euphorbia fastuosa Sessé & Moc.	81	76	1140$^{\text{cn}}$	Euphorbia pulcherrima Kl.[1,2]
92	Psidium pomiferum [L.]	82	77		Psidium guajava L.[2]
93	Prunus virginiana [L.]	83	78	306★	Cerasus capollin DC. ex Ser. (Type)
94☆	Cactus phyllantus [L.]	82	77	?407$^{\text{cdc}}$	Epiphyllum oxypetalum (DC.) Haw.[2]
95	Sesuvium portulacastrum [L.]	84	79		Sesuvium portulacastrum L.[2]
96	Mentzelia aspera [L.]	87	81	357$^{\text{c}}$	Mentzelia hispida Willd.[1,2]
97	Cistus mexicanus Sessé & Moc.	87	82	46	Helianthemum glomeratum (Lag.) DC.[2]; H. obcordatum Dun. in DC. (Type).
98	"Cactus coronatus"	[Unpublished]		?397$^{\text{cdc}}$	Mammillaria lanifera Haw.[1]
99	Argemone mexicana [L.]	88	82		Argemone platyceras Link & Otto[2]
100	Annona squamosa [Jacq.?]	[90]	[84]		Annona squamosa L.[2]
101	"Scutellaria tuberosa N."	[Unpublished]		981	Scutellaria sp.[1]
102	Phlomis purpurea [L.]	[93]	[87]		Unknown;♦ Stachys sp.?
103	Castilleja integrifolia [L.f.]	95	89	960∗$^{\text{cn}}$	Castilleja integrifolia L.f.[2]; C. tenuiflora Benth.[2]
104	Castilleja pulcherrima Sessé & Moc.	95	89	959	Castilleja arvensis Cham. & Schlecht.[2]
105	Castilleja fissifolia [L.f.]	95	89	961	Castilleja sp.[1]
106	Rhinanthus capensis [L.]	96	89	968	Lamourouxia tenuifolia Mart. & Gal.[2]
107	Rhinanthus bipinnatifidus Sessé & Moc.	96	90	972	Lamourouxia multifida H.B.K.[1,2]
108	"Melampyrum barbatum N."	[Unpublished]		966	Lamourouxia sp.[1]; Penstemon barbatus (Cav.) Roth[2]
109◇	Erinus humilis Sessé & Moc.	101	95	934	Bacopa procumbens (Mill.) Greenm.[1,3]
110	Bignonia stans [L.]	99	92		Tecoma stans (L.) H.B.K.[2]
111	Ruellia depressa [L.f.]	100	93	1040	Dyschoriste microphylla (Cav.) Ktze.[2]

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†This is *Ornithogalum graminifolium* of Pl. Nov. Hisp. ed. 2. 51. and of Fl. Mex. 94 (ed. 2. 86). The plate is cited in Fl. Mex. only. The descriptions, and the references to Hernández in these works, both apply to a species of *Hypoxis*. The name *Anthericum graminifolium* was at one time applied to the plant of plate 60, a *Hypoxis*, but the name was not published.

†This plate was apparently made in 1787–88; another plate thought to represent the same species, no. 323, was probably made during the "Second Excursion" in 1789.

‡Number published as "87" in Pl. Nov. Hisp.; correctly given as "85" in the manuscript of that work.

★The plate, if it actually represents a *Prunus*, is extraordinarily badly drawn. The plant described in Pl. Nov. Hisp. is apparently *P. serotina* subsp. *capuli* (Cav.) McVaugh.

☆No. 94 was used erroneously in Pl. Nov. Hisp. for *Convolvulus nutans*, no. 194; the latter is cited in the manuscript of Pl. Nov. Hisp.

♦Mill. Ic. 202 is cited in synonymy in Pl. Nov. Hisp. The plate in Miller's *Figures of the . . . plants . . . in the Gardeners Dictionary*, is a *"Phlomis"* with large purplish flowers.

◇This plate was apparently made in 1787–88; another plate thought to represent the same species, no. 458, was probably made during the "Third Excursion," 1790–91. It represents quite a different plant.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex.		Madrid plate no.	de Candolle plate no.	Identification
		Ed. 1	Ed. 2			
112	Ruellia strepens [L.]	99	93		1041	Ruellia hirsuto-glandulosa (Oerst.) Hemsl.[2]
113	Capraria verticillata Sessé & Moc.	98	92		949	Russelia sp.[1]
114†	Chelone mexicana Sessé & Moc.	FM164-	FM150-		837	Penstemon aff. kunthii G. Don[1]
115†	"Chelone integerrima"	[Unpublished]			835	Penstemon sp.[1]
116	Buchnera asiatica [L.]	101	94		954	Agalinis peduncularis (Benth.) Pennell[1,2]
117	Martynia annua [L.]	103	96		?832[cn]	Proboscidea triloba (Cham. & Schlecht.) Decne.[1,2]
118	Cleome gigantea [L.]	105	98		20[cn]	Cleome speciosa Raf.[2]; C. cardinalis DC. (Type)
119	Geranium alchimiloides [L.?]	107-	100-		147	Geranium hernandesii DC.[2] (Type)
120	Sida anoda Sessé & Moc.	109-	102			Anoda cristata (L.) Schlecht.[2,3]
121	"Sida obliqua Fl. Mex."	[Unpublished]			66	Sida bicolor Cav.[1]; S. rhombifolia L.[2]
122†	Portulaca patens [L.]	[77]	[72]	M3	391[c]	Talinum sp.[1]; T. paniculatum (Jacq.) Gaertn.[2]
123	Sida palmata [Jacq.]	110	102		?64[cn]	Neobrittonia acerifolia (Lag.) Hochr.[1,2]
124	Hibiscus malvaviscus [L.]	112	105			Malvaviscus arboreus Cav.[2]
125	Hibiscus rigidus [L.f.]	[113]	[105]		76	Hibiscus spiralis Cav. (ex DC.)[1]
126	Astragalus mexicanus Sessé & Moc.	119	111			Brongniartia sp.[2,3]
127	Aphanes arvensis [L.?]	[19]	[18]			Alchemilla sp.[3]
128	Phaseolus alatus [L.]	117	109		246	Phaseolus anisotrichus Schlecht.[1]
129	"Phaseolus auritus"	[Unpublished]				Phaseolus heterophyllus Humb. & Bonpl.[2]
130‡	Hedysarum diphyllum [L.]	122	114		273*[cn]	Zornia diphylla (L.) Pers.[2]
131	Glycine ensiformis Sessé & Moc.	124	116		241	Canavalia villosa Benth.[2]
132	Phlox divaricata [L.]	26	24	M s.n.		Bonplandia geminiflora Cav.[1]
133★	Phlox violacea Sessé & Moc.	26	25	M27		Loeselia cf. glandulosa (Cav.) G. Don[1]
134	Phlox spinosilla Sessé & Moc.	26	24			Loeselia mexicana (Lam.) Brand[2,3]
135	[No reference found to this number]					
136☆	Psoralea citrodora [Cav.?]	120	112		232	Dalea sp.[1]
137	Psoralea alopecurus Sessé & Moc.	120	112		231	Dalea sericea Lag.[2]
138	"Clitoria mariana"	[Unpublished]			276	Cologania sp.[1]; Galactia radicata DC. (Type)
139	"Stelina [Staehelina] viscosa"	[Unpublished]				Baccharis heterophylla H.B.K.[2]; Haplopappus venetus (H.B.K.) Blake[2]
140◆	Athanasia pumilla [L.f.]	137	128		675[cn]	Tridax coronopifolia (H.B.K.) Hemsl.[2]
141	Ageratum febrifugum Sessé & Moc.	135	126		551	Piqueria trinervia Cav.[1,2]
142	Ageratum viscosum Sessé & Moc.	135	126		550[cn]	Stevia pilosa Lag.[2]; Stevia sp.[2]
143	Ageratum purpureum Sessé & Moc.	135	126		549[cn]	Stevia pilosa Lag.[2]; ?Stevia viscida H.B.K.[1]
144	Cacalia sonchifolia [L.?]	[131]	[122]			Senecio callosus Sch. Bip.[3]

145	Cacalia nutans Sessé & Moc.	132	123	524	Pericalia sessilifolia (Hook. & Arn.) Rydb.[2]
146	Cacalia sinuata Sessé & Moc.	[131]	[122]	522^{cn}	Odontotrichum sp.[1]
147	"Pteronia atropurpurea"	[Unpublished]			Vernonia alamanii DC.[2]
148◇	Eupatorium triangulare Sessé & Moc.	134	125	560^{cdc}	Eupatorium deltoideum Jacq.[1,2]
149■	Tagetes patula [L.]	141	132		Tagetes tenuifolia Cav.[2]
150	Tagetes anethina Sessé & Moc.	142	132		Tagetes lucida Cav.[2]
151	Buphthalmum heliantoides [L.]	145	135	699	?Zexmenia sp.[1]
152□	Pectis ciliaris [L.]	143	133	?670	Pectis canescens H.B.K.[2]; P. prostrata Cav.[3]
153	Zinnia pauciflora Sessé & Moc.	FM206-	FM188-	DC-^{cdc}	Zinnia leptopoda DC.[1]; Z. peruviana (L.) L.[2]
154	Bidens tetragona Sessé & Moc.	131	122	603	Verbesina tetraptera (Ort.) A. Gray[2]; Actinomeris tetragona DC. (Paratype)
155	Spilanthus heterophyllus Sessé & Moc.	130	121	673^{cn}	Verbesina crocata (Cav.) Less. ex DC.[1,2]
156▲	Perdicium decurrens Sessé & Moc.	139	130	513	Trixis decurrens DC. (Type)
157	Perdicium cordatum Sessé & Moc.	139	130	512,512*	Perezia hebeclada (DC.) A. Gray (Paratypes)
158	Coreopsis coronata [L.]	147	137		Dahlia coccinea Cav.[2]
159	Coreopsis verticillata [L.]	147	137	609	Cosmos crithmifolius H.B.K.[2]
160△	Helianthus altissimus [L.]	FM211-	FM193-	600	Tithonia tubaeformis (Jacq.) Cass.[1]

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†Listed under this name among the plates made in 1787–88; in the same list Ic. 115 is called *Chelone integerrima.* Both no. 114 and 115 are cited in Pl. Nov. Hisp. under the name *Chelone pentstemon* [L.]. Leaves of both *C. mexicana* and *C. pentstemon* are described as entire, except that the latter is said to have a variant with "foliis omnibus serratis." DC. plate 837 evidently represents this variant. Ic. 115 represents a species with very narrow entire leaves.

†No. 122 was not used in the list of plates made in 1787–88, and was probably assigned to the *Portulaca* in the later stages of preparation of the manuscript of Pl. Nov. Hisp. Originally the species was assigned the number 413, which was cited in Fl. Mex. 132 (ed. 2. 121). Presumably the painting was made in 1790–91, on the "Third Excursion."

‡See also Ic. 350, which was cited in Pl. Nov. Hisp. as 130.

★See also Ic. 333, which was cited in Pl. Nov. Hisp. as 133.

☆This plate was apparently made in 1787–88; another plate thought to represent the same species, no. 307, was probably made during the "Second Excursion," 1789.

◆See also Ic. 410, which was cited in Fl. Mex. 243 (ed. 2. 222) as 140.

◇No. 148 was never cited in Pl. Nov. Hisp. for *E. triangulare,* but only for *Tagetes patula,* no. 149. No. 172 was the number assigned to *E. triangulare* before the new numbers were assigned to the Ic. Fl. Mex. (see p. 108, above), and this was cited by oversight in Pl. Nov. Hisp. The list of plates made in 1787–88 includes *E. triangulare* under no. 148.

■Cited in Pl. Nov. Hisp. as 148; cited as 149 in the manuscript of Pl. Nov. Hisp. and in other lists of plates.

□Cited in Pl. Nov. Hisp. as 452, apparently because the number as written in the manuscript could be taken for either 152 or 452. In the list of plates from the "First Excursion," 1787–88, the number is 152. No. 152 was cited in Pl. Nov. Hisp. for *Erinus portulacaster* Sessé and Moc. (p. 101; ed. 2. 94); this is probably the same species as no. 458, *Erinus humilis.*

▲No. 156 is also cited under "Daphne pontica?" in the manuscript of Fl. Mex. and in the published texts (p. 102; ed. 2. 94). I have not seen the plate, nor any specimens referred to this species, and cannot guess the identity of the plant.

△Through what may or may not have been a coincidence, "Jacq. Hort. [Vindob.] t. 160" was cited in Fl. Mex.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex.		Madrid plate no.	de Candolle plate no.	Identification
		Ed. 1	Ed. 2			
161	Achras capiri Sessé & Moc.	51	48	M96	749[cn]	Lucuma? capiri A.DC. (Type); Mastichodendron capiri (A.DC.) Cronq.
162	Eriocephalus antemisifolius [sic] Sessé & Moc.	150	139		703g[cn]	?Parthenium hysterophorus L.[1]
163	Solidago sinuata Sessé & Moc.	[141]	[131]		578*†	Senecio praecox (Cav.) DC.[2]
164	Eupatorium uniflorum Sessé & Moc.	132	123		526	Vernonia salicifolia (DC.) Sch. Bip. (Paratype)
165	Lobelia tupa [L.]	150	140		705	Lobelia cardinalis subsp. graminea (Lam.) McVaugh[2]
166	Lobelia triquetra [L.]	150	140		?713[c]	?Lobelia gruina Cav.[2]
167	Lobelia cardinalis [L.]	151	140		?706[c]	Lobelia cardinalis subsp. graminea (Lam.) McVaugh[2]
168	Lobelia spicata Sessé & Moc.	[151]	[141]		712	Lobelia fenestralis Cav.[1,2]
169	"Lobelia sempervirens N."	[Unpublished]			711	Lobelia laxiflora var. angustifolia A.DC.[1]
170	"Lobelia pumila N."	[Unpublished]			710	Lobelia sp.[1]
171†	"Lobelia debilis"	[Unpublished]			709	Diastatea micrantha (H.B.K.) McVaugh[1,2]
172‡	Serapias longifolia [L.]	153	142			Unknown
173	Ophrys peregrina Sessé & Moc.	[153]	[142]		1220	Spiranthes cinnabarina (Ll. & Lex.) Hemsl.[2]; S. orchioides (Sw.) A. Rich.[1]
174	Ophrys pubescens Sessé & Moc.	153	142		1221	?Spiranthes cinnabarina (Ll. & Lex.) Hemsl.; S. montana (ex A. Rich., 1847)[1]
175	"Ophrys diphylla"	[Unpublished]			1219	Malaxis myurus (Lindl.) Ktze.[1,2]
176	Ophrys fastigiata Sessé & Moc.	153	142		1219*	Malaxis fastigiata (Reichb.f.) Ktze.[1,2]
177	Zea mayz [L.]	159	147			Zea mays L.[3]
178	Ambrosia artemisifolia [L.]	161	150		639	Ambrosia artemisiifolia L.[2]
179★	Sicyos angulata Sessé & Moc.	169	157		?355*[cdc]	Sechium edule (Jacq.) Sw.[3]
180	Acalypha villosa [Jacq.]	165-	153-			Acalypha subviscida S. Wats.[2]
181	"Smilax rotundifolia"	[Unpublished]			1276	Smilax moranensis Mart. & Gal.[1,2]
182	Schinus molle [L.]	173-	160-			?Schinus molle L.[3]
183	Dioscorea sativa [L.]	172	159		1274♂,1274♀	Dioscorea galeottiana Kunth[2]
184	Mimosa peregrina [L.]	175	163		207	Calliandra anomala (Kunth) Macbr.[1]; Inga anomala β pedicellata DC. (Lectotype)
185	Mimosa esculenta Sessé & Moc.	178	165		209[cn]	Leucaena esculenta (DC.) Benth. (Type)
186	Polypodium aureum [L.]	181	168			Polypodium aureum L.[2]
187	Adiantum digitatum Sessé & Moc.	182	169		1301	Pteris cretica L.[1,2]
188	Petiveria octandra [L.]	55	51	M21		Petiveria alliacea L.[1]
189☆	Combretum secundum [Jacq.]	56	52		346[c]	Combretum farinosum H.B.K.[2]
190	Justicia pulchella Sessé & Moc.	4	4		1067	Carlowrightia glandulosa Rob. & Greenm.[1]; Justicia pringlei Rob.[2]

191	Fuchsia arborea Sessé & Moc.	58	54	M11	366^{c}	Fuchsia arborescens Sims[1]
192	Justicia pulcherrima [L.f.]	2	2		1069	Aphelandra deppeana Schlecht. & Cham.[2]
193	Varronia tuberosa Sessé & Moc.	30	28		882	Cordia alliodora (Ruiz & Pav.) Oken[2]
194♦	Convolvulus nutans Sessé & Moc.	[24]	[22]		860	Porana velutina (Choisy) O'Don.[2]; Ipomoea nutans Choisy (Type)
194♦	Celosia dioica Sessé & Moc.	40	38		1091^{cn}	Iresine sp.[1]
195	Fuchsia racemosa Sessé & Moc.	58	54		?362^{c}	Fuchsia fulgens DC. (Type)
196	Rhus tridentatum [L.f.]	47	44		192	Rhus toxicodendron L.[1]; Rhus saxatilis DC. (Type)
197	Convolvulus quahutzehuatl Sessé & Moc.	[23]	[22]		851	Ipomoea murucoides Roem. & Schult.[2]
198	Sapindus trifoliatus [L.]	60	56		122	Thouinia? villosa DC. (Type)
199	Amyris ambrosiaca [L.f.]	58	54		196	Bursera sarcopoda P.G. Wilson[2]; Icica? serrata DC. (Type)
200	Dodonaea viscosa [Jacq.]	59	55			Dodonaea viscosa Jacq.[2]
201◇	Convolvulus bractiflorus Sessé & Moc.	23	22		854	Exogonium bracteatum (Cav.) Choisy[2]
202	Sida quinqueloba Sessé & Moc.	110	103		63	Anoda acerifolia (Zuccag.) DC.[1]
203	Cassia fistula [L.]	[63]	[59]		DC-^{cdc}	?Cassia fistuloides Collad. (Type)
204	Solanum capense [L.f.]	35	33			Solanum hernandesii Dun.[2,3] (?Type)
205	Mimosa inga [L.]	175	162		213	Inga eriocarpa Benth.[2]; I. schiedeana Steud.[2]
206	Carolinea princeps [L.f.]	113	106		97	Bombax ellipticum H.B.K.; Carolinea fastuosa DC. (Type)
207■	Datura maxima Sessé & Moc.	25	23			Solandra nitida Zucc.[2]
208	Erythrina corallodendron [L.]	115	107		253	Erythrina coralloides DC. (Type)
209	Justicia coccinea Sessé & Moc.	3	3		1065	Jacobinia spicigera (Schlecht.) Bailey[2]
210	Convolvulus muricatus [L.]	[22]	[21]		844	Calonyction aculeatum (L.) House[1,2]

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†An original painting, but without name or number as used by Sessé & Mociño.

†No. 171 was used erroneously in Fl. Mex. ed. 2. 99, and in the manuscript of that work, for *Bauhinia purpurea,* no. 271.

‡See no. 148, *Eupatorium triangulare,* for a misuse of no. 172.

★This plate probably is the *Sicyos angulata* of Pl. Nov. Hisp., cited as Ic. 364, although the latter was another plate, probably painted during the "Second Excursion" in 1789.

☆In Fl. Mex. (p. 11; ed. 2. 10), "Ic. 189" is cited under *Piper reticulatum.* This should read "Ic. [Herb. no.] 189"; it is a part of the numbering system commenced in Spain for the entire herbarium, under which "Piper tuberosum N." was no. 189.

♦No. 194 was used twice in the list of plates from the "Second Excursion"; see also no. 94.

◇The number is cited as 207 in both editions of Pl. Nov. Hisp., but DC. plate 854 is clearly labelled "201," and that number is used for *C. bractiflorus* in the list of plates of the "Second Excursion," 1789.

■See footnote to no. 201.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
211	"Echites annularis"	[Unpublished]			?795†	Prestonia mexicana A. DC.[1,2]; Haemadictyon mexicanum A. DC. (Type)
212	Stapelia pancololote Sessé & Moc.	[41]	[39]		763^{cdc}	Gonolobus uniflorus H.B.K.[2]
213	Tillandsia recurvata [L.]	50	46		1255	Tillandsia ionantha Planch.[1]; T. streptophylla Scheidw.[2]
214	Paullinia mexicana [L.]	59	55		120	Serjania mexicana (L.) Willd.[1,2]
215	Laurus indica [L.]	62	57			Unknown
216	Magnolia glauca [L.]	90	84		6	Talauma mexicana (DC.) G. Don[1,2] (Type)
217	Bignonia muricata Sessé & Moc.	99	92		820	Pithecoctenium muricatum DC. (Type)
218	Cornutia ternata Sessé & Moc.	103	96		1026	Vitex mollis H.B.K.[1,2]
219	Theobroma guazuma [L.]	126	117		114	Guazuma tomentosa H.B.K.[1]
220	Croton aromaticum [L.]	165	154		1113	Croton morifolius Willd.[1,2]
221	Croton humile [L.]	166	154		1120*	Croton ciliato-glanduliferus Ort.[1,2]
222	Carica papaya [L.]	172	160	M76		Carica papaya L.[1,3]
223	Malpighia glabra [L.]	[72]	[68]		137	Malpighia glabra L.[2]
224	Swietenia mahagoni [L.]	68	64		152^{cn}	Swietenia humilis Zucc.[2]
225	Rauwolfia nitida [Jacq.]	32	30			Rauwolfia sp.[2]
226†	Randia mitis? [L.]	33	31	M s.n.	472^{c}	Randia sp.[1]
227	Astragalus formosus Sessé & Moc.	119	111		249	Harpalyce formosa DC. (Type)
228‡	"Cordia elliptica N."	[Unpublished]				Unknown
229★	Aeschynomene pumilla [L.]	[122]	[114]			Aeschynomene scabra G. Don[2]
230	Nicotiana pusilla [L.]	FM41	FM37		910	Nicotiana plantaginea Dun. (Type)
231	Mirabilis longiflora [L.]	19	18			Mirabilis longiflora L.[2]
232	Mimosa unguis cati [L.]	175	162		212	Pithecellobium dulce (Roxb.) Benth.[1]
233	Ternstroemia meridionalis [L.f.?]	86	80		735^{cdc}	Ternstroemia lineata DC. (Type); T. pringlei (Rose) Standl.[2]
234	Spermacoce capitata Sessé & Moc.	17-	16-		497	Crusea calocephala DC.[1,2] (Paratype)
235	Ceanothus africanus [L.]	39	36	M22	175^{c}	Ceanothus pauciflorus DC. (Type)
236☆	Cynanchum hirsutum Sessé & Moc.	FM76-	FM70-			Matelea congestiflora (Donn. Sm.) Woodson[2]
237	Mussaenda spinosa [Jacq.?]	36	34		469	Randia echinocarpa DC. (Type)
238	Jatropha urens [L.]	[167]	[155]			Cnidoscolus sp.[3]
239◆	Melia americana Sessé & Moc.	68	64			Trichilia pavoniana C. DC.[2]
240	Asclepias scandens Sessé & Moc.	43	41			?Matelea sp.[3]
241◇	Cerbera cuneifolia Sessé & Moc.	32	30		793	Thevetia ovata (Cav.) A. DC.[1]
242	Tabernaemontana grandiflora [Jacq.]	[29]	[27]		789	Stemmadenia sp.[1,2]
243	Hamellia patens [L.]	37	34		489	Hamelia patens γ ? quinifolia DC. (Type)

244	Datura ferox [L.]	24	23			Datura sp.[3]
245	Bignonia paniculata [L.]	99-	92		828	Amphilophium mutisii H.B.K.[1]; A. paniculatum (L.) H.B.K., var.[2]
246	Turraea viridis Sessé & Moc.	68	63		158	Amyris rekoi Blake[1,2]
247■	Rhus tetlatziam Sessé & Moc.	47	44		189	Rhus filicina DC. (Type)
248	Amyris silvatica [Jacq.]	57	53		195	Bursera tecomaca (DC.) Standl.[1,2] (Type)
249	Jatropha janipha [L.]	167	155		1133	Manihot stenoloba Muell. Arg.[1]
250	Prockia crucis [L.]	89	83		309	Prockia crucis L., var.[1]
251	Rhus pterocarpus Sessé & Moc.	[47]	[45]	M71	190[c]	Pseudosmodingium perniciosum (H.B.K.) Engl.[1,2]; Spathelia? rhoifolia DC. (Type)
252	Varronia curassavica [L.]	30	28		885	Cordia curassavica (Jacq.) Roem. & Schult.[2]
253	Serapias lurida Sessé & Moc.	153	143		1190	Epidendrum radiatum Lindl.[1]
254	Besleria ["Besteria"] cristata [Jacq.]	103	97		932[cn]	Alloplectus glaber DC. (Type)
255	Stapelia campanulata Sessé & Moc.	41	39		804	Dictyanthus pavonii Decne.[2]
256	Hymenaea courbaril [L.]	67	63			Hymenaea courbaril L.[2]
257	Sapindus amolli Sessé & Moc.	60	56			Sapindus saponaria L.[3]; Thouinidium decandrum (Humb. & Bonpl.) Radlk.[2]
258	Serapias palmifolia Sessé & Moc.	153	143		1196□	Govenia sp.[3]
259	Viola calceolaria [L.]	152	141		35	Hybanthus sp.[1]; Ionidium? calceolarium Ging. (Type)

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†An original painting, but without name or number as used by Sessé & Mociño.

†No. 226 is also cited under *Aeschynomene pumilla;* the correct number, as cited in the manuscript of Fl. Nov. Hisp., is 229, q.v.

‡Neither painting nor specimens with this name have been found. "Cordia elliptica" appears under no. 228 in the list of plates made on the "Third Excursion," 1790–91, and in the final list, compiled by Mociño, of plates 1–416. The type of *Elaphrium copalliferum* DC. is an original painting (DC. plate 202) numbered 228, but not otherwise identified with any plant named by Sessé & Mociño.

★See footnote to no. 226.

☆This is *Cynanchum maritimum* [Jacq.] of Pl. Nov. Hisp. 41 (ed. 2. 39), where Ic. 236 is cited.

♦Published as 339; and so written in the manuscript of Pl. Nov. Hisp.; both *Mimosa trunca* and *Melia americana* were listed under no. 339 among the plates from the "Second Excursion," 1789. In Mociño's final list of plates 1–416, *Melia americana* was first listed under both 239 and 339, but 339 was later changed in that list to *Mimosa trunca.* Apparently Mociño entered the wrong number in compiling the manuscript for the flora.

◇Published as 247, but correctly written as 241 in the manuscript of Pl. Nov. Hisp.

■Published as 217 in Pl. Nov. Hisp. and so cited by other authors. The plate bears the number 247, and it appears under this number in the list of plates of the "Second Excursion," 1789.

□Apparently Ic. 258 was cited through some oversight, under *Serapias palmifolia,* instead of under *S. diphylla* Sessé & Moc. (Pl. Nov. Hisp. 153, ed. 2. 143). Plate 1196 is labelled "258" and "Serapias diphilla Sp. N."; it appears to represent a species of *Bletia.* Herbarium material of "Serapias diphylla" has been named *Bletia reflexa* Lindl.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex.		Madrid plate no.	de Candolle plate no.	Identification
		Ed. 1	Ed. 2			
260	Malpighia crassifolia [L.]	73	68		134	Byrsonima pulchra DC. (Type)
261†	Hippomane fruticosa Sessé & Moc.		FM226-		1127	?Sebastiania pavoniana (Muell. Arg.) Muell. Arg.[1]
262	Polygonum scandens [L.]	61	57	M s.n.	1098^{c}	Antigonon leptopus Hook. & Arn.[1,3]
263	Carissa verticillata Sessé & Moc.	29	27		801	Rauwolfia longifolia A. DC.[1]
264	Mimosa intsia [L.]	176	164		211	Schrankia distachya DC. (Type)
265	Loranthus ramiflorus Sessé & Moc.	51	47		448	Psittacanthus ramiflorus (DC.) G. Don; Loranthus ramiflorus DC. (Type)
266	Byttneria scabra [L.]	39	37		103^{c}	Byttneria aculeata (Jacq.) Jacq.[2]; B. lanceolata DC. (Type)
267	Apocynum proliferum Sessé & Moc.	42	39		775	Sarcostemma pannosum Decne.[2]
268	Lupinus altissimus Sessé & Moc.	116	108		243	Crotalaria mollicula H.B.K.[1,2]
269	Petesia stipularis [L.]	16	15		483	Anisomeris protracta (Bartl. ex DC.) Standl.[2]
270	Bauhinia aculeata [L.]	62	58	M10	?223^{c}	Bauhinia leptopetala DC. (Type)
271†	Bauhinia purpurea [L.]	62	58	M s.n.	224^{c}	Bauhinia spathacea DC. (Type); B. subrotundifolia Cav.[2]
272	"Solanum tubulosum"	[Unpublished]			913	Saracha procumbens (Cav.) Ruiz & Pav.[2]
273	Parkinsonia aculeata [L.]	62	58			Parkinsonia aculeata L.[2]
274	Echites quinqueangularis [L.?]	27	26		796	Mandevilla sp.[2]; Echites cordata A. DC. (Type)
275	Rondeletia volubilis Sessé & Moc.	36	34		463	Paederia ciliata (DC.) Standl.[2]; Lygodysodea ciliata Bartl. ex DC. (Paratype)
276	Poinciana hirsuta Sessé & Moc.	66	62			Caesalpinia sp.[3]
277‡	Guaiacum afrum [L.]	68	64	M s.n.	160^{c}	Guaiacum coulteri A. Gray[1]
278★	Hippomane spinosa [L.]	168	156		1126	?Stillingia zelayensis (H.B.K.) Muell. Arg.[1]
279	Cassia atomaria [L.]	63	59			Cassia sp.[3]
280☆	Hermannia corymbosa Sessé & Moc.	[106]	[99]		93	Melochia rhodocalyx C. Koch & Bouché[1]; Riedleia corymbosa DC. (Type)
281	Tradescantia parviflora Sessé & Moc.	50	47		1287	Aneilema holosericea (Kunth) Woodson[1]
282	Costus arabicus [L.]	1	1			Unknown
283	Grislea umbellata Sessé & Moc.	57	53		328^{cdc}	Adenaria floribunda H.B.K.[2]
284	Banisteria laurifolia [L.]	73	68	M37	130^{c}	Mascagnia macroptera (DC.) Ndzu. (Type)
285	Begonia palmata Sessé & Moc.	163	151			Begonia palmaris A. DC.[2]; B. biserrata Lindl.[2]
286	Corchorus siliquosus [L.]	88	82			Corchorus siliquosus L.[2]; C. hirtus L.[2]
287	Cactus frutescens Sessé & Moc.	82	77		?411^{cdc}	Pereskia rotundifolia DC. (Type)
288	Symphitum fruticosum Sessé & Moc.	21	20		901	Antiphytum mexicanum DC. (Type)

289	Antirrhinum uniflorum Sessé & Moc.	102	95		725	Gesneria? uniflora DC. (Paratype)
290[♦]	Pinguicula lusitanica [L.] (fig. 1)	6	5		1071	Pinguicula obtusiloba A. DC. (Type)
290[♦]	Pinguicula vulgaris [L.] (fig. 2)	6	5		1071	Pinguicula oblongiloba A. DC. (Type)
290[♦]	Pinguicula villosa [L.] (fig. 3)	6	5		1071	Pinguicula crenatiloba A. DC. (Type)
291	Ruellia fruticosa Sessé & Moc.	100	94		1070	Ruellia sp.[2]
292[◇]	Ehretia cuneifolia Sessé & Moc.	FM51	FM47		887	Bourreria spathulata (Miers) Hemsl.[2]
293	Echium longiflorum Sessé & Moc.	20	19		903	Macromeria exserta D. Don[1,2]
294	Cypripedium turgidum Sessé & Moc.	154	143		1225	Cypripedium irapeanum Ll. & Lex.[1,2]
295[■]	Pergularia laevis Sessé & Moc.	FM78	FM72		770	Cynanchum foetidum (Cav.) H.B.K.[2]
296	Melochia rotundifolia Sessé & Moc.	106	99		93*	Pterostemon mexicanus Schauer[1,2]
297	Phaseolus linearis Sessé & Moc.	117	109		248	Phaseolus leptophyllus G. Don[2]
298[□]	Phyllanthus americanus Sessé & Moc.	159-	148-			Phyllanthus galeottianus Baill.[2]
299	Ayenia magna [L.]	154	143		104	Ayenia fruticosa Rose, var.[2]
300	Quassia amara [L.]	69	64	M84		Quassia amara L.[1,2]
301	Ptelea trifoliata [L.]	17	16		200[c]	Ptelea trifoliata L.[2]; P. podocarpa DC. (Type)[▲]
302[△]	Salvia fastuosa Sessé & Moc.	7	7		983[cn]	Salvia sessei Benth.[1,2]

[†] This is *Hippomane biglandulosa* [L.] of Pl. Nov. Hisp. (168; ed. 2. 156), where plate 261 was cited. The plant described in Pl. Nov. Hisp., however, is probably *Stillingia zelayensis* (H.B.K.) Muell. Arg., which seems to be the plant depicted in Ic. 278 (DC. plate 1126), which is cited under *Hippomane spinosa* [L.], but is labelled "*Hippomane biglandulosa.*" Evidently the plate-numbers were interchanged in publication.

[†] Cited as 171 in Fl. Mex. ed. 2. 99.

[‡] No. 277 was originally used for *Ophrys imbricata* Sessé & Moc., as indicated on DC. plate 1197, an original painting apparently depicting *Lockhartia oerstedii* Reichb. f. The number 277 appears in the manuscript of Pl. Nov. Hisp. but not in the printed version (p. 153, ed. 2. 142).

[★] See footnote under 261.

[☆] Probably Sessé & Mociño confused two species under one name and number. Ic. 280 was first painted during the "Second Excursion," that to Guerrero in 1789. The description in Pl. Nov. Hisp., "petalis vix calice longioribus" probably applied to this plant. The cited locality, however (Tepalcatepec), may have been that of DC. plate 93, in which the petals are long-exserted.

[♦] Listed 290 in Mociño's final enumeration of plates 1–416; the number 290 appears on the plate itself. It was cited in Pl. Nov. Hisp., and in the manuscript of that work, as Ic. 11. "Ic. 11, f. 1," correctly identified in the manuscript, was published as "Ic. 11, f. 3."

[◇] Named *Ehretia exsucca* [L.] in Pl. Nov. Hisp. 31 (ed. 2. 29), and the number published as 298 (correctly given as 292 in the manuscript). Herbarium specimens are marked "Ehretia cuneifolis olim exsucca."

[■] *Pergularia tomentosa* [L.] of Pl. Nov. Hisp. (42; ed. 2. 40), where the plate is also cited.

[□] The same name is applied to Ic. 460. Evidently Sessé & Mociño had this first plate made during the "Second Excursion," in 1789, as the locality for *P. americanus* is cited as "Mazatlán." Ic. 298 is assigned to this species in Mociño's final list of nos. 1–416. No. 460, however, was probably painted during the "Third Excursion," 1790–91, as DC. plate 1109 is a copy of a plate forwarded to Madrid at the end of that Excursion. The identity of Ic. 298 remains in doubt.

[▲] Reported in *Calques des Dessins* as an original painting; it is in fact a copy by Mlle. Baulaire.

[△] *Salvia calyciinflata* Sessé & Moc. Fl. Mex. 7 (ed. 2. 7), where Ic. 302 is also cited.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
303	Echites uniflora Sessé & Moc.	28	27		794	Macrosiphonia hypoleuca (Benth.) Standl.[2]
304	Erythrina horrida Sessé & Moc.	115	107		252	Erythrina horrida DC. (Type)
305	Polymnia wedalia [L.]	148	138	M s.n.	653[c]	?Sigesbeckia jorullensis H.B.K.[1]
306	Grislea herbacea Sessé & Moc.	57	53	M28	329[c]	Ammania auriculata Willd.[1]
307†	Psoralea citrodora [Cav.?]	120	112		230	Dalea sp.[1]
308	Psoralea dalea [L.]	120	112		228	Dalea acutifolia DC. (Type); D. cliffortiana Willd.[1]
309	Cotyledon spatulata Sessé & Moc.	74	69		?420[cdc]	Sedum jaliscanum S. Wats.[2]
310	Psoralea procumbens [Mill.?]	120	112		229	Dalea procumbens DC. (Type); Marina procumbens (DC.) Barneby
311	Indigofera eneaphylla [L.]	124	116		267	Indigofera miniata Ort.[2]
312†	"Verbesina pinnatifolia"	[Unpublished]			696	Dyssodia tagetiflora Lag.[2]
313	Helianthus ? atro-rubens [L.]	[146]	[136]		602	Simsia sanguinea A. Gray[1]; Aspilia purpurea Greenm.[2]
314	Passiflora tilliaefolia [L.]	154	144		31	Passiflora serratistipula DC. (Type)
315	Fritillaria meleagris [L.]	54	51		1268	Calochortus sp.[1]
316	Hibiscus vitifolius [L.]	112	105		83	Hibiscus tubiflorus DC. (Type); Kosteletzkya tubiflora (DC.) Blanch. & McVaugh
317	Coreopsis artemisifolia Sessé & Moc.	148	137		615	Cosmos sulphureus Cav.[1,2]
318	Citrus decumanus [L.]	127	118			Citrus sp.[3]
319	"Tradescantia cordifolia"	[Unpublished]			1291	Tripogandra cf. amplexicaulis (Kl.) Woodson[1]
320	Cissus sicyoides [L.]	18	17		146	Cissus tuberosa DC. (Type)
321	Ignatia amara [L.f.]	21	20		468	Posoqueria latifolia (Rudge) Roem. & Schult.[2]
322	Gronovia scandens [L.]	FM71	FM65			Gronovia scandens L.[2]
323‡	Polianthes tuberosa [L.]	54-	50-		1251	Agave (Manfreda) sp.[1]
324	Veratrum luteum [L.]	174	162		1281	Schoenocaulon officinale (Cham. & Schlecht.) A. Gray[2]
325	Ayenia pusilla [L.]	154	143		105	Ayenia pusilla L.[2]; A. cordifolia DC. (Type)
326	Indigofera atropurpurea Sessé & Moc.	125-	117-		266	Indigofera thibaudiana DC.[1,2]
327	Spigelia anthelmia [L.]	22	21		?811[c]	Spigelia mexicana A. DC. (Paratype)
328	Cacalia pinnatifida [L.?]	132	123		525	Odontotrichum amplifolium (DC.) Rydb.[1]; Cacalia sinuata Cerv.[2]
329	Jatropha curcas [L.]	167	155		1131	Jatropha curcas L.[1]
330	Gesneria maculata Sessé & Moc.	97	91		721	Gesneria maculata DC. (Type)
331	Jatropha triloba Sessé & Moc.	167	155		1134	Jatropha triloba Sessé in Cerv.[1,2]; Manihot triloba (Sessé) Miranda.

332	Zinnia elegans [Jacq.?]	142	133		571*[cdc]	Zinnia violacea Cav.[2,3]
333★	Croton verticillatum Sessé & Moc.	166	154		1114	Croton adspersus Benth.[1,2]
334	Diospyros t[l] iltzapotl Sessé & Moc.	179	166		756[c]	Diospyros ebenaster Retz.[2]
335	Triumfetta bartramia [L.]	76	71		119	Triumfetta semitriloba Jacq.[2]; T. oxyphylla DC. (Type)
336	Crescentia ternata Sessé & Moc.	94	88		926	Crescentia alata H.B.K.[1,2]
337	Scutellaria indica [L.]	93	87		982	Scutellaria multiflora Benth.[2]
338	Mimosa nivea Sessé & Moc.	179	166			Unknown
339☆	Mimosa trunca Sessé & Moc.	178	165		214	Calliandra emarginata (Humb. & Bonpl.) Benth.[1,2]
340	Capparis umbellata Sessé & Moc.	87	81	M98		Capparis angustifolia H.B.K.[1]
341	Lythrum cordifolium Sessé & Moc.	78	73		320	Cuphea coccinea DC. (Type)
342◆	Euphorbia geniculata Sessé & Moc.	81	75		1141	Euphorbia schlechtendalii Boiss.[2]
343	Echites cimicida Sessé & Moc.	28	27		797	Haplophyton cimicidum A. DC. (Paratype)
344	Antirrhinum maculatum Sessé & Moc.	102	95		716	Gloxinia antirhina DC. (Paratype)
345	Arbutus ferruginea [L.f.]	71	66	M64		Arctostaphylos pungens H.B.K.[2]
346	Aralia chilapensis Sessé & Moc.	48	45		436	Aralia humilis Cav.[1]
347	"Triumfetta poliandra"	[Unpublished]			117	Triumfetta polyandra DC. (Type)
348	Sida crispa [L.?]	[109]	[102]			Gayoides crispum (L.) Small[2,3]; Bastardia viscosa (L.) H.B.K.[2]
349	Crataegus inermis [L.?]	84	79	M51		Amelanchier denticulata (H.B.K.) Koch[1,2]
350◇	Milleria quinqueflora [L.]	148	138		DC-[cdc]	Milleria quinqueflora L.[2]
351	Sida rhombifolia [L.]	108	101		62	Sida rhombifolia L.[2]
352	Heisteria coccinea [Jacq.]	69	65		1100	Licaria sp.[1]
353	Malpighia urens [L.]	73	68		136	Malpighia sp.[1]
354■	Melochia conglobata Sessé & Moc.	106	99		92	Melochia nodiflora Sw.[1,2]
355	Passiflora punctata [L.]	155	144		29	Passiflora trisetosa DC. (Type)
356	Cactus cochenillifer [L.]	82	77		?413[cdc]	?Opuntia hernandesii DC. (Syntype)
357	Gesneria tomentosa [L.]	97	91		722	Kohleria deppeana (Schlecht. & Cham.) Fritsch[1]

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†The same name was applied to Ic. 136; see the footnote under that number.

†No. 312 was first used in the list of plates of the "Second Excursion," in 1789, for this species and also for *Spondias mombin.* It was used for the *Spondias* in the manuscript of Pl. Nov. Hisp. and in the published text of that work. In the final list of plates 1–416, made by Mociño, the *Verbesina* replaced *Spondias* as 312, and *Spondias* was entered under 372.

‡See also no. 68, for what is presumably another plate cited under the same name.

★Published as 133, but correctly written as 333 in the manuscript of Pl. Nov. Hisp.

☆No. 339 also cited in error for 239, *Melia americana;* see footnote under 239.

◆Cited in Pl. Nov. Hisp. as 349, but correctly written as 342 in the manuscript of that work.

◇Cited as 130 in the Pl. Nov. Hisp., but correctly written as 350 in the manuscript of that work.

■This number was also cited under *Erythrina herbacea;* the correct number for that species, as written in the manuscript of Pl. Nov. Hisp., is 399.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
358†	Gesneria acaulis [L.]	97	91		719, no.2	Achimenes tenella DC. (Type)
358†	Gesneria longiflora Sessé & Moc.	97	91		719, no.1	Achimenes longiflora DC. (Type)
359	Euphorbia heterophylla [L.]	79	74		1140*	Euphorbia heterophylla L.[2]
360	Euphorbia edulis Sessé & Moc.	81	76		1139	Euphorbia graminea Jacq.[2]; E. delicatula Boiss.[2]
361	Elaterium digitatum Sessé & Moc.	158	147		350[cdc]	Cyclanthera pedata (L.) Schrad.[2]
362	Passiflora normalis [L.]	155	155		28†	Passiflora dictamo DC. (Type)
363	Perdicium mexicanum Sessé & Moc.	139	129		514	Perezia reticulata (D. Don) A. Gray[1,2]
364‡	Sicyos angulata [L.]		FM229-			Sicyos microphyllus H.B.K.[2]
365	Melastoma scabrosa [L.]	70	65		332	Clidemia rubra (Aubl.) Mart.[2]; Heterotrichum octonum (Humb. & Bonpl.) DC.[2]
366	Sicyos palmata Sessé & Moc.	170	158		355	Microsechium palmatum (Ser.) Cogn.; Sechium palmatum Ser. (Type)
367	Phaseolus helvolus [L.]	[116]	[109]		244	Phaseolus atro-purpureus DC. (Type)
368	Poinciana horrida Sessé & Moc.	66	61		219	Caesalpinia cacalaco Humb. & Bonpl.[1,2,3] Coulteria mexicana DC. (Type)
368★	Caesalpinia vesicaria [L.]	67	62			Haematoxylon brasiletto Karst.[2,3]
369	Euphorbia tithymaloides [L.]	79	74			Pedilanthus (3 species)[2]
370	Muntingia calabura [L.]	88	82	M80		Muntingia calabura L.[1]
371	Heliocarpus americana [L.]	78	73			Heliocarpus reticulatus Rose[2]; H. velutinus Rose[2]
372☆	Spondias mombin [L.]	75	70			Spondias mombin L.[3]
373	Crescentia edulis Sessé & Moc.	95	89		830	Parmentiera edulis DC. (Type)
374	Buchnera physaloides Sessé & Moc.	FM163	FM149		975[c]	Melasma physalodes (D. Don) Melch.[1,2]
375	"Lippia ["Phryma"] arborea Sp. N."	[Unpublished]			1017[cn]	Lippia callicarpaefolia H.B.K.[2]
376◆	"Hibiscus flavidus"	[Unpublished]			87	Malvaviscus? flavidus DC. (Type)
377	Erythrina latiflora Sessé & Moc.	115	107		251	Erythrina breviflora DC. (Type)
378	Eupatorium thyrsoideum Sessé & Moc.	133	124		561	Eupatorium thyrsoideum DC. (Paratype)
379	Tagetes punctata ["punctates"] Sessé & Moc.	142	132		DC-[cdc]	Tagetes sp.[3]
380	Aristolochia anguicida [L.]	156	145		1107	Aristolochia (3 species)[2]
381	"Fraxinus ternata"	[Unpublished]				Unknown
382◇	"Buchnera depressa"	[Unpublished]			952	Undetermined[1]; Silvia serpyllifolia (H.B.K.) Benth.[2]
383	Cleome pentaphylla [L.]	105	98		?22*[cn]	Cleome gynandra L.[2]; C. speciosa Raf.[2]
384	Antirrhinum elatine? [L.]	102	95		942	Maurandya sp.[1]
385	Rheedia lateriflora [L.]	86	80	M s.n.	1179[c]	Rheedia edulis (Seem.) Tr. & Planch.[1,2]

386	Paullinia tomentosa [Jacq.?]	60	56	M82	121^{c}	Paullinia pteropoda DC. (Type)
387■	Cassia alata [L.]	64	60	M4		Cassia polyantha Collad.[1]
388	Achras mamosa [L.]	51	48		746^{cn}	Fam. Sapotaceae[1]
389	Poinciana elata [L.]	65	61			Caesalpinia coriaria (Jacq.) Willd.[2]
390□	Euphorbia pithyusa? [L.?]	[81]	[75]		1146	Euphorbia calyculata H.B.K.[1,2]; E. fulva Stapf[2]
391	Elaterium glandulosum Sessé & Moc.	158	147		$xxxviii^{c}$,$?349^{cdc}$	Cyclanthera biglandulifera Cogn.[2]
392	Hibiscus brasiliensis [L.]	[Unpublished]			86	Hibiscus oxyphyllus DC. (Type); Pavonia melanommata Rob. & Seat.[2]
393	Capraria crustacea [L.]	98	92		948^{c}	Stemodia verticillata (Mill.) Sprague[2]
394	Bocconia frutescens [L.]	76	71	M14	14^{c}	Bocconia arborea S. Wats.[1,2]; B. frutescens β cernua DC. (Type)
395	Hydrolea tetragynia Sessé & Moc.	44	41		$873*^{cn}$	Hydrolea spinosa L.[2]
396▲	Rauwolfia o[p]positiflora Sessé & Moc.	32	30	M42		Vallesia glabra (Cav.) Link[1]
397	"Cytinus hypocistis[hipocistus]"	[Unpublished]			$?979^{c}$	Undetermined; "Orobanche cytinoides"[1]
398	Lobelia patzquarensis Sessé & Moc.	152	141	M8	707^{c}	Lobelia laxiflora var. mollis (Vatke) Zahlbr.[1,2]
399△	Erythrina herbacea [L.]	115	107		$?250^{c}$	Erythrina leptorhiza DC.[2] (Type)
400	Bombax gossypinum [L.]	107	100		95^{c}	Cochlospermum vitifolium (Willd.) Spreng.[2]; C. serratifolium DC. (Type)
401	Jacquinia armillaris [L.]	29	27			Jacquinia aurantiaca Ait.[2]
402	Cytisus cayanus? [L.]	[125]	[117]			Cajanus bicolor DC.[2]
403	Malachra hispida Sessé & Moc.	110	103	M89		Malachra alceifolia Jacq.[1]

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†DC. plates 719 ("719, no. 2") and 720 ("719, no. 1") are two figures on the same plate, listed as 719 and 720 in the index to the plates, but as "719, no. 1" and "719, no. 2" in the *Calques des Dessins.* In the manuscript of Pl. Nov. Hisp., Ic. 358, fig. 2 is cited under *longiflora,* whereas in the published text it is 358, fig. 3.

†This is an original plate, but it was reported in *Calques des Dessins* as a "Colored copy." It bears the number 362 in Mociño's hand, and is watermarked J KOOL.

‡*Sicyos angulata* of Pl. Nov. Hisp. is Ic. 179, cited as 364; I have seen neither Ic. 179 nor Ic. 364.

★No. 368 is cited in Pl. Nov. Hisp., and in the manuscript of that work, both for *Caesalpinia vesicaria* and for *Poinciana horrida.* Evidently two species are involved. *Poinciana horrida,* from the description, is the plant shown in DC. plate 219, whereas *Caesalpinia vesicaria,* from the description, is *Haematoxylon brasiletto.*

☆See footnote under 312, the number cited for this species in Pl. Nov. Hisp.

◆The number "376" and "Hibiscus flavidus" are written on the plate, but this number is listed among the plates from the "Second Excursion," that of 1789. as *Hibiscus mutabilis.*

◇The plant depicted in DC. plate 952 has pinkish or lavender flowers. Herbarium specimens plainly labelled "Buchnera depressa" and "ic," were named *Silvia serpyllifolia* (a yellow-flowered species) by Standley.

■The type of *C. polyantha* (Collad. Hist. Cass. *pl. 2.* 1816) is copied from M4, which is presumably Ic. 387.

□Apparently Sessé & Mociño confused two similar species under this name.

▲Cited as 397 in Pl. Nov. Hisp., but as 396 in the list of plates of the "Third Excursion," where *Cytinus hypocistis* is listed as 397.

△Cited in Pl. Nov. Hisp. as 354; see footnote under that number.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
404	Thrianthema monogynia [L.]	71	67	M70		Trianthema portulacastrum L.[2]
405	Convolvulus queretarensis Sessé & Moc.	24	23	M65	849[c]	Ipomoea longifolia Benth.[1]
406	Schinus occidentalis Sessé & Moc.	173	161	M44		Bursera fagaroides (H.B.K.) Engl.[1]
407	Rhamnus maculatus Sessé & Moc.	[38]	[35]			Karwinskia sp.[3]
408	Echites revoluta Sessé & Moc.	28	26	M61		Apocynum cannabinum L.[2]
409	Hibiscus pedunculatus [L.f.?]	113	105	M60		Malvaviscus candidus DC.[2] (Type)
410†	Croton vulpinum Sessé & Moc.	166	155	M17	1116	Croton dioicus Cav.[2]
411	Saururus cernuus [L.]	55	52	M52	1300[c]	Anemopsis californica (Nutt.) Hook. & Arn.[1]
412	Sida triloba Sessé & Moc.	110	103	M15	65[c]	?Wissadula trilobata (Hemsl.) Rose[2]; Sida oxyphylla DC. (Type)
413†	Bignonia salicifolia Sessé & Moc.	99	93	M91	824[c]	Astianthus viminalis (H.B.K.) Baill.[1,2]
414‡	Bignonia leucoxylon [L.]	99	92	M90		Tabebuia sp.[1]
415	Xanthium fruticosum [L.f.]	161	149	M6		Franseria ambrosioides Cav.★
416	Buchnera grandiflora [L.f.]	[101]	[94]	M31	956[c]	Escobedia longiflora Pennell[2]
417	Cytharexylum quadrangulare [Jacq.]	103	96	M48		Citharexylum affine D. Don[1,2]; C. sessei D. Don[2]
418	Cytharexylum racemosum Sessé & Moc.	103	96	M55		Citharexylum racemosum Sessé & Moc.[1,2]
419☆	Ruellia amoena Sessé & Moc.	100	93	M88		Ruellia sp.[1]
420	Stemodia siliquosa Sessé & Moc.	98	91		974	Schistophragma pusilla Benth.[1,2]
421	Hibiscus fragrantissimus Sessé & Moc.	[113]	[105]			Unknown; Hibiscus sp. ?[3]
422	Urena lobata [L.]	111	104	M87	85[c]	Hibiscus fasciculatus DC. (Type)
423♦	Clitoria racemosa Sessé & Moc.	124	116		?240[c]	"Clitoria racemosa"[1]; ?Centrosema plumieri (Turp. ex Pers.) Benth.
424	Polygala baccifera Sessé & Moc.	[114]	[106]	M75		Monnina sp.[1]
425	Symplocos martinicensis [Jacq.?]	127	118	M46		Symplocos prionophylla Hemsl.[1,2]
426	Passiflora obtusifolia Sessé & Moc.	156	145	M2	30[c]	Passiflora coriacea Juss.[1,2]
427	Begonia tuberosa Sessé & Moc.	162	150			Begonia gracilis var. martiana (Link & Otto) A. DC.[2]
428	Begonia syphillitica Sessé & Moc.	[162]	[150]	M97		Begonia monoptera Link & Otto[2]
429	Begonia macrophylla Sessé & Moc.	162	151			Begonia barkeri Knowles & Westc.[2]
430	Platanus orientalis [L.]	163	152			Platanus mexicana Moric.[2]
431	Dalechampia scandens [L.]	164	152	M s.n.		Dalechampia scandens L.[1,2]
432	Hura crepitans [L.]	168	156	M s.n.	1128	Hura polyandra Baill.[1,2]
433	Momordica operculata [L.]	168	156	M32		Schizocarpum sp.[1]
434	Sicyos triquetra Sessé & Moc.	170	158		354[cdc]	Sechiopsis triquetra (Ser.) Naud.; Sicyos triqueter Ser. (Type)

435	Cecropia peltata [L.]	170	158	M s.n.	1157^{c}	Cecropia obtusifolia Bertol.[2]
436	Carica heptaphylla Sessé & Moc.	172	160		1163^{cn}	Jacaratia mexicana A. DC. (Type)
437	Coriaria cuneifolia Sessé & Moc.	173	161	M69	737^{cdc}	Saurauia serrata DC. (Type)
438	Cissampelos pareira [L.]	173	161			Cissampelos pareira L.[2]
439	Musa sapientium [L.]	174	162		1229^{cn}	Musa sp.[1]
440	Clusia alba [L.]	179	166			Clusia sp.[3]
441	Phylica scandens Sessé & Moc.	39	37		178^{cn}	Gouania stipularis DC. (Type)
442	Jatropha dioica Sessé	[Unpublished]◇			1176	Jatropha dioica Sessé[1,2]
443■	Euphorbia junciformis ["inciformis"] Sessé & Moc.	FM133	FM122	M s.n.	1142^{c}	Euphorbia sp.[1]
444	Hedysarum grandiflorum Sessé & Moc.	123	115	M5	275^{c}	Amicia zygomeris DC.[2] (Type)
445	Cassia biflora [L.]	64	59			Cassia biflora L.[2]
446	Dorstenia drackenia [L.]	19	18	M s.n.	1161^{c}	?Dorstenia crispata S. Wats.[1]
447□	Nerium oleander [L.]▲	27-	26-	?M s.n.		?Lochnera rosea (L.) Reichenb.[1]
448	"Aristolochia sagittifolia N."	[Unpublished]		M s.n.		Aristolochia sp.[1]; A. pentandra Jacq.[2]; A. pringlei Rose[2]
449	Tillandsia secunda Sessé & Moc.	FM88-	FM81-			Pitcairnia palmeri S. Wats.[2]
450	Turnera pumilea [L.]	FM84-	FM77-	M s.n.		Turnera palmeri S. Wats.[1,3]; T. callosa Urb.[2]
451△	"Banisteria hispida N."	[Unpublished]		M s.n.		?Gaudichaudia sp.[1,2]

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†Published as no. 140, under the name of *Croton dioicum* Sessé & Moc., in Fl. Mex. 243 (ed. 2. 222). The number is correctly written as 410 in the manuscript of that work.

†See also Ic. 122, which was cited in Fl. Mex. as 413.

‡This number was erroneously cited for *Ruellia amoena* in Pl. Nov. Hisp. 100 (ed. 2. 93). The correct number, as written in the manuscript of that work, is 419.

★Contemporary determination by Lagasca, from the plate at Madrid.

☆Also cited as 414; see the footnote under that number.

♦"Clitoria racemosa fl. mex. ic. ined." was cited by de Candolle (in DC. Prodr. 2: 234. 1825) in synonymy under *Centrosema plumieri* Turp. ex Pers.

◇One of the few names published by Sessé in his lifetime (in Cerv. Gaz. Lit. Mex. 3: suppl. 4. 1794), but not mentioned in either of the posthumous floras under a recognizable binomial. DC. plate 1176 is a good representation of this species, and bears the number "442."

■The epithet is written "iunciformis" on the plate at Madrid, and in the list of plates of the "Third Excursion."

□Nos. 447–460, inclusive, are known only from the list of plates made during the "Third Excursion"; none is published.

▲The plate at Madrid is labelled "Nerium disentericum." As it was probably painted during the "Third Excursion," it is assumed to be the plant listed as "Nerium oleander."

△The plate at Madrid, named "Banisteria hispida," is a later version of, but not an exact copy of, DC. plate 127, the type of *Hiraea ? podocarpa* DC. The latter is an original painting, almost certainly representing a species of *Gaudichaudia*. In the plate at Madrid the fruits and inflorescences have been so modified that neither is typical of *Gaudichaudia*.

Ic. Fl. Mex. no.	Name used by Sessé & Mociño	Page in Pl. Nov. Hisp. or Fl. Mex. Ed. 1	Ed. 2	Madrid plate no.	de Candolle plate no.	Identification
452†	"Gentiana corymbosa N."	[Unpublished]		M s.n.	872^{cn}	Nama undulatum H.B.K.[1,2]
453	Achras pruniformis Sessé & Moc.	52-	49-	M s.n.	750^{c}	Fam. Sapotaceae[1]
454	"Cistus? palmata N."	[Unpublished]				Unknown
455	Mimosa procumbens Sessé & Moc.†	FM256-	FM234-	M s.n.	205^{c}	Mimosa geminata DC. (Type)
456‡	Salvia aegyptiaca [L.]	7	6	M47	991^{c}	Salvia linearis Ort.[1]
457★	Ipomoea hederifolia [L.?]	27-	25-			Quamoclit vitifolia (Cav.) G. Don[2]
458☆	Erinus humilis Sessé & Moc.	101	95	M s.n.		Bacopa monnieri (L.) Wettst.[1]
459◆	"Tarchonanthus purpureus N."	[Unpublished]		M101	571	Lagascea mocinniana DC. (Paratype)
460◇	Phyllanthus americanus Sessé & Moc.	159-	148-	M s.n.	1109^{c}	Phyllanthus galeottianus Baill.[1,2]

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†In the list of plates from the "Third Excursion," no. 452 was omitted and no. 457 was used twice, once for *Gentiana corymbosa* and once for *Ipomoea hederifolia*. The plate at Madrid is labelled "Gentiana corymbosa"; DC. plate 872 is labelled "Hydrolea radians" and bears the number "452." Presumably Mociño decided eventually to use no. 452 for the "Gentiana."

†Two different species are described on the same page under the name *Mimosa procumbens*. Apparently the plates represent the one listed first on the page, its habitat "in clivo colli."

‡The same name was applied to Ic. 7 and to Ic. 456, but two different species are involved. It is probable that no. 7 came from near Mexico City; it was listed only among the plates of the "Second Excursion," of 1789. No. 456 was listed only among the plates of the "Third Excursion." According to a contemporary note by Lagasca, it represents *Salvia angustifolia* Cav. (= *S. linearis* Ort.).

★See footnote under 452. Identification of this name depends upon a contemporary determination by Lagasca, of a Sessé & Mociño specimen.

☆See footnote under 109, the number cited for this species in Pl. Nov. Hisp.

◆Ic. 459 and DC. plate 571, both original paintings, are not exact copies, but are evidently made from the same model.

◇See footnote under no. 298.

LITERATURE AND ABBREVIATIONS CITED IN THE TEXT

AGH. Archivo General de la Nación (Historia) [México]. References are to volumes, parts ("expedientes"), and pages, e.g., 527^1: 15 is a reference to volume 527, first *expediente*, page 15.

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INDEX TO SCIENTIFIC NAMES IN TABLE 1

Contr. Univ. Mich. Herb. 14:141–152. 1980.

KARWINSKI'S ITINERARIES IN MEXICO, 1827–1832 AND 1841–1843

Rogers McVaugh
University of Michigan

Much of the early botanical exploration of Mexico was carried out by Europeans who came to America for the purpose of collecting plants, which were then taken back to European gardens and museums. Of all the botanical specimens collected in Mexico before 1875, few remain in that country. Of all the thousands of new species of plants described from Mexico in the 19th century, hardly any is represented by a holotype in Mexico. Most of the early holotypes are in London or Paris or Geneva or Madrid or Brussels or some other European city. Because these types are so important in the proper interpretation of Mexican species, it is also very important for us to know where the early travelers went in Mexico, and where they collected plants.

In the years following the establishment of the Mexican republic, that is to say especially in the years between 1825 and 1850, a succession of industrious and dedicated European collectors worked in Mexico and took out large collections of herbarium specimens. Most of the work of these early collectors was concentrated in Veracruz, Hidalgo, and Oaxaca. One of the earliest, still little-known to botanists, was Wilhelm Friedrich Freiherr von Karwinski von Karwin. He was born February 19, 1780, in Hungary, into a family of the Central European nobility, and died March 2, 1855, shortly after his 75th birthday. He was educated in Vienna, became a mining engineer of some distinction, then after working more than a decade in Spain he inherited some property in Bavaria and moved there in 1815. He became interested in traveling to America, and after unsuccessful attempts to associate himself with the Brazilian expeditions of Martius and later with those of Langsdorf, he visited Brazil, apparently at his own expense, in 1821–23. His later trips, to Mexico, were at the behest of mining interests in Europe or with the support of scientific societies or academies. A brief account of his life was published by Urban (Mart. Fl. Bras. 1, pt. 1: 35, 1906).

Karwinski's death elicited a brief obituary including a reference to his 5-year botanical expedition to "Oaxaca," and to the many plants, especially cacti, that he had introduced into European gardens (Flora 38: 160. 14 Mar 1855). Historians both before and after his death have treated him very briefly. Lasègue (1845, p. 212) says merely that Karwinski was in Mexico from 1827 to 1832, and mentions 8 localities in Oaxaca where he collected. In another note (p. 469) Lasègue says Karwinski travelled in Veracruz with Liebmann from February to May, 1841. Hemsley (1887, p. 123) says that Karwinski was sent to Mexico in 1826, and remained five years, "chiefly in the province of Oaxaca," and about "Ixmiquilpan, Zimapan, &c." Hemsley says further that Karwinski made a second trip to Mexaco, 1840–1843.

Karwinski's first expedition to Mexico seems to have been supported at least in part by what Hemsley calls the "German-American Mining Society of Dusseldorf," that is, the *Deutsch-amerikanischen Bergwerksverein zu Elberfeld.* There seems to be general agreement that the botanical collections from this trip went to the Botanical Garden in Munich.

The *Acquisitions-Journal* at the Botanische Staatssamlung in Munich shows that from 1832 to 1838 Mexican plants were purchased from Karwinski at five different times. One accession included collections in spirits only; the other four presumably consisted of herbarium material. The total paid, exclusive of the material in spirits, was more than 232 gulden. At the then current prices of specimens, as indicated by actual examples in the same journal, it may be supposed that the Karwinski collection at Munich comprised more than 1000 and perhaps as many as 2000 specimens. A short note in *Flora* (vol. 15, p. 480, 14 Aug 1832) says that Karwinski has returned to Munich with a herbarium of 1200 species. Whether or not this number represents the sum total of what the collector obtained in Mexico, or merely what he carried with him on his return, I cannot say. Zuccarini (Flora 15: 586–592. 7 Oct 1832) says that in addition to what Karwinski has sent back over the years, he now has a herbarium of 700 species from the mountains of Oaxaca. A note in *Flora* for 1832 (vol. 15, p. 407), says that the museum in Vienna bought 194 of Karwinski's Mexican plants in 1830, two years before he returned to Europe. Martius (Flora 11: 367. 21 Jun 1828), in a note written on June 12, recorded the receipt from Karwinski of a collection of about 40 species of cacti, thought to have come mostly from Oaxaca. Other notes published between 1828 and 1832 attest the fact that collections of Karwinski's plants, both living and dried, were being received in Munich.

Within a few months after Karwinski's return to Munich in 1832, Zuccarini began publishing accounts of the collections. A preliminary note, listing some new species by name, has already been mentioned (Flora 15: 586–592). An expanded study by the same author was then published in a long *Beiblatt* accompanying *Flora* for 1832.

Specific Mexican localities visited by Karwinski on his first trip have occasionally been cited in botanical literature, but by far the greatest numbers of his specimens have been cited merely with a very general locality, e.g. "Mexico" or "Oaxaca." There seems to be a good reason for this. The herbarium in Munich (M) contains many Karwinski specimens, but on the basis of sampling carried out over a period of two days in 1966,[1] I estimate that three quarters of them, or perhaps even more, are labelled simply "Mexico" or "in Imperio Mexicano." Some of the remainder bear short hand-written labels, presumably by Karwinski himself, recording the place of collection and the month and year. Oddly enough most of the dated collections were taken between May, 1827, when the collector was working in the mining districts near Pachuca, Hildalgo, and October, 1827, when he was in Mexico City after returning from a trip to another mining area, that near Sultepec, Edo. de México. It seems clear from data taken from rather numerous specimens, that Karwinski was in Hidalgo in May, June, and July. In August he was near Mexico City. His trip to the west, including the ascent of the Nevado de Toluca and a descent into the hot country of the Balsas valley below Sultepec, took place in September. In October he was again collecting near Mexico City (Figure 1).

Except for those described above, I have seen only two dated collections, one from Cristo [near Sultepec] with date May 1828, and one from near Tehuantepec, March 1831. I cannot explain why there are so few labelled collections after a certain date. One possibility is that during the early part of his trip, in the spring and summer of 1827, Karwinski made a practice of labelling specimens individually. Perhaps after completing his work near Mexico in October, 1827, he sent off to Europe all the collections he had accumulated up to that time, before he himself began a new excursion. Later collections, from Oaxaca or from other parts of Mexico, may have been provided with no labels at all, or merely with general designations for each bundle; it seems impossible to say.

Presumably Karwinski travelled to Oaxaca via Tehuacán, then spent most of his time collecting near the mining centers, or on trips toward the Pacific coast. At the time of his visit, and for some years thereafter, centers of the Mexican silver-mining industry were at Yavesía and San Pedro Nolasco, near Ixtlán, across the mountains from the

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[1] For many courtesies during my visit, I am very grateful to the Director, Prof. Dr. H. Merxmüller, and to Dr. Annelis Schreiber.

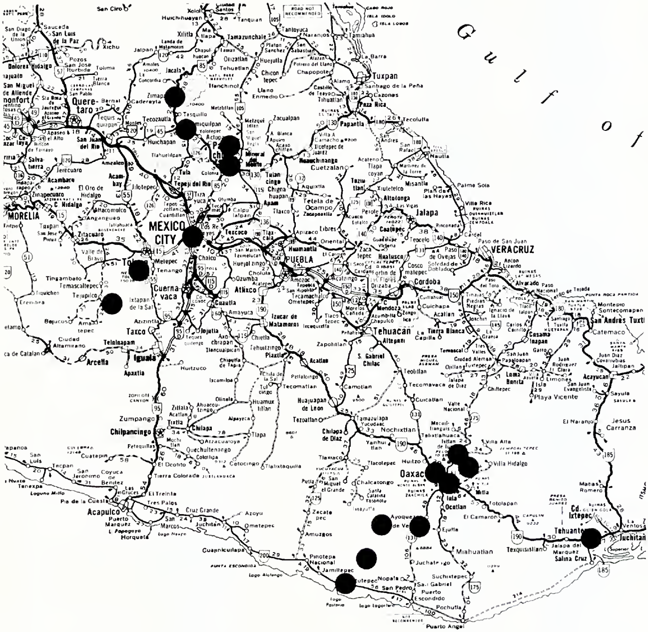

FIG. 1. (above). Localities in México and Hidalgo at which Karwinski is known or reported to have collected plants, 1827–1828; data from the literature and from dated herbarium specimens. (below). Localities in Oaxaca at which Karwinski is reported to have collected plants, presumably 1828–1832; all data from the literature, except for one herbarium specimen from Tehuantepec.

capital city of Oaxaca. The mines were to a large extent supported and staffed by Europeans, and Karwinski, like many other collectors in the ensuing years, apparently found it convenient to make his headquarters at the mines, while collecting in the vicinity.

Localities (all without dates) that have been cited in the literature as sources for Karwinski's plants, include the following from the mining regions north of Oaxaca: Capalalpan [Capulalpan], Ixtlán, San Pedro Nolasco. One place, "in summo monte Tanga, 10,000 [ft.]" I have not located.

In Karwinski's time it was also possible to travel south from the city of Oaxaca, via Sola de Vega, Teojomulco, and Juquila, to the Pacific coast. Zuccarini says that Karwinski found *Cheirostemon,* the famous "hand-tree," in the region of San Juan Quieixe and Juquila, and that he found *Magnolia mexicana* in the same general region, near Jocotepec and Tututepec, and *Lopezia grandiflora* near "Sant Jago el grande" not far from the ocean. A few other localities cited by different authors probably are from this southern part of Oaxaca (e.g. St. Augustino, San Bartolo). Karwinski also collected near the capital (Oaxaca), at Santa María del Tule and, as already mentioned, near Tehuantepec. Liebmann, almost 15 years after Karwinski's time, travelled along the Pacific Coast from near Pochutla to Tehuantepec and then returned to Oaxaca by the inland route, but whether or not Karwinski did the same cannot be ascertained at present.

In spite of these known localities, and the inferences that may be drawn from them, almost nothing is known about where Karwinski went or what routes he employed, or how long he stayed, after he returned to Mexico City late in 1827. As most of the localities cited in literature are from Oaxaca, it seems likely that he spent a considerable amount of time in that state. His obituary, as already noted, refers to his "5 jährigen Aufenthalt in Oaxaca." Lasègue (p. 212) says Karwinski's plants were "récoltées principalement dans l'État d'Oaxaca."

Anyone who finds a Karwinski specimen with locality or date, or both, especially from this first trip of 1827–32, will do well to record the data and keep an index to all such specimens.

Karwinski's second trip to Mexico (1841–43) was undertaken when he was 60 years old, under the auspices of five different sponsors in St. Petersburg (now Leningrad). By the terms of his agreement he was to look for plants and animals, and also, primarily, to search for minerals in commercial deposits. His trip was very successful, botanically speaking. He brought back more than 2000 gatherings, in 6 major sets. These were partly named, and distributed about 1851 by the botanist F. J. Ruprecht, who was then working in St. Petersburg.[1] The first set, with the original hand-written field data, went to the herbarium of the Imperial Botanical Garden of St. Petersburg, whereas the duplicates were distributed like any other specimens, but mostly without name or other data. Because so few of the specimens have been distributed to herbaria outside the Soviet Union, and because Russian botanists for the most part have not been actively interested in Mexican botany, the specimens have been little used and seldom cited. Of those that have been noted in the literature, however, not a few are types.

Only Fournier (1886) seems to have made a concerted effort to examine all of Karwinski's specimens of any major group of plants. In the introduction to his work on Mexican grasses, he acknowledges the kindness of [Eduard] Regel, who had placed at his disposition, among other things, "l'importante collection de Graminées de Karwinsky. Bien que récoltée en 1842, cette collection n'avait jamais été l'objet d'un travail d'ensemble et renfermait encore des nouveautés." Fournier cited about 100 gatherings made by Karwinski, including most of the numbers from 943 to 1015 and from 1463 to 1486, in addition to many unnumbered collections (the numbers were those assigned by Ruprecht, after the plants had been arranged in some systematic order).

Most of the specimens collected on Karwinski's journeys from 1841 to 1843 were from the lowlands of northern Veracruz, where few collectors had preceded him, or from the lowlands and mountains of Tamaulipas, where hardly anyone except Berlandier had collected before. As far as I can ascertain, Karwinski was the first collector to reach the uplands of Tamaulipas between Victoria and Miquihuana. As the localities he visited include mines, ranches and other places not on ordinary maps, and as the original hand-

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[1] According to Ruprecht's notations the sets were distributed as follows:

1) Pro horto Imper. botan. Petrop.
2) Pro museo botanico Academiae Imp. Petrop.
3) Pro museo scholae saltuariae Petrop.
4) Universitate Moscoviensi
5) Universitate Kazaniensi
6) Universitate Helsingforsiensi

written labels are often cryptic or misleading, it is desirable to describe his itineraries in some detail.[1]

The detailed itineraries for 1841 and 1842, as set forth below, are based primarily on a series of notes preserved in the herbarium archives at LE. It seems to have been Karwinski's practice to pack his specimens in bundles, either from individual localities or from a series of localities visited on a given trip, and to number and label each bundle. About 35 separate clippings, taken from bundles labelled in this way, have been preserved. When these are arranged in numerical order (which also appears to be chronological order), a reasonably complete picture of localities and routes emerges. Additional information can often be supplied from the original labels on individual specimens, but these of course usually do not provide anything of note about the relation of one locality to another.

Apparently bundles I–X included all the plants collected between Papantla and Huejutla, and near Huejutla during the summer months of 1841. Bundles 1–10 included plants collected at Huejutla beginning in October 1841 and on a trip to Horcasitas from which Karwinski returned in December of the same year. A second series of bundles numbered 1–12 included the plants collected from June to August, 1842, on a trip from Victoria across the Sierra Madre and return.

Sometimes the information on a bundle was very specific, e.g.

"No. IX. Huichichilingo 9 Leguas de Huejutla."

"No. 1. Huejutla a fine Octobri 1841 usque ad 5 Nov^{re}."

Other bundles evidently included plants from various localities, e.g.

"No. 1. Plantae lectae in proximitate oppido San Miguel de Aguayo (nunc Victoria) in montibus Sierra Madre et in planitie mens. Junii et Jul. 1842."

Still others referred to plants from a part of a long trip. e.g.

"No. 4. Plantae lectae in itinere a Huejutla ad Horcasitas. De San Vicente al Tamuin ad marginibus flum. Panuco 14 leguas in una die pereundas per desertum sine gentes nec agua."

Many of the localities are still well-known today, and those that cannot be located on modern maps can usually be assigned approximate positions because of Karwinski's practice of recording the distances in leagues ("leguas") between successive localities. The Spanish land-league as used in Mexico was about 4.24 km. Karwinski's estimates agree for the most part with the actual distances, after due allowance for the well-known elasticity of distances in areas remote from urban centers, and the differences between modern roads and the more devious routes of the year 1840.

The archives apparently do not include any of the bundle-wrappings (if indeed any were prepared) for the plants collected in 1843. Usually, however, as in 1842 and sometimes before, Karwinski prepared one small field-label for each gathering. These were usually in Latin, occasionally in Spanish or German. The label usually includes no more than a brief locality-name, and the month and year of collection (these latter often

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[1] For essentially all the information presented here on Karwinski's collections in 1841–43, I am indebted to the authorities of the Komarov Botanical Institute of the Academy of Sciences, USSR. The herbarium of the Institute (LE) was very graciously made available to me during my visit in July 1975, when I was permitted to consult not only the original specimens and such duplicates as have gravitated to Leningrad since 1850, but also to use and study material on Karwinski from the herbarium archives. I am especially grateful to Dr. I. A. Linczevski, who aided me in many ways.

I have tried to set forth as far as possible the details of the itineraries of 1841–43, as these were derived from documents at LE and from other sources. I have not tried to supply background information on Karwinski himself, or on the circumstances of his journey. There is much additional information in the archives in Leningrad, and it is to be hoped that botanists in the Soviet Union will eventually complete the study of which this is a small part. A note on Karwinski was published by V. I. Barabanov in 1974, among the abstracts of papers presented at a meeting in honor of the bicentennial of G. I. Langsdorf (Kalesnik, 1974). I am grateful to Dr. Andrei Bobrov for calling this to my attention.

omitted). Occasionally there are notes on vernacular names or local uses, sometimes a Latin binomial.

The specimens were not consistently numbered by the collector. Sometimes he began short series of numbers for specimens from a single locality, or for different species of one genus (e.g. numbers up to at least 31 were assigned to specimens from Tanquecillos in October, 1842). When the entire collection was returned to St. Petersburg, however, it was sorted into systematic order by family and genus, and numbers were arbitrarily assigned, presumably by Ruprecht. The series began with the Ranunculaceae (*Clematis*), and ended with the non-vascular cryptogams. According to Ruprecht's notes, the set put aside for the Imperial Botanical Garden at St. Petersburg included 2177 numbers, but in the enumeration compiled by the same author, only 1136 numbers are listed, including 1096 from Mexico, 26 from Havana, 11 from Florida, and 3 from Dog Key, Bahamas.

Few data were copied from the original set when the duplicates were distributed, so most of the duplicate sheets bear no more information than the number assigned by Ruprecht, plus in some few instances the name of the plant. Mostly, therefore, locality-data for any particular number must be sought on the primary set at LE, to which the original field-labels were attached.

Itineraries of 1841–1842

Karwinski arrived in the West Indies in the early autumn of 1840. At one point he was interrupted by a shipwreck. He spent at least a short time in the Bahamas; he collected a few specimens near Apalachicola, Florida (November), and several more near Havana (December, and January 1841). From Havana he took ship for Veracruz, where he arrived about the first of February. The Danish botanist F. M. Liebmann, after a trip of 56 days from Europe, landed in Veracruz on 7 February 1841 (Dansk Ugeskr. II. 1: 186. 1842), and joined forces with Karwinski for a joint pack trip northward through the lowlands. As Liebmann wrote on February 21st,

> Mexico's present situation makes it to a certain extent advisable with combined strengths to brave the dangers with which a completely demoralized population, anarchy and lawlessness will each day confront us . . . . The interior swarms with bandits who unpunished rob and murder with the utmost audacity . . . . The only part of the Mexican population which one still dares to trust are the Indians, and we have therefore, on our journey decided to choose the Indian districts as much as possible for our stays.

On 26 February the two travelers set out (DU II, 1: 201) for the north by the coastal road to Tuxpan. They seem to have spent about two weeks on the road, and collected at least at the following localities, turning away from the coast at Rancho Nuevo:

La Antigua [Veracruz]	19° 19′ N
San Carlos	19° 24′ N
Paso de Doña Juana	19° 29′ N
Laguna Verde	19° 44′ N
El Morro de Boquilla	19° 51′ N
Rancho Nuevo	19° 57′ N
Hda. de Sta. Bárbara	19° 58′ N, 96° 36′ W

From near Santa Bárbara the party turned southwest some 12–13 km to Colipa, where they spent the next 27 days (DU II, 1: 202), or apparently about until the first of April. Liebmann commented on Colipa as follows:

> Colipa, which is the first purely Indian town we have come to on our trip, lies 10 leagues from the coast between mountains covered by the most luxurious virgin forests of whose wealth of trees

one can best form an idea when I note that Karwinsky together with an Indian in 8 days got a wood collection of 100 different hardwoods in specimens an ell long and 6 inches thick. Our stay in Colipa was extended to 27 days partly because of the rich returns, partly because of the impossibility of getting lodgings in Misantla, the main depot of the vanilla trade, as we had first decided.

From Colipa Liebmann and Karwinski moved to Jicaltepec, some 8 km SW of Nautla. Liebmann left for the south probably toward the end of April, and Karwinski continued to turn inland and toward the north. He seems to have reached Papantla, Ver., before mid-May, then to have continued without much pause to Huejutla, in the lowlands of northeastern Hidalgo, which was to be his base of operations for the next 5 or 6 months (Figure 2).

FIG. 2. Karwinski's route from Veracruz to Huejutla, and that from Huejutla into eastern Tamaulipas, both in 1841; data from Veracruz to Papantla are taken chiefly from Liebmann's collections, and for the other localities from the archives at LE.

Papantla to Huejutla [May–Jun 1841].[1]

Papantla, Ver.	
Coazintla [Coatzintla, Ver.]	[20° 29′ N, 97° 27′ W]
Rancho de Mesa de Mecatepec, Ver.	[20° 33′ N, 97° 30′ W]
Tihuatlán, Ver.	[20° 44′ N, 97° 32′ W]
Paso Real, Ver.	[20° 55′ N, 97° 36′ W]
Hda. de Chapopote, Ver.	[20° 56′ N, 97° 41′ W]
Hda. de Tamatoc [Tamatoco], Ver.	[21° 04′ N, 97° 51′ W]
Rancho de Monte Grande, Ver.	[21° 07′ N, 98° 02′ W]
Rancho de la Pastoría, Ver.	[21° 06′ N, 98° 08′ W]
Huejutla, Hgo.	[21° 08′ N, 98° 25′ W]

By August 4 Karwinski was making an excursion from Huejutla to the nearby settlement of Ixcatán, so he may well have been established in Huejutla by mid-July.[2] The airline distances along his routes from Papantla to Huejutla amount to something on the order of 175 km, and the trails and packroads of Karwinski's time were certainly longer than this; the entire journey may have taken some weeks. If he spent 3 weeks to a month in Papantla in May, and a month *en route* between Papantla and Huejutla, he could have been in the latter place as early as the beginning of July. From Huejutla Karwinski seems to have made several excursions, both long and short, on botanical business, during the second half of the year 1841.

There are various indications among the materials at LE that Karwinski made a trip from Huejutla to Tampico, but I have not been able to establish firm dates or a precise itinerary for this. Some herbarium labels read: "Plantae lectae in itinere ab Huejutla ad Tampico." At least one original label (no. 846, *Sabal mexicana*) reads "in magna silva palmera incipiens ad Tantoyucca usque Tampico 35 leguas." About 1856, and presumably for some years before (Alvarez & Durán, 1856, p. 286), the regular stage route from Mexico City to Tampico passed through Tantoyuca and continued on to the northeast, the distance from Tantoyuca recorded as 34 leagues. It is possible (but I have no evidence for this) that Karwinski went to Tampico and returned to Huejutla in September or October, 1841. Notes referring to some plant-specimens from Huejutla state specifically that these plants were collected "a fine Octobri usque ad 5 Nov^{re}," so that the collector may have been traveling before this time.

There are also notes suggesting that Karwinski was in Tantoyuca in February 1842, perhaps at that time on his way to Tampico. I cannot account for his time between February and June, 1842; in the latter month he was in Ciudad Victoria, Tamps., ready to begin a long trip into the mountains to the westward.

Fournier (1886) cites specimens collected at or near Córdoba ["Cordova"], Ver., some of them in February. It may be that Karwinski travelled from Huejutla to Córdoba early in 1842, although this seems rather unlikely; perhaps more likely is the suggestion that after his first arrival in Veracruz early in 1841, he made a quick trip up to Córdoba and returned to Veracruz in time to go north with Liebmann, who was not ready to travel until late in February.

Information from herbarium labels and other materials at LE indicates that Karwinski made short excursions from Huejutla, e.g. to Ixcatán, Hgo., in early August, and to Huichichilingo [Huitzitzilingo, Hgo.], probably about the same time. By his own statement he was in Huejutla in October and early November, 1841, and again from the end of December 1841 to early January, 1842. In the intervening time he made a trip

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[1] In the lists below, modern equivalents of place-names are given in square brackets if necessary, as are coordinates in latitude and longitude if known. Distances in leagues are those given on the original papers. Dates in brackets are approximate.

[2] Numerous specimens among the duplicates at LE are labelled as from Colipa, with the date 22 July 1841. I suspect that this is an error, as other indications point to Karwinski's having become established at Huejutla by this time or before.

of some weeks' duration through the coastal lowlands of northern Veracruz, eastern San Luis Potosí, and southern Tamaulipas; he probably did not return to Huejutla until almost the end of December.

from	Huejutla, Hgo.	[21° 08′ N, 98° 25′ W]	["4 leg^{s}"]
to	Chiconamel, Ver.	[21° 14′ N, 98° 27′ W]	[3 leg^{s}]
to	Rancho de las Piedras, [S.L.P.?]	[21° 22′ N, 98° 30′ W]	[3 leg^{s}]
to	Rancho de Limón [not located]		[6 leg^{s}]
to	Corozal, Ver.	[21° 33′ N, 98° 32′ W]	[7 leg^{s}]
to	Rancho del Humo [not located]		[3 leg^{s}]
to	San Vicente, S.L.P.	[21° 44′ N, 98° 34′ W]	[14 leg^{s}]
to	Tamuin, S.L.P.	[22° N, 98° 46′ W]	[9 leg^{s}]
to	Hda. del Limón, S.L.P.	[22° 11′ N, 98° 44′ W]	[3 leg^{s}]
to	Rancho del Tulillo, S.L.P.	[22° 17′ N, 98° 41′ W]	[7 leg^{s}]
to	Hda. del Naranjo, Tamps.	[22° 29′ N, 98° 38′ W]	[10 leg^{s}]
to	Cerro Bernal, Tamps.	[22° 47′ N, 98° 37′ W]	
	via Tantoyuquita, Tamps.,	[22° 33′ N, 98° 34′ W]	
	Tantasneque [Tancasnequi, Tamps.]	[22° 34′ N, 98° 32′ W]	
	and Rancho del Carrizo, Tamps.	[22° 44′ N, 98° 29′ W]	

From the peak of Bernal, Karwinski undertook a short trip to the Hda. del Cojo, said to be 5 leagues distant. Returning by the same route, he continued as follows:

from	Hda. del Cojo	[22° 52′ N, 98° 23′ W]	[7 leg^{s}]
to	Horcasitas [Magiscatzin, Tamps.]	[22° 48′ N, 98° 42′ W]	[10 leg^{s}]
to	Escandón [Xicoténcatl, Tamps.]	[23° N, 98° 59′ W]	[16 leg^{s}]
to	Santa Bárbara [Ocampo, Tamps.]	[22° 50′ N, 99° 20′ W]	[8 leg^{s}]
to	Palmitas [not located]	["et retro ad Horcasitas"].	

On the return from Horcasitas to Huejutla, "in mense Decembri 1841," the route was as follows:

from	Horcasitas		[5 leg^{s}]
to	Cardiel, Tamps.	[22° 41′ N, 98° 40′ W]	[8 leg^{s}]
to	Hda. del Naranjo, Tamps.		[10 leg^{s}]
to	Hda. del Limón, S.L.P.		[5 leg^{s}]
to	Rancho de Tampacoala [Tampacualab, S.L.P.]	[ca 22° 10′ N, 98° 52′ W]	[8 leg^{s}]
to	Tamuin, S.L.P.		[thence]
to	Chico[namel] "prope Huejutla"		

On this last trip Karwinski, according to notations on herbarium specimens, was at the Hda. del Naranjo in "mid-December," and at El Tamuin on December 19, 1841. This fits in with the suggestion, previously made, that he returned to Huejutla just before the end of the month.

Travels in the mountains of Tamaulipas and Nuevo León

This trip, during July and August, 1842, is well documented by the notes taken from the wrappings of Karwinski's plants (Figure 3). The collector apparently left from Victoria in the latter part of June and returned in the latter part of August. Traveling at first toward the southwest and then westward, he crossed the Sierra Madre near Miquihuana, turned northward into the desert of southern Nuevo León, then again eastward into the upper canyons of the Rio Blanco[1] drainage near present Aramberri.

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[1] Fournier and others have cited specimens from "between Victoria and Río Blanco," as if there were two contiguous or at least nearby localities. Evidently, however, such a phrase as written merely means that the specimen was collected somewhere between the two ends of the journey.

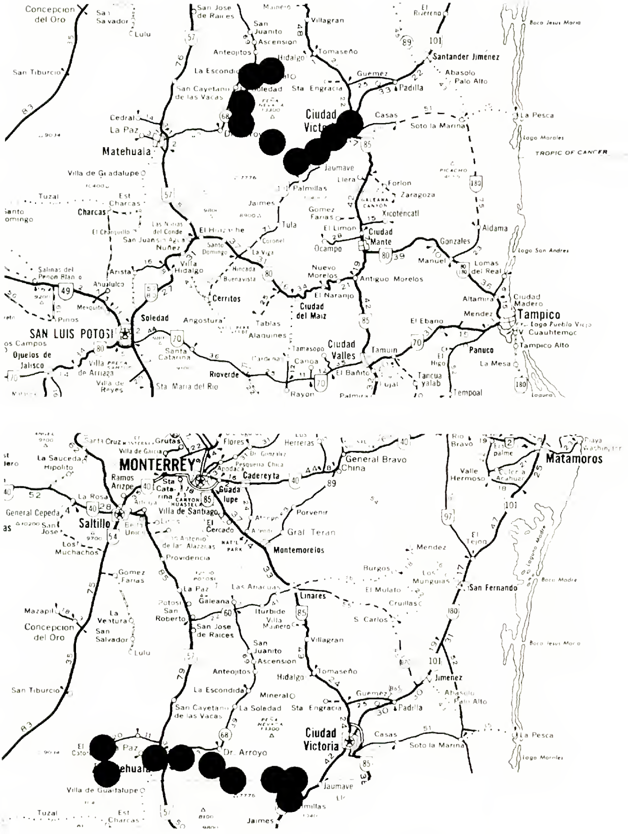

FIG. 3. (above). Karwinski's route between Victoria and Río Blanco, 1842; data chiefly from the archives at LE. (below). Karwinski's route to Matehuala and Catorce, 1843; data chiefly from the archives at LE.

He returned to Victoria by essentially the same route, collecting at this season also. His itinerary was as follows:

from	Victoria, "per Cañon de las Minas"		[14 leg^{S}]
to	La Mula, [Tamps.]	[23° 36′ N, 99° 17′ W]	[12 leg^{S}]

to	Hda. de Hernández ["per Valle de Jaumave"; not located]		[6 leg^{s}]
to	Hda. Santyaguillo [Santiaguillo, Tamps.]	[23° 27′ N, 99° 34′ W]	[6 leg^{s}]
to	[or through] Cañon de Palmillas [not located]		[6 leg^{s}]
to	Tanque Colorado [not located]		[5 leg^{s}]
to	La Miquiguana [Miquihuana, Tamps.]	[23° 35′ N, 99° 47′ W]	[5 leg^{s}]
to	Tanque de Miquiguana [not located; possibly the same as Tanque de Equia, Tamps.]	[23° 34′ N, 99° 55′ W]	[14 leg^{s}]
	[via "La Baxada del Puerto del Rancho de la Bolsa" (N.L.), 23 Jul 1842; 23° 44′ N, 100° 02′ W]		
to	Tanquecillo(s), N.L.	[23° 53′ N, 100° 02′ W]	[12 leg^{s}]
	[via Cañon de Pastli]		
to	La Escondida, N.L.	[24° 07′ N, 99° 55′ W]	[6 leg^{s}]
	[via Cañon de Pastli]		
to	Río Blanco, N.L.	[ca 24° 06′ N, 99° 49′ W]	

The return to Victoria seems to have been by essentially the same route. Many collections were made in July and August on the way out, and in August on the return, from "La Miquiguana in sumitatibus montium et in planitie," from "Tanque Colorado per sumitate montium (la Cumbre)" to Santiaguillo, through the valley of Jaumave, and finally down the Cañon de las Minas to Victoria "fin. Aug. 1842."

I cannot account well for Karwinski's time during the rest of the year 1842. Rather numerous specimens dated "Oct 1842" are labelled as from Santiaguillo, or from Tanquecillo. Most of the plants so labelled appear to be characteristic species of the forested semi-arid interior valleys, not desert species, so it may be that this Tanquecillo is not the same as the one where Karwinski collected in July and August. At the former locality he collected such well-known desert plants as *Larrea tridentata* and *Parthenium argentatum.*

Trip to Matehuala and Catorce, Jan–Apr 1843

During the first 4 months of the year 1843, Karwinski collected many specimens in the vicinity of the mines at Matehuala and Catorce, San Luis Potosí, and along his routes to these places and on the return to the vicinity of Santiaguillo, Tamps. No direct records of his travels have been preserved, but from original notations on herbarium specimens at LE the following provisional itinerary is suggested. The dates are those recorded on the specimens.

Jan	Santyaguillo [Santiaguillo, Tamps.]	[23° 27′ N, 99° 34′ W]	
Feb	from Palmillas, Tamps.	[23° 18′ N, 99° 32′ W]	[6 leg^{s}]
	to Rancho de Palo Blanco, Tamps.	[23° 27′ N, 99° 42′ W]	
	[then via ?Bustamante and/or Miquihuana]		
	to Medina, N.L.	[23° 24′ N, 100° 07′ W]	[6 leg^{s} "W"]
	to Las Boquillas, N.L.	[23° 33′ N, 100° 19′ W]	
Feb–Mar	to San Antonio, S.L.P.	[23° 41′ N, 100° 29′ W]	["prope"]
Feb–Mar	Matehuala, S.L.P.	[23° 39′ N, 100° 38′ W]	
Feb	via Rancho de la Palma [not located]		
Feb	to Catorce, S.L.P.	[23° 41′ N, 100° 53′ W]	["prope"]
Feb–Mar	Sierra de Marroma [Maroma], S.L.P.	[ca 23° 32′ N, 100° 51′ W]	
	[return via Matehuala?]		
Apr	"prope Calabacita [not located] et Medina"		
Mar	La Santoña [not located; see below]		
Apr	"de La Santoña al Pantano" [see below]		
	"El Pantano et a Tanque Colorado" [see below]		
	"El Pantano et in Santyaguillo" [see below]		
	Palmillas, Tamps.	[23° 18′ N, 99° 32′ W]	
	[?to] La Guazacana [Huazacana, Tamps.]	[23° 08′ N, 99° 28′ W]	
	[?to] "Rancho San Rafael prope Sta. Barbara" [see below]		
May	Tampico "ad littore mare."		

I have not been able to place on any map the localities called Calabacita, La Santoña, El Pantano, Tanque Colorado, or Rancho San Rafael. It may be supposed that Calabacita is near Medina, though this is not necessarily so. Evidently San Rafael is near Santa Bárbara, that is to say Ocampo, Tamps. The other three names are associated so many times, either in time or by direct mention, with known localities, that it seems clear they are all in the mountains of Tamaulipas in the general area of Palmillas, Santiaguillo, and Miquihuana. On the trip out in 1842, Tanque Colorado was said to have been 6 leagues from Cañon de Palmillas, and 5 leagues from La Miquihuana. Among the collections made in July and August of that year, there are several with such notations as "Cañon Palmillas de Santyaguillo al Tanque Colorado." A note in the archives at LE gives the distance from Tanque Colorado to Santyaguillo, on Karwinski's return trip in August, as 7 leagues.

I suspect that El Pantano was the mine at nearby Bustamante, the so-called Real del Pantano. At this period the mine was active, as were the mines at Miquihuana (cf. Alvarez & Durán, 1856, pp. 446, 449; García Cubas, 1884, p. 221). Probably Karwinski's visits to the Miquihuana–Bustamante–Santiaguillo area were all related to his interest in mining; presumably he visited the Matehuala–Catorce area for the same reason.

There is no direct reference to the whereabouts of La Santoña that I can find, except that on some labels the locality is given as "de la Santoña al Pantano," suggesting that it is not far from Bustamante; it may have been another mine.

When the chronological sequence of the above localities is considered, it suggests that Karwinski returned from Matehuala late in March, 1843, to spend some weeks in the Miquihuana–Bustamante–Santiaguillo area. The other dated localities in April and May suggest that he turned south from Palmillas and travelled by way of Huazacana to Santa Bárbara (i.e. Ocampo). From Santa Bárbara the lowland routes to the coast were already known to him from his travels in 1841. The discovery of additional dated specimens from other localities may confirm or discredit these suggestions.

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THE TAXONOMY OF *CAREX* SECTION *STELLULATAE* IN NORTH AMERICA NORTH OF MEXICO

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INTRODUCTION

The genus *Carex* is one of the largest amphimictic genera of vascular plants with an estimated 1,000 (Hitchcock et al., 1969) to 2,500 (Nelmes, 1952a) species. While size alone does not necessarily indicate taxonomic difficulty, *Carex* is a genus that does often plague taxonomists. One of the most problematic sections in *Carex* is the *Stellulatae.* It should be noted here that the nomenclatural difficulties surrounding the infrageneric taxa in *Carex* are formidable (Voss, 1966). Because of this, the currently accepted nomenclature of the subdivisions of the genus (Mackenzie, 1931, 1935) is here followed without further comment.

As defined by Mackenzie (1931), section *Stellulatae* is best developed in eastern North America. Here Mackenzie recognized 16 species: *Carex echinata* Murray (*C. muricata auct. non* L.), *C. cephalantha* (Bailey) Bicknell, *C. angustior* Mackenzie, *C. laricina* Bright, *C. sterilis* Willdenow, *C. interior* L. H. Bailey, *C. exilis* Dewey, *C. josselynii* (Fernald) Pease, *C. elachycarpa* Fernald, *C. mohriana* Mackenzie, *C. atlantica* L. H. Bailey, *C. incomperta* Bicknell, *C. howei* Mackenzie, *C. seorsa* E. C. Howe, *C. ruthii* Mackenzie, *C. wiegandii* Mackenzie. Some of these species he considered transcontinental. *Carex phyllomanica* W. Boott, *C. ormantha* (Fernald) Mackenzie, and *C. laeviculmis* Meinschausen were considered by Mackenzie to be endemic to western North America. One species, *C. townsendii* Mackenzie, was restricted to Mexico.

Outside of North America, *Carex echinata* is known throughout much of Europe (Jermy and Tutin, 1968) and also in the south temperate zone in New Zealand (Moore and Edgar, 1970) and Victoria and New South Wales, Australia (Moore, 1893; Ewart, 1930; Willis, 1970). *Carex omiana* Franch. & Savat., *C. echinata,* and *C. angustior* are reported from eastern Asia (Egorova, 1960, 1966; Ohwi, 1936). In addition, three species which have been referred to the *Stellulatae* are isolated endemics on tropical mountains: *C. gajonum* Nelmes (1952b) in Sumatra, *C. svenonis* Skottsberg (1944) in Hawaii and *C. perileia* S. T. Blake (1947) in New Guinea.

In North America, there has been vast divergence in the taxonomic treatments of this group. In northeastern North America alone the number of species recently recognized has varied from nine (Gleason, 1952; Gleason and Conquist, 1963) to 14 (Fernald, 1950) and even 15 (Mackenzie, 1931). The number of species reported from Canada has varied from 12 (Mackenzie, 1931) to three (Boivin, 1967).

MATERIALS AND METHODS

This study was based on examination of about 8,000 specimens located in the following herbaria: ACAD, ALTA, CAN, CM, DAO, F, FLAS, GA, GH, MICH, MIN, NCU, NY, PH, QK, SHER, SIU, TEX, TRT, TRTE, UARK, UBC, UC, WIS. In addition, the species were studied in the field in Ontario from 1974 to 1977 and along the east coast of North America from Nova Scotia and southern Quebec to Massachusetts in 1975 and 1978.

Citations of representative specimens are available from the senior author upon request.

TAXONOMIC CHARACTERS

A wide variety of characters are available within the genus *Carex.* In compiling features for examination in this work, keys and descriptions in a number of previous treatments of this section were consulted. Especially useful in this respect were Mackenzie (1931), Hermann (1941), Fernald (1950), Gleason (1952), and Voss (1972), and more generally Damman (1964) and Jermy and Tutin (1968). In addition a thorough search was made for new features that might be of use.

The vegetative organs and flowers are rather simple; thus, most of the characters are concentrated in the inflorescence and infructescence. Fruiting characters specifically are used a great deal and, in this investigation, were unavoidably the most numerous character type. Nevertheless, the obvious utility of fruiting characters and the dubious success of vegetative keys except in relatively depauperate *Carex* floras (Damman, 1964; Jermy and Tutin, 1968) should not obscure the usefulness of some nonfruiting characters. In this investigation, leaf width, leaf section type, and distance between adjacent spikes on the culm were found to be quite useful.

As it is potentially of considerable significance, the precise manner in which some of the characters were measured will be briefly discussed. In the *Stellulatae,* perhaps the most critical decision is which perigynium should be measured. Many keys contain a general statement that the perigynia in the middle of the spike are most characteristic and should be used for comparison. A check on this initially obvious statement revealed that it is indeed not so obvious at all. It was evident that, at least in the *Stellulatae,* the perigynium length/width ratio is most different between species and least variable within a species on the *lowest* perigynia of the spikes. The middle and certainly the uppermost perigynia are more variable and, in fact, perigynia of all species converge in shape towards the apex of the spike so that they become essentially indistinguishable (Reznicek, 1978). If there are relatively few perigynia in the spike, often only the lowest one or two are suitable for measurement as characteristically developed for the species.

The perigynium beak was on occasion difficult to define. It was measured from the first inflection point in the curve at the transition from beak to body to the tip of the teeth at the apex of the beak. The width of the perigynium was always measured at the widest point, regardless of its location, and the number of nerves of the perigynium was counted over the achene on the adaxial surface above the basal spongy layer. Throughout the text the terms nerve and vein have been used interchangeably.

When leaves were measured, the largest culm leaf was always used. This was usually the uppermost leaf (except in *Carex exilis*). The widest leaf on the plant proved a significant character. In its measurement, all leaves were considered, including the dried up leaves of the previous year. These old leaves, usually produced on sterile shoots after the plants have fruited, are sometimes much larger than culm leaves and, as is the case with the shape of the lowest perigynia on a spike, better express the potential variation of the plant. For this reason, plants of this group should not be cleaned of their dead leaves when preparing specimens.

RELATED SECTIONS AND LIMITS OF THE *STELLULATAE*

It is clear that a complete revision of group boundaries even in one section of *Carex* like the *Stellulatae* cannot be attempted without examination of world-wide material which is beyond the scope of this work. However, some discussion of relationships and minor realignments of North American species seems necessary at this point.

The *Stellulatae,* as defined by Mackenzie (1931), are close to three other sections of *Carex* in North America: the notoriously difficult *Ovales,* the boreal *Heleonastes,* and the primarily woodland *Deweyanae.* These groups and the *Stellulatae* all have in common gynecandrous, simple spikes and a usually cespitose habit. The *Ovales* characteristically have more or less scale-like perigynia appressed and more or less overlapping in a dense head. The perigynia are thin-margined, sometimes even winged and often stramineous. The *Heleonastes,* excluding *C. disperma* Dewey (Ohwi, 1936; Toivonen and Timonen, 1976), characteristically have short-beaked or essentially beakless, plump, ascending to spreading perigynia that are not spongy-thickened at the base and usually appear minutely whitish puncticulate. The *Deweyanae* have ascending or even appressed-ascending perigynia. The plants themselves have a lax and spreading habit. The *Stellulatae* are characterized by spreading to reflexed perigynia that are prominently beaked, spongy at base, thick-margined, not white puncticulate and with a usually serrulate beak.

As Mackenzie (1931) defined the section, the *Stellulatae* included 20 species in North America. In addition, a few other North American species have been included in it in the past. *Carex gynocrates* and its relatives, now placed in the *Dioicae,* were placed here by Fernald (1902) and Holm (1903) but these differ strongly in being much smaller, slender, delicate, dioecious mat-formers. *Carex illota* was included by Mackenzie (1917, 1922) but later aligned with the *Ovales* (Mackenzie, 1931). Moore and Calder (1964) concurred with this placement. Since the species has more or less sharp-edged, ascending perigynia without a spongy base and a smooth-margined beak that is not bidentate, the plant certainly does not belong in the *Stellulatae.*

Mackenzie (1931) separated the *Stellulatae* from the *Deweyanae* by "perigynia spreading or ascending at maturity" for the former contrasted with "perigynia appressed" for the latter. However, Mackenzie included three species in the *Stellulatae* which differed considerably from the above description: *Carex laeviculmis,* which was described as having perigynia "appressed or ascending," *C. elachycarpa* with pergynia "closely appressed," and *C. josselynii* with pergynia "appressed-ascending." The taxonomic position of *C. josselynii* and *C. elachycarpa,* considered endemic to northern Maine, has already been discussed (Reznicek and Ball, 1979) and they were shown to be based on abnormal individuals of species with normally spreading to reflexed perigynia. *Carex laeviculmis,* on the other hand, is a widespread species of western North America ranging from Alaska to California. In addition to appressed or ascending perigynia, it has a lax, spreading habit. These characteristics, along with its overall aspectual similarity to *C. deweyana* and *C. bromoides,* place it clearly with the *Deweyanae,* not the *Stellulatae.* As it was at one time described as a variety of *C. deweyana* (Bailey, 1888), it is difficult to understand Mackenzie's placement of it in the *Stellulatae* without any mention that it was unusual in the group. Fernald (1902) noted that it was similar to *C. seorsa* in having a smooth-beaked perigynium and this may have been partly responsible for Mackenzie's decision. It is here considered as a member of the *Deweyanae* and will not be discussed further.

The exclusion of *Carex laeviculmis* from the *Stellulatae* leaves a uniform group of cespitose sedges with gynecandrous spikes of widely spreading to reflexed perigynia that are planoconvex to more or less biconvex, thick-margined, and have a prominent serrulate, bidentate beak and spongy base. Only three species differ slightly from this description.

Carex exilis has involute leaves and usually solitary spikes. It may also occasionally be dioecious. These features have led to its placement in the *Dioicae* by some authors (Tuckerman, 1843; Kükenthal 1909). This placement was also supported by Savile and Calder (1953) using evidence derived from the phylogeny of *Carex*-infecting smuts. Comparison of micromorphological features of the perigynium and achene epidermis of *C. exilis* with *C. echinata, C. interior, C. dioica* L. and *C. parallela* (Laest.) Sommerf. was also interpreted as providing support for the placement of *C. exilis* in the *Dioicae* (Toivonen and Timonen, 1976). However, *Carex exilis* is not normally dioecious and may be multiple-spiked. Additionally, characters of the perigynium such as shape, beak-toothing and marginal serration are those of the *Stellulatae*. Multiple-spiked individuals, save for involute leaves, very closely resemble other species of *Stellulatae* and would seem to indicate a close relationship of *C. exilis* to the *Stellulatae* rather than to the normally dioecious and exclusively single-spiked *Dioicae*. This relationship has been noted by several authors (Boott, 1858; Holm, 1901, 1903; Nelmes, 1952a). *Carex exilis* is here placed in the *Stellulatae* pending further evidence from additional characters and examination of other relevant species in the *Dioicae*. With its stiff involute leaves and usually single spikes, *C. exilis* is a plant of striking appearance and is here regarded as a specialized and somewhat isolated species within the group.

Carex sterilis differs slightly in being incompletely or even completely dioecious. In all other features it is very similar to other species of *Stellulatae*. Dioecious *Carex* are rare and most have single spikes. The only other more or less dioecious, multiple-spiked *Carex* known to the authors in North America are several species in the *Divisae* (Mackenzie, 1931; Reznicek, Catling, and McKay, 1976; Hudson, 1977). It should be noted here that most keys to *Carex* segregate the *Stellulatae* using the gynecandrous nature of the spikes, especially the terminal spike. Clearly, *C. sterilis* cannot be keyed correctly using this feature.

Carex seorsa, while of typical sex distribution and spike number, differs slightly in having a smooth perigynium beak with the widest part of the perigynium only slightly below the middle.

The remaining species of *Stellulatae* are all extremely similar in morphology. Thus, even with the rather specialized *Carex exilis*, the group is a very uniform and well defined natural taxon.

THE DELIMITATION OF SPECIES IN SECTION *STELLULATAE*

While the *Stellulatae* as a whole present extreme taxonomic difficulties, there nevertheless are some taxa that are distinctive. In dealing with the taxonomy of the group it is best to discuss these distinctive plants first and leave the problem areas for detailed discussion.

The most distinctive member of the *Stellulatae* is *Carex exilis*. It is amply distinguished from all other members by its usually single spike (Fig. 36), involute, stiff leaves, and large anthers.

Carex seorsa is also a distinctive species. It is a more or less lax plant with soft leaves contrasting with the often stiff clumps of the other species. It is unique in the *Stellulatae* in having a totally smooth-margined beak. The perigynium is also widest closer to the middle and has a more tapering base than most individuals of other species. The perigynium is not, however, widest near the middle as described by numerous authors. Figures 1 and 35 both illustrate that it is in fact usually widest somewhat below the middle. The plant also usually has a shorter beak and longer ligule than other members of the *Stellulatae*.

Carex sterilis is a most interesting species. It was the first exclusively American species to be described (Willdenow, 1805). In some recent works it is not recognized (Boivin, 1967) or only recognized at varietal level (Gleason, 1952; Gleason and Cronquist, 1963). Nevertheless, the plant is quite distinct from all other members of the *Stellulatae*. It is striking that in an overwhelming majority of cases the terminal spike is strongly unisexual, being either all pistillate with rarely 1 or 2 staminate flowers at the base or all staminate with rarely a few pistillate flowers. Virtually never does the terminal spike have the clavate base formed by staminate flowers that is so characteristic of all other members of the *Stellulatae* (Fig. 37). The lateral spikes are also strongly unisexual but

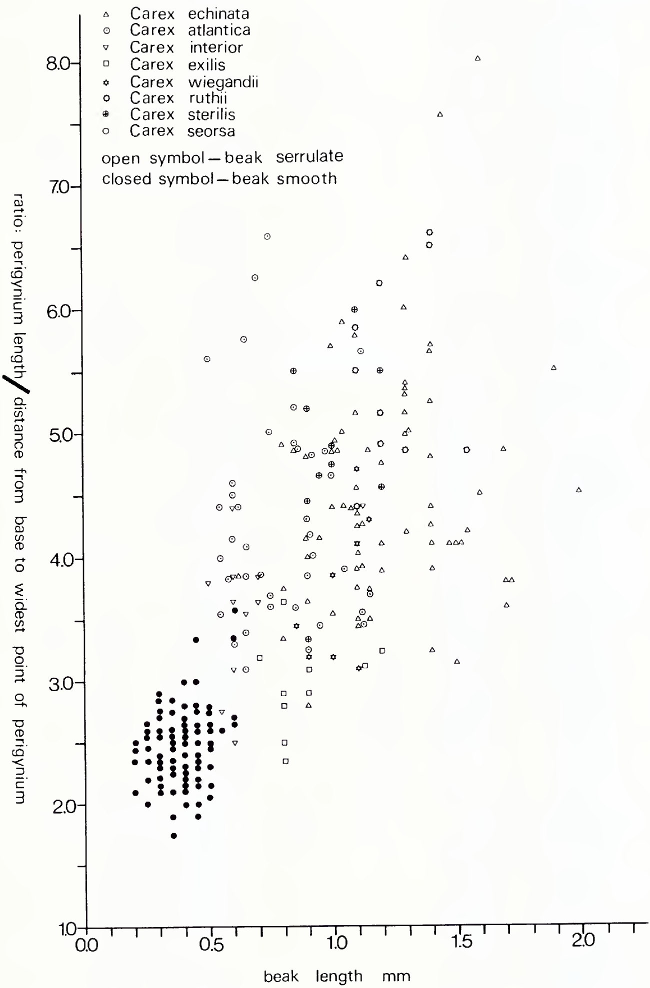


FIG. 1. Ratio of perigynium length and distance from base to widest point of perigynium plotted against beak length for *Carex echinata, C. atlantica, C. interior, C. exilis, C. wiegandii, C. ruthii, C. sterilis* and *C. seorsa.*

less so than the terminal spike. *Carex sterilis* does not have a regular arrangement of male and female flowers even on one spike and often the plants are more or less completely dioecious. Both these features, as noted before, make keying the species very difficult. Staminate specimens are particularly difficult to place if not recognized to species. A helpful clue (see key) is that they have larger anthers than most other species of *Stellulatae. Carex sterilis* also has more or less obtuse pistillate scales that are strongly castaneous with a usually broad hyaline tip and margin and usually castaneous perigynia with soft, hyaline-bordered teeth. These features also help separate it from other species in the group, which usually have lighter coloured perigynia and scales.

The remaining species are much more difficult. The correlations among characters are more obscure and the aspect of all species is quite similar. A close examination of leaf widths disclosed that the widest leaves found in the group, about 5 mm, were confined to two geographical regions and that certain morphological features were correlated with the leaf widths in each of the two areas. The two units correspond to Mackenzie's (1931) species *Carex ruthii,* confined to the southern Appalachian mountains, and *C. wiegandii,* whose range was centered about the Gulf of St. Lawrence. The two taxa are easily separated from one another by their distinctive infructescence structure (Fig. 2). *Carex ruthii* has an extremely open, elongate infructescence with considerable space between the lowest spikes (Fig. 43) whereas *C. wiegandii* has a dense, in some cases almost capitate, infructescence with even the lowest spikes closely approximate (Fig. 39). Further examination indicated that these two taxa can possess leaves as narrow as 2.8 mm in some cases, thus overlapping with *C. echinata* and *C. atlantica* which may occasionally have leaves broader than 2.8 mm (but never up to 5 mm). *Carex echinata* can easily be separated from *C. wiegandii* and *C. ruthii* by its longer, often acute pistillate scales. Both *C. ruthii* and *C. wiegandii* have shorter, more or less obtuse pistillate scales. Figure 3 shows clearly that the pistillate scale length of broad-leaved individuals of *C. echinata* is greater than that for specimens of *C. ruthii* and *C. wiegandii* with comparable leaf widths. Broad-leaved individuals of *C. atlantica* can usually be separated from *C. ruthii* and *C. wiegandii* by the extremely broad perigynia, normally 2 mm or more wide and 1.1 to 1.6 times as long as wide as shown in Fig. 4. In the rare case of overlap of features, the distinctive infructescence and restricted distribution of *C. ruthii* and *C. wiegandii* help to distinguish them.

Carex echinata and *C. atlantica* are, for convenience, treated as part of the narrow-leaved segment of the *Stellulatae* though they may sometimes have leaves greater than 2.8 mm wide. This group is by far the most variable and difficult.

Throughout the midwestern states and the southern Canadian prairie provinces there occurs only one species of *Stellulatae.* This is the common plant with diminutive spikes of small, short-beaked perigynia appropriately described by Bailey (1893) as *Carex interior.* This plant is remarkably uniform throughout its extensive range, which proved to include all provinces and territories of Canada, most of the northern and western United States, and Mexico south to the vicinity of Mexico City. *Carex interior* can sometimes be difficult to separate from related species where they are sympatric. However, from *C. echinata* it is relatively easily distinguished by beak length (Fig. 5). In the rare case of ambiguity, other less reliable features must be used, for example, the perigynium beak/body ratio, perigynium length/width ratio, venation of the perigynia, and the nature of the pistillate scales as outlined in the key and descriptions. *Carex interior* is much more difficult to separate from small plants of *C. atlantica.* The perigynia of *C. interior* have a distinctive shape. The sides are nearly straight to slightly convex and, in the taper to the beak, there is mostly a "shoulder" or second inflection point before a final concave taper. This "shoulder" is well illustrated by Boott (1858, *sub C. stellulata* var. *scirpoides*) who obviously clearly understood this plant. Nevertheless, it is a subtle distinction and easily missed if one is not familiar with this character. In addition, the perigynia of *C. interior* are usually nerveless on the adaxial surface whereas those of

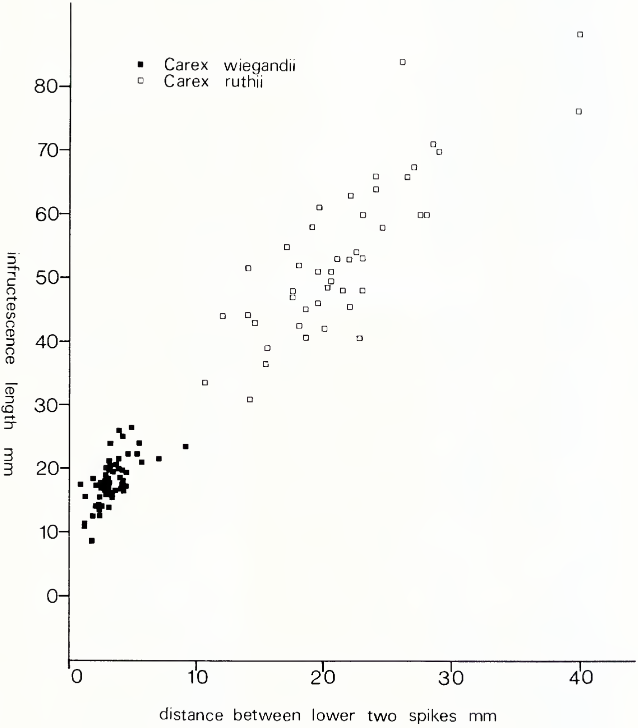


FIG. 2. Scatter plot of infructescence length and distance between the lower two spikes for *Carex ruthii* and *C. wiegandii.*

C. atlantica are usually nerved. *Carex interior* also usually has brownish or somewhat castaneous perigynia when mature while those of *C. atlantica* are usually greenish except when overripe. As well, on the beak and up to 1.0 mm below, the margins of the perigynia of *C. interior* are usually densely serrulate and often more or less setulose. The marginal teeth of *C. atlantica* are more sparse, arising singly and often with discernible space between the teeth. The perigynia of *C. interior* are 1.4–2.0 (2.2) times as long as wide and those of *C. atlantica* are 1.1–1.7 (1.9) times as long as wide. Although there is great overlap, this feature is helpful in separating specimens that may be ambiguous for some other features. Some of these features are illustrated in Fig. 6, which shows both the difficulty of separating the two species and that two groups are indeed present.

Including *Carex echinata* and *C. atlantica,* not yet discussed except as they related to species already mentioned, 11 species recognized by Mackenzie (1931) still remain to be dealt with. These are *C. atlantica, C. echinata* (*C. muricata* auct. *non* L.), *C. mohriana, C. howei, C. incomperta, C. laricina, C. cephalantha, C. phyllomanica, C. ormantha, C. angustior,* and *C. townsendii.* When specimens representing this group of names were carefully analyzed, it was found that they fell into two clear-cut groups based on perigynium length/width ratios, beak length, perigynium colour, beak/body ratios, geographic distribution, and other features. The perigynium length/width ratio and beak length for the two groups are illustrated in Fig. 7. The group with longer, narrower perigynia with length/width ratios ranging from 1.75–3.6 and beak lengths from 0.85–2.05 mm includes *C. echinata, C. laricina, C. phyllomanica, C. ormantha, C. angustior, C. cephalantha,* and *C. townsendii.* The group with broader perigynia 1.1 to 1.9 times as long as wide and beaks 0.45 to 1.25 mm long includes *C. atlantica,*

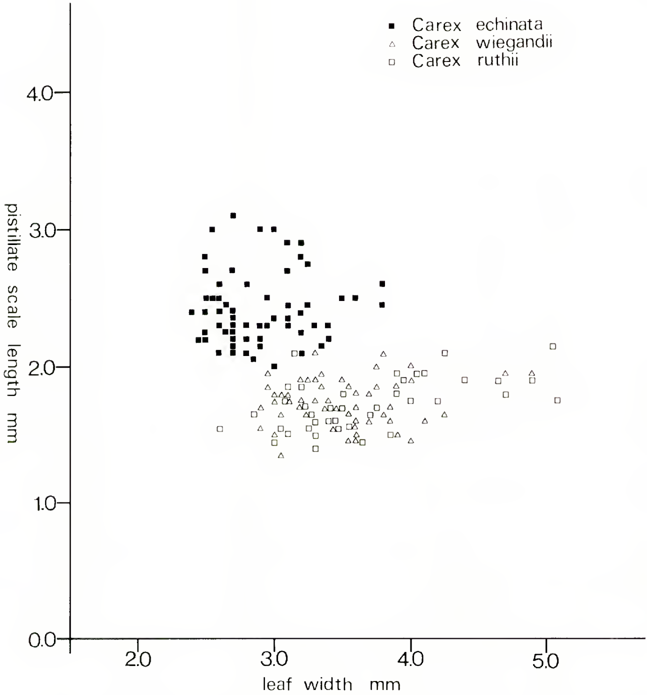


FIG. 3. Scatter plot of pistillate scale length and maximum leaf width for *Carex ruthii, C. wiegandii* and broad-leaved individuals of *C. echinata.*

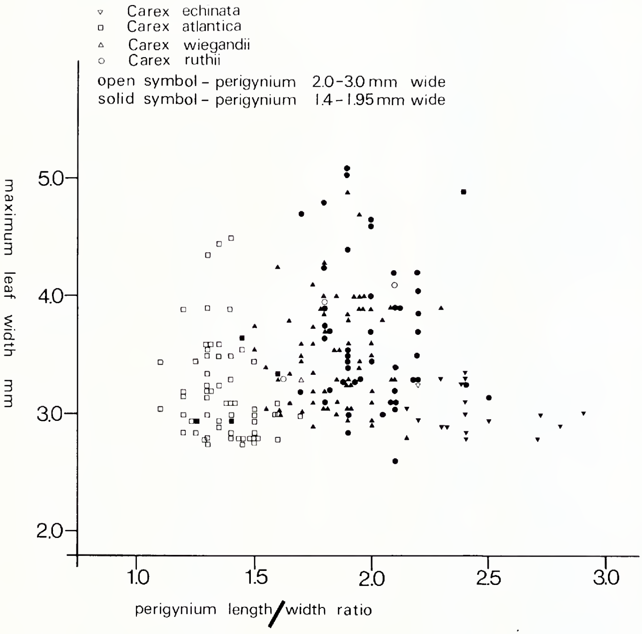


FIG 4. Perigynium length/width ratio plotted against maximum leaf width for *Carex ruthii, C. wiegandii* and broad-leaved individuals of *C. echinata* and *C. atlantica.*

C. mohrina, C. incomperta, and *C. howei.* Only the names *C. echinata* and *C. atlantica* appear on Fig. 7 and it will be convenient to refer to the *C. atlantica* complex and the *C. echinata* complex containing respectively the names associated in the two groups listed above.

The *Carex atlantica* Complex

The four taxa in the *Carex atlantica* complex, *C. atlantica, C. incomperta, C. howei,* and *C. mohriana,* were separated on the basis of perigynium size, infructescence length, leaf width, pistillate scale length and acuteness, and geographical distribution among other features. In Mackenzie's (1931) monograph, they fell into two groups. *C. howei* and *C. mohriana* were separated from *C. atlantica* and *C. incomperta* by the key couplet "perigynia small, 2.25–3.25 mm long, the beak very shallowly bidentate one fourth to one third length of the body; scales half to two thirds length of bodies of perigynia" for *C. howei* and *C. mohriana* versus "perigynia 2.75–4.75 mm long, with beak sharply bidentate and ventral false suture conspicuous" for *C. atlantica* and *C. incomperta.* Fig. 8 shows a frequency diagram of perigynium length for the complex. It is evident that perigynium length is a unimodal curve with the mean of this sample being 2.75 mm. Careful examination of perigynium beak teeth indicated that in the *C. atlantica* complex, the length of the teeth is closely correlated with beak length and both correlate closely with perigynium size and follow the same pattern as shown in Fig. 8.

Carex mohriana was separated from *C. howei* by the couplet "spikes strongly separate; leaf-blades 0.25–1 mm wide" for *C. howei* and "spikes aggregated in a dense head; leaf-blades 1–2.5 mm wide" for *C. mohriana*. Examination of a wide selection of material showed that plants with densely aggregated spikes are of sporadic occurrence throughout the range of the *C. atlantica* complex and also occur through the entire range of leaf widths shown by the complex. Mackenzie (1931) considered the plant a central Florida endemic. Close inspection has not revealed any further diagnostic features. Isotypes of *C. mohriana* have some culms with elongate heads typical of the *C. atlantica* complex as a whole mixed with culms with dense heads. This segregate is a slight variant not worthy of recognition.

The separation of *Carex incomperta* and *C. atlantica* has been discussed by Hermann (1965). He summarized key characters from various treatments, concluded that the two taxa were conspecific, and reduced *C. incomperta* to varietal status as *C. atlantica* var. *incomperta* (Bicknell) Hermann. Further to this end, a comparison has been made of two of the major key differences noted by Hermann (1965), the proportionate lengths of pistillate scale and perigynium body and the leaf width. *Carex incomperta* is described as having the pistillate scales two-thirds to fully as long as the body of the perigynium and leaves 1.5 to 2.5 mm wide and *C. atlantica* as having the pistillate scales half to two-thirds the length of the body and leaves 1.5 to 4.0 mm wide. Figure 9 clearly shows that the variation in leaf width is hardly correlated with that of the pistillate scale length/perigynium body length proportion. Two groups cannot be sorted out here. As all other characters examined followed the same pattern, it would

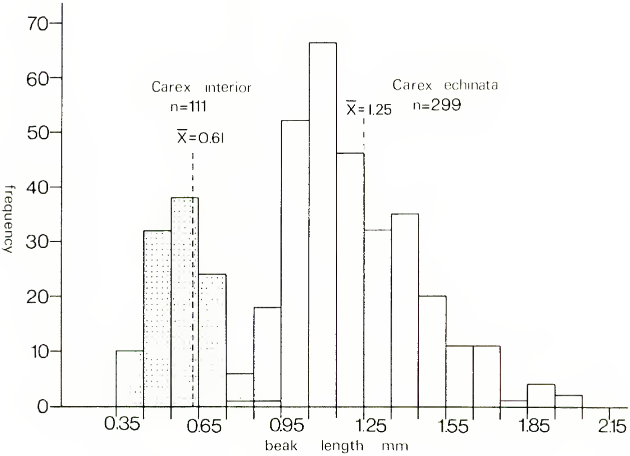


FIG. 5. Frequency diagram of beak length for *Carex interior* and *C. echinata*.

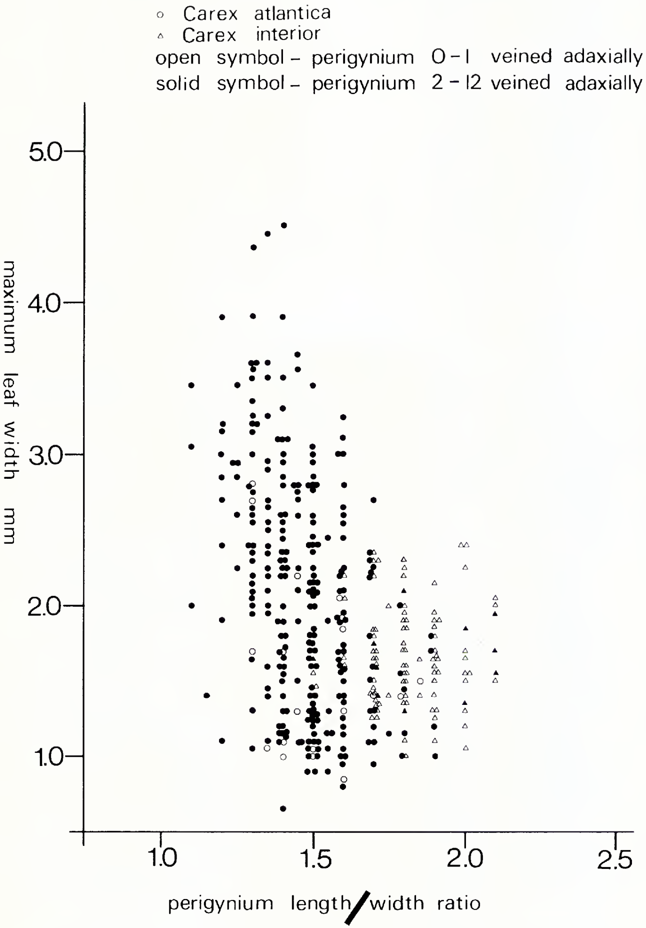


FIG. 6. Scatter plot of perigynium length/width ratio and maximum leaf width for *Carex atlantica* and *C. interior*. Disposition of specimens as *C. atlantica* or *C. interior* based on other features as noted in text.

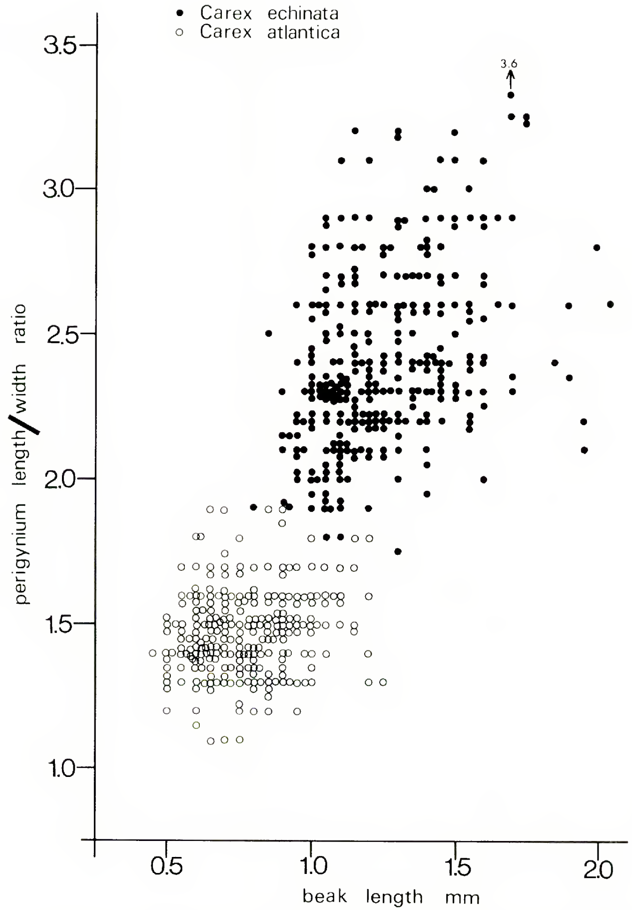


FIG. 7. Beak length plotted against perigynium length/width ratio for *Carex echinata* and *C. atlantica.*

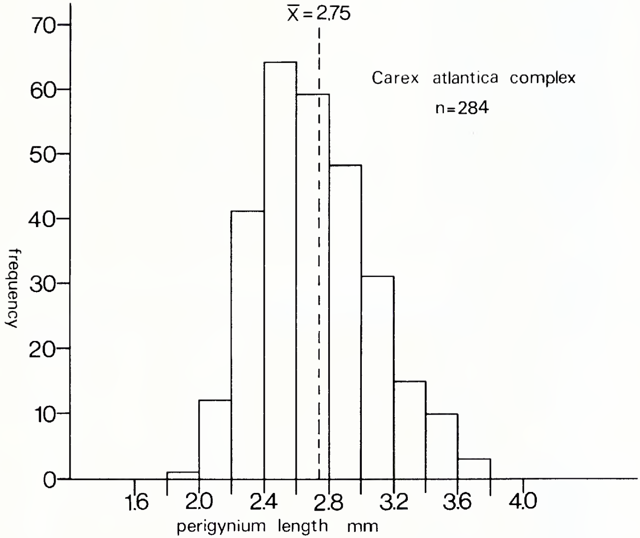


FIG. 8. Frequency diagram of perigynium length for *Carex atlantica.*

seem that *C. atlantica* and *C. incomperta* are certainly conspecific as shown by Hermann (1965) and, more than that, not even different at varietal level.

One of the most interesting aspects of this study was the investigation of the relationships of *Carex howei.* From the time the taxon was first described by L. H. Bailey (1893), as *C. interior* var. *capillacea,* to the present, all authors in their keys, descriptions, and discussions have associated this species with *C. interior.* No mention was ever made of precisely how the plant was to be separated from *C. incomperta* and *C. atlantica* except for the standard key characters noted before. We discovered that not only is the true relationship of *C. howei* with *C. atlantica* and its relatives, but in fact it is conspecific with them and not closely related to *C. interior* at all. The differences between *C. interior* and the *C. atlantica* complex have been discussed already. Plants fitting the description of *C. howei* have usually green perigynia 1.1 to 1.7 (–1.9) times as long as wide, veined on the adaxial surface with margins of beak and upper portion of body sparsely serrulate and no "shoulder" as described for *C. interior.* This is clearly in line with plants described as *C. atlantica* and *C. incomperta.* Figure 6 shows leaf width plotted against perigynium length/width ratio for *C. interior* and the *C. atlantica* complex. Narrow-leaved (less than 1.6 mm wide) plants of the *C. atlantica* complex fit the description of *C. howei.* One can see here that they generally fit into the pattern of variation shown by the rest of the *C. atlantica* complex rather than fitting with the "bulge" shown by *C. interior. Carex howei* clearly represents the smallest variants of the *C. atlantica* complex and is not related to *C. interior.* Figure 10, perigynium length plotted against perigynium width, was coded for leaf widths that correspond to the description of the three taxa. The maximum leaf width given in keys for *C. howei* was 1.0 mm (Fernald, 1950; Gleason and Cronquist, 1963; Voss, 1972) and the range for *C. incomperta* 1.5 to 2.5 mm and for *C. atlantica* 1.5 to 4.0 mm (Mackenzie, 1931; Hermann, 1965). However, there are quite a number of plants of the *C. atlantica* complex with maximum leaf widths between 1.0 and 1.5 mm. Thus, the limits used on the graph were adjusted according to measurements of herbarium specimens determined by Mackenzie. Plants named *C. howei* often had leaves to 1.6 mm wide for even slightly wider in rare instances as pointed out by Voss (1972). The two larger groups, representing *C. atlantica* and *C. incomperta,* also had their limits adjusted according to measurements of herbarium specimens as above. It can be seen here that rather than the presence of two or three taxa, the graph again shows a uniform pattern of variation for the entire

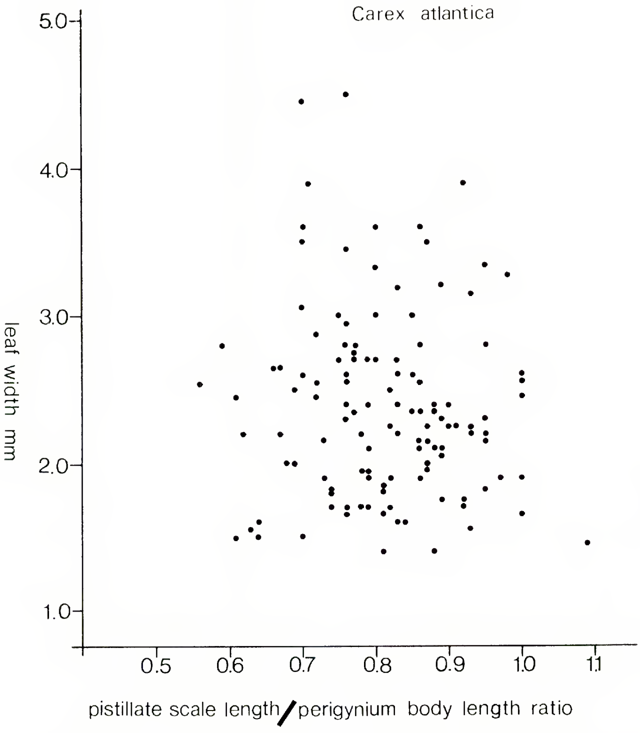


FIG. 9. Maximum leaf width plotted against ratio of pistillate scale length and perigynium body length for *Carex atlantica.*

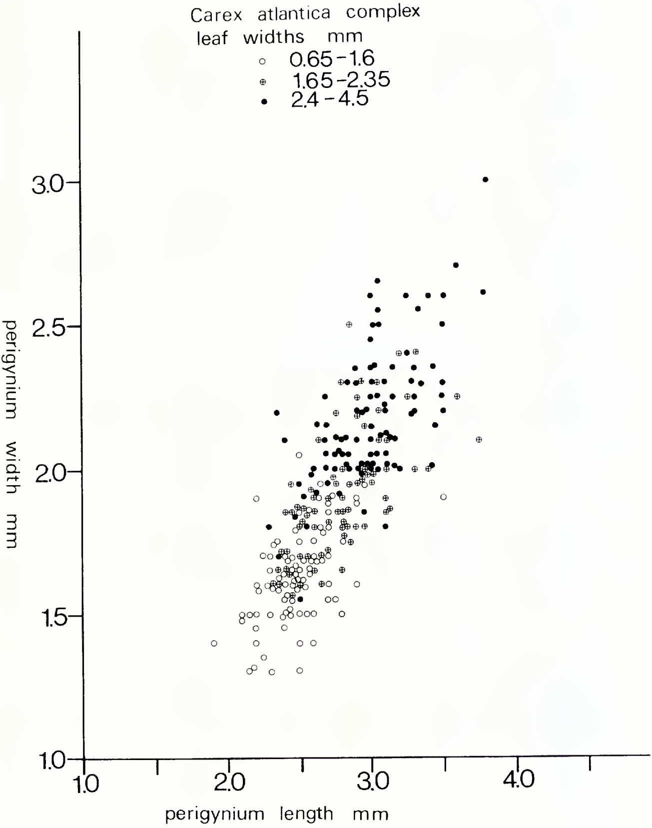


FIG. 10. Scatter plot of perigynium length and perigynium width for *Carex atlantica.*

C. atlantica complex and, obviously, that smaller plants have smaller perigynia but of the same shape. Again on this graph, as noted on Fig. 6, plants answering the description of *C. howei* are at the smallest end of the uniform variation spectrum shown by the *C. atlantica* complex just as plants called *C. atlantica* form the large end and *C. incomperta* the middle. However, no discontinuities are detectable. The unimodal nature of the distribution of perigynium lengths has already been demonstrated (Fig. 8). Figure 6 also clearly shows that there are many plants with leaves 1.0 to 1.5 mm wide, as pointed out previously.

However, the situation is not as simple as presented thus far. Although there is a lack of discontinuities in the *Carex atlantica* complex, characters show a definite segregation on a geographical basis. This is especially true for leaf width. Figure 11 demonstrates this differing abundance graphically for two areas, Nova Scotia and Georgia. In Nova Scotia, plants with widest leaves 1.5 mm to 1.9 mm are quite rare and a definite discontinuity of variation exists, whereas in Georgia a unimodal curve is indicated.

The taxonomic disposition of this kind of variable complex is always exceedingly unsatisfactory. This is especially so here since taxonomists working in local areas, for example Nova Scotia, will find "distinct" taxa because the total range of variability of the complex is not expressed throughout its entire range. Thus, a revision of the taxonomy based on specimens from a local area may well give different results from one including the entire range of the complex.

From the discussion above, it is evident that there is only one taxon at the species level in the *Carex atlantica* complex. Although the complex patterns of variation within that species are describable, they are very difficult to fit into the standard taxonomic hierachy. It is felt that intergradation between plants fitting the description of *C. incomperta* and *C. atlantica* is so complete over such a large area that recognition of two taxa, even at varietal level as proposed by Hermann (1965), is not feasible. Because the fine-leaved plants, fitting the description of *C. howei,* form recognizable populations with a distinctive distribution (Fig. 22) that may grow with broad-leaved plants without intergradation, they are here recognized at subspecific level as *C. atlantica* subsp. *capillacea.*

The *Carex echinata* Complex

Seven species were recognized by Mackenzie (1931) in the *Carex echinata* complex: *C. echinata* (*C. muricata auct. non* L.), *C. ormantha, C. phyllomanica, C. townsendii, C. angustior, C. laricina,* and *C. cephalantha. Carex townsendii* was described from Chihuahua, Mexico, but so few Mexican specimens of this complex have been examined that no further treatment is here possible.

The *Carex echinata* complex is widely distributed both on the eastern and western sides of the continent. In the east, the group has a more or less continuous range from Newfoundland and Labrador to western Ontario south to New Jersey, Iowa, and in the Appalachian mountains to southern North Carolina. In the west, the complex occurs on mountain chains and along the coast from Alaska to southern California and Colorado and again in Mexico. Specimens from the interior boreal region are extremely few. Of the species recognized by Mackenzie (1931) only two, *C. phyllomanica* and *C. ormantha,* were considered exclusively western North American and one, *C. laricina,* exclusively eastern North American. *Carex cephalantha, C. angustior,* and *C. echinata* were considered to occur on both sides of the continent. *Carex laricina* has, however, been united by recent authors with *C. cephalantha* (Fernald, 1950; Voss, 1972). Furthermore, the original description of *C. ormantha,* as *C. echinata* var. *ormantha* Fernald (1902), included Rhode Island and Connecticut plants. This leaves only *C. phyllomanica* considered as exclusively western by all authors.

Mackenzie's major division of these seven species was based on the nature of the pistillate scales. *Carex echinata, C. ormantha,* and *C. phyllomanica* were considered to have "obtuse or obtusish" scales, chestnut brown with bright white margins, not sharply keeled and with the midvein obscure at the apex. *Carex angustior, C. cephalantha,* and *C. laricina* were described as having pistillate scales "obtusish to cuspidate," yellowish brown with a narrow, opaque or dull white margin and a midvein prominent to the apex. When the pistillate scales were closely examined, they were found to be tremendously

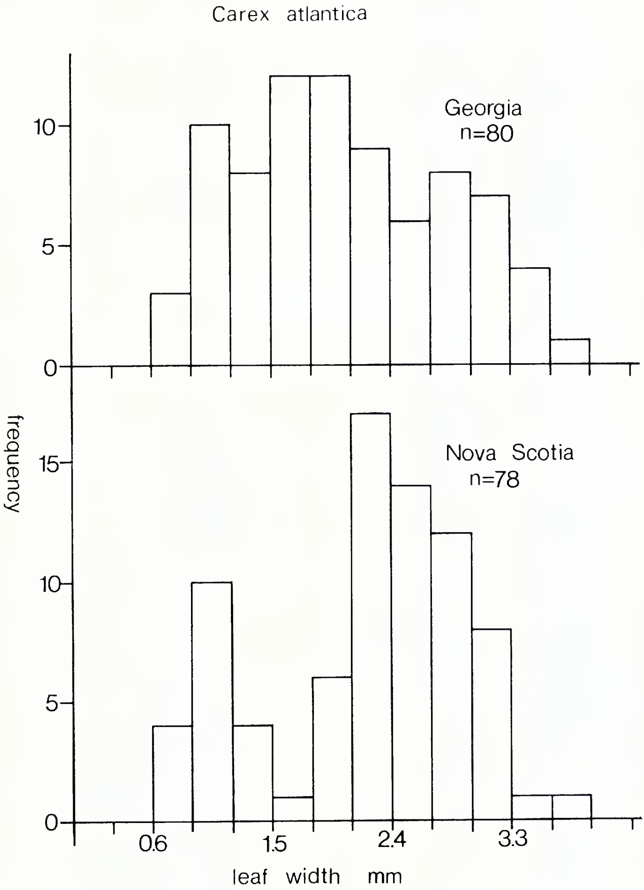


FIG. 11. Frequency diagrams of maximum leaf width for all specimens examined of *Carex atlantica* from Georgia (above) and Nova Scotia (below).

variable, both on the same spike and between plants. The variability on a single spike paralleled that of the perigynia as discussed earlier and variability between plants ranged more widely, even with plants of similar appearance. A brief survey of plants named *C. ormantha, C. phyllomanica,* and *C. echinata* by Mackenzie revealed that, of 23 examined, 7 had primarily obtuse or "obtusish" scales and 16 had mostly acute scales. In the same manner, an examination of 26 plants of *C. angustior, C. cephalantha,* and *C. laricina* disclosed 23 with acute scales and 3 with obtuse or "obtusish" scales. Variability of even greater magnitude crossing Mackenzie's specific boundaries was observed in the venation and bordering of scales.

Carex echinata was separated from *C. ormantha* and *C. phyllomanica* by its ovate perigynium and nerveless adaxial surface as contrasted with a many-nerved adaxial surface and "narrower" perigynia. When actual measurements and observations were made, the circumstances under which this separation was derived became puzzling for, of 74 specimens named *C. ormantha* and *C. phyllomanica,* including a considerable proportion named by Mackenzie himself, 20 were nerveless or with one faint nerve and 54 were 2–11-nerved. In addition, the perigynium length/width ratio ranged from 1.95 to 3.2 (3.6) times as long as wide. These values entirely encompassed those obtained for "authentic" *C. echinata.* The problems do not end here for, in distinguishing *C. ormantha* and *C. phyllomanica,* Mackenzie (1931) relied on the separation of the spikes in the infructescence and perigynium length. *Carex ormantha* was described as having a very open infructescence and perigynia 3.5 to 4.0 mm long and *C. phyllomanica* a very dense infructescence and perigynia 3.75 to 4.5 mm long. The best way found to express the nature of the differences was to use the ratio of culm length/infructescence length. Figure 12 shows how the two classes of plants segregate with regard to these two characters. It can be readily seen that the separation is anything but clear-cut. Perigynium length and infructescence density do not correlate well at all. Although the dense-headed plants are primarily coastal, the separation of the two taxa on these characters at specific level is not feasible. As well, western plants fitting the descriptions of *C. cephalantha, C. echinata,* and *C. angustior* were excluded from the graph. They are somewhat intermediate between *C. phyllomanica* and *C. ormantha* for these characters.

A close examination of *Carex angustior, C. laricina,* and *C. cephalantha* is also in order. *Carex angustior* was considered to have very narrow, lanceolate perigynia nerveless on the adaxial surface with a beak equalling or exceeding the length of the body and the achene much longer than wide. Both *C. laricina* and *C. cephalantha* were described as having perigynia ovate, the beak much shorter than the body, the achenes about as wide as long, and perigynia nerved on the adaxial surface. Figure 13 shows the pattern of beak length/body length ratio, number of nerves on the adaxial surface, and perigynium length/width ratio for the *C. echinata* complex. In this revealing figure, it can be seen that perigynium beak/body ratio, perigynium length/width ratio, and the number of nerves on the adaxial surface of the perigynium are only loosely correlated. Certainly, no discontinuous clusters of variation are evident. In addition, variation in these characters in the east of North America is nearly paralleled by that in the west. At the very least, if there are separate species in the complex, they cannot be distinguished using these features. However, it is notable that the plants with the narrowest perigynia were both invariably nerveless and from the east. The achene length/width ratio could not be placed on Fig. 13 without confusion but it shows parallel variation to the perigynium length/width ratio in the *C. echinata* complex. *Carex angustior* was also characterized as being a delicate plant with narrow leaves and a dense infructescence (Mackenzie, 1931) but these characters also show great variability.

Carex cephalantha and *C. laricina* have been united by a number of authors (Fernald, 1950; Voss, 1972). Mackenzie (1931) separated the two mainly on the basis of perigynium length. *Carex laricina* he indicated had perigynia 2.75 mm to 3.5 mm long and *C. cephalantha* 3.5 mm to 4.0 mm long. Hermann (1941), adjusted the range of

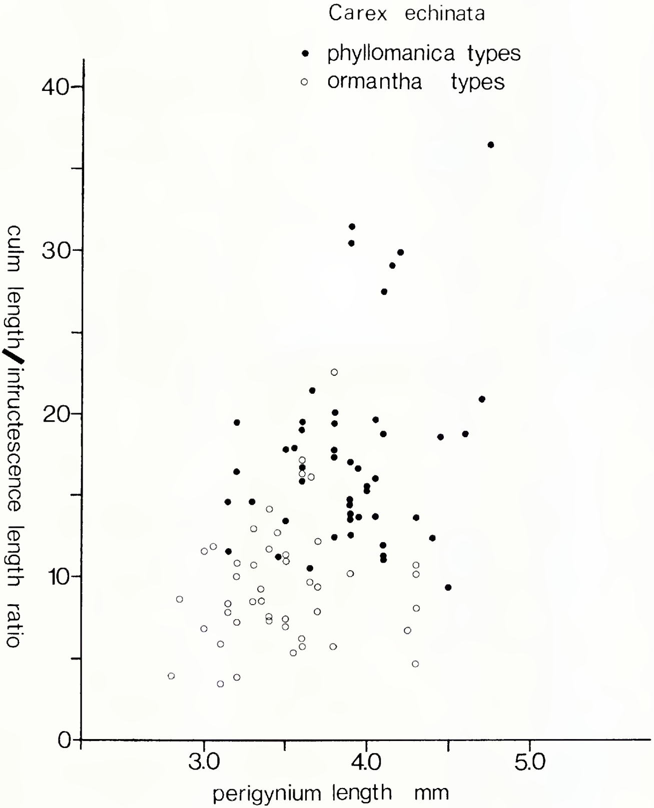


FIG. 12. Scatter plot of perigynium length and ratio of culm length to infructescence length for *Carex echinata* subsp. *phyllomanica* and "*ormantha* types."

C. laricina to 2.75 mm to 3.3 mm. Thus, it would seem that a frequency diagram of a wide selection of specimens of these plants should show few plants with perigynia 3.3 mm to 3.5 mm long. However, when such measurements are made on a large sample (Fig. 14) this is not the case. In fact, the sample formed a unimodal curve with a mean of 3.33 mm. The decisions of Fernald (1950) and Voss (1972) not to recognize *C. laricina* as distinct were clearly correct.

The problems are yet more involved, as up to now the two groups based on pistillate scale characters have been mostly discussed separately. As shown earlier, the features do not work reliably and, therefore, a cross-comparison of some of the species recognized by Mackenzie is in order. *Carex echinata* and *C. angustior* are both said to be nerveless on the adaxial surface but *C. echinata* should have ovate perigynia with short beak and *C. angustior* lanceolate perigynia with long beak. Figure 13, discussed earlier, shows that

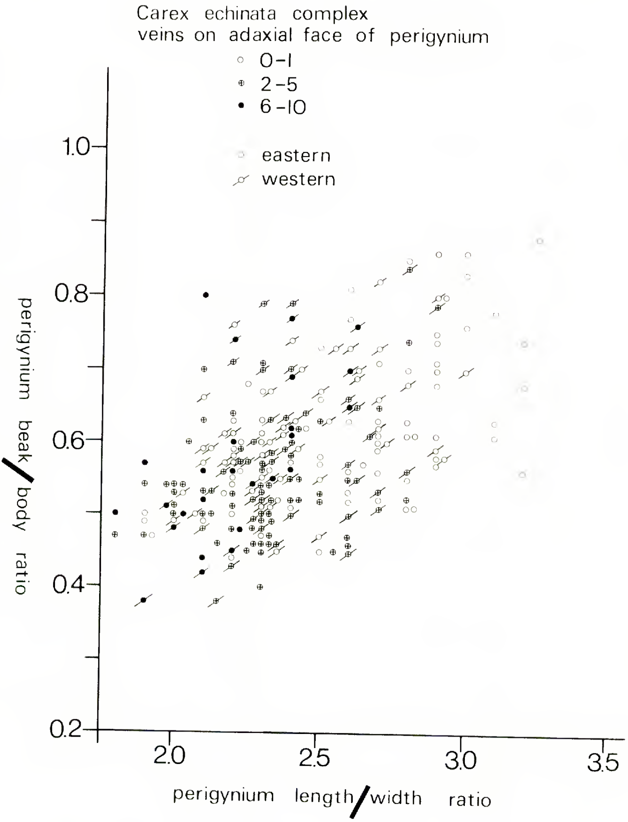


FIG. 13. Scatter plot of perigynium length/width ratio and perigynium beak length/perigynium body length ratio for *Carex echinata*.

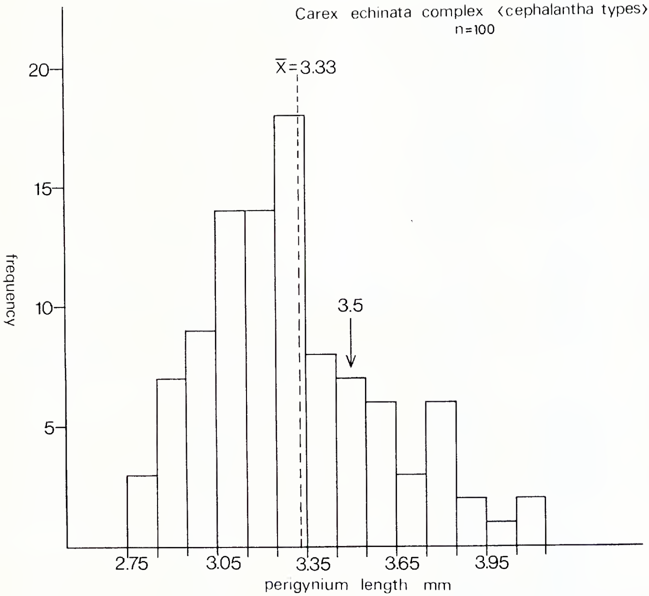


FIG. 14. Frequency diagram of perigynium length for *Carex echinata "cephalantha* types."

nerveless perigynia occur over a wide range of perigynium length/width ratios and perigynium beak/body ratios. No discontinuities were evident.

The variability of plants in western North America is such that Mackenzie (1931) had to recognize *Carex cephalantha* in collections of western plants and indeed, plants fitting this description do occur frequently in some parts of the west coast. Also, as noted earlier, plants with the very loose infructescences and long clavate terminal spikes characteristic of *C. ormantha,* as circumscribed by Mackenzie (1922, 1931), occur in the east (Fernald, 1902). Mackenzie separated the western and eastern plants by the nature of the pistillate scales but the unreliability of this feature has already been noted.

As in the *Carex atlantica* complex, the demonstration of discontinuities at the specific level has not been possible. Again, like the *C. atlantica* complex, the situation is more difficult than merely reducing the entire complex to one undivided species. A close examination of the complex throughout its range revealed a great deal of geographically correlated variation, thought not always in characters used by Mackenzie (1931). Western plants, regardless of their perigynium shape and inflorescence form, tend to be broader leaved. There is much overlap and, in essence, only the coastal plants that have been called *C. phyllomanica* have consistently much broader leaves than the extremes of the east. These coastal plants form a striking variant in the extreme but they do intergrade with *C. echinata* in the west and, rarely, plants similar in form will be found in other parts of the species range. These coastal plants, with usually large perigynia, dense heads and broad leaves are here recognized as a well marked subspecies, *C. echinata* subsp. *phyllomanica.*

In New England and to a lesser extent in adjacent areas and the northern Great Lakes region, there occurs a somewhat higher proportion of narrow-leaved plants than in other areas. Exact proportions of western plants are: leaves less than 1.6 mm wide 4%, 1.6 to 2.55 mm wide 68%, and leaves greater than 2.55 mm wide 28%. Respective figures for all eastern plants are 34%, 56% and 10% and for New England only 65%, 23%, 12%. It is notable also that, as in the *Carex atlantica* complex and the western plants of the *C. echinata* complex, the widest-leaved plants in the east tend to be found near the coast. There is no doubt that all species of *Stellulatae* except *C. interior, C. sterilis,* and *C. ruthii* reach their greatest abundance and largest size in coastal regions. The eastern plants with narrow leaves are interesting. The narrowest-leaved extremes are often plants with extremely narrow perigynia, *ca.* 3 times as long as wide, and essentially nerveless on the adaxial surface. These plants correspond to the extreme of Fig. 13 with very narrow, nerveless perigynia. They have been called *C. angustior* Mackenzie. Mackenzie considered *C. angustior* to be a smaller plant with a denser infructescence than other species he recognized in the *C. echinata* complex, but these characters do not correlate well. This lack of correlation was responsible, in fact, for the description of *C. angustior* var. *gracilenta* (Clausen and Wahl, 1939) as that name refers to plants with elongate infructescences but narrow perigynia. Figure 13 also shows that these plants merely form a rare extreme of *C. echinata* with otherwise no significant trends present in the characters presented.

When the situation is examined in more detail, further resolution becomes difficult. Figure 15 shows the relationship of perigynium length/width ratio for samples from various portions of the range of *Carex echinata.* Figure 15A shows eastern *C. echinata* from the area where the plants with narrow perigynia tend to occur most frequently. It can be seen that the pattern is the same as in Fig. 13 with the plants with the narrowest perigynia being rare extremes. The length/width ratio is variable but no bimodality is evident. Figure 15B shows western North American plants referred by authors to *C. angustior, C. cephalantha,* and *C. echinata.* No extremes with very narrow perigynia are present in the sample examined. In Europe, perigynia ranged to approximately 2.8 times as long as wide in the limited sample examined. However, *C. angustior* has been reported for Asiatic U.S.S.R. (Egorova, 1960). The distribution of perigynium length/width ratio for the entire *C. echinata* complex in North America is shown in Fig. 15C. It can be seen that the pattern has changed little from Fig. 15A. The distribution is more or less skewed but with no clear-cut bimodality.

The feature of perigynium length/width ratio is one not equally expressed in all parts of the species' vast range. However, the extremes noted, although they mostly occur in northeastern North America, intergrade so completely that they cannot here be given formal taxonomic recognition. They are certainly not compatible with the morphogeographical subspecies recognized in this work. If it is desired to draw attention to this variant, the name *Carex echinata* Murray var. *angustata* (Carey) L. H. Bailey is available.

When western North American plants referred by Mackenzie and others to *Carex ormantha* were examined in detail, it was found that a higher proportion of plants with loose, long infructescences occurred in the Sierra Nevada of California than in other areas. However, as noted earlier, plants of the *C. echinata* complex with loose infructescences also occur in the east. No other characters were seen that correlated closely with the infructescence type. Like perigynium length/width ratio and leaf width, infructescence density is a feature whose expression is not equal throughout the range of the species. The lack of correlation of other features with infructescence type in plants with a lax infructescence and the lack of a precise geographical segregation of this variant make recognition of these plants as a separate taxon impossible. Again, if it

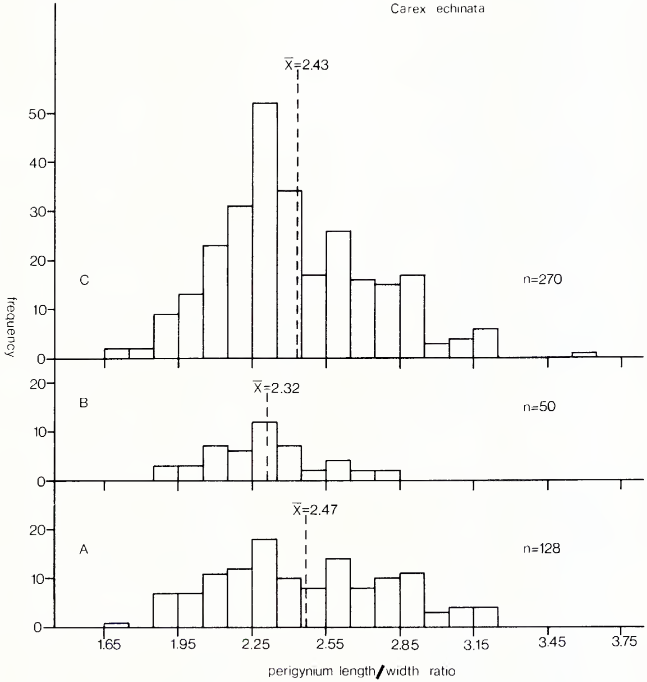


FIG. 15. Frequency diagram of perigynium length/width ratio for *Carex echinata* subsp. *echinata*, (A) selected specimens from Maine, Vermont, New Hampshire, Nova Scotia, Newfoundland, Quebec, New Brunswick, northern and central Ontario, northern New York, upper peninsula of Michigan, northern Wisconsin and northern Minnesota, (B) selected specimens from western North America, (C) selected specimens from throughout the North American range of the species.

is desired to draw attention to this variant, the name *C. echinata* Murray var. *ormantha* Fernald is available.

The Identity of North American and European *Carex echinata*

The relationship of North American plants to European plants has been often disputed. Most authors have been forced to admit this European species to the North American flora although its occurrence is often relegated to a restricted area. Mackenzie (1931) recognized it from only two areas of North America: in the east from Labrador, Newfoundland, and the Mingan Islands, Quebec, and in the west from Alberta and Alaska. However, Alberta specimens named *C. echinata* by Mackenzie are *C. interior.*

A summary of distinctions from all other North American species of the *Carex echinata* complex recognized by Mackenzie (1931) indicated *C. echinata sensu stricto* as having ovate, short-beaked perigynia, nerveless on the adaxial surface with obtuse or obtusish pistillate scales. In his description, Mackenzie notes the perigynia as being 2.5 to 3.0 mm long and 1.2 to 1.8 mm wide. His description also calls for a plant 15 to 35 cm high with 2 to 3 spikes and leaves 1.0 to 2.0 mm wide (Table 1).

When a selection of 56 specimens representing a wide geographical range from Spain and the Azores to Scandinavia and Russia was examined for these and other features, the results were quite interesting. The absolute range of perigynium length was 2.65 to 4.3 mm and the mean of the sample was 3.42 mm. This mean is well beyond the maximum size given for *Carex echinata* perigynia by Mackenzie (1931). Perigynium width ranged from 1.2 to 2.05 mm. The length/width ratio ranged from 1.75 to 2.8. The number of spikes ranged up to 5 and leaf width up to 2.8 mm even in the limited sample examined. Plants examined ranged to over 40 cm tall and, although no fully elongated fruiting specimens were seen, some had broken culms of the previous year that indicated that they were quite tall when fully grown. Division of the lower pistillate scales into acute and obtuse classes disclosed that, of 55 specimens, 34 had acute and 21 obtuse scales. The pistillate scale apex is also described and pictured as acute in Jermy and Tutin (1968). Accurate comparison with Mackenzie's description is made rather difficult by his use of the term "obtusish."

Table 1: Comparison of measurements from 56 European *Carex echinata* with values given for North American *C. echinata* by Mackenzie (1931) for specific characters.

Character	Mackenzie (1931)	European *C. echinata*	
Culm length	15–35 cm	10–42 cm	(maximum value not observed)
Widest leaf	2.0 mm	2.8 mm	
No. spikes	2–3	2–5	
Perigynium length	2.5–3.0 mm	2.65–4.3 mm	
Perigynium width	1.2–1.8 mm	1.2–2.05 mm	

Plants with perigynia both nerved and not nerved on the adaxial surface are found in Europe. From a sample of 56 plants, 21 had 2–6 veins on the adaxial surface and 35 had 1 vein or none. As well, there is great variability in beak length and the portion of the body below the beak that is serrulate-margined. Infructescence density is also quite variable. In Europe as in North America, it may range from loose with widely spaced spikes to dense infructescences reminiscent of *C. echinata* subsp. *phyllomanica* of the west coast of North America. *Carex echinata* in Europe is quite variable, just as it is in North America.

It is evident from the previous discussion that if Mackenzie's (1931) delimitations of species are used objectively on European specimens, then surely almost all North American taxa of the *Carex echinata* complex recognized by Mackenzie would also have to be recognized in Europe. Mackenzie's description of *C. echinata* does not fit the common "Star Sedge" of Europe. Even on the basis of the limited sample of European *C. echinata* examined, the plant is much more variable than allowed by Mackenzie for North American *C. echinata*. Mackenzie's delimitation of the species was much too narrow. It is likely that Mackenzie felt that the European species should occur in North America only at high latitudes and altitudes and in subarctic habitats. The opinion that only arctic and subarctic species were likely to be common to Europe and North America was also held by Bailey (1893). Mackenzie may well have based his description and delimitation of the species on these dwarfed plants, without taking into account the variation found in Europe. The recognition of different species in North America has been shown to be untenable. Also, although there is little doubt that the species is more variable in North America, much of the variability shown by North American plants can be found in European plants, as pointed out long ago by Fernald (1902).

Löve (1954a, b) has argued that the European *Carex echinata, C. cephalantha,* and *C. angustior* are distinct species because they differ in chromosome number. The European plants are reported to have a chromosome number of $2n = 58$ whereas *C. angustior* and *C. cephalantha* have had counts noted of $2n = 50$ and $2n = 52$ respectively. No morphological discussion in support of this was presented. The blanket statement that they must be different species if their chromosome numbers (here determined on a very limited sample) are different is unacceptable in *Carex*. The various problems hampering the free use of chromosome data in *Carex* have been discussed previously (Moore and Calder, 1964; Faulkner, 1972; Reznicek, 1978).

Carex echinata of Europe and Asia and the *C. echinata* complex in North America are here viewed as a single, variable species. This places it with other variable circumboreal species such as *C. curta* Good., (*C. canescens auct. non* L.), *C. diandra* Shrank, *C. brunnescens* (Pers.) Poir., *C. aquatilis* Wahl., *C. magellanica* Lam., *C. livida* (Wahl.,) Willd., *C. vaginata* Tausch, *C. capillaris* L., and *C. rostrata* Stokes. Some of these species, such as *C. curta, C. diandra,* and *C. magellanica,* are also, like *C. echinata,* found in the temperate parts of the southern hemisphere.

Comments on Taxonomic difficulties in the *Stellulatae*

Both in the *Carex atlantica* complex and the *C. echinata* complex other characters were examined and had the same basic geographical trends of variation as the examples discussed above. No other patterns that could be resolved into morphogeographical variants susceptible of recognition in a formal taxonomic hierarchy could be discerned.

The basic problems with the previous taxonomy of the *Stellulatae,* especially the *Carex atlantica* and *C. echinata* complexes, were the arbitrary division of continuous series of variation in certain characters into artificial taxa, and, concomitant with this, a much too narrow circumscription of taxa. Specific limits were occasionally placed in such a manner that they fell near the mode of the variation in certain characters. It is no wonder that this group has gained notoriety as an extremely difficult area of the genus *Carex*. The after-effects of such problematical taxonomy are not desirable.

First, the group gains a perhaps unwarranted reputation for being difficult and thus taxonomists working on a flora are unlikely to deal adequately with it. Also, if taxonomists examine their plants closely and find that in their area they do not compare accurately with published species descriptions, they are liable, if a complete revision of the group is not undertaken, to describe new varieties *ad infinitum* to account for variation that should have been included with the description of the species in the first place. This phenomenon has been noted for other critical groups (Davis and Heywood, 1963) and such may have been the case with *C. interior* subsp. *charlestonensis* Clokey (1939), *C. interior* var. *keweenawensis* Hermann (1941), *C. angustior* var. *gracilenta* Clausen and Wahl (1939), and *C. sterilis* var. *rousseauiana* Raymond (1950). As well, more or less intermediate plants may be considered hybrids, as is evident from annotations on herbarium specimens. Lastly, taxonomists may examine the variation of alleged species based on specimens in herbaria, throw up their hands in frustration, and place everything into one species. None of these alternatives is desirable.

TAXONOMIC TREATMENT

Carex L. section *Stellulatae* Kunth, Enum. Pl. 2: 399. 1837.

Rhizomes short; plants cespitose; roots pale yellow to dark brown, smooth. Culms aphyllopodic with persistent basal sheaths; leaves all in basal third, usually plicate to flat, upper blades usually larger than lower; sheaths covering nodes, usually glabrous. Spikes usually gynecandrous; pistillate scales ovate, obtuse to acute, one-veined, usually yellow to castaneous with green center and hyaline margins, staminate scales lanceolate to ovate, usually acute, usually yellow to castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to usually reflexed at maturity, lanceolate to suborbicular, tapering to a beak, plano-convex to slightly biconvex, sessile, spongy-thickened at base surrounding achene, nerveless or several-nerved adaxially, usually several- to many-nerved abaxially; beak usually serrulate on margin and toothed apically; achenes usually ovate to suborbicular, biconvex, sessile; style deciduous; stigmas 2; anthers 3..

The *Stellulatae* are very widespread in North America. At least one species is found in every province and territory of Canada and all states of the United States except, as yet, Oklahoma. Southward, it is found through Mexico and Guatemala. Worldwide, the section is known from Europe, north-eastern Asia to Japan, New Zealand, Australia, New Guinea, and Sumatra. However, the greatest diversity of species is in North America, especially in eastern regions.

Although occurring in a wide range of habitats the *Stellulatae* nevertheless exhibit a number of common preferences. They are all species of open wetlands, only occasionally ranging into wet forests. Quite frequently, they occur in bogs, fens, and wet meadows but much less commonly in taller wetland vegetation such as *Typha* or *Scirpus* marshes or shrub carrs.

The section is very difficult taxonomically in North America and most species can overlap slightly with each other in all characters although, of course, all characters never overlap on any one plant. Identification is, therefore, quite difficult. In using the key, dimensions must be carefully measured and the best fitting lead of the couplet selected after examination of all characters given. In case of doubt, identifications should always be confirmed by comparison with authentically determined herbarium material.

KEY TO *STELLULATE* OF NORTH AMERICA

1. Spikes usually solitary; leaves involute; anthers 2.0–3.6 mm. 1. *C. exilis*
1. Spikes 2–8; leaves flat or plicate; anthers 0.6-2.2 (2.35) mm. 2.
2. Perigynium beak smooth-margined. 8. *C. seorsa*
2. Perigynium beak at least sparsely serrulate on margins. 3.
3. Widest leaves 2.8–5.0 mm wide. 4.
3. Widest leaves 0.8–2.7 mm wide. 7.
4. Lower perigynia of spikes mostly 1.1–1.6 times as long as wide, mostly 2.1–3.0 mm wide. 6a. *C. atlantica* subsp. *atlantica*
4. Lower perigynia of spikes (1.5) 1.7–3.0 times as long as wide, mostly 1.2–2.0 mm wide. 5.
5. Longer pistillate scales 2.1–3.1 mm long; west coast of North America. 7b. *C. echinata* subsp. *phyllomanica*
5. Longer pistillate scales 1.4–2.2 mm long; eastern North America. 6.
6. Infructescences mostly 15–30 mm long, lowest 2 spikes 1.3–9.5 mm distant. 4. *C. wiegandii*
6. Infructescences mostly 30–85 mm long, lowest 2 spikes 10–40 mm distant. 5. *C. ruthii*
7. Terminal spikes entirely staminate; anthers (1.0) 1.2–2.2 (2.35) mm long. 2. *C. sterilis*
7. Terminal spikes partly or wholly pistillate; anthers 0.6–2.2 (2.35) mm long. 8.
8. Terminal spikes without a distinct clavate base of staminate scales, staminate portion less than 1 mm in length; anthers (1.0) 1.2–2.2 (2.35) mm long. 2. *C. sterilis*
8. Terminal spikes with a distinct clavate base 1.0–16.5 mm long of staminate scales; anthers 0.6–1.6 (2.0) mm long. 9.
9. Lower perigynia 2.0–3.0 mm wide. 6a. *C. atlantica* subsp. *atlantica*
9. Lower perigynia 0.9–1.95 mm wide. 10.
10. Lower perigynia mostly 1.9–3.0 mm long, 1.0–2.0 (2.2) times as long as wide; beaks mostly 0.4–0.95 mm long, mostly 0.2–0.5 times as long as body. 11.
10. Lower perigynia mostly 2.85–4.75 mm long, (1.7) 1.8–3.6 times as long as wide; beaks mostly 0.95–2.0 mm long, mostly 0.45–0.85 times as long as body. 13.
11. Perigynia mostly nerveless over achene on adaxial surface; beak of perigynium conspicuously setulose-serrulate; perigynia often more or less convexly tapered from widest point to beak, forming a "shoulder." 3. *C. interior*

11. Perigynia mostly 1–10-nerved over achene on adaxial surface; beak of perigynium more sparsely serrulate with definite spaces between the often single teeth; perigynia mostly more or less cuneate or even concavely tapered from widest point to beak. 12.
12. Widest leaves 1.6–2.7 mm wide, infructescence mostly 18–45 mm long. 6a. *C. atlantica* subsp. *atlantica*
12. Widest leaves (0.65) 0.8–1.6 mm wide, infructescence mostly 8–20 mm long. 6b. *C. atlantica* subsp. *capillacea*
13. Heads very dense, 12–25 (40) mm long; distance between lower 2 spikes usually less than length of lowest spike. 14.
13. Heads more lax, usually 25–80 mm long; distance between lower 2 spikes usually more than length of lowest spike. 7a. *C. echinata* subsp. *echinata*
14. Perigynia 2.85–3.6 (4.0) mm long, often nerveless over achene on adaxial surface; widest leaves 1.0–2.4 (2.7) mm wide; widespread. 7a. *C. echinata* subsp. *echinata*
14. Perigynia (3.1) 3.5–4.75 mm long, usually 2–12-nerved over achene on adaxial surface; widest leaves (1.7) 2.3–2.7 mm wide; west coast of North America. 7b. *C. echinata* subsp. *phyllomanica*

1. Carex exilis Dewey, Am. Jour. Sci. Arts 14: 351. 1828. Holotype in herb. Dewey: Danvers [Massachusetts], Oakes, GH(!). Isotypes GH(!) NY(!) WIS(!).

C. exilis var. *squamacea* Dewey, Am. Jour. Sci. Arts 14: 351. 1828. Holotype in herb. Dewey: Ipswich, Mass., Oakes. GH(!). Isotypes PH (2 sheets) (!), NY (2 sheets) (!), WIS (2 sheets) (!).

C. exilis var. *androgyna* Dewey *in* Wood, Class Book of Botany: 750. 1861. Probable isotype: Manchester, Essex Co., N. Y. P. D. K[nieskern]. GH(!).

Rhizomes short; plants densely cespitose; roots smooth, pale yellow to dark grey-brown; culms 12–80 cm, erect, elongating in fruit, phyllopodic, obtusely trigonous, smooth; basal sheaths persistent, dark brown. Leaves 2–6 per culm, all in basal third, usually shorter than culms in fruit; blades 4–70 cm X 0.4–1.5 mm in diameter, involute, smooth or antrorsely scabrous; lower blades of culms often longer than upper and blades of sterile shoots longer; widest leaf 0.8–1.5 mm in diameter. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–21 cm; inner band hyaline, not purple-dotted; sheath apex concave, scarcely thickened; ligule 0.8–1.8 mm X 0.6–1.6 mm, rounded. Infructescence 6–40 mm; spike solitary (occasionally 1 or 2 (3) smaller accessory spikes below main one), pistillate above and staminate below or plants sometimes dioecious. Pistillate portion of spike 5.0–9.5 mm wide, up to 27-flowered; staminate portion of spike 1.0–3.0 mm wide, up to 50-flowered. Pistillate scales 1.8–3.3 mm X 1.3–2.2 mm, ovate, one-veined, acute, castaneous with green center and hyaline margins. Staminate scales 1.7–5.5 mm X 1.0–2.2 mm, lanceolate to ovate, one-veined, acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, lanceolate-ovate to very broadly ovate, 2.6–4.7 mm X 1.25–2.3 mm, 1.3–2.65 times as long as wide; tapering to a beak, plano-convex or slightly biconvex, castaneous when first ripe, dark brown when over-mature; more or less sessile, spongy-thickened at base surrounding achene; adaxial veins up to 7, faint; abaxial veins up to 15, faint; serrulate on margins up to 1.2 mm below base of beak. Beak 0.5–1.7 mm, 0.2–0.65 times as long as body; serrulate on margins, toothed apically; teeth blunt, soft, sometimes obsolete or up to 0.35 mm. Achenes 1.4–2.2 mm X 1.2–1.7 mm, ovate, biconvex; style deciduous, stigmas 2. Anthers 3, (2.0) 2.2–3.6 mm. Fig. 26 (perigynia) and 36 (infructescences).

This very distinctive member of the *Stellulatae* is notable for its striking, large, single spikes. It was described early and its nomenclature and typification present no problems.

Although very distinct from all other *Stellulatae*, perigynium shape and size in this species are quite variable as shown in Fig. 26. The perigynia range from very narrowly ovate to very broadly ovate and beak length is exceedingly variable as well. Plants with accessory spikes below the main one may resemble other species of *Stellulatae* but are separable by their involute leaves, large anthers, and the fact that the terminal spike is much larger than the laterals. Other *Stellulatae* may have the terminal spike slightly larger than the laterals but not strikingly so. These multiple-spiked plants, when growing with both single-spiked *Carex exilis* and other species of *Stellulatae*, are likely responsible for reports of hybrids (Mackenzie, 1931; Raymond, 1952; Moore and Calder, 1964) as discussed by Marie-Victorin and Rolland-Germain (1969).

The position of *Carex exilis* in the *Stellulatae* is quite isolated. Boott (1858) felt that it was allied with *C. sterilis*. This is plausible as the species do share certain features such as large anthers, a more densely cespitose habit than most other *Stellulatae*, and a tendency to be more or less dioecious. In any case, it appears that the plant is not close to members of the *Dioicae* group as has been proposed by Tuckerman (1843), Kükenthal (1909), Savile and Calder (1953), and Toivonen and Timonen (1976).

The distribution of the species is quite interesting (Fig. 16). From Delaware northwards to Massachusetts it is continuous along the coast. From there it occurs inland through New York to western Ontario and Minnesota and north along the coast to central Labrador. Southwards from Delaware, it is known from two isolated localities, one in Moore County, North Carolina, (record from Radford, Ahles, and Bell, 1964) and one from George County, Mississippi (At Miss.-Ala. line; off Hwy 98 about 200–300 yds.

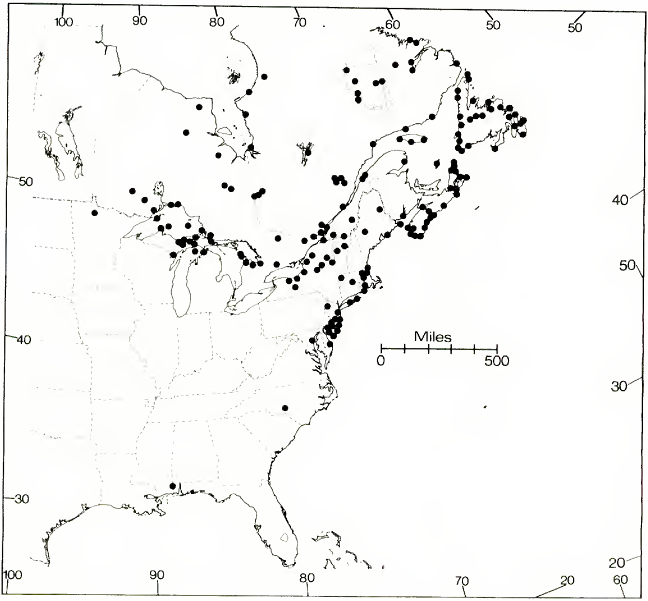


FIG. 16. Distribution of *Carex exilis*.

to right (south) of Hwy. Ken E. Rogers 2919, April 12, 1970, NCU). These southern records are likely relicts of a former wider distribution in the wetlands of the southern coastal plain during the glacial maxima. The species found the vast bogs and fens of newly deglaciated territory a very suitable habitat and spread widely from the area where glaciated territory touched the coastal plain as in New Jersey and Long Island, New York. *Carex exilis* is probably still in the process of migration northwards and westwards. Such a pattern is also shown by *Sarracenia purpurea,* a frequent associate of *C. exilis* in bogs and fens (Gleason and Cronquist, 1964).

The ecology of *Carex exilis* is quite restricted. It grows in extreme fens and bogs and, like *Sarracenia purpurea* mentioned above, with little regard for calcareous or acidic habitats but always in open, wet sites of low cover.

2. **Carex sterilis** Willdenow, Sp. Pl. 4: 208. 1805. Holotype in herb. Willdenow: No. 17109b "Pennsylvania, Muhlenberg." B, photo TRTE(!). Probable isotypes GH(!), PH (3 sheets) (!).

C. stellulata Gooden. var. *sterilis* (Willd.) Carey, Carices N. U.S. 554. 1847.

C. elachycarpa Fernald, Proc. Am. Acad. Arts Sci. 37: 492. 1902. Holotype: Fort Fairfield, Valley of Aroostook River, Aroostook Co., Maine. Mabel P. Cook, Elsie L. Shaw, M. L. Fernald, June 29, 1899. GH(!). Isotypes GH(!), NEBC(!).

Kobresia elachycarpa (Fern.) Fernald, Rhodora 5: 251. 1903.

C. sterilis Willd. var. *rousseauiana* Raymond, Nat. Can. 77: 62. 1950. Holotype: Anticosti, Rivière Chicotte: berge graveleuse à L'embouchure. 17 juillet 1942. Rousseau 52 333 MT(!). Isotypes MTJB(!), MICH(!).

C. X*minganinsularum* Raymond, Bull. Soc. Bot. France 99: 197. 1952. Lectotype (*des. nobis*): Québec: [comté de Saguenay]. Archipel de Mingan: île à la Proie, Marie-Victorin, Rolland-Germain et Louis-Marie 20.116, 22 juillet 1925. MT(!). Isolectotype MT(!).

C. muricata L. var. *sterilis* (Willd.) Gleason, Phytologia 4: 22. 1952.

Rhizomes short; plants cespitose, often densely so; roots smooth, pale yellowish to brown; culms 10–75 cm, erect, elongating in fruit, aphyllopodic, scabrous on angles above; basal sheaths persistent, brownish. Leaves 3–5 per culm, all in basal third, shorter than culms in fruit; blades 7.5–25 cm X 1.2–2.6 mm, plicate, antrorsely scabrous above; upper blades of culm much longer than lower and blades of sterile shoots longer; widest leaf 1.6–2.6 mm wide. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 4.0–13 cm; inner band hyaline; sheath apex concave, scarcely thickened; ligule 0.3–1.7 mm, rounded to obtuse. Infructescence 0.9–4.0 cm, densely crowded above but often with the lower spikes more or less separate; spikes 3–8. Plants more or less dioecious; pistillate plants with rarely a few staminate flowers; predominately staminate plants sometimes with a few pistillate flowers scattered on the spikes or occasionally entirely pistillate spikes mixed with entirely staminate ones in the same infructescence. Terminal spikes 3.5–13.7 mm, usually unisexual, 4.5–7.2 mm wide and 5–26-flowered when pistillate, 1.2–2.6 mm wide and 6–31-flowered when staminate. Lateral spikes 3.0–13.5 mm, similar to terminal spikes. Distance between upper 2 spikes 0.3–1.5 (5) mm; distance between lower 2 spikes 3.8–15.5 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.8–2.9 mm X 1.0–1.8 mm, ovate, one-veined, acute, castaneous with green center and usually conspicuous, broad hyaline margins. Staminate scales 2.2–3.3 mm X 1.1–1.8 mm, ovate, one-veined, acute, castaneous with green center and broad hyaline margins. Lower perigynia of spikes spreading to reflexed, ovate to deltoid, 2.1–3.8 mm X 1.2–2.2 mm, 1.4–2.3 (2.7) times as long as wide, tapering to a beak, plano-convex, castaneous when first ripe, almost black when over-mature, sessile, spongy-thickened at base surrounding achene; adaxial veins absent or up to 10; abaxial veins 5–12; strongly setulose-serrulate on margins to 0.2–0.8 mm below base of beak. Beak 0.65–1.6 mm, 0.45–0.8 times as long as body, copiously setulose-serrulate on margins, toothed apically; teeth soft, often flexuous, whitish, 0.15–0.5 mm. Achenes 1.0–1.7 mm

× 0.9–1.3 mm; ovate to suborbicular, biconvex, sessile; styles deciduous; stigmas 2. Anthers 3, (1.0) 1.2–2.2 (2.35) mm. Figs. 27 (perigynia) and 37 (infructescences).

In its tendency to a dioecious habit, *Carex sterilis* is very unusual among plurispicate *Carex*. It was the first exclusively North American species to be described and its nomenclature and typification are straightforward. Fernald's (1902) use of the name for what is now called *C. atlantica* was clearly an error, as pointed out by Mackenzie (1910). Willdenow's type is dioecious as both male and female spikes are clearly visible on the sheet.

Carex sterilis presents an unusual array of infructescence types. All-male plants are intermingled with all-female plants and occasional intermediate forms. In the very rare instance of an individual of *C. sterilis* having a more or less gynecandrous terminal spike, close examination is necessary to place it. The most reliable feature is the long anthers of the plant, up to 2.2 (2.35) mm. This is longer than any species except the distinctive *C. exilis*. *Carex sterilis* also has more prominent castaneous and hyaline margins to the pistillate scales, a more densely setulose-serrulate margin to the beak, and less stiff, often more hyaline apical teeth on the beak than is usual for most individuals of other species. These features are of particular assistance when comparative material is available.

Carex sterilis does not have any very close relatives in the *Stellulatae*. It is similar to *C. interior* in its blunt scales with broad hyaline margins and its densely setulose-serrulate perigynium beak, but *C. interior* has small anthers, a gynecandrous terminal spike, and a beak less than 0.45 times as long as the perigynium body. The similarity of *C. sterilis* to *C. exilis* in some respects has already been discussed under the latter species.

As noted before, most species of *Stellulatae* tend to be coastal (or montane) but *Carex sterilis* is primarily a plant of the interior. Its range is divided into two parts (Fig. 17). The major portion centers on the Great Lakes region. In certain areas here the plant is quite common in its habitat. Outlying areas occur in Minnesota, Manitoba, and Saskatchewan; the central part of northern Ontario, north to James Bay; and, in the east, to eastern Pennsylvania, eastern New York, and rarely to extreme western Connecticut and

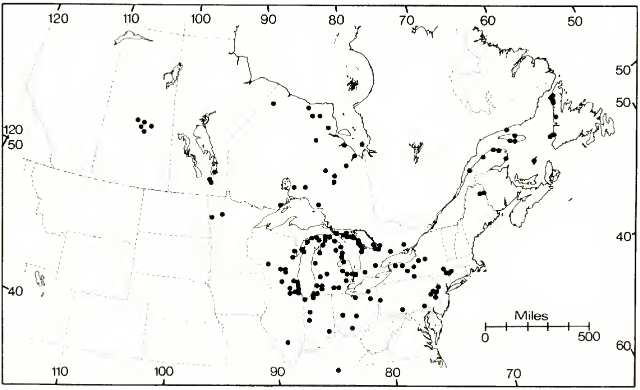


FIG. 17. Distribution of *Carex sterilis*.

Massachusetts. There is then a large gap in the species range until the region of the Gulf of St. Lawrence. There, the species occurs sparingly from the Aroostock River Valley of northern Maine to the Mingan Islands, Quebec, and east to western Newfoundland. It is a calciphile and the gap is likely due to a scarcity of suitable habitats. No significant differences were noted between plants from the Gulf of St. Lawrence and the Great Lakes region. Reports of *C. sterilis* in older literature from other parts of North America are due to past misuse of the name for *C. atlantica* or *C. echinata. Carex sterilis* has virtually its entire range in newly glaciated territory and presumably survived glaciation in suitable habitats just south of the glacial front.

The preferred habitat of this species is quite restricted. It is an obligate calciphile occurring in fens, marl meadows, calcareous lake and river shores, moist limestone flats, wet prairie, and open, calcareous Cedar and Tamarack swamps. The habitat of the plant is of considerable help in identification as most other *Stellulatae* except *C. interior* and *C. exilis* prefer acidic sites. In its favoured habitat, the plant may be abundant, sometimes dominating small areas. Its stiff culms in dense clumps are a distinctive feature of many fens, marly meadows, and calcareous shores.

3. **Carex interior** L. H. Bailey, Bull. Torr. Bot. Club 20: 426. 1893. Lectotype (*des. nobis*): Penn Yan, New York, No. 36, H. P. Sartwell, Carices Americae Septentrionalis Exsiccatae, Pars 1, 1848. GH(!). Isolectotypes NY(!), PH(!).

C. scirpoides Willdenow, Sp. Pl. 4: 237. 1805. *Non C. scirpoidea* Michaux, Fl. Bor. Am. 2: 171. 1803.

C. stellulata Gooden. var. *scirpoides* (Willd.) Darlington, Fl. Cestrica 31. 1837.

C. stellulata Gooden. var. *scirpina* Tuckerman, Enumeratio Methodica Caricum Quarundam. 9. 1843. *Nom. illeg.* Based on *C. scirpoides* Willd.

C. sterilis Willd. forma *flexibilis* Farwell, Ann. Rep. Mich. Acad. Sci. 21: 362. 1920. Holotype: Lakeville [Oakland Co., Michigan]. O. A. F[arwell] 4887, June 2, 1918. BLH n.v. Isotype MICH(!).

C. interior L. H. Bailey subsp. *charlestonensis* Clokey, Bull. S. Calif. Acad. Sci. 38: 1. 1939. Holotype: Charleston Park, Charleston Mts., Clark Co. Nevada. I. W. Clokey 7468, June 19, 1937. UC(!). Isotypes GH(!), PH(!), TEX(!), UC(!), MICH(!), CM(!).

C. interior L. H. Bailey var. *keweenawensis* F. J. Hermann, Am. Midl. Nat. 25: 19. 1941. Holotype: Southeast of Eagle Harbor, Keweenaw Co. Michigan, F. J. Hermann 7985, July 13, 1936. GH(!). Isotypes PH(!), MICH(!).

C. interior L. H. Bailey forma *keweenawensis* (F. J. Hermann) Fernald, Rhodora 44: 284. 1942.

Rhizomes short; plants cespitose; roots smooth, yellowish to dark brown; culms 10–95 cm, erect, elongating in fruit, aphyllopodic, smooth; basal sheaths persistent, light brown. Leaves 3–5 per culm, all in basal third, often shorter than culms in fruit; blades 6–31 cm X 0.6–2.4 (2.7) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 1.0–2.4 (2.7) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 1.8–13.0 cm; inner band hyaline, sometimes purple dotted; sheath apex concave, not or scarcely thickened; ligule of uppermost culm leaf 0.6–2.2 mm, obtuse to rounded. Infructescence 8–37 mm, dense to more or less lax; spikes 2–5 (6). Terminal spike 5.2–20 mm, staminate at base, pistillate above; staminate portion 2.2–14.5 mm X 0.7–1.4 mm, 3–10-flowered; pistillate portion 3.0–7.0 mm X 4.0–5.8 mm, 4–16-flowered. Lateral spikes 3.0–9.5 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 2.2 mm and 3-flowered; pistillate portion 2.3–8.0 mm, 3–18-flowered. Distance between upper 2 spikes 0.4–5.8 mm, distance between lower 2 spikes 2.1–11.0 mm; lateral spikes with short scale-like bracts. Pistillate scales 1.2–2.1 (2.4) X 1.0–1.6 mm, ovate, one-veined, usually obtuse, castaneous with green center and broad hyaline margins. Staminate scales 1.4–2.9 mm X 1.0–1.3 mm, ovate, one-nerved, obtuse to acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, ovate to broadly ovate, 1.95–3.0 (3.3) mm X 1.1–1.8 mm, 1.4–2.0 (2.2) times as long as wide; tapering to a beak, plano-convex to slightly biconvex, green to mostly castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins up to 1.0 mm below base of beak; adaxial veins over achene none or occasionally up to 6; abaxial veins 4–12, sometimes faint. Beak 0.4–0.95 mm, 0.18–0.44 times as long as body, setulose-serrulate on margins, apex toothed; teeth more or less blunt, 0.15–0.4 mm. Achenes 1.2–1.8 mm X 0.95–1.5 mm, ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.6–1.4 mm. Figs. 28 (perigynia) and 38 (infructescences).

Over much of North America, especially the central parts, this small species is the commonest or only representative of the *Stellulatae.* The plant was long known as *Carex scirpoides* Willd. However, since that name differs only in the last letter of the Latin termination from the earlier *C. scirpoidea* Michaux, it is here regarded as a later homonym. Bailey's name was the next available for the taxon at the specific level and is in common use in all floristic and taxonomic works at the present time.

For such a wide-ranging taxon, the uniformity of *Carex interior* over its range is surprising. Virtually no attempts have been made to segregate the species into several taxa except for the description of the form with perigynia nerved on the adaxial surface as both *C. interior* subsp. *charlestonensis* and *C. interior* var. *keweenawensis.* The nerved form, although occurring sporadically throughout the range of *C. interior,* is apparently more frequent than the nerveless form in the Rocky Mountain states (Hermann, 1970).

Rarely, specimens were seen that were intermediate in beak length, perigynium length and perigynium shape between *Carex interior* and *C. echinata.* These plants may represent hybrids although they appear fertile on superficial examination. These plants were often similar to the description of *C. laricina.* Interestingly enough, although this species has been aligned with *C. atlantica* subsp. *capillacea* in the past, no intermediates were noted in this study.

Carex interior, with its wide distribution in the southwestern United States and Mexico as well as across the continent farther north, is not a recently evolved species (by *Stellulatae* standards). Over wide areas of its range, it is not now sympatric with other species of *Stellulatae.* Its nearest relatives in the *Stellulatae* are *C. echinata,* noted above, and also, more interestingly, the broad-leaved *C. wiegandii,* a rare species of northeastern North America. The small anthers and short, usually obtuse pistillate scales of *C. wiegandii* are similar to those of *C. interior* and, although *C. wiegandii* is a larger plant, there is much overlap in perigynium length, beak length, and perigynium length/width ratio. The distant similarity of *C. interior* to *C. sterilis* has already been noted.

The distribution of *Carex interior* is shown in Fig. 18. Additional Mexican localities are noted in Hermann (1974). The species is reported, undoubtedly correctly, from New Mexico as well (Wooton and Standley, 1915). In the east, the plant has been reported from West Virginia (Core, 1938) and Virginia (Harvill, 1973). As it occurs in adjacent southern Pennsylvania, the species may well occur in these states, but all specimens examined have been either *C. atlantica* or *C. echinata.*

The preferred habitats of *Carex interior* are calcareous, although it is not so specific as *C. sterilis* in this regard. It never grows in acidic *Sphagnum* bogs or similar sites but is found in a wide variety of lake, river, and stream shores, ditches, sedge meadows, wet prairies, fens, Cedar, Tamarack, and Spruce swamps and, occasionally, wet mixed woods.

4. **Carex wiegandii** Mackenzie, N. Am. Fl. 18: 108. 1931. Lectotype (*des. nobis*): Silurian hills back of Birchy Cove (Curling), Region of Humber Arm, Bay of Islands, Western Newfoundland, M. L. Fernald and K. M. Wiegand 2776, July 21, 1910. GH(!). Isolectotype F(!).

Rhizomes short; plants cespitose; roots smooth, pale yellow-brown to dark grey-brown; culms 10–105 cm, erect, elongating in fruit, aphyllopodic, smooth to slightly scabrous above; basal sheaths persistent, brown. Leaves 3–8 per culm, all in basal third,

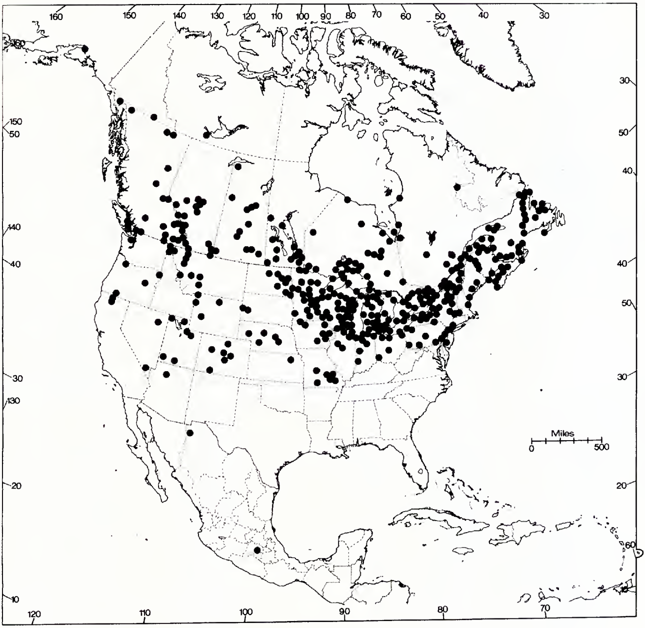


FIG. 18. Distribution of *Carex interior.*

usually shorter than culms in fruit; blades 11–45 cm X 1.7–5.0 mm, plicate, antrorsely scabrous above, upper blades of culm much longer than lower and blades of sterile shoots longer; widest leaf 2.8–5.0 mm. Sheaths covering nodes, tight, glabrous or sometimes hispidulous on the veins, that of uppermost leaf 4–23 cm; inner band hyaline, rarely purple dotted; sheath apex concave, strongly thickened; ligule 0.9–2.5 mm, rounded to obtuse. Infructescence 8.6–30 mm, dense; spikes 4–6. Terminal spike 6.1–14.5 mm, staminate at base, pistillate above; staminate portion 2–8.6 mm X 0.8–1.3 mm, 5–20-flowered; pistillate portion 3.0–8.0 mm X 5.0–7.3 mm, 7–25-flowered. Lateral spikes 4.5–8.0 mm, sessile, pistillate at apex and staminate at base; staminate portion (0) 0.5–2.0 mm, (0) 1–3-flowered; pistillate portion 3.0–8.0 mm, 5–21-flowered. Distance between upper 2 spikes 0.8–3.0 mm, distance between lower 2 spikes 1.3–9.5 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.45–2.0 (2.2) mm X 1.3–1.9 mm, ovate, one-veined, obtuse to subacute, sometimes shortly mucronate, castaneous with green center and hyaline margins. Staminate scales 1.2–2.3 mm X 1.4–1.8 mm, ovate, one-veined, obtuse to acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, broadly ovate, 2.55–3.75 mm X (1.25) 1.4–2.0 (2.1) mm, (1.4) 1.6–2.5 times as long as wide, tapering to a beak, plano-convex, green to castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene; adaxial veins absent or up to 10, faint; abaxial veins 5–18; serrulate on margins to 0.1–0.8 mm below base of beak. Beak 0.55–1.1 (1.35) mm, 0.25–0.55 times as long as body, serrulate on margins, toothed apically; teeth more or less blunt, 0.2–0.5 mm. Achenes 1.4–1.9 mm X 1.1–1.55 mm, ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.7–1.3 mm. Figs. 29 (perigynia) and 39 (infructescence).

Before it was recognized and described by Mackenzie, specimens of this species were for many years identified as either *Carex atlantica* or *C. echinata.* When robust, it is an unmistakable plant with its broad leaves and dense heads of closely aggregated spikes. There are no problems of nomenclature or typification with this species.

Carex wiegandii is a rare species of restricted range. Few specimens have been examined. Nevertheless, it does not seem to be a variable species. The plant is quite uniform in appearance throughout its range.

Its relationships in the rest of the *Stellulatae* are with *Carex interior* as noted before, and to some extent, *C. atlantica.* Occasional specimens with very broad perigynia may resemble *C. atlantica* but they can usually be separated by the dense infructescence of *C. wiegandii.* As well, the perigynia of *C. wiegandii* are sometimes only faintly nerved or even nerveless on the adaxial surface. The ranges of the two species barely overlap. As *C. wiegandii* is similar in some of its features to *C. interior* it provides an interesting connection between *C. interior* and *C. atlantica.* It is possible that *C. wiegandii* may have been derived from past hybridisation of *C. interior* and a broad-leaved race of *C. atlantica.*

The range of *Carex wiegandii* is centered on the Gulf of St. Lawrence with stations sparingly inland to Ontario and south, very sparingly, to Maine, extreme northern Massachusetts, and recently discovered sites in Pennsylvania (Rothrock, 1978) (Fig. 19). It has been reported from northern New York (Mackenzie, 1931; Fernald, 1950) but no specimens have been seen from there. As it occurs in adjacent Quebec, its occurrence there is probable. Its previously unreported occurrence as far west as the Lake Superior region is interesting (Corbeil Pt. Algoma Dist. Ontario, T. M. C. Taylor et al. 438, July 26, 1935, CAN, GH; 471, July 22, 1935, CAN; 15 mi N. of Sault Ste. Marie [Algoma Dist.] Ontario, J. K. Jeglum, D. E. Harvey 3317, Aug. 7, 1970, SSMF). The species should be sought in suitable habitats elsewhere in the Lake Superior region and throughout central and eastern Canada and the northern United States.

Carex wiegandii is a plant of relatively restricted habitat. It occurs in *Sphagnum* bogs or boggy thickets and lake shores and sometimes along more open trails or ditches through bogs.

5. **Carex ruthii** Mackenzie, N. Am. Fl. 18: 112. 1931. Holotype: Craggy Mt. N. C. Albert Ruth, July 1900. NY(!).

C. muricata L. var. *ruthii* (Mackenzie) Gleason, Phytologia 4: 22. 1952.

Rhizomes short; plants cespitose; roots smooth, pale yellowish-brown to dark grey-brown; culms (23) 30–100 cm, erect, elongating in fruit, aphyllopodic, scabrous above; basal sheaths persistent, pale to dark brown. Leaves 3–7 per culm, all in basal third, more or less equalling culms in fruit; blades 30–70 cm X 1.6–5.0 mm, plicate to flat, antrorsely scabrous margined, upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf (2.6) 2.9–5.0 mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 6–18 cm; inner band hyaline to straw coloured, sometimes purple dotted above; sheath apex concave, more or less thickened; ligule 1.0–2.5 mm; rounded. Infructescence (22) 30–85 mm, lax; spikes 3–8. Terminal spike 7–15.5 mm, staminate at base, pistillate above; staminate portion 2.0–11.0 (14.0) mm X 0.8–1.6 mm, 3–14-flowered; pistillate portion 4.1–8.0 mm X 6.1–7.7 mm, 10–25-

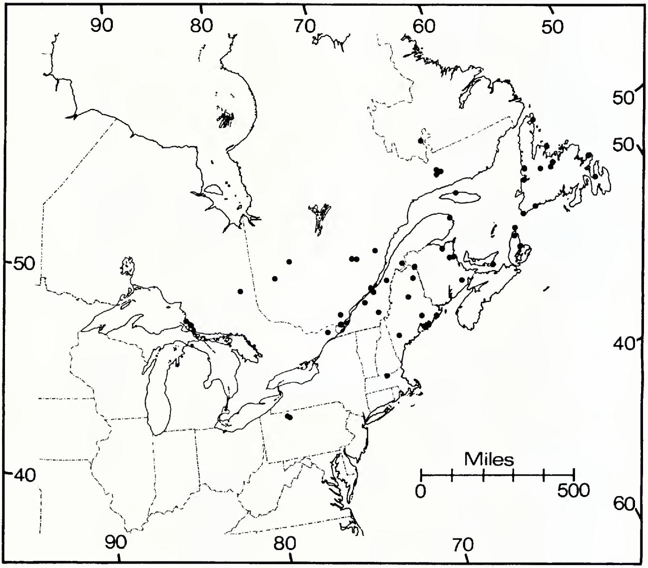


FIG. 19. Distribution of *Carex wiegandii.*

flowered. Lateral spikes 3.6–11.2 mm, sessile, pistillate or sometimes staminate at base and pistillate above; staminate portion up to 1 mm and 2-flowered; pistillate portion 3.6–11.2 mm, 6–28-flowered. Distance between upper 2 spikes 0.3–4.5 (8.0) mm, distance between lower 2 spikes (5) 10–40 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.4–2.2 mm X 1.1–2.0 mm; ovate, one-veined, obtuse to acute, usually castaneous with green center and hyaline margins. Staminate scales 1.6–2.4 mm X 1.1–1.9 mm; narrowly ovate, one-veined, obtuse to acute; castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, broadly to narrowly ovate, (2.8) 3.0–4.4 mm X 1.3–1.9 (2.1) mm, (1.6) 1.8–2.5 times as long as wide, tapering to a beak, plano-convex, olive-green; sessile, spongy-thickened at base surrounding achene; adaxial nerves absent or up to 5; abaxial nerves 6–14; smooth margined below base of beak. Beak 0.9–1.75 mm, 0.43–0.85 times as long as body, serrulate on margins, toothed apically; teeth stiff, 0.15–0.35 mm. Achenes 1.1–1.8 mm X 0.9–1.4 mm; ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.8–1.45 mm. Figs. 30 (perigynia) and 43 (infructescence).

This restricted endemic of the southern Appalachian mountains is a striking plant with a very elongate infructescence. There are no problems in nomenclature and typification associated with it.

The few specimens examined were all very similar. The elongate infructescence combined with very broad leaves is not shown by any other species of *Stellulatae.*

Occasionally, specimens with broad perigynia may appear similar to *Carex atlantica* but the nature of the infructescence and the usually long-beaked perigynia, serrulate only on the beak, help to separate the two. Although allied by Mackenzie (1931) to *C. cephalantha* as well as to *C. atlantica* and *C. wiegandii,* it appears that its closest relative in the *Stellulatae* is *C. atlantica.* It differs from the *C. echinata* complex in its short pistillate scales, broad leaves, and elongate infructescence as well as the green colour of the perigynia.

The distribution of the species (Fig. 20) is limited to the Appalachian Mountains from southwestern Virginia to extreme northern Georgia and South Carolina. This is a distribution characteristic of many restricted Appalachian endemics such as *Diphylleia cymosa, Chelone lyonii, Pieris floribunda, Cymophyllus fraseri, Buckleya distichophylla,* and *Saxifraga careyana.* It occurs, according to herbarium labels, in moist forests, especially along trails, ditches, and streams through forests; boggy meadows and balds; and around seepage areas and springs.

6. Carex atlantica L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893. Based on *C. stellulata* Gooden. var. *conferta* Chapman.

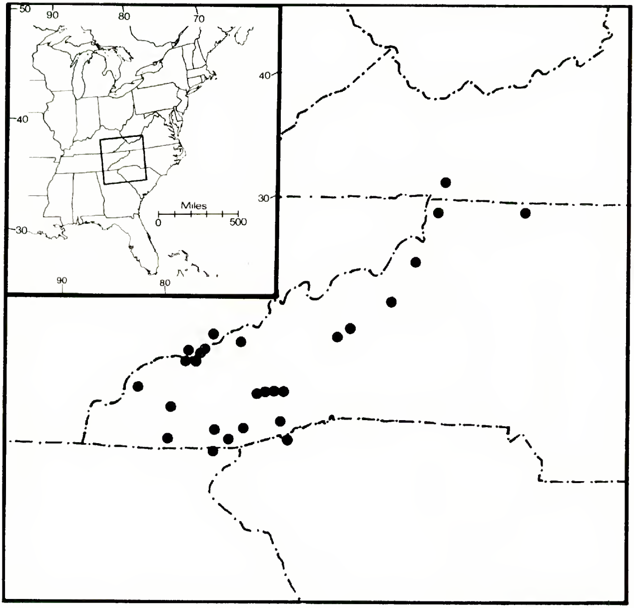


FIG. 20. Distribution of *Carex ruthii.*

C. stellulata Gooden. var. *conferta* Chapman, Fl. S. U.S. 534. 1860. Lectotype (*des. nobis*): Gadsden Co. Florida, Chapman. NY(!).

C. echinata Murr. var. *conferta* (Chapman) L. H. Bailey, Cat. N. Am. Carices 2. 1884.

C. incomperta Bicknell, Bull. Torr. Bot. Club 35: 494. 1908. Holotype: Bog below the "Cliff," foot of the Sea Cliff Inn, Nantucket Island, Massachusetts, Eugene P. Bicknell, June 20, 1908. NY(!). Isotypes GH(!), PH(!).

C. atlantica Bailey var. *incomperta* (Bicknell) F. J. Hermann, Rhodora 67: 362. 1965.

Rhizome short; plants cespitose; roots smooth, yellowish to grey-brown; culms 10–110 cm, erect to more or less spreading, elongating in fruit, aphyllopodic, scabrous margined above; basal sheaths persistent, light brownish. Leaves 3–5 per culm, all in basal third, equalling to shorter than culms in fruit; blades 8–60 cm X 0.4–4.0 (4.5) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 0.8–4.0 (4.5) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–24 cm; inner band hyaline, sometimes purple dotted above; sheath apex concave, more or less thickened; ligule of uppermost culm leaf 0.5–3.7 mm, rounded to obtuse. Infructescence 8–55 mm, dense to lax; spikes 2–8. Terminal spike 4.8–23.7 mm, staminate at base, pistillate above; staminate portion 1.8–13.5 mm X 0.8–1.3 mm, 2–21-flowered; pistillate portion 3.0–11.0 mm X 4.4–7.5 mm, 4–38-flowered. Lateral spikes 3.1–13.1 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 6.5 mm and 10-flowered; pistillate portion 2.5–12 mm, 3–40-flowered. Distance between upper 2 spikes 0.6–12.5 mm, distance between lower 2 spikes 1.5–18.0 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.2–2.4 mm X 1.2–2.0 mm, ovate to more or less suborbicular, one-veined, obtuse to more or less acute, green with hyaline margins, rarely castaneous. Staminate scales 1.3–3.5 mm X 0.8–1.4 mm, ovate-lanceolate to ovate, one-veined, acute to obtuse, green with hyaline margins, rarely castaneous. Lower perigynia of spikes spreading to reflexed, broadly ovate to suborbicular, 1.9–3.8 mm X 1.3–3.0 mm, 1.1–1.7 (1.9) times as long as wide, tapering to a beak, plano-convex, green, rarely more or less castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins to 0.7 mm below base of beak; adaxial veins over achene (0) 1–12; abaxial veins 6–13. Beak 0.45–1.25 mm, 0.23–0.5 (0.63) times as long as body, serrulate on margin, apex toothed; teeth stiff, 0.15–0.45 mm. Achenes 1.0–1.9 mm X 1.0–1.7 mm, deltoid to rhombic-orbicular, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.6–1.5 (1.8) mm.

This is the only species of *Stellulatae* in much of the southeastern United States. Mackenzie (1931) stated that the type of *Carex stellulata* var. *conferta* Chapman was from "Apalachicola, Florida" but the specimen so labelled in herb. Chapman was called by Chapman *C. stellulata,* not *C. stellulata* var. *conferta,* and cannot be the type. The lectotype is here chosen to be a specimen labelled Gadsden Co. Florida and named *C. stellulata* var. *conferta* by Chapman.

Carex atlantica, including the subspecies *capillacea,* is a very variable species. In size it ranges from over 1 m tall with leaves up to ca. 4 mm wide to delicate plants scarcely 20 cm high with leaves less than 1 mm wide. Normally distinguished by its very broad perigynia, 1.1–1.7 times as long as wide, a very few specimens are intermediate in colour, perigynium length/width ratio, and beak length between this species and *C. echinata.* These plants may be hybrids or rare, extreme variants of *C. echinata.* Some apparently intermediate plants are found north of the range of *C. atlantica.*

The closest relatives of *Carex atlantica* are *C. echinata, C. ruthii,* and *C. wiegandii.* From all these species it is usually distinguishable by its broad perigynia. Its wide range in the south and its distinctive perigynium shape and colour and overall aspects indicate that it is an old species that has been able to occupy a niche no other extant species of *Stellulatae* has entered.

The distribution of *Carex atlantica* (Figs. 21, 22) covers essentially all of the eastern United States, extending very sparingly into Canada in Nova Scotia and Quebec. It is, however, clearly most abundant on the coast. Its occurrence as a disjunct at the head of Lake Michigan, in Michigan and Indiana, is, as noted with *C. seorsa*, characteristic of coastal species. Most of the range of *C. atlantica* is in unglaciated territory but it has been able to spread into wetlands in glaciated territory to some extent, although less so than *C. echinata* or *C. interior.*

The habitats of *Carex atlantica* in the north are primarily bogs and wet, acid thickets and forest edges. It does not inhabit calcareous sites. In the south, where the species is more common, it occupies, judging from herbarium labels, a wide range of wetland habitats, usually on sandy or peaty acid soil.

6a. Carex atlantica subsp. atlantica

Culms usually 25–110 cm; leaves usually 1.0–4.0 (4.5) mm wide, widest leaf usually 1.55–4.0 (4.5) mm; infructescence usually 15–55 mm with 3–8 spikes; perigynia 2.3–3.8 mm × 1.5–3.0 mm, 1.1–1.7 times as long as wide; beak usually 0.6–1.25 mm. Figs. 31 (perigynia) and 40 (infructescences).

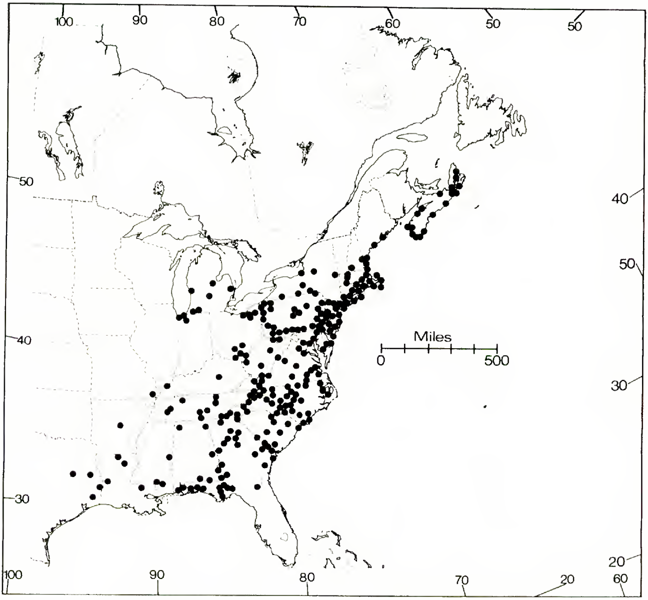


FIG. 21. Distribution of *Carex atlantica* subsp. *atlantica.*

This subspecies is the common large *Stellulatae* of the southeastern United States. Often particularly robust near the coast, the plant is also widely present inland. Its distribution is shown in Fig. 21. The possible evolutionary relationships of *C. atlantica* subsp. *atlantica* and subsp. *capillacea* are discussed under the latter subspecies.

6b. Carex atlantica subsp. **capillacea** (L. H. Bailey) Reznicek *comb. nov.*

C. interior L. H. Bailey var. *capillacea* L. H. Bailey, Bull. Torr. Bot. Club 20: 426. 1893. Lectotype (*des. nobis*): Arlington [Massachusetts] June 21, 1885. W. Boott. GH(!).

C. scirpoides Willd. var. *capillacea* (L. H. Bailey) Fernald, Rhodora 10: 47. 1908.

C. delicatula Bicknell, Bull. Torr. Bot. Club 35: 495. Nov. 1908. not *C. delicatula* C. B. Clarke, Kew Bull. Misc. Inf. Add. Ser. 8: 79. Aug. 1908.

C. stellulata Gooden. var. *scirpoides* (Willd.) Darlington forma *capillacea* (L. H. Bailey) Kükenthal, Das Pflanzenriech 4: 20. 231. 1909.

C. howei Mackenzie, Bull. Torr. Bot. Club 37: 245. 1910. Based on *C. interior* L. H. Bailey var. *capillacea* L. H. Bailey.

C. mohriana Mackenzie, N. Am. Fl. 18: 106. 1931. Holotype: Swamp near Wauchula, S. Florida, A. H. Curtiss 6761, Apr. 15, 1901. GH(!). Isotypes QK(!), UC(!), MIN(!), MICH(!).

The smallest extreme of *C. atlantica.* Culms usually 10–60 cm; leaves 0.4–1.55 mm wide; widest leaf (0.65) 0.8–1.55 mm; infructescence usually 8–20 mm long with 2–5 spikes; perigynia 1.9–3.0 mm X 1.3–2.0 mm, (1.15) 1.3–1.7 (1.9) times as long as wide; beak 0.45–0.95 mm. Figs. 32 (perigynia) and 41 (infructescence).

This taxon was long known as *Carex howei* or *C. interior* var. *capillacea.* Its affinities have been shown above to be with *C. atlantica,* with which it in fact intergrades. Bailey (1893) described *C. interior* var. *capillacea* from "Eastern Massachusetts, New Jersey and central Pennsylvania." Mackenzie (1931) states "specimens collected in eastern Massachusetts by Wm. Boott, who first called attention to the plant, are taken as the type of *C. interior* var. *capillacea* . . . ." Of several specimens from Boott's herbarium, all presumably seen by Bailey, "Arlington, June 21, 1885 W. Boott" (GH) is selected as the lectotype.

This delicate sedge is quite distinct in some parts of its range, especially north of the glacial boundary as pointed out earlier, but plants grading imperceptibly into *Carex atlantica* subsp. *atlantica* are not infrequent over much of the range of the species. Thus, recognition at subspecific level seems much more to represent the evolutionary relationships of the taxon. The area south of the glacial boundary and inland from the coastal plain is the oldest part of the species range. *Carex atlantica* presumably migrated from there onto the outer coastal plain and newly deglaciated territory as these areas became open for colonization. Differentiation accompanied migration until the frequencies of occurrence of character states are quite different in these different areas. The segregation is most pronounced in the northeast of the species' range where *Carex atlantica* subsp. *atlantica* and subsp. *capillacea* are quite distinct and may grow together without intergrading. *C. atlantica* subsp. *capillacea* is likely an incipient species, as yet only partially differentiated. The range of the taxon is from Nova Scotia to Texas along the Atlantic Coast and locally inland in New York, Pennsylvania, Quebec, Ohio, and Michigan as shown in Fig. 22.

7. Carex echinata Murray, Prod. Stirp. Gott. 76. 1770. Lectotype (*des. nobis*): plate 284, Flora Danica (Oeder, 1766).

C. leersii Willdenow, Fl. Berol. Prod. 29. 1787. *Nom Illeg.*

C. stellulata Goodenough, Trans. Linn. Soc. 2: 144. 1794. Type not traced.

C. stellulata Gooden. var. *angustata* Carey, Carices N. U.S. 544. 1847. Lectotype (*des. nobis*): Fairfield, New York. K, Photo TRTE(!). Isolectotype GH(!).

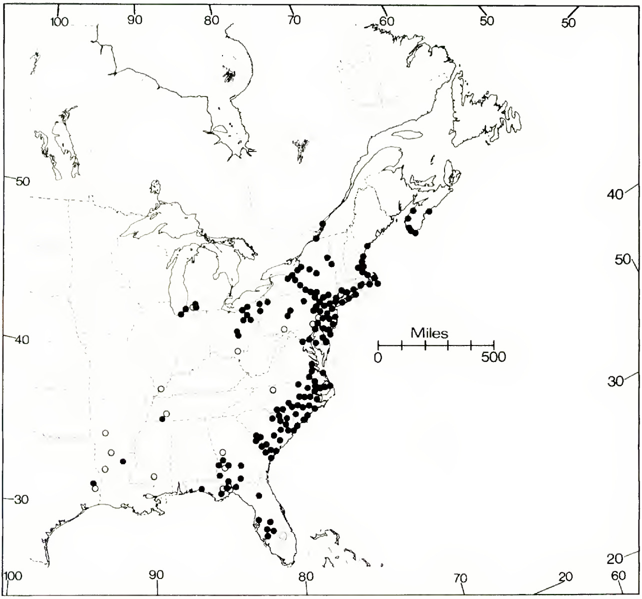


FIG. 22. Distribution of *Carex atlantica* subsp. *capillacea.* Open circles indicate intermediates with *C. atlantica* subsp. *atlantica.*

C. echinata Murr. var. *cephalantha* L. H. Bailey, Mem. Torr. Bot. Club 1: 58. 1889. Lectotype (*des. nobis*): Ashland, Mass. June, 1879, Thomas Morong. (GH)(!).

C. echinata Murr. var. *angustata* (Carey) L. H. Bailey, Mem. Torr. Bot. Club 1: 59. 1889.

C. sterilis Willd. var. *angustata* (Carey) L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893.

C. sterilis Willd. var. *cephalantha* (L. H. Bailey) L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893.

C. sterilis Willd. var. *excelsior* L. H. Bailey, Bull. Torr. Bot. Club 20: 424. 1893. Holotype: Junius, New York, No. 35, H. P. Sartwell, Carices Americae Septentrionalis Exsiccatae, Pars 1, 1848. GH(!). Isotype NY(!).

C. sterilis Willd. var. *aequidistans* Peck *ex* E. C. Howe, Ann. Rep. N.Y. State Mus. 48: 137. 1897. Type locality: Oneida and Essex Counties, N.Y. Type not traced.

C. echinata Murr. var. *ormantha* Fernald, Proc. Am. Acad. Arts Sci. 37: 483. 1902. Lectotype (*des.* Mackenzie): Bog along Strawberry Creek, Sierra Nevada Mts., El Dorado Co., California, Ezra Brainerd 160, July 18, 1897. GH(!).

C. echinata Murr. var. *excelsior* (L. H. Bailey) Fernald, Proc. Am. Acad. Arts Sci. 37: 484. 1902.

C. stellulata Gooden. var. *ormantha* (Fernald) Fernald, Rhodora 4: 222. 1902.

C. stellulata Gooden. var. *cephalantha* (L. H. Bailey) Fernald, Rhodora 4: 222. 1902.

C. stellulata var. *excelsior* (L. H. Bailey) Fernald, Rhodora 4: 222. 1902.

C. interior L. H. Bailey var. *josselynii* Fernald, Rhodora 8: 115. 1906. Holotype: Wet sandy river-bank, Fort Kent, Valley of the St. John River, Aroostook Co., Maine, M. L. Fernald, July 6, 1904. GH(!). Isotypes NY(!), MICH(!, fragment).

C. scirpoides var. *josselynii* (Fernald) Fernald, Rhodora 10: 48. 1908.

C. cephalantha (L. H. Bailey) Bicknell, Bull. Torr. Bot. Club 35: 493. 1908.

C. stellulata Gooden. var. *sterilis* (Willd.) Carey forma *excelsior* (L. H. Bailey) Kükenthal, Das Pflanzenreich 4: 20. 231. 1909.

C. leersii Willd. var. *angustata* (Carey) Mackenzie *ex* Small & Carter, Fl. Lancaster Co. 55. 1913.

C. leersii Willd. var. *cephalantha* (L. H. Bailey) J. K. Henry, Fl. S. Brit. Col. 60. 1915.

C. angustior Mackenzie *in* Rydberg, Fl. Rocky Mts. Adj. Plains Ed. 1. 124. 1917.

C. ormantha (Fernald) Mackenzie, Erythea 8: 35. 1922.

C. josselynii (Fernald) Mackenzie *ex* Pease, Proc. Bost. Soc. Nat. Hist. 37: 188. 1924.

C. muricata L. var. *cephalantha* (L. H. Bailey) Wiegand & Eames, Cornell Univ. Agr. Exp. St. Mem. 92: 120. 1926.

C. laricina Mackenzie *ex* Bright, Trillia 9: 4. 1930. Holotype: Presque Isle, low wet, sandy, back shores. June 16, 1927. John Bright. Location of type not known.

C. angustior Mack. var. *gracilenta* Clausen & Wahl, Rhodora 41: 30. 1939. Holotype: Moist woodland along stream at Ingleby, 2 mi. east of Coburn, Centre Co., Pennsylvania, R. T. Clausen and H. A. Wahl 2532, June 6, 1937. GH(!). Isotypes CU n.v., BH n.v.

C. muricata L. subsp. *cephalantha* (L. H. Bailey) Clausen, Cornell Univ. Agr. Exp. St. Mem. 291: 10. 1949.

C. muricata L. var. *angustata* (Carey) Gleason. New Britton and Brown Illus. Fl. 1: 318. 1952.

C. muricata L. var. *laricina* (Bright) Gleason, Phytologia 4: 22. 1952.

C. phyllomanica W. Boott var. *angustata* (Carey) Boivin, Phytologia 43: 51. 1979.

C. phyllomanica W. Boott var. *ormantha* (Fernald) Boivin, Phytologia 43: 51. 1979.

Rhizomes short; plants cespitose; roots smooth, yellowish to brown; culms 10–90 (135) cm, erect to more or less spreading, elongating in fruit, aphyllopodic, scabrous on margins above; basal sheaths persistent, light brown. Leaves 3–6 per culm, all in basal third, shorter than to equalling culms in fruit; blades 5–40 cm X 0.7–3.3 (3.8) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots much longer; widest leaf 1.0–3.3 (3.8) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 1.8–2.5 cm; inner band hyaline, sometimes purple dotted above; sheath apex concave, scarcely thickened; ligule of uppermost culm leaf 0.6–2.5 (4.5) mm, rounded to more or less acute. Infructescence 7–78 mm, dense to very lax; spikes (2) 3–8. Terminal spike 5.0–24.0 mm, staminate at base, pistillate above; staminate portion 2.0–16.5 mm X 0.9–2.0 mm, 2–17-flowered; pistillate portion 2,6–9.0 mm X 4.9–9.1 mm, 4–26-flowered. Lateral spikes 3.0–15.5 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 8.2 mm and 7-flowered; pistillate portion 2.5–11 mm, 3–32-flowered. Distance between upper 2 spikes 0.6–14.5 mm, distance between lower 2 spikes 1.7–42.0 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.4–3.1 mm X 0.7–2.3 mm, ovate, one-veined, acute to sometimes obtuse, castaneous with green center and hyaline margin. Staminate scales 1.3–3.8 mm X 0.8–1.7 mm, ovate-lanceolate to ovate, one-veined, acute, castaneous with green center and hyaline margins. Lower perigynia of spike spreading to reflexed, lanceolate to ovate, (2.65) 2.85–4.75 mm X 0.8–2.1 mm, (1.7) 1.8–3.2 (3.6) times as long as wide, tapering to a beak, plano-convex, green to castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins to 0.85 mm below beak; adaxial veins over achene none or up to 12; abaxial veins 2–14. Beak 0.85–2.0 mm, (0.4) 0.45–0.86 times as long as body, serrulate on margins, apex usually toothed, teeth stiff, sharp (0) 0.15–0.5 mm. Achenes 1.3–2.1 mm X 0.8–1.55 mm, ovate-lanceolate to rhombic ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.8–1.6 (2.0) mm.

Synonymy given for this species includes only names that have been widely used in North America or are based on North American types. Complete synonymy, including names of varieties and forms, is found in Kükenthal (1909) and Mackenzie (1931).

The correct name for this widespread species has been the subject of much dispute. Four names have been applied with some regularity: *Carex muricata* Linneaus (1753), *C. echinata* Murray (1770), *C. leersii* Willdenow (1787), and *C. stellulata* Goodenough (1794).

Mackenzie (1923) argued for the applicability of the name *Carex muricata* L. He noted that the plant was described by Linnaeus (1745) in his "Flora Suecica" and the description was nearly the same as in the later "Species Plantarum." This plant, he argued, grew in wetlands and Mackenzie (1923) stated "there never has been any doubt that the plant of wet places, which occurs especially in north Sweden and which is, undoubtedly to be taken as, the type of *Carex muricata* is the same as *Carex stellulata* L. [sic]." He noted that "the botanists immediately following Linnaeus seem to have been quite unanimous in applying the name *Carex muricata* to what has in more recent times usually been called *Carex stellulata* Good." However, Mackenzie did not mention that Goodenough (1794), in describing *C. stellulata,* noted at that early date that the botanists immediately following Linnaeus were in error in their application of this name and that the Linnaean herbarium confirmed this. Mackenzie (1923) dismissed the Linnaean herbarium by noting that Kükenthal (1909) stated that there was a mixture in Linnaeus' specimens. On that basis, Kükenthal in fact rejected the name *C. muricata* altogether. However, when the Linnaean herbarium is consulted, there is found a sheet labelled "8 *muricata.*" The name and number directly connect that sheet with the name and number in Species Plantarum Ed. 1. The other sheet in the Linnaean herbarium, the basis of Kükenthal's (1909) "mixture," is unnamed and has no bearing on the application of the name *C. muricata.* The Linnaean plant clearly has androgynous spikes and is a member of the section *Bracteosae.* Mackenzie's arguments, based on pre-1753 literature, are not to the point. At best, Mackenzie could have shown that Linnaeus had changed his mind between Flora Suecica and Species Plantarum Ed. 1. As has been pointed out by David (1976), there can be no confusion as to the application of the name *C. muricata* L. Continued use of the name for species of *Stellulatae* by recent authors (Gleason, 1952; Gleason and Cronquist, 1963; Boivin, 1967; Hitchcock and Cronquist, 1973) is incorrect.

Carex echinata Murray (1770) was based on a description by Haller (1768) and plate 284 of "Flora Danica" (Oeder, 1766). Haller (1768) also refers to Oeder's illustration. Haller's description and Oeder's plate are clearly the common "Star Sedge" of Europe. Oeder's plate is designated the lectotype of *C. echinata* Murray.

Fernald (1902) noted, quoting a letter from C. B. Clarke, that "*C. echinata* Murr. is = *C. divulsa* Gooden. and not near *C. stellulata* Gooden. The original sheet of Murray is in the British Museum, inscribed in his own hand as his *echinata;* it is a very good specimen and Jas. Britten (or any other botanist at the British Museum) will tell you that there can be no dispute about this identification." However, Murray's new name was validated by his citation of Haller's (1768) polynomial epithet and the typification must be based on Haller's work. Murray's specimen is irrelevant to the selection of a type. This same case has been argued by Britten (1907), Kovacs (1910), Briquet (1910), Fernald (1917), de Langhe (1944), and David (1976) who all concurred with this application of the name *C. echinata.* The use of the name *C. echinata* for a member of the *Bracteosae,* as has been done by Kükenthal (1905, 1909), is in error.

Carex leersii Willdenow (1787) was clearly described and there is no doubt his name applies to the plant previously named *C. echinata.* However, since Willdenow cited the type of *C. echinata,* his name is illegitimate. *Carex stellulata* Goodenough was also clearly described and applies to *C. echinata* but is a later synonym. There can be no doubt that the correct name for the species in question here is *C. echinata* Murray.

Carex echinata, including the robust, coastal subspecies *phyllomanica,* is the most variable species of *Stellulatae* in North America. It ranges in height from 10 to rarely over 90 cm; the perigynia vary from slightly under 3 to well over 4 mm in length and in shape from lanceolate to more or less broadly ovate. The infructescence may be very lax and open to quite compact. Furthermore, as discussed previously, variations in these and other characters are often only loosely correlated with each other. As well, a large portion of the variation is expressed in Europe.

Carex echinata is most similar to *C. atlantica* and *C. interior.* Its separation from these two species and the occurrence of rare intermediates has been discussed under these species.

At present, the range of *Carex echinata* is essentially divided into two parts in North America (Figs. 23, 24). Although *C. echinata* is most abundant and robust near the east and west coasts, the virtual absence of the species in the boreal region of the center of North America may well be due to the species having been eliminated by Pleistocene glaciation. Its absence in the center of boreal North America is paralleled by its apparent absence from the center of boreal Russia (Egorova, 1960). In western North America, the species likely survived glaciation in the southern mountains, along the southern coast, and perhaps in coastal refugia northwards as discussed by Calder and Taylor (1968). In the east, it survived also in the southern mountains and along the southern coast. It is here postulated that the species is still actively migrating and, in future millenia, will colonize the boreal region of northern Canada and have a continuous distribution across the continent.

The splitting of the species range into parts during the glacial maximum is probably at least partly responsible for the great variability of the taxon. Also, as the species migrated into new territory after deglaciation, the migration was accompanied by further differentiation. As suggested earlier, the species is probably still actively migrating and evolving at the present. One of the consequences of this is the taxonomic difficulty of the *C. echinata* complex.

Carex echinata is primarily a species of acidic wetlands such as *Sphagnum* bogs, peaty or sandy lake and river shores, boggy meadows, and openings in coniferous forest. Along the northeast coast of North America, where the species is especially common, it may grow in roadside ditches, wet pastures and meadows, and even as a weed in commercial cranberry bogs.

7a. **Carex echinata** subsp. **echinata**

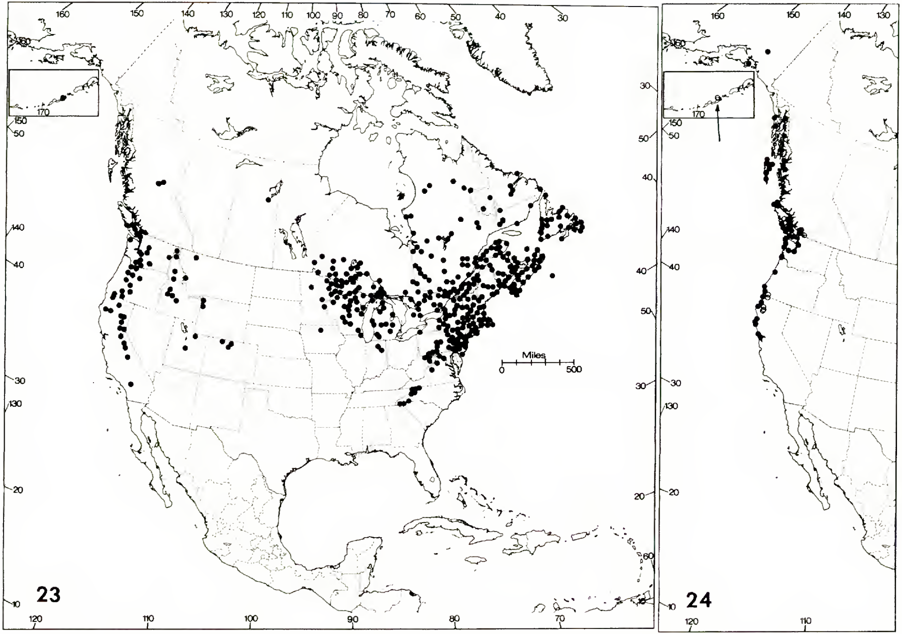
Culms 10–90 (135) cm; leaves usually 0.7–2.7 (3.3) mm wide; widest leaf 1.0–2.7 (3.3) mm wide; infructescence 7–78 mm, lax to dense; perigynia (2.65) 2.85–3.6 (4.6) mm, nerved or not over achene on adaxial surface; often serrulate on margins below base of beak. Figs. 33 (perigynia) and 44 (infructescences).

This widespread subspecies is abundant and variable throughout all the range shown in Fig. 23, except that it is largely replaced on the west coast of North America by *Carex echinata* subsp. *phyllomanica.* It is also widespread in Europe. The exact taxonomic disposition of Asiatic and southern hemisphere representatives of the *C. echinata* complex is not known.

7b. Carex echinata subsp. **phyllomanica** (W. Boott) Reznicek *comb. nov. C. phyllomanica* W. Boott *in* Watson, Bot. Calif. 2: 233. 1880. Holotype: In swamps, Mendocino City, California. H. N. Bolander 4746, 1866. GH(!). Isotypes NY(!), UC(!).

Culms 20–80 cm; leaves 1.0–3.3 (3.8) mm wide; widest leaf (1.7) 2.3–3.3 (3.8) mm wide; infructescence 12–25 (40) mm, very dense; distance between lower 2 spikes usually less than length of lowest spike; perigynia (3.1) 3.5–4.75 mm; usually 2–12 nerved over achene on adaxial surface; usually not serrulate below base of beak. Figs. 34 (perigynia) and 42 (infructescence).

This striking, broad-leaved western coastal race is distinctive in its extreme but forms that intergrade with *Carex echinata* subsp. *echinata* are scattered throughout its



FIGS. 23–24. Distribution of *Carex echinata*. 23. *C. echinata* subsp. *echinata*. 24. *C. echinata* subsp. *phyllomanica*. Open circles indicate intermediates with *C. echinata* subsp. *echinata*.

range, especially somewhat inland from the coast. It is widespread from Santa Cruz County, California (Munz, 1959) to the coastal regions of Alaska east of Prince William Sound (Fig. 24). It is especially robust and abundant on the Olympic peninsula, Washington, Vancouver Island, and the Queen Charlotte Islands. It occurs in bogs and along streams and lakeshores in the coastal forests.

8. **Carex seorsa** E. C. Howe *in* Gordinier & E. C. Howe, Fl. Renss. Co. N.Y. 39. 1894. Holotype: Border of shaded swamp, Lansings' Grove, Lansingburgh, N.Y. E.C. H[owe], May 1866. NYS n.v. Isotype NY(!).

C. rosaeoides E. C. Howe *in* Gordinier & E. C. Howe, Fl. Renss. Co. N.Y. 33. 1894. Not validly published. Name rejected by author; *C. seorsa* was substituted for it in same publication.

Rhizomes short; plants cespitose; roots smooth, yellowish to brown; culms 15–75 cm, erect to more or less spreading, elongating in fruit, aphyllopodic, smooth; basal

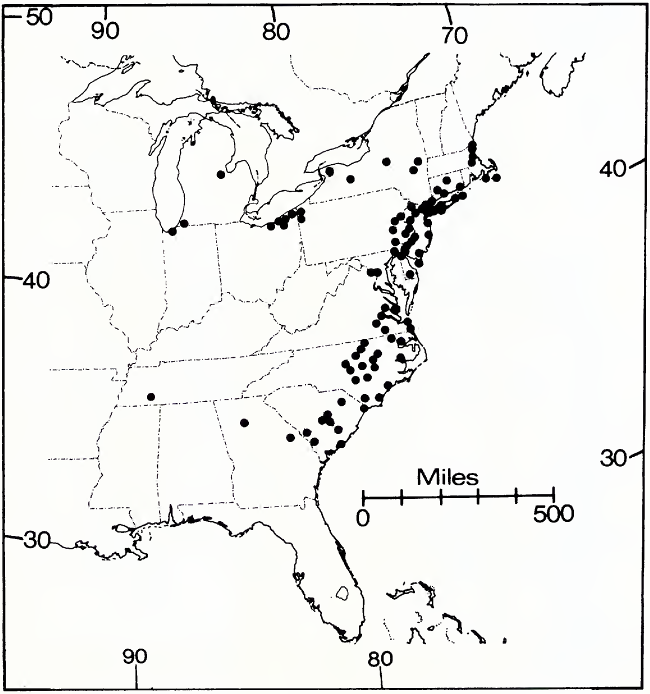
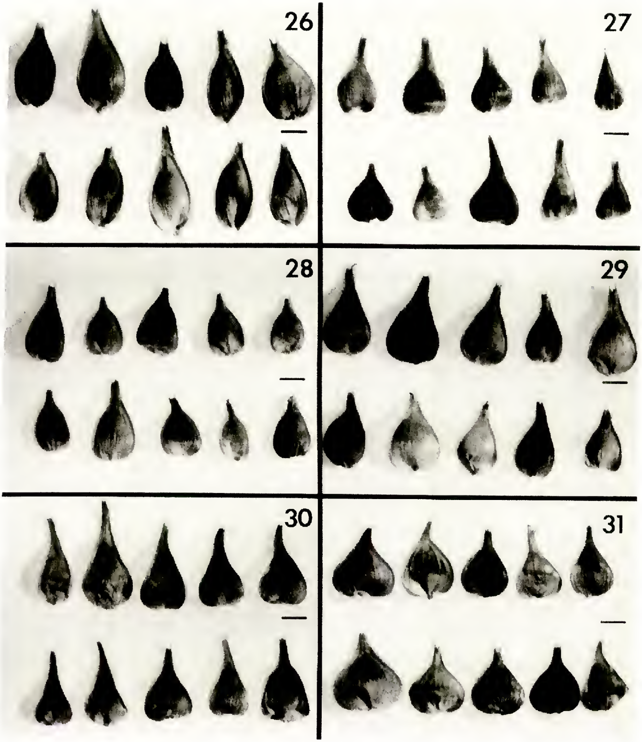


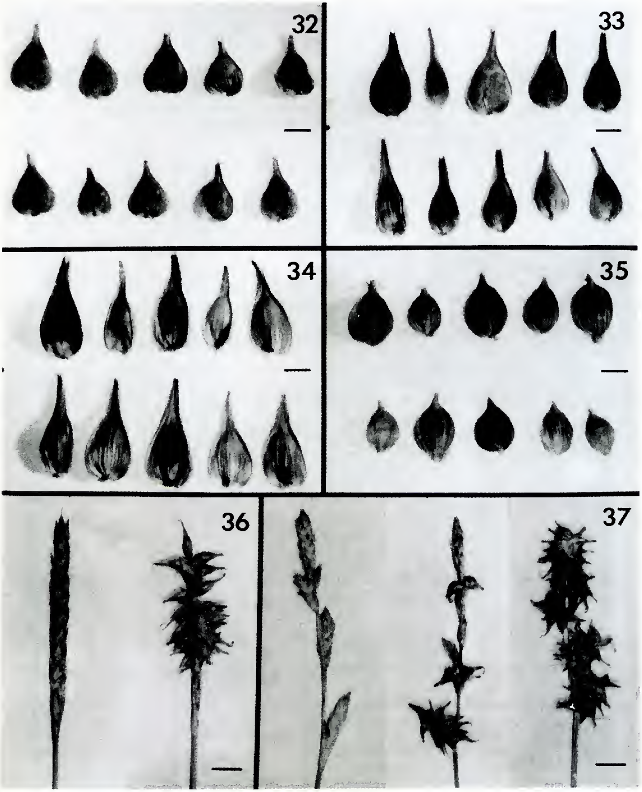
FIG. 25. Distribution of *Carex seorsa*.



FIGS. 26–31. Variation in perigynia of *Carex*. 26. *C. exilis*. 27. *C. sterilis*. 28. *C. interior*. 29. *C. wiegandii*. 30. *C. ruthii*. 31. *C. atlantica* subsp. *atlantica*. The bar equals 1 mm in all figures.

sheaths persistent, light brown. Leaves 2–4 per culm, all in basal third, usually shorter than culms in fruit; blades 9–50 cm X 0.8–3.9 mm, plicate to flat, antrorsely scabrous on margins above, upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 2.1–3.9 mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–12 cm; inner band hyaline; sheath apex deeply concave, not thickened; ligule 1.7–7.0 mm, acute or often with an emarginate apex. Infructescence 18–70 mm, lax; spikes 4–8. Terminal spike 4.7–16.5 mm, staminate at base, pistillate above; staminate portion 1.8–12.7 mm X 0.9–2.1 mm, 3–13-flowered; pistillate portion 2.8–7.3 mm X 4.4–6.0 mm, 6–23-flowered. Lateral spikes 2.8–10.8 mm sessile, pistillate with often a few staminate flowers at base; staminate portion (0) 0.8–4.6 mm, (0) 1–6-

flowered; pistillate portion 2.0–7.6 mm, 4–25-flowered. Distance between upper 2 spikes 0.6–5.5 mm, distance between lower 2 spikes 5–27 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.2–2.2 mm X 1.0–1.6 mm, ovate, one-nerved, acute, green with hyaline margins. Staminate scales 1.7–3.3 mm X 1.0–1.4 mm, ovate, one-veined, acute, green with hyaline margins. Lower perigynia of spikes spreading to reflexed, elliptic to elliptic-ovate, 1.8–2.9 mm X 1.0–1.9 mm, 1.2–2.1 times as long as



FIGS. 32–37. Variation in perigynia and infructescences of *Carex*. 32. *C. atlantica* subsp. *capillacea*. 33. *C. echinata* subsp. *echinata*. 34. *C. echinata* subsp. *phyllomanica*. 35. *C. seorsa*. 36. *C. exilis*. 37. *C. sterilis*. The bar equals 1 mm in Figs. 32–35 and 3 mm in Figs. 36 and 37.

FIGS. 38–45. Infructescences of *Carex*. 38. Variation in infructescences of *C. interior.* 39. Typical infructescence of *C. wiegandii.* 40. Variation in infructescences of *C. atlantica* subsp. *atlantica.* 41. Typical infructescence of *C. atlantica* subsp. *capillacea.* 41. Typical infructescence of *C. echinata* subsp. *phyllomanica.* 43. Typical infructescence of *C. ruthii.* 44. Variation in infructescences of *C. echinata* subsp. *echinata.* 45. Typical infructescence of *C. seorsa.* The bar equals 3 mm in all figures.

wide, tapering to a beak, plane-convex, green when ripe, brownish when over-mature, sessile, spongy-thickened at base surrounding achene, not serrulate on margins; adaxial nerves over achene absent or up to 6; abaxial nerves 6–14. Beak 0.2–0.6 mm, 0.09–0.33 times as long as body, smooth margined, apex truncate or obscurely blunt-toothed to 0.2 mm. Achenes 1.2–1.6 mm X 0.85–1.4 mm, ovate to orbicular, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 1.0–1.9 mm. Figs. 35 (perigynia) and 45 (infructescence).

The nomenclature and typification of *Carex seorsa* is straightforward. The name *C. rosaeoides* is not validly published as it was not accepted by the author when published (Stafleu, Voss et al. 1978, Art. 34. 1).

Carex seorsa is isolated in the *Stellulatae* with no near relatives. It is easy to separate from all other species and no intermediates are known. The species is very uniform throughout its range and no infraspecific taxa have been proposed.

The species is more or less restricted to the coastal plain in the south of its range but has penetrated newly glaciated territory to some extent in the north from northern Massachusetts to eastern Ohio (Fig. 25). The disjunct stations mapped near the head of Lake Michigan in Michigan and Indiana are characteristic of many more coastal species (Peattie, 1922; Voss, 1972).

Carex seorsa is somewhat different from the rest of the *Stellulatae* in its ecology. It is primarily a wet forest species. It appears to occur frequently on forest edges but is not a species of open wetlands.

Nomen Dubium

Carex echinata Murr. var. *microstachys* Boeckeler, Linnaea 39: 125. 1875.

The type of this variety was in the Berlin Herbarium (B) and was destroyed during World War II. The range of the taxon was given as "America borealis." There is no possibility of being certain of the application of this name from the description. It was placed by Mackenzie (1931) in synonomy with *Carex angustior.*

ACKNOWLEDGEMENTS

We wish to thank Dr. E. G. Voss for his helpful comments on the manuscript. This work was supported by the Canadian National Research Council Grant A6494 to P. W. Ball and Canadian National Research Council Postgraduate Scholarships and Ontario Graduate Scholarships to A. A. Reznicek.

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NOTES ON MARINE ALGAE FROM THE TROPICAL ATLANTIC OCEAN–VIII[1]

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A few years ago I published a large number of new stations for marine algae in the West Indies, particularly the Lesser Antilles, and a bibliography supplementing that which I had prepared earlier (Taylor 1960, 1969). The collecting had been done between January and April. A short trip was made during November 1972 to determine the condition of the marine flora at that time. It was found to be an unfavorable one, and while the intertidal vegetation differed little, that a bit deeper seemed less luxuriant and very little indeed was drifted ashore. The main attention was given to Grenada, but nearly as much to Barbados where I had given three previous periods to field study. The additions which I was able to make to their recorded floras were few, but they do help respecting continuity of range.

The small chain of islands between Grenada and St. Vincent, collectively called the Grenadines, had almost no recorded algal flora before 1966, when I spent a profitable day on the northernmost, Bequia Island (Taylor 1969, p. 139) and found a quite varied flora. This time I spent a day on the southernmost, Carriacou Island, and because of the season and the nature of the coast did not do quite so well. Politically it is a dependency of Grenada, as Bequia Island is of St. Vincent. However, there are most promising shoals inside a fringing reef which a person staying on the island and doing simple snorkeling and scuba diving would undoubtedly find most rewarding. Close to shore the vegetation was dominated by *Hypnea cervicornis* in spectacular golden masses, with *H. musciformis* and particularly *Spyridia filamentosa,* but there were a number of other things associated. For this island I have no previous records whatever, unless they are concealed among the very few listed collectively as from the Grenadines (Taylor 1960), and it is very worthy of detailed attention. It may be expected to show many things absent from or little known on Grenada, Barbados or other islands nearby lacking extensive reef-protected shoals.

Omitting the many collections I made in 1972 which added nothing new to the islands concerned, though they commonly were from new stations, I can offer the following supplementary list, using the sequence adopted in 1960.

LIST OF SPECIES

CHLOROPHYCEAE

Chaetomorpha nodosa Kütz.:–Grenada, St. Andrew Parish, Grand Mal Bay no. 72–50; Martins Bay, coll. J. G. Taylor from intertidal rocks, no. 72-125.

Chaetomorpha crassa (C. Ag.) Kütz.:–Carriacou I., 72-107C.

Chaetomorpha ? *aerea* (Dillw.) Kütz.:–Barbados, St. John Parish, Conset Bay, abundant on intertidal rocks, no. 72-184.

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[1] This study was in part supported by Grant no. GB-3186 from the National Science Foundation, for which help thanks are rendered.

Cladophora fuliginosa Kütz.:—Grenada, St. Andrew Parish, Grenville Beach, near the end of the airstrip at the north end of the beach, no. 72-66. The runway for the airplanes comes down essentially to the upper beach line.

Cladophora prolifera (Roth) Kütz.:—Grenada, St. Andrew Parish, Grenville Beach near the airstrip, no. 72-70.

Valonia ventricosa J. Ag.:—Carriacou I., no. 72-104.

Ernodesmis verticillata (Kütz.) Bǿrg.:—Carriacou I., no. 72-106.

Halimeda simulans Howe:—Grenada, St. George Parish, Morne Rouge Bay, no. 72-30.

Codium taylori Silva:—Grenada, St. George Parish, Morne Rouge Bay, washed ashore as a particularly dense, firm ball, no. 72-39.

PHAEOPHYCEAE

Ectocarpus coniferus Bǿrg:—Barbados, St. Lucy Parish, River Bay, on rocks in the little cove at the mouth of the intermittent "river," no. 72-163.

Giffordia indica (Sond.) Papenf. & Chihara:—It is perhaps well to indicate here that in a paper (Taylor 1973) dealing primarily with Pacific algae (and so quite easily missed by students of the Western Atlantic flora) I reported that after thorough study of type material, the literature, and of my Bermuda and West Indian material I felt constrained to agree that *G. duchassaingiana* (Grun.) Taylor should go under *G. indica* as a synonym. It accompanied *E. coniferus* at the above station and was present at Six Mens Bay in St. Peter Parish, but these are not new island records.

Sphacelaria tribuloides Menegh.:—Grenada, St. George Parish, Martins Bay, coll. J. G. Taylor from intertidal rocks, no. 72-127A; Grand Mal Bay, also on intertidal rocks, no. 72-55.

Dictyota dichotoma (Huds.) Lamx.:—Carriacou I., in shallow water on stones no. 72-115.

Dictyota divaricata Lamx.:—Grenada, St. George Parish, Morne Rouge Bay, washed ashore in abundance no. 72-24.

Dictyota cervicornis Kütz.:—Carriacou I. on stones in shallow water no. 72-116.

Padina gymnospora (Kütz.) Vick.:—Grenada, St. Andrew Parish, Marquis, no. 72-87; Carriacou I. on stones in shallow water, nos. 72-107A, 72-114B.

Sargassum vulgare C. Ag.:—Carriacou I., no. 72-108.

Sargassum hystrix J. Ag.:—Carriacou I., no. 72-107B.

Sargassum hystrix var. *spinulosum* (Kütz.) Grun.:—Carriacou I., no. 72-109.

RHODOPHYCEAE

Erythrotrichia carnea (Dillw.) J. Ag.:—Grenada, St. George Parish, L'Emboucherie, on *Padina*, no. 72-46.

Galaxaura oblongata (Sol.) Lamx.:—Grenada, St. George Parish, Morne Rouge Bay, no. 72-36.

Pterocladia pinnata (Huds.) Papenf.:—Grenada, St. George Parish, Morne Rouge Bay, on intertidal rocks, no. 72-32.

Fosliella lejolisii (Rosan.) Howe:—Carriacou I., on *Valonia ventricosa* no. 72-104, p.p.min.

Amphiroa fragilissima (L.) Lamx.:—Carriacou I., no. 72-120.

Amphiroa rigida Lamx. var. *antillana* Bǿrg.:—Grenada, St. George Parish, Morne Rouge Bay, no. 72-40A.

Gracilaria damaecornis J. Ag.:—Grenada, St. George Parish, Point Salines, Black Bay, no. 72-15.

Gracilaria cervicornis J. Ag.:—Carriacou I., no. 72-101.

Gracilaria foliifera (Forssk.) Bǿrg.:—Carriacou I., no. 72-102.

Gracilaria foliifera toward *v. angustissima* (Harv.) Taylor:–Carriacou I., no. 72-113.

Gracilaria sjostedtii Kylin:–Carriacou I., no. 72-110.

Solieria tenera (J. Ag.) Wynne and Taylor:–Grenada, St. Andrew Parish, Marquis, drifted ashore in some quantity, no. 72-83A. This is not a new island record, though the station is a new one. It is introduced to call attention to the change of generic assignment from *Agardhiella* which was foretold in Taylor and Rhyne (1970 p. 10) and effected by Wynne and Taylor (1973), after a study of a species lectotype and the cystocarp structure required this change.

Hypnea cervicornis J. Ag.:–Carriacou I., no. 72-111, -112. This plant was exceedingly abundant in shallow water near shore, forming great golden yellow masses.

Hypnea musciformis (Wulf.) Lamx.:–Carriacou I., no. 72-105.

Spyridia filamentosa (Wulf.) Harv.:–Carriacou I., no. 72-119. Abundant, with *H. cervicornis.*

Dasya collinsiana Howe:–Grenada, St. Andrew Parish, Grenville Beach north end near the airstrip, no. 72-67.

Polysiphonia ferulacea Suhr:–Grenada, St. Andrew Parish, Grenville Beach, north end near the airstrip, no. 72-68.

Polysiphonia opaca (C. Ag.) Zanard.:–Barbados, St. John Parish, Conset Bay, on higher intertidal rocks, associated with the more abundant *Murrayella,* no. 72-185B.

Bostrychia ?moritziana Mont.:–Carriacou I., on intertidal mangrove roots, ill-developed, no. 72-114A.

Acanthophora spicifera (Vahl) Børg.:–Carriacou I., no. 72-117A.

Laurencia papillosa (Forssk.) Grev.:–Carriacou I., on intertidal rocks, no. 72-117B.

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BOREOTHAMNION (CERAMIACEAE, CERAMIALES), A NEW RED ALGAL GENUS FROM ALASKA

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Collections of benthic marine algae were made at Amchitka Island in the Aleutians, Alaska, during the late 1960's and early 1970's in conjunction with the participation of University of Washington's Fisheries Research Institute in the United States Atomic Energy Commission's program of bioenvironmental studies conducted there. These collections have proved to be a rich source of material from a relatively remote oceanic region. The high incidence of undescribed taxa, including new species and some new genera (Wynne, 1970a, 1970b, 1972, 1977, in press; Lebednik, 1977) is a reflection of both the inaccessibility of the site and the fact that many specimens were obtained from SCUBA-collections or in the "drift," cast up from the sublittoral zone. Ecological observations on the benthic marine organisms have already been reported (Dayton, 1975; Lebednik and Palmisano, 1977), but the taxonomic investigations on the algae continue. Such an analysis is worthwhile owing to the location of Amchitka Island in an intermediate position between the western and eastern Pacific Ocean as well as its bordering the southern Bering Sea. This paper and the accompanying paper (Wynne, 1980) contribute toward further elucidating this flora.

Boreothamnion Wynne, gen. nov. (Ceramiaceae)

Thalli robusti, ramis principalibus distinctis, distiche ordinatis, irregulariter enascentibus; axes monopodiales in uno plano iacentes; cellula apicalis transverse se dividens; omne segmentum axium indeterminatorum quattuor (interdum tres) verticilli-ramulos in duobus paribus inaequalibus efficiens, ut axes compressi aut applanati sint; par primum formatum verticilli-ramulorum ex adverso ordinatorum valdius evolutum quam par secundum; corticatio rhizoidea e cellula basali verticilli-ramulorum vicina apici omnium axium indeterminatorum effecta et deorsum crescens; verticilli-ramuli axem primarium habentes, i.e. rachem percurrentem conspicuam, pinnatim aut quaternatim ramosam; axes indeterminati e cellulis axialibus pro verticilli-ramulis directe effecti; cellulae vegetativae uninucleatae; axes non mucosi; glandicellulae nullae; tetrasporangia tetraedrice divisa; plantae sexuales non visae.

Species typica: *Boreothamnion villosum* Wynne.

Thalli robust, with distichously arranged main branches that arise irregularly; monopodial axes lying in one plane; apical cell transversely dividing; each segment in the indeterminate axes producing four (at times 3) whorl-branchlets in two unequal pairs, resulting in compressed or flattened axes; the first-formed pair of oppositely placed whorl-branchlets more strongly developed than the second pair; rhizoidal cortication produced from basal cell of whorl-branchlets close to apex of all indeterminate axes and growing downward; whorl-branchlets with a primary axis, i.e., a conspicuous percurrent rachis that is pinnately or quaternately branched; indeterminate axes produced directly from axial cells in place of whorl-branchlets; vegetative cells uninucleate; axes not slimy; gland cells absent; tetrasporangia tetrahedrally divided; sexual plants not seen.

Characteristic features of the genus include the production of 4 (3) non-equivalent whorl-branchlets from each axial cell of the indeterminate axes, the percurrent branched whorl-branchlets, the rhizoidal cortication of the indeterminate axes, the uninucleate condition of the vegetative cells, the non-slimy consistency of the axes, the tetrahedrally divided sporangia, and the absence of gland cells.

Boreothamnion villosum Wynne, sp. nov. Figurae 1, 3, 5–9, 11–14.

Thalli 5–15 (–25) cm alt., per hapteron discoideum stuposum affixi; rami principales distiche ordinati, axes compressos 1–2 mm lat. habentes, verticilli-ramulis determinatis qui texturam coactam non-mucosam efficiunt dense obtectos; axes indeterminati in plana singula plerumque iacientes; 4 (interdum 3) verticilli-ramuli (in duobus paribus inaeque evolutis, morphologicaliter, autem, similibus) per omnem cellulam axialem producti; membra paris plus evoluti verticilli-ramulorum 600–700 μm long.; verticilli-ramuli distaliter directi, dense superpositi et tomentum continuum vel uniformem super axes efficientes; verticilli-ramuli rachem primariam pinnate ramosam habentes, ramulis lateraliter denuo ramosis; nonnullae cellulae horum ramusculorum in processus spinosus desinentes; rami indeterminati pro uno membro paris magis evoluti verticilli-ramulorum producti; cellulae vegetativae uninucleatae; cellulae axiales axium indeterminatorum usque ad c. 200 μm long., 160 μm lat.; corticatio rhizoidea e cellula basali verticilli-ramulorum evoluta, ut cellulas axiales omnino includant, et aliquot strata incrassatione facta, deorsum patens; axes corticati (verticilli-ramulis exclusis) 320–540 μm diam. facti; tetrasporangia spherici-ovoidea, 28–36 μm lat., 34–40 μm long., in verticilli-ramulis e cellula terminali et in pinnulis lateralibus verticilli-ramulorum effecta; plantae sexuales non visae.

Thalli 5–15 (–25) cm tall, attached by a discoid, stupose holdfast; distichously arranged main branches with compressed axes 1–2 mm broad, very densely covered with determinate whorl-branchlets that give a non-slimy, felted texture; indeterminate axes lying generally in a single plane; 4 (at times 3) whorl-branchlets (in two unequally developed but morphologically similar pairs) produced by each axial cell; the members of the more developed pair of whorl-branchlets 600–750 μm in length; whorl-branchlets distally directed, densely overlapping and effecting a continuous or uniform tomentum over the axes; whorl-branchlets with a primary rachis that is pinnately branched; the ramuli being further branched laterally; some cells of these ramuli terminating in spine-like processes; indeterminate branches produced in place of one member of the more developed pair of whorl-branchlets; vegetative cells uninucleate; axial cells of indeterminate axes to about 200 μm long, 160 μm broad; rhizoidal cortication developed from basal cell of whorl-branchlets, extending downward to completely enclose the axial cells and becoming several layers in thickness; corticated axes (excluding whorl-branchlets) becoming 320–540 μm in diam.; tetrasporangia spherical-ovoid, 28–36 μm broad, 34–40 μm long, produced terminally on whorl-branchlets and on lateral pinnules of the whorl-branchlets; sexual plants not seen.

Holotype: collected by P. A. Lebednik *AM126*, 22. xii. 1968, in drift, Top Camp (Lat. 51° 34.7′ N; Long. 178° 50.5′ E), Amchitka Island, the Aleutians, Alaska, U.S.A. Tetrasporic. Deposited in the University of Michigan Herbarium. Isotype in UC.

Other collections: ALASKA. Amchitka Island (the Aleutians), St. Makarius Bay: 7. ix. 1967 (*Weinmann 134*), 9. ix. 1967 (*Weinmann 4*), 10. ix. 1967 (*Weinmann 168*), 13. iii. 1968 (*Wynne 1313;* tetrasporic), 16. iii. 1968 (*Wynne 1354;* tetrasporic), 23. iii. 1968 (*Wynne 1478*), 13. viii. 1970 (*Wynne AM451*), 14. viii. 1970 (*Wynne AM479*); St. Makarius Point: 14. iii. 1968 (*Wynne 1324;* tetrasporic), 23. iii. 1968 (*Wynne 1478*); west of St. Makarius Point: 20. ix. 1968 (*Lebednik AM103*); Constantine Harbor: 1. ix. 1967 (*Weinmann 81*), 25. iii. 1968 (*Wynne 1509*); 2. v. 1969 (*Lebednik AM319*); Square Bay: 8. ix. 1967 (*Weinmann 132*), 14. ix. 1967 (*Weinmann 203*); Duck Cove: 16. vi. 1969 (*Lebednik AM376*); one mile off Duck Cove: 13. vi. 1969 (*Lebednik AM366*); Top Camp: 17. viii. 1970 (*Wynne AM578*); Kirilof Point: 11. vi. 1969 (*Lebednik AM362*); Bat Island off north side of

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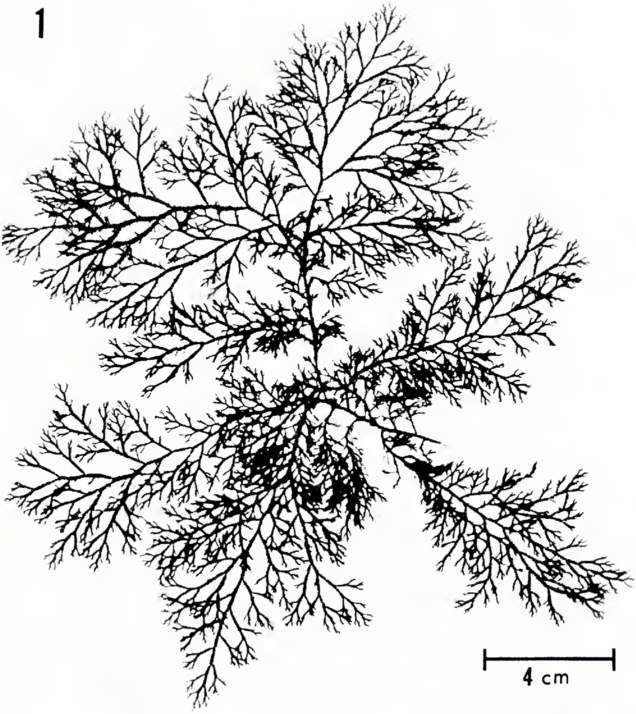

FIG. 1. *Boreothamnion villosum* (*AM479*).

Amchitka Island: 5. x. 1969 (*Lebednik AM415*); Rifle Range Point: 19. iii. 1968 (*Wynne 1442;* tetrasporic). Akutan Island, Hot Springs Bay: 15. vii. 1966 (*K. Baillie & R. Driskill 13736 = UBC A26763, A26765*).

Boreothamnion serratum Wynne, sp. nov. Figurae 2, 4, 10, 15, 16.

Thalli 6–10 (–12) cm alt., per hapteron stuposum affixi, ex axibus ramosissimis compressis, ad 1 mm lat., et distiche ordinatis constantes; axes plerumque in uno plano iacentibus, verticilli-ramulos in duobus paribus inaeque evolutis efficiens, pari magis evoluto, 3–6 segmentis e cellula apicali remoto, primum effecto; verticilli-ramuli laterales ad axem indeterminatum perpendiculariter dispositi, ita ut ambitus interruptus pectinatusve sint; verticilli-ramuli 3 vel 4 ramusculos e plerisque cellulis primariis ferentes, his vicissim denuo ramosis; nonnullae cellulae horum ramusculorum in processus spinosus desinentes; cellulae vegetativae uninucleatae; cellulae axiales axium indeterminatorum usque ad c. 230 μm long., 120 μm lat.; corticatio e cellulis basilibus verticilli-ramulorum evoluta, deorsum crescens ut axes omnino includant; tetrasporangia subglobosa, 28–30 μm lat., 32–36 μm long., in pinnuli lateralibus verticilli-ramulorum effecta; plantae sexuales non visae.

Thalli 6–10 (–12) cm tall, attached by a stupose holdfast, consisting of irregularly, abundantly branched axes that are compressed, to 1 mm broad, and distichously arranged; axes generally lying in one plane, covered with determinate whorl-branchlets; each axial cell producing 4 whorl-branchlets in two unequally developed pairs, the more developed pair being produced first, 3–6 segments from the apical cell; the lateral whorl-branchlets perpendicularly oriented with respect to the indeterminate axis, resulting in an interrupted or serrate contour; whorl-branchlets bearing 3 or 4 ramuli from most primary cells, and these in turn are further branched; some cells of these ramuli terminating in spine-like processes; vegetative cells uninucleate; axial cells of indeterminate axes to about 230 μm long, 120 μm broad; cortication developed from basal cells of whorl-branchlets, growing downward to completely enclose the axes; tetrasporangia

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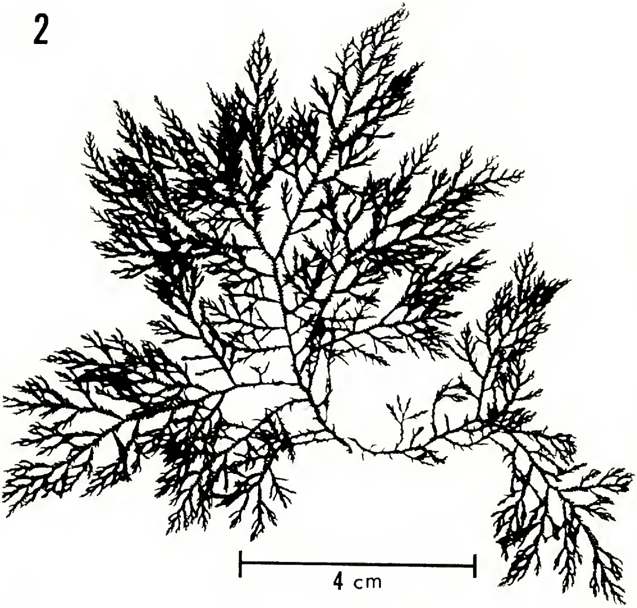
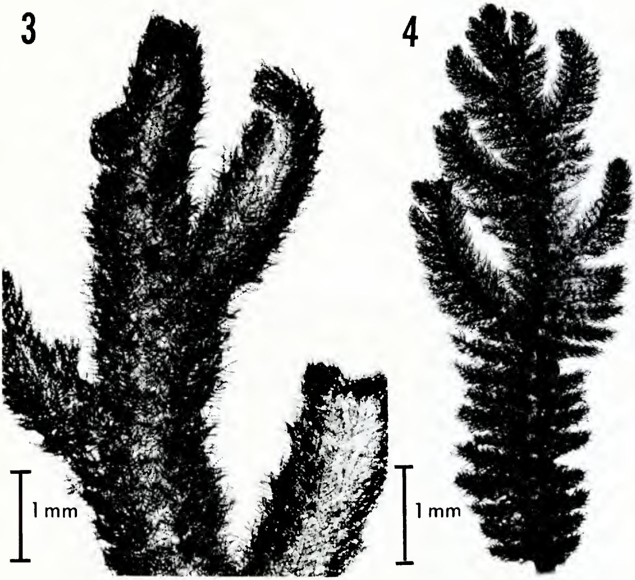


FIG. 2. *Boreothamnion serratum* (*AM626*).



FIGS. 3–4. Fig. 3. *Boreothamnion villosum.* Portion of a thallus near apex; Fig. 4. *Boreothamnion serratum.* Portion of a thallus near apex.

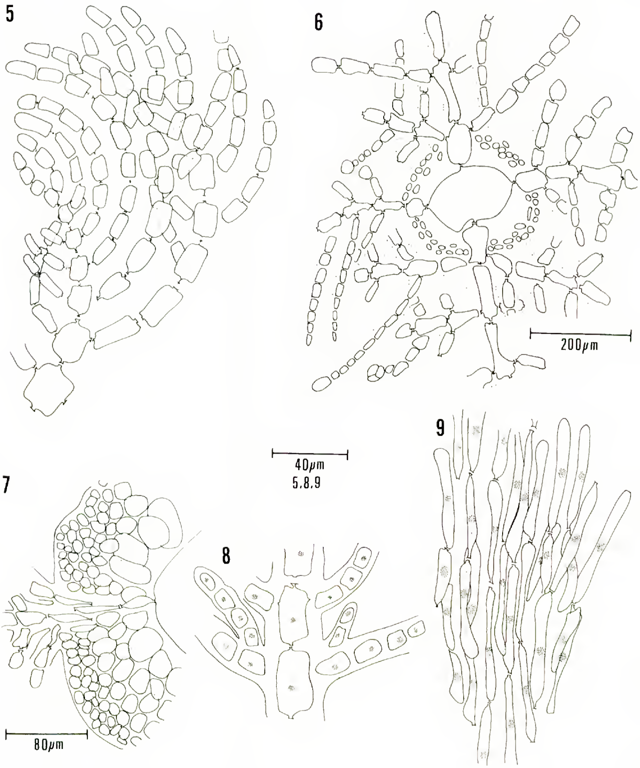
sub-globose, 28–32 μm broad, 32–36 μm long, produced on lateral pinnules of whorl-branchlets; sexual plants not seen.

Holotype: collected by Fred C. Weinmann *205,* tetrasporic, 10. ix. 1967, St. Makarius Bay (Lat. 51° 22.0′ N; Long. 179° 14.7′ E), In drift. Amchitka Island, the Aleutians, Alaska, U.S.A. Deposited in the University of Michigan Herbarium. Isotype in UC.

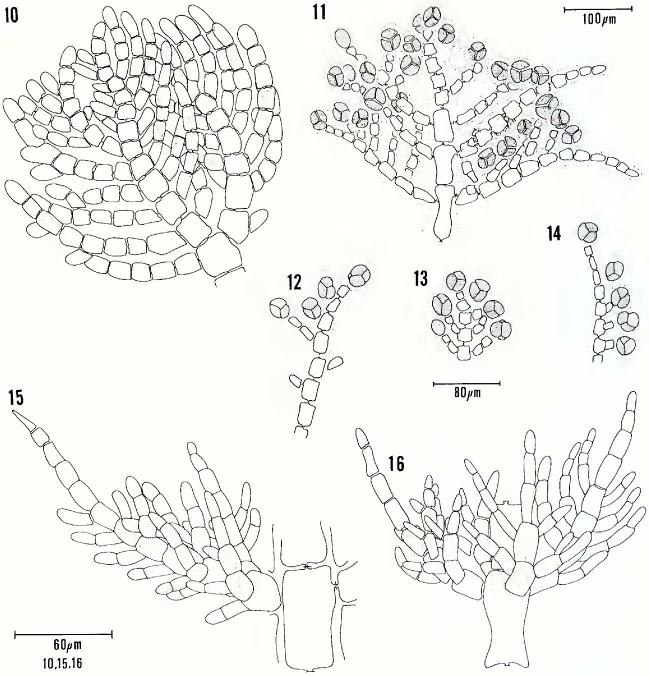
Other collections: ALASKA. Amchitka Island (the Aleutians), Constantine Harbor: 12. ix. 1968 (*Lebednik AM39*), 31. xii. 1968 (*Lebednik AM217A*), 13. iv. 1969 (*Lebednik AM252*), 2. v. 1969 (*Lebednik AM319*), 18. viii. 1970 (*Wynne AM626*), 21. x. 1972 (*Lebednik AM1177*); Kirilof Point: 2. v. 1969 (*Lebednik AM362*). Unalaska Island, Staraya Bay: 16. vii. 1966 (*A. Cattell & Baillie 13759 = UBC A26762*).

For a macroscopic differentiation of the two species (Figs. 1–4) one can see that *Boreothamnion villosum* is relatively less branched than *B. serratum* in regard to the indeterminate branching. The width of the axes of *B. villosum* exceeds that of the axes of *B. serratum.* One can also detect that the axes of *B. villosum* have a smooth, continuous contour with a villous or tomentose aspect (Fig. 3) due to the overlapping of whorl-branchlets; the axes of *B. serratum* have a more interrupted or serrate contour

(Fig. 4) due to the essentially perpendicular orientation of the whorl-branchlets in respect to the axes that bear them. This distinction is based on the different shapes of the whorl-branchlets in the two species: in *B. villosum* the rachis is pinnately branched, the whorl-branchlet having a triangular shape (Fig. 11) but in *B. serratum* the rachis is branched usually from four sides (Fig. 16), the laterals at the tip of the rachis being only slightly shorter than basal laterals and most laterals being further branched, resulting in a



FIGS. 5–9. *Boreothamnion villosum.* Fig. 5. Camera lucida drawing of apical portion (in part); not all cells are included due to their congested and overlapping arrangement; Fig. 6. Cross section of an axis, showing the production of 2 pairs of whorl-branchlets from each axial cell; their dimorphic nature is not evident in this drawing; Fig. 7. Cross-section of a portion of an axis showing the cortex; Fig. 8. Portion of a whorl-branchlet that has been stained to demonstrate the uninucleate condition of the cells; Fig. 9. Surface view of cortex that has been stained to show nuclei.



FIGS. 10–16. Figs. 10, 15, 16. ***Boreothamnion serratum.*** Figs. 11–14. ***B. villosum.*** Fig. 10. Camera lucida drawing of apical region of an indeterminate axis; Fig. 11. Whorl-branchlet bearing tetrasporangia. Figs. 12–14. Tetrasporangia in both terminal and sessile positions. Fig. 15. Young whorl-branchlet, showing the rachis terminating in a spine-like cell; Fig. 16. Lower portion of a whorl-branchlet with four pinnules developed from the basal cell.

stiff, bushy whorl-branchlet. For both species the terminal cells of these lateral branches are often attenuated into spine-like processes. In addition, in *B. serratum* some of the corticating cells were observed to bear extensions at right angles to their long axis, i.e., extending outward from the main axis of the alga.

Key to distinguish the two species of *Boreothamnion*

Axes of thallus to 2 mm broad, with a uniform contour; whorl-branchlets distally directed and overlapping one another, bearing opposite ramuli from most rachis cells. *B. villosum.*

Axes of thallus to 1 mm broad, with an interrupted, serrate contour; whorl-branchlets somewhat perpendicularly directed with respect to the indeterminate axis, bearing 3 or 4 ramuli from most rachis cells. *B. serratum.*

The lack of female plants in *Boreothamnion* makes it difficult to assign this genus to a tribe in the Ceramiaceae in that the position of the carpogonial branch is regarded as a critical taxonomic criterion within this family (Kylin, 1930; Feldmann-Mazoyer, 1940; Feldmann and Feldmann, 1966). The recent recognition by Itono (1977) of three sub-families is based almost entirely on features of the procarp.

Sixteen tribes are presently recognized (Schmitz, 1889; Feldmann-Mazoyer, 1940; Kylin, 1956; Hommersand, 1963; Wollaston, 1968, 1971; Gordon, 1972; Itono and Tanaka, 1973; Baldock, 1976; Itono, 1977): Crouanieae, Warrenieae, Dohrnielleae, Heterothamnieae, Delesseriopsieae, Antithamnieae, Ceramieae, Callithamnieae, Spyridieae, Wrangelieae, Ptiloteae, Dasyphileae, Griffithsieae, Spermothamnieae (including Ptilothamnieae), Sphondylothamnieae, and Compsothamnieae (including Pleonosporieae and Spongoclonieae). The vegetative characteristics along with the tetrasporangial features permit some comparison with certain of these tribes. Guiry (1978) has indicated that most genera of the Ceramiaceae have tetrahedrally divided tetrasporangia, cruciate division occurring in only a few tribes and being considered as more primitive. In general, a given tribe is characterized by one mode of division, although some exceptions have been noted (cf. Guiry, 1978, Table III).

Boreothamnion is similar to the tribe Crouanieae in having whorl-branchlets in whorls of 3 or 4, tetrahedrally divided tetrasporangia, and rhizoidal cortication. Among genera of Crouanieae *Euptilocladia* most resembles *Boreothamnion* in that both genera have flattened, monopodial axes, with alternate distichous branching from the edges, heavily corticated and bearing four whorl-branchlets from each axial cell in opposite pairs with one pair longer than the other (Wollaston, 1968). However, *Euptilocladia* has numerous short determinate branches in addition to the indeterminate branches and the whorl-branchlets; such determinate branches are absent in *Boreothamnion*. Another difference is that branches are initiated from the basal cell of the whorl-branchlets in *Euptilocladia* (Wollaston, 1968, Figs. 13J, 14J), whereas in *Boreothamnion* the branches arise directly from the axial cell and replace the lateral whorl-branchlet. The other distinction is the structure of the whorl-branchlet: a pinnately or quaternately branched percurrent rachis in *Boreothamnion* but a series of successive whorls of 2–4 cells each terminating in a chain of small cells in *Euptilocladia*. This type of branching by successive whorls each of 2–4 cells is true of the whorl-branchlets in all the Crouanieae and thus makes the placement of *Boreothamnion* in that tribe untenable.

In looking at the Antithamnieae, we see some points of agreement between this tribe and *Boreothamnion*, such as the whorl-branchlet having the form of a pinna, this term employed by Wollaston (1968) to designate those whorl-branchlets with a central rachis bearing distichously arranged pinnules and typical of most genera of this tribe. Among the Antithamnieae *Platythamnion* appears to bear the greatest resemblance to *Boreothamnion* in that both genera have four whorl-branchlets (a pair of lateral longer ones and a pair of transverse shorter ones) from each axial cell (Wollaston, 1972). The only corticated species in *Platythamnion* is *P. nodiferum* (J. Ag.) Wollast. from southern Australia (Wollaston, 1968). The characteristic deflection of the apex of the main axis observed in *Platythamnion* does not occur in *Boreothamnion*. In addition, the gland cells and the cruciately divided tetrasporangia present in *Platythamnion* and in this tribe are not found in *Boreothamnion*. These differences effectively preclude the assignment of *Boreothamnion* to the Antithamnieae.

Boreothamnion is unlike Heterothamnieae (Wollaston, 1968) in that this tribe lacks the distinct holdfast and the corticating rhizoids seen in this genus. Also, gland cells are typical for this tribe but are lacking in *Boreothamnion*. Similarities exist, such as the tetrahedrally divided tetrasporangia and the presence of 2, 3, 4, or 5 whorl-branchlets per cell, but these whorl-branchlets are usually branched by successive whorls of cells as in the Crouanieae, unlike the pinnate form of the whorl-branchlets in *Boreothamnion*. *Antithamnionella* and *Trithamnion* in the Heterothamnieae do have whorl-branchlets that may be distichously branched (or simple), but both of these genera have significant differences from *Boreothamnion,* such as the presence of gland cells in both, the variable form and number of the whorl-branchlets in *Antithamnionella,* and the unilateral placement of the whorl-branchlets in *Trithamnion.*

The vegetative cells of *Boreothamnion* are uninucleate,[1] which is the condition in Wrangelieae (containing the single genus *Wrangelia*), but the indeterminate branches in *Wrangelia* originate from the basal cells of whorl-branchlets (Gordon, 1972), unlike their origin in the position of whorl-branchlets directly on axial cells. Such traits as the multinucleate condition of the vegetative cells and/or lack of whorl-branchlets further prevent us from associating *Boreothamnion* with the Spermothamnieae, Griffithsieae, Sphondylothamnieae, or Compsothamnieae (L'Hardy-Halos, 1970; Gordon, 1972).

Although the nuclear condition in most genera of the Ptiloteae has not been reported, the uninucleate condition is present in *Plumaria* (L'Hardy-Halos, 1970) and also in *Ptilota, Neoptilota,* and *Tokidaea* (unpubl. obs.). Although most genera of the Ptiloteae are characterized by a regular alternation of long and short branches along the axes and pseudoparenchymatous cortication (Erskine, 1955; Kylin, 1956), this pattern is not true of all the genera. In *Tokidaea,* a recently described genus (Yoshida, 1974), each axial cell bears a pair of lateral whorl-branchlets, at times accompanied by a third little-developed whorl-branchlet inserted perpendicular to the first two. Other features of *Tokidaea,* including the transverse segmentation of the apical cells, rhizoidal cortication developed from the basal cell of whorl-branchlets, and tetrahedrally divided tetrasporangia, are shared with *Boreothamnion.*

A sample of *Tokidaea corticata* (Tokida) Yoshida kindly provided[2] by Dr. T. Yoshida was examined and compared with *Boreothamnion. Tokidaea* is a much less robust plant than the two species of *Boreothamnion,* as is evident from Tokida's illustrations (1932, fig. 3, pl. IIIb–d, as *Antithamnion corticatum*). The transverse whorl-branchlets, which are not even mentioned in Tokida's original account, are figured as very rudimentary in Yoshida's description and do not match the well developed pair of transverse whorl-branchlets in *Boreothamnion.* The apices in *B. villosum* are usually completely covered by the distally arching whorl-branchlets in this species and thus hardly discernible. The apices of the axes in *B. serratum* are less covered but still more occluded than in *Tokidaea.* The cortication in *Boreothamnion* begins very close to the apex, whereas the upper portions of *Tokidaea* are free of cortication.

The position of the tetrasporangia is a characteristic that is regarded (Wollaston, 1968; Itono, 1977) as of limited taxonomic utility, being at times useful at the generic level. It is true that for a given genus tetrasporangia are usually borne as either sessile or pedicellate structures (Feldmann-Mazoyer, 1940). *Boreothamnion* would appear to be somewhat atypical in having tetrasporangia both with and without stalk cells (Figs. 12–14). The tetrasporangia are produced on the lateral pinnules of the whorl-branchlets for both species of *Boreothamnion* and additionally at the terminal ends of the whorl-branchlets in *B. villosum.* In the Crouanieae Wollaston (1968) showed that the tetrasporangia are borne on the basal cell of whorl-branchlets in *Crouania* and *Gattya,* whereas their position ranges from the basal cell to the outer cells of the whorl-branchlets in the various species of *Ptilocladia* and *Euptilocladia.* The terminal position of some of the tetrasporangia in *Boreothamnion* resembles that of *Gymnothamnion* in the Ptiloteae (Feldmann-Mazoyer, 1940). There is also similarity to the aforementioned *Tokidaea* (Yoshida, 1974), in which tetrasporangia occur in both sessile and pedicellate

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[1] Both acetocarmine and Wittman's iron hematoxylin stains were employed in demonstrating nuclei in the two species.

[2] Legit M. Kurogi and I. Yamada, 30. ix. 1970, Nemuro, Hokkaido, Japan.

positions on the adaxial surface of the whorl-branchlets but apparently not in terminal positions from the primary rachis as in *Boreothamnion.*

The quadri-verticillate whorls of branchlets in *Boreothamnion* and the cutting off of the pericentral cells (i.e., the basal cells of the four whorl-branchlets) in opposite pairs rather than in a rhodomelacean sequence would be regarded as generally primitive features in the family. The same would apply to the manner in which cortication is produced by the basal cell (pericentral cell) of the whorl-branchlets and the fact that the cortication consists of rhizoidal downgrowths rather than a condensation of the whorl-branchlets as seen in the Ceramieae and some of the Ptiloteae. The tetrahedrally divided tetrasporangia, the absence of gland cells, the dimorphism of the whorl-branchlets, and a highly elaborate thallus structure would be regarded as generally more advanced traits. In summary, *Boreothamnion* exhibits greatest affinity for the tribe Ptiloteae, resembling *Tokidaea* most closely but differing from the genus in several respects.

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BERINGIELLA (RHODOMELACEAE, CERAMIALES), A NEW RED ALGAL GENUS FROM ALASKA

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Even with the recent tally (Lindstrom, 1977) of 376 species of benthic marine algae that have been recorded from Alaska, it is evident that the waters along the extensive coastline[1] of this state hold yet a large number of undescribed taxa. An explanation lies in the fact that much of the coastline has been little explored phycologically on account of both the frequency of weather conditions unfavorable for collecting and the inaccessibility of most sites. Fairly intensive collecting carried on at Amchitka Island (cf. accompanying paper, Wynne, 1980, for background) provides evidence that a close scrutiny of both eulittoral and sublittoral habitats of this one relatively small area can turn up a surprisingly high number of new taxa. An additional new genus containing a single species is described in this paper.

Beringiella Wynne, gen. nov. (Rhodomelaceae)

Thalli ramosissimi, teretes, crescentes e singula cellula apicali exposita, quae radialiter instituta et ramos determinatos indeterminatosque holoblasticaliter efficit; quinque (interdum quattuor) cellulae pericentrales in axibus et determinatis et indeterminatis effectae, hae cellulae pericentrales singulae transverse se dividentes, cellula superiore cellula centrali semper connexa; hae cellulae deinde et anticlinaliter et periclinaliter se dividentes diametrum axium augentes; axes et determinati et indeterminati cellulas corticales parvas in dispositione pseudoparenchymatica atque cellulas interiores longitudinaliter sectatas habentes; cellulae pericentrales in transectione non manifestae; trichoblastae vegetativae nullae.

Procarpus in trichoblasta portatus, pericarpo tectus quum trichogyne receptoria est; cystocarpus maturus pericarpum bene evolutum habens. Tetrasporangia tetraedrice divisa, in axibus immutatis singulatim in unoquoque segmento axiali effecta. Plantae masculae non visae.

Species typica: *Beringiella labiosa* Wynne.

Thalli much branched (Fig. 1), terete, with growth from a single exposed apical cell, which is radially organized and holoblastically produces determinate and indeterminate branches; five (at times four) pericentral cells produced in both determinate and indeterminate axes (Figs. 2–4, 6, 7), these pericentral cells each undergoing a transverse division, the upper cell retaining connection with the central cell; these cells then undergoing both anticlinal and periclinal divisions, increasing the diameter of the axes; both indeterminate and determinate axes with small cortical cells in a pseudoparenchymatous arrangement (Fig. 8) and inner longitudinally coursing cells; pericentral cells not evident in transection; vegetative trichoblasts absent.

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[1] About 10,600 km (6,600 miles) of coast fronting the sea and about 55,000 km (34,000 miles) of indented tidal coastline comprise Alaska's three faces to the sea (New Encyclopaedia Britannica, 1978).

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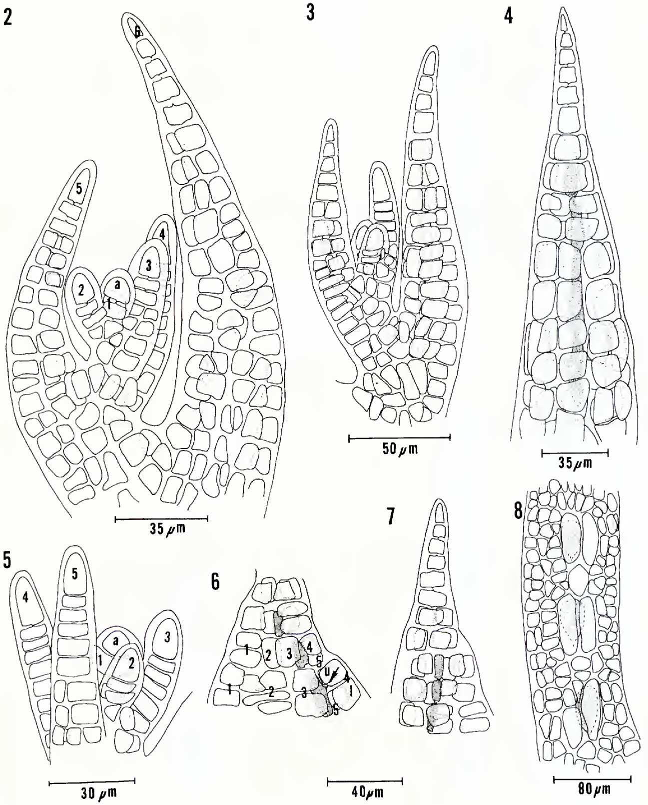
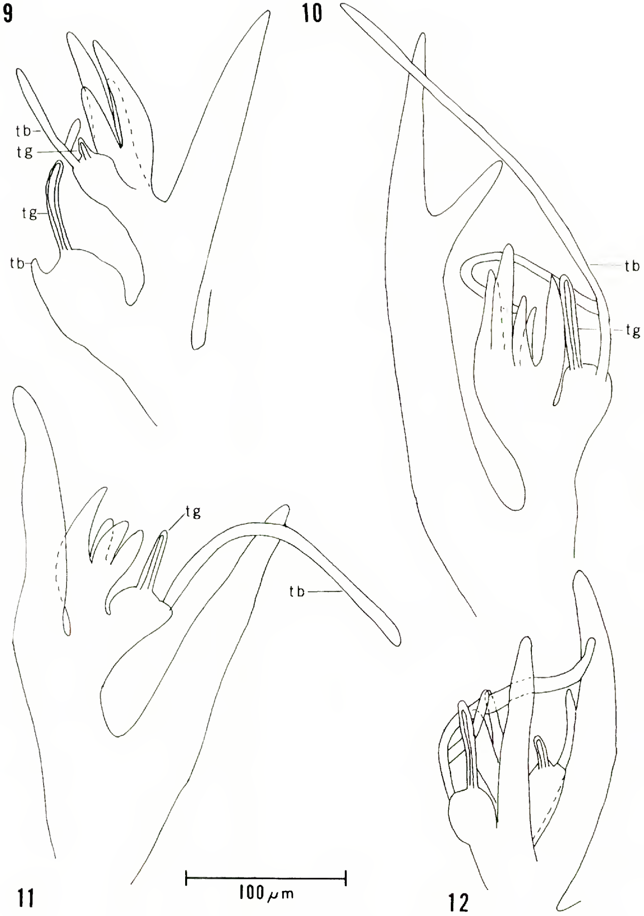
FIG. 1. ***Beringiella labiosa.*** Portion of the holotype specimen (*AM360*).

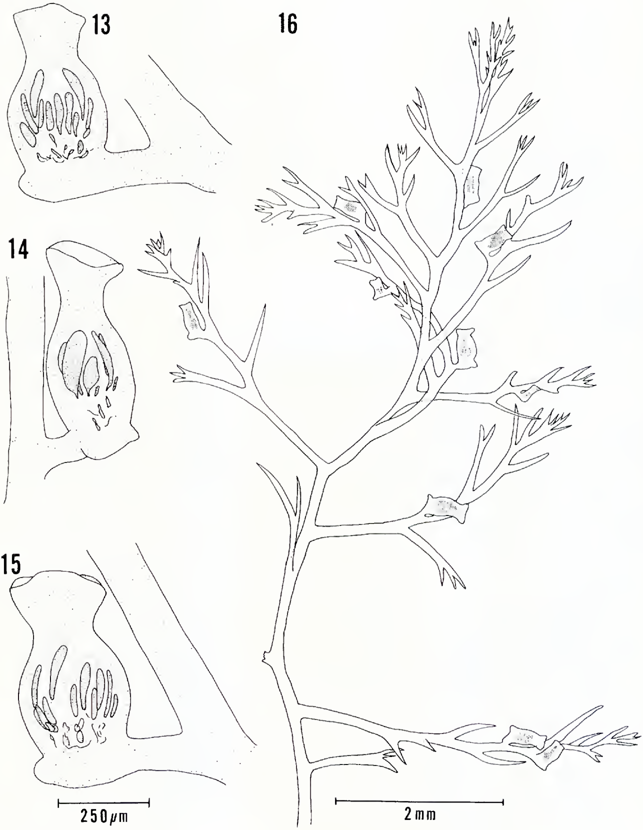
Procarp borne on a trichoblast (Figs. 9–12), covered by pericarp when trichogyne is receptive; mature cystocarp with a well developed pericarp (Figs. 13–16). Tetrasporangia tetrahedrally divided, produced singly per axial segment in unmodified axes (Figs. 17–19). Male plants not seen.



FIGS. 2–8. *Beringiella labiosa.* Fig. 2. Apical region of indeterminate axis, showing the apical cell (a) and spirally arranged lateral branches numbered in their sequence of formation, 1 being newly formed; Fig. 3. Apical region of indeterminate axis with determinate laterals; Fig. 4. Apex of a determinate branch showing evidence of 4 pericentral cells and their transverse division; Fig. 5. Apex of an indeterminate axis, showing exogenous production of lateral branches from each axial segment, the youngest (1) in the process of being cut off and the others (2–5) being later stages; Fig. 6. Portion of an axis (slightly squashed) with 5 pericentral cells and evidence of their transverse division and the connection of an axial cell (stippled) to the upper product of the transverse division of a pericentral cell (arrow); Fig. 7. Apex with production of 5 pericentral cells; Fig. 8. Portion of a tetrasporic axis with young sporangia and their cover cells.



FIGS. 9–12. *Beringiella labiosa.* Tips of female plants bearing procarps, their association with trichoblasts (tb) and the trichogynes (tg) extending from the pericarp.

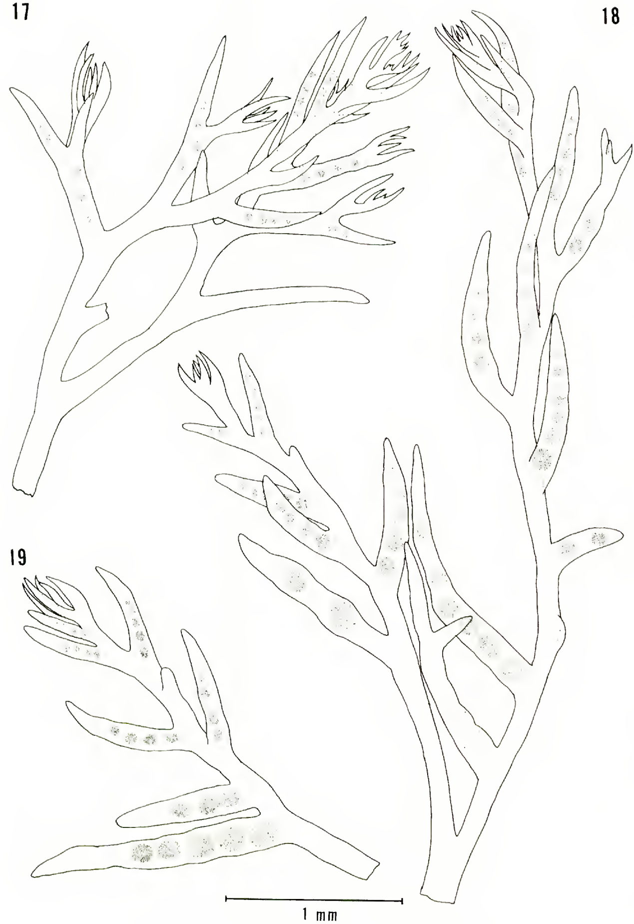


FIGS. 13–16. *Beringiella labiosa.* Figs. 13–15. Mature cystocarps. Fig. 16. Cystocarpic thallus.

Beringiella labiosa Wynne, sp. nov.

Thalli 6–10 (–14) cm alt. ramosissimi ad multos ordines ramificationis; axes prope basim thallorum circa 1 mm lat.; thalli porphyrei ad atropurpureos.

Procarpi multi prope cacumina ramorum, ad basim trichoblastae reductae effecti; pericarpus conspicuus, urceolatus, 570–600 µm long., 245–380 µm lat.; os pericarpi



FIGS. 17–19. *Beringiella labiosa.* Tetrasporic branches.

manifeste expansum, bucciniforme; cystocarpus carposporangia ovoidea, 150–160 μm long. et 32–40 μm lat. continens; tetrasporangia 115–160 μm diam., tetraedrice divisa, in seriebus 4–6, in ordinibus ultimatis penultimatisque ramorum immutorum reperta.

Thalli 6–10 (–14) cm tall, profusely branched, to many orders of branching; axes near base of thalli about 1 mm wide; thalli brownish-red to dark purple.

Procarps occurring in abundance near tips of branches, produced at base of a reduced trichoblast; pericarp conspicuous, ureolate, 570–600 μm long by 345–380 μm broad; mouth of pericarp distinctively flared, bugle-shaped (Figs. 13–15); cystocarp containing carposporangia that are ovoid, 150–160 μm long and 32–40 μm broad; tetrasporangia 115–160 μm in diam., tetrahedrally divided, in series of 4–6 in ultimate and penultimate orders of unmodified branches.

Holotype (Fig. 1): collected by P. A. Lebednik *AM360,* 11. vi. 1969, 20–26 m depth, Kirilof Point (Lat. 51° 24.4′ N; Long. 179° 18.2′ E), Amchitka Island, the Aleutians, Alaska, U.S.A. Cystocarpic. Deposited in the University of Michigan Herbarium (MICH). Isotypes have been deposited in the United States National Herbarium, Smithsonian Institution (US) and the herbaria of the University of California, Berkeley (UC), University of British Columbia, Canada (UBC), and Hokkaido University, Japan (SAP).

Other collections: ALASKA. Amchitka Island (the Aleutians), St. Makarius Bay: 9. ix. 1967 (*Weinmann 21;* drift collection); entrance to Constantine Harbor: 12. ix. 1968 (*Lebednik AM40;* 13 m depth; tetrasporic), 26. iv. 1969 (*Lebednik AM292;* 16–26 m depth; cystocarpic), 28. iv. 1969 (*Lebednik AM308;* 12–15 m depth; cystocarpic), 2. v. 1969 (*Lebednik AM313, Lebednik AM321;* 6 m & 13 m depths; tetrasporic).

This alga is known only from Amchitka Island. *Beringiella* refers to the Bering Sea; *labiosa* (Lat., having large lips) refers to the out-flared rim of the pericarp.

Development in *Beringiella*

Actively growing tips of *Beringiella* are comprised of a congested cluster of closely over-arching lateral branches, most of which are of a determinate type and others of an indeterminate type. A close examination of these tips reveals that the primary axis has a large dome-shaped apical cell cutting off flattened, discoid segments proximally (Fig. 5). It appears that each segment produces a branch by the lateral outward protrusion of the segment (Fig. 5). This exogenous, or holoblastic, development of branches occurs as early as the first segment. Spirally arranged determinate branches can be seen to be associated with each successive central cell of the primary axis (Figs. 2, 5). These polysiphonous radial branches of limited growth are referred to as "brachyblasts" by Hommersand (1963) and represent one type of modified holoblastic branching. In *Beringiella* they appear as undivided, spinelike laterals.

An indeterminate lateral branch is produced in the same manner as that of the determinate branches. The apical cell of an indeterminate axis is dome-shaped, and the polysiphonous condition develops within two or three segments from the apical cell; the apical cell of a determinate axis is attenuated, and several distal segments remain undivided (Figs. 3, 4). Although the usual number of pericentral cells appears to be five (Fig. 6), four pericentral cells have also been observed (Fig. 4). These pericentral cells each undergo a transverse division, the upper product of this division retaining the pit connection with the central cell (Fig. 6, arrow). This connection was difficult to detect, and several stains[2] were used in attempting to demonstrate this critical taxonomic

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[2] These included aniline blue, lactophenol-cotton blue, Delafield's hematoxylin (Johansen, 1940), and Wittmann's aceto-iron-hematoxylin chloral hydrate (Wittmann, 1965). A treatment (Morrill, 1976) of 1% aniline blue acidified with a drop of 0.5% HCl and mounted in glycerine gave best results.

feature. Gentle squashing of the stained material was necessary to reveal the structure of the apices.

Discussion

The transverse division of pericentral cells is of relatively limited occurrence in the Rhodomelaceae, restricted to three tribes: Bostrychieae, Rhodomeleae, and Rhodolachneae. Since this criterion is of such fundamental taxonomic significance, it facilitates the search for close relatives of this new genus. Other morphological features of *Beringiella* can be compared with members of these three tribes.

In respect to the pericentral cells, the number varies from 4 to 10 in the Bostrychieae, although 5 and 6 are the more common numbers. These pericentral cells may undergo additional transverse divisions following the first such division, resulting in several tiers of cells per central cell. The lower pericentral cells in *Bostrychia* and in *Benzaitenia* (Morrill, 1976) are in pit-connection with the central cell.

In the Rhodomeleae 6 (–7) pericentral cells are present in *Rhodomela* (Kylin, 1914) and 4 primary ones in *Odonthalia* (Falkenberg, 1901; Kylin, 1934), and here also several transverse divisions may occur, bringing about several tiers of cells per central cell. The upper pericentral cells in *Beringiella* are in pit-connection with the central cells. In *Rhodolachne* (the only genus in the Rhodolachneae) there are only 4 pericentral cells, each of which undergoes a single transverse division (Womersley and Bailey, 1970; Wynne, 1970); the lower pericentral cells are in pit-connection with the central cell. *Beringiella,* which has an original group of 4 or 5 pericentral cells that retain connection between the upper cells (after division) and the central cell, would agree with the Rhodomeleae. A variable number of pericentral cells is encountered in other genera of the family, such as *Benzaitenia* (Morrill, 1976), *Rhodomela* (Kylin, 1914), and within single species of *Polysiphonia* (Hollenberg, 1944).

Trichoblasts are entirely lacking in the Bostrychieae and the Rhodolachneae. In Bostrychieae the procarp is borne naked, originating on pericentral cells along the axes of ordinary branches, and no pericarp is present until after fertilization (Hommersand, 1963). In the Rhodomeleae vegetative trichoblasts are lacking in *Odonthalia* but are present as deciduous structures in *Rhodomela.* Both of these genera have fertile trichoblasts on which the procarps are borne, this being a point of agreement with *Beringiella.*

Another similarity with *Beringiella* is the radial symmetry of the axes in the Rhodomeleae and Rhodolachneae, unlike the dorsiventral symmetry of the axes in Bostrychieae. Axes may be partially prostrate in the Bostrychieae and Rhodolachneae, but they are entirely erect in *Beringiella* as well as the Rhodomeleae. Cortication is well developed in the Rhodomeleae and most species of Bostrychieae, this feature conforming with *Beringiella.* Rhodolachneae, on the other hand, has uncorticated axes.

Tetrasporangia are borne in opposite pairs in the Rhodomeleae and Rhodolachneae. In the Bostrychieae sporangia may occur in whorls of up to 6 per segment. If there are only two per segment in *Bostrychia,* they occur in two longitudinal series on one side of the fertile axis, reflecting the dorsiventral nature of the axes in this tribe. The production of a single tetrasporangium per segment in *Beringiella* is a difference from these three tribes.

The available evidence suggests that *Beringiella* fits most comfortably with the Rhodomeleae, the majority of points of agreement being with this tribe. The production of a single sporangium per segment in *Beringiella* is the main discrepancy with *Odonthalia* and *Rhodomela.* In the Rhodomelaceae there are instances of genera in the same tribe having differing number of sporangia per segment (e.g., Polysiphonieae, Lophothalieae, and Lophosiphonieae) and even of this variability present in a single genus (e.g., *Bostrychia*). So there is precedence for having such variation within a single tribe.

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