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COVER IMAGE

Fire storm working its way along the lower portion of Market Street, San Francisco. Facing northeast, looking toward the Call (or Spreckels) Building (center, 4th building counting from the right edge) on the south side of Market Street at 3rd and Market. The California Academy of Sciences' Market Street building is the second on the right (south side, near 4th and Market); the Emporium is the first building on the right (south side, between 4th and 5th and Market). Although these buildings had some level of reinforced steel construction, none was adequately fireproofed. Initial reports indicated that they withstood the shock of the earthquake but not the fire that followed. (A 1906 colorized image. California Academy of Sciences Archives, San Francisco Earthquake 1906.)

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The California Academy of Sciences, Grove Karl Gilbert, and Photographs of the 1906 Earthquake, mostly from the Archives of the Academy

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In the early morning hours of 18 April 1906, a catastrophic earthquake struck the San Francisco region of central California. Buildings were severely damaged, transportation systems disrupted, water mains broken. When fires broke out in the downtown area, firefighters had no means to control them. The California Academy of Sciences museum building lay in the path of advancing fires and in time was consumed, as were most of the buildings in the downtown section of the city. The Academy, founded in 1853, included among its founders and earliest members, John Boardman Trask who had an abiding interest in the history of California earthquakes and, as early as 1855, published a first catalogue of such events dating from 1812 to 1855. Following the 1868 "Haywards" earthquake in the East Bay and the aborted effort of the Chamber of Commerce Committee to write a comprehensive report on the event, interest in earthquakes waned among Academy members and the public-at-large as well. At the time of the 1906 event, Grove Karl Gilbert, a geologist with the U.S. Geological Survey, was on the scene having been assigned to study the effects of hydraulic mining. Gilbert was tapped immediately to participate in an investigation into the causes and effects of the earthquake. The study was undertaken by the California State Commission for the Investigation of the Earthquake, appointed by California's Governor Pardee and funded by a grant from the Carnegie Institution of Washington, D.C. Andrew Lawson of the University of California, Berkeley, chaired the Committee. Gilbert's assignment was to investigate the effects of the earthquake in Marin County. Accompanied by Alice Eastwood, the California Academy of Sciences' curator of Botany, he traveled as far north as Inverness and Pt. Reyes taking photographs and amassing field notes describing the changes in the landscape. Gilbert gave Alice Eastwood a large number of original prints of the many photographs he took. These were placed in the Academy's archives together with photographs taken by members of the Academy's staff or others who were living in the Bay Area at the time. A selection of these photographs is presented here, some appearing in print for the first time.

Dedication

This contribution is dedicated to the memory of our friend and former director of the University of California's Seismographic Station, Bruce Alan Bolt, with whom we shared a common interest in the history of earthquake studies in California

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PREFACE

April 18, 2006 marks the 100th anniversary of the earthquake and fire that devastated San Francisco and resulted in the near total destruction of the California Academy of Sciences. The value of the loss of the Academy's prize possessions, its library, its collections of natural history objects, and its Archives, which included more than 50 years of Academy and local history, can scarcely be imagined. Even a cursory glance at what is known of the Academy's first 50-plus years (see Leviton and Aldrich 1997) whets the appetite for more details. Yet, the Academy as an institution, both cultural and scientific, having survived the ravages of the devastation, gathered strength across the decades so that it now stands as one of the world's leading natural history museums, supporting imaginative educational and research programs. What follows attempts to place the Academy and a few of the individuals associated with it in perspective with respect to the events of 1906 and the study of earthquakes in California to that time.

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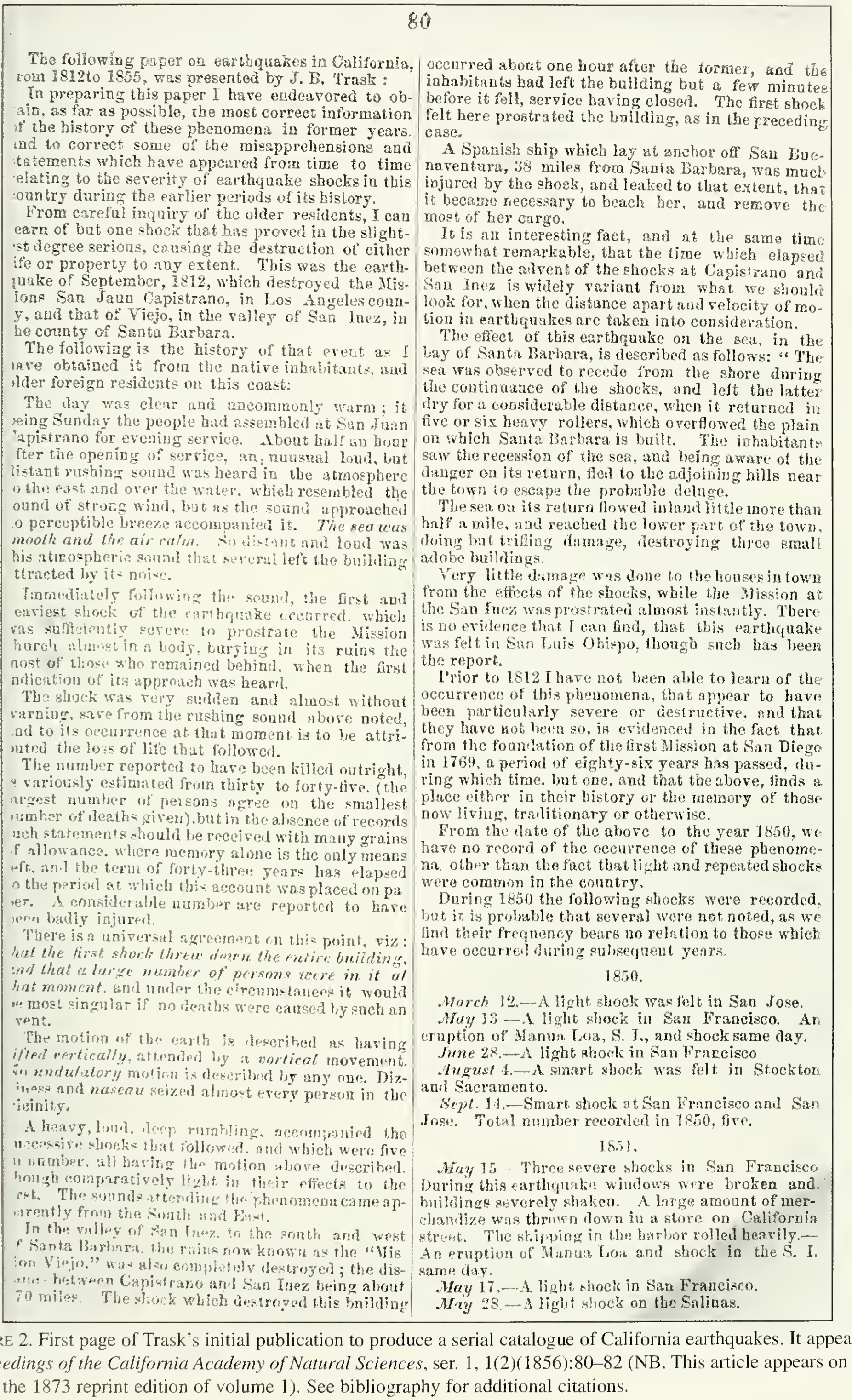
THE CALIFORNIA ACADEMY OF SCIENCES AND EARTHQUAKE STUDIES IN CALIFORNIA BEFORE 1906

Earthquakes are as much a part of the California scene as are the Sierra Nevada, Death Valley, Yosemite Valley, the California coast line, the Golden Gate. All have attracted the attention of the public and of scientists worldwide who have come to study the state's deserts and mountains, its valleys and coast, its natural history, and, most notably, its earthquakes.

Although earthquakes have been part of California's written history since the Spanish missionaries entered what was then called Alta California, scientific interest in them did not emerge until the early 1850s, with the founding of the California Academy of Natural Sciences in San Francisco on 4 April 1853. On that day, seven individuals met in the offices of one Lewis J. Sloat to organize the Academy. Among this group was medical practitioner and unofficial California State Geologist, John Boardman Trask (Fig. 1). Although Trask's interests in natural history centered mostly on topics other than geology following his third report to the California State Legislature on California geology in 1856, he nonetheless began compiling information on earthquakes in California and, shortly thereafter, to publish annual reports summarizing reported seismic activity within the state (Fig. 2). Largely cataloguing events, with dates and times and commentaries by local observers, Trask rarely speculated on the underlying causes of the seismic activity until 1864 when, in his catalogue of earthquakes in California for 1800 to 1864, he presented his views on the topic. Trask focused on what was conventional wisdom of the period, that earth-

FIGURE 1. John Boardman Trask, ca. 1863, as Assistant Surgeon, Union Army. Courtesy California Academy of SciencesArchives.



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The following paper on earthquakes in California, rom 1812to 1855, was presented by J. B. Trask :

In preparing this paper I have endeavored to obtain, as far as possible, the most correct information of the history of these phenomena in former years. and to correct some of the misapprehensions and statements which have appeared from time to time relating to the severity of earthquake shocks in this country during the earlier periods of its history.

From careful inquiry of the older residents, I can earn of but one shock that has proved in the slightest degree serions, causing the destruction of either life or property to any extent. This was the earthquake of September, 1812, which destroyed the Misions San Jaun Capistrano, in Los Angeles couny, and that of Viejo, in the valley of San Inez, in he county of Santa Barbara.

The following is the history of that event as I have obtained it from the native inhabitants, and older foreign residents on this coast:

The day was clear and uncommonly warm ; it being Sunday the people had assembled at San Juan Capistrano for evening service. About half an hour fter the opening of service, an; nuusual loud, but distant rushing sound was heard in the atmosphere o the east and over the water, which resembled the ound of strong wind, but as the sound approached no perceptible breeze accompanied it. *The sea was mooth and the air calm.* So distant and loud was his atmospheric sound that several left the building ttracted by its noise.

Immediately following the sound, the first and eaviest shock of the earthquake occurred. which was sufficiently severe to prostrate the Mission hurch almost in a body, burying in its ruins the most of those who remained behind, when the first ndication of its approach was heard.

The shock was very sudden and almost without warning, save from the rushing sound above noted, and to its occurrence at that moment is to be attributed the loss of life that followed.

The number reported to have been killed outright, is variously estimated from thirty to forty-five. (the argest number of persons agree on the smallest number of deaths given).but in the absence of records uch statements should be received with many grains of allowance. where memory alone is the only means left. and the term of forty-three years has elapsed o the period at which this account was placed on paper. A considerable number are reported to have been badly injured.

There is a universal agreement on this point, viz : *hat the first shock threw down the entire building, and that a large number of persons were in it at hat moment.* and under the circumstances it would be most singular if no deaths were caused by such an vent.

The motion of the earth is described as having *ifted vertically*, attended by a *vortical* movement. No *undulatory* motion is described by any one. Dizziness and *naseau* seized almost every person in the vicinity.

A heavy, loud, deep rumbling, accompanied the uccessive shocks that followed. and which were five n number, all having the motion above described. though comparatively light in their effects to the first. The sounds attending the phenomena came apparently from the South and East.

In the valley of San Inez. to the south and west f Santa Barbara, the rains now known as the "Mision Viejo," was also completely destroyed ; the distance between Capistrano and San Inez being about 70 miles. The shock which destroyed this building occurred abont one hour after the former, and the inhabitants had left the building but a few minutes before it fell, service having closed. The first shock felt here prostrated the building, as in the preceding case.

A Spanish ship which lay at anchor off San Buenaventura, 38 miles from Santa Barbara, was much injured by the shock, and leaked to that extent, that it became necessary to beach her, and remove the most of her cargo.

It is an interesting fact, and at the same time somewhat remarkable, that the time which elapsed between the advent of the shocks at Capistrano and San Inez is widely variant from what we should look for, when the distance apart and velocity of motion in earthquakes are taken into consideration.

The effect of this earthquake on the sea, in the bay of Santa Barbara, is described as follows: "The sea was observed to recede from the shore during the continuance of the shocks, and left the latter dry for a considerable distance, when it returned in five or six heavy rollers, which overflowed the plain on which Santa Barbara is built. The inhabitants saw the recession of the sea, and being aware of the danger on its return, fled to the adjoining hills near the town to escape the probable deluge.

The sea on its return flowed inland little more than half a mile, and reached the lower part of the town, doing but trifling damage, destroying three small adobe buildings.

Very little damage was done to the houses in town from the effects of the shocks, while the Mission at the San Inez was prostrated almost instantly. There is no evidence that I can find, that this earthquake was felt in San Luis Obispo, though such has been the report.

Prior to 1812 I have not been able to learn of the occurrence of this phenomena, that appear to have been particularly severe or destructive. and that they have not been so, is evidenced in the fact that from the foundation of the first Mission at San Diego in 1769, a period of eighty-six years has passed, during which time, but one, and that the above, finds a place either in their history or the memory of those now living, traditionary or otherwise.

From the date of the above to the year 1850, we have no record of the occurrence of these phenomena, other than the fact that light and repeated shocks were common in the country.

During 1850 the following shocks were recorded, but it is probable that several were not noted, as we find their frequency bears no relation to those which have occurred during subsequent years.

1850.

March 12.—A light shock was felt in San Jose.

May 13 —A light shock in San Francisco. An eruption of Manua Loa, S. I., and shock same day.

June 28.—A light shock in San Francisco

August 4.—A smart shock was felt in Stockton and Sacramento.

Sept. 14.—Smart shock at San Francisco and San Jose. Total number recorded in 1850, five.

1851.

May 15 —Three severe shocks in San Francisco During this earthquake windows were broken and. buildings severely shaken. A large amount of merchandize was thrown down in a store on California street. The shipping in the harbor rolled heavily.—An eruption of Manua Loa and shock in the S. I. same day.

May 17.—A light shock in San Francisco.

May 28.—A light shock on the Salinas.

FIGURE 2. First page of Trask's initial publication to produce a serial catalogue of California earthquakes. It appeared in the *Proceedings of the California Academy of Natural Sciences*, ser. 1, 1(2)(1856):80–82 (NB. This article appears on pages 85–89 in the 1873 reprint edition of volume 1). See bibliography for additional citations.

quakes were associated with volcanic activity. His writing on this topic is at times labored inasmuch as he clearly had difficulty in associating many of the reported tremors in central and southern California with active or even dormant volcanoes. Nonetheless, he made a valiant attempt to fit observations to theory without stretching credibility or invoking marginal theories such as roof collapse of subterranean caverns, violent gaseous explosions, or climatic conditions, all of which had been advanced by one or more of his Academy colleagues (see, for example Winslow 1855; also Leviton and Aldrich 1997:108, 114, 120–122, 129). Trask's last publication on earthquakes appeared in 1866, and, save for a paper in 1869 by Joshua Clayton, no further articles on earthquakes appeared among the Academy's scientific publications.

But, the discussion of matters relating to earthquakes did not disappear entirely from the consciousness of Academy members. The "Haywards" earthquake of 1868, which caused moderate damage in San Francisco, was of sufficient concern that it was suggested that the Academy establish a committee to investigate the event because it would be expected to do so by the public (Aldrich et al. 1986:71; Leviton and Aldrich 1997:104). At the meeting of the Academy held on 2 November 1868), on a resolution entered by Col. Leander Ransom, Drs. James Blake and James Cooper, and Mr. Gregory Yale were appointed to the committee. At that same meeting, Blake observed "that it was not the purpose of the Academy to advance theories as to the cause of earthquakes since that had been done by men who had made these phenomena a life study. Time was required for scientific investigations and as soon as these could be made the results would be given to the public" (see Aldrich et al. 1986:71 for details).

However, before a proper study could be initiated by the Academy's committee, the San Francisco Chamber of Commerce, prodded by George Gordon, a prominent San Francisco businessman, preempted the Academy and established a committee to make a comprehensive study of the earthquake, its effects, and ways to mitigate future damage. The history of this committee and its failure to submit a final report are detailed by Aldrich et al. (1986). The Academy made no further effort to study the 1868 event but, at subsequent meetings, it did entertain discussions relating to earthquakes in general, with few concrete results. Theories were advanced, most of which were debunked by Blake, even though he was unable to advance an alternative. The more humorous of the remarks centered on the gas theory of earthquakes, wherein the sudden release of accumulated underground gases, not necessarily related to volcanoes, would produce convulsions. In response, one member suggested that the Academy should appoint a curator of earthquakes, "whose duty it would be to collect specimens of earthquakes and place them in the museum, taking care, however, to purge such specimens of their gases to avoid dangerous consequences." (Leviton and Aldrich 1997:114). Another "tongue in cheek" suggestion was that, "for the protection of the City of San Francisco, an artificial volcano should be got up in the neighborhood for the escape of the gases coming this way and producing so much uneasiness." (Leviton and Aldrich, *loc. cit.*). In a more serious vein, at the members meeting held on 18 April 1870 Josiah Dwight Whitney moved that a committee be appointed "to inquire as to the best instrument for recording such [earthquake] phenomena, and the proper place to fix it." The motion was adopted and Whitney, Henry Gibbons, George Davidson, and Robert Stockton Williamson were appointed to it. Regretably, the matter came to naught with Whitney's departure from San Francisco following the failure of the State legislature to provide further financial support for the State Geological Survey.

Although other unpublished oral presentations dealing with earthquakes took place at Academy meetings between 1870 and 1906, interest in earthquakes seemed to diminish in importance as other topics captured the members' attention. Furthermore, the scientific study of earthquakes moved from San Francisco to the fledgling University of California at Berkeley and somewhat later Stanford University. At these institutions, persons with professional credentials in geology, receptive to new ideas, and with the aid of newly designed, sensitive seismograph instruments, began the kinds of scientific investigations called for by James Blake in November, 1868. At Berkeley, Edward Singleton Holden, astronomer, librarian, and university president, established the first seismographic stations in the Western Hemisphere (Campbell 1916; Rodda and Leviton 1982:52; Gerschwind 2001:15). Not long afterwards, Andrew Lawson joined the Berkeley faculty, and John C. Branner was brought in to head the geology program at Stanford University, which opened its doors in the early 1890s.

Major theoretical breakthroughs in the understanding of earthquakes came slowly. It was not until late in the 19th century that the idea that earthquakes could be related to movement along fractures in the earth's crust was posited, even though the existence of those fractures had been well known to geologists for many years (for a more complete discussion of this topic see Dean 1993). Indeed, fractures were, more often than not, thought to have resulted from earthquakes; thus, movement along them was not thought to be the source of disturbances. In the United States, one highly experienced field geologist, Grove Karl Gilbert, early in the 1880s, did make the association, but at the time it attracted little attention (Gilbert 1883; but see also Gilbert 1906:272–273, 1908:30–35; Wallace 1980:38).

GROVE KARL GILBERT ON EARTHQUAKE AND FAULTS BEFORE 1906

According to Robert Wallace (1980), Grove Karl Gilbert (1843–1918; Fig. 3) dealt with issues of earthquakes and faults as part of his general studies of mountain building processes. Gilbert's geological training had come mostly in the 1860s during an apprenticeship to John Strong Newberry, then Ohio state geologist but known also for his studies in Western paleontology and stratigraphy. Newberry lobbied to get Gilbert the appointment to the Wheeler survey of the American West (formally titled the United States Geographical Survey West of the 100th Meridian but usually named after its leader, Lieutenant George Wheeler). Gilbert first addressed faults and earthquakes in his field work for the Wheeler Survey from 1871 to 1874 on the Basin and Range topography of Nevada. In 1875, Gilbert switched to the Powell Survey (United States Geological and Geographical Survey of the Rocky Mountains, short-titled after its leader, the charismatic John Wesley Powell). Gilbert stayed with Powell until Gilbert transferred to the newly formed United States Geological Survey (USGS) in 1879, where he spent the rest of his career (Pyne 1980, 1999).


FIGURE 3. Grove Karl Gilbert, ca. 1882. (Courtesy Smithsonian Institution Archives [SIA Merrill Collection, RU 7177, Box 4, Folder 30].)

Geologists, among them Clarence King (in 1868; he directed the Survey of the 40th Parallel, contemporary with the Wheeler and Powell Surveys and eventually became the first head of the U.S. Geological Survey), initially, had attributed the Basin and Range region's geological history to the folding of strata. This mechanism best explained the creation of the ridges and valleys of the

Appalachian Mountains in the American East, where most early American geologists had been trained. Gilbert challenged this, arguing that the Nevada mountains were uplifted blocks bounded on both sides by deep-seated vertical or high-angle faults, with down-dropped basins between the blocks. Within the blocks, folded strata could be detected, but folding did not cause the main uplifting that shaped the modern landscape. John Wesley Powell also adopted a fault-block mechanism to explain these mountains, and eventually most others came to agree, including Clarence King in 1878 (Wallace 1980).

Gilbert first thought about earthquakes in connection with the 1872 Owens Valley shocks along the eastern margin of the Sierra Nevada; he was aware that fault scarps like those seen elsewhere in the Basin and Ranges developed in conjunction with that episode. Thus, in 1872 and again in 1875, Gilbert argued that the fault-bounded blocks accounted for the Basin-Range topography. The final link between faults and earthquakes was yet to come, but it was only a matter of time. During 1877–1883, Gilbert focused on the Lake Bonneville area, writing about the earthquakes and faults that bounded that basin. His field work on the western face of the Wasatch Range of Utah extended his thinking on the subject. There he found small, fresh scarps that he hypothesized were the most recent evidence of the forces that uplifted the range. Gilbert said earthquakes raised the mountains along the faults a few feet at a time. This led him to warn Utah residents in 1883–1884 of the possibility of more earthquakes along the mountain front, including possibly at Salt Lake City; this was an early instance of earthquake prediction (Wallace 1980). At this time, and until 1906, Gilbert focused on the relation of earthquakes to vertical displacement. But this was to change.

GILBERT AND THE EARTHQUAKE OF 1906

In 1906, Gilbert was in California to study the effects of hydraulic mining (Fig. 4), not earthquakes. But decades of field work and writing about the role of faults and earthquakes in mountain

FIGURE 4. Hydraulic mining at the Esperance Mine. French Corrall. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [331.1.6.1; envelope #4], Alice Eastwood Archive, California Academy of Sciences Archives.)

building had prepared him for rapid field observations and clear thinking about what happened on April 18, 1906.

It was a little after 5 a.m. of that day that a rumbling of the earth awakened the residents of San Francisco and other Bay Area communities. Light tremors had been felt before, but nothing like this, and nothing so sustained. The intensity increased and quickly people poured out of their homes, hotels, and other buildings, dazed and awed by the event. The shaking stopped, but more was in store for the nervous onlookers. Small fires broke out, but, because of broken water mains, firefighters found they could not respond. The fires spread and in a short time the downtown area of the city became an inferno. The California Academy of Sciences' buildings were in the path of the advancing fire (Fig. 30). At the time, its properties included a commercial building, which faced onto Market Street, and a museum building, which was located directly behind. Both had been constructed in the late 1880s with funds and on land donated to the Academy by San Francisco entrepreneur and recluse James Lick and had opened to the public only a few years earlier (1891). Although there was nothing that could save the buildings and most of their precious contents, a few dedicated Academy staff hastened downtown to rescue the few items they could before the buildings were enveloped in flames (Figs. 33–34, 37; see Leviton and Aldrich 1997: 471–473). Among them were Richard Loomis, then director of the museum, Mary Hyde, Academy Librarian, John Van Denburgh, M.D., curator of herpetology, and Alice Eastwood, curator of botany.

Alice Eastwood (Fig. 5) engages our attention here. Miss Eastwood came to the Academy in 1892. She was brought in as understudy to the then curator of botany, Mary Katharine Layne Curran, the future Katharine Brandegee. With Brandegee's departure from the Academy in 1893, Eastwood was appointed curator, a position she held for most of the next 57 years. We do not know when or where Alice Eastwood first made the acquaintance of Grove Karl Gilbert.[1] Gilbert was a widower, having lost his wife some years earlier (Pyne 1999). And, in 1906, he was living in Berkeley. Thus, it could have been on any one of several occasions during his geological studies in California in the

FIGURE 5. Alice Eastwood, circa 1900. (California Academy of Sciences Archives.)

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[1] We know little about the relationhsip of Alice Eastwood and Grove Karl Gilbert save for what Steve Pyne was able to uncover in his researches for his biography of Gilbert (Pyne 1980:262–263). That the two had decided to marry in 1918 is well established. At this time Alice was 59 and Grove Karl 74. How long had he and Alice Eastwood known one another is an open question. The only tease is a note that Gilbert wrote in early 1918, "Alice and I have been lovers for years" (see Pyne 1980:262). In early 1918, Gilbert was returning from a trip to the East. He stopped in Michigan to visit his sister, and while there he suddenly took ill and died. Alice Eastwood remained unmarried for the rest of her long life. She passed away in 1953 at the age of 94. Following the untimely loss of her impending husband, Alice Eastwood devoted the rest of her life to the California Academy of Sciences, to her botanical studies, and to the local botanical club, which she continued to sponsor after the departure of Mary Katharine ("Kate") Brandegee. For a brief biographical sketch of Alice Eastwood, see Ogilvie (1986:79–80).

early 1900s. Although there is nothing in the available records to show that Gilbert attended meetings of the California Academy of Sciences on or before 1906, it is known that Alice Eastwood made occasional trips to the East Bay, to the University of California at Berkeley herbarium, and it may have been on one of these visits that she and Gilbert met. On the other hand, both were Sierra Club enthusiasts, and according to Stephen Pyne, the two met during Sierra Club outings (Pyne 1980:262). Whatever the case, after the earthquake and fire, the two ventured forth on an extended excursion to Marin County, as far as Inverness and Point Reyes, to study the effects of the earthquake and to take photographs showing the impact of the ground movements on the landscape.[2] Because of disruptions of life at the Academy brought on by the earthquake and fire, and exacerbated by clashes with the Academy's Director, Leverett Mills Loomis, in the latter part of April, and for some time thereafter, Alice Eastwood, left San Francisco to spend time working at other institutions. Initially, and at the invitation of John Galen Howard, she took up residence at Howard's home in Berkeley to be close to the university's herbarium and library to continue her botanical studies (see comments by Duncan [2006] relating to this period and to Eastwood's botanical relationship with Berkeley botanist Edward Lee Greene).

Gilbert published a short general article on earthquakes on April 28, 1906 in the *Mining and Scientific Press*, an influential San Francisco technical journal. In that article, he distinguished earthquakes caused by volcanoes from those caused by mountain-building (tectonic in his words), stating that the 1906 earthquake was of the latter type. Often, tectonic forces manifested themselves in the folding of rocks, but when the forces built up rapidly or the rocks were resistant, the rocks ruptured and an earthquake took place, sometimes marked at the surface by a fault (a fracture in the earth along which motion takes place). The shock waves from this rupture were of two kinds, longitudinal and transverse, and different types of rocks reacted variously to them. Alluvial rocks and "made ground" were especially susceptible to damaging shaking from transverse waves. This article did not report Gilbert's field work in Marin and was not illustrated by pictures.

On the same page, the *Press* announced the creation of an earthquake commission by the governor of California, and Gilbert's appointment to it with seven other scientists. Andrew Lawson of the University of California at Berkeley chaired the group, and the Carnegie Institution of Washington funded the project with a grant of $5,000. The commission divided the field investigations, with John Branner of Stanford in charge of the San Francisco peninsula, Lawson in the area to the south of that, and Gilbert in Marin County and northward (Geschwind 2001:33–35). Furthermore, the United States Geological Survey set up an investigative team headed by Gilbert. Both groups made substantial reports in which Gilbert had a major place, and in which many of his photographs were a crucial part of the evidence for the teams' findings.

The Lawson group issued a preliminary report of twenty pages in early summer 1906; thousands of copies were distributed, and it was reprinted in *Science* and the *Press*. With Lawson's permission, Gilbert published a paper, with his findings and some of those of the commission, in the August 1906 issue of *Popular Science Monthly*. In that article, he repeated the distinction between tectonic and volcanic earthquakes and again noted the association of the former with faults. He added that once a fault zone was established, it became a site of weakness along which further earthquakes were more likely to take place than in undisturbed ground. The 1906 quake occurred in such a setting, along the San Andreas fault, which had been mapped and defined as early as 1893 by Lawson. The area through which this fault passed was marked by linear ridges, elongated lakes, and lines of springs that were characteristic of faulted ground (Figs. 8, 22–23). A significant finding of the 1906 quake was the amount of horizontal (strike-slip or lateral) displacement, compared to the vertical uplift that Gilbert had emphasized in his pre-1906 publications on faults and earth-

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[2] A selection of Gilbert and other photographs are included in the Photographic Portfolio following the bibliography.

quakes. Gilbert described, but did not name, the different kinds of surface cracks that appeared along the rift and, most importantly, illustrated them with his photographs (Figs. 7–12). He noted that the commission was using U.S. Coast and Geodetic Survey maps and data to determine whether only one side of the fault had moved, or both equally. He concluded with a plea that the commission answer the vexing questions of when and where and how severe an earthquake was likely to hit the Bay Area again. However, in private correspondence with Lawson, Gilbert later worried that the commission should not get into the question of forecasting (Geschwind 2001:35–36).

The USGS report appeared in the second half of 1907, with Gilbert as senior author. He wrote the first section of thirteen pages about "the earthquake as a natural phenomenon" and his coauthors did the rest of the book, over 125 pages detailing structural damage to the built environment and recommending better construction techniques (separate sections written by Humphrey,[3] Sewell, and Soulé 1907). Gilbert's section used evidence from earthquake damage within San Francisco as well as in his field areas in Marin and northward to make his points. As he described each feature of the earthquake, he referenced specific photographs in the book that showed what he discussed. The monograph included 100 photographs, 11 of them taken by Gilbert. Some of the material had appeared in his earlier publications but these sections he reworked and edited, changing "rift" to "fault trace" in conformity with the Lawson commission's terminology, for example. The new material included information about the relative motion of the rocks on either side of the fault and about the propagation of waves of force by the earthquake. The latter material depended heavily on his fieldwork in the mudflats at Tomales Bay. Gilbert paid particular attention to this locality because the land had the same character as the wet "made ground" along the San Francisco Bay shoreline that had failed so badly during the tremors of 1906. Although he did not mention it, his observations on the mudflats were also related to the work he was doing at the same time using flume experiments to study stream erosion. Evidence from the landscape, anecdotes, and building damage formed the basis of his tentative generalizations about the earthquake's motion and distribution of intensity, because the array of seismographs in the Bay Area was too thin to provide the data to support these conclusions.

In 1908, Gilbert published several sections in the report of the California Earthquake Commission. The volumes, collectively known as the Lawson report after the chair of the investigation, were written sometimes by individual authors (Harry Reid wrote all of volume two), but Andrew Lawson exercised editorial control over the document and kept the eight scientists working on schedule, thus deserving the credit he is given by the short-title of "Lawson report". In one five-page section, Gilbert generalized about the features of the rift caused by the 1906 earthquake, summarizing it as the "surface expression of a great shear-zone, or compound fault" (Gilbert in Lawson 1908:33). Here Gilbert also named and described "fault sags," depressions caused by the earthquake and often marked by wet spots after rainfall (Figs. 22–23). In discussing the drainage of the fault zone, he noted that some stream valleys were shaped more by earthquake fractures than by erosion (Figs. 18–19).

In longer sections later in the Lawson report, Gilbert provided excruciating detail on the effects of the tremors on the country between Bolinas Lagoon and Tomales Bay. In part, he used this essay to sort and validate conflicting information from local observers. His writing is more than descriptive, however. Gilbert promulgated the classification of the fault trace into three phases: ridge, trench, and echelon (Gilbert in Lawson 1908:66), each illustrated by numerous photographs. He used the detailed observations of damage to fences, gardens, tree lines, and other features to calcu-

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[3] R.L. Humphrey includes a brief statement relating to the loss of the Academy's buildings (then located at 819 Market Street). Two photographs (pls. 24A and 25B showing damage to the Academy) are included among the plates showing the effect of earthquake and fire on many of San Francisco's buildings.

late the amount of offset along the fault, taking into account not just lateral and vertical movement but also twisting, gaping, and shearing. Gilbert found that these motions complicated the answer to the question of how much movement there was during the earthquake; and instead of seeking one numerical answer, he gave ranges and averages. Gilbert stated that, in the Bolinas-Tomales area, the left side of the fault moved northward relative to the right side (Gilbert in Lawson 1908:70); but this was a general conclusion of the Commission, not uniquely his finding. He illustrated all of these phenomena with photographs mostly by himself but sometimes by others (Table 1). His long section had 44 of them plus a number of diagrams. Gilbert also published a brief summary of the Lawson report in the *American Journal of Science* (1909b) but did not include photographs.

TABLE 1. Photographs in the Lawson Report (1908)

Photographer	*Number photos*	*Percent photos*
G.K. Gilbert	58	17.4
A.C. Lawson	40	12.0
F.E. Matthes	36	10.8
H.W. Fairbanks	29	8.7
J.C. Branner	23	6.9
R.S. Holway	21	6.3
H.O. Wood	20	6.0
A.S. Eakle	10	3.0
R.L. Humphry	6	1.8
Other, signed	48	14.4
Unattributed	43	12.9
Total	334	100.2*

* Rounding error

Gilbert devoted his presidential address to the Association of American Geographers on New Year's Day 1909 to the topic of earthquake forecasting; *Science* published it as the lead article in its January 22 issue. He may have used lantern slides to illustrate it, but the published version did not include photographs or diagrams.[4] Gilbert dealt with the issues of predicting what localities are earthquake prone, and what the prospects were for predicting when great shocks would occur again. In discussing place, he drew upon the delineation of earthquake features from the Lawson report as indicative of a landscape prone to horizontal movement along a fault, and mentioned briefly that fault scarps in other regions were evidence of vertical movements associated with earthquakes. He reported that the Lawson team had already located another area marked by the same peculiar terrain as found between Bolinas and Tomales, along the Hayward fault in northern California. Predicting the timing of a future earthquake was unlikely, Gilbert said; there were lots of theories but little reliable evidence. He argued that forecasting place was important but time was not; structures in a suspect region should be designed to withstand earthquakes regardless of whether the quake was expected tomorrow or decades ahead. Gilbert excoriated city planners in the Bay Area for their emphasis on the damage caused by the fire, and included a calculation showing destruction due to the earthquake alone was at least as great. (A few photographs of buildings destroyed by the quake alone would have made the point as well.) As Gerschwind remarks (2001:20), Gilbert's paper was the first clear statement by a scientist of the lessons of the earthquake of 1906 for rebuilding the city, but it would take decades for the state to work out a rational and coherent policy of dealing with seismic risk.

Photographs documenting the devastation wrought by the earthquake and fire in San Francisco and elsewhere in the San Francisco Bay Area have engaged the attention of viewers for many decades. Grove Karl Gilbert's photographs, mostly taken to document landform changes, reflect the eye of an experienced field geologist and reveal much about the surface appearance of catastrophic offsets along active faults. But Gilbert also took photographs in San Francisco; these are to be found in the photo archives of the U.S. Geological Survey in Denver, Colorado, and were meant specifically to document the failure of selected structures and structural materials (Figs. 26–27).

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[4] James McKeen Cattell, the editor of *Science*, often included graphs, diagrams, and tables in the journal, but rarely photographs. He did use photographs frequently in *Popular Science Monthly*, which he also edited. (Michael Sokol biographer of Cattell, pers. commun.)

They are clearly identified and annotated as to what they are by Gilbert.As noted, Gilbert's landscape photographs appeared in an article in *Popular Science Monthly* in August 1906, were reprinted in a volume edited by David Starr Jordan in 1907, and most importantly were included in the Lawson report (1908). Many scientists are well aware that a large number of Gilbert's photographs are in the photographic archives of the USGS in Denver, Colorado. What is not as well known is that an original set of prints of the photographs Gilbert and Eastwood took during the weeks that immediately followed the earthquake were in Alice Eastwood's possession and are now preserved in the archives of the California Academy of Sciences. Other Gilbert photographs, mostly geological in nature and mostly taken on trips to the Sierra Nevada, are included in this collection. The Academy also houses in its archives photographs of the 1906 event taken by U.S. Department of Agriculture horticulturist and Academy Board of Trustees Secretary Gulian Pickering Rixford (e.g., Figs. 31–32), Academy curator of geology Frank Marion Anderson (e.g., Fig. 33, and possibly Fig. 34 [although this one may have been taken by Richard Lewis Humphry]), entomology curator Gustav Eisen (e.g., Fig. 37), and others, few of which have attracted the attention of earthquake specialists.

"AFTER SHOCK"

After 1909, Gilbert returned to his dual study of hydraulic mining and stream erosion. He had built a flume on the Berkeley campus to conduct experiments on stream flow, deposition, and erosion (Gilbert 1914), but, as Leopold (1980) notes, this device had a constant slope, which limited the conclusions Gilbert could draw from it. The hydraulic mining paper (1917) presented data (and photographs) that led to the end of this environmentally destructive process of extracting gold from California sediments. Gilbert also contributed to the development of the theory of isostacy and completed his Great Basin studies in a paper that was published after his death (Pyne 1999). His relationship with Alice Eastwood came to a bittersweet end: they had decided to marry, and he was traveling West to join her in May 1918 when a heart attack killed him during a stopover at a family home in Michigan. Alice Eastwood remained single for the rest of her life, and left an enduring legacy of him by saving his California photographs among her own papers.

As for the Academy. Following the earthquake and fire, it, like San Francisco, took stock of what had happened. The outlook was grim, but not hopeless. Word was received that the Schooner *Academy* was due back from the Galapagos expedition in the late Fall, and on board it carried core collections that would mark the Academy's rebirth — a large collection of plants, mollusks, insects, and reptiles, including the most complete series of Galapagos tortoises, representing all extant populations in the islands, to be found in any museum, and more. To provide temporary housing for this treasure would be a challenge, but the Academy's director, Leverett Mills Loomis, and curator of herpetology, John Van Denburgh, rose to the occasion. Whereas the Academy's commercial building lay in ruins, the museum building, though it suffered grievously from the fire, was still more or less intact. At Loomis' direction, part of the ground floor was walled off and temporary shelving installed so that when the *Academy* arrived in port at the end of November, its precious cargo could be immediately relocated (Fig. 35).

In the meantime, institutions and individuals from around the world donated library materials to help rebuild (Fig. 36) what had been the premier natural history library in the United States west of the Eastern seaboard. Library materials were received from no fewer than 42 individuals, 49 United States institutions and societies, 2 Canadian institutions, 1 South African organization, 18 museums and societies in Asia, Australia, and New Zealand, 84 museums, universities and societies in Europe, 10 in Central and South America, and 7 book dealers.[5]

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[5] A complete list is to be found in Leviton and Aldrich 1997:561–563.

During the nearly 10 years that elapsed between the time of the earthquake and fire and the reopening of the Academy's new museum facilities in Golden Gate Park in 1916, much of the Academy's research program went on as usual. Although a few staff took temporary leave to continue their studies elsewhere (Alice Eastwood among them), several carried on in temporary facilities in San Francisco. John Van Denburgh and Joseph Slevin, for instance, managed the relocation of the herpetological collections to a downtown warehouse and from them there followed a steady stream of publications.

Thus, although suffering a brief interruption in production, on 20 December 1907, the first issue of series 4, volume 1 of the Academy's scientific publications, the *Proceedings*, appeared. And, perhaps appropriately enough, its title was "Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. Preliminary descriptions of four new races of gigantic land tortoises from the Galapagos Islands" by John Van Denburgh.

The Academy was back in business!

♣♣♣♣♣♣♣♣♣♣♣♣♣♣♣

One hundred years have now passed since that fateful day in April when so much of the past lay in ruins. But, the San Francisco Bay area recovered; the cities, towns, and villages, the universities, private and public enterprises came roaring back so that City by the Golden Gate is once again the Queen city of the West. It is, therefore, on the occasion of this, the 100th anniversary of the San Francisco earthquake and fire that we celebrate the Academy's persistence in the face of adversity. The photographic portfolio of images that is appended here includes material mostly drawn from the archives of the Academy. Many are Gilbert photographs, some appearing for the first time in print, whereas others are from the U.S. Geological Survey Photographic Archives, Denver, Colorado, the Smithsonian Institution Archives, Washington, D.C., and the Academy's Rixford, Anderson, and Barclay Stephens record units.

Finally, we take note that as devastating as it was, 1906 was not the only occasion on which the Academy suffered the effects of severe earthquakes. Scarcely 15 years ago, following the Loma Prieta Earthquake in 1989, the Academy buildings, then located in Golden Gate Park, were so severely stressed that there was serious doubt about their safety should another earthquake occur. Thus, for a second time within a hundred years, the Academy faced the prospect of rebuilding, although this time with all of its collections, its library, and its other scientific and cultural assets intact. That once again the Academy will emerge from these trials there can be little doubt.

ACKNOWLEDGMENTS

We take this opportunity to thank the Library staff of the California Academy of Sciences, and specifically Larry Currie, Academy Librarian, for many courtesies extended to us in gathering material for this paper. We are indebted also to Ellen Alers (Smithsonian Institution Archives), Tommie Ann Gard (U.S. Geological Survey Library, Denver), Rebecca Pappert (Young Science Library, Smith College), and Pamela Skinner (Neilson Library, Smith College). We are grateful to colleagues who critiqued both an earlier version of this paper and then reviewed later iterations, J. Thomas Dutro (U.S. Geological Survey [ret.]), Terrence M. Gosliner (Provost, CAS), Tomio Iwamoto (Ichthyology, CAS), Gary Williams (Invertebrate Zoology, CAS), and Mark Aldrich (Smith College); all also responded to our plea for rapid turnaround reviews. Also thanks to Hallie Brignall (Herpetology, CAS) who helped with the images. Our reviewers caught many errors and infelicities, but those that remain are solely the responsibility of the authors. Michael Sokal (Worcester Polytechnic Institute) advised us on the Science Press's practice of illustrating articles.

Finally, we thank Ellis L. Yochelson (Research Associate, Paleobiology, Smithsonian Institution) for drawing our attention to Gilbert photos on the USGS Library website.

NOTE ON SOURCES

Information on earthquakes and the Academy can be gleaned from Leviton and Aldrich's edition of Theodore Hittell's history of the CAS (1997) and from the CAS *Proceedings* volumes before 1906. Pyne (1980) published a full-length, analytic biography of Gilbert; for a compact sketch on Gilbert, see Pyne (1999). Wallace (1980) wrote a perceptive essay on Gilbert's ideas on earthquakes and faults. In his prize-winning book, Geschwind (2001) analyzes the scientific and politic response to earthquakes in California; the first two chapters were especially useful for our article. Dean (1993) presents a thoughtful and exhaustive paper on thinking about the San Francisco earthquake and seismic theories that predated it. Of the recent general books on the San Francisco earthquake of 1906, we found Fratkin (2005) a scholarly but readable account as a piece of history. Winchester's (2005) gossipy account is marred by presentism. The main collections of Gilbert (and others) photographs we drew upon are in the CAS Archives and the USGS Library in Denver. Many of the USGS 1906 earthquake images are now downloadable from its website.

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Portfolio of Earthquake Images by Grove Karl Gilbert and others, mostly from the Archives of the California Academy of Sciences

The Gilbert images are from a collection of original prints given to Alice Eastwood by G.K. Gilbert and, although separately boxed and stored, they are part of the Eastwood Archive at the Academy. Copies of many of the Gilbert images are also in the U.S. Geological Survey Photographic Archive in Denver, Colorado, and some are now available on line <*http://libraryphoto.cr.usgs.gov/*>.

The Gulian Pickering Rixford Archive includes glass plate negatives and prints of of photographs taken by Rixford in San Francisco some days after the earthquake and fire. They are not dated.

Photographs of downtown San Francisco and of the skeleton remains of the California Academy of Sciences were taken by Academy curator Frank Marion Anderson.

The photograph of the wooden Japanese statue, one of the few objects to survive both earthquake and fire, was taken by Drs. Peter S. Bruguiere and Academy curator Gustav Eisen.

Except as otherwise noted, all images are from the Academy's Archives. A number of the images have not been published before. Others were used by Gilbert to illustrate his reports on the earthquake published between 1906 and 1908.

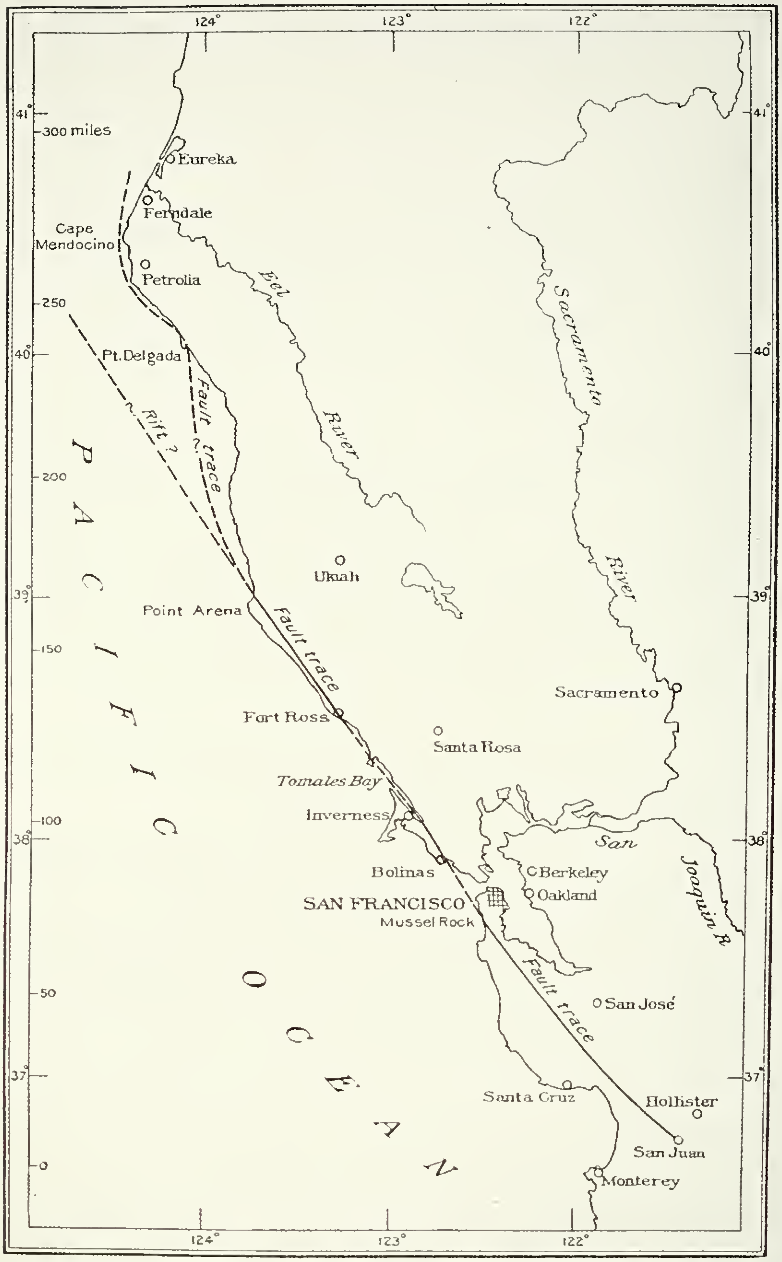

FIGURE 6. Map of the fault trace. Broken lines indicate alternative hypotheses as to its extension north of Point Arena. (From G.K. Gilbert 1907b:3.)

FIGURE 7. On the edge of the rift. Marin County. The woman in the picture is almost certainly Alice Eastwood (see also below). Photograph by G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #36; Envelope 8], California Academy of Sciences Archives.)

FIGURE 8. Fault trace two miles north of Skinner Ranch at Olema. View is to the northwest. Illustrates ridge phase of fault trace. The woman in the photo is almost certainly Alice Eastwood (Pyne 1980: 263). Photograph by G.K. Gilbert. (G.K. Gilbert Collection, [N7583-A], California Academy of Sciences Archives.) (Also in Gilbert in Lawson 1908, pl. 40, fig. A.])

FIGURE 9. Fault trace west of Olema, looking southeast. Photograph by G.K. Gilbert. Woman in the picture is unidentified. (G.K. Gilbert Collection [331.6.1, #2924; Envelope 7], California Academy of Sciences Archives.) (An image similar to this was included in Gilbert in Lawson 1908, pl. 40, fig. B].)

FIGURE 10. Fault scarp on earthquake crack. Vertical displacement about five feet. Photography by G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #2965; Envelope 7], Alice Eastwood Archive, California Academy of Sciences Archives.) (Also in Gilbert in Lawson 1908, pl. 53, fig. A.)

FIGURE 11. Road bed between Olema and Inverness. Collapse of road bed gives appearance of a vertical displacement about 5 feet. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [N7583-E], California Academy of Sciences Archives.)

FIGURE 12. Road bed between Olema and Inverness. Road bed probably destroyed by shaking of soft ground beneath. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [N-7583-F], California Academy of Sciences Archives.)

FIGURE 13. Fence offset 8.5 feet. Trace of fault barely visible, running from lower right to upper left through offset. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [N7583-C], California Academy of Sciences Archives.) (Also in Gilbert 1907b, pl. 1, fig. B.)

FIGURE 14. Buried water pipe upended by earthquake motion. Five miles west of Stanford University along Portola Valley Road. Although among the Gilbert images, we suspect that this one was taken by John Branner, or a Branner student at Stanford University, and given to Gilbert. (G.K. Gilbert Collection [N7583-B], California Academy of Sciences Archives.)

FIGURE 15. Bailey's Pier at Inverness. Photo taken by Martha P. Schreiber before 18 April 1906 (from Gilbert in Lawson, 1908, pl. 58, fig. B).

FIGURE 16. Photo by G.K. Gilbert taken after the 18 April earthquake. (for another view, see Gilbert in Lawson 1908, pl. 58, fig. A). (G.K. Gilbert Collection [331. 6.1, #472; Unnumbered white envelope], California Academy of Sciences Archives.)

FIGURE 17. Panorama taken in the vicinity of Olema. Fault trace passes from lower right to left, offsetting hedge in center. Composite photo taken in three parts by G.K. Gilbert and assembled digitally here (G.K. Gilbert Collection [331.6.1; Envelope 8, #s 3010-3012], Alice Eastwood Archive, California Academy of Sciences Archives.)

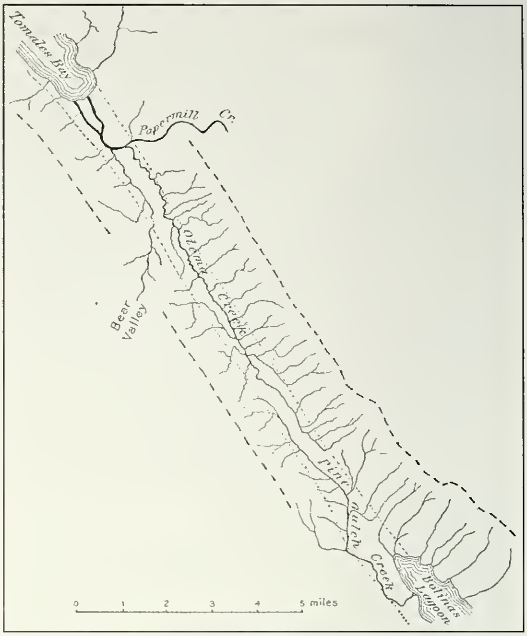

FIGURE 18. Drainage map of Bolinas-Tomales Valley (from Gilbert in Lawson, 1908:31, fig. 2). Heavy broken lines show crests of bounding ridges; light broken lines indicate limits of rift topography.

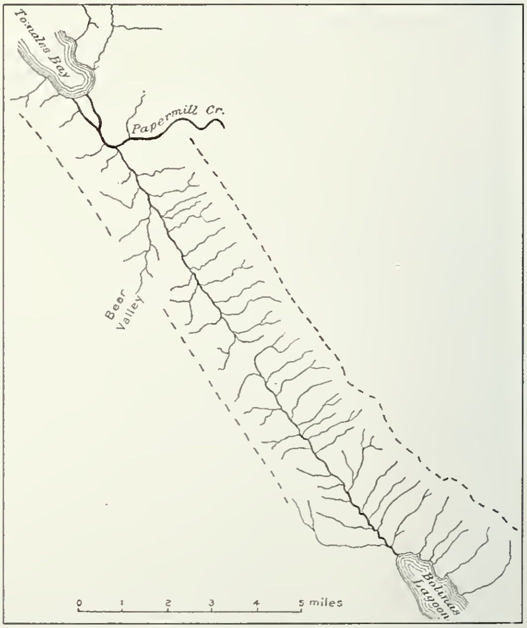

FIGURE 19. Hypothetical drainage map of Bolinas-Tomales Valley if developed without influence of rift displacement (compare with fig. 18 above) (from Gilbert in Lawson, 1908:32, fig. 3).

FIGURE 20. Row of eucalyptus offset (center) by earthquake, ½ mile west of Woodville. Photo G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #2946; Envelope 7], Alice Eastwood Archive, California Academy of Sciences Archives.)

FIGURE 21. Branch of fault-trace in north part of Bolinas, looking NNW, illustrating diagonal cracks. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #165; Unnumbered white envelope], Alice Eastwood Archive, California Academy of Sciences Archives.) (Also in Gilbert in Lawson 1908, pl. 39, fig. A).

FIGURE 22. Looking southeast from point near Shafter's Ranch, Olema. Ponds in trace of fault. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #3046; Envelope 7], Alice Eastwood Archive, California Academy of Sciences Archives.) (Also in Gilbert in Lawson 1908, pl. 42, fig. B.)

FIGURE 23. Sag ponds south of Shafters Ranch occupying trace of fault. Photograph by G.K. Gilbert. (G.K. Gilbert Collection [331.6.1, #3043; Envelope 7], Alice Eastwood Archive, California Academy of Sciences Archives.)

FIGURE 24. Fire cloud over San Francisco. Photograph by G.K. Gilbert, probably taken from somewhere in the East Bay while he was recording damage done to buildings in Oakland and Berkeley as well as landscape changes caused by the earthquake. (G.K. Gilbert Collection [331.6.1, #124; Envelope 7], California Academy of Sciences Archives.)

FIGURE 25. Fault trace 1.5 miles south of Olema, looking SE. Fault trace touches sag ponds, as seen by the jagged trace between them. (G.K. Gilbert Collection [331.6.1; Envelope 7], Alice Eastwood Archive, California Academy of Sciences Archives.) (Also in Gilbert in Lawson 1908, pl. 43, fig. A.)

FIGURES 26–27. Figure 26 (left). Howard near 17th, San Francisco. Buckling of rails by compression. G.K. Gilbert photograph [GKG 2879], U.S. Geological Survey Photographic Archives, Denver, Colorado (also pl. 91 in Lawson [1908]). Figure 27 (right). Howard Street near 17th (East side of street). All houses shifted toward left. Tall house (center) dropped from its south foundation. G.K. Gilbert photograph [GKG 2893], U.S. Geological Survey Photographic Archives, Denver, Colorado.

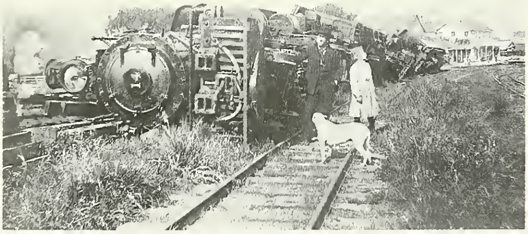

FIGURE 28. Point Reyes Station. Train overturned by the earthquake. G.K. Gilbert photograph [GKG 3400]. U.S. Geological Survey Photographic Archives, Denver, Colorado.

FIGURE 29. Downtown Oakland, California, before noon, 18 April 1906. Wall failure to building containing Oakland Cyclery and J.A. Munro & Co., Auctioneers. G.K. Gilbert photograph [GKG 2889], U.S. Geological Survey Photographic Archives, Denver, Colorado.

FIGURE 30. Fire storm working its way along the lower portion of Market Street, San Francisco. Facing northeast, looking toward the Call (or Spreckels) Building (center, 4th building counting from the right edge) on the south side of Market Street at 3rd and Market. The California Academy of Sciences' Market Street building is the second on the right (south side, near 4th and Market); the Emporium is the first building on the right (south side, between 4th and 5th and Market). Although these buildings had some level of reinforced steel construction, none was adequately fireproofed. Initial reports indicated that they withstood the shock of the earthquake but not the fire that followed. (A 1906 colorized image. California Academy of Sciences Archives [San Francisco Earthquake 1906 File].)

FIGURES 31 (above) and 32 (below). Previously unpublished photos showing the devastation of downtown San Francisco. (Gulian Pickering Rixford Collection, California Academy of Sciences Archives (above N21179; below N21194).

FIGURE 33. The remains of the California Academy of Sciences' commercial and museum buildings following the earthquake and fire. The elevator shaft (center) survived, as did the exterior walls of the museum building (center left). Photograph by Frank Marion Anderson, Curator of Geology, California Academy of Sciences. (California Academy of Sciences Archives.)

FIGURE 34. Interior of the Academy's museum building following the earthquake and fire. Note that the steel-reinforced floors and columns are intact. Photographer not identified (also in Leviton and Aldrich 1997:474). (California Academy of Sciences Archives.)

FIGURE 35. Temporary storage for the Galapagos collections in a walled-off section of the old Museum building of the Market Street complex, December 1906 (also in Leviton and Aldrich 1997:481). (California Academy of Sciences Archives.)

FIGURE 36. The "new" library of the Academy, temporarily located at 1812 Gough Street. The rapid recovery of the library was the result of the extraordinary outpouring of good will and publications from individuals and institutions worldwide (also in Leviton and Aldrich 1997:478). (California Academy of Sciences Archives.)

FIGURE 37. Wooden Japanese god that emerged unscathed from the Academy's building after the fire. Photograph by Drs. Peter S. Bruguiere and Academy curator Gustav Eisen. (California Academy of Sciences Archives N23046.)

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES
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Systematics of the Garden Lizards, *Calotes versicolor* Group (Reptilia, Squamata, Agamidae), in Myanmar: Central Dry Zone Populations

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The Burmese garden lizards represent a complex of several species. DNA sequence and morphological analyses reveal that two species occur sympatrically in the Central Dry Zone of Myanmar. These two new species are described herein. Additionally, the molecular data demonstrate that *Calotes versicolor* represents multiple species and at least two clades: one from India-Myanmar and another from Myanmar-Southeast Asia. The morphological investigation does not currently recognize unique trait(s) for each clade, but it does establish a set of morphometric, scalation, and quantitative coloration traits that permit statistical comparison of intra- and interpopulational variation in the *versicolor* species group.

Calotes versicolor and *Calotes mystaceus* are the most commonly seen diurnal lizards in Myanmar. Both appear to be forest-edge species, hence readily adapted to the fence-row, roadside and garden habitats created by humans. Our collaborative (CAS-NWCD-SI[5]) survey and inventory of the Burmese herpetofauna have enabled us to document the distribution of these lizards and many other amphibians and reptiles, and critically, to obtain tissue samples and adequate voucher series to initiate studies of regional differentiation at both the morphological and molecular levels in a variety of common Burmese frogs and lizards.

Our attention has become increasingly focused on the "common" species. We have discovered from our earliest site-specific surveys that a common species often consisted of two species, often within the same paddy or forest fragment. We further noted that individuals of the same species from distant localities regularly appear subtly different. These differences are sufficiently muted that they can be easily overlooked, and in hurried inventories of sites, it is easier and more expedient to label a specimen with a readily available name. The unfortunate consequence of this practice is an underestimate of a site's true biodiversity and more broadly the biodiversity of the region or country being surveyed and inventoried.

The Chatthin Wildlife Sanctuary (23°35′N, 95°44′E) was the first site surveyed (Zug et al. 1998) in our country-wide inventory of the Myanmar herpetofauna. It lies at the northern end of the Central Dry Zone and is largely a secondary or recovering indaing forest surrounded by paddies.

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[5] CAS=California Academy of Sciences; NWCD=Nature and Wildlife Conservation Division, Forest Department, Myanmar; SI=Smithsonian Institution.

The garden lizard is only modestly abundant at this site and did not attract any special attention until J. Schulte began a regional analysis of molecular differentiation of *Calotes versicolor* populations and discovered that two "*versicolor*" species occur at Chatthin. His continuing analysis has identified other "*versicolor*" species, on which we will report subsequently. Here our focus is on a preliminary definition of the "*versicolor*" group and the description of two Chatthin species. The latter has called our attention to the uncertainty of which population represents true *Calotes versicolor*, i.e., *Agama versicolor* Daudin, 1802. We examine that question briefly owing to its importance in diagnosing the new species. That question will be addressed more critically subsequently in a broader regional study.

TAXONOMIC HISTORY OF *CALOTES VERSICOLOR*

Calotes versicolor was described by Daudin in 1802, then a half-dozen more times by 19th century biologists. All these descriptions apply to Indian populations and, where the type-locality is designated, to populations on the east coast of India (Pondicherry, Chenai [Madras], and Kolkata [Calcutta]). Remarkably, this wide ranging and abundant lizard of gardens and fence-rows has not had populations recognized as distinct species in other parts of Asia. This phenomenon derives from the seeming uniformity of "*versicolor*" populations and, as noted above, the ease of labeling them with the "*versicolor*" epithet. This uniformity is more apparent than real, because even without close examination, we recognized that the *C. versicolor* from different areas in Myanmar were subtly different. We certainly are not the first to notice such differences. Auffenberg and Rehman (1993, 1995) recognized two distinct morphologies in Pakistan and described one of them as a new subspecies (*farooqi*). Kästle (in Schleich and Kästle 2002) noted that the Nepal *C. versicolor* consist of several varieties, and he seems to have been the first to label these strictly *C. versicolor*-morphs as the *C. versicolor* complex. This narrower usage differs from that of Malcolm Smith's *versicolor* group, and we believe that this recognition of a distinct *versicolor* group/complex is a useful phenetic hypothesis prior to a full scale phylogenetic analysis.

Using Malcolm Smith's "Fauna of British India" (1935) as a historical marker, *Calotes* consisted then of four species groups: *cristatellus*; *microlepis*; *versicolor*; *liocephalus*; and unassigned, *C. kingdonwardi* and two dwarf species (*C. ellioti*, *C. rouxii*). Subsequently, no one appears to have examined the relationship within or among these groups until the 1980s. At that time, Moody, in his unpublished dissertation (1980), examined morphological variation in the Agamidae and provided the first phylogenetic analysis of intrafamilial relationships. To ensure a comprehensive study of the family with a full representation of all agamid clades (= genera and subgenera), Moody examined more than 95% of the types of the then described species. This examination resulted in his decision to recognize 53 clades in contrast to the 34 genera listed in Wermuth's 1967 agamid checklist. Moody's nomenclatural groupings were defined only by their species composition (1980: Appendix A). Owing to the thoroughness and scope of this dissertation, Moody's nomenclature was broadly accepted even though he never published formal descriptions of the new and resurrected taxonomic groups. Smith's *cristatellus* group was assigned to the genus *Bronchocela* Kaup, 1827 (see Hallermann's [2005] taxonomic review of the genus). The *liocephalus* and *versicolor* groups remained in *Calotes* Cuvier, 1817. The *microlepis* group became *Pseudocalotes* Fitzinger, 1843 (see Hallermann and Böhme [2000] for generic diagnosis, species content, and nomenclatural history), and Smith's recognition of C. *kakhiensis* as an aberrant member of *Calotes* was "corrected" by placement in the genus *Salea* Gray, 1845. Ota and Hikida (1991) described *Calotes nigrigularis* from Mt. Kinabalu, Sabah. Subsequently, Manthey and Grossmann (1997) erected the genus *Complicitus* for this peculiar lizard, and in 2000, Manthey and Denzer proposed a new genus, *Hypsicalotes* for *C. kinabaluensis*. The validity of these monotypic taxon has not yet been tested.

Smith (1935:183) recognized that his *versicolor* group was "not very homogeneous" because the included taxa shared only a few features. Subsequent studies of *Calotes, sensu* Moody, have examined neither the species composition nor the interspecific relationships within this taxon or the intraspecific ones among *versicolor* populations. We have initiated a morphological review of the species of *Calotes* with the intent of determining phylogenetic relationships based on shared-derived morphological features. That review is still in its earliest stages; nonetheless, we propose that the *versicolor* group (phenetic now) consists of *Calotes* species sharing the following traits: 1) pre-axillary scales uniform-sized, i.e., absence of a crescent-shaped patch of granular scales (pigmented or unpigmented) in front of the shoulder; 2) trunk scales somewhat smaller than or equal to size of ventral scales; 3) dorsal crest scales in a continuous row to (at least) above the shoulders; 4) supratympanic area with a pair of spine patches or patches fused as a single longitudinal series; and 5) multiple (2–4) distinctly linear rows of elongate loreal and subocular scales above the supralabial scales. Each of these traits occurs in other species of *Calotes* but only in combination in the *versicolor* group.

MATERIALS AND METHODS

The present study focuses on the two *versicolor* morphotypes of Myanmar's Central Dry Zone. DNA sequence data (Fig. 3) demonstrate their genetic distinctiveness from one another and other *versicolor* group populations in Myanmar and elsewhere. This discovery resulted from J. Schulte's on-going investigations of relationships among agamid "genera." The initial discovery of striking genetic differences among a few Burmese "*versicolor*" populations led to an increase sampling of populations throughout Myanmar. All these tissue samples derive from the Myanmar Herpetological Survey. The origin of these samples and those from other areas of southern Asia are detailed in Appendix, section C. Methodology for the extraction of DNA and its subsequent analysis are in Appendix, section A.

The DNA data were examined phylogenetically using PAUP* beta version 4.0b10 (Swofford 2002) and implementation of a heuristic search with TBR branch swapping and 1000 random taxon additions using maximum parsimony (MP). Bootstrap resampling (Felsenstein 1985) assessed the support for individual nodes using 1000 bootstrap replicates with TBR and 100 random taxon additions per replicate. Decay indices (= "branch support" of Bremer 1994) were calculated for all internal branches using TreeRot.v2c (Sorenson 1999) and heuristic searches as conducted above for each node present in the overall MP tree(s).

Data examination also included maximum-likelihood (ML) analyses. Simultaneous optimization of ML parameters and phylogenetic hypotheses for this data set were computationally impractical. Iterative searches were conducted for these mtDNA data using a successive approximations approach (Swofford et al. 1996; Sullivan et al. 2005). To reduce computation time, the program ModelTest v3.7 (Posada and Crandall 1998) was used to find the best fitting model of sequence evolution for a tree reconstructed using neighbor joining (NJ), as it has been determined that the starting tree does not significantly influence the estimated model discovered by ModelTest (Posada and Crandall 2001). These parameters were fixed in the initial searches. Heuristic search conditions were: 1) Starting trees were obtained via NJ; 2) TBR branch-swapping; 3) reconnection limit set to eight. Tree(s) obtained from this search protocol were used to estimate new parameter values under an identical model. These new parameter values were fixed in a second search with the same conditions as the initial run. This process was repeated until the same tree and parameter values were found in two successive searches. Bootstrap resampling was applied using ML with 100 replicates and heuristic searches as above except that successive approximations were not conducted for each replicate. In our evaluation of branch support strength, we consider a bootstrap value of 95% and above as strongly supported (Felsenstein and Kishino 1993), 95–70% as moderately supported, and below 70% as poorly supported.

For morphological comparisons, we assembled a small set of *Calotes versicolor* samples from throughout Myanmar to examine the variation within and between select Myanmar populations and two external samples (Pondicherry, India [the putative type-locality of *Agama versicolor* [Daudin] and eastern Thailand) for a perspective on the intra-Myanmar variation. The composition of these samples is presented in the Appendix C.

Our preliminary examination of morphological differences between the genetically distinct units at Chatthin identified several scalation and coloration differences. From this initial comparison and examination of the *Calotes* literature, we developed a set of 25 mensural, 12 meristic (scalation), and 10 coloration traits; definitions of these traits are presented in Appendix section B. Each trait has a unique abbreviation and those are used throughout the following text. Each specimen was dissected to examine the gonads to determine sex and maturity. Data were gathered by HB and GZ, who, periodically and independently, would record data from the same subsample of specimens to ensure that they were measuring and counting identically. The same protocol was followed by JV and GZ for CAS specimens. SYSTAT version 10.2 was used for all statistical analyses.

A map showing principal localities in Myanmar for the major samples of specimens examined in this study will be found in the Appendix (Fig. 11).

OBSERVATIONS ON MOLECULAR SEQUENCE DIFFERENTIATION AMONG POPULATIONS OF MYANMAR *CALOTES* "*VERSICOLOR*"

The twenty-one new mitochondrial DNA sequences range in size from 1702–1728 base pairs and were aligned with 33 additional draconine sequences from Macey et al. (2000) and Schulte et al. (2002, 2004) for a total of 1915 aligned positions. All sequences are inferred to be authentic mitochondrial DNA rather than nuclear encoded copies based on the criteria discussed in Schulte et al. (2004). Site homology was inferred to be ambiguous at 408 nucleotide positions. In the phylogenetic analysis of 1507 unambiguously aligned sites in 54 DNA sequences, 888 were phylogenetically informative (parsimony criterion) and 1028 were variable.

Analysis of DNA sequence data containing 1507 aligned positions produced one overall most parsimonious phylogenetic hypothesis with a length of 6452 steps. Overall phylogenetic relationships among draconine genera are similar to those reported in Macey et al. (2000) and Schulte et al. (2004) (Fig. 1). Differences among intergeneric relationships are restricted to those branches that are weakly supported by bootstrap values and decay indices. All *Calotes* species were recovered as monophyletic with strong support (bootstrap 100%, decay index 39). Two sequences of the recently described species *C. chincollium* (Vindum et al. 2003) were recovered as the sister group to a sample identified tentatively as *C. emma* from Rakhine State in Myanmar (bootstrap 100%, decay index 34) with these three samples forming a strongly supported monophyletic group to a sample of *C. emma* from Vietnam (bootstrap 100%, decay index 44).

The clade containing sequences of *C. calotes, C. htunwini, C. irawadi,* and *C.* "*versicolor*" is strongly supported (bootstrap 98%, decay index 11). The four DNA sequences representing *Calotes htunwini* form a strongly supported monophyletic group (bootstrap 100%, decay index 39) that is the sister group to all remaining species in this clade. All samples of *C.* "*versicolor*" and *C. irawadi* form a monophyletic group with strong support (bootstrap 100%, decay index 52) exclusive of *C. calotes*. The four DNA sequences of *C. irawadi* are monophyletic (bootstrap 100%, decay index 19) but are nested within sequences of *C.* "*versicolor*" with weak support (bootstrap 58%, decay index 3). DNA sequences of *C.* "*versicolor*", except the sample from Rakhine State, are moderate-

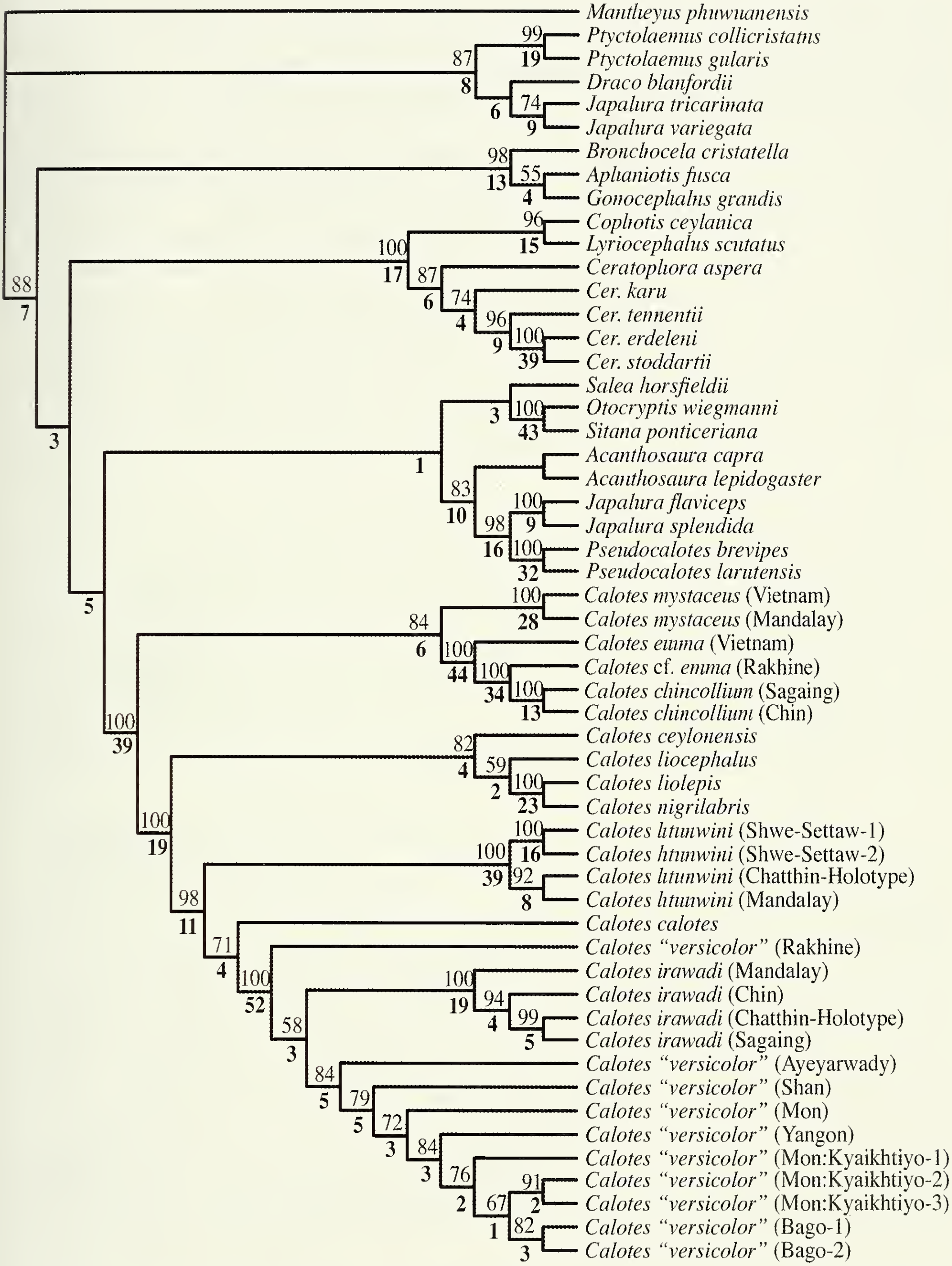

FIGURE 1. Phylogenetic relationships among agamid lizards based on maximum parsimony analysis of DNA sequence data (length = 6452 steps). Bootstrap values are presented above branches and decay indices are shown in bold below branches on the cladogram.

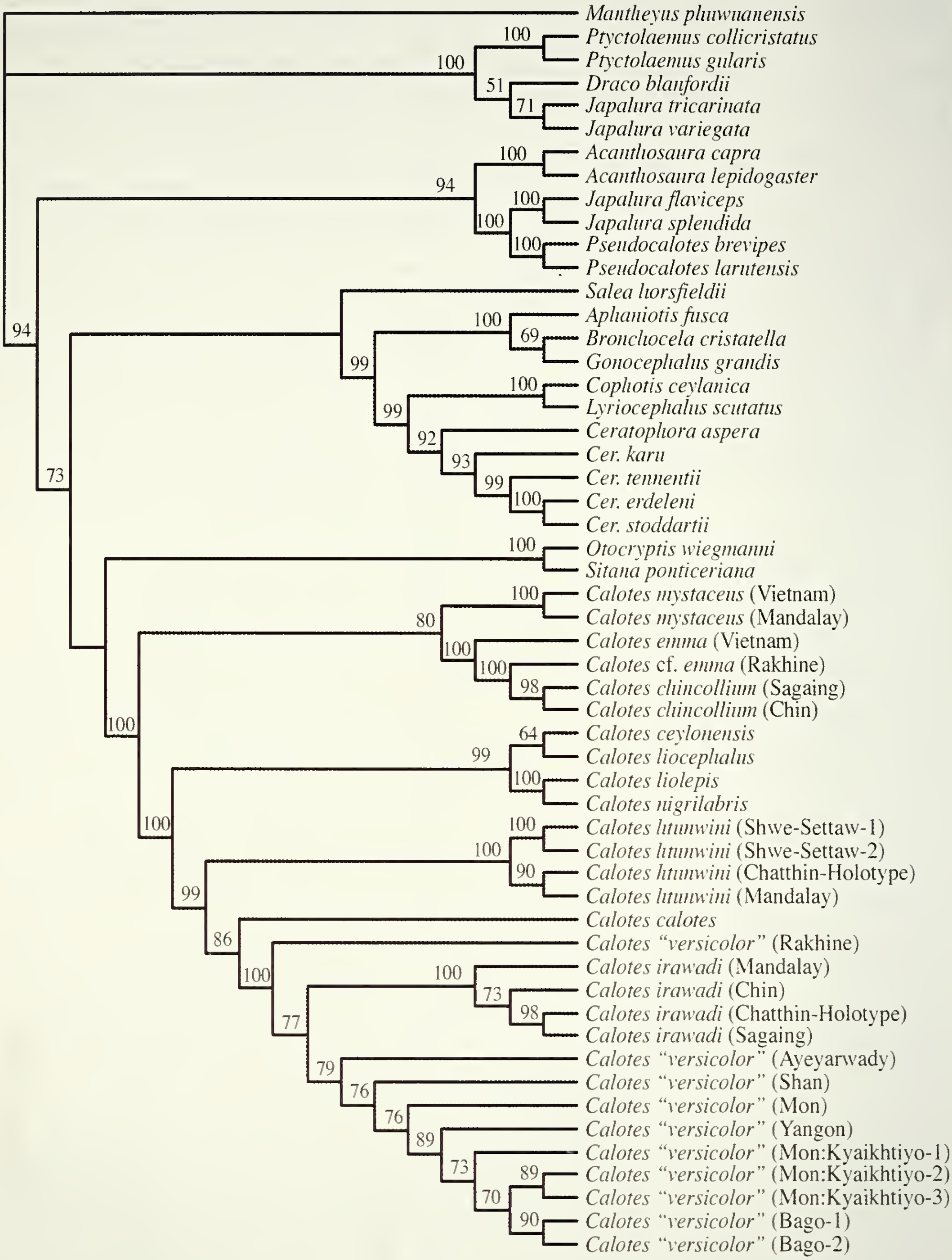

FIGURE 2. Phylogenetic relationships among agamid lizards based on maximum likelihood analysis using GTR + I + G model (mean -log-likelihood = 27680.88). Outgroups are identical to those presented in figure 1.

ly supported as a monophyletic group (bootstrap 84%, decay index 5).

Hierarchical likelihood ratio tests conducted using ModelTest found that the most complex model (GTR + I + G) best explains the aligned sequences and a neighbor joining topology. Model selected was identical when using the overall most parsimonious tree. Model parameters identified using successive approximations were as follows: a= 0.658; proportion of invariant sites = 0.238; substitution rates R(a) = 0.314, R(b) = 4.742, R(c) = 0.345, R(d) = 0.295, R(e) = 2.55, and R(f) = 1.000; and estimated base frequencies A = 0.383, C = 0.330, G = 0.075, and T = 0.212. Using the aligned DNA sequence data (992 unique site patterns) and model parameters from the successive approximations ML analysis, a single topology (Fig. 2) was found (-lnL = 27680.88). Relationships among most sequences representing *Calotes* species in ML analyses were identical to those found from MP analyses. Topological differences between these hypotheses are restricted to weakly supported intergeneric relationships at deeper nodes in the trees. There are several nodes within *Calotes* where ML bootstraps are noticeably higher than MP bootstraps including the group composed of *C. ceylonensis, C. liocephalus, C. liolepis,* and *C. nigrilabris* and the clade containing *C. calotes, C. irawadi*, and all *C. "versicolor"* populations, whereas ML bootstraps support for the class containing *C. irawadi* sequences from Chin, Chatthin, and Sagaing was much lower than the MP bootstrap value.

Maximum likelihood-corrected distances between previously published sequences of *Calotes* species, the *C. versicolor* group, *C. htunwini,* and *C. irawadi* exhibited extensive molecular variation (Fig. 3). The average pairwise genetic difference between *C. htunwini* and all other samples of *Calotes* was 25.8% whereas average pairwise differences between *C. irawadi* and all other samples of *Calotes* were 29.5%. Within the group previously referred to as *C. versicolor,* sequences of *C. htunwini* and *C. irawadi* compared to all other specimens were 21.3% and 9.5% different, respectively. Within the clade containing all populations of *C. "versicolor"* and *C. irawadi,* the latter species was 4.6% different based on maximum likelihood corrected distances. Interestingly, the specimen of *C. "versicolor"* from Rakhine State was found to be 20.6% divergent from *C. htunwini,* 4.4% different from *C. irawadi,* and 3.8% different from the remaining specimens of *C. "versicolor."*

OBSERVATIONS ON MORPHOLOGICAL VARIATION IN MYANMAR *CALOTES VERSICOLOR* GROUP

Preliminary analysis delineated six OTUs (operational taxonomic units) among ten sample localities, two of which (Htunwini and Irawadi) are described subsequent to this examination of morphological variation within and among samples. The latter two OTUs occur together broadly throughout the Central Dry Zone from Chatthin Wildlife Sanctuary southward to Shwe-Settaw W.S.; the Irawadi morphotype also occurs alone on the western edge of the Shan Plateau in the Pyin-Oo-Lwin area (900–1000 m). The garden lizards at the other Myanmar sample localities (Moyingyi and Nat-Ma-Taung), Pondicherry, and Thai-East, each represents a different OTU. Subsequent remarks on morphological variation use these OTU labels (Htunwini, Irawadi, and locality names).

SEXUAL DIMORPHISM.— None of the individual locality samples is sufficiently large to reliably test (Students' t for measurements and scalation, χ^2 for coloration) for sexual or juvenile-adult dimorphism. We, nonetheless, present the result (Table 1) because these dimorphisms regularly occur in other *Calotes* and our preliminary data indicate that these dimorphisms also occur widely in Myanmar *Calotes "versicolor."*

Adult females and males differ in size. Females average smaller than males, and this feature is statistically significant for most measurements in the combined samples of Htunwini and Irawadi

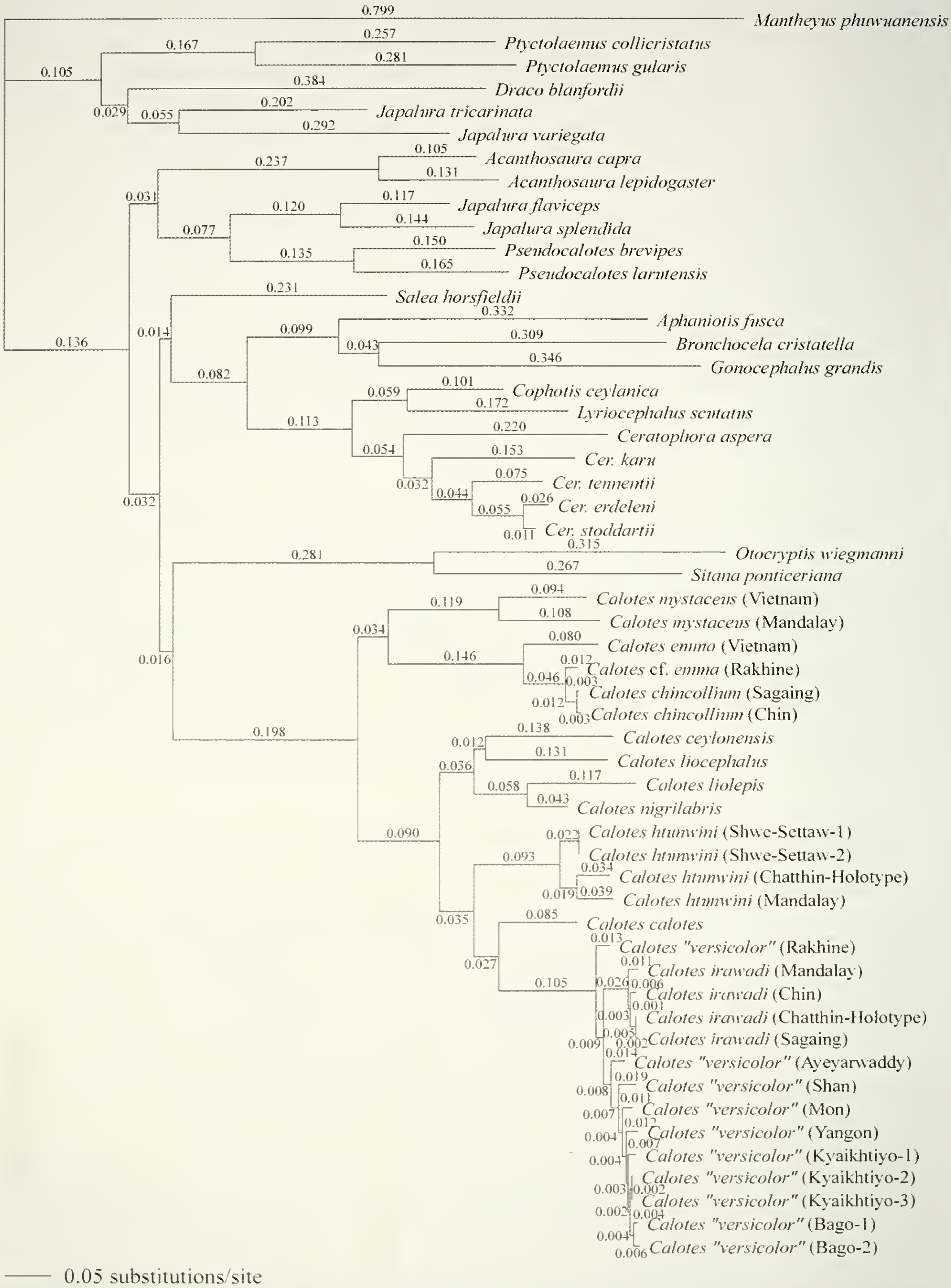

FIGURE 3. A phylogram depicting the phylogenetic relationships and relative divergence of DNA sequence data between species of draconine lizards and populations of the *Calotes versicolor* group. Branch length values represented by estimated number of nucleotide substitutions per site are depicted adjacent to branches.

TABLE 1. Summary of sexual dimorphic traits in *Calotes "versicolor"* samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses: adult females, adult males, juveniles.

Htunwini
  Alaungdaw Kathapa (4, 3, 1). TailW, 4ToeLng; Dorsal; ForearmSt.
  Chatthin (3, 0, 7). Not testable.
  Popa (0, 1, 3). Not testable.
  Shin-Ma-Taung (5, 4, 0). EyeEar, TailH, TailW, UpArmL, UpLegL; Dorsal; color - ForearSt.
  Shwe-Settaw (0, 0, 12). Not testable.
  combined samples (14, 11, 21). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, SnW, Interorb, SVL, TrunkL, TailH, TailW, PectW, SnForel, UpArmL, LoArmL, UpLegL, CrusL, HindfL, 4ToeLng; Dorsal, 4ToeLm; color – MidvLine, ForearSt.

Irawadi
  Alaungdaw Kathapa (2, 14, 1). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb, SVL, TrunkL, TailL, TailH, TailW, PectW, PelvW, SnForel, UpArmL, LoArmL, 4FingLng, UpLegL, CrusL, HindfL; 4ToeLm; color – DorsSt, TrnkBand.
  Chatthin (2, 1, 4). Not testable.
  Popa (3, 4, 3). TailL, HindfL, 4ToeLng; no scalation dimorphism; no color dimorphism.
  Pyin-Oo-Lwin (5, 0, 1). Not testable
  Shwe-Settaw (1, 7, 1). Not testable
  combined samples (14, 30, 13). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb, TailL, TailH, TailW, PectW, SnForel, UpArmL, LoArmL, UpLegL, CrusL, HindfL, 4ToeLng; Eyelid, Dorsal, 4FingLm, 4ToeLm; color – ThroatSt, ThroatPa, CheekCol, DorsSt, TrnkBand.

Moyingyi (3, 7, 1). HeadL, HeadW, JawW, HeadH, EyeEar, SnW, TailH, TailW, PectW, PelvW, SnForel, UpLegL, HindfLng; Dorsal; color - CheekCol.

Nat-Ma-Taung (5, 3, 7). EyeEar, TailH, HindfLng; no scalation dimorphism; DorsSt, ForearSt

Pondicherry (2, 11, 2). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb; SVL, TrunkL, TailL, TailH, TailW, PectW, PelvW, SnForel, LoArmL, ForefL, 4FingLng, UpLegL, CrusL, HindfLng, 4ToeLng; no scalation dimorphism; state of preservation prevented test of color dimorphism.

Thai-East (2, 10, 1). JawW, HeadH, NarEye, EyeEar, SnW, Interorb, TailH, TailW, SnForel, UparmL; Dorsal, 4ToeLm; no color dimorphism.

(Table 1). Overall size differences between the sexes would presumably cause all component measurements to differ in average lengths. That a number of traits do not is noteworthy, and especially so when the differences are shared between the Htunwini and Irawadi samples. The shared non-dimorphic traits are: ForelL, 4FingLng, PelvW. Additional non-dimorphic traits are 4ToeLng for Htunwini and SnW, SVL for Irawadi. An explanation for this non-dimorphism is not immediately evident; perhaps larger samples and covariance analyses would determine if it is a biological reality. Size dimorphism is evident in the other two Myanmar samples (Table 1) as well as the extralimital ones.

Male *Calotes "versicolor"* are the larger sex, strikingly so in the Pondicherry sample, in which there is no overlap in SVL of adult females and males (Table 2). Tiwari and Aurofilio (1990) reported similar results from a Chennai (approx. 120 km N of Pondicherry) sample (10–12 females, 19–23 males). Overlap in SVL and other measurements occurs in all our other samples. This SVL overlap occurred also in Auffenberg's and Rehman's (1993) Myanmar sample. Their Myanmar sample consisted mainly of Yangon individuals, and the size dimorphism (SVL marginally significant difference) was diluted by the inclusion of specimens from three other distant Burmese localities, representing different OTUs.

The sexual differences in scalation are slight (Table 1).The widespread occurrence of Dorsal differences in Htunwini, Irawadi, Moyingyi, and Thai-East samples suggest that this difference is not a statistical artifact. Females have more Dorsals (means of females and males: 50.0, 44.6

TABLE 2. Summary of select measurement characters in adults of the *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses. All measurements are in mm: mean ± s, minimum and maximum values.

Sample	*SVL*	*TrunkL*	*SnForel*	*HindfLng*	*HeadL*	*HeadW*	*EyeEar*	*Interorb*
Htunwini								
F(14)	69.9±6.12	34.7±2.73	25.0±2.59	21.1±2.14	16.5±1.51	13.8±2.34	3.9±0.42	8.6±1.21
	61.3–84.3	30.3–41.9	20.9–28.8	17.4–23.9	14.6–20.6	10.2–17.5	3.2–5.0	6.2–11.0
M(11)	78.5±6.89	37.4±3.51	28.4±2.50	24.3±2.36	18.5±3.03	16.6±2.64	4.9±0.60	9.8±0.76
	67.9–91.4	31.9–44.7	25.5–32.3	20.6–27.8	10.6–21.6	12.5–21.1	4.0–6.0	8.4–11.0
Irawadi								
F (14)	77.4±7.91	40.6±4.3	26.6±3.32	24.5±1.59	17.6±1.82	14.3±1.92	4.3±0.60	8.3±1.04
	64.3–90.3	32.1–44.9	20.8–32.1	21.0–26.5	13.9–21.4	11.2–17.8	3.1–5.5	6.9–10.7
M (30)	82.4±8.09	41.4±5.34	29.2±2.17	26.8±2.22	20.1±1.78	19.1±3.60	5.8±0.86	9.4±0.88
	66.4–106.8	31.7–56.9	25.4–33.7	23.0–34.1	16.9–24.9	13.3–28.3	4.2–7.9	7.9–11.3
Nat-Ma-Taung								
F (5)	79.4±13.63	41.6±8.72	28.2±4.12	24.5±2.77	18.1±2.85	17.1±4.04	4.8±0.75	8.5±1.21
	56.1–89.4	27.7–49.3	21.2–31.2	19.6–26.3	13.0–19.8	9.9–19.4	3.5–5.3	6.4–9.3
M (3)	88.3±1.17	46.2±1.07	31.2±0.92	28.6±0.61	21.7±0.62	21.0±1.77	6.4±0.10	10.1±0.40
	87.0–89.3	45.5–47.4	30.2–32.0	28.2–29.3	21.0–22.0	19.0–22.2	6.3–6.5	9.6–10.3
Moyingyi								
F (3)	83.4±4.92	41.4±2.65	30.7±1.47	27.0±1.22	17.9±1.34	14.4±1.77	4.2±0.35	8.9±0.91
	78.2–88.0	38.5–43.7	29.0–31.8	26.2–28.4	16.9–19.4	13.2–16.4	4.0–4.6	8.1–9.9
M (7)	91.4±4.52	43.5±2.97	35.4±2.50	30.1±1.35	21.0±1.34	20.1±2.03	6.1±0.71	9.6±0.36
	82.9–97.5	39.9–47.3	31.6–37.7	27.5–31.8	19.1–23.5	17.7–24.1	4.7–6.8	9.1–10.0
Pondicherry								
F (2)	92.9	45.2	31.3	28.4	21	18.1	5.5	11
	89.9–95.9	44.6–45.8	30.2–32.3	27.3–29.4	20.5–21.4	17.6–18.6	5.5	10.6–11.3
M (11)	119.3±8.69	52.5±4.23	45.7±4.88	37.2±2.00	28.3±1.91	29.4±4.05	9.6±1.26	14.0±0.93
	106.7–131.2	46.0–59.5	38.0–52.9	33.7–40.0	25.2–30.9	22.4–33.7	7.3–11.0	12.3–15.1
Thai-east								
F (2)	73.6	35.8	27.5	22.9	17.9	14.2	4.3	9.2
	71.2–76.0	34.4–37.1	26.3–28.6	22.1–23.7	17.7–18.0	13.5–14.8	4.2–4.3	9.1–9.3
M (10)	81.2±6.11	35.6±3.20	32.5±3.01	25.6±2.18	20.0±1.41	18.9±2.77	5.8±0.54	10.5±0.77
	69.9–90.1	30.2–41.1	26.8–36.1	23.2–30.0	17.9–22.8	13.8–23.3	4.8–6.7	8.9–11.6

Htunwini; 51.6, 48.2 Irawadi; 56.3, 49.5 Moyingyi; 47.5, 44.2 Thai-East). Presumably, the higher number of Dorsal in females reflects an increased abdominal volume, although circumference is not enlarged relative to an increase in Midbody. An explanation for slightly more 4ToeLm in males is not immediately evident.

Calotes "*versicolor*" are well known for bright head, neck, and fore-trunk coloration in sexually ready males. These bright reds and oranges soon disappear in preserved specimens; however, we have not observed these bold shades in mature males of the Htunwini, Irawadi, Moyingyi, and Nat-Ma-Taung populations. The preserved sexual coloration differences of the four dimorphic Burmese populations are largely non-overlapping (Table 1 and 4) except for the usual presence of ForearSt in Htunwini and Nat-Ma-Taung females, and the distinct DorsSt in Irawadi and Nat-Ma-Taung females. Clearly, the coloration of living adults of all Myanmar populations requires more attention and better cataloging.

MENSURAL TRAITS.— Amidst the four Burmese OTUs, the Moyingyi population has the largest average body size even though the Moyingyi sample does not contain the largest Burmese individual (an Irawadi male; Table 2) among our Burmese samples. Htunwini adults are the smallest garden lizard of the four Burmese OTUs. Nat-Ma-Taung and Irawadi adults are approximately equal in size and the Moyingyi lizards the largest. We anticipate that these relative size differences will only be strengthened as sample sizes are enlarged.

There is a strong positive linear association among all the mensural traits and SVL, usually with coefficients of determination (R^2) greater than 0.80, confirming that regression equations account for a significant percentage of the variation. Regression slopes were not compared statistically. Visually, body-segment lengths appear to increase proportionately faster (i.e., higher slope values) in males than females for both Htunwini and Irawadi samples. Regression slopes for female Htunwini and Irawadi, and for male Htunwini, Irawadi, and Pondicherry samples are also similar. Thus, assuming that regressions reflect growth trajectories, females and males within a population possess different growth allometries, whereas the same sexes from different populations have similar allometries. This interpretation requires testing.

The Irawadi OTU is represented by individuals from seven areas (Alaungdaw Kathapa [AK], Chatthin, Popa, Pyin-Oo-Lwin, Yamethin, Yin Mar Bin, and Shwe-Settaw), but adults are available from six areas and only two (AK, Shwe-S) have enough adult males to hint that the more northerly populations might average somewhat smaller (SVL) than the Shwe-S area. The availability of adequate adults of Htunwini is similar and limits the evaluation of geographic variation. There are no adults from Shwe-S, and AK has the largest (mean SVL) males, and Chatthin the smallest females.

Because of the correlation among all the measurements, principal components analysis (PCA) results reflect only aspects of body size, and expectedly, the major loading variable is SVL, whose loading is double or more that of any other measurement. Preliminary PCA comparison of all adults and all measurements identified SVL, TrunkL, HeadW, and SnForel (ordered by loading rank) as the major loadings on the first component (PC1), and TrunkL for the second component (PC2) in adult females; PC1 explains 80% of total variance and PC2 the remaining variance. Results were similar for adult males: PC1 loading—SVL, TrunkL, UpLegL, PectW, and HindfL; PC2—TrunkL; PC1 80.6% of variance, PC2 22.4%. We used the preceding seven measurements and JawW in PC analysis to examine regional variation individually in adult females and males of the Htunwini and Irawadi samples. These four comparisons revealed no geographic structuring of either sex of each OTU (see Fig. 4A).

A PCA of adult males (n = 71) of the combined "*versicolor*" sample (n = 160) shows a segregation of the Pondicherry males from the Myanmar and Thai males (Fig. 4B). SVL is the major loading on PC1, TrunkL and HindfL on PC2, 93.6% and 3.4% of variance, respectively. Hence, the PC graph emphasizes the significantly larger bodied Pondicherry males on the PC1 axis and the similarity of body proportions on the PC2 axis. This size difference is best evaluated by minimum size at attainment of sexual maturity: males—106.7 mm SVL Pondicherry, 69.8 mm Thailand, 82.9 mm Moyingyi, 87.0 mm Nat-Ma-Taung, 67.9 mm Htunwini, and 66.4 mm Irawadi; females—89.9 mm SVL Pondicherry, 71.2 mm Thailand, 78.2 mm Moyingyi, 56.1 mm Nat-Ma-Taung, 61.3 mm Htunwini, and 64.3 mm Irawadi. The minimum mature sizes highlight the major size difference of the Pondicherry OTU in contrast to the Burmese and Thai OTUs.

SCALATION.— Of the 12 scalation traits recorded, no sample displays a unique meristic aspect of scalation, i.e., unique in the sense of no or minimal overlap of one or a set of traits among the OTUs. All traits have either broad overlap or near identity of range of values (see Table 3). Although ranges overlap, four meristic traits (Dorsal, Midbody, 4FingLm, 4ToeLm) show differ-

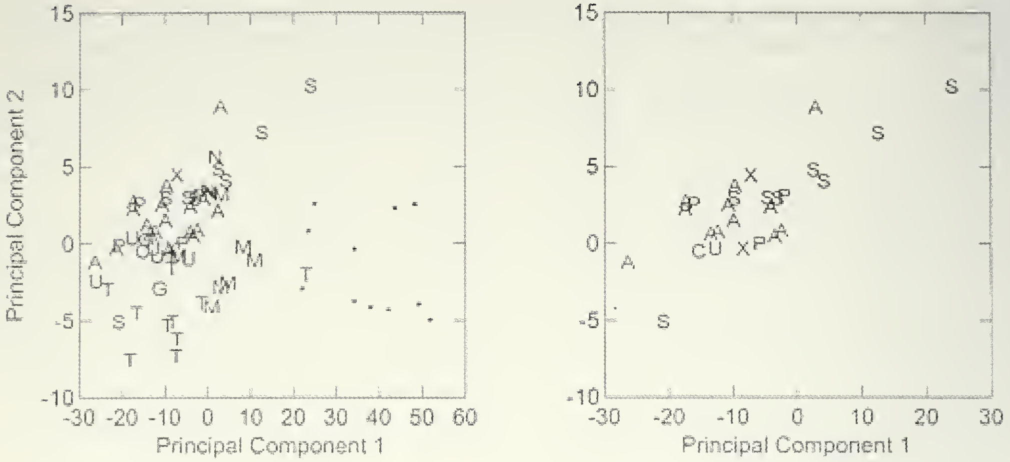

FIGURE 4. Principal components comparisons of *Calotes "versicolor"* samples using select mensural traits (JawW, SVL, TrunkL, PectW, SnForel, UpLegL, HindfL). Left. Adult males of the combined regional samples. Right. Adult males of the Irawadi regional samples. Abbreviations: *, Pondicherry, India; A, Alaungdaw Kathapa; C, Chatthin; G, Min-Gon-Taung; M, Moyingyi; N, Nat-Ma-Taung; P, Popa; S, Shwe-Settaw: T, eastern Thailand;. U, Shin-Ma-Taung; X, Yamethin.

ences of means among the six OTUs. Nat-Ma-Taung has the highest number of Dorsal (mean, 52.2) and Pondicherry the lowest (40.8). Table 3 shows the distribution of the Dorsal means, and a mean of the means is 48.2, confirming the outlier status of Nat-Ma-Taung. Neither of these samples displays sexual dimorphism of Dorsal or other scalation traits (Table 1). Pondicherry has the lowest Midbody meristic (42.8), and it is similarly distant from the mean of means (46.3). *Htunwini* has the lowest means for 4FingLm (16.9) and 4ToeLm (22.7), contrasting to the mean of means, 20.0 and 24.8, respectively.

Regional or intrapopulational variation can be examined only in Htunwini and Irawadi, and even in these OTUs, the data must be viewed cautiously owing to small sample sizes. For Htunwini, the means of the scalation traits for the five sample localities (Alaungdaw Kathapa, Chatthin, Popa, Shin-Ma-Taung, Shwe-Settaw) are very similar with a range of 1 or less for head scalation traits, and five or less for Dorsal and Midbody. The ranges are also small for 4FingLm (<1.5) and 4ToeL (<1.3), although the Chatthin sample is an outlier (difference > half of range) for both traits (16.4,

TABLE 3. Summary of select scalation characters in juvenile and adults of the *Calotes "versicolor"* samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses.

Sample	*HeadSTr*	*Dorsal*	*Midbody*	*4FingLm*	*4ToeLm*
Htunwini (49)	12.3±1.23	47.3±4.37	47.1±2.73	16.9±1.47	22.7±1.83
	10–15	38–57	39–53	15–20	18–26
Irawadi (57)	12.1±1.24	48.9±3.92	45.6±2.22	20.2±1.52	24.9±1.46
	10–15	36–59	40–51	17–24	22–29
Nat-Ma-Taung (15)	11.7±1.10	55.2±3.91	49.4±2.67	20.6±0.91	25.9±1.60
	10–14	49–60	45–55	19–23	24–29
Moyingyi (11)	12.4±1.21	52.1±4.81	48.7±2.10	21.1±1.81	24.8±1.53
	11–15	46–61	46–53	18–24	23–28
Pondicherry (15)	12.7±1.22	40.8±3.08	42.8±2.37	21.5±1.92	26.5±1.89
	11–14	36–45	37–46	16–24	23–30
Thai-east (13)	13.2±0.80	44.9±2.22	44.6±2.47	19.5±1.39	24.0±1.08
	12–15	41–48	41–48	17–22	22–26

20.9). The uniformity of ranges and means is similar for the Irawadi samples (AK, Chatthin, Popa, Pyin-Oo-L, Shwe-S). Outlier values occur only for HeadSTr (AK, Chatthin) and Midbody (Pyin-Oo-L).

A PCA of all juveniles and adults of the combined "*versicolor*" sample shows a broad clustering (Fig. 5A; components 1 and 2) of the OTUs with no individual OTU separated by a hiatus from the other OTUs; however, internal structuring or aggregation is present. Pondicherry lizards lie largely in the upper left quadrant of the graph, overlapping somewhat with Irawadi lizards. Htunwini lizards occupy the bottom half of the cluster with little overlap with the other OTUs, and especially with minimal overlap (Fig. 5B) with sympatric Irawadi. There are four moderately strong loadings of traits on the first four components; these PCs accounts for 58, 16, 11, and 4% (= 89%) of the total variance. Dorsal and Midbody are major loading traits on PC1, 4FingLm and 4ToeLm on PC2, Midbody on PC3, and HeadSL on PC4. Thus, PCA discerns the lower values of Dorsal and Midbody for Pondicherry and similarly the low 4FingLm and 4ToeLm of Htunwini in the placement of these two OTUs in multicharacter hyperspace, that is, PC1 is a vector principally of trunk scalation and PC2 of digital lamellae.

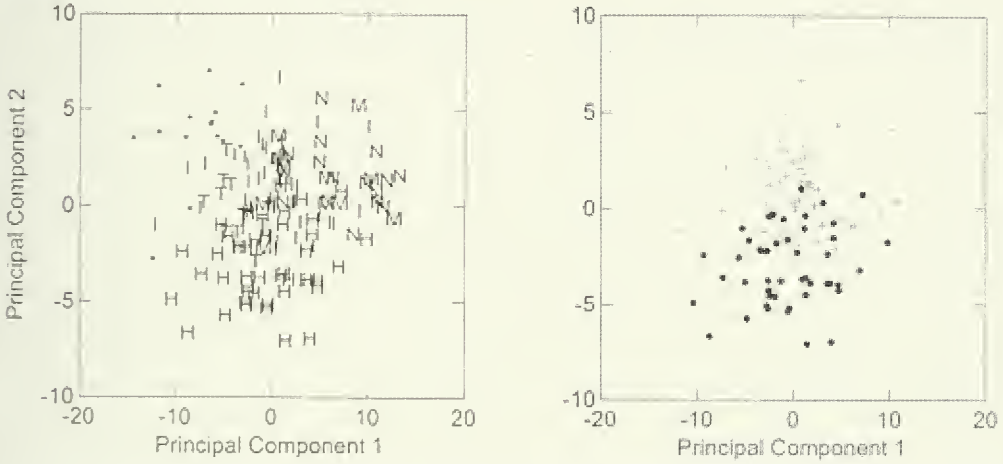

FIGURE 5. Principal components comparisons of *Calotes* "*versicolor*" samples using all scalation traits. Left. Juvenile and adult lizards of the combined regional samples. Right. Juveniles and adults of the Htunwini and Irawadi OTUs. Abbreviations: *, Pondicherry, India; H, circle, Htunwini OTU; I, +, Irawadi OTU; M, Moyingyi; N, Nat-Ma-Taung; T, eastern Thailand:.circle. H, Htunwini OTU; +, I, Irawadi OTU.

Other scalation features are less easily quantified and several of these traits are strikingly different among the "*versicolor*" OTUs examined in this study. The orientation of scales on the side of the neck and adjacent supra-axillary area is obliquely upward to vertical (Fig. 8) in all OTUs except Htunwini. Scale orientation in the latter is horizontal to slightly upward oblique. This orientation feature is confined to the cervical and supra-axillary area; posteriorly on the anterior trunk, the trunk scale orientation of Irawadi and all other "*versicolor*" lizards is obliquely upward.

Keels are variously developed on the neck, trunk, limbs, and caudal scales. Within a sample or OTU, the relative height of keels is usually equivalent in adult females and males. All OTUs share distinctly keeled caudal scales (dorsally and ventrally), although keeling seems slight to modest in Nat-Ma-Taung individuals. The extent of limb scale keeling varies among the OTUs. On the forelimb, keels are well developed on the dorsal and ventral surfaces of the upper and lower arms in Htunwini, Irawadi, Moyingyi, and Thai OTUs. Keels are similarly present on these surfaces in Nat-Ma-Taung individuals although seemingly lower than in the geographically adjacent Htunwini and

Irawadi. The relative height and their body location of keels may be sexually dimorphic in Pondicherry lizards; however, the state of preservation and the few females of our samples may have biased our observation. Adult Pondicherry females have low to modest keeling on all limb surfaces, adult males have reduced or no keeling on dorsal surface of the upper arm. For hindlimbs, the general pattern (Htunwini, Irawadi, Moyingyi, Thai, Pondicherry) is distinct keels on dorsal surface of thigh and crus, distinct keels ventrally on crus, and weak to no keels on underside of thigh. Nat-Ma-Taung individuals match the general pattern but with weaker keels. Keeling is well developed on the ventral scales, from throat to vent, of all OTUs. The strengthening of keeling on the dorsal and lateral surface of the neck and trunk is more variable. For Htunwini and Moyingyi, keels are well developed throughout. Keel height is moderate to low on these surfaces in Irawadi. Some Thai specimens match the Irawadi condition, others have no to low keels, and Pondicherry individuals have smooth dorsal scales.

Description and comparison of the dorsal crest in "*versicolor*" lizards represent a challenge. The degree of development of crest is ontogenetically and sexually variable. Adult males definitely have the strongest development of the crest in each of OTUs, but our observations suggest that crest-scale development is also affected by the hormonal or territorial status of individual males because slightly smaller adult males have less well-developed crests. Another challenge is determining the last "true" crest-scale. The anterior crest-scales are unquestionably present; however, there is a gradual transformation in shape and size diminution posteriorly. As we began data collection, we assumed that our Dorsal trait would delineate some of the differences in dorsal crests; however, it became evident quickly that Dorsal simply was a count of the number of middorsal scales from the first distinct, although short, spine to the middorsal scale above the vent. We have not yet developed a reliable means of defining where "spines" end and the first peaked middorsal scales begin. This ambiguity is reflected in the subsequent description of crest variation.

Of the six OTUs, the crest is best developed in the Pondicherry males. The crest begins with one or two short spines, then jumps to a spine with a length equal to tympanum diameter, quickly grading upward to spines of 2.5–3.0 × diameters at the rear of the neck and then gradually decreasing in length to about 0.75–1.0 × diameters at the base of the tail. The crest of adult Pondicherry females is less well-developed: the longest spines are slightly greater than tympanum diameter on the anterior neck declining to half that length on the anterior trunk, and flat middorsal scales by mid-trunk. The nature of dorsal spines in Myanmar OTUs is similar to the Pondcherry females except the crest does run with elevated spines to base of the tail in most males. The crest is modestly developed in Moyingyi males. The spines quickly reach a length of 75–100% tympanum diameter and remain a constant length to the supra-axillary and then shorten gradually to the base of the tail where the middorsal scale tips are still pointed and slightly elevated. Moyingyi females have slightly shorter spines anteriorly and largely mimic the male condition until midtrunk where the middorsal scales flatten and match the parasagittal dorsal scales in appearance. The preceding male and female patterns occur in Htunwini and Irawadi. In the former, the neck spine-lengths are less than tympanum diameter; in the latter, lengths equal the diameter. The neck spine in Irawadi are straighter and more numerous on the neck than in Htunwini (compare in Fig. 8) and other OTUs. The condition in Nat-Ma-Taung is similar to the Pondicherry lizards, although the maximum spine length never exceeds 1.5 × tympanum diameter in adult males and barely larger than a diameter in females. Thai males have a pattern like Moyingyi males, although an occasional Thai male can have one or two larger (to 2 × diam.) neck spines.

Initially, we had the impression that Htunwini lizards had somewhat larger surpaocular scales than those of Irawadi individuals. The HeadSTr trait was an attempt to quantify this difference but did not succeed. To ensure consistency in data collection, we used a transverse axis defined by anterior border of the interparietal scale. Because of posterior position of the axis, it inadequately addressed the supraocular size issue. The poorly defined medial supraocular ring does not permit consistency in data-gathering. A difference in supraocular size might be a diagnostic feature; however, our current impression is that variation within the Htunwini or Irawadi OTU encompasses the variation of a combined sample. The Pondicherry, Thai, and Moyingyi samples match the preceding observation. Nat-Ma-Taung lizards appear to have the largest, hence fewer, supraoculars, but this appearance cannot be confirmed without a consistent quantitative measure.

The interparietal scale is typically the largest dorsal head scale. It is variously rectangular in shape. The shape variation in one OTU seemingly encompasses the variation in the total sample.

Calotes versicolor group members are characterized by a pair of supratympanic spines (= paroccipital spines of Moody) on each side of the head. Each spine is actually a cluster of scales with a single large center spine surrounded by lower spine-like scales. The anteriormost spine is also the dorsalmost one, lying well above the anterior half of the tympanum. The posterior spine is closer to the tympanum (3–4 scales separation) and commonly level with the posterior edge of the tympanum. The spines vary ontogenetically, becoming distinctly enlarged as an individual approaches maturity. They are also somewhat larger in adult males than in females, but this dimorphism is not great in our samples. With maturity, the basal scales become increasingly pointed and projecting. The Thai and Myanmar OTUs have modestly developed spines, their lengths half or less the maximum diameter of the tympanum. The spines in both female and male Pondicherry lizards are two-thirds or more tympanum diameter.

Coloration.— Our samples and coloration coding permit an explicit comparison of coloration differences in five OTUs. The Pondicherry sample presumably was held too long in formalin. and all specimens are a unicolor dark butterscotch brown. The quantification of coloration traits (Table 4) reveals that each OTU has a unique set of traits and that most adult females and males can be distinguish from each other in each OTU (except Thailand). This sexual differentiation is often not statistically significant (hence unreported above) when examining single color traits but is functional when using sets of traits. For example, Htunwini females (adult) regularly have ForearSt, NucSpot. TrnkBand. and MidvLine, which occur less frequently in males. Irawadi females typically lack CheekCol and have DorsSt and TrnkBand, the opposite condition in males. Nat-Ma-Taung males lack DorsSt and ForearSt, and these traits are almost always present in females. Moyingyi males regularly have CheekCol and ThroatPa, which are absent in females.

Geographic variation in coloration among Htunwini and Irawadi sample-localities cannot be accurately assessed owing to low numbers of adults at most localities. Possibly, Alaungdaw-Kathapa male Irawadi have darker and more frequent CheekCol than other Irawadi populations. No other regional coloration differences were noted in other Irawadi populations or in any Htunwini populations.

Amongst the OTUs, the Thai sample is the most readily differentiated. No Thai adults have DorsSt, ForearSt, NucSpot, ThroatPa, and TrunkSt; most adults have CheekCol. Except for Htunwini, males commonly have CheekCol; however, the intensity and size seemingly varies among the OTUs. Htunwini females and males also have reduced ThroatSt and TrunkSt. In contrast, Irawadi, Nat-Ma-T, and Moyingyi adults almost always have ThroatSt, and roughly half of the adult Irawadi and Nat-Ma-T females have TrunkSt.

Morphological differentiation.— We noted in the introduction that we recognized two genetically distinct "*versicolor*" lizards at Chatthin. The preceding genetic and morphological analyses confirm the distinctiveness of these lizards and demonstrate that the two lizards co-occur broadly throughout Myanmar's Central Dry Zone. These analyses also demonstrate the presence of other populations of "*versicolor*" lizards, representing distinct lineages.

TABLE 4. Summary of occurrence of color traits in adults of the *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses. All values are percent present.

Sample	*CheekCol*	*DorsSt*	*ForearSt*	*NucSpot*	*TrnkBand*	*MidvLine*	*ThroatSt*	*ThroatPa*	*TrunkSt*
Htunwini									
F (14)	0	64	57	93	86	100	29	14	14
M (11)	0	73	18	64	45	64	9	0	0
Irawadi									
F (14)	7	50	78	86	100	93	100	29	50
M (30)	50	20	67	60	43	90	100	3	40
Nat-Ma-Taung									
F (5)	60	80	100	80	100	100	100	0	40
M (3)	67	0	0	100	67	67	100	0	0
Moyingyi									
F (3)	0	67	100	100	100	100	100	0	0
M (7)	86	43	86	100	43	100	86	57	0
Thai-east									
F (2)	100	0	0	0	100	50	100	0	0
M (10)	60	0	0	0	100	50	100	0	0

A variety of morphological traits allows us to differentiate these lineages. Briefly those traits are: 1) body size at sexual maturity and degree of sexual dimorphism of adults; 2) Dorsal, Midbody, 4FingLm, and 4ToeLm of scalation; and 3) a variety of coloration traits. Because our study focuses on the Central Dry Zone "*versicolor*", these two species are described below. A subsequent study will examine the more "peripheral" populations in the bordering mountain ranges and the coastal/southern populations from Rakhine to Mon State.

SPECIES DESCRIPTIONS

Calotes htunwini Zug and Vindum, sp. nov.

Figs. 6–8.

HOLOTYPE.— USNM 524044, an adult female from MYANMAR: **Sagaing Division**, Chatthin Wildlife Sanctuary, San Myaung Camp (23°34′27.6″N, 95°44′15.6″E; ca. 110 m), approx. 2 km WNW of Chatthin, collected by Htun Win, 22 May 1998.

PARATYPES.— MYANMAR: **Sagaing Division**, Alaungdaw Kathapa National Park CAS 215741, USNM 562980; Chatthin Wildlife Sanctuary CAS 231832, USNM 520545, 524045, 562967–968; Kabaing CAS 215811; Mintaingbin CAS 215368; Yin Ma Bin CAS 215347–348, 215448, 215457–458, USNM 562981; **Magway Division**, Shwe-Settaw Wildlife Sanctuary CAS 213607, 213620, 213741, 213786, 213789, USNM 562974–975.

DIAGNOSIS.— *Calotes htunwini* is a member of the *C. versicolor* species group and differs from all other members of this group by the horizontal orientation of the scale-rows on the side of the neck and adjacent supra-axillary area; scale-row orientation in the other *C. versicolor* members is obliquely posteriorad or vertical. Further, it differs from the sympatric *C. irawadi* by its slightly smaller adult body size (means 69.9, 78.5 mm SVL; female, male respectively), fewer 4FingLm (mean 16.9), absence of CheekCol, and infrequent presence of ThroatSt.

ETYMOLOGY.— We name this species in fond memory of Htun Win and to honor him for his contribution to Burmese herpetology. Htun Win grew up in Chatthin village and joined the Chatthin Wildlife Sanctuary in January 1993 as a day-worker and was appointed as a NWCD forester in January 1995. He began his herpetological work as the team leader of GZ's Chatthin W.S. herpetofauna monitoring-inventory project in August 1997 and then became the leader of our CAS-

NWCD-SI Herpetological Survey team in November 1999. His commitment to our survey project and his expanding knowledge of the Burmese herpetofauna were major factors for the success of the survey. He became ill while surveying the herpetofauna of Kachin State and died in June 2004. The epithet is proposed as a noun in apposition.

Description of holotype.— An adult female of 64.0 mm SVL, 22.2 mm SnForel, 33.8 mm TrunkL, 135 mm TailL (about ⅛ tip regenerated, tail now in 2 pieces), 6.4 mm TailH, 5.6 mm TailW, 9.1 mm PectW, 11.2 mm UpArmL, 11.0 mm LoArmL, 10.2 mm ForefL, 6.8 mm 4FingLng, 13.5 mm UpLegL, 12.8 mm CrusL, 18.2 mm HindfL, and 9.5 mm 4ToeLng. Head pentagonal (dorsal outline) covered largely with small, mostly smooth scales slightly overlapping; 14.7 mm HeadL, 10.3 mm HeadW, 10.0 mm JawW, 12.1 mm HeadH, 6.6 mm SnEye, 3.5 mm NarEye, 3.7 mm EyeEar, 4.6 mm SnW, and 6.7 mm InterOrb.

Head distinct from neck; snout to eye broadly acute and triangular, snout-tip blunt; head behind eyes with edges slightly bowed outward by jaw muscles but edges largely parallel; sides of head flat, descending perpendicular downward from sharp canthus rostralis and supraciliary edge to lips, posterior to eye slightly rotund; eyes, slightly protruding, just barely extending beyond canthus-supraciliary border; chin and throat generally flat. Dorsal head scales (Fig.7) variably sized and smooth surfaced, most equivalent in size to dorsal trunk scales; no distinct plates, rostral equivalent to supralabials in height above lip with 7 SnS; 8/8 (left/right) elongate and sharply folded CanthR, scales somewhat enlarged in supraocular area but not forming distinct supraocular plates; 13 HeadSL and 12 HeadSTr; posteriorly slightly enlarged, irregularly diamond-shaped interparietal with distinct medial parietal eye. Laterally head with single large nasal scale on each side abutting rostral and perforated by large naris; loreal and preocular area with small scales, those above supralabials arranged in two parallel longitudinal rows extending to posterior margin of orbit; 11/11 Suplab; eye covered with "sock" of small, nearly granular-sized scales and opening border by double row of eyelid scales, outermost row of ridged scales, inner row smooth and flat 12/13 Eyelid; postocular and temporal scales modest sized, smooth laterally and lightly keeled dorsolaterally; tympanum large (subequal eye-opening diameter) and naked; pair of spines or spine-clusters in supratympanum area, anterior one dorsolaterally directly above anterior half of tympanum separated by 6 scales, posterior one level with posterior edge of tympanum separated by 3 scales, a single narrow, dagger-like scale (length about ⅛ tympanum maximum diameter) projecting upward; 10/11 rectangular Inflab along mouth margin, bordered below by 3–4 rows of narrow and elongate, longitudinally arranged smooth scales; medially the chin throat scales triangular and strongly keeled; single median pentagonal mental scale between left and right Suplab.

Trunk scalation generally keeled dorsally and laterally; middorsal crest of elongate scales, occiput origin separated from interparietal by 3 rows of dorsal scales, dorsal spine-scales relatively small (lengths about 1.5 × length of adjacent parasagittal scales) and first 5–6 more equilateral-triangular than spine-like, length of crest-scales decreasing by midneck and flattened like adjacent dorsal scales by anterior trunk; 49 Dorsal, 48 Midbody; all trunk scales keeled, increasing in size from neck onto trunk, neck and supra-axillary scales horizontal (Fig. 8) with orientation gradually shifting diagonally upward although not near-vertical; dorsal trunk scales large and subequal ventral trunk scales; preaxillary scales modest sized and most smooth; ventral scales large and uniform sized from throat to vent and strongly keeled.

Limbs with modest to large scales, all keeled; fingers (21/21 4FingLm) and toes (27/28 4ToeLm) each with 3–4 modestly keeled scales dorsally and strongly bicarinate lamellae ventrally; claws long, thin and sharply pointed on all digits. Tail scalation similar to trunk with progressive loss of scale rows distally.

Coloration in preservation beige to light tan background dorsally and laterally; head scales

FIGURE 6. *Calotes htunwini* in life. Upper. Holotype, adult female [USNM 524044] – Chatthin (photographed by G. Zug). Left Paratype, adult female [USNM 524045] – Chatthin (G. Zug). Right. Paratype, subadult male [USNM 562997] – Shwe-Settaw (G. Zug).

speckled with dark brown dorsally; pair of dark brown, cream-centered nuchal spots, one on each side of posterior border of interparietal scale and not contacting one another; 4 dark brown line radiating posteriorly and ventrally from the orbit. Indistinct and discontinuous middorsal light line, broader dorsolateral light stripes also discontinuous; eight dark brown dorsal blotches cleft by light middorsal line and edged laterally by the dorsolateral light stripe on each side, each of the blotches separated front and behind by narrow light bar, which extends onto sides of trunk; 1 blotch on neck, 6 on trunk, and smaller and narrower onto tail base; laterally neck dark above and lighter below, trunk similar except generally darker. Fore- and hindlimbs banded, narrow light edges define broader dark bands; banding lighter on forelimb in contrast to darker, more distinct banding on hindlimb; pale stripe along posterior margin of crus. Ventrally dusky beige with faded palmate dark striping on throat (ThroatSt) and faded dark midventral stripe on trunk (MidvLine). In life (Fig. 6), colors brighter and bolder; distinct orange to rufous tint on top and side of head, dorsally on neck and anterior trunk; ventrally white with beige tint and brown markings, throat faded orange.

VARIATION OF PARATYPES.— The paratypic series contains 7 adult females, 4 adult males, and 15 juveniles. The juveniles range in SVL from 34.5 to 75.7. The adult females range in SVL from 61.3 to 84.3 mm (mean, 69.6). Means for the females other measurements (all in mm) are: TrunkL 34.5; TailL 152; TailH 7.3; TailW 7.4; PecW 11.4; PelvW 7.4; SnForeL 25.0; UpArmL 13.7; LoArmL 12.3; ForefL 12.6; 4FingLng 8.2; UpLegL 15.6; CrusL 15.8; HindfL 21.1; 4ToeLng 11.5; HeadL 16.6; HeadW 13.4; JawW 11.7; HeadH 13.3; SnEye 6.8; Nareye 3.6; EyeEar 3.9; SnW 4.7; Interorb 8.5. The adult males range in SVL from 71.6 to 91.4 mm (mean, 81.4). Means for the males other measurements (all in mm) are: TrunkL 39.6; TailL 148.6; TailH 11.8; TailW 10.9; PecW 14.9; PelvW 8.2; SnForeL 28.8; UpArmL 15.5; LoArmL14.1; ForefL 14.0; 4FingLng 9.3; UpLegL 18.3; CrusL 18.3; HindfL 25.1; 4ToeLng 14.2; HeadL 19.9; HeadW 17.8; JawW 14.0; HeadH 13.3; SnEye 5.3; Nareye 4.2; EyeEar 5.1; SnW 5.3; Interorb 10.0.

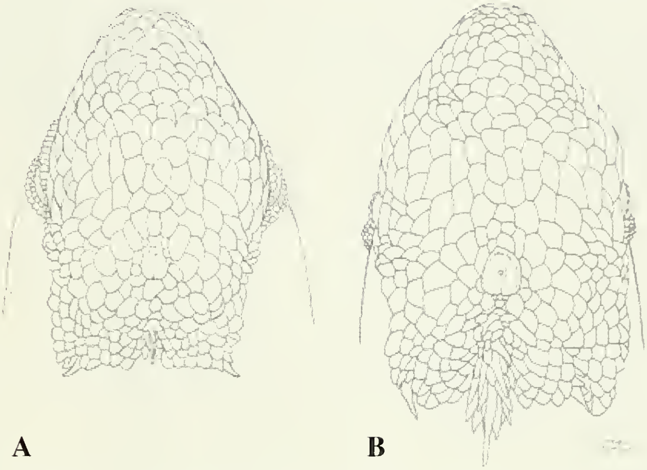

FIGURE 7. Dorsal view of the top of the head of (A) *Calotes htunwini* (USNM 5240440) and (B) *Calotes irawadi* (USNM 520543). Drawn by Molly Dwyer Griffin, 2005.

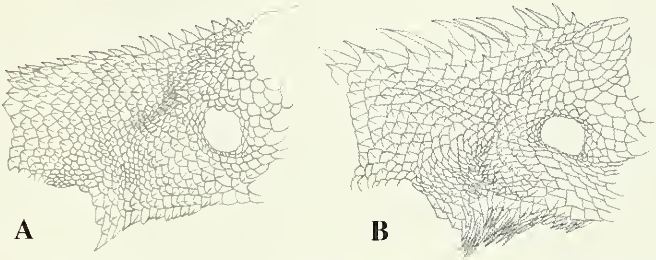

FIGURE 8. Lateral view of the side of the neck and shoulder of (A) *Calotes htunwini* (USNM 5240440) and (B) *Calotes irawadi* (USNM 520543). Drawn by Molly Dwyer Griffin, 2005.

Means for scalation traits for the entire paratypic sample is: SnS 6.7; HeadSTr 12.3; HeadSL 14.1; Canthr 8.0; EyeLd 11.2; Suplab 11.1; Inflab 10.1; TempSp 2.0; Dorsal 48.1; Midbody 47.4; 4FingLm 17.0; 4ToeLm 22.5.

Coloration in adults has a few sexual dimorphic aspects: MidvLine present in all females and half of the males: ForearSt in half of females and in no males. Both sexes lack ThroatPa and CheekCo, and TrunkSt are regularly absent. NucSpot occurs in most adults.

DISTRIBUTION AND NATURAL HISTORY.— *Calotes htunwini* occurs throughout the lower elevations of Myanmar's Central Dry Zone (Fig. 9). It is represented by vouchers from Chatthin W.S. southward to Shwe-Settaw W.S. and from Alaungdaw Kathapa N.P. eastward to the base of the Shan Plateau in the vicinity of Mandalay. Our field notes indicate that *C. htunwini* is a forest lizard.

At Chatthin, it occurs within the indaing forest. At Shwe-Settaw, it co-occurs with *C. irawadi* in the scrubby woodland bordering the Namada River. It was also found along a dry forest stream in the center of of the Shwe-Settaw reserve. At Popa and AK, the field notes are inadequate to differentiate between in forest and roadside-agricultural habitats. All the preceding forest records are of open forest, commonly with a scattered grass understory.

Calotes irawadi Zug, Brown, Schulte, and Vindum, sp. nov.

Fig. 7–8, 10

Holotype.— USNM 520543, an adult male from Myanmar: **Sagaing Division**, Chatthin Wildlife Sanctuary, San Myaung Camp (23°34′27.6″N, 95°44′15.6″E; ca. 110 m), approx. 2 km WNW of Chatthin by local collector, 17 July 1997.

Paratypes.— Myanmar: **Sagaing Division**, Alaungdaw Kathapa National Park CAS 215535, 215641, 215709, USNM 562986–990, 562993; Chatthin Wildlife Sanctuary CAS 231833, USNM 520546, 524043, 562994; Kabaing CAS 215787; Khim Aye CAS 215423, 215426–429, USNM 562991–992. Magway Divis., Le Kaing CAS 213663, 213685, 213726–727; Shwe-Settaw Wildlife Sanctuary CAS 213865, 213891, 213899 USNM 562997–999; **Mandalay Division**, Popa Mountain Park USNM 562995-996.

Diagnosis.— *Calotes irawadi* is a member of the *versicolor* species group and shares the obliquely posteriorad or vertical scale-row orientation on the neck and adjacent supra-axillary area with all other *versicolor* group members except *C. htunwini*. It differs from *C. versicolor* (Pondicherry population) by a much smaller body size (female, male means 77.4, 82.4 mm SVL vs. 93 mm, 119 mm, respectively), and more Dorsal (means 48.9 vs. 40.8) and Midbody (47.1 vs 42.8).

Middorsal crest scales in *C. irawadi* are smaller (equal to tympanum diameter) and are straighter and more numerous than *C. versicolor* (Pondicherry) with crest scales to 2.5–3.0 × diameter of tympanum. Lengths of supratympanic spines in *C. irawadi* are half or less the diameter of tympanum and ⅔ or more tympanum diameter in *C. versicolor* (Pondicherry). *C. irawadi* averages smaller than Moyingyi and Nat-Ma-Taung "*versicolor*" and has fewer Dorsal. It differs from eastern Thailand "*versicolor*" by more Dorsal and in coloration by the usual presence of DorsalSt and NucSpot.

Etymology.— Irawadi is a variant spelling of Ayeyarwaddy and is used as a noun in apposition. Our use of Irawadi refers to the broad distribution of this species in the central portion of the Ayeyarwaddy River basin.

Description of holotype.— An adult male of 75.7 mm SVL, 28.0 mm SnForel, 36.7 mm TrunkL, 218 mm TailL (entire), 10.0 mm TailH, 9.4 mm TailW, 10.9 mm PectW, 14.9 mm UpArmL, 14.5 mm LoArmL, 14.6 mm ForefL, 9.7 mm 4FingLng, 20.3 mm UpLegL, 19.0 mm CrusL, 27.3 mm HindfL, and 15.9 mm 4ToeLng. Head pentagonal (dorsal outline) covered largely with small, mostly smooth scales slightly overlapping: 17.9 mm HeadL, 15.5 mm HeadW, 12.8 mm JawW, 14.0 mm HeadH, 7.6 mm SnEye, 3.7 mm NarEye, 4.5 mm EyeEar, 4.6 mm SnW, and 8.4 mm InterOrb.

Head distinct from neck; snout to eye broadly acute and triangular, snout-tip blunt; head behind eyes with edges slightly bowed outward by jaw muscles but edges largely parallel; sides of head flat, descending perpendicular downward from sharp canthus rostralis and supraciliary edge to lips, posterior to eye slightly rotund; eyes, slightly protruding, just barely extending beyond canthus-supraciliary border; chin and throat generally flat. Dorsally head scales (Fig.7) variably sized and smooth surfaced, most equivalent in size to dorsal trunk scales; no distinct plates, rostral equivalent to supralabials in height above lip with 7 SnS; 7/8 (left/right) elongate and sharply folded CanthR, scales somewhat enlarged in supraocular area but not forming distinct supraocular plates, 16 HeadSL and 15 HeadSTr, posteriorly slightly enlarged; irregularly bell-shaped interparietal with distinct medial parietal eye. Laterally head with single large nasal scale on each side abutting rostral and perforated by large naris; loreal and preocular area with small scales, those above supralabials arranged in two parallel longitudinal rows extending to posterior margin of orbit; 11/10 Suplab; eye covered with "sock" of small, nearly granular-sized scales and opening border by double row of eyelid scales, outermost row of pyramidal scales, inner row smooth and flat 13/15 Eyelid; postocular and temporal scales modest to small, smooth laterally and dorsolaterally; tympanum large (subequal eye-opening diameter) and naked; pair of spines or clusters in supratympanum area, anterior one dorsolaterally directly above anterior half of tympanum separated by 5–6 scale rows, posterior one level with posterior edge of tympanum separated by 3 scale rows, a single narrow, spine-like scale (length about ¼ tympanum maximum diameter) projecting upward; 10/10 rectangular Inflab along mouth margin, bordered below by 3–4 rows of narrow and elongate, longitudinally arranged smooth scales; medially the chin throat scales triangular and smooth to lightly keeled; single median triangular mental scale between left and right 1st supralabials and barely larger than them.

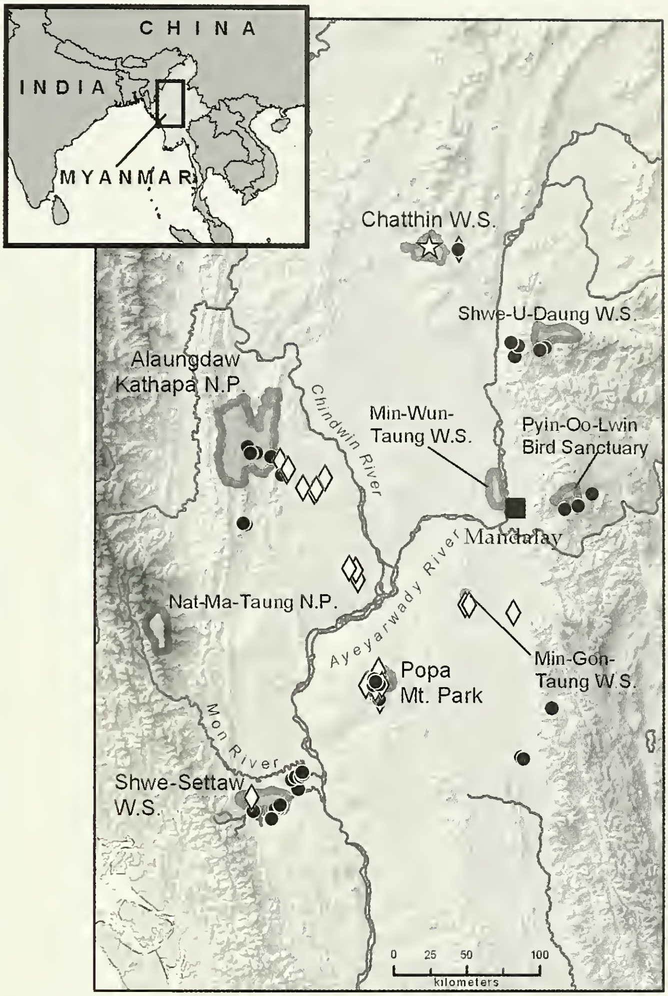

FIGURE 9. Geographic occurrence of *Calotes htunwini* and *Calotes irawadi* in the central dry zone of Myanmar. Symbols: star, type locality of both species, Chatthin Wildlife Sanctuary; solid circle, *Calotes htunwini*; diamond, *Calotes irawadi*. Map produced by Michelle Koo.

Trunk scalation generally keeled (moderately) dorsally and laterally; middorsal crest of elongate scales, occiput origin separated from interparietal by 2 rows of dorsal scales, dorsal spine-scales of moderate length (2–3 × length of adjacent parasagittal scales; midneck ones nearly equal maximum tympanum diameter) and blade-like, laterally compressed to supra-axillary as their lengths visibly decline, becoming more keeled scale-like but retaining projecting and hooked median tip to the base of the tail although flatten like adjacent dorsal scales; 49 Dorsal, 48 Midbody; all trunk scales keeled, weakly so on ventrolateral half of neck and trunk, keel and scale orientation diagonally upward from neck and supra-axillary area (Fig. 8) to base of tail, nearly vertical on anterodorsal surface of neck; preaxillary scales modest sized and most smooth; ventral scales large and uniform sized from throat to vent and strongly keeled.

Limbs with modest to large scales, all keeled; fingers (21/21 4FingLm) and toes (27/28 4ToeLm) each with 3–4 modestly keeled scales dorsally and strongly bicarinate lamellae ventrally; claws long, thin and sharply pointed on all digits. Tail scalation similar to trunk although more strongly keeled with progressive loss of scale rows distally.

Coloration in preservation dusky tan background dorsally and laterally; head scales speckled with dark brown dorsally; pair of dark brown nuchal spots, one on each posterolateral edge of interparietal scale and not contacting one another; 2 faded dark brown lines radiating posteroventrally from the orbit; dusky brown cheek patch (CheekCol). Indistinct small brown dorsal blotches across middorsal crest; none on neck, 6 on trunk, and darker, broader as regular bands on tail; laterally neck light above and dark below, trunk ground color mute brown throughout. Fore- and hindlimbs banded, narrow light defining broader dark bands; banding faded but distinct on fore- and hindlimb; faded pale stripe along posterior margin of crus. Ventrally light dusky beige with strongly faded palmate striping on throat (ThroatSt) and barely visible dark midventral stripe on trunk (MidvLine). In life (not photographed), brief color notes: "dorsum bronzy brown, ear drum and shoulder spot light green."

Variation of paratypes.— The paratypic series contains 5 adult females, 21 adult males, and 7 juveniles. The juveniles range in SVL from 41.9 to 81.5mm. The adult females range in SVL from 64.3 to 77.9 mm (mean, 71.6). Means for the females other measurements (all in mm) are: TrunkL 38.5; TailL 203.0; TailH 6.8; TailW 6.7; PecW 11.6; PelvW 7.4; SnForeL 23.4; UpArmL 14.1; LoArmL 13.2; ForefL 13.7; 4FingLng 9.7; UpLegL 16.9; CrusL 17.1; HindfL 23.8; 4ToeLng 13.8; HeadL 16.6; HeadW 13.6; JawW 11.8; HeadH 12.1; SnEye 7.5; Nareye 4.0; EyeEar 4.0; SnW 4.9; Interorb 8.0. The adult males range in SVL from 66.4 to 106.8 mm (mean, 83.3). Means for the males other measurements (all in mm) are: TrunkL 42.1; TailL 231.5; TailH 10.2; TailW 9.8; PecW 14.9; PelvW 8.6; SnForeL 29.3; UpArmL 17.1; LoArmL 15.8; ForefL 14.9; 4FingLng 10.7; UpLegL 20.1; CrusL 19.3; HindfL 26.5; 4ToeLng 16.1; HeadL 20.3; HeadW 19.6; JawW 16.3; HeadH 15.1; SnEye 8.6; Nareye 4.3; EyeEar 5.9; SnW 5.4; Interorb 9.5.

Means for scalation traits for the entire paratypic sample are: SnS 6.8; HeadSTr 12.3; HeadSL 14.3; Canthr 7.9; EyeLd 12.5; Suplab 10.9; Inflab 10.4; TempSp 2.0; Dorsal 48.4; Midbody 45.0; 4FingLm 20.1; 4ToeLm 24.8.

Coloration (Fig. 10) in adults shows no "either/or" sexual dimorphism. NucSpot is present in all females and only half of the males. Similarly ForeArSt is present in all females and ⅔ of males; TrunkSt is absent in half of females, ⅔ of males; and DorsSt is absent in most males and half of females. MidvLine is usually present in both sexes, ThroatSt always present, and ThroatPa commonly absent in both.

Distribution and natural history.— Of the two new taxa, *Calotes irawadi* has the broadest occurrence in Myanmar's Central Dry Zone (Fig. 9). It is represented by vouchers from Chatthin W.S. southward to Shwe-Settaw W.S. and from mid-elevations at Alaungdaw Kathapa N.P. eastward to edge of the Shan Plateau at Pyin-Oo-Lwin (approx. 1000 m elevation). Field observations indicate that *C. irawadi* is an open-forest lizard but also persists in fence-row habitats and cut-over woodland. Where it co-occurs with *C. htunwini* at Shwe-Settaw, the "forested" habitat is patches of secondary growth scrub <maximum tree height to 10 m> intermixed with small garden-field plots, and here it was found equally in both the forest and agricultural lands. At AK *C. irawadi* occurred mainly in forest habitats, at Popa in gardens and in the second-growth scrub adjacent to the more densely forested mountain-sides.

FIGURE 10. *Calotes irawadi* in life. Upper. Holotype, adult male [USNM 520543] – Chatthin (G. Zug). Left. Paratype, subadult male [USNM 562997] – Shwe-Settaw (G. Zug).Right. adult female [USNM 563004] – Pyin-Oo-Lwin (G. Zug).

Biogeographic Comments on Burmese Calotes

Geologically, Myanmar consists of several Gondwanan blocks that sequentially collided with the southeastern edge of the Laurasian plate beginning in the mid to late Triassic. The Sinoburmalayan (Sibumasu) block with smaller Gondwanan terranes moved "northeastward" closing the Mesotethys Sea and then collided with the Asian plate in the Late Cretaceous. This second collision produced the first stage of mountain building of the Sinoburman Range. The Burman plate collided with the southern edge of Sinoburmalayan block and continues to slide northward along the contact zone. This collision resulted in further mountain building and the initial uplift of the Shan Plateau on the Sinoburmalayan block. The collision of the Indian plate with the Eurasian plate at the end of the Early Eocene and its subsequent subduction beneath the Burman plate (late Miocene) initiated the building of the Indoburman Range and the isolation of the central lowlands of Myanmar from those of Indian and Indochina (Bender 1983; Hutchinson 1989; Hall 1998; Metcalfe 1998).

Acrodont lizard clades (Agamidae and Chamaeleonidae) are tightly associated with the Gondwanan tectonic plates (Macey et al. 2000). Of the three acrodont clades of Southeast Asia, two (the *Leiolepis* and *Hydrosaurus* clades) are hypothesized as faunal components of Gondwanan plates that joined Asia between 65 and 120 MYBP (Macey et al. 2000). The draconine clade (see Fig. 3) either entered Asia from the Indian plate (ca. 20 MYBP) or from an earlier terrane accretion; however, Macey et al. (2000) were unable to delimit the origin of the Draconinae as Southeast Asian or Indian. Our genetic data do not address the draconine origin question or whether *Calotes* arose in India or Southeast Asia. The data do demonstrate that the *Calotes versicolor* group has distinct Indian and Southeast Asian branches. We cannot address the origins of these two branches or when they arrived in Burma, because the data of phylogenetic relationships and estimates of branching age among the various *C. versicolor* populations and species are still too incomplete.

Table 5. Amphibians and reptiles confined to the Central Dry Zone of Myanmar. Herein, this zone is the area between 19.5°to 24.5°N and elevations below 1000 m.

Amphibia

Microhylidae

Microhyla sp-miniature

Ranidae

Fejervarya limnocharis complex sp

Reptilia

Agamidae

Calotes htunwini
Calotes irawadi
Liolepis peguensis

Gekkonidae

Cyrtodactylus brevidactylus
Cyrtodactylus chrysopylos

Colubridae

Oligodon splendidus

Elapidae

Bungarus magnimaculatus
Naja mandalayensis

The central lowlands of Myanmar (the Central Dry Zone) is a distinct climatic zone, created by the previously mentioned mountain building. The Central Dry Zone and its flora and fauna had gained its isolation and likely its strong seasonal aridity by, at least, the Late Miocene. Falling and rising sea-levels during the Pleistocene (embayment to Mandalay at least once during this period) regularly changed the landscape of the central Ayeyarwaddy River Valley. Exactly how these briefly described geological events affected the dispersal and isolation of the biota remains unknown. Our growing knowledge of the biodiversity of this central valley attests to major landscape changes producing multiple isolation events and opportunities for differentiation and speciation.

Reporting the discovery of *Naja mandalayensis*, Slowinski and Wüster (2000:269) noted "likely that additional field work will reveal that the central dry zone is a [*sic*] area of significant herpetological endemism." Field and laboratory studies are demonstrating that this central dryland and adjacent foothills have a more species-rich herpetofauna and more endemics (Table 5) than previously reported. Much of the evidence for this endemicity remains unpublished, although some reports are in various stages of analysis and writing. For example, our surveys regularly reveal that most areas have two sympatric *Fejervarya limnocharis* group frogs, either a large and medium-sized frog pair or a medium-sized and small frog pair. A miniature *Microhyla* sp. occurs at least from Chatthin to Mandalay. These taxa, along with *Calotes htunwini*, *C. irawadi*, and *N. mandalayensis* highlight the Central Dry Zone as a center of speciation and, further, suggest the ability of this herpetofauna to withstand major human perturbations, because all of preceding taxa are found in paddies and other human-disturbed habitats as well as fragments of natural habitats.

A historical explanation is not presently available to offer a sequence of isolation events to permit regional differentiation and eventual speciation in this area. We doubt that the various embayments of the Pleistocene offer an appropriate isolation mechanism. We have not found any detailed geologic histories of central Burma that might offer clues to a landscape history with the appearance and disappearance of habitat islands for biotic differentiation. The present dry zone is not floristically uniform. It contains three major forest types and a Euphorbia semi-desert in its center (Kress et al. 2003). Our data on the habitat occurrence of *Calotes htunwini* and *C. irawadi* are not sufficiently precise to identify the habitat preference or restriction of these two species, but the broad dry zone distribution of both shows that they occupy a variety of forests within the broader classification of mixed deciduous and dry forest.

On a broader scale, the phylogenetic hypothesis generated herein and preliminary unpublished data show these newly recognized species represent different evolutionary lineages. *Calotes htunwini* and its ancestor represent an early branching within the *C. versicolor* group with affinities to Indian species and populations. *Calotes irawadi* is more closely allied with populations of *C.* "*versicolor*" from Myanmar and East Asia, i.e., China, Cambodia, Laos, and Vietnam (Schulte, Stuart, and Bauer, unpublished data). That these two species share a similar distribution indicates that their ancestors were likely central Burma residents and shared the same history of geographic isolation.

Key to Myanmar[6] *Calotes*

1. Scales on side of trunk obliquely upward 2
1. Scales on side of trunk obliquely downward . . . . *C. kingdonwardi*

2. Crescent-shaped patch of small granular scales in front of forelimb insertion 6
2. No patch of granular scales in front of forelimb insertion; this preaxillary area with moderate to large scales (*C. versicolor* group) 3

3. Scales on side of neck and adjacent shoulder area horizontal; keels on these scales modestly to strongly developed . . . . *C. htunwini* sp. nov.
3. Scales on side of neck and adjacent shoulder area obliquely upward; keels on these scales weakly to strongly developed 4

4. Females and males sexually mature at SVL of 78 mm or larger; adult females and male without diagonal dark stripes on chest and belly . . . . Yangon-Moyinge OTU
4. Females and males sexually mature at SVL of 60 mm or larger; some adults with diagonal dark stripes on chest and belly 5

5. Adults with narrow dorsal bars middorsally, bars often offset on opposite sides of dorsal crest . . . . *C. irawadi* sp. nov.

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[6] For *C. versicolor* group from central Myanmar, 16°N to 24°N.

5. Adults with broad dorsal bars middorsally, bars commonly congruent on opposite sides of dorsal crest . . . . Nat-Ma-Taung OTU

6. Two parallel rows of compressed scales above tympanum . . . . *C. jerdoni*
6. No parallel rows of compressed scales above tympanum 7

7. Large postorbital spine present. . . . . *C. emma*
7. No postorbital spine 8

8. Midbody scale rows 47-57, tail not swollen posterior to base in males . . . . *C. mystaceus*
8. Midbody scale rows 59-74, tail swollen posterior to base in males . . . . *C. chincollium*

ACKNOWLEDGMENTS

The Myanmar Herpetological Survey is a country-wide species inventory designed to uncover the full diversity of the Burmese herpetofauna by surveying broadly but focusing on the forest and wildlife reserves of the Myanmar Forestry Department, Ministry of Forestry. The Survey owes it success to the administrative and logistic support of U Shwe Kyaw, Director General, Forestry Department, and U Khin Maung Zaw, Director, and U Tin Tun, Deputy Director, of the Nature and Wildlife Conservation Division (NWCD, Forestry Dept.), and critically to the NWCD staff (U Htun Win, Daw Thin Thin, U Kyi Soe Lwin, U Awan Khwi Shein, U San Lwin Oo, Sai Wunna Kyi) who have been the core of our survey team. The Survey is a collaborative effort among the staff of NWCD, the California Academy of Sciences, and the Smithsonian's National Museum of Natural History (SI-NMNH). The latter two institutions have provided a variety of administrative and financial support. We thank all the above individuals and institutions for their past and ongoing support.

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Appendix

A. Methodology for Obtaining Molecular Data

Genomic DNA was extracted from liver using the DNeasy Tissue Kit® (Qiagen, Inc.). Amplification of genomic DNA was conducted in a DNA Engine® (PTC-200TM) Peltier Thermal Cycler (MJ Research) using a denaturation at 94C for 35 s, annealing at between 45–54°C for 35 s, and extension at 70C for 150 s for 30–35 cycles with Life Technologies (Gibco) Taq polymerase. Negative controls were run on all amplifications to check for contamination. Amplified products were purified with AMPure® magnetic beads (Agencourt). Cycle-sequencing reactions were run using ABI Prism Big Dye Terminator chemistry version 3.1 (Perkin-Elmer) with a denaturation at 96C for 10 s, annealing at 50C for 10 s, and extension at 60C for 4 min for 35–40 cycles. Sequencing reactions were run on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems).

Amplifications of the mitochondrial ND1 gene through the COI gene from genomic DNA were prepared with several primer combinations. All samples were amplified with L3914 in combination with H4980 or H5617a, as well as L4437 in combination with H5934a or H6159. Both strands were sequenced using L3914, L4160, L4178a, H4419b, H4419d, L4437, H4618b, L4831a, L4831c, L4882b, H4980, L5002, L5417, L5549b, H5617a, L5631, L5638b, H5692, H5934a, H5937c, H6030. and H6159. Most primers are as described by Macey et al. (1997) except L3914, which is reported in Macey et al. (1998) as L3878. Additional primers used include L4160 (Kumazawa and Nishida 1993), H4419b and L4882b (Macey et al. 2000), L5549b (Schulte et al. 2003), and H6159 (Weisrock et al. 2001). Several new primers were designed for this study: H4419d (5’ – GGYATGGGCCCAAYTGCTT – 3`); H4618b (5’ – TTGTGGCAGCTTCRATTGCNCGTGG – 3’); L4831c (5’ – TGACTACCAGAAGTACTNCAAGG – 3’); L5417 (5’ – ACATCAGCAACAAARTGACG – 3’); L5631 (5’ – CATCAYCTGAATGCAACYCAG – 3’); H5937c (5’ – TAYAATGTTCCRATATCTTTRTG – 3`); and H6030 (5’ – CCMARAGCTTGTCCTGGTTG – 3’). Primer numbers refer to the 3’ end on the human mitochondrial genome (Anderson et al. 1981), where L and H denote primers whose extension produces the light and heavy strands, respectively. Voucher specimen information and GenBank accession numbers for newly reported sequences are provided in the material examined section. Aligned DNA sequences are available in TreeBASE (Study accession number = S1461: Matrix accession number = M2627).

DNA sequences were aligned initially by eye. Positions encoding part of ND1, all of ND2, and part of COI were translated to amino acids using MacClade 4.08 (Maddison and Maddison 2003) for confirmation of alignment. Alignments of sequences encoding tRNAs were based on secondary structural models. Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes using these models. Gaps are treated as missing data. Unalignable regions were excluded from phylogenetic analyses due to ambiguity in our hypotheses of homology for these aligned data.

B. Definition of Morphological Characters

Each character and its abbreviation follow; we include a definition only where we record character differently than preceding researchers. Abbreviations follow Zug (1998) for ease of recognition. All characters reported for right side, all measurements in millimeters.

Mensural Characters

A. Head

Eye-ear length: **EyeEar** — Distance from anterior edge of tympanum to posterior of orbit (not pupil opening).

Head height: **HeadH** — Dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws.

Head length: **HeadL** — Distance from anterior edge of tympanum to tip of snout.

Head width: **HeadW** — Distance from left to right outer edge of temporal or jaw muscles at their widest point without compression of soft tissue.

Interorbital width: **Interorb** — Transverse distance between anterodorsal corners of left and right orbits.

Jaw width: **JawW** — Distance from left to right outer edge of jaw angles; this measurement excludes jaw musculature broadening of head.

Naris-eye length: **NarEye** — Distance from anterior edge of orbit to posterior edge of naris.

Snout-eye length: **SnEye** — Distance from anterior edge of orbit to tip of snout (rostral scale).

Snout width: **SnW** — Internasal or internarial distance of other authors; transverse distance between left and right nares.

B. Body and Limbs

4th finger: **4FingLng** — Distance from juncture of 3rd and 4th digits to distalmost extent (outer/distalmost surface of claw) of 4th finger.

4th toe: **4ToeLng** — Distance from juncture of 3rd and 4th digits to distal end of 4th digit on hindfoot.

Crus length: **CrusL** — Length of crus (tibia) from knee to heel.

Forefoot length: **ForefL** — Distance from proximal end of forefoot to tip of fourth digit.

Hindfoot length: **HindfL** — Distance from proximal end (heel) of hindfoot to distalmost surface of fourth toe.

Lower arm length: **LoArmL** — Distance from elbow to distal end of wrist, or just before underside of forefoot.

Pectoral width: **PectW** — Distance between left and right axilla (posterior to forelimb insertions) measured on ventral side.

Pelvic width: **PelvW** — Distance between left and right inguen (posterior to hindlimb insertions).

Snout-vent length: **SVL**.

Snout-forelimb length: **SnForel** — Distance from anterior of forelimb, or shoulder, to tip of snout.

Tail height: **TailH** — Distance from dorsal to ventral surface of tail base measured just posterior to vent.

Tail length: **TailL** — Distance from vent to distal end of tail; noting completeness or regeneration of tail.

Tail width: **TailW** — Distance from left to right side of tail base just posterior to vent.

Trunk length: **TrunkL** — Body length or axilla-groin length of others; distance between posterior edge of forelimb insertion (axilla) to anterior edge of hindlimb insertion (inguen).

Upper arm length: **UpArmL** — Distance from anterior insertion of forelimb, or shoulder, to elbow.

Upper leg length: **UpLegL** — Distance from anterior edge of hindlimb insertion to knee.

Meristic Characters

A. Head

Canthus rostralis: **CanthR** — number of elongate scales along 'dorsolateral snout ridge' from above posterodorsal corner of nasal scale to and including posteriormost supraciliary scale.

Dorsal eyelid scales: **Eyelid** — Number of scales found along dorsal edge of eyelid.

Dorsal head scales: **HeadSLn** — Number of scales longitudinally on midline between interparietal and rostral scale.

Head scales: **HeadSTr** — Number of scales in transverse line between posteriormost left and right supraciliary scales, just anterior of interparietal.

Infralabials: **Inflab** — posterior end defined by posteriormost enlarged scales that touches with Suplab at rear corner of mouth.

Snout scales: **SnS —** Number of scales on line transversally between left and right nasal scales (single scale surrounding naris).

Supralabials: **Suplab —** posterior end defined by posteriormost enlarged scales that touches Inflab at rear corner of mouth.

Temporal spines: **TempSp —** Number of distinctly enlarged spine-like scales in patches above and posterior of tympanum, exclusive of dorsal or head crest spines.

B. Body and Limbs

Forefoot lamellae (scansors): **4FingLm** — Number of 4th digit lamellae; from 1st lamella at digits' cleft that is wider than deep and touches dorsal digital scale (on at least one side) to most distal lamella; fragmented proximal scales are excluded.

Hindfoot lamellae (scansors): **4ToeLm** — As for 4FingLm.

Dorsal scales or spines: **Dorsal —** Number of middorsal scales (spines or not), beginning with first enlarged spine-like scale on nape to above vent.

Midbody scale rows: **Midbody —** Number of scale rows around trunk at midbody.

Coloration of Preserved Specimens

A. Dorsal color characters

Cheek Color: **CheekCol —** Presence (1) or absence (0) of dark patches on jowl muscles.

Paired Dorsolateral Stripes: **DorsSt —** Presence (1) or absence (0) of pair of dorsolateral light stripes, one on each side of trunk.

Forearm Stripe: **ForearSt** — Presence (1) or absence (0) of longitudinal light stripe on the outer surface of forearm.

Paired Nuchal Spots: **NucSpot —** Presence (1) or absence (0) of pair of dark spots just posterior and abutting interparietal scale.

Dark Bands on Trunk: **TrnkBand —** Number of dark bands (bars) on dorsum of trunk between axilla and inguen, not including bands over shoulder or pelvis.

B. Ventral color characters

Midventral Dark Line: **MidvLine —** Presence (1) or absence (0) of dark line on venter midline from throat to pelvis.

Throat Stripes: **ThroatSt —** Presence (1) or absence (0) of striping on throat.

Colored Throat Patch: **ThroatPa —** Presence (1) or absence (0) of colored patch or band on throat.

Ventral Trunk Striping: **TrunkSt —** Striping ventrally on trunk, none (0), irregular or broken striping (1), or continuous striping (2). This character excludes MidvLine.

Ventral Color: **VenColor —** Ventral background coloration, white to cream (0), light tan to beige (1), or pinkish to light brown or dusky (2).

SEX AND MATURITY.— Examination of gonads revealed sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males when testes and epididymides were enlarged, supplemented by presence of secreting precloacal or femoral pores.

COMMENTS ON CHARACTERS.— Several researchers have attempted to quantify digit shape and length, as well as other traits. Although we support quantification because it permits statistical analysis and presumably removes a degree of bias or subjectivity, many voucher specimens are not carefully prepared resulting in bent or folded specimens or parts thereof. Thus, we believe that quantification of some characters implies a degree of accuracy that does not exist. Our selection of mensural characters emphasizes those possessing termini ending on bone and along axes that have rigorous bony struts reducing compression or bending. SnForel and TrunkL, for example, are two useful measurements but also two that can have significant variation resulting from poor preparation.

C. SPECIMENS EXAMINED

Museum symbolic codes follow Leviton et al. (1985) except for the Wildlife Heritage Trust, Colombo, Sri Lanka (WHT), Bombay Natural History Society (BNHS), and the newly established Myanmar Biodiversity Museum (MBM). The code BNHS-AMB is followed by the field number for Aaron M. Bauer for an uncatalogued specimen being deposited at the designated institution.

1. Tissue vouchers

The DNA sequence data derives from new sequences and previously reported data
(Type specimens in bold)

Newly reported sequences are: *Calotes chincollium* (Chin – CAS 220582, DQ289458; Sagaing – CAS 215505, DQ289459); *Calotes* cf. *emma* (Rakhine – CAS 223062, DQ289460); *Calotes htunwini* (Chatthin – USNM **524044**, DQ289461; Mandalay – CAS 204851, DQ289462; Shwe-Settaw1 – USNM **562976**, DQ289463; Shwe-Settaw2 USNM **562977**, DQ289464); *Calotes irawadi* (Chatthin – USNM **520543**, DQ289465; Chin – CAS 219911, DQ289466; Mandalay – USNM 563005, DQ289467; Sagaing – CAS 204862, DQ289468); *Calotes "versicolor"* (Ayeyarwaddy – CAS 205008, DQ289469; Bago1 – CAS 206551, DQ289470; Bago2 – USNM563012, DQ289471; Mon – CAS 222606, DQ289472; Mon:Kyaik.1 – MBM.USNM/fs 35783, DQ289473; Mon:Kyaik.2 – MBM.USNM/fs 35815, DQ289474; Mon:Kyaik.3 – MBM.USNM/fs 35831, DQ289475; Rahkine – CAS 204991, DQ289476; Shan – CAS 230481, DQ289477; Yangon – CAS 208157, DQ289478).

Previously reported sequences used here are reported in Macey et al. (2000) and Schulte et al. (2002, 2004): *Acanthosaura capra* (MVZ 222130, AF128498); *Acanthosaura lepidogaster* (MVZ 224090, AF128499); *Aphaniotis fusca* (TNHC 57874, AF128497); *Bronchocela cristatella* (TNHC 57943, AF128495); *Calotes calotes* (WHT 1679, AF128482); *Calotes ceylonensis* (WHT 1624, AF128483); *Calotes emma* Vietnam (MVZ 224102, AF128489); *Calotes liocephalus* (WHT 1632, AF128484); *Calotes liolepis* (WHT 1808, AF128485); *Calotes mystaceus* Myanmar (CAS 204848, AF128488); *Calotes mystaceus* Vietnam (MVZ 222144, AF128487); *Calotes nigrilabris* (WHT 1680, AF128486); *Ceratophora aspera* (WHT 1825, AF128491); *Ceratophora erdeleni* (WHT 1808, AF128522); *Ceratophora karu* (WHT 2259, AF128520); *Ceratophora stoddartii* (WHT 1512, AF128492); *Ceratophora tennentii* (WHT 1633, AF128521); *Cophotis ceylanica* (WHT 2061, AF128493); *Draco blanfordii* (MVZ 222156, AF128477); *Gonocephalus grandis* (TNHC 56500, AF128496); *Japalura tricarinata* (CAS 177397, AF128478); *Japalura variegata* (ZIL 20922, AF128479); *Japalura flaviceps* (MVZ 216622, AF128500); *Japalura splendida* (CAS 194476, AF128501); *Lyriocephalus scutatus* (WHT 2196, AF128494); *Mantheyus phuwuanensis* (FMNH 255495, AY555836); *Otocryptis wiegmanni* (WHT 2262, AF128480); *Pseudocalotes brevipes* (MVZ 224106, AF128502); *Pseudocalotes larutensis* (previously reported as *Pseudocalotes flavigula* – TNHC 58040, AF128503); *Ptyctolaemus collicristatus* (USNM 559811, AY555837) *Ptyctolaemus gularis* (CAS 221515, AY555838); *Salea horsfieldii* (BNHS-AMB5739, AF128490); *Sitana ponticeriana* (WHT 2060, AF128481).

Several corrections are made to the identifications as reported in Macey et al. (2000). *Calotes emma* (MVZ 222144) is *Calotes mystaceus; Calotes versicolor* (MVZ 224102) is *Calotes emma*; sequences reported as *Aphaniotis fusca* and *Bronchocela cristatella* should be switched, that is AF128497 is *Aphaniotis fusca* and. AF128495 is *Bronchocela cristatella*.

2. Morphological vouchers

(Type specimens in bold)

Calotes htunwini: MYANMAR: **Sagaing Division.** Alaungdaw Kathapa National Park CAS **215741**, 215764, USNM **562980**; Chatthin Wildlife Sanctuary CAS **231832,** USNM **520545**, 520547, **524044–045**, **562967–968,** 562983–985; Kabaing CAS 210517, 215801, **215811**; Mintaingbin CAS **215368**; Yin Ma Bin CAS **215347–348**, **215448**, **215457–458**, USNM **562981**; Yingpaungtaing CAS 215381–382. **Magway Division.** Shin-Ma-Taung Forest Reserve CAS 210709, 215836, 215838–839, 215870; Shwe-Settaw Wildlife Sanctuary CAS **213607**, **213620**, **213741**, **213786**, **213789**, 213841, USNM **562974–975**. **Mandalay**

FIGURE 11. The localities identified on the map represent the major samples of the Specimens Examined section. DNA samples are identified in the above list by abbreviated names. Their equivalents are: Ayeyarwady = Mwe Hauk; Chin = Nat-Ma-Taung; Mon &/or Kyaik = Kyaikhtiyo; Sagaing = Alaungda Kathapa; Shan (not on map) = Pyadalin Cave W.S. (21°06'N 96°21'E).

Division, 96 km S of Mandalay CAS 204851; Min-Gon-Taung Wildlife Sanctuary CAS 216013, 216045, USNM 562982; Popa Mountain Park CAS 214021–022, 214090, 214114.

Calotes irawadi: Myanmar: **Sagaing Division**, Alaungdaw Kathapa National Park CAS **215535**, **215641**, **215709**, USNM **562986–990**, **562993**; Chatthin Wildlife Sanctuary CAS **231833**, USNM **520542**, **520543**, **520546**, **524043**, **562994**, 563000; Kabaing CAS 215787; Khim Aye CAS **215423**, **215426–429**, USNM **562991–992**. **Magway Division**, Le Kaing CAS **213663**, **213685**, 213702, **213726–727**; Shin-Ma-Taung Forest Reserve CAS 216136; Shwe-Settaw Wildlife Sanctuary CAS **213865**, **213891**, **213899**, USNM **562997–999**. **Mandalay Division**, Popa Mountain Park CAS 213954, 214009, 214015, 214086, 214140, 231230, USNM **562995–996**, 563001–002; Pyin-Oo-Lwin USNM 563003–008; Yamethin CAS 210565, 210605; Yin Ma Bin CAS 215293.

Calotes "tiedemanni-versicolor": India: **Tamil Nadu State**, Pondicherry [11°57′N, 79°48′E] CM 152047–054, 152068–072, USNM cm152066–067.

Calotes "*versicolor*": Myanmar: **Bago Division**, Moyingyi Wetland Bird Sanctuary [17°35′N, 96°34′E] USNM 563012–014, fs 36572, 36579–581, 36589–590, 36606–607; **Chin State**, Nat-Ma-Taung Wildlife Sanctuary. [21°12′N, 94°5′E) CAS 219911–916, 219918–919, 219921–927. Thailand: Ubon Ratchathani [15°14′N, 104°53′E] USNM 206049–050, 206052–054, 206057, 206059–62, 206071–072, 206080.

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A Revision of the Malagasy Ants Belonging to Genus *Monomorium* Mayr, 1855 (Hymenoptera: Formicidae)

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In this revision of the Malagasy *Monomorium* ant fauna, thirty-six species are recognized, nineteen of them here described as new. The new species are *Monomorium adiastolon*, sp. nov., *M. aureorugosum*, sp. nov., *M. bifidoclypeatum*, sp. nov., *M. chnodes*, sp. nov., *M. clarinodis*, sp. nov., *M. denticulus*, sp. nov., *M. ferodens*, sp. nov., *M. fisheri*, sp. nov., *M. flavimembra*, sp. nov., *M. gongromos*, sp. nov., *M. infuscum*, sp. nov., *M. lepidum*, sp. nov., *M. micrommaton*, sp. nov., *M. nigricans*, sp. nov., *M. notorthotenes*, sp. nov., *M. platynodis*, sp. nov., *M. robertsoni*, sp. nov., *M. versicolor*, sp. nov., and *M. xuthosoma*, sp. nov. Five species (four described from African material) pass into synonymy: *M. leopoldinum* Forel 1905 with *M. madecassum* Forel 1892, *M. binatu* Bolton 1987, *M. exchao* Santschi 1926 and *M. imerinense* Forel 1892 with *M. termitobium* Forel 1892 and *M. valtinum* Bolton 1987 with *M. hanneli* Forel 1907. Seventeen species remain unchanged. *Monomorium minutissimum* Santschi 1937 is transferred from synonymy under *Monomorium mictile* Forel 1910 to become a junior synonym of *Monomorium exiguum* Forel 1894. The Malagasy species are distributed among seven species groups. Previously recognized in the literature are the *destructor*-, *hanneli*-, *latinode*-, *monomorium*- and *salomonis*- groups. The *hildebrandti* species group comprises six new species as well as those formerly assigned to the *fossulatum* species group. (Prior to this revision, *fossulatum* Emery 1895 was relegated to synonymy under *sechellense* Emery 1894, and *hildebrandti* Forel 1892 is the earliest described species in this group.) The *shuckardi* species group, here erected, appears to be unique to Madagascar, and comprises a group of four Malagasy *Monomorium* with several plesiomorphic characters. A key to workers of the 36 Malagasy *Monomorium* species is provided.

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Genus *Monomorium* Mayr

INTRODUCTION

Monomorium is one of the more significant genera of myrmicine ants. Not only does the genus have endemic representatives in all major land masses, but those of its species with tramp tendencies have been spread by human commerce to countries that do not have a native *Monomorium* fauna (McGlynn 1999) and in those countries can often be considered pests. In his Catalogue of the world's ant species, Bolton (1995) listed a world total of 293 species for the genus. Since that time broad revisionary studies have added additional species: 43 have been described from Australia (Heterick 2001; Heterick 2003) and 30 from Arabia (Collingwood and Agosti 1996). Other research has also resulted in the description of new taxa, including that of two new *Monomorium* from Brazil (Fernandez, in press), two from China (Zhou 2001) and one from Japan (Terayama 1996) and southern Europe respectively (Radchenko 1997). Two species have also been transferred to genus *Monomorium* from *Antichthonidris* (synonymy Heterick 2001). Allowing for loss of other species-level names due to synonymy arising from the work of the abovementioned authors, the current world tally stands at 359 species.

The classic text for information on the *Monomorium* species of tropical Africa has been Bolton's (1987) monograph. In this work, Bolton alluded to one Malagasy *Monomorium* species-group with a very primitive palp formula (PF) of 5,3 and mentioned in his discussion of individual species several whose distribution included Madagascar. However, he made no attempt to provide a description of the indigenous *Monomorium* fauna of Madagascar, which lay outside the monograph's terms of reference, in its own right. This work attempts to provide a comprehensive survey of the *Monomorium* species of Madagascar, and is part of an ongoing effort to inventory and describe the life forms of this fascinating and biodiverse large island. Keys are provided here to enable researchers to identify workers of endemic Malagasy *Monomorium* as well as those introduced to the island.

MONOMORIUM: A GENUS BADLY IN NEED OF REINTERPRETATION.— Unlike the case with a number of myrmicine genera that have a clearly defined diagnosis based on a few salient characters, the concept of the genus *Monomorium* in recent years has ballooned to the point where it has become unwieldy, and in great need of redefinition. The genus, as it stands at the moment, lacks clearly defined autapomorphies. A complete reappraisal of *Monomorium* is not possible in this paper, partially because this is intended as a monograph of a regional fauna rather than a review of the genus on a world basis, and partially because such a redefinition will require examination of reproductive and worker castes of all the known species groups. Genitalic characters, particularly of the males, and generation of molecular sequences should be a mandatory part of the analysis. As it is at the moment, *Monomorium* has become almost a *meta*-genus that is continuing to swallow up previously discrete genera. Since 1987 these have included *Chelaner* and *Syllophopsis* (Bolton 1987), *Antichthonidris* (Heterick 2001) and *Epelysidris*, *Nothidris* and *Phacota* (Fernandez, in press). I report in this work on a Malagasy species in which the worker has a PF of 3,2, a condition in *Monomorium* previously recorded only for males of two species formerly placed in *Antichthonidris* (Snelling 1975; Heterick 2001). Interestingly, this new species is not an isolated taxon, but evidently a member of a significant Afrotropical and Malagasy species group (the *M. hildebrandti* species group) in which all the other known members have a PF of 2,2. The change in the diagnosis of *Monomorium* brought about by this and other recent discoveries (e.g., see Heterick 2003, Fernandez, in press) means that the autonomy of the small solenopsidine genera *Anillomyrma*, *Megalomyrmex* and, possibly, *Bondroitia* is under threat. Genera linked with *Solenopsis* and with *Allomerus*, which have a broader suite of distinctive anatomical features than the abovementioned (see Bolton 1987 for details of shared characters), stand somewhat further apart from the current concept of *Monomorium* and are likely to remain so.

SYSTEMATICS

Taxonomic background of Malagasy *Monomorium*

The first described *Monomorium* species, the tramp species now known as *Monomorium pharaonis*, was placed in the then portmanteau genus *Formica* as '*Formica pharaonis*' (Linnaeus 1758). The genus *Monomorium* originated with Mayr in 1855. An account of the general history of the various generic and subgeneric names now synonymized under *Monomorium* is given in Bolton (1987) and so is not reproduced here. The later synonymization of *Antichthonidris*, *Epelysidris*, *Nothidris* and *Phacota* is mentioned above.

Six taxa assigned to *Monomorium* have been described from material collected from Madagascar. *Monomorium hildebrandti*, *Monomorium imerinense* and *Monomorium madecassum* were described by Forel in the same publication as supposed races of *Monomorium minutum* Mayr (Forel 1892c). All three taxa were raised to full species by Dalla Torre (Dalla Torre 1893). Also in 1892, in a separate publication (Forel 1892b), Forel described *Monomorium termitobium* as a species in its own right. *Monomorium shuckardi* was published by this author three year later (Forel 1895). In 1922, Emery positioned this latter species under the subgenus *Notomyrmex* in which similar South American and Australian forms had already been placed. *Notomyrmex* was raised to genus by Kusnezov in 1957, but reduced to a synonym of *Chelaner* by Ettershank in 1966 (*Chelaner* becoming in turn a junior synonym of *Monomorium* with Bolton's 1987 revision). In Ettershank's work, non-Australasian taxa previously incorporated under *Notomyrmex* were separated from the new genus of *Chelaner*, and the species *shuckardi* was returned to *Monomorium*. The final *Monomorium* species described from Madagascar was *Monomorium sakalavum* (Santschi 1928). In addition to the above taxa, four *Monomorium* species described from material collected elsewhere have been recorded from Madagascar, namely *Monomorium destructor* (Jerdon) (Mamet 1954; Bolton 1987; Fisher 2003), *Monomorium pharaonis* (Fisher 2003) *Monomorium robustior* Forel (Wheeler 1922; Bolton 1987; Fisher 2003) and *Monomorium subopacum* Smith (Bolton 1987; Fisher 2003). In terms of the smaller islands in the Malagasy region, Mamet (1954) lists *M. destructor* and *Monomorium floricol*a (Jerdon) from Mauritius, *M. floricola* from Reunion, and *Monomorium elongatum* Smith and *M. floricola* (as *M. impressum*, now a synonym of *M. florico-*

la) from Rodriguez. Of these species only *M. elongatum*, from Rodriguez, was described from material collected from the region.

In general, *Monomorium* workers and queens can be separated from other Malagasy myrmicines by a combination of their eleven or twelve-segmented antenna with three-segmented club, lack of antennal scrobes, presence of distinct frontal lobes, lack of spines or sharp denticles on the propodeum and nodes, and, in most specimens, the presence of a single anteromedian clypeal seta. Some *Cardiocondyla* species and occasional specimens of a few species of *Nesomyrmex* also have an anteromedian clypeal seta. However, *Cardiocondyla* possesses a dentate propodeum, the postpetiole is much larger than the petiole in dorsal view, and the clypeus forms a raised, projecting shelf that covers the base of the mandibles, and in *Nesomyrmex* the central seta is very short and unobtrusive - unlike that of *Monomorium*. Those *Nesomyrmex* workers that possess the median clypeal seta also have a rather angular mesosoma and low node, unlike Malagasy *Monomorium*. The petiole does not bear a large, plate-like anteroventral process in *Monomorium*, nor does the sting possess a membranous extension at its apex. The masticatory margin of the mandible has a maximum of five distinct teeth (though sometimes an additional tiny denticle is present because of the bifurcation of a tooth). In the reproductive wing, the vein RS curves towards but does not meet the anterior wing margin to form a closed radial cell.

A summary of what was known about the *Monomorium* fauna of Madagascar and associated islands before the commencement of this project is provided below. 'from inspection' refers to placement of a taxon in a particular species group as a result of examination of material during this project. These taxa had not been assigned to a species group or category prior to this project, although an available group did exist. No group was available for *Monomorium shuckardi* Forel, and I have not seen material belonging to *Monomorium elongatum* Smith. (Nb: With the exception of the *M. hildebrandti* species group, the groups mentioned are those recognized by Bolton (1987) in relation to the Afrotropical fauna):

TAXON	DISTRIBUTION
***Monomorium destructor* group**	
Monomorium destructor (Jerdon)	Madagascar, Mauritius
Monomorium robustior (Forel)	Madagascar
***Monomorium hildebrandti group* (= *M. fossulatum* group)**	
Monomorium hildebrandti Forel (from inspection)	Madagascar
***Monomorium monomorium* group**	
Monomorium floricola (Jerdon)	Mauritius, Reunion, Rodriguez
Monomorium imerinense Forel	Madagascar
Monomorium madecassum Santschi	Madagascar
Monomorium sakalavum Santschi (from inspection)	Madagascar
Monomorium termitobium Forel (from inspection)	Madagascar
***Monomorium salomonis* group**	
Monomorium pharaonis (L.)	Madagascar
Monomorium subopacum Smith	Madagascar
Unassigned	
Monomorium elongatum Smith	Rodriguez
Monomorium shuckardi Forel	Madagascar

Monomorium salomonis (L.) has also been listed as occurring in Madagascar (Fisher 1997 (citing Wheeler 1922: 870), McGlynn 1999; Fisher 2003). The occurrence of *Monomorium salomonis* in Madagascar is doubtful.

SYNONYMIC LIST OF MALAGASY SPECIES OF *MONOMORIUM*

- ***shuckardi* group**
  - ***clarinodis*** Heterick, sp. nov.
  - ***notorthotenes*** Heterick, sp. nov.
  - ***robertsoni*** Heterick, sp. nov.
  - ***shuckardi*** Forel
- ***destructor* group**
  - ***destructor*** (Jerdon)
    - *basale* Smith (‘*Myrmica basalis*’)
    - *ominosum* Gerstäcker (‘*Myrmica ominosa*’)
    - *atomarium* Gerstäcker (‘*Myrmica atomaria*’)
    - *gracillimum* Smith (‘*Myrmica gracillima*’)
    - *vexator* Smith (‘*Myrmica vexator*’)
  - ***robustior*** Forel
- ***salomonis* group**
  - ***pharaonis*** (L.)
    - *antiguense* Fabricius (‘*Formica antiguensis*’)
    - *domesticum* Shuckard (‘*Myrmica domestica*’)
    - *minutum* Jerdon (‘*Atta minuta*’)
    - *vastator* Smith (‘*Myrmica vastator*’)
    - *fragile* Smith (‘*Myrmica fragilis*’)
    - *contiguum* Smith (‘*Myrmica contigua*’)
  - ***subopacum*** (Smith)
    - *glyciphilum* Smith (‘*Myrmica glyciphila*’)
    - *mediterraneum* Mayr
    - *salomonis* subsp. *subopacum* var. *senegalensis* Santschi (unavailable name) (unnecessary replacement names *claveaui* Emery and *santschiellum* Wheeler also unavailable)
    - *salomonis* subsp. *planidorsum* Emery (‘*Monomorium salomonis* subsp. *planidorsa*’)
    - *surconfi* Santschi (‘*Paraphacota surconfi*’)
    - *cabrerai* Santschi (‘*Paraphacota cabrerai*’)
    - *cabrerai* st. *obscuripes* Santschi (‘*Paraphacota cabrerae* [sic] st. *obscuripes*’)
    - *subopacum* var. *intermedium* Santschi
    - *subopacum* var. *apuleii* Santschi
    - *salomonis* subsp. *subopacum* st. *liberta* Santschi (unavailable name)
    - *subopacum* var. *ebraicum* Menozzi
    - *subopacum* var. *adoneum* Santschi
    - *subopacum* subsp. *italica* Baroni Urbani
  - ***willowmorense*** Bolton
    - *salomonis* r. *herrero* [sic] var. *willowmorensis* Forel (unavailable name)
    - *salomonis* r. *herrero* [sic] var. *belli* Forel (unavailable name)
- ***latinode* group**
  - ***latinode* Mayr**
    - *latinode* var. *brunneum* Emery
    - *voeltzkowi* Forel
- ***monomorium* group**
  - ***bifidoclypeatum* Heterick, sp. nov.**
  - ***chnodes* Heterick, sp. nov.**
  - ***denticulus* Heterick, sp. nov.**
  - ***exiguum*** Forel
    - *exiguum* var. *bulawayense* Forel (‘*Monomorium exiguum* var. *bulawayensis*’)
    - *faurei* Santschi

        - *exiguum* r. *flavescens* Forel
        - *minutissimum* Santschi, **syn. n.**
    - ***flavimembra* Heterick, sp. nov.**
    - ***floricola*** (Jerdon)
        - *cinnabari* Roger
        - *poecilum* Roger
        - *specularis* Mayr
        - *impressum* Smith
        - *floricola var. philippinense* Forel ('*Monomorium floricola* var. *philippinensis*')
        - *floricola* var. *furinum* Forel ('*Monomorium floricola* var. *furina*')
        - *floreanum* Stitz
        - *angusticlava* Donisthorpe
    - ***lepidum* Heterick, sp. nov.**
    - ***madecassum*** Forel
        - *minutum* var. *leopoldinum* Forel, **syn. n.**
        - *explorator* Santschi
        - *aequum* Santschi
        - *estherae* Weber
    - ***micrommaton* Heterick, sp. nov.**
    - ***nigricans* Heterick, sp. nov.**
    - ***platynodis* Heterick, sp. nov.**
    - ***sakalavum*** Santschi
    - ***termitobium*** Forel
        - *minutum* r. *imerinense* Forel, **syn. n.**
        - *exchao* Santschi **syn. n.**
        - *binatu* Bolton **syn. n.**
    - ***versicolor* Heterick, sp. nov.**
    - ***xuthosoma* Heterick, sp. nov.**
- ***hanneli* group**
    - ***hanneli*** Forel
        - *moestum* Santschi
        - *valtinum* Bolton **syn. n.**
- ***hildebrandti* group**
    - ***adiastolon* Heterick, sp. nov.**
    - ***aureorugosum* Heterick, sp. nov.**
    - ***cryptobium*** (Santschi)
    - ***ferodens* Heterick, sp. nov.**
    - ***fisheri* Heterick, sp. nov.**
    - ***gongromos* Heterick, sp. nov.**
    - ***hildebrandti*** Forel
    - ***infuscum* Heterick, sp. nov.**
    - ***modestum*** Santschi
        - *modestum* var. *boerorum* Santschi
        - *modestum* var. *transwaalense* Emery ('*Monomorium modestum* (*Syllophopsis*) *modestum transwaalensis*') (first replacement name)
        - *modestum* var. *smutsi* Wheeler (unnecessary second replacement name)
    - ***sechellense*** Emery
        - *fossulatum* subsp. *sechellense* Emery
        - *sechellense* Bolton (*sechellense* has priority over *fossulatum*)

MATERIALS AND METHODS

Material examined

Most specimens examined were part of the very extensive collection of ants gathered from Madagascar over a number of years by Brian Fisher and his team, and curated in the California Academy of Sciences (CAS) Insect Collection. Where, under the subheading 'OTHER MATERIAL EXAMINED', no institution is indicated by parentheses at the end of an item, a (CAS) holding can be assumed. Pinned *Monomorium* specimens from the Harvard Museum of Comparative Zoology (MCZ) and University of California-Davis (UCDC) were also examined. Specimens were initially sorted phenotypically. However, in view of the extreme variability of some taxa, both in terms of color and morphology, wet material belonging to these problematic taxa was forwarded to Guelph University for DNA molecular analysis sequencing cytochrome oxidase (COI) in order to evaluate their species status more accurately. At the time of writing this program has yet not produced publishable results, but if completed, the results of this analysis will be reported elsewhere. [Note: '1×2' (with the appropriate caste symbol) refers to one pin bearing two specimens; '2×1' (also with appropriate caste symbol) refers to two separate pins, each bearing a specimen.]

Distribution data

Geographic data from individual specimen labels were used to generate distribution maps. The mapping program used was ArcView GIS 3.3. Along with the taxonomic methods mentioned above, these maps were sometimes found to be useful in differentiating between very similar species on the basis of their biogeography.

Sources of borrowed material

The following institutions provided material. An asterisk (*) denotes collections containing types.

BMNH	Entomology Department, Natural History Museum, London, UK*
CAS	California Academy of Sciences, San Francisco California., USA*
MCSN	Museo Civico di Storia Naturelle 'G. Doria', Genoa, Italy*
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts., USA*
MHNG	Musée d'histoire naturelle, Genève, Switzerland*
NHMB	Musée d'histoire naturelle, Basel, Switzerland*
NMW	Naturhistorisches Museum, Wien, Austria*
UCDC	University of California-Davis, Davis, California, USA
OXUM	Hope Entomological Collections, Oxford Museum of Natural History, Oxford, UK*

Use of DELTA program for generating natural language descriptions

Standardized descriptions of each Malagasy *Monomorium* species were generated using the DELTA (DEscription Language for TAxonomy) computer program (Dallwitz, Paine, and Zurcher 2000). The procedure followed is outlined in Heterick (2001). In the current project, also utilizing only morphological characters, there were 57 worker characters, 43 queen characters, and 32 male characters.

WORKER CHARACTERS USED IN CREATING NATURAL LANGUAGE DESCRIPTIONS (CHARACTER NUMBERS IN BRACKETS) (Figs. 1–5, 13):

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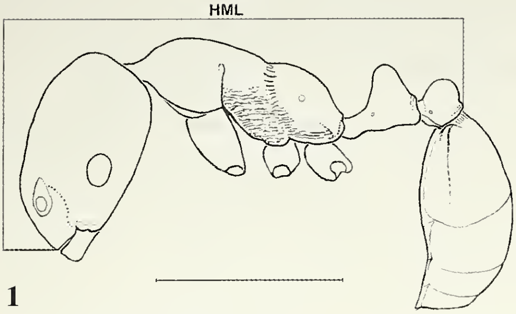
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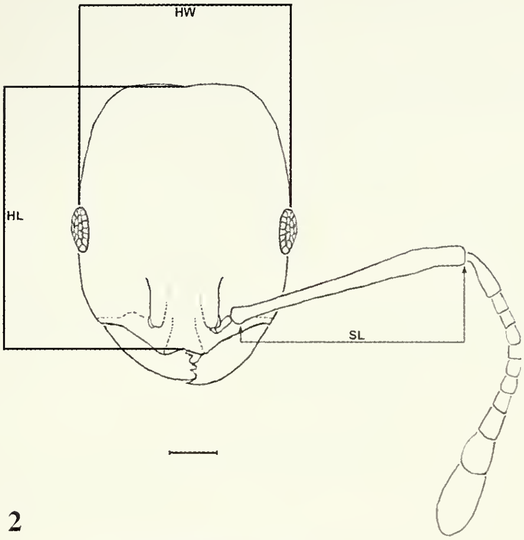
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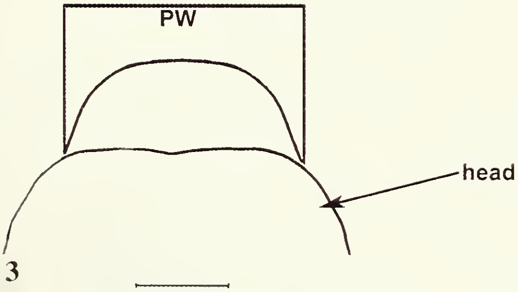
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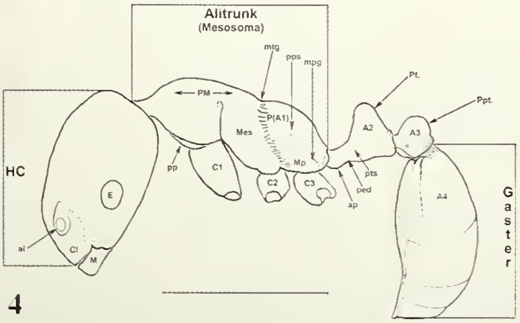
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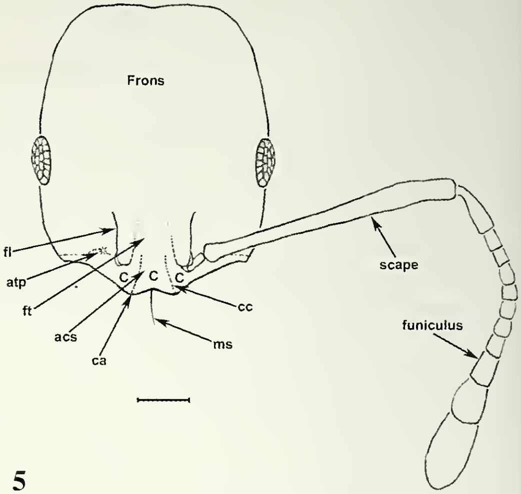
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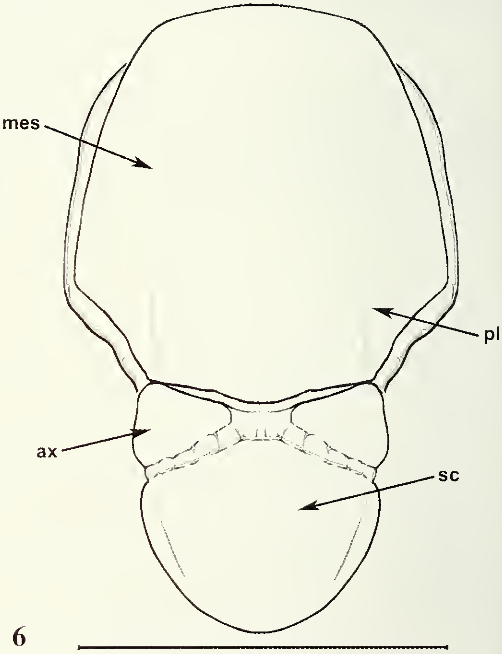
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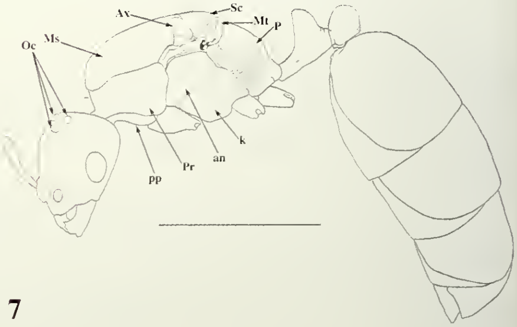
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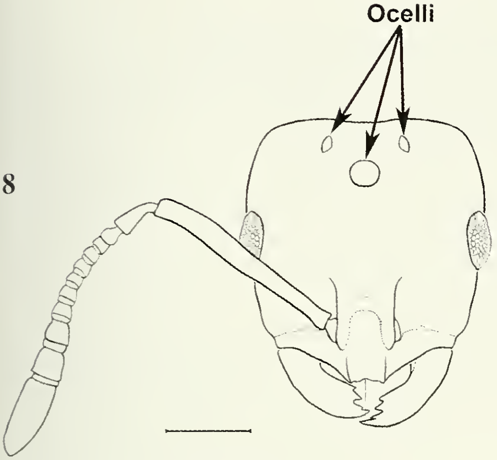

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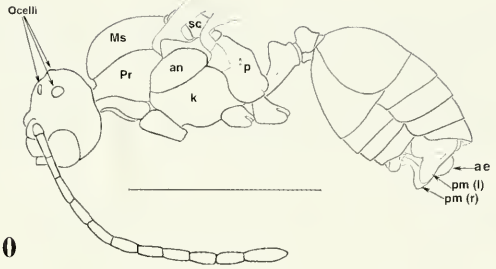

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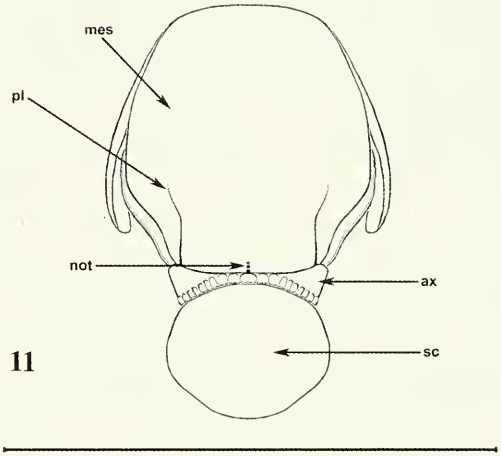

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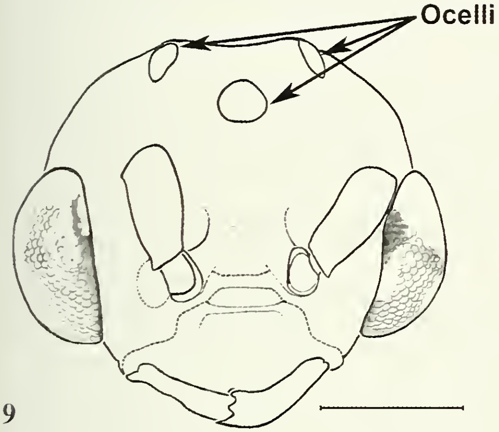

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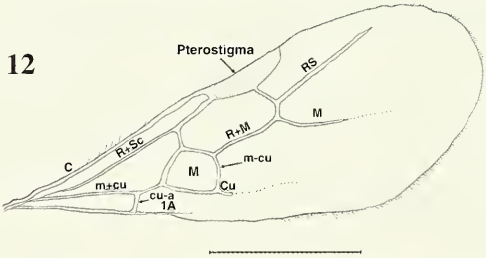

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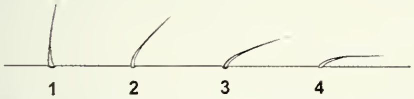

FIGURES 1–13. **Figures** 1–3: Measurements used in this study (*M. sakalavum* worker) (1) HML, length of head +mesosoma (alitrunk)+petiole+postpetiole: (2) HL, head length; HW, head width; SL, scape length; (3) PW, promesonotal width. (Pilosity is omitted in Figs. 1-12.) Scale bars: Fig 1 = 0.5 mm; Figs 2–3, = 0.1mm. **Figure** 4. Profile of *M. sakalavum* worker. A1-4, abdominal segments; ai, antennal insertion; ap, anteroventral process; E, eye; HC, head capsule; Mes, mesopleuron (Nb. In some species, the mesopleuron may be divided by a furrow into an upper anepisternum and a lower katepisternum); Mp, metapleuron; mpg, metapleural gland bulla; mtg, metanotal groove; P, propodeum (= first abdominal segment); ped, peduncle of petiole; PM, promesonotum; pp, propleuron; pps, propodeal spiracle; Ppt, postpetiole; Pt, petiole; pts, petiolar spiracle. Scale bar = 0.5 mm. **Figure** 5. Full-face view of head of *M. sakalavum* worker. acs, anteromedian clypeal sector; C, clypeus; ca, clypeal angle (may be produced as denticle or tooth); cc, median clypeal carina; f, funiculus of antenna; fl, frontal lobe; frons, frons of head capsule; ft, frontal triangle; ms, median seta; scape, scape of antenna. Scale bar = 0.1 mm. **Figure** 6. Dorsal view of *M. sakalavum* queen thorax. Scale bar = 0.5 mm. **Figure** 7. Profile of *M. sakalavum* queen. an, anepisternum; ax, axilla; k, katepisternum; Ms, mesoscutum; Mt, metanotum; Oc, ocelli; P, propodeum; pp, propleuron; Pr, pronotum; Sc, scutellum. Scale bar = 1 mm. **Figure** 8. Full-face view of head of *M. sakalavum* queen. Scale bar = 0.2 mm. **Figure** 9. Full-face view of head of *M. sakalavum* male. Scale bar = 0.2 mm. **Figure** 10. Profile of *M. sakalavum* male. ae, aedeagus; An, anepisternum; ax, axilla; k, katepisternum; Ms, mesoscutum; P, propodeum; pm (l), left paramere; pm (r), right paramere; Pr, pronotum. Scale bar = 1 mm. **Figure** 11. Dorsal view of *M. sakalavum* male thorax. ax, axilla; mes, mesosoma; not, notaulus (vestigial here); pl, parapsidal line; sc, scutellum. Scale bar = 1 mm. **Figure** 12. Wing of *M. fisheri* showing the maximum complement of wing veins found in *Monomorium*. Scale bar = 1 mm. **Figure** 13. Inclination of a seta on body surface (terms used are taken from Dubois 1986). 1, erect; 2, suberect 3, decumbent 4, appressed.

(13–17), labial and maxillary segment count (18), and characteristics of the mandibles (19–22) were all characters used to create a morphological profile for the worker of each species.

MESOSOMA (Figs. 1, 3–4, 13).— In the same way, the appearance and pilosity of the promesonotum (23–27), the degree of impression of the mesonotal groove (28), and the appearance and pilosity of the propodeum and metapleuron (29–37) were also selected.

PETIOLE AND POSTPETIOLE (Figs. 1, 4).— The appearance of the petiole and postpetiole was scored, also the morphometric relationships between node face and node in profile, node height and postpetiole height and postpetiole height and length (38–48).

OTHER CHARACTERS (Fig. 13).— Those selected included pilosity of the first gastral tergite, color and presence or absence of worker polymorphism (49–50).

MEASUREMENTS OF GROSS MORPHOLOGY.— Seven measurements of the gross morphology were taken for the worker, these being expressed in millimeters (51–57). The head-mesosoma-petiole-postpetiole length (HML) (Fig. 1) was preferred to a total length measurement, since the gaster in myrmicine ants can be either distended or shrunk in individual specimens, resulting in an inordinately large variance in length readings. The first component of the HML is the head length (see following), followed by a modified Weber's length (WL). For the latter, a measurement was taken from the anterior base of the promesonotal hump (i.e., where the vertex of the head capsule would reach if the ant's head was tilted right back) to the apex of the metapleural lobe. The third component is the length of the combined petiole and postpetiole (measured from the apex of the metapleural lobe to the posterior margin of the postpetiole). These measurements were performed with the body of the ant viewed in profile. Head length (HL) (Fig. 2) is here defined as the length of the head capsule in full-face view as measured by a straight line from the midpoint of the anteromedian clypeal margin to the midpoint of the margin of the vertex. Head width (HW), also calculated with the ant in full-face view, involved measuring the maximum width of the head of the ant, disregarding the bulge made by the compound eyes. In most cases maximum width was just posteriad of the eyes. The cephalic index (CeI) was determined by the formula:

$$\text{CeI} = \text{HW}/\text{HL} \times 100$$

Antennal scape length (SL) (Fig. 2) is the maximum length of the scape, excluding the condylar bulb and its associated neck. The right scape was measured, except where this organ was missing or damaged, in which case the left scape was measured instead. The scape index (SI) was determined by the formula:

$$\text{SI} = \text{SL}/\text{HW} \times 100$$

The promesonotal width (PW) (Fig. 3) is the maximum width of the promesonotum viewed from the front, from a slightly elevated position so that the broadest extent of the promesonotum is visible.

NB. Measurements were obtained from dried, pointed specimens. These were examined under a stereomicroscope fitted with an ocular micrometer. Measurements were made to 0.01 mm. Provided that number was available, at least twenty worker specimens from each species were measured, many more in the case of problematic taxa. The maximum number of queens and males that could be reliably associated with the workers of a given species was also measured, this usually being less than twenty except for a few taxa like *M. termitobium* where the number of reproductives was very large. Drawings (Figs 1–13) were made by manipulation and overdrawing of images obtained from a Leica M420 microscope linked to an Automontage (Syncroscopy) program and imported into Adobe Photoshop 7.0.

QUEEN CHARACTERS (Figs. 6–8, 12): Characters selected for the head (1–7), propodeum (14–20), petiole and postpetiole (24–32), pilosity of the first gastral tergite (33) and color (34) were as for the worker. Gross measurements (37–43) were also carried out in the same way as those for the worker. Characters of the thorax differ from those of the conspecific worker, however, because of the presence of wings in the queen for part of her life history. These additional characters related to the appearance and pilosity of the combined pronotum, mesoscutum and mesopleuron, including degree of separation of the axillae (8–13) and the venation of the wing (21–23). Additional characters concerned presence or absence of brachypterous queens (35) and ergatoid or worker-queen intercastes (36).

MALE CHARACTERS (Figs. 9–10, 12): Seven characters were chosen for the male head, these including head-mesosoma width ratio, appearance of the frons and compound eyes, the position of the lower margin of the compound eye in relation to the posterior margin of the clypeus, the appearance of the ocelli, the ratio of the first segment of the antennal funiculus to the second segment, and the number of teeth and denticles. The mesosoma characters (8–12) were the profile and appearance of the pronotum + mesoscutum + mesopleuron, the appearance of the parapsidal furrows and notauli, and the degree of separation of the axillae. Wing vein characters (13–15) were as for the queen. Petiole and post-petiole characters (16–23), pilosity of the first gastral tergite (24), color (25) and gross morphological measurements (26–32) were as for the worker and queen.

GENUS *MONOMORIUM* MAYR

Monomorium Mayr 1855:452. Type-species: *Monomorium monomorium* Bolton (replacement name for *Monomorium minutum* Mayr, 1855:453, a junior secondary homonym of *Atta minuta* Jerdon 1851:105 [= *M. pharaonis* (L.) 1758: 580]); by monotypy (Bolton 1987:287).

Phacota Roger 1862a: 260. Type-species: *Phacota sichelii*, by monotypy. *Phacota* junior synonym of *Monomorium*: Ettershank 1966:82, syn. rev. Bolton 1987:281. [Synonymy by Fernandez (in press) 2.]

Nothidris Ettershank 1966:105. Type species: *Monomorium latastei* by original designation. [Synonymy by Fernandez (in press) 2.]

Antichthonidris Snelling 1975:5. Type-species: *Monomorium denticulatum*, by original designation. [Synonymy of genus by Heterick 2001:361 without species-level nomenclatural changes, synonymy of *A. denticulata* Fernandez (in press) 2.]

Epelysidris Bolton 1987:279. Type-species: *Epelysidris brocha*, by original designation. [Synonymy by Fernandez (in press) 2.]

(For synonymy in the genus *Monomorium* prior to 1988, see Bolton, 1987:287-288.)

DIAGNOSIS OF WORKER OF MALAGASY SPECIES.— Minute to moderate (total length approximately 1.5–4.5 mm) monomorphic to polymorphic myrmicine ants. Palp formula 5,3, 3,3 3,2, 2,2 or 1,2. Mandible smooth or longitudinally striolate, with three to six teeth and denticles, apical tooth always much larger than the preceding tooth; basal tooth often reduced to a small or minute denticle or angle but enlarged in one species, basal tooth often separated by a diastema from remainder of the dentition in members of the *M. hildebrandti* group; mandibular shape triangular, linear-triangular, or strap-like with inner and outer edges parallel or nearly so. Median clypeal seta conspicuous in most Malagasy species and positioned at or slightly above a distinct anteromedian clypeal margin except in *M. hildebrandti* group, where it is positioned on underside of a protruding shelf, near to the true anteromedian clypeal margin; paired setae (one often shorter than the other) straddling midpoint of anteromedian clypeal margin present in some large workers of *M. aureorugosum*, *M. fisheri* and *M. infuscum* and some queens of *M. fisheri*. Clypeus raised medially, usually bicarinate, though carinae may be obscure or in form of multiple weak ridges; in full-face view, the anteromedian clypeal margin often narrow and projecting, but this sector broad and abruptly declivous (i.e., when viewed in profile) in several members of *M. monomorium* and *M. hildebrandti* groups. Frontal carinae straight or diverging slightly posteriad, absent behind frontal lobes. Frontal lobes weakly sinuate or more-or-less parallel in full-face view. Antennal scrobes absent. Antennae

11- to 12-segmented; club usually with three distinct segments, sometimes four, or without a distinct club, but club never two-segmented. Eyes often reduced (sometimes to one or two ommatidia) in *M. hildebrandti* group, small to fairly large in other groups; in full-face view, eyes generally set at about midline of head capsule, or slightly above or below, but occasionally set well into anterior sector of head capsule; in profile, eyes usually set at about midline or behind midline of head capsule, rarely in front of midline; eye shape usually elliptical, with more pronounced curvature of the inner margin, but can be elongate or ovoid and narrowed to a point anteriad.

Mesosoma with standing setae in most groups, these setae lacking in some members of *M. salomonis* group; standing setae short and bristle-like in members of *M. shuckardi* group. Metanotal groove most commonly deeply impressed, but weakly impressed, vestigial or absent in some taxa. Propodeal dorsum rounded onto declivitous surface, weakly or strongly angulate or armed with short denticles, spines lacking in Malagasy species; standing propodeal setae absent in some cases. Propodeal spiracle distinctly circular or nearly so, usually situated at about midlength, but placed anteriad or posteriad of midlength in some taxa, and close to propodeal dorsum in members of *M. shuckardi* group. Metapleural glands of moderate to small size, never hypertrophied. Propodeal lobes often small to vestigial, rarely acute-angled and prominent. Fore coxae larger than middle or hind coxae. Petiolar peduncle often with small anteroventral flange or protuberance, but this feature vestigial in many species. Petiolar spiracle well in front of node in several endemic species, slightly in front of or in anterior sector of node in remaining taxa, often rather dorsally situated. Petiolar node shape ranging from low and broadly conical or tumular to cuneate and strongly tapered, thick and asymmetrical in profile in some members of *M. hildebrandti* group, but never regularly cuboidal in Malagasy species; underside of node and peduncle commonly with fine, transverse rugulae in larger species of *M. hildebrandti* group. Anteroventral margin of postpetiolar sternite often conspicuous, this feature reduced or absent in members of *M. destructor*, *M. pharaonis* and *M. monomorium* groups. Gaster dorsoventrally compressed, with blunt lateral carinae on gastral tergites. Sting not prominent in Malagasy species.

Diagnosis of queen of Malagasy species.— Larger than conspecific worker, but not greatly so in some taxa. Palp formula, number of mandibular teeth and denticles and number of antennal segments as for conspecific worker. Ocellar triangle of three ocelli typical, but posterior ocelli may occasionally be reduced in size. Eyes large, generally elliptical, sometimes with a concavity in upper outer margin, but circular, semi-circular and ovoid eye shapes also occur.

Seen in profile, mesoscutum ranges from broadly convex to convex anteriad and flattened or even faintly sinuate posteriad. Mesoscutal pilosity always present. Pronotum, mesoscutum and mesopleuron often smooth and shining, but may be striolate or punctate to a greater or smaller degree; mesopleuron always divided by transverse furrow into upper anepisternum and lower katepisternum. Length-width ratio of mesoscutum and scutellum from near 7:3 to about 3:2. Axillae mostly well separated but may be contiguous or even reduced to a strip of thin cuticle, each individual axilla being indistinct. Metapleural sculpture most commonly in form of longitudinal striolae or striae, propodeum often unsculptured except for costulae on declivitous face, but where present frequently more marked than in conspecific worker. Dorsal propodeal face characteristically sloped, often almost vertical. Propodeal processes, where present, in form of small denticles or flanges, at most. Wing veins tubular and sclerotised in *M. notorthotenes*, *M. hanneli*, and in *M. hildebrandti* group, predominantly weak and depigmented in most *M. monomorium* group species, though wing veins are darkly pigmented without accompanying sclerotization in some species. Cross-vein m-cu present in all queens of *M. hildebrandti* group, in all *M. notorthotenes* queens and some *M. hanneli* queens, absent in other *M. hanneli* queens, rarely present in reproductives of *M. destructor* group (per Bolton 1987), and always absent in reproductives of *M. monomorium* and *M.*

salomonis groups (information on the latter coming from Bolton 1987). Cross-vein cu–a always present in *M. notorthotenes*, *M. hanneli* and all members of *M. hildebrandti* group, always absent as a distinct vein in members of *M. monomorium* group (very rarely present as a vague shadow). (Alate queens seen only for *M. hanneli*, and M. *hildebrandti*, *M. monomorium* and *M. shuckardi* groups.) Petiole as for that of conspecific worker. No brachypterous queens seen among Malagasy *Monomorium*. Ergatoid females seen for both *M. hildebrandti* and *M. monomorium* groups.

Diagnosis of male of Malagasy species.— I have seen males only for *M. notorthotenes*, *M. hanneli* and the *M. hildebrandti* and *M. monomorium* groups, and can associate males with just 12 of the 36 Malagasy *Monomorium* species identified in this work. This is too incomplete a record for a proper diagnosis to be made, but of those males seen, all, except members of the *M. salomonis* group, possess conspicuous, often turreted ocelli. The compound eyes are almost invariably protuberant, tending to elongate in some species. The wing of the male, on the other hand, generally has the same venation as the conspecific female, but vein cu–a is lacking in all males of *M. notorthotenes* and *M. hanneli*. The males of the endemic *M. notorthotenes* are very small in relation to the conspecific queen, even smaller than many workers of this species, and have a distinctly fly-like *habitus*. Identified males of the *M. hildebrandti* group are also relatively small in relation to the queen and approximately the same size or smaller than the worker. However, the size disparity between queen and male is much less among *M. monomorium* group reproductives, in contrast to the often minute workers, e.g. the HML of the *Monomorium madecassum* queen is 3.01–3.12 mm, compared with 2.80–2.84 mm for the male. (By way of contrast, the HML for the *M. madecassum* worker is only 1.14–1.27 mm).

MALAGASY SPECIES GROUPS RECOGNIZED AS A RESULT OF THIS PROJECT

Despite the fact that Madagascar was separated from Africa in the late Jurassic about 165 MYBP, and from India only 88 MYBP (Krause 2003), the Malagasy *Monomorium* fauna has strong African affinities, and shares a number of species with eastern and southern Africa. However, several shared taxa have their distribution primarily in the middle and western parts of Africa. By way of contrast, the Malagasy representatives of another myrmicine genus, *Pyramica*, have much more decidedly Asian affinities (Fisher 2003).

Of most interest are four species of a group restricted to Madagascar that has not been previously categorized. I have called this the *Monomorium shuckardi* species group after the only member described prior to this work. Members of this group possess some of the most plesiomorphic characters known for the genus *Monomorium*, most notably a PF of 5,3. The placement of the petiolar spiracle well anteriad of the node and near to the midlength of the petiole is also a primitive feature shared only with a few Australian species in the *M. bicorne*, *M. insolescens* and *M. kilianii* species groups (Heterick 2001), and with members of the *M. scabriceps* group (Bolton 1987). However, other morphological features suggest a relationship at a basal level with the *Monomorium destructor* and *Monomorium salomonis* groups. These include the specialized small males (albeit, only known for *Monomorium notorthotenes* Heterick, sp. nov.) also found in the *M. destructor* group (Bolton 1987), and the finely microreticulate or striolate body sculpture and lack of standing setae on the propodeum, both characteristic of various members of the *M. salomonis* group. All members of the *M. shuckardi* species group also share a sculptured mandible with the other two groups, the sculpture in this case being predominantly longitudinal striolae or striae. Virtually all collections have been in the south of the island, in Toliara Province.

Two other groups found naturally on Madagascar are the *M. hanneli* and *M. hildebrandti* groups. The *M. hanneli* group (one Malagasy species) is otherwise restricted to West Africa and

Kenya, but members of the *M. hildebrandti* group (ten Malagasy species) in which the eye is reduced to one or two ommatidia are also widespread in Africa, Indo-Australia, Australasia, and the Pacific (Wilson and Taylor 1967; Heterick 2001). *Monomorium subcoecum* (not found in Madagascar) was described by Emery from the Antilles, in the Caribbean (Emery 1894b). However, whereas these two entities appear to constitute only a minor fraction of the African *Monomorium* fauna (with the exception of the widespread *Monomorium cryptobium*), several of the species recognized in this work are abundant and widespread throughout Madagascar. As understood in this work, the *M. hildebrandti* species group includes those species placed by Bolton in the *M. fossulatum* species group. The name *hildebrandti* is here preferred as the designation of this group because this was the earliest named species, and the name '*fossulatum*' has been synonymized under *sechellense* (Bolton 1995).

Monomorium hanneli bears a strong superficial resemblance to members of the *M. hildebrandti* group in which the clypeal carinae are well-developed and the clypeus is projected forward. The appearance of the mesosoma is also similar, if not identical, and the compound eye in workers of *M. hanneli* and workers of most *M. hildebrandti* group species is reduced. However, as Bolton (1987) correctly adjudges, the appearance of both groups is due to convergence. The most highly visible way workers of the two groups are separable is the appearance of the smooth, vertically attenuate node and the smooth, elevated postpetiole found in the *M. hanneli* group. A slightly more subtle but equally important difference is in the placement of the median seta, which, with the ant in full-face view, is set at or slightly above the midpoint of the true anteromedian clypeal margin in *M. hanneli* and its African relatives (i.e., *M. guineense*, *M. invidium* and *M. jacksoni*), and well underneath a protrusive ledge in those members of the *M. hildebrandti* group with a projecting clypeus. The wing is more strongly sclerotized in those members of the *M. hildebrandti* group that I have seen than it is in *M. hanneli*, and all of the former possess vein m–cu, whereas that vein is missing in *M. hanneli* males and at least some queens.

While the workers of most members of the *M. hildebrandti* group have eyes that are comparatively very small, usually being less than the greatest width of the antennal scape, this is not a universal trait. The general reduction in the size of the worker eye is perhaps a function of a cryptic or mainly subterranean lifestyle, since the colonies of most species in this group appear to favour rotting wood and leaf mould. Transverse ventral rugulae found under the petiole of the medium-size and larger species are absent from the small workers of *M. cryptobium*, *M. ferodens*, *M. modestum* and *M. sechellense*. Very smooth workers of some populations of *M. hildebrandti* also lack these rugulae. Apart from the almost total loss of vision, the species formerly recognized as belonging to the *fossulatum* group (including all those formerly placed in the genus *Syllophopsis*) share a gestalt common to *M. hildebrandti* and its allies. The very large *Monomorium aureorugosum* and *Monomorium infuscum* workers have distinctively triangular mandibles, well-separated antennal lobes and are heavily sculptured, but share the same petiolar structure (including the fine, transverse, ventral petiolar rugulae and asymmetrical nodal dorsum) of other large members of the species group. *Monomorium ferodens* has an aberrant PF of 3,2, but otherwise clearly belongs here. In summary, this group has the following shared worker apomorphies: (1) smooth, linear-triangular mandibles with a strongly oblique masticatory margin (except for *M. aureorugosum* and *M. infuscum*), (2) an anteromedian clypeal seta (more rarely, paired setae) positioned well under a protrusive ledge, and (3) a primitively asymmetrical dorsum to the petiolar node. Reduced eyes and transverse, ventral petiolar rugulae are also found in many *M. hildebrandti* group species. Workers of most species in this group share with the *M. hanneli* group and several members of the *M. monomorium* group narrowly separated frontal lobes.

The *M. destructor* and *M. salomonis* species groups are represented by few species, and these are mainly tramp ants. Within the *M. destructor* group, *Monomorium destructor* is adventive to the island, having been brought across by human commerce at some time in the past, but the widespread distribution of *Monomorium robustior* suggests endemicity (thus also Bolton 1987). Within the *M. salomonis* group, *Monomorium pharaonis* and *Monomorium subopacum*, members of different complexes but with similar tramp tendencies, have clearly been introduced. The presence of *Monomorium willowmorense*, known from one worker collected from the north-east coast, is more puzzling. The monotypic *Monomorium latinode* species group is represented by *M. latinode*, which also has tramp tendencies, and is well-dispersed across the Indo-Australian region (Bolton 1987).

Monomorium monomorium species group members found in Madagascar are often abundant, but are not particularly diverse compared with the Afrotropical fauna, only 15 species being recognized here. It should be said, however, that the variability of several nominal species like *M. termitobium* is so great that molecular-based systematics is probably needed to give the taxonomy strong definition. Some of the taxa appear to belong to complexes identified by Bolton (1987), while others seem not to be closely related to members of the group found on the African mainland. Of the described species, *M. madecassum* is clearly referable to Bolton's *leopoldinum* complex, albeit *M. leopoldinum* itself becomes a junior synonym of *M. madecassum* in this work. *Monomorium exiguum* and *M. floricola* were placed in the *boerorum* complex by Bolton, but this was confessedly for convenience, and even aside from the difference in antennal count (i.e., 11 antennomeres in *M. exiguum* and 12 in *M. floricola*), the queens of the two species do not appear very similar. *Monomorium exiguum* is actually closely related to the Afrotropical *Monomorium rosae* (see my comments under the former). The other *Monomorium* with an 11-segmented antenna, *M. nigricans*, is of uncertain affinities, but may also belong to the *M. exiguum* complex.

Monomorium termitobium is here regarded as the senior synonym of *M. binatu*, *M. exchao* and *M. imerinense*. Through *M. binatu* and *M. exchao*, *M. termitobium* (along with the apparently closely related *M. xuthosoma* and *M. sakalavum*) is associated with Bolton's *rhopalocerum* complex, but as here conceived, the morphological parameters of that complex far exceed those designated by Bolton. Workers of *Monomorium micrommaton* and *M. chnodes* bear a close resemblance to hirsute, yellow workers of *M. termitobium*. The queen of *M. micrommaton* is relatively large, with a proportionately massive mesosoma and a broad, cordate head, quite different characters from those of the queen of *M. termitobium*. *Monomorium chnodes* possesses a square propodeum (unlike that seen in any workers of *M. termitobium*) with a large propodeal spiracle, and some queens and workers have a five-toothed mandible — a feature otherwise unknown in the *M. monomorium* species group. However, preliminary molecular data place *Monomorium chnodes* close to *M. platynodis*, and both species possess a very short clypeus that, when seen in profile, descends towards the arc of the mandibles at almost 90 degrees. *Monomorium platynodis*, in fact, may represent a radiation derived from *M. chnodes*, with a reduction in the size and dentition of the mandible.

In *Monomorium chnodes*, *M. flavimembra*, *M. lepidum*, *M. platynodis,* and *M. versicolor*, the clypeal carinae are obsolete or only weakly defined and the anteromedian clypeal margin is depressed and moderately to strongly declivous when seen in profile — in the case of *M. chnodes* and *M. platynodis* being almost vertical, as mentioned above. In four of these species, the fourth (i.e., basal) tooth is greatly reduced or absent. Only *M. chnodes* has a strongly defined basal tooth. In *M. chnodes*, *M. flavimembra*, and *M. lepidum*, the petiolar node is more-or-less conical and the postpetiole is rounded, but in *M. platynodis* and *M. versicolor* the nodes are high and the petiolar node is strongly cuneate. The group is here called the *flavimembra* complex. *Monomorium bifidoclypeatum* is very similar to these species and almost certainly also belongs to this complex. *Monomorium denticulus* is a small member of the *M. schultzei* complex but does not appear to be conspecific with any of the described African forms.

Key to Malagasy *Monomorium* workers

1. Antenna 11-segmented (*M. monomorium* species group) 2
1'. Antenna 12-segmented (various species groups) 3
2. Metanotal groove weakly impressed; in profile, propodeum rather elongate and petiolar node always conical, its dorsum tapered (depigmented yellow to brown) (Figs. 51–52) . . . . *M. exiguum* Forel
2'. Metanotal groove strongly impressed; in profile, propodeum evenly rounded and petiolar node may be thick, broadly rounded (dark reddish-brown to black) (Figs. 65–66) . . . . *M. nigricans* Heterick, sp. nov.
3. Palps long (PF 5,3); propodeum usually lacking standing setae, where present these short and fine; occipital carina strongly defined and conspicuous along rear margin of head when head viewed in profile; mandible armed with five distinct teeth (*M. shuckardi* species group). . . . 4
3'. Palps shorter (PF 3,3 or less); propodeum usually with standing setae, but if these lacking, then mandible armed with four teeth, or with three distinct teeth and a small to minute denticle or angle; occipital carina vestigial or short, not conspicuous along rear margin of head when head viewed in profile 7
4. Head and mesosoma finely striolate; in profile, propodeum without a distinct angle between its dorsal and declivitous faces (Fig. 37). *M. robertsoni* Heterick, sp. nov.
4'. Head and mesosoma finely striolate-microreticulate, microreticulate-punctate with or without unsculptured areas, or head and dorsum of mesosoma smooth and shining; propodeum in profile with blunt to sharply defined propodeal angle 5
5. Antennal scape very long, extending beyond vertex of head capsule (SI 113–132) larger (HW 0.62–0.72 mm), depigmented yellow ants (Figs. 85–86) . . *M. notorthotenes* Heterick, sp. nov.
5'. Antennal scape shorter, barely or not attaining vertex (SI 90–108); if yellowish, then much smaller (HW 0.35–0.47 mm compared with 0.62–0.72 mm) 6
6. In full-face view, frons of head capsule densely microreticulate-punctate; generally larger species (HW 0.46–0.72 mm, usually 0.55 mm<) (Figs. 38–39). . . . . *M. shuckardi* Forel
6'. In full-face view, frons of head capsule finely striolate-microreticulate or smooth and shining; generally smaller species (HW 0.35–0.47 mm compared with 0.46–0.72 mm, usually 0.55 mm ≥); (Figs. 35–36) . . . . *M. clarinodis* Heterick, sp. nov.
7. Mandible distinctly longitudinally striate, maximum number of teeth four 8
7'. Mandible smooth and shining, except for piliferous pits, with three to five teeth 12
8. In full-face view, frons of head capsule smooth, with exception of piliferous punctures, fine rugulae on vertex (*M. destructor*) and fine, circular striolae around antennal insertions (*M. destructor* species group) (e.g.. Fig. 41) 9
8' In full-face view, frons of head capsule sculptured, sculpture varying from superficial reticulation to shagreenate-punctate (*M. salomonis* species group) (e.g., Fig. 43). 10
9. Head and mesosoma brown to dark brown . . . . *M. robustior* Forel
9'. Head and mesosoma yellow to light brownish-yellow . . . . *M. destructor* (Jerdon)
10. Mesosoma possessing one or more pairs of erect and/or sub-erect setae (Fig. 91) . . . . *M. pharaonis* (L.)
10'. Mesosoma without standing setae 11
11. In full-face view, frons of head capsule shining, with surface sculpture confined to faint reticulation, the vertex more noticeably shagreenate; scape shorter (SI < 100) . . . . *M. willowmorense* Bolton
11'. In full-face view, frons of head capsule opaque, reticulate to shagreenate-punctate; scape longer (SI 100 >) (Figs. 42–43). . . . . *M. subopacum* (Smith)

12. Either frontal lobes separated by a strip of posterior sector of clypeus that is clearly wider than either of them, *or*, if frontal lobes closely approximated, metanotal groove strongly indented and propodeum smooth; propodeal dorsum rounding into declivitous face without distinct angle; propodeal denticles always absent; fine, transverse ridges always absent from underside of petiolar peduncle and node; anteroventral postpetiolar process commonly vestigial or absent, rarely an inconspicuous lip and prominent only in *M. latinode* (e.g., Fig. 94). 13

12'. Frontal lobes usually closely approximated, and separated by a strip of posterior sector of clypeus that is narrower than either of them, *or*, if frontal lobes well separated, and metanotal groove deeply impressed, then propodeal dorsum meeting declivitous face at a distinct angle; propodeum often armed with flanges or denticles; several to many fine, transverse ridges present on underside of petiolar peduncle and node; anteroventral postpetiolar process usually distinct as sharp angle, conspicuous lip or spur (*M. hanneli* and *M. hildebrandti* species groups.) (e.g., Fig. 102) 26

13. Mandible armed with five teeth; PF 3,3; propodeum elongate, its dorsum and sides finely and densely striolate (*M. latinode* species group) (Figs. 44–45). . . . . *M. latinode* Mayr

13'. Mandible armed with three or four teeth (five teeth very rarely present in *M. chnodes*); PF 2,2 or 1,2; propodeum not as above, usually smooth on dorsum and sides (*M. monomorium* species group) 14

14. In full-face view, clypeus strongly bidentate, each clypeal carina terminating in a sharp angle or denticle, the anteromedian clypeal margin between the clypeal projections often straight; eyes large, eye length between ¼th and ⅕th length of side of head capsule (body of ant concolorous yellow or brown, gaster may be slightly darker shade than mesosoma) (e.g., Fig. 90) 15

14'. In full-face view, clypeus usually weakly emarginate to weakly convex, if clypeus tending to bidentate then anteromedian margin of clypeus usually indented between anteromedian clypeal projections, body of ant is distinctly bicolored or eye is smaller, eye length ⅕th < length of side of head capsule (eg. Fig. 54) 16

15. Propodeal spiracle very large, ≈ same width as antennal segments a3–9; petiolar node higher, tending to cuneate (Figs. 59–60) . . . . *M. madecassum* Forel

15'. Propodeal spiracle minute, pinhole-like, width << antennal segments a3–9; petiolar node lower, conical (Fig. 50). . . . . *M. denticulus* Heterick, sp. nov.

16. Mandible *always* clearly armed with three teeth with no trace of a smaller, basal tooth or denticle. 17

16'. Mandible characteristically armed with four teeth, albeit basal tooth may be reduced to a minute, offset denticle or angle (rarely absent in individuals of *M. flavimembra*, whose workers have a bright reddish- or yellowish-brown body and yellowish appendages), rarely with five teeth (some *M. chnodes*) 18

17. In profile clypeus sloping towards mandibles at acute angle; in full-face view clypeus projecting forward so that its anterior margin adjoins or partially obscures basal margin of mandibles; metanotal groove deeply impressed but almost always without broad cross-ribs; variously colored from orange to dark reddish-black or bicolored, but where head is light colored, antennal scape is conspicuously darker than head capsule (Figs. 67–68)
. . . . *M. versicolor* Heterick, sp. nov.

17'. In profile, clypeus almost at right angle to mandibles; in full-face view, anterior margin of clypeus largely straight, clypeus not projecting forward, leaving a gap between clypeus and mandibles; metanotal groove deeply impressed, broad cross-ribs always present; concolorous orange, with antennal scape of same color as head capsule (Figs. 63–64)
. . . . *M. platynodis* Heterick, sp. nov.

18. Head and gaster uniformly dark brown to black, contrasting with yellowish or bicolored yellow-and-brown mesosoma; petiolar node low, broadly conical to tumular, scarcely higher than postpetiole (Figs. 55–56) . . . . *M. floricola* (Jerdon)

18'. Either concolorous, or head and gaster not both uniformly dark in color with a lighter colored mesosoma; petiolar node variable but usually distinctly higher than postpetiole. 19

19. In profile, mesosoma straight and at higher level than propodeum; propodeal spiracle very large, ≈ diameter of antennal segments a3–a9; five teeth occasionally present, all non-apical mandibular teeth usually of same size; propodeum short, about as long as high; antennal scape relatively short (SI 67–76) (densely hairy, bright yellow ants) (Figs. 48–49) . . . . *M. chnodes* Heterick, sp. nov.

19'. In profile, mesosoma, if straight, on same level as propodeum; propodeal spiracle generally smaller, commonly pinhole-like; maximum of four teeth, basal tooth frequently distinctly smaller than other non-apical teeth and reduced to minute denticle or angle in several taxa; propodeum usually longer than high; antennal SI usually 80> 20

20. In full-face view, antennal scapes very long, scapes normally reaching or even slightly exceeding vertex of head capsule (SI 100 >), in rare, very small individuals with scape index slightly less than 100, head darker than mesosoma; profile of combined mesosoma and propodeum straight (except for indentation of metanotal groove), propodeum elongate with indistinct angle between propodeal dorsum and its declivitous face; mesosoma often with 8> pairs of setae; mesopleuron usually with distinct sculpture, often reticulate-punctate (reddish-brown ants which normally have darker head and gaster) (Figs. 1–4). . . . . *M. sakalavum* Santschi

20'. In full-face view, antennal scapes usually shorter, if exceeding vertex, and profile of combined mesosoma and propodeum straight, then mesopleuron smooth, or head of same color intensity as mesosoma and mesosoma with only three prominent pairs of standing setae, or propodeum rounded in a convex curve towards its declivitous face 21

21. With combination of: head and mesosoma brownish-yellow to orange (normally concolorous, head may be of slightly darker shade than mesosoma), gaster brown; clypeus projected forward, clypeal carinae strongly developed and moderately divergent anteriad; propodeal spiracle relatively large, ≈ diameter of antennal segments a3–a9; in profile, postpetiole visibly higher than wide (Fig. 69) . . . . *M. xuthosoma* Heterick, sp. nov.

21'. Without this combination of characters (similar species most easily distinguished by smaller, pinhole- like propodeal spiracle, or rounded postpetiole which is as high as wide, or weakly developed or indistinct clypeal carinae) 22

22. In full-face view, clypeal carinae well developed and strongly divergent anteriad, anteromedian clypeal margin straight and broad, sometimes reaching almost to genae; in profile, clypeus meeting mandibles at angle of ≈ 90°; petiolar node often very small and low for size of ant, with a distinct ventral lobe in some specimens; head rather broad (CeI 86–94) (gracile, yellow or brown species) (Figs. 46–47) . . . . *M. bifidoclypeatum* Heterick, sp. nov.

22'. In full-face view, if clypeal carinae well developed, then clypeus with carinae sub-parallel or only slightly divergent, or, if anteromedian clypeal margin straight and broad, then clypeal carinae obsolete or only weakly developed. 23

23. Concolorous reddish-brown to yellowish-brown species with yellow to brownish-yellow appendages, clypeus also yellowish, in contrast with color of head capsule; clypeal carinae obsolete or feebly indicated, clypeus only weakly projected forward and depressed medially, anteromedian clypeal margin broad and straight to weakly emarginated (Figs. 53–54) . . . . *M. flavimembra* Heterick, sp. nov.

23'. Either color pattern not as above, or clypeal carinae distinct, anteromedian clypeal margin narrow, and clypeus strongly projected forward. 24

24. Bicolored species with head and mesosoma yellow to orange, gaster brown to shining black, sometimes with paler, yellowish or orange area at base of first gastral tergite; in full-face view, clypeal carinae weak or obsolete, anteromedian clypeal margin broad and straight or slightly emarginate; head generally broader (CeI 82–88); basal tooth reduced to minute angle and strongly offset (Figs. 57–58) . . . . *M. lepidum* Heterick, sp. nov.

24'. Concolorous yellow or brown to bicolored yellow and brown or black, but if bicolored as above, then clypeal carinae distinct in full-face view, often sharply defined and sub-parallel, anteromedian clypeal margin narrow, its outline slightly convex, straight or concave; head of these bicolored specimens generally narrower (CeI 74–83); basal tooth variably developed, but usually a distinct denticle (several specimens may need to be examined as mandibular teeth are sometimes abraded) 25

25. Eye very small (8 ommatidia <), its diameter ≤ greatest width of antennal scape; in profile, clypeus broadly convex, angle formed by anterior clypeal margin usually indistinct; in full-face view clypeus bulbous, clypeal carinae weakly developed and frontal carinae separated by barely greatest width of antennal scape (hairy, concolorous, depigmented yellow ants) (Figs. 61–62) . . . . *M. micrommaton* Heterick, sp. nov.

25'. Eye almost always larger (10 ommatidia ≥), its diameter > greatest width of antennal scape (extremely rarely, eye small with some ommatidia reduced in size , in which case gaster and sometimes head have brownish tinge, totally lacking in *M. micrommaton*); in profile, descending outline of clypeus in most cases sloping rather than broadly convex, with distinct angle at anterior clypeal margin; in full-face view, clypeus usually less bulbous and clypeal carinae often weakly to strongly developed; frontal carinae most commonly separated by more than width of antennal scape at its widest point (body color highly variable, ranging from pale yellow through various shades of brown to chocolate or bicolored yellow or orange and brown/black) (Fig. 93–94). . . . . *M. termitobium* Forel

26. In full-face view, clypeus projected forward with well-defined clypeal carinae, median seta positioned at or slightly posteriad of (i.e., above) the projecting anteromedian clypeal margin; petiolar node smooth, thin, tapered and often scale-like; postpetiole elevated, smooth, usually distinctly higher than wide; underside of petiolar peduncle and node smooth, without hint of fine, transverse ridges (concolorous yellow to tawny-orange species) (*M. hanneli* species group) (Fig. 70–71). . . . . *M. hanneli* Forel

26'. In full-face view, either clypeus not projected forward with strong carinae, or anteromedian seta set well anteriad of (i.e., underneath) apparent anteromedian clypeal margin; petiolar node variable but never thin, tapered and scale-like; postpetiole usually rounded, if elevated and distinctly higher than wide, then strongly sculptured; underside of petiolar peduncle with several to many fine, transverse ridges in medium-sized and larger species (*M. hildebrandti* species group) 27

27. PF 3,2; four mandibular teeth, apical tooth twice as large as t3, sharp and downcurved (depigmented, pale yellow species) (Fig. 77) . . . . *M. ferodens* Heterick, sp. nov.

27'. PF 2,2; four or five mandibular teeth, with apical tooth usually same size as t3; sometimes with broad base but never downcurved (color variable, often brown, bright yellow-orange or bicolored) 28

28. Promesonotum, petiolar node and postpetiole coarsely striate; in full-face view, mandibles broadly triangular with at least five distinct teeth arranged vertically on masticatory margin, additional denticle may be present; eye size moderate, diameter of eye ≈ equal to greatest width of antennal scape (very large, blackish-red or orange-and-yellow ants with HW > 0.85 mm,

often >1mm). 29

28'. Promesonotum and petiolar node, at least, without coarse striae; either smooth, or with weak striolae posteriad (promesonotum) or with faint, lateral, longitudinal striolae (petiolar node); in full-face view, mandibles linear-triangular in most specimens, number of teeth and denticles four to five, but four is most common; HW 85 <, except in very large workers of M. fisheri, in which eye is very small (eye width < greatest diameter of antennal scape.) 30

29. Blackish-red species; average scape length shorter (SI 92–99) . . . . *M. infuscum* Heterick, sp. nov.

29'. Orange species; average scape length longer (SI 98–103) (Figs. 73–74) . . . . *M. aureorugosum* Heterick, sp. nov.

30. Eye point-like, consisting of one or two ommatidia (small, depigmented, yellow species). . 31

30'. Eye often small, but of normal appearance, consisting of four ommatidia ≥ 33

31. Mesopleuron microreticulate (Figs. 82–83) . . . . *M. sechellense* Emery

31'. Mesopleuron smooth 32

32. In profile, metanotal groove deeply impressed; propodeal angle distinct with clear separation of dorsal and declivitous faces; smaller ants (HW 0.27–0.30 mm) (Figs. 75–76) . . . . *M. cryptobium* Santschi

32'. In profile, metanotal groove usually weakly impressed; propodeal angle indistinct, propodeum without clear separation of dorsal and declivitous faces; larger ants (HW 0.36–0.42 mm) (Figs. 80–81) . . . . *M. modestum* Santschi

33. In full-face view, humeri of promesonotum armed with a small, bluntly rounded angle, tubercle or rugosity . . . . *M. gongromos* Heterick, sp. nov.

33'. In full-face view humeri of promesonotum not armed with a small, bluntly rounded angle, tubercle or rugosity, though they may be flattened and project as flanges over sides of mesopleuron 34

34. With combination of: eyes relatively large (eye width ≥ greatest width of antennal scape, and number of ommatidia ≥ 16); postpetiole attenuated anteriad; weak, longitudinal striolae nearly always present on sides of petiole; maximum of four mandibular teeth and denticles; promesonotum always smoothly rounded on to humeri (HW 0.63–0.70 mm; SI 88–100) (Fig. 72). . . . . *M. adiastolon* Heterick, sp. nov.

34'. Without above combination of characters (eyes usually small, eye width < greatest width of antennal scape, other characters vary with species) 35

35. Petiolar node thick, posterior face descending at right angle to petiole, dorsum broadly rounded and sides lacking longitudinal striolae; five mandibular teeth and denticles often present; promesonotum flattened and projecting as flange in smooth, shining specimens; anteromedian margin of clypeus indented, straight or narrowly convex with indistinct clypeal carinae; propodeal angle always square, lacking short denticles; nest series show allometric monophasy, some southern populations distinctly polymorphic with large-headed major workers; average size larger (HL 0.64–1.23 mm; HW 0.50–1.26 mm) (Figs. 78–79) . . . . *M. fisheri* Heterick, sp. nov.

35'. Petiolar node usually distinctly asymmetrical or narrow tending to cuneate, if node thick and erect, then often finely longitudinally striolate with dorsum narrowly rounded and posterior surface distinctly sloping at angle of 90° <; maximum of four mandibular teeth or denticles; promesonotum always rounded; anteromedian margin of clypeus straight to indented, extension of clypeal carinae usually forming blunt angles; propodeal angle often armed with short denticles or flanges; nest series monomorphic with, at most, slight variation in size; average size smaller (HL 0.44–0.73 mm: HW 0.36–0.61 mm) (Figs. 101–105). . *M. hildebrandti* Forel

The shuckardi-group

Monomorium clarinodis Heterick, sp. nov.

Figs. 14, 35–36.

Etymology.— Latin '*clarus*' ('shiny') + pl. of '*nodus*' (masc. 'knot')

Material examined.— Holotype: ☿, **Prov. Toliara**, 6.1 km 182 S Marovato 25°35′S, 45°18′E, 20 m. 14.ii.2002, Fisher et al. BLF#5528 /under stone spiny forest/thicket/ CASENT 0453886 (CAS). Paratypes: **Prov. Toliara** (all specimens with same collection data as holotype): 1☿ (ANIC); 21☿ (BMNH); 21☿ (CAS); 31☿ (MCZ).

Other material examined: **Prov. Toliara:** Beza-Mahafaly ['Mahafely'], 27 km E Betioky 23.iv.1997 B.L. Fisher (3☿, 1♀); Cap Sainte Marie, 12.3 km 262 W Marovato 11–15.ii.2002 Fisher *et al.* (6♀); Ehazoara Canyon, 26 km E Betioky 27.iv.1997 B.L. Fisher (1☿); Forêt Beroboka, 5.9 km 131 SE Ankidranoka 12–16.iii.2002 Fisher *et al.* (2☿); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i.–1.ii 2001 B.L. Fisher (16☿); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* (16☿); Mahafaly ['Mahafely'] Plateau 6.2 km 74 ENE Itampolo, 21–25.ii.2002, Fisher *et al.* (7☿); Mandarano ['Manderano'], 10.iv.2002, Frontier Project MG030 (1☿); 6.1 km 182 Marovato 14.ii.2002 Fisher *et al.* (1☿); P. N. Ambovo Springs, 29.3 km 4 N Ranohira, 9–14.ii.2003, B.L. Fisher (2☿); P. N. Kirindy Mite, 16.3 km 127 SE Belo sur Mer 6–10.xii.2001 Fisher *et al.* (1☿); P.N. Andohahela, 1.7 km 61 ENE Tsimelahy 16–20.i.2002 Fisher *et al.* (6☿); P.N. Andohahela, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (4☿); Tsimanampetsotsa, 6.7 km 130 SE Efoetse, 18–22.iii.2002 B.L. Fisher (8☿); Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka, 22–26.iii.2002 B.L. Fisher (1☿).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons ranging from shining, smooth with almost effaced reticulation to shining and finely punctate-reticulate; pilosity of frons consisting of a few short, thick, erect setae interspersed with short, appressed setulae. Eye moderate, eye width 1–1.5x greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin broadly convex; paraclypeal setae short and thickened, not reaching basal margin of closed mandibles; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 5,3. Mandibular teeth five; mandibles triangular and mainly smooth (weakly striate basally); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present).

Mesosoma: Promesonotum shining and microreticulate, microreticulation reduced on humeri, or, shining and smooth on dorsum, lower mesopleuron strongly punctate; (viewed in profile) promesonotum broadly convex, or, anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae very variable, from one or two to up to a dozen; standing promesonotal setae consisting of short, erect or semi-erect bristles; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove vestigial. Propodeum with reduced sculpture, generally smooth dorsally, metapleuron punctate; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle, but dorsal and declivitous faces separated when seen in profile; standing propodeal setae absent; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer declivitous face of propodeum than metanotal groove. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle laterodorsal and situated well anteriad of petiolar node; node (viewed in profile) cuneate, vertex rounded; appearance of node shining and faintly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole shining, with vestigial sculpture; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, short, thick, erect setae interspersed with minute, appressed setulae.

GENERAL CHARACTERS: Color from orange or yellowish with gaster light brown, through to uniform chocolate. Worker caste monomorphic.

HOLOTYPE WORKER MEASUREMENTS: HML 1.55 HL 0.53 HW 0.44 CeI 83 SL 0.40 SI 91 PW 0.32.

OTHER WORKER MEASUREMENTS: HML 1.22–1.57 HL 0.45–0.55 HW 0.35–0.47 CeI 78–87 SL 0.32–0.43 SI 90–97 PW 0.26–0.35 (n=20).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex always planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on dorsum of pronotum and mesoscutum. Propodeum shining and microreticulate; propodeum distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Propodeal lobes present as vestigial flanges only, or absent.

WING: Wing not seen (queen dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and microreticulate; postpetiolar sternite not depressed, in form of narrow, rectangular projection.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, short, thick, erect setae interspersed with minute, appressed setulae.

GENERAL CHARACTERS: Color brownish-yellow, gaster darker. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 2.29 HL 0.66 HW 0.61 CeI 92 SL 0.52 SI 85 PW 0.52 (n=1).

REMARKS.— This species appears to have a wider distribution than other members of the *M. shuckardi* group, with most specimens being obtained from sifted litter in spiny forest in Toliara Province. The species has also been collected, however, in pitfall traps, from under a stone and from within a rotten log in tropical dry forest. Workers are very variable in appearance, and range from shining with largely effaced sculpture on the frons and most of the promesonotum to uniformly granulose-reticulate on the mesosoma with a striolate-reticulate frons, the latter form resembling members of the *M. salomonis* species group. Color is similarly variable, and ranges from uniformly pale yellowish or bicolored orange-and-brown to dark chocolate, some of the latter workers exhibiting a rather mottled appearance (not unlike blended white and dark chocolate confectionery). One of the dark workers possesses numerous differences from similarly dark specimens taken in the same pitfall trap. The propodeum is more elongate and positioned relatively lower to the promesonotum so that there is no metanotal groove, the eye is slightly larger, the appendages are longer, and there is more extensive sculpture and erect pilosity. In other, respects, however, it conforms to the *habitus* of the other dark workers. This specimen does not appear to be an ergatoid, and the reason for the aberrant appearance is not known.

Monomorium notorthotenes Heterick, sp. nov.

Figs. 14, 85–89.

Etymology.— Greek '*noton*' (neut. 'back') + '*orthotenes*' ('stretched out')

Material examined.— Holotype: ☿, **Prov. Toliara**, Rés Cap Sainte Marie 14.9 km 261 W Marovato 25°36′S, 45°09′E, 160 m. 13–19.ii.2002, Fisher et al. BLF# 5740/under stone spiny forest/thicket/ CASENT 0002257 (CAS). Paratypes: **Prov. Toliara** (all specimens with same collection data as holotype): 1×2☿ (one with head missing) (ANIC); 1×2☿ (BMNH); 1♀+2♂ (5741) (CAS); 2☿+1♀ (MCZ).

Other material examined: **Prov. Toliara:** Cap Sainte Marie 14.9 km 261 W Marovato, 13–19.ii.2002, Fisher et al. (23☿, 4♀, 3♂); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* (27☿, 6♀, 6♂); 4.4 km 148 SSE Lavanono, 17.ii.2002, Fisher *et al.* (37☿, 4♀, 4♂); Mahafaly ['Mahafely'] Plateau 6.2 km 74 ENE Itampolo, 21–25.ii.2002, Fisher *et al.* (48☿, 4♀, 3♂); Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka, 22–26.iii.2002 B.L. Fisher (15☿, 1♀).

Worker description.— Head: Head rectangular; vertex planar; frons shining and finely striolate and microreticulate; pilosity of frons consisting mainly of short, appressed setulae with a few stout, erect and semi-erect setae on vertex. Eye large, eye width 1.5× greater than greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club four-segmented. Clypeal carinae indistinct; anteromedian clypeal margin broadly convex; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 5,3. Mandibular teeth five; mandibles triangular and striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present).

Mesosoma: Promesonotum shining and microreticulate throughout; (viewed in profile) promesonotum broadly convex; promesonotal setae seven to twelve; standing promesonotal setae consisting of short, erect or semi-erect bristles; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove weakly impressed, with faint costulae or costulae lacking. Propodeum shining and microreticulate; propodeal dorsum convex; propodeum smoothly rounded or with indistinct angle, but dorsal and declivitous faces separated when seen in profile; standing propodeal setae absent; appressed propodeal setulae abundant, particularly on dorsum of propodeum; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle laterodorsal and situated well anteriad of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining and distinctly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 1:1 and 3:4; height–length ratio of postpetiole between 1:1 and 3:4; postpetiole shining and microreticulate; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, short, thick, erect setae interspersed with minute, appressed setulae.

GENERAL CHARACTERS: Color depigmented ochre. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 2.77 HL 0.88 HW 0.76 CeI 86 SL 0.86 SI 113 PW 0.49.

OTHER WORKER MEASUREMENTS: HML 2.39–2.80 HL 0.75–0.90 HW 0.62–0.78 CeI 81–86 SL 0.82-0.96 SI 115–132 PW 0.42–0.50 (n=20).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex always planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin;. (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on dorsum of pronotum and mesoscutum. Propodeum shining and microreticulate; propodeum distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing first discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and microreticulate; postpetiolar sternite not depressed, in form of narrow, rectangular projection.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, short, thick, erect setae interspersed with minute, appressed setulae.

GENERAL CHARACTERS: Color brownish- yellow, gaster darker. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 3.98–4.39 HL 1.14–1.21 HW 1.11–1.23 CeI 95–103 SL 1.00–1.09 SI 85–98 PW 0.90–1.04 (n=13).

MALE DESCRIPTION.— HEAD: (In full-face view) head width-mesosoma width ratio between 4:3 and 1:1; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 2:3 and 1:2. Maximum number of mandibular teeth and denticles three.

Mesosoma: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to lower katepisternum; parapsidal furrows vestigial or absent; notauli absent; axillae separated by width of at least one axilla.

Wing: Wing veins tubular and strongly sclerotised; vein m–cu absent; vein cu–a present.

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) evenly tumular; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole about 3:4; postpetiole shining and smooth.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae.

General characters: Color a depigmented ochre.

Male measurements: HML 2.01–2.23 HL 0.46–0.53 HW 0.48–0.54 CeI 94–106 SL 0.11–0.14 SI 21–26 PW 0.58–0.71 (n=15).

Remarks.— This species appears to be restricted to spiny forest and associated thickets in coastal localities in the extreme south and south-west of Madagascar. Collections have been made from colonies under stones, or of foraging workers. Workers of the species are much more uniform in appearance than those of *Monomorium clarinodis* but, apart from their larger size and longer antennae, closely resemble pale workers of that ant. Superficially, workers of this species may be confused with *Aphaenogaster* because of their elongate bodies and spindly appendages.

Monomorium robertsoni Heterick, sp. nov.

Figs. 14, 37.

Etymology.— In honour of Dr. Hamish Robertson (South African Museum).

Material examined.— Holotype: **Prov. Toliara**, Ranobe, 23°02′03″S, 43°36′43″E, 30 m., 13–19.ii.2002. Frontier Project, MGF056/sifted litter spiny forest/thicket/ CASENT 0003501 MGF056(5) (CAS). Paratypes: **Prov. Toliara**: one ☿ with same collection data as holotype, collection code MGF054 (MCZ); two ☿'s, Mandarano ['Manderano'], 23°31′38″S, 44°05′15″E, 70m, 10.v.2002 Frontier Project, MGF030/ sifted litter gallery forest (1☿ - CAS) (1☿ - BMNH).

Other material examined: Ifaly, 17.ix.1993 W.E. Steiner and R. Andriamasimanana (4☿) (MCZ).

Worker description.— Head: Head square; vertex planar; frons finely striolate throughout; pilosity of frons a mixture of well-spaced, erect and semi-erect setae interspersed with appressed setulae only. Eye large, eye width 1.5x greater than greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head. Antennal segments 12; club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin broadly convex; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 5,3. Mandibular teeth five; mandibles triangular and striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present).

Mesosoma: Promesonotum finely striolate throughout; in profile broadly convex anteriad, convexity reduced posteriad; promesonotal setae seven to twelve; standing promesonotal setae consisting of short, erect or semi-erect bristles; appressed promesonotal setulae few, mainly on dorsum of promesonotum. Metanotal groove vestigial. Propodeum uniformly finely striolate; propodeal dorsum flat throughout most of its length; always smoothly rounded, no separation between dorsal and declivitous faces when seen in profile; standing propodeal setae absent; appressed propodeal setae very scarce or absent; propodeal spiracle nearer declivitous face of propodeum than metanotal groove; vestibule of propodeal spiracle absent or not visible; propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle laterodorsal and situated slightly anteriad of petiolar node. Node (viewed in profile) conical, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1. Anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole shining and smooth; postpetiolar sternite depressed near its junction with gaster, and sloping anteriad at angle of 45–60 to form large conspicuous lip at its anterior end.

Gaster: Pilosity of first gastral tergite consisting mainly of short, appressed setulae, together with a few erect and semi-erect setae.

General characters: Color of head, mesosoma and nodes orange, legs, mandibles and apical portion of gaster straw-colored, basal portion of gaster brown. Worker caste monomorphic.

Holotype measurements: HML 1.50 HL 0.53 HW 0.45 CeI 86 SL 0.45 SI 100 PW 0.32.

Paratype worker measurements: HML 1.50–1.82; HL 0.53–0.61; HW 0.45–0.54; CeI 83–88; SL 0.45–0.52; SI 97–104; PW 0.32–0.40 (n=3).

Other worker measurements: HML 1.49–1.67; HL 0.52–0.58; HW 0.43–0.49; CeI 81–84; SL 0.44–0.51; SI 99–107; PW 0.32–0.36 (n=4).

Remarks.— This species appears to have a very restricted distribution. The few known specimens are all workers, and have been collected from Ifaly, Mandarano and Ranobe in south-western Toliara Province. Collections have been made in sifted litter in spiny forest and associated thickets, in a pitfall trap at the base of a baobab, and in a malaise trap. The latter capture suggests this species may forage arboreally. *Monomorium robertsoni* is characterized by its low propodeum, which lacks a separate dorsal and declivitous face, and by its finely striolate exoskeleton.

Monomorium shuckardi Forel

Figs. 14, 38–39.

Monomorium shuckardi Forel 1895:251. holotype, Madagascar: Moramanga (MHNG) [examined].
Monomorium (*Notomyrmex*) *shuckardi* Emery 1922: 170.

Material examined— Holotype: Madagascar, Moramanga, coll. [F.] Sikora (MHNG). (NB. The symbol used in the original publication is that for the worker, i.e., "☿", but in fact, the specimen is a queen. That a dealated queen is here described rather than a worker is evident from Forel's use of the term 'scutellum', and also his mention of propodeal 'teeth', which are not found in the worker. The total specimen length given by Forel for the type specimen agrees exactly with my own measurement, and given that there is no indication in the published description that any other specimens were examined by Forel, a holotype status fixed by monotypy (Code 73.1.2) is here assumed.).

Other material examined: **Prov. Toliara:** 18 km NNW Betroka, 29.xi.–24.xi.1994 M. A. Ivie & D. A. Pollock (30☿, 1♀) (MCZ); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i.–1.ii 2001 B.L. Fisher (6☿); Mahafaly ['Mahafely'] Plateau, 6.2 km 74 ENE Itampolo 21–25.ii.2002 B.L. Fisher (2☿); Reserve Berenty, 9.ii.1993 P.S. Ward (3☿); (MCZ) (4☿) (UCDC); Tsimanampetsotsa, Bemanateza, 23.0 km 131SE Beheloka, 22–26.iii.2002 B.L. Fisher (4☿).

Worker description.— Head: Head square; vertex planar or weakly concave; frons shining and densely microreticulate; pilosity of frons consisting of a few short, thick, erect setae interspersed with short, appressed setulae; Eye large, eye width 1.5x greater than greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set anteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club four-segmented. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin broadly convex; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits equidistant from antennal fossae and mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 5,3. Mandibular teeth five; mandibles triangular and striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present).

MESOSOMA: Promesonotum shining and microreticulate throughout; (viewed in profile) anterior promesonotum smoothly rounded anteriad, thereafter more-or-less flattened, promesonotum raised well above propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of short, erect or semi-erect bristles; appressed promesonotal setulae few, mainly on dorsum of promesonotum. Metanotal groove vestigial. Propodeum shining and densely microreticulate, with distinct striolae on metapleuron; propodeal dorsum slightly elevated anteriad and sloping away posteriad, or, sloping posteriad and depressed between raised propodeal angles; when seen obliquely, propodeum smoothly rounded or with indistinct angle, but dorsal and declivitous faces separated when seen in profile; standing propodeal setae decumbent and short, rarely also with very short erect and suberect setae; appressed propodeal setulae abundant, particularly on dorsum of propodeum; propodeal spiracle nearer declivitous face of propodeum than metanotal groove. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

POSTPETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node. node (viewed in profile) cuneate, vertex rounded, or, conical, vertex rounded; appearance of node shining and faintly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole about 1:1; postpetiole shining and microreticulate; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting mainly of short, appressed setulae, together with a few erect and semi-erect setae.

GENERAL CHARACTERS: Color orange, head slightly to moderately darker, gaster chocolate. Worker caste monomorphic.

OTHER WORKER MEASUREMENTS: HML 1.51–2.32 HL 0.53–0.78 HW 0.45–0.72 CeI 84–95 SL 0.46–0.71 SI 94–105 PW 0.27–0.49 (n=16).

QUEEN DESCRIPTION (holotype).— HEAD: Head oval; vertex convex; frons shining and finely longitudinally striolate and microreticulate; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; sides of mesoscutum and mesopleuron faintly longitudinally striolate, dorsum of mesoscutum mainly smooth; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2. Axillae narrowly separated (i.e., less than width of one axilla). Standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mesoscutal and mesopleural setulae few, mainly on dorsum of pronotum and mesoscutum. Propodeum shining and densely striolate over whole surface; distinctly angulate, propodeal angle sharp; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of a few decumbent setae only; appressed propodeal setulae well-spaced and sparse; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges.

WING: Wing not seen (queen dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node, in profile cuneate, vertex tapered; appearance of node shining and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1. Anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and microreticulate; postpetiolar sternite not depressed, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color ferruginous. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

HOLOTYPE MEASUREMENTS: HML 3.16 HL 0.81 HW 0.88 CeI 109 SL 0.79 SI 89 PW 0.82.

OTHER QUEEN MEASUREMENTS: HML 3.34 HL 0.88 HW 0.86 CeI 98 SL 0.74 SI 86 PW 0.76 (n=1).

REMARKS.— Worker specimens are readily separable from other members of the *M. shuckardi* group by the densely microreticulate sculpture of their frons. The worker of this species also bears a superficial resemblance to that of *Monomorium subopacum*, but can be distinguished from it by a number of features, apart from those mentioned in the key, including the presence of erect setae on the promesonotal dorsum, the elongate petiolar peduncle, the anterior placement of the petiolar spiracle and the placement of the propodeal spiracle (more dorsal and nearer propodeal declivity compared with more lateral and nearer metanotal groove). Populations are fairly widespread in dry, spiny forest regions in Toliara Province. Like many other Malagasy *Monomorium*, this species will make opportunistic use of dead twigs above ground for its nests. Other specimens have been collected in pitfall traps, under stones and as ground foragers. Oddly enough, the holotype queen is recorded as having being collected by Sikora in Moramanga, Toamasina Province, hundreds of kilometers from its known current range. This record may be in error, as the vegetation community of Moramanga is very different from that to which this species seems adapted.

THE *DESTRUCTOR*-GROUP

Monomorium destructor (Jerdon)

Figs. 15, 40–41.

Atta destructor Jerdon 1851:105. Syntype ☿'s, INDIA [no types known to exist].
Monomorium destructor (Jerdon): Dalla Torre 1893:66.
Monomorium (*Parholcomyrmex*) *destructor* (Jerdon): Wheeler, W.M. 1922: 874.
Myrmica basalis Smith 1858:125. Syntype ☿ (lectotype here designated), SRI LANKA (BMNH) [examined].
Monomorium basale (Smith): Mayr 1865:92. Syn. under *M. destructor* (Jerdon): Forel 1894a: 86.
Myrmica ominosa Gerstäcker 1859:263. Syntype ☿'s MOZAMBIQUE [no types known to exist].
Monomorium ominosum (Gerstäcker): Roger 1863b:31. Syn. under *M. destructor* (Jerdon): Dalla Torre 1893: 66.
Myrmica atomaria Gerstäcker, 1859:263. Syntype ☿'s MOZAMBIQUE [no types known to exist]. Syn. under *M. ominosum* (Gerstäcker): Roger 1863b:31.
Myrmica gracillima Smith 1861a:34. Holotype ☿ ISRAEL [type presumed lost]
Monomorium gracillimum (Smith): Mayr 1862:753.

Monomorium (*Parholcomyrmex*) *gracillimum* (Smith): Emery 1915b:190.
Monomorium destructor r. *gracillimum* Forel 1913a:437. Syn. under *M. destructor* (Jerdon): Bolton 1987:324.
Myrmica vexator Smith 1861b:47. Syntype ☿'s (lectotype here designated) INDONESIA: Ternate Isl. (OXUM) [examined]. Syn. under *M. destructor* (Jerdon): Donisthorpe 1932:468.

MATERIAL EXAMINED.— ***M. basale***: LECTOTYPE: ☿, Sri Lanka ("Ceylon"), no collector named (BMNH). The ant on the LHS (seen from the rear) on a rectangle containing three syntype workers is designated the lectotype for *Monomorium basale*, so that the name can be fixed. This and other early collections of *Monomorium destructor* were given separate species-level names, presumably on the basis of quite minute differences in color or morphology, and, possibly, their provenance. The antennal club in *M. basale* is described by Smith as 'dark fuscous', and the termination of the flagellum in *M. vexator* as 'slightly fuscous', otherwise their respective descriptions by Smith read much the same. PARALECTOTYPES: Two workers on the same card rectangle as the lectotype (BMNH). No attempt has been made to separate the carded specimens, which are damaged and fragile. ***M. vexator***: LECTOTYPE: ☿, J. Smith. (OXUM) (The collection locality, which does not appear on the labels but in the publication, is Ternate Island, [Indonesia.]) The middle ant of the three carded syntype specimens is here designated the lectotype to fix the name of this taxon. *Monomorium destructor*, because of its ubiquity and its allometric variation, has attracted half-a-dozen synonyms. PARALECTOTYPES: Two workers on the same card rectangle as the lectotype (OXUM). Carded specimens as above.

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** 10km NE Antsiranana, 14.ii.1991, G.A. Alpert (14☿) (MCZ); 15km NE Antsiranana, 14.ii.1991, G. A. Alpert (2☿); (MCZ); 3 km S Namakia, 19.iii.1993 P. Rabeson (2☿, 2♂) (MCZ). **Prov. Mahajanga:** Mahavavy River, 6.2 km 145 SE Mitsinjo 1–5.xii.2002 Fisher *et al.* (10☿); Mahavavy River, 10.6 km 148 SSE Mitsinjo 4.xii.2002 Fisher *et al.* (9☿); P. N. Namoroka, 17.8 km 329 WNW Vilanandro, 12.ii.2002 Fisher *et al.* (1☿).

WORKER DESCRIPTION.— HEAD: Head square; vertex planar or weakly concave; frons longitudinally finely striolate anteriad (striolae curving inwards around antennal insertions), smooth and shining posteriad, except for a few transverse rugulae on upper vertex; pilosity of frons consisting mainly of appressed and decumbent setulae with a few erect setae on vertex. Eye large, eye width 1.5× greater than greatest width of antennal scape to moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin broadly convex to straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Weak psammophore present. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, lower mesopleuron strongly punctate; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum uniformly finely striolate, some punctation on metapleuron; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae variable in number and arrangement, when present usually one prominent pair at propodeal angles or at midlength, with other shorter setae very sparse or absent; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral or laterodorsal and situated within anterior sector of petiolar node or just at front of node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 1:1 and 3:4; height–length ratio of postpetiole between 4:3 and 3:4; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

Mesosoma: Color yellow-orange to brownish-orange, gaster chocolate with or without yellowish area on anterior sector of first gastral tergite. Worker caste monophasically allometric, i.e., with variable size, but not morphology among workers from same nest.

Lectotype measurements (*M. basale*): HML 1.70 HL 0.66 HW 0.58 CeI 88 SL 0.48 SI 83 PW 0.34.

Lectotype measurements (*M. vexator*): HML 1.78 HL 0.68 HW 0.62 CeI 91 SL 0.50 SI 81 PW 0.36.

Other worker measurements (non-types): HML 1.31–1.92 HL 0.49–0.76 HW 0.38–0.68 CeI 78–89 SL 0.39–0.52 SI 76–103 PW 0.25–0.40 (n=20).

Queen description.— Head: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits and striolae around antennal sockets, frontal carinae and below the eyes, and fine rugulae near posterior margin of vertex; frons consisting mainly of decumbent setae, with two longitudinal, parallel rows of erect setae straddling the midline. Eye elongate, elliptical and oblique; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 7:3 and 2:1. Axillae a strip of thin cuticle separating mesoscutum and scutellum, each individual axilla indistinct. Standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae abundant, particularly on mesoscutum. Propodeum shining and smooth, with a few weak striolae on metapleuron; always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of one pair anteriad, with or without another pair posteriad; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

Wing: Wing not seen (queen dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; (viewed in profile) node conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1. Anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining, with vestigial sculpture; postpetiolar sternite with anterior and posterior margins convergent, forming a narrow wedge.

Gaster: Pilosity of first gastral tergite consisting mainly of appressed setae with a few erect and semi-erect setae.

General characters: Color of foreparts tawny-yellow, gaster brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 3.22–3.46 HL 0.83–0.84 HW 0.76–0.80 CeI 92–95 SL 0.60–0.62 SI 78 PW 0.68–0.89 (n=2).

Remarks.— *Monomorium destructor* is very similar to the closely related *Monomorium robustior*, but is lighter in color and the eyes tend to be less elongate. Workers within nests also show more allometric variation than is found in *M. robustior*. Samples of this tramp species have been taken in tropical dry forest in north and north-western Madagascar in the Antsiranana and Mahajanga Provinces, where they have been collected under stones, from a dead branch and by sweeping. Populations also may be expected to occur generally in severely damaged habitats in these regions.

Monomorium robustior Forel

Figs. 15, 90.

Monomorium gracillimum r. *robustior* Forel 1892a:352. Syntype ☿'s (lectotype here designated), Somalia (MHNG) [examined]. [NB. Misspelled as *Monomorium gracillimum* r. *robustius* Forel 1894b:228.]
Monomorium (*Parholcomyrmex*) *gracillimum* r. *robustior* Wheeler W.M. 1922:875.
Monomorium robustior Forel: Bolton 1987:328.

Material examined.— Lectotype: ☿, Somalia. C. Keller (MHNG). A lectotype has been chosen to fix the name for the species, which was originally described as simply a race of *Monomorium gracillimum*, itself now a synonym for *Monomorium destructor*. The specimen, originally on a pin holding three pointed specimens, has been transferred to a single pin, along with the original labels and a lectotype label. Paralectotypes: Two pins with 12 and 13 workers, respectively, data the same as for the lectotype (MHNG). Photocopies of the original labels have been affixed to the pin with the two specimens.

Other material examined: **Prov. Antananarivo:** Antananarivo, 14.xi.1990 P. S. Ward (2☿) (MCZ); Lac Alarobia ['Alarobie'], 10 km NE Antananarivo 10.iii.1991, G.D. Alpert (2☿) (MCZ). **Prov. Fianarantsoa:** Forêt Analalava, 29.6 km 280 W Ranohira 1–5.ii.2003 Fisher *et al.* (1☿). **Prov. Mahajanga:** Station Forestière Ampijoroa, 22.xi.1990 (2☿) (MCZ). **Prov. Toliara:** 18 km NNW Betroka, 29.xi.–4.xii.1994 M.A. Ivie & D.A. Pollock (8☿) (MCZ); Ehazoara Canyon, 26 km E Betioky 27.iv.1997 B.L. Fisher (8☿); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i.–1.ii 2001 Fisher *et al.* (37☿); Forêt Mite, 20.7 km 29 WNW Tongobory 27.ii–3.iii. 2002 Fisher *et al.* (79☿); Mahafaly Plateau, 6.2 km 74 ENE Itampolo 21–25.ii.2002 Fisher *et al.* (10☿); Rés. Berenty, Forêt Bealoka, 14.6 km 329 NNW Amboasary 3–8.ii.2002 Fisher *et al.* (3☿); Res. Beza Mahafaly ['Mahafely'], 18.xi.1984 R. L. Brooks (17☿) (MCZ); Tsimanampetsotsa, Bemanateza, 23.0 km 131SE Beheloka, 22–26.iii.2002 Fisher *et al.* (14☿).

Worker description.— Head: Head square; vertex planar or weakly concave; frons longitudinally finely striolate anteriad (striolae curving inwards around antennal insertions), smooth and shining posteriad; pilosity of frons consisting of abundant, incurved, appressed setulae only. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule to set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elongate with or without eye narrowed to point anteriad. Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore present. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, striate; masticatory margin of mandibles strongly oblique;

basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, lower mesopleuron strongly punctate; (viewed in profile) promesonotum broadly convex; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum with sculpture reduced dorsally, metapleuron punctate; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised; propodeum angulate, propodeal angle blunt; length ratio of propodeal dorsum to its declivity about 1:1; standing propodeal setae consisting of two or more pairs of longer, suberect setae near propodeal angles, with shorter setae anteriad; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth with vestigial microreticulation anteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole about 1:1; sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, short, thick, erect setae interspersed with minute, appressed setulae.

GENERAL CHARACTERS: Color brown, gaster chocolate. Worker caste monomorphic.

LECTOTYPE MEASUREMENTS: HML 1.83 HL 0.68 HW 0.68 CeI 100 SL 0.56 SI 82 PW 0.38.

OTHER WORKER MEASUREMENTS (non-types): HML 1.65–1.97 HL 0.62–0.76 HW 0.64–0.75 CeI 95–103 SL 0.51–0.61 SI 75–85 PW 0.36–0.46 (n=20).

REMARKS.— *Monomorium robustior* has a wider known distribution than *M. destructor* in Madagascar, mainly in more southerly regions (Antananarivo, Fianarantsoa, Mahajanga and Toliara Provinces). Specimens have been collected by a variety of means in dry tropical and spiny forest. In Africa, this species has been recorded from Kenya and Somalia (Bolton 1987).

THE *SALOMONIS*-GROUP

Monomorium pharaonis (Linnaeus)

Figs. 16, 91–92.

Formica pharaonis L. 1758:580. Syntype ☿'s, EGYPT [whereabouts of type material unknown]

Monomorium pharaonis (L.): Mayr 1862:752.

Formica antiguensis Fabricius 1793:357. Syntype ☿, WEST INDIES: Antigua [whereabouts of type material unknown]. Syn. under *M. pharaonis* (L.): Roger 1862b: 294.

Myrmica domestica Shuckard 1838:627. Syntype ☿'s, , GREAT BRITAIN: London [no types known to exist]. Syn. under *M. pharaonis* (L.): Roger 1862b:294.

Atta minuta Jerdon 1851:105. Syntype ☿'s, INDIA [no types known to exist]. Syn. under *M. pharaonis* (L.): Emery 1892:165.

Myrmica vastator Smith 1857:71. Syntype ☿'s (lectotype here designated), SINGAPORE (OXUM) [examined].

Monomorium vastator (Smith): Mayr 1886:359. Syn. under *M. destructor* (Jerdon): Dalla Torre 1893: 66. Syn. under *M. pharaonis* (L.): Donisthorpe 1932:449.

Myrmica fragilis Smith 1858:124. Syntype ☿'s (lectotype here designated), SINGAPORE (BMNH) [examined]. Syn. under *M. pharaonis* (L.): Mayr 1886:359.

Myrmica contigua Smith 1858:125. Holotype , SRI LANKA (BMNH) [examined]. Syn. under *M. pharaonis* (L.): Mayr 1886:359.

MATERIAL EXAMINED.— ***M. vastator***: LECTOTYPE: ☿, Singapore, J. Smith (OXUM). Four syntype workers are carded, two above and two below, on the one pin. The worker on the lower left-hand side (viewed from the rear of the pin) is here designated a lectotype to fix the name '*vastator*' in the interests of stability. *Monomorium pharaonis* belongs to a small complex of closely related ants, and was also confused with *Monomorium destructor* by early researchers (Bolton 1987). PARALECTOTYPES: Three workers, same data as the lectotype (OXUM). (The lectotype and three paralectotypes are covered with a uniform, thin layer of glue and cannot be separated.). ***M. fragile***: LECTOTYPE: ☿, Singapore, J. Smith (BMNH). Four syntype workers carded on one rectangle. The worker on the lower right (viewed from the rear) is here designated a lectotype to fix the name '*fragile*' in the interests of nomenclatural stability. PARALECTOTYPES: Three workers, same data as the lectotype (BMNH). (The lectotype and three paralectotypes are glued and could not be separated without serious risk of damage.). ***M. contiguum***: HOLOTYPE: ♀, Ceylon. J. Smith (BMNH).

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (1☿); Sambava, 7.xi.1992 Solomon (1♀) (MCZ). **Prov. Fianarantsoa:** Ranomafana NP, Talatakely 14.iv.1998 M.E. Irwin & E.I. Schlinger (4☿). **Prov. Mahajanga:** P.N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (1☿).

WORKER DESCRIPTION.— HEAD: Head oval; vertex weakly convex; frons shining and finely striolate and microreticulate; pilosity of frons consisting of a few short, thick, erect setae interspersed with short, appressed setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin broadly convex; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles with sub-parallel inner and outer margins, striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and microreticulate throughout; (viewed in profile) promesonotum broadly convex; promesonotal setae two to six; standing promesonotal setae consisting of very short, incurved decumbent setae only; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and microreticulate; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as blunt-angled flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining and distinctly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole shining and microreticulate; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color yellowish, gastral tergites with brown infuscation in basal sector. Worker caste monomorphic.

Lectotype measurements (*M. vastator*): The physical condition and alignment of the worker does not permit ready measurements.

Lectotype measurements (*M. fragile*): HML 1.52 HL 0.56 HW 0.42 CeI 75 SL 0.48 SI 114 PW 0.23.

Other worker measurements: HML 1.39–1.48 HL 0.53–0.56 HW 0.42–0.45 CeI 78–81 SL 0.45–0.49 SI 105–111 PW 0.22–0.28 (n=8).

Queen description.— Head: Head square; vertex always planar; frons matt and uniformly reticulate-punctate; frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; eyes (in full-face view) set at about midpoint of head capsule; eyes (viewed in profile) set around midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron uniformly reticulate-punctate, punctations tending to form fine striolae on dorsum of mesoscutum; length-width ratio of mesoscutum and scutellum combined between 7:3 and 2:1. Axillae narrowly separated (i.e., less than width of one axilla). Standing pronotal/mesoscutal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed pronotal, mescoscutal and mesopleural setulae well-spaced over entire surface. Propodeum uniformly reticulate-punctate; always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of two or more pairs of prominent setae anteriad, with a few decumbent setae around declivitous face; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as bluntly angled flanges.

Wing: Wing not seen (queen dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node matt and reticulate-punctate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1. Anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole about 4:3; postpetiole matt and reticulate-punctate; postpetiolar sternite forming a narrow wedge-shaped projection through strong convergence of its anterior and posterior ends.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color orange-yellow, gaster brown, with large, yellow sector at apex of first tergite. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Holotype measurements (*M. contiguum*): HML 2.43 HL 0.68 HW 0.63 CeI 93 SL 0.62 SI 98 PW 0.73.

Other queen measurements: HML 2.37 HL 0.66 HW 0.62 CeI 94 SL 0.58 SI 94 PW 0.52 (n=1).

Remarks.— One of several tramp species in the *M. destructor* and *M. salomonis* groups found in Madagascar, *M. pharaonis* has recently been recorded from tropical dry forest and secondary rainforest. However, because of its anthropophilic nature, this ant probably has a wider distribution in Madagascar than these few (non-urban) records suggest.

Monomorium subopacum (Smith)

Figs. 16, 42–43.

Myrmica subopaca Smith 1858:127.

Monomorium subopacum (Smith): Mayr 1862:753. Syntype ☿'s, 's, (lectotype here designated) MADEIRA (BMNH) [examined].

Monomorium (*Xeromyrmex*) *subopacum* (Smith): Wheeler W.M. 1922:871.

[*Xeromyrmex* a junior synonym of *Monomorium*: Ettershank 1966:82].

Myrmica glyciphila Smith 1858: 125. Syntype ☿'s, (lectotype here designated) Sri Lanka (BMNH) [examined]. Syn. under *M. subopacum* (Smith): Bolton 1987:360.

Monomorium mediterraneum Mayr 1861:72 (diagnosis in key). Syntype ☿ (see comments below - lectotype here designated) Spain: Cadiz (NMW) [examined]. Syn. under *M. subopacum* (Smith): Mayr 1862:763.

Monomorium (*Xeromyrmex*) *salomonis* subsp. *subopacum* var. *senegalensis* Santschi 1913: 306 Syntype ☿'s, SENEGAL: Saint-Louis (NHMB) [not seen] [Unavailable name]. Syn. under *M. subopacum* (Smith): Bolton 1987: 360 (along with proposed replacement names *claveaui* Emery 1922:178 and *santschiellum* Wheeler, W.M. 1922: 872). See also comment under *liberta*, below.

Paraphacota surcoufi Santschi 1919a:90, fig. 1. Syntype ♂'s (lectotype here designated), ALGERIA: Biskra (NHMB) [examined].

Monomorium subopacum v. *surcoufi* Santschi 1927:243. Syn. under *M. subopacum* (Smith): Bolton 1987:360.

Paraphacota cabrerai Santschi 1919b:405, fig. 1. Holotype ♂, CANARY ISL: Tenerife, Laguna (NHMB) [examined].

Monomorium subopacum var. *cabrerai* Santschi 1927:241. Syn. under *M. subopacum* (Smith): Bolton 1987:360.

Paraphacota cabrerae [sic] st. *obscuripes* Santschi 1921a:169. Syntype ♂'s (lectotype here designated), CANARY ISL., Tenerife, Bajamar (NHMB) [examined]. Syn. under *M. subopacum* Santschi 1927:241.

Monomorium (*Xeromyrmex*) *subopacum* var. *intermedium* Santschi 1927:242 Syntype ♂'s (see comments below—lectotype here designated), CANARY ISLANDS, Haria, Lanzarote (MCZ) [examined]. [First available use of *Monomorium* (*Xeromyrmex*) *salomonis* subsp. *subopacum* var. *intermedium* Wheeler 1927:108; unavailable name]. Syn. under *M. subopacum* (Smith): Hohmann et al. 1993:155.

Monomorium (*Xeromyrmex*) *subopacum* var. *apuleii* Santschi 1927:243. Syntypes ☿, ♀, ♂, TUNISIA: Hammamat (?NHMB) [not seen].

Monomorium (*Xeromyrmex*) *subopacum* var. *liberta* Santschi 1927:243. [First available use of *Monomorium* (*Xeromyrmex*) *salomonis* subsp. *subopacum* st. *liberta* Santschi 1921c:170; unavailable name]. Syn. under *M. subopacum* Bolton 1987: 360. (NB. *M. liberta* syntypes are same specimens as *senegalensis* above).

Monomorium (*Xeromyrmex*) *subopacum* var. *ebraicum* Menozzii 1933:62. Syntypes ☿, ♂, ISRAEL: Tel Aviv (?Instituto di Entomologia, Universitá di Bologna "Guido Grandi" [IEGG]) [not seen]. Nominal subspecies of *M. subopacum* Bolton 1995:261.

Monomorium (*Xeromyrmex*) *subopacum* var. *adoneum* Santschi 1936:41, fig. 22 [spelled "*adonis*" under fig.]. Syntype ☿'s, LEBANON: Djbeil ou Djbla (?NHMB) [not seen]. Nominal subspecies of *M.subopacum* Bolton 1995:258.

Monomorium (*Xeromyrmex*) *subopacum* subsp. *italica* Baroni Urbani 1964:154, figs. 2–3. Holotype ☿, ITALY: Gambarie (not seen) (Museo Civico di Storia Naturale di Verona [MSNV]) [not seen]. Syn. under *M. subopacum* (Smith): Baroni Urbani 1968:450.

MATERIAL EXAMINED.— ***M. subopacum***: LECTOTYPE: ☿, Madeira, T.V. Wollaston (BMNH). In view of the subtle differences that separate genuine good species in the *M. salomonis* group, I am designating a lectotype to fix the name '*subopacum*', the type worker material of which is a richer reddish brown than the type material for *M. glyciphilum*. The syntype material is on a single card rectangle. The lectotype worker is the third worker from the RHS, seen from the rear. PARALECTOTYPES: Three workers and three queens, carded on the same rectangle as the holotype (BMNH). No attempt has been made to separate the ants. ***M. glyciphilum***: LECTOTYPE: ☿, Sri Lanka ("Ceylon"), no collector named (BMNH). The syntype material seen (three carded workers) is darker than that of *M. subopacum*. The lectotype is the RHS specimen (seen from the rear). The rationale for choosing a lectotype is given above under *M. subopacum*. PARALECTOTYPES: Two workers on the same card as the lectotype (BMNH). No attempt has been made to separate the workers. ***M. mediterraneum***: Lectotype: I have seen five specimens labeled 'type' (NMW). These comprise four workers and one queen. The collection locality reads 'Rotes Meer' (Red Sea), collector (the queen, at least) Frauenfeld (handwritten label). I have also inspected four additional workers, not labeled 'type'. One worker, from Cadiz (Spain), coll. (?)Rogenhofer (partly illegible handwriting), (NMW) also possesses a label indicating it was seen by Mayr in 1862, and I think it reasonable to assume it was one of the specimens, possibly a *M. mediterraneum* syntype, examined by that researcher when he synonymized *mediterraneum* with *subopacum* in the same year. A third label reads '*Monom. subopacum* det. Mayr'. Two of the remaining workers carry only the determination label, while the third has an additional slip: 'Frfld Rothes [*sic*] Meer 1855'. The label data presents a conundrum: all nine workers are not only morphologically identical but have been mounted in identical fashion; i.e., one ant glued lengthwise at the end of a point so its head overhangs the apex of the triangle. Even the points, pins and glue are identical. The queen is mounted in similar fashion. The handwriting on the four specimens not designated 'type', however, is that of a different person to the one who labeled the five specimens designated 'type'.

There are not sufficient data in either Mayr's original description or on the labels to answer the question of the type status of these specimens definitively. Mislabeling, possibly by an assistant, also appears to have occurred. The original description, however, does reveal that Mayr examined one queen and multiple workers from southern Spain. In the interests of the stability of the name *mediterraneum*, and based on the likelihood that it is in fact part of the original type series, I am designating the Cadiz specimen a lectotype. ***Monomorium surcoufi***: Lectotype: ♂. Algeria, Biskra, August 1919. at light ('à la lumiere') (NHMB – Reg. No. 213). The lectotype (top rectangle) fixes the name for this taxon in which the clypeus and male reproductive structures are said by Santschi to differ from those of *M. cabrerai* which has similarly colored legs. Paralectotype: ♂, on same pin as the lectotype and with same data (NHMB – Reg. No. 213). ***Monomorium cabrerai***: Holotype: ♂, Canary Isl., Tenerife, Laguna, 25.VII.1903. [Published collector A. Cabrera y Diaz] (NHMB – Reg. No. 213). This male was designated a 'holotype' by Bolton (1987), and since the length is given as single measurement, it seems clear no other specimens were examined. Bolton's 1987 revision is therefore deemed to have given this specimen support for a holotype status (Code 73.1.2). Nb.: the labels on both this specimen and the type specimens of its putative subspecies '*obscuripes*' read '*cabrerae*', but in the published description of the former the rendition is *M.* '*cabrerai*' and that of the supposed subspecies is '*M. cabrerae*'. All of this is part of the general confusion and inconsistent taxonomy that has bedeviled this species. Since the worker after whom the ant was named was presumably a male (the Christian name of A. Cabrera y Diaz was 'Anatael'), '*cabrerai*' should be the correct spelling, and is followed here. However, researchers have generally adopted '*cabrerae*', as per the labels (e.g., Wheeler 1922; Bolton 1995 – but see Bolton 1987). ***Monomorium cabrerai obscuripes***: Lectotype: ♂, Canary Isl., Tenerife, Bajamar, 10.X.1909, A. Cabrera (NHMB – Reg. No. 213). The designation of a lectotype fixes the name for this taxon in which the male has uniformly dark legs. Paralectotype: ♂, same locality as lectotype, 20.IX.1909 (NHMB – Reg. No. 213). ***Monomorium subopacum intermedium***: Lectotype: ☿, Canary Islands, Haria, Lanzarote, 1000 ft, 8 Jan. 1925 ['8. 1. 25'] W.M. Wheeler. MCZ cotype [syntype] 3–5 20875 (MCZ). The lectotype fixes the taxon name for populations of *M. subopacum* found on the Canary Islands. The lectotype worker has been repinned with the original labels. The subgenus *Xeromyrmex* represents an outmoded way of looking at *Monomorium* species related to the *M. salomonis* group, and the possibility of its use being revived is highly remote, to say the least (see Bolton 1987), even if *intermedium* is brought out of synonymy in the future. Paralectotypes: Ten workers (several damaged) with the same collection data as the lectotype (MCZ). Two workers, originally on the same pin as the lectotype, have been repinned with photocopies of the original labels. NB. The original syntype series of 43 workers included a worker of another species, whose appearance agrees with the description of *Monomorium medinae* Forel (type material not seen). This is a member of the *M. salomonis* group, endemic to the Canary Islands (Bolton 1987), in which the body sculpture of the worker is largely effaced. I have repinned this worker with photocopies of the original labels and an additional label stating that it does not belong to the taxon *Monomorium subopacum* var. *intermedium* Santschi.

Other material examined: **Prov. Toliara:** Sakaraha, 15.ii.1993 P.S. Ward 11937.5773/4 (3☿) (MCZ) 11937 (3☿) (UCDC) 11932 (3☿) (UCDC).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and finely microreticulate; pilosity of frons consisting of abundant, incurved, appressed setulae only. Eye large, eye width 1.5× greater than greatest width of antennal scape; eyes (in full-face view) set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; club three-segmented. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth four: mandibles with sub-parallel inner and outer margins, striate; masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and microreticulate throughout; in profile broadly convex anteriad, convexity reduced posteriad; promesonotal setae absent; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove weakly to strongly impressed, with distinct transverse costulae. Propodeum shining and microreticulate; propodeal dorsum flat throughout most of its length; angulate, propodeal angle blunt; length ratio of propodeal dorsum to its declivity between 2:1 and 4:3; standing propodeal setae absent; appressed propodeal setulae well-spaced and sparse; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; vestibule of propodeal spiracle absent or not visible; propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral or laterodorsal and situated within anterior sector of petiolar node. Node (viewed in profile) cuneate, vertex rounded, or, conical, vertex rounded: appearance of node shining and distinctly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4. Anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present, but weakly developed to vestigial. Height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole between 1:1 and 3:4; postpetiole shining and microreticulate; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting mainly of short, appressed setulae, together with one to several pairs of erect and semi-erect setae.

GENERAL CHARACTERS: Color mesosoma, nodes and legs orange-yellow, head and antennae brown, gaster dark brown. Worker caste monomorphic.

LECTOTYPE MEASUREMENTS (*M. subopacum*): HML 1.81 HL 0.67 HW 0.54 CeI 81 SL 0.56 SI 104 PW 0.35.

LECTOTYPE MEASUREMENTS (*M. glyciphilum*): HML 2.03 HL 0.72 HW 0.60 CeI 83 SL 0.62 SI 104 PW 0.39.

LECTOTYPE MEASUREMENTS (*M. mediterraneum*): HML 1.92 HL 0.70 HW 0.55 CeI 79 SL 0.58 SI 105 PW 0.36.

LECTOTYPE MEASUREMENTS (*M. subopacum intermedium*): HML 1.93 HL 0.71 HW 0.58 CeI 82 SL 0.59 SI 102 PW 0.36.

OTHER WORKER MEASUREMENTS (non-types): HML 1.77–2.12 HL 0.64–0.73 HW 0.52–0.61 CeI 80–85 SL 0.54–0.64 SI 104–108 PW 0.34–0.42 (n=9).

QUEEN DESCRIPTION (based on three paralectotype queens of '*Monomorium subopacum*' and one queen of '*Monomorium mediterraneum*').— HEAD: Head square; vertex always planar; frons shining and finely longitudinally striolate and microreticulate; pilosity of frons consisting of well-spaced appressed setulae only. Eye roundly elliptical; in full-face view, eyes set above midpoint to of head capsule; in profile, eyes set posteriad of midline of head capsule.

MESOSOMA: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron uniformly finely punctate-microreticulate; length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2. Axillae narrowly separated (i.e., less than width of one axilla). Standing pronotal/mesoscutal setae sparse or absent; appressed pronotal, mescoscutal and mesopleural setulae well- spaced over entire pronotum/mesonotum. Propodeum entirely microreticulate-striolate; propodeum smoothly rounded or with indistinct angle; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised; standing propodeal setae absent; appressed propodeal setulae well-spaced and sparse; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges or bluntly angled flanges.

WING: Wing not seen (queens dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node, in profile, cuneate, vertex rounded; appearance of node matt and microreticulate, rugose posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1. Anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole between 3:2 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and microreticulate; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of long, appressed setae and one or two semi-erect setae, or, standing setae completely absent.

GENERAL CHARACTERS: Color tawny, variegated brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 3.13–3.43; HL 0.91–0.92; HW 0.79–0.86; CeI 89–93; SL 0.70–0.79; SI 89–92; PW 0.68–0.74 (n=4).

MALE.— I have only seen damaged male specimens (lectotypes for the taxa *Monomorium surconfi*, *M. cabrerai* and *M. cabrerai obscuripes*). As there has been controversy over the assignment to *M. subopacum* of at least the males of *Monomorium cabrerai obscuripes* and the other males are tattered and lack body parts, no formal description of the abovementioned males is included here.

MALE TYPE MEASUREMENTS: LECTOTYPE MEASUREMENTS (*Monomorium surconfi*): HL 0.88 HW 0.98 CeI 111. (NB. Lectotype lacks antennae, postpetiole and gaster). HOLOTYPE MEASUREMENTS (*Monomorium cabrerai*): HML (Holotype lacks postpetiole and gaster) HL 0.89 HW 0.96 CeI 108 SL 0.29 SI 30 PW 1.00. LECTOTYPE MEASUREMENTS (*Monomorium cabrerai obscuripes*): HML 3.17 HL 0.79 HW 0.86 CeI 109 SL 0.30 SI 35 PW 0.80.

REMARKS.— Bolton (1987) recognized this species from Madagascar on the basis of a short series from Maevatanana ("Maevantanara"); however, there are no Malagasy specimens in the CAS, despite the huge amount of *Monomorium* material collected by Brian Fisher and his teams since the early 1990s. The Malagasy component in the description and measurements provided above includes details from six specimens held at UCDC and three specimens from the same series held at MCZ. *Monomorium subopacum* is very similar to *Monomorium willowmorense* (below), but those worker specimens I have seen of the former can be distinguished from *M. willowmorense* by their finely granulate-reticulate frons, uniformly sculptured promesonotal humeri and a longer antennal scape (SI > 100 in *M. subopacum* and < 100 in *M. willowmorense*). Nonetheless, the differences that separate the two are small, and in view of the variability to be found in *M. subopacum* (note the voluminous entries above!) I would not be surprised if molecular–based investigations resulted in *M. willowmorense* being added to the already overburdened synonymic list for *M. subopacum*.

Several of the synonyms are those of taxa originally described from males. The spurious genus '*Paraphacota*' incorporated three such taxa, and what appears to me to be two distinct species. The male of *Monomorium surcoufi* and that of *M. cabrerai* are obviously identical, and easily recognized by their long, bicolored legs and completely hyaline wings. On the other hand, the male of *Monomorium cabrerai obscuripes* has relatively shorter, uniformly dark legs and brown wing veins. I have not seen nest material of *Monomorium subopacum* that has included males, but Bolton (1987) was in no doubt that the descriptions of *M. surcoufi* and *M. cabrerai* were based on ordinary males of *M. subopacum*. He followed Santschi in also placing *M. cabrerai obscuripes* under *M. subopacum* but allowed that it could be the male of *M. medinae* Emery, a Canary Islands endemic, a view first broached by Wheeler (1927). Hohmann *et al.* (1993) included the two *cabrerai* taxa under *Monomorium medinae*, but omitted *Monomorium surcoufi*. This seems to me an odd judgement, and, indeed, Bolton (1995) did not mention these authors at all in relation to '*Paraphacota*', but continued to consign all three taxa to synonymy under *Monomorium subopacum*. (NB. Dr. Xavier Espadaler [pers. commun.] also places *M. cabrerai* under *M. subopacum*, leaving *M. cabrerai obscuripes* as an unresolved puzzle, but has indicated that none of the males originally placed under '*Paraphacota*' belongs to *Monomorium medinae*.)

Monomorium subopacum, like *Monomorium pharaonis*, is something of a tramp, and its occurrence in Madagascar and other regions well away from its natural area of occurrence is certainly due to human activities (Bolton 1987).

Monomorium willowmorense Bolton

(Fig. 16)

Monomorium willowmorense Bolton 1987:364, fig. 54. South Africa: Willowmore (BMNH, MHNG) [material pertaining to '*willowmorensis*' and '*belli*' examined].

Monomorium salomonis r. *herrero* var. *willowmorensis* Forel 1914:245 [unavailable name]. Syntype ☿'s, South Africa: Willowmore (BMNH, MHNG).

Monomorium salomonis r. *herrero* var. *belli* Forel 1914:245 [unavailable name]. Syntype ☿'s (lectotype for the taxon '*willowmorense*' here designated from the '*belli*' material [MHNG], the remaining '*belli*' and '*willowmorense*' material becoming paralectotypes) South Africa: Willowmore (BMNH, MHNG, MCZ).

Material examined.— Lectotype: ☿ (unavailable name "*belli*"), South Africa, Cape Province, Willowmore, 8. 1. 1914 [G.] Arnold (MHNG). A lectotype has been chosen to fix the name, '*Monomorium willowmorense*' for the taxon, which is morphologically similar to *M. subopacum*. The specimen, originally on a pin holding three pointed specimens, has been transferred to a single pin and the original labels and a lectotype label have been appended to that pin. Paralectotypes: (i) Two workers ("*belli*"), data the same as for the lectotype (MHNG). Repinned with photocopies of the original labels. (ii) Two workers ("*belli*") on separate pin, data as for lectotype (MHNG). (iii) Five workers (unavailable name "*willowmorensis*"), on two separate pins (i.e., 12 (both damaged) + 13) coll. 1.1.1914, otherwise data same as for lectotype (MHNG). (NB. The measurements of twelve workers from the then syntype series are provided in Bolton 1987).

Other material examined: **Prov. Toamasina:** S.F. Tampolo, 10 km NNE Fenoarivo Atn. 10.iv.1997 B.L. Fisher (1 ☿).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and finely striolate and microreticulate; pilosity of frons consisting of abundant, incurved, appressed setulae only. Eye large, eye width 1.5× greater than greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin broadly convex; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2.2. Mandibular teeth four; mandibles with sub-parallel inner and outer margins, striate; masticatory margin of mandibles strongly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and microreticulate, microreticulation reduced on humeri; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae absent; standing promesonotal setae consisting of three pairs of longer, incurved, erect or semi-erect setae with occasionally a shorter seta between first anterior pair; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and densely microreticulate, distinct striolae present on metapleuron; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised; propodeum angulate, propodeal angle blunt; standing propodeal setae absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and faintly microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole about 1:1; postpetiole shining and microreticulate; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

Gaster: Pilosity of first gastral tergite consisting mainly of short, appressed setulae, together with a few erect and semi-erect setae.

General characters: Color reddish- brown, gaster chocolate. Worker caste monomorphic.

Lectotype measurements: HML 1.54, HL 0.60, 0.49, CeI 82, SL 0.46, SI 94, PW 0.32.

Other worker measurements: HML 1.50 HL 0.60 HW 0.47 CeI 78 SL 0.45 SI 96 PW 0.31 (n=1).

Remarks.— One worker of this otherwise South African species is known from Toamasina Province.

THE *LATINODE*-GROUP

Monomorium latinode Mayr

Figs. 16, 44–45.

Monomorium latinode Mayr 1872:152. Syntype ☿ (lectotype here designated), Malaysia: Sarawak, Borneo (BMNH) [material examined].

Monomorium latinode var. *bruneum* Emery 1893:243. Syntype ☿'s (lectotype here designated), Sri Lanka: Kandy (MCSN) [material examined]. Syn. under *Monomorium latinode* Mayr: Bolton 1987:429.

Monomorium voeltzkowi Forel 1907b:78. Syntype ☿'s (lectotype here designated), Tanzania: Chake-Chake, Pemba (MHNG) [material examined]. Syn. under *Monomorium latinode* Mayr: Bolton 1987:429.

Material examined.— ***M. latinode***: Lectotype: ☿, Borneo Sarawak (Malaysia), G. Doria (BMNH). A single carded worker labeled syntype is here designated lectotype to fix the name for populations of *M. latinode*, which has a more convex outline to the vertex than *M. latinode bruneum* or *M. voeltzkowi*. Other syntype specimens may still exist (seen by Bolton in 1987), and THESE SHOULD BE TREATED AS PARALECTOTYPES. ***M. latinode bruneum***: Lectotype: ☿, Ceylon, Kandy, [E.] Simon (MCSN). Label data reads '*brunneum*', but published name is *bruneum*. A lectotype has been chosen to fix the name for the taxon, which is darker than typical *M. latinode*. The specimen, originally on a pin holding four carded specimens, has been transferred to a single pin and the original labels and a lectotype label have been appended to that pin.

PARALECTOTYPES: Three workers, data the same as for the lectotype, photocopies of original labels attached (MCSN). ***M. voeltzkowi***: LECTOTYPE: ☿, Chake-Chake, Pemba, "East Africa" [Tanzania] (MHNG). A lectotype has also been chosen to fix the name *voeltzkowi*, whose proportions were thought by Forel to differ from those of *M. latinode*. The lectotype has been repinned as above. PARALECTOTYPES: (i) One worker, data the same as for the lectotype, photocopies of original labels attached (MHNG). (ii) Three workers, data as for the lectotype (MHNG).

OTHER MATERIAL EXAMINED: COMOROS ISLANDS: Mayotte, Majimbini, 21.vii.1998 R. Jocqué (2☿). MADAGASCAR: **Prov. Antsiranana:** Nosy Be, 2 km ENE Andoany (= Hellville), 1.v.1989 P.S. Ward (6☿) (MCZ). **Prov. Fianarantsoa:** 3km S Namakia, 5.iv.1993 P. Rabeson (96☿) (MCZ).

WORKER DESCRIPTION.— HEAD: Head oval; vertex weakly convex; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin straight, or, emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 3,3. Mandibular teeth five; mandibles triangular and smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth smaller than t4 (five teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, entire lower mesopleuron distinctly striolate; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed promesonotal setulae very sparse or absent. Metanotal groove vestigial. Propodeum uniformly finely striolate; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae numerous, wholly or mainly erect or suberect, without conspicuous paired setae evident; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as blunt-angled flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite depressed near its junction with gaster, and sloping anteriad at angle of 45–60 to form large conspicuous lip at its anterior end.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color head, mesosoma and appendages brownish-yellow, gaster brown. Worker caste monophasically allometric, i.e., with variable size, but not morphology among workers from same nest.

LECTOTYPE MEASUREMENTS (*M. latinode*): HML 2.02 HL 0.72 HW 0.59 CeI 81 SL 0.60 SI 103 PW 0.42.

LECTOTYPE MEASUREMENTS (*M. latinode bruneum*): HML 2.03 HL 0.73 HW 0.59 CeI 81 SL 0.56 SI 95 PW 0.46.

LECTOTYPE MEASUREMENTS (*M. voeltzkowi*): HML 1.66 HL 0.60 HW 0.46 CeI 77 SL 0.46 SI 100 PW 0.36.

OTHER WORKER MEASUREMENTS (non-types): HML 1.83–2.29 HL 0.65–0.83 HW 0.52–0.73 CeI 79–88 SL 0.50–0.62 SI 85–98 PW 0.38–0.49 (n=20).

REMARKS.— This species, currently the sole member of the *M. latinode* group, has an appearance somewhat suggestive of taxa from the Australasian *M. rubriceps* species group. However, none of the latter has a PF of 3,3. and this count may represent an ancestral plesiomorphy, if indeed the ant is a member of that group. Certainly, the species has no close connections with the remaining African and Malagasy *Monomorium* fauna. The type specimens for the nominal taxa currently associated with *M. latinode* (i.e., '*M. latinode*', '*M. latinode bruneum*' and '*M. voeltzkowi*') show variation in color and size, and the lectotype of *M. latinode* also exhibits some differences in the appearance of the head capsule. Apart from an excellent series from the Province Fianarantsoa and a small number from Province Antsiranana (MCZ) from tropical and lowland rainforest, I have seen no other Malagasy material pertaining to this tramp species. Malagasy specimens have been collected on low vegetation and on the ground.

THE *MONOMORIUM*-GROUP

Monomorium bifidoclypeatum Heterick, sp. nov.

Figs. 17, 46–47.

ETYMOLOGY.— Latin '*bifidus*' ('split into two parts') +'*clypeatus*' ('provided with a shield')

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Antsiranana**, RS Manongarivo 17.3 km 218 SW Antanambao 1580 m 14°01′3″S, 48°25′1″E, 160 m. 27.x.1998, B.L. Fisher 1972# /beating low vegetation montane rainforest/ 1972(05)–1 (CAS). PARATYPES: **Prov. Antsiranana:** (all specimens with same collection data as holotype): 1☿ (ANIC); 1☿ (BMNH); 1♀ (CAS); 1☿ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** R. S. Manongarivo, 17.3 km 218 SW Antanambao 27.x.1998 B.L. Fisher (1☿); R.S. Manongarivo, 20.4 km 219 SW Antanambao 3.xi.1998 B.L. Fisher (6☿). **Prov. Fianarantsoa:** 36 km S Ambalavao, Res Andringitra 29.x.1993 B.L. Fisher (1☿).

WORKER DESCRIPTION.— HEAD: Head square, or rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye large, eye width 1.5× greater than greatest width of antennal scape, to moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin straight between strongly divergent clypeal carinae, clypeus descending almost vertically to arc of mandibles and sometimes transversely carinate below level of antennal insertions; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae, or, approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex; promesonotal setae seven to twelve; standing promesonotal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as rounded flanges, or, present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered, or, conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:4 and 2:3; anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole about 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color yellow to light brown, gaster often darker than head and mesosoma. Worker caste monomorphic.

HOLOTYPE: HML 1.22 HL 0.47 HW 0.42 CeI 88 SL 0.34 SI 82 PW 0.25.

OTHER WORKER MEASUREMENTS: HML 1.07–1.47 HL 0.43–0.55 HW 0.37–0.52 CeI 86–94 SL 0.32–0.44 SI 85–92 PW 0.21–0.29 (n=9).

QUEEN DESCRIPTION.— HEAD: Head square; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length-width ratio of mesoscutum and scutellum combined about 3:2; axillae separated by width of at least one axilla; standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeum always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of one pair of prominent setae anteriad, with a few smaller, erect to decumbent setae on and around dorsal and declivitous faces; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining, with vestigial sculpture; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

WING: Wing not seen (queen dealated).

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color yellow or yellowish-brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 2.18 HL 0.61 HW 0.58 CeI 95 SL 0.48 SI 83 PW 0.44 (n=1).

REMARKS.— This species appears to belong to a complex of very similar ants in which the head of the worker is relatively broad and the body is shiny and somewhat streamlined. *Monomorium bifidoclypeatum* has strongly defined clypeal carinae, and the anteromedian sector of the clypeus is depressed so that it forms an almost vertical, triangular plate. Seen in profile, the clypeal angle is approximately 90º. In other members of this complex, however, the clypeal carinae are poorly developed or obsolete, although the general conformation of the clypeus is the same. *Monomorium bifidoclypeatum* also has a distinct basal mandibular tooth, this anatomical feature being much reduced or even absent in the other species, except for *M. chnodes*. The sole known queen is rather similar in appearance to queens of *M. termitobium* (typical form). All but one of the specimens I have seen come from Antsiranana Province, where they were collected by beating low vegetation or by sifting litter from montane rainforest. One worker was collected as a forager in montane rainforest in Andringitra Reserve, Fianarantsoa Province.

Monomorium chnodes Heterick, sp. nov.

Figs. 17, 48–49.

ETYMOLOGY.— Greek '*chnodes*' ('downy')

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Toamasina**, Mont Akirindro 7.6 km 341 NNW Ambinanitelo 15°17′3″S, 49°32′9″E 600 m, 17–21.iii.2003, Fisher *et* al. BLF8250/ sifted litter rainforest/ CASENT 0025716 8250(50) (CAS). PARATYPES: **Prov. Toliara** (all specimens with same collection data as holotype; one worker with collection code 8250, other specimens with collection code 8322): 13☿ (ANIC); 13☿ (BMNH); 1♀ (CAS); 13☿ + 1♀ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Toliara:** 6.9 km NE Ambanizana 2.xii.1993 B.L. Fisher (9☿, 2♀). **Prov. Toamasina:** Mont. Akirindro, 7.6 km 341 NNW Ambinanitelo 17–21.iii.2003 Fisher *et* al. (25☿, 6♀); Mont Anjanaharibe, 18.0 km 21 NNE Ambinanitelo 8–12.iii.2003 Fisher *et al*. (32☿, 6♀); Mont Anjanaharibe, 19.5 km 27 NNE Ambinanitelo 12–16.iii.2003 Fisher *et al*. (16☿, 6♀).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth five, or, four; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t4 (five teeth present), or, approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) anterior promesonotum smoothly rounded anteriad, thereafter more-or-less flattened, promesonotum raised well above propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, metapleuron with a few weak striolae; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 3:2; height–length ratio of postpetiole between 1:1 and 3:4; postpetiole shining and smooth; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina, or, without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color yellow. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.11 HL 0.42 HW 0.34 Cel 81 SL 0.23 SI 68 PW 0.23.

OTHER WORKER MEASUREMENTS: HML 1.05–1.19 HL 0.41–0.44 HW 0.34–0.37 CeI 79–88 SL 0.23–0.27 SI 67–76 PW 0.23–0.27 (n=20).

QUEEN DESCRIPTION.— HEAD: Head oval; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule;

MESOSOMA: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeum smoothly rounded or with indistinct angle; propodeal dorsum convex; standing propodeal setae consisting of two or more pairs of prominent setae anteriad, often with another pair of prominent setae posteriad, along with shorter, decumbent setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Propodeal lobes present as vestigial flanges only, or absent.

WING: Wing not seen (queens dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite not depressed, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color bright yellow. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 1.46–1.58 HL 0.45–0.51 HW 0.40–0.44 CeI 83–89 SL 0.28–0.33 SI 67–76 PW 0.29–0.35 (n=12).

REMARKS.— Despite a resemblance to workers from some populations of *M. termitobium*, *M. chnodes* has several distinct features that place it apart from other small Malagasy *Monomorium* in the *M. monomorium* group. The shape of the mandible tends towards linear-triangular, not unlike that seen in the *M. hanneli* species group, and the dentition consists of four, occasionally five teeth or denticles of approximately equal size. The spiracle of the propodeum is large, as is that of the petiole, and the body and head are covered in abundant, downy setae. Nonetheless, molecular indicators place *M. chnodes* right within populations of what are here regarded as *termitobium*, and also close to *M. platynodis*. *Monomorium chnodes* has a restricted distribution in the Ambinanitelo region in Toamasina Province where workers and queens have been taken in sifted litter, from rotten logs and in pitfall traps in montane rainforest. This species also appears to have an association with the plant family Melistomataceae, which could be worthy of research.

Monomorium denticulus Heterick, sp. nov.

Figs. 17, 50.

ETYMOLOGY.— Latin dim. of '*dens*' (masc. 'tooth').

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Mahajanga**, P. N. Ankarafantsika, Ankoririka, 10.6 km 13° NE Tsaramandroso 16°16′S, 47°3′E 210 m, 9–14.iv.2001 E. Rabeson *et al*. BLF 3664/ sifted litter tropical dry forest/ CASENT 0470359 3664(11) (CAS). PARATYPES: **Prov. Mahajanga** (all specimens with same collection data as holotype, one worker with collection code 3664, three workers with collection code 3662): 1☿ (BMNH); 13☿ (MCZ). OTHER MATERIAL EXAMINED: **Prov. Fianarantsoa:** P. N. Isalo, Ambovo Springs, 29.3 km 4 N Ranohira 9–14.ii.2003 Fisher *et al*. (1☿). **Prov. Mahajanga:** P. N. Baie de Baly, 12.4 km 337 NNW Soalala 26–30.xi.2002 Fisher *et* al. (1☿). **Prov. Toliara:** Forêt Beroboka, 5.9 km 131 SE Ankidranoka 12–16.iii.2002 Fisher *et al*. (1☿); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al*. (1☿).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye large, eye width 1.5× greater than greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule to set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate or straight, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits);

masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of one prominent pair anteriad and a less prominent pair posteriad, smaller, decumbent setae few or absent: appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum to equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges to present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered, or, conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole between 4:3 and 3:4; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color yellow to brown. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.14 HL 0.43 HW 0.35 CeI 80 SL 0.35 SI 101 PW 0.22.

OTHER WORKER MEASUREMENTS: HML 1.01–1.29 HL 0.40–0.48 HW 0.32–0.38 CeI 76–84 SL 0.31–0.38 SI 88–106 PW 0.21–0.25 (n=7).

REMARKS.— *Monomorium denticulus* is the only member of the otherwise exclusively Afrotropical *M. schultzei* species complex represented in Madagascar. This ant is smaller than *M. schultzei* and is separable from other members of the complex by virtue of its shallow metanotal groove with short cross-ribs, its pinhole-like propodeal spiracle and its distinct clypeal denticles. The elongate mesosoma bears a superficial resemblance to that of *M. exiguum*. This yellow or brown species is distributed in a surprising variety of habitats in three provinces in Madagascar, but colonies appear to be very rare, being represented by a handful of workers. These have been collected in pitfall traps or from sifted litter in *Uapaca* woodland, tropical dry forest, spiny forest and rainforest.

Monomorium exiguum Forel

Figs. 18, 51–52.

Monomorium exiguum Forel 1894a:85. Syntype ☿'s (lectotype here designated), ETHIOPIA: (locality on label now illegible, but given as 'Südabessinien' in Bolton 1987) (MHNG) [examined].

Monomorium (*Martia*) *exiguum* Forel 1913b:351.

Monomorium (*Lampromyrmex*) *exiguum* Forel: Wheeler W.M. 1922:876.

Monomorium (*Mitara*) *exiguum* var. *bulawayensis* [*sic*] Forel 1913c:217. Syntype ☿'s (lectotype here designated), ZIMBABWE: Bulawayo (MHNG) [examined].

Monomorium (*Lampromyrmex*) *exiguum bulawayensis* Forel: Wheeler, W.M. 1922:876. Syn. under *Monomorium exiguum* Forel: Bolton 1987:388.

Monomorium (*Mitara*) *faurei* Santschi 1915: 260, fig. 10 (☿). Syntype ☿'s (lectotype here designated), GABON (MHNG) [examined].

Monomorium (*Lampromyrmex*) *faurei* Santschi: Wheeler, W.M. 1922:876. Syn. under *Monomorium exiguum* Forel: Bolton 1987:388.

Monomorium (*Mitara*) *exiguum* r. *flavescens* Forel 1916:418. Syntype ☿'s, DEMOCRATIC REPUBLIC OF CONGO: St. Gabriel, Stanleyville (MHNG) [examined].

Monomorium (*Lampromyrmex*) *exiguum flavescens* Forel: Wheeler, W.M. 1922:876. Syn. under *Monomorium exiguum* Forel: Bolton 1987:388.

Monomorium minutissimum Santschi 1937:225, figs. 27, 28. Syntype ☿ (lectotype here designated), ANGOLA, Ebanga Rd. (NHMB) [examined]. syn. n. Syn. under *Monomorium mictile* Forel: Bolton 1987:388.

MATERIAL EXAMINED.— ***M. exiguum***: LECTOTYPE: ☿, Ethiopia, Ilg (MHNG). In view of the variability, particularly in color, that led researchers to erect new 'varieties' for this species, a lectotype has been chosen for *M. exiguum* that fixes the species name for populations with dark, longer-headed specimens that have the characteristics mentioned in the original description. This particular specimen has been glued in the normal way, dorsal surface uppermost. PARALECTOTYPE: ☿, same data as lectotype, here designated for a specimen that has been pointed on the same pin as the lectotype and glued on its back. This specimen has been repinned with photocopies of the original labels (MHNG). ***M. exiguum bulawayense*** (corrected ending): LECTOTYPE: ☿. Zimbabwe, Arnold (MHNG). The lectotype fixes this name for populations with dark, shorter headed specimens as mentioned in the description for *M. exiguum bulawayense*. The carded lectotype specimen is the one glued on the RHS of the card (the head of the LHS specimen is damaged). PARALECTOTYPE: ☿, same data as lectotype (MHNG). (No effort has been made to separate the fragile, carded lectotype and paralectotype.). ***M. faurei***: LECTOTYPE: ☿, Gabon, F. Faure, 1914 (NHMB Reg. No. 203). The lectotype fixes the name for populations of *M. exiguum* with a slightly bicolored appearance (i.e., yellowish-brown head and gastral apex and yellowish mesosoma, nodes, appendages and gastral base. The sides of the gaster in this form are often infuscated). The carded lectotype is the single specimen on the top card rectangle on a pin holding three rectangles. PARALECTOTYPES: (i) Four carded workers, same data as the lectotype (bottom two rectangles) (NHMB). (ii) One worker and two detached worker heads mounted between two cover clips, these held by a pinned slip of cardboard, 'Guinea fr.' [Guinea], Mamou, Silvestri (NHMB). ***M. exiguum flavescens***: LECTOTYPE: ☿, Democratic Republic of Congo: St. Gabriel, Stanleyville, Kohl (MHNG). The lectotype fixes the name for populations with relatively pale workers with a strongly constricted mesosoma as mentioned in the description of *M. exiguum flavescens*. PARALECTOTYPE: (i) One worker, same data as lectotype (MHNG). This paralectotype has been removed from the same pin as the lectotype and repinned with photocopies of the original labels. (ii) Two workers, same data as the lectotype (MNHG). ***M. minutissimum***: LECTOTYPE: ☿, Angola, Ebanga Rd., A. Monard, 16.xi.1932 (NHMB – Reg. No. 207). The lectotype fixes the name for populations of this taxon, which appears to be essentially the same as *M. faurei*, though said by Santschi to have a more deeply incised metanotal groove. The lectotype is headless. (NB. This specimen is described as a 'holotype' by Bolton (1987), but Santschi clearly examined more than one specimen as is indicated by the range of body length given in his description. However, no other syntype specimens are known to still exist.).

OTHER MATERIAL EXAMINED: **Prov. Antananarivo:** Rés Ambohitantely, 24.1 km 59 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (1☿); Ambohitantely, 20.9 km 72 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (4☿). **Prov. Antsiranana:** Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (1☿); Résérve Ambre, 3.5 km 235 SW Sakaramy 26–31.i.2001 Fisher *et al.* (1☿); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (1☿) 6–20.iii.2001 R. Harin Hala (6♂). **Prov. Fianarantsoa:** 28 km SSW Ambositra, Ankazomivady 9.i.1998 (4☿, 1♀), 11.i.1998 (3♀), 14.i.1998 (1☿) B.L. Fisher. **Prov. Mahajanga:** P. N. Ankarafantsika, Ampijoroa, 40 km 306 NW Andranofasika 26–31.iii.2001 Fisher *et al.* (2☿); P. N. Ankarafantsika, Ampijoroa, 5.4 km 331 NW Andranofasika 26–31.iii.2001 Rabeson *et al.* (26☿, 1♀); P. N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (9☿); P. N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (5♂); P. N. Tsingy de Bemaraha, 10.6 km 123 ESE Antsalova 16–20.xi.2001 Fisher *et al.* (4☿). **Prov. Toamasina:** SF Tampolo, 10 km NNE Fenoarivo Atn. 10.iv.1997 B.L. Fisher (1☿). **Prov. Toliara:** Beza-Mahafaly, 27 km E Betioky 23.iv.1997 B.L. Fisher (49☿, 7♀); Cap Sainte Marie, 12.3 km 262 W Marovato 11–15.ii.2002 Fisher *et al.* (6♀); Cap Sainte

Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (3☿); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (59☿, 7♀); Forêt de Petriky, 12.5 km W 272 Tolagnaro 22.xi.1998 B.L. Fisher (3☿); Mahafaly Plateau, 6.2 km 74 ENE Itampolo 25.ii.2002 Fisher *at al.* (7♂); P. N. Kirindy Mite, 16.3 km 127 SE Belo sur Mer 6–10.xii.2001 Fisher *et al.* (3♀); P. N. Andohahela, 1.7 km 61 ENE Tsimelahy 16–20.i.2002 Fisher *et al.* (40☿, 7♀); 2.7 km WNW Ste Luce, 9–11.xii.1998 B.L. Fisher (1☿); Vohibasia Forest, 59 km NE Sakaraha 13 i. 1996 B.L. Fisher (6☿).

Worker description.— Head: Head rectangular, vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 11: antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened; promesonotum on same plane as propodeum, promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae, or, metanotal groove vestigial. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node: node (viewed in profile) conical, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole about 1:1: postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color variable, pale yellow to brown. Worker caste monomorphic.

Lectotype worker measurements (*M. exiguum*): HML 0.93 HL 0.36 HW 0.28 CeI 78 SL 0.22 SI 79 PW 0.18.

Lectotype worker measurements (*M. exiguum bulawayense*): HML 1.00 HL 0.39 HW 0.32 CeI 81 SL 0.26 SI 83 PW 0.20.

Lectotype worker measurements (*M. faurei*): HML 0.88 HL 0.35 HW 0.29 CeI 83 SL 0.22 SI 76 PW 0.18.

Lectotype worker measurements (*M. exiguum flavescens*): HML 0.89 HL 0.36 HW 0.30 CeI 82 SL 0.22 SI 75 PW 0.18.

Lectotype worker measurements (*M. minutissimum*): No measurements taken as lectotype is headless.

Other worker measurements (non-types): HML 0.79–0.97; HL 0.33–0.39 HW 0.26–0.29 CeI 73–81 SL 0.22–0.26 SI 81–93 PW 0.16–0.20 (n=20).

Queen description.— Head: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, margin sometimes shallowly concave; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae contiguous, or nearly so; standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeum smoothly rounded or with indistinct angle; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 2:1 and 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and weakly striolate posteriad; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial (NB. May be confused with rear margin of postpetiolar sternite, which does project as a spur, length of sternite being much reduced).

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color yellowish-brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes seen.

Queen measurements: HML 1.55–2.00 HL 0.45–0.55 HW 0.39–0.54 CeI 83–98 SL 0.34–0.42 SI 75–90 PW 0.28–0.55 (n=19).

Male description.— Head: (In full-face view) head width-mesosoma width ratio between 1:1 and 3:4; frons finely micropunctate. Compound eyes protuberant and elliptical tending to elongate; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 1:1 and 3:4. Maximum number of mandibular teeth and denticles three.

MESOSOMA: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; parapsidal furrows vestigial or absent; notauli absent; axillae widely separated (i.e., by width of at least one axilla), axilla fused with scutellum to narrowly separated (i.e., less than width of one axilla).

WING: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) conical, vertex tapered, appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 1:1 and 3:4; height–length ratio of postpetiole between 2:1 and 4:3; postpetiole shining, with vestigial sculpture.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color light to medium brown, appendages pure brown to off-white.

MALE MEASUREMENTS: HML 1.37–1.96 HL 0.41–0.51 HW 0.42–0.48 CeI 102–116 SL 0.10–0.19 SI 24–34 PW 0.44–0.66 (n=11).

REMARKS.— *Monomorium exiguum* ranges throughout Madagascar, but is most abundant in Toliara Province, where is it is often among the most commonly collected *Monomorium* in sifted litter samples. Interestingly, the paler '*flavescens*' and '*bulawayense*' forms also occur in Madagascar, along with *M. exiguum* sensu stricto. In the taxon *faurei* the head is darker than the mesosoma, and the gaster is pale with darker infuscation on its basal half, as well as on the sides of the first gastral tergite. This variant, too, is quite common on Madagascar. *Monomorium exiguum* workers from Madagascar tend to have a slightly more tapered petiolar node than their counterparts on the African mainland.

Based on comparative type material I have seen, *Monomorium exiguum* is part of a complex that includes, at least, the exclusively African *Monomorium mictile* Forel, *Monomorium rosae* Santschi and *Monomorium taedium* Bolton. An 11-segmented antenna, an elongate and flattened head capsule, weakly developed clypeal carinae, a dorsally rather flattened rather than evenly convex propodeum and the low, strongly conical form of the petiole are common to all of these taxa. *Monomorium rosae* is placed in a different complex by Bolton (1987) on the basis of the appearance of the worker postpetiole, but in actual fact, the shape of the postpetiole in larger, darker specimens of *Monomorium exiguum* approaches that of *M. rosae*, if it is not identical. The degree of obliqueness seen in the posterior face of the postpetiole appears to be proportional to the size of the worker, rather than a distinct feature at the species level, let alone the species-complex level, in all three species mentioned above.

The distinction between the above four species, if indeed it truly exists, is minimal. In appearance the workers form a continuum, with the bright yellow *M. mictile* being the smallest species and the very dark *M. rosae* the largest. To give just one instance, the relevant measurements supplied by Bolton (1987) for *M. exiguum* (40 specimens) and *M. rosae* (12 specimens) certainly give this reviser pause for thought! With *M. exiguum* in regular font, *M. rosae* in bold, these read: TL (i.e., total length); 1.5–1.7/**1.6–2.0** HL 0.36–0.42/**0.42–0.50**, HW 0.28–0.32/**0.33–0.40** CI (=CeI) 74–80/**76–82** SL 0.22–0.27/**0.28–0.35** SI 74–84/**85–94** PW 0.17–0.21/**0.21–0.25** AL (i.e., mesosoma length) 0.36–0.44/**0.42–0.56**. Apart from the larger size, the only real difference that I can discern between a *M. rosae* Santschi syntype from the Democratic Republic of Congo and large, brown specimens of *M. exiguum* I have seen from Madagascar is the presence of faint sculpture on the lower mesopleuron in *M. rosae*. Fresh *M. rosae* material, which I have not seen, is said by

Bolton to be 'blackish-brown to black'.

Monomorium mictile is separated from *M. exiguum* by Bolton (1987) on the basis of the presence or absence of erect infrahumeral setae. These are supposedly absent in *M. mictile* and long and erect in *M. exiguum.* In fact the setae are present, but short and appressed in *M. mictile.* This particular character does not seem to be useful as a means of separating similar species in the *M. monomorium* species group, at least in Madagascar. Where hundreds or even thousands of workers are available for examination, I have noticed variability in the number, length and alignment of the promesonotal setae, including differences in the length and alignment of the infrahumeral setae. This phenomenon may not be recognizable where only a few, isolated specimens are available for study. For now, I would allow for the separation of *M. mictile* from *M. exiguum*, as all Malagasy specimens I have seen of the latter have erect or semi-erect infrahumeral setae (albeit of different lengths). The same applies to *Monomorium taedium*, for which I have seen three paratype workers. Apart from their somewhat larger size (HW = 0.34 mm) and lack of erect infrahumeral setae they look exactly like brown *M. exiguum.* Interestingly, the postpetiole of the paratype specimens of *M. taedium* is quite globose, as in smaller *M. exiguum.*

As well as six syntypes of *M. mictile*, I have also examined 15 syntype workers of the form *Monomorium exiguum mictile* '*sudanicum*' and the lectotype worker of *Monomorium minutissimus*, both of which taxa Bolton regarded as conspecific with *M. mictile.* The '*sudanicum*' workers are certainly the same species as the *M. mictile* syntypes and share the same uniform, bright yellow coloration, but I differ with Bolton on the identity of the headless lectotype worker of *M. minutissimum.* Leaving aside the absence of the head (which was said by Santschi to be yellowish-brown like the gaster), the morphology of this specimen is identical with that of the *M. faurei* type material, and has the typical coloration of this form of *M. exiguum.* I therefore consider this taxon to be a junior synonym of *M. exiguum* rather than *M. mictile.* (NB. Because of the way the ant is glued on its side to its rectangle, the infrahumeral setae are not readily apparent, and may have been destroyed during the mounting process.)

Monomorium flavimembra Heterick, sp. nov.

Figs. 19, 53–54.

Etymology.— Latin '*flavus*' (yellow) + pl. of '*membrum*' (neut. 'member')

Material examined.— Holotype: ☿, **Prov. Antsiranana**, Réserve Spéciale Ambre, 3.5 km 235 SW Sakaramy 325m, 12 29'S, 49 15'E, 26–31.i.2001, Fisher et al. BLF# 2676 /ex rotten log tropical dry forest/ CASENT 0401520 (CAS). Paratypes: **Prov. Antsiranana** (three workers and three queens collection code 2676, seven workers collection code 2679, otherwise data as for the holotype): 12☿ (ANIC); 1☿ + 12♀ + 12☿ (BMNH); 1☿ (CAS) 1♀ + 12☿ + 2☿ (MCZ). Other material examined: **Prov. Antsiranana:** Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (2☿); Résérve Spéciale Ambre, 3.5 km 235 SW Sakaramy 26–31.i.2001 Fisher *et al.* (15☿, 1♀); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (67☿); Rés. Spéc. Ankarana, 13.6 km 192 SSW Anivorano Nord 16–21.ii.2001 Fisher *et al.* (2☿)

Worker description.— Head: Head oval; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin broadly convex; paraclypeal setae short and thickened, not reaching basal margin of closed mandibles; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as blunt-angled flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered to conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina, or without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color light to dark reddish brown, gaster darker brown, appendages yellowish. Worker caste monomorphic.

Holotype measurements: HML 1.33 HL 0.48 HW 0.43 CeI 89 SL 0.40 SI 94 PW 0.25.

Other worker measurements: HML 1.12–1.31 HL 0.41–0.50 HW 0.37–0.43 CeI 83–89 SL 0.34–0.42 SI 89–101 PW 0.23–0.27 (n=20).

Queen description.— Head: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae contiguous, or nearly so; standing pronotal/mesoscutal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron; propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeum smoothly rounded or with indistinct angle; propodeal dorsum flat throughout most of its length; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 2:1 and 4:3; postpetiole shining and weakly striolate posteriad; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Wing: Wing not seen (queens dealated).

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color foreparts reddish brown, gaster brown, appendages yellow. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 1.55–1.57 HL 0.51 HW 0.47–0.49 CeI 92–96 SL 0.43–0.45 SI 88–95 PW 0.34–0.35 (n=4).

Remarks.— *Monomorium flavimembra* is similar in morphology to *M. bifidoclypeatum*, but the anteromedian clypeal sector is only weakly carinate, and the petiolar node is higher and less sharply conical. The basal tooth is usually present as a small obtuse angle but may be absent altogether. The rich, russet color of the upper part of the frons and mesosoma contrasts with the bright yellow clypeus, mandibles and appendages in most specimens, but the legs may have a brownish tinge. The four known queens, all dealated, are very small and ergatoid-like. Queens of more regular proportions (for a *Monomorium* whose workers reach about 2 mm TL) may exist among the unclassifiable CAS *Monomorium* queen material that cannot be associated with workers.

This taxon has a localized distribution in Antsiranana Province, in far northern Madagascar. Workers have been collected in tropical dry forest as ground foragers, in sifted litter and from colonies in wood (rotted logs and twigs) and root mats.

Monomorium floricola (Jerdon)

(Figs. 19, 55, 56)

Atta floricola Jerdon 1851:107. Syntype ☿s, India [no types known to exist].

Monomorium floricola – (Jerdon): Mayr 1879:671.

Monomorium cinnabari Roger 1863a:199. Syntype ☿s, Cuba [whereabouts of type material unknown]. Syn. under *M. floricola* (Jerdon): Wheeler, W.M. 1913:388.

Monomorium poecilum Roger 1863a:199. Syntype ☿s, Cuba [whereabouts of type material unknown]. Syn. under *M. floricola* (Jerdon): Emery 1894b:51.

Monomorium specularis Mayr 1866:09. Syntype ☿s (see comments below – lectotype here designated) Samoa: Upolu (NMW) [examined]. Syn. under *M. floricola* (Jerdon): Mayr 1879:71.

Monomorium impressum Smith 1876:47. Syntype ♀s, ♂ (lectotype here designated) Rodriguez Isl.: (BMNH) [examined]. Syn. under *M. floricola* (Jerdon): Bolton 1987:88.

Monomorium floricola var. *philippinensis* Forel 1910a: 23. Syntype ☿s, ♀s, Philippines, Manila, Luzon Isl. (?NHMB) [not seen].

Monomorium floricola philippinense Forel: Bolton 1995

Monomorium floricola var. *furina* Forel 1911:21. Syntype ☿s, Sri Lanka: Peradeniya (?NHMB) [not seen].

Monomorium floricola furinum Forel: Bolton 1995

Monomorium floreanum Stitz 1932:68, fig. 1 (☿). Syntype ☿s, ♀s, Galapagos Isl., Floreana [whereabouts of type material unknown]. Syn. under *M. floricola* (Jerdon): Linsley and Usinger 1966:75.

Monomorium (*Monomorium*) *angusticlava* Donisthorpe 1947:89. Syntype ☿s (lectotype here designated from CAS material), Irian Jaya: Maffin Bay (CAS, BMNH) [examined]. Syn. under *M. floricola* (Jerdon): Bolton 1987:88.

Material examined.— ***M. specularis***: Lectotype: Two workers from Upolu, Samoa, G. Mayr Collection (NMW), may include one or both of the two syntype workers from the same locality mentioned in Mayr's publication of *M. specularis*. Label data indicates that these specimens were held by the Godeffroy Museum (stated as the repository for the type material by Mayr). Although the label data does not include the word 'type' or its equivalent, I am designating a lectotype to fix the name for the species, as these specimens agree closely with the description of M. *specularis*, and the issue of type status in view of the paucity of available data is otherwise unlikely to be resolved definitively. Paralectotype: ☿, data as above (NMW). ***M. impressum***: Lectotype: ♀, Rodriguez Island, Gulliver (publ. name of collector) (BMNH). The lectotype is designated to fix the name *impressum* for populations of putative *M. floricola* in which the queen has a dark head and gaster and a very pale mesosoma. The lectotype is on a card rectangle including a second queen and a male, and is the queen on the LHS (seen from the rear). Paralectotypes: One queen and one male on the same card rectangle as the lectotype (BMNH). No attempt has been made to separate these ants. ***M. angusticlava***: Lectotype: The California Academy of Science (CAS) possesses a specimen which bears a red bordered circle reading 'type'. The material received from the BMNH is mounted on pins bearing yellow bordered circles reading 'paratype'. However, Donisthorpe specifically states that he used sixteen workers in describing *M. angusticlava*, so there can be no assumption of a holotype. Since all specimens have the same collecting data, they should be treated as syntypes. I have selected the CAS specimen as a typical worker for this taxon, as it is described. A second worker appears to have been included on the same point, but has been largely destroyed, leaving a postpetiole and gaster. The lectotype details are: ☿, Maffin Bay, Dutch New Guinea (Irian Jaya), E.S. Ross, viii 1944 (CAS). The choice of a lectotype fixes the name for this taxon, which was thought by Donisthorpe to be generally more gracile than *M. floricola*. Paralectotypes: Two pins (12 and 11) of pointed workers and one pin of two separately carded workers. Collection data exactly as for lectotype (BMNH).

Other material examined: **Prov. Antsiranana:** 18 km N Antalaha, Ampahana, Gary D. Alpert (1♀) (MCZ); Nosy Be, Ambatoloaka, 12.viii.1992 Alpert *et al.* (1♀) (MCZ). **Prov. Mahajanga:** P.N. Namoroka, 17.8 km 329 NW Vilanandro 8–12.xi.2002 B.L. Fisher (1☿); P.N. Namoroka, 16.9 km 317 NW Vilanandro 12–16.xi.2002 B.L. Fisher (1☿); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 (2☿). **Prov. Toamasina:** 9.7 km NNE Mahalevona 12.xii.1993 B.L. Fisher (1☿); Mahavavy River, 6.2 km 145 SE Mitsinjo 1–5.xii.2002 B.L. Fisher (12☿). **Prov. Toliara:** Beza-Mahafaly ['Mahafely'], 27 km E Betioky 23.iv.1997 B.L. Fisher (1☿); Forêt Mite, 20.7 km 29 WNW Tongobory 27.ii–3.iii.2002 B.L. Fisher (4☿).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elongate; Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 1,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, striolae, if present, usually vestigial and confined to lower anterior mesopleuron, in some populations entire lower mesopleuron distinctly striolate; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae seven to twelve; standing promesonotal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with multiple hair like striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) evenly tumular to roundly conical; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few short, appressed setulae.

General characters: Color head, gaster brown, mesosoma tawny yellow or variegated yellow-and-brown, appendages yellow or yellowish-brown. Worker caste monomorphic.

Lectotype measurements (*M. specularis*): HML 1.09 HL 0.42 HW 0.33 CeI 77 SL 0.28 SI 86 PW 0.20.

Lectotype measurements (*M. angusticlava*): HML 1.15 HL 0.43 HW 0.34 CeI 79 SL 0.29 SI 87 PW 0.21.

Other worker measurements: HML 1.00–1.21 HL 0.39–0.43 HW 0.31–0.34 CeI 79–85 SL 0.27–0.31 SI 81–90 PW 0.20–0.23 (n=19).

Queen description.— Head: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits and striolae around antennal sockets, frontal carinae and below the eyes; frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined about 2:1. Axillae narrowly separated (i.e., less than width of one axilla). Standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, metapleuron with a few distinct striolae; propodeum always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae well-spaced and sparse; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle lateroventral and situated within anterior sector of petiolar node; node, in profile conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth to greatest node width about 1:1. Anterior petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color head, gaster brown, mesosoma and nodes yellowish. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Lectotype measurements (*M. impressum*): HML 1.88 HL 0.72 HW 0.59 CeI 81 SL 0.60 SI 103 PW 0.42.

Other Queen measurements: HML 1.75–1.88 HL 0.54–0.55 HW 0.44–0.46 CeI 82–85 SL 0.39–0.40 SI 85–89 PW 0.31–0.33.

Male description.— Head: Head width–mesosoma width ratio between 4:3 and1:1; frons smooth to finely striolate. Compound eyes protuberant and elliptical; margin of compound eye margin of compound eye nearly abutting clypeus. Ocelli weakly turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 3:4 and 2:3. Maximum number of mandibular teeth and denticles three.

Mesosoma: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum. Parapsidal furrows vestigial or absent; notauli absent. Axillae narrowly separated (i.e., less than width of one axilla).

Wing: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node. Petiolar node, (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1. Anterior petiolar process absent or vestigial. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 2:1 and 3:2; postpetiole shining and microreticulate.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae interspersed with a few appressed setulae.

General characters: Color uniformly brown.

Male measurements: HML 1.68 HL 0.46 HW 0.50 CeI 109 SL 0.16 SI 0.32 PW 0.44.

Remarks.— Workers of this species bear a striking resemblance in appearance and morphology to dark-headed, bicolored specimens of *Monomorium termitobium*, but can be distinguished by the combination of a uniformly dark brown or chocolate head *and* gaster. In *M. termitobium* the gaster is not uniformly dark brown or black, although it may be a dingy brownish-yellow or yellow with dark infuscation. The petiolar node in all Malagasy specimens of *M. floricola* that I have seen is also very low and broadly conical to tumular, barely higher than the postpetiole. The ventral surface of the petiole lacks a lobe of any description. *Monomorium termitobium* workers possess a petiolar node that is distinctly higher than the postpetiole, even when it is low conical in shape, and a subpetiolar lobe of varying degrees is always present.

Monomorium floricola, an exotic introduction, has been collected throughout Madagascar, but populations are principally in the drier, western parts of the island. Material in the CAS collection comes mainly from gallery forest, where individual workers have been taken in malaise traps and by beating. One small series has also been collected from an above ground rot pocket in a tree.

Monomorium lepidum **Heterick, sp. nov.**

Figs. 20, 57–58.

Etymology.— Latin '*lepidus*' ('elegant')

Material examined.— Holotype: ☿, **Prov. Mahajanga**, Forêt de Tsimembo, 11.0 km 346 NNW Soatana, 50 m 19°00′S, 44°27′E, 21–25.xi.2001, Fisher *et al.* BLF/ex dead twig above ground tropical dry forest/ CASENT 0442208 4561 (CAS). Paratype: **Prov. Mahajanga** (all specimens with same collection data as holotype): 1☿ (ANIC); 1♀ + 13☿ (BMNH); 1☿ (CAS); 23☿ (MCZ).

Other material examined: **Prov. Antsiranana:** R. S. Manongarivo, 12.8 km 228 SW Antanambao 11–17.x.1998 B.L. Fisher (9☿); R. S. Manongarivo, 10.8 km 229 SW Antanambao 8.xi.1998 B.L. Fisher (1☿); **Prov. Mahajanga:** Forêt de Tsimembo 11.0 km 346 NNW Soatana 21–25.xi.2001 Fisher *et* al. (4☿); Forêt de Tsimembo 8.7km km 336 NNW Soatana 21–25.xi.2001 Fisher *et* al. (16☿); P.N. Baie de Baly, 12.4 km 337 NNW Soalala 26–30.xi.2002 Fisher *et* al. (27☿, 2♀); P.N. Namoroka, 9.8 km 300 WNW Vilanandro, 4–8.xi.2002 Fisher *et al.* (20☿); P.N. Namoroka, 17.8 km 329 WNW Vilanandro, 8–12.xi.2002 Fisher *et al.* (4☿); P.N. Namoroka, 16.9 km 317 NW Vilanandro, 12–16.xi.2002 Fisher *et al.* (10☿, 1♀); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (24☿); P.N. Tsingy de Bemaraha, 2.5 km 62 E Bekopaka 11–15.xi.2001 Fisher *et al.* (21☿); P.N. Tsingy de Bemaraha, 10.6 km 123 ESE Antsalova 16–20.xi.2001 Fisher *et al.* (3☿); P.N. Zombitse, 19.8 km 84 E Sakaraha 5–9.ii. 2003 Fisher *et al.* (21☿); Res. Bemarivo, 23.8 km 223 SW Besalampy 19–23.xi.2002 Fisher *et al.* (25☿); **Prov. Toliara:** Kirindy, 15.5 km 64 ENE Marofandilia 28.xi–3.xii.2001 Fisher *et al.* (17☿); Rés. Berenty, Forêt Bealoka, 14.6 km 329 NNW Amboasary 3–8.ii.2002 Fisher *et al.* (25☿); Rés. Berenty, Forêt Bealoka, 8.6 km 314 NW Amboasary 6.ii.2002 Fisher *et al.* (3☿); Vohibasia Forest, 59 km NE Sakaraha 13 i. 1996 B.L. Fisher (2☿).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae partially developed or indistinct; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae; anterior tentorial pits situated nearer mandibular insertions than antennal fossae. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum, or, equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color of foreparts tawny-yellow to orange (postpetiole sometimes darker), gaster chocolate. Worker caste monomorphic.

Holotype measurements: HML 1.25 HL 0.48 HW 0.40 CeI 84 SL 0.36 SI 90 PW 0.25.

Other worker measurements: HML 1.09–1.38 HL 0.44–0.54 HW 0.37–0.47 CeI 82–88 SL 0.34–0.42 SI 89–96 PW 0.22–0.29 (n=20).

Queen description.— Head: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits and a few striolae around antennal sockets and frontal carinae; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally. interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron; propodeum shining and smooth, with multiple hair like striolae on metapleuron. Propodeum always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges; Petiolar spiracle lateral and situated within anterior sector of petiolar node.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: node (viewed in profile) conical, vertex rounded; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and weakly striolate posteriad; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

General characters: Color of foreparts yellow-orange, gaster chocolate. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 1.99–2.34 HL 0.56–0.59 HW 0.55–0.58 CeI 96–105 SL 0.47–0.49 SI 82–86 PW 0.40–50 (n=3).

Remarks.— This handsome, bicolored species can easily be mistaken for the '*binatu*' form of

M. termitobium, but lacks the sharply defined, narrowly separated clypeal carinae and strongly projecting clypeus of the latter. The proper affinities of this ant lie with *M. flavimembra* and its allies. Workers within a series are of uniform appearance, either bright yellow or orange with a dark brown gaster. The gaster is typically uniformly dark, but the base of the first gastral tergite may be a cloudy brownish-yellow. Sometimes the postpetiole is also dark brown. As with *M. flavimembra*, the basal mandibular tooth is greatly reduced, but is at least represented by a faint angle in all specimens seen.

Monomorium lepidum has a scattered distribution in western and southern parts of the island. Most records have come from Mahajanga Province. As with many of these small *Monomorium*, the species has a predilection for rotten twigs and tree stumps, but also features prominently in sifted litter and pitfall-trapped samples. Tropical dry forest is a typical habitat, but several series have come from rainforest.

Monomorium madecassum Forel

Figs. 21, 59–60.

Monomorium minutum r. *madecassum* Forel, 1892c:255. Syntype ☿s (lectotype here designated). MADAGASCAR: Imerina (MHNG) [examined].

Monomorium madecassum Dalla Torre, 1893:67.

Monomorium minutum var. *leopoldinum* Forel, 1905:179 Syntype ☿s (lectotype here designated), DEMOCRATIC REPUBLIC OF CONGO: St. Gabriel, Stanleyville (MHNG) [examined]. Syn. nov.

Monomorium leopoldinum Bolton, 1987:397

Monomorium explorator Santschi, 1920:12, figs 1a–b. Holotype ☿, GABON: Samkita (NHMB) [examined]. Syn. under *M. leopoldinum* Bolton, 1987:397.

Monomorium aequum Santschi, 1928:195, fig.3b. Holotype ☿, DEMOCRATIC REPUBLIC OF CONGO: Stanleyville (NHMB) [examined]. Syn. under *M. leopoldinum* Bolton, 1987:397.

Monomorium (*Monomorium*) *estherae* Weber, 1943:361. Syntype ☿s (lectotype here designated), SUDAN, Imatong Mts. (MCZ) [examined]. Syn. under *M. leopoldinum* Bolton, 1987:397.

MATERIAL EXAMINED.— ***M. madecassum***: LECTOTYPE: ☿, Madagascar, Imerina, coll. [P.] Camboué (MHNG). This specimen is designated the lectotype to fix the name for the species. Malagasy workers are generally smaller and less hairy than workers collected in Africa. PARALECTOTYPES: (i) ☿, Madagascar, Imerina, coll. [F.] Sikora (MHNG). (ii) ♀, Madagascar, Imerina, coll. [P.] Sikora (MHNG). ***M. leopoldinum***: LECTOTYPE: ☿, DEMOCRATIC REPUBLIC OF CONGO: St. Gabriel, Stanleyville, P. Kohl (MHNG). A lectotype is designated to fix the name '*leopoldinum*' under which were placed certain African populations of what is here regarded as *M. madecassum*. PARALECTOTYPES: Two workers, same data as lectotype (MHNG). Repinned, with photocopies of the original labels. ***M. explorator***: HOLOTYPE: ☿, Gabon, Samkita, F. Faure (NHMB – Reg. no. 206). Santschi mentions only the one specimen was used for his description. ***M. aequum***: HOLOTYPE: ☿, Democratic Republic of Congo, Stanleyville, Reichensperger (NHMB – Reg. No. 216). This worker was designated a 'holotype' by Bolton (1987), and since the length is given as a single measurement, it seems clear no other specimens were examined. A holotype status fixed by monotypy (Code 73.1.2) is here assumed. ***M. estherae***: LECTOTYPE: ☿, Sudan, Imatong Mts., 24 July–5 Aug. 1943, N.A. Weber. 1423 (MCZ). The publication and the type label describe these two specimens as 'cotypes', but 'syntypes' is clearly intended. A lectotype is designated to fix the name '*estherae*' for this taxon, whose representatives are slightly less hairy than those of *M. leopoldinum*. PARALECTOTYPE: ☿, same data as lectotype (MCZ). Repinned, with photocopies of the original labels.

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (4☿); R.S. Manongarivo, 10.8 km 229 SW Antanambao 8.xi.1998 B.L. Fisher (5☿). **Prov. Fianarantsoa:** 28 km SSW Ambositra, Ankazomivady, 9.i.1998 (1☿), 11.i.1998 (12☿, 1♀), 13.i.1998 B.L. Fisher (6☿); P.N. Andringitra, Forêt Ravaro, 12.5 km SW Antanitotsy 10–15.i.2000 S. Razafimanimby (6♀). **Prov. Mahajanga:** Mahavavy River, 6.2 km 145 SE Mitsinjo 1–5.xii.2002 Fisher *et al.* (3☿); P.N. Ankarafantsika, Tsimaloto, 18.3 km 46 NE Tsaramandroso 2–8.iv.2001 Rabeson *et al.* (4☿); P.N.

Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (1☿); P.N. Tsingy de Bemaraha, 2.5 km 62 ENE Bekopaka 11–15.xi.2001 Fisher *et al.* (1☿). **Prov. Toamasina:** Morarano-Chrome forêt, 25 km W, xi.1991 A. Pauly (1♀, 1♂ (*in cop.*)); S.F. Tampolo, 10 km NNE Fenoarivo Atn. 10.iv.1997 B.L. Fisher (2☿). **Prov. Toliara:** Cap Sainte Marie, 12.3 km 262 W Marovato 11–15.ii.2002 Fisher *et al.* (64☿, 1♀); Ehazoara Canyon, 26 km E Betioky 27.iv.1997 B.L. Fisher (2☿); Forêt Beroboka, 5.9 km 131 SE Ankidranoka 12–16.iii.2002 Fisher *et al.* (2☿); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i–1.ii.2002 Fisher *et al.* (4☿); Forêt Mite, 20.7 km 29 WNW Tongobory 27.ii–3.iii.2002 Fisher *et al.* (1☿); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* (73☿); southern Isoky-Vohimena Forest, 21.i.1996 B.L. Fisher (2☿); P.N. Andohahela, Manantalinjo, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (2☿); P.N. Tsimanampetsotsa, 6.7 km 130 SE Efoetse, 18–22.iii.2002 Fisher *et al.* (1☿);. P.N. Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka 22–26.iii.2002 Fisher *et al.* (2☿); P.N. Tsimanampetsotsa, Mitoho, 6.4 km 77 ENE Efoetse 18–22.iii.2002 Fisher *et al.* (4☿); P.N. Zombitse, 19.8 km 84 E Sakaraha 5–9.ii. 2003 Fisher *et al.* (1☿); Ranobe, Frontier Project 17–21.ii.2003, MGFO61 (1☿); Rés. Berenty, Forêt Anjapolo, 21.4 km 325 NW Amboasary 7.ii.2002 Fisher *et al.* (15☿).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye large, eye width 1.5× greater than greatest width of antennal scape, to moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 1,2; Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, entire lower mesopleuron often distinctly striolate but sculpture may be vestigial; (viewed in profile) promesonotum broadly convex; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae well-spaced over entire promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with multiple hair like striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae usually consisting of one prominent pair anteriad, with other shorter setae very sparse or absent, more rarely consisting of two anterior pairs or three or four pairs ranged along either side of the propodeal dorsum; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered, or, cuneate, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; ventral petiolar lobe weakly present to absent; height ratio of petiole to postpetiole between 3:2 and 4:3; height-length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color light brownish-yellow to brown, gaster darker. Worker caste monomorphic.

LECTOTYPE MEASUREMENTS (*M. madecassum*): HML 1.24 HL 0.49 HW 0.40 CeI 82 SL 0.35 SI 86 PW 0.26.

LECTOTYPE MEASUREMENTS (*M. leopoldinum*): HML 1.41 HL 0.53 HW 0.44 CeI 84 SL 0.39 SI 89 PW 0.29.

LECTOTYPE MEASUREMENTS (*M. explorator*): HML 1.34 HL 0.51 HW 0.42 CeI 82 SL 0.36 SI 86 PW 0.28.

LECTOTYPE MEASUREMENTS (*M. aequum*): HML 1.48 HL 0.52 HW 0.45 CeI 87 SL 0.37 SI 82 PW 0.30.

LECTOTYPE MEASUREMENT (*M. estherae*): HML 1.34 HL 0.51 HW 0.41 CeI 80 SL 0.35 SI 85 PW 0.27.

OTHER WORKER MEASUREMENTS (non-types): HML 1.14–1.27 HL 0.46–0.51 HW 0.37–0.41 CeI 78–83 SL 0.32–0.37 SI 83–93 PW 0.23–0.27 (n=20).

QUEEN DESCRIPTION.— HEAD: Head square; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron; propodeum shining and smooth, with multiple hair like striolae on metapleuron; propodeum always smoothly rounded; propodeal dorsum flat throughout most of its length; standing propodeal setae consisting of a few decumbent setae only; appressed propodeal setulae well-spaced and sparse; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Propodeal lobes present as bluntly angled flanges.

WING: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu always absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite not depressed, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 3.01–3.12 HL 0.76–0.77 HW 0.74–0.75 CeI 96–99 SL 0.56–0.58 SI 76–77 PW 0.88–0.92 (n=2).

Male description.— Head: Head width–mesosoma width ratio between 1:1 and 3:4 to less than 1:2; frons finely longitudinally striolate. Compound eyes protuberant and elliptical tending to elongate; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli turreted. Ratio of length of first funicular segment of antenna to second funicular segment about 1:3. Maximum number of mandibular teeth and denticles four.

Mesosoma: Mesoscutum broadly convex; mesoscutum with a few vestigial striolae on its dorsum, otherwise both pronotum and mesonotum smooth and shining. Parapsidal furrows vestigial or absent; notauli vestigial. Axillae widely separated (i.e., by width of at least one axilla), axilla fused with scutellum.

Wing: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node. Petiolar node, (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1. Anteroventral petiolar process absent or vestigial. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 1:1; postpetiole shining, with vestigial sculpture.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

General characters: Color chocolate, tibia and tarsi pale brownish-yellow.

Male measurements: HML 2.80–2.84 HL 0.70 HW 0.72–0.74 CeI 104–106 SL 0.21–0.22 SI 28–31 PW 0.90–0.94 (n=2).

Remarks.— Workers of *Monomorium madecassum* are immediately recognizable by virtue of their large propodeal spiracle, clypeal denticles, and relatively large eyes. The petiolar node and postpetiole also tend to be high and narrow in most specimens. The taxon *Monomorium leopoldinum*, described from African material, is morphologically indistinguishable from *M. madecassum* and is here made a junior synonym of the earlier name. *Monomorium aequum* was collected in the same locality (Stanleyville, Democratic Republic of Congo) as *M. leopoldinum*, and apart from smaller eyes and a broad head the lectotype is virtually indistinguishable from that of *M. leopoldinum*. *Monomorium explorator* Santschi, from Gabon, has a smooth mesopleuron without any hint of sculpture. Otherwise, however, it conforms closely to *M. madecassum*. African populations of *M. madecassum* are on average larger than Malagasy populations of this species. Workers also tend to be more hirsute, with more than two pairs of erect propodeal setae, according to Bolton (1987). By way of contrast, Malagasy workers usually have one or two pairs of erect propodeal setae, but a series from Ankarafantsika, Mahajanga Province, is pilose like the African workers. (As mentioned under 'Remarks' for *Monomorium exiguum*, degree of pilosity does not appear to be useful as a diagnostic character at a species level for many small *Monomorium*.) The type specimens of *Monomorium estherae* are altogether like *M. madecassum*. The queen and male of *M. madecassum* are both very large for members of the *M. monomorium* group, and each, like the worker, possesses a very large propodeal spiracle. The compound eye of the male is elongate-oval. The reproductive wing is a pale off-white, although its veins are fairly well-defined.

Monomorium madecassum is the only member of its complex found on Madagascar, where it can be found throughout the island. Most CAS material has been collected in Toliara. Although not as abundant in samples as several other small species, this ant has been taken from different vegetation assemblages, ranging from spiny forest to rainforest, and can exist in disturbed forest areas and even in grassland. Various collection methods have been successful, and its inclusion in malaise trap samples indicates this species will forage arboreally. The ant appears to have catholic tastes in terms of nest sites, colonies having been sampled in a dead branch above ground and also under stones.

Monomorium micrommaton Heterick, sp. nov.

Figs. 22, 61–62.

Etymology.— Greek '*mikrommatos*' ('small-eyed')

Material examined.— Holotype: ☿, **Prov. Toamasina**, P.N. Mantadia 895 m, 18°47′5″S, 48°25′6″E, 28.xi–1.xii.1998 H.J. Ratsirarson 112/sifted litter (leaf mold, rotten wood) rainforest/112(32)–51 (CAS). Paratypes: **Prov. Toamasina** (all specimens with same collection data as holotype): 32♀ + 1♀ (ANIC); 42☿ + 1♀ (BMNH); 32☿ + 1 (CAS); 42☿ + 1♀ (MCZ).

Other material examined: **Prov. Antsiranana:** 12.2 km WSW Befingotra, Res. Anjanaharibe-Sud, 19.x.1994 B.L. Fisher (19☿). **Prov. Fianarantsoa:** 45 km S Ambalavao 25.ix.1992 B.L. Fisher (24☿); 43 km S Ambalavao, Res. Andringitra 10.x.1993 B.L. Fisher (120☿); Parc Nat. de Ranomafana , 11.v.1991 L. Bartolozzi, S. Tiati & C. Raharimina (1☿); P.N. Ranomafana, Vatoharanana 4.1 km 231 SW Ranomafana 27–31.iii.2003 Fisher *et* al. (25☿); Ranomafana N.P. 1.i.1992 E. Rajeriarison (3☿) (MCZ); W.E. Steiner (1♀) (MCZ); Ranomafana N.P. 7 km (*sic*!) 8.x.1988 W.E. Steiner (1♀) (MCZ); 3 km W Ranomafana, nr. Ifanadiana 27.iv. 1989 P.S. Ward (4☿) (MCZ); 7 km W Ranomafana , 10.ix.1993 W. E. Steiner *et al.* (2☿) (MCZ); 7 km W Ranomafana , 23.ix.1993 M. Stebbins, W. E. Steiner *et al.* (2♀) (MCZ); 7 km W Ranomafana, 14.x.1993 W.E. Steiner *et al.* (1♀); (MCZ) R.S. Ivohibe, 7.5 km ENE Ivohibe, 7–12.xi.1997 B.L. Fisher (24☿); R. S. Ivohibe, 9.0 km NE Ivohibe, 12–17.xi.1997 B.L. Fisher (3☿). **Prov. Toamasina:** 6.9 km NE Ambanizana 2.xii.1993 B.L. Fisher (20☿); 6 km ESE Andasibe (- Périnet) 17. xi. 1990 P.S. Ward (4☿) (MCZ); F.C. Andriantantely 4–7.xii.1998 H.J. Ratsirarson (11☿); F.C. Didy, 16–23.xii.1998 H.J. Ratsirarson (10☿); P.N. Mantadia, 28.xi–1.xii.1998 H.J. Ratsirarson (2☿).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae: Eye small, eye width less than 1× greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye more-or-less circular, or, elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin emarginate, clypeal carinae indistinct; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits equidistant from antennal fossae and mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent;

propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 3:2; height–length ratio of postpetiole between 1:1 and 3:4; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

General characters: Color yellow. Worker caste monomorphic.

Holotype measurements: HML 1.02 HL 0.39 HW 0.32 CeI 82 SL 0.27 SI 84 PW 0.22.

Other worker measurements: HML 0.92–1.11 HL 0.36–0.43 HW 0.30–0.35 CeI 78–84 SL 0.24–0.28 SI 78–87 PW 0.20–0.26 (n=20).

Queen description.— Head: Head square; vertex always planar; frons shining and smooth except for piliferous pits; frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye elliptical, outer margin may be shallowly concave; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Mesoscutum broadly convex; pronotum ,mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2. Axillae narrowly separated (i.e., less than width of one axilla). Standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, metapleuron with a few distinct striolae; propodeum smoothly rounded or with indistinct angle; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as vestigial flanges only, or absent.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered, to cuneate, vertex rounded; appearance of node shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1. Anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 2:1 and 4:3; postpetiole shining and smooth to shining, with vestigial sculpture; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

General characters: Color bright orange-yellow. Brachypterous, alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 2.87–2.98 HL 0.67–0.70 HW 0.68–0.71 CeI 99–104 SL 0.53–0.58 SI 76–82 PW 0.74–0.96 (n=5).

Remarks.— *Monomorium micrommaton* workers are similar to the yellow, typical form of *M. termitobium*, but, unlike the latter, appear to be restricted to cryptic environments. The queens are also clearly separable from those of the latter species. All collections have been made in rainforest on the east coast of Madagascar in the provinces of Antsiranana, Fianarantsoa and Toamasina, usually in sifted leaf litter, mould or rotten wood. The very reduced eyes and depigmented coloration suggest this species is strongly adapted to a cryptic lifeway.

Monomorium nigricans Heterick, sp. nov.

Figs. 20, 65–66.

Etymology.— Latin '*nigricans*' ('blackish').

Material examined.— Holotype: ☿, **Prov. Toliara**, Rés. Cap Sainte Marie, 12.3 km 262° W Marovato 25°34′90″S, 45°10′10″E 200 m, 11–15.ii.2002 B. Fisher *et al.* BLF 5500/ sifted litter, spiny forest/thicket/ CASENT 0020200 5500(LO) (CAS). Paratypes: **Prov. Toliara** (one worker collection code 5500, one worker collection code 5502, eleven males collection code 5504, otherwise data as for the holotype): 12♂ (ANIC); 13♂ + 1☿ (BMNH); 12♂ (CAS); 13♂ + 1♂ + 1☿ (MCZ).

Other material examined: **Prov. Toliara:** 18 km NNW Betroka, 29.xi.–4.xii.1994 M.A. Ivie & D.A. Pollock (18☿) (MCZ); Res. Beza Mahafaly ['Mahafely'], 18.xi.1984 R.L. Brooks (14☿) (MCZ); Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (14☿); Forêt Mahavelo, Isantoria Riv. 5.2 km 44 NE Ifotaka 28.i–1.ii.2002 B.L. Fisher (1♂); Forêt Mite, 20.7 km 29 WNW Tongobory 27.ii–3.iii.2002 Fisher *et al.* (1☿); Mahafaly Plateau, 6.2 km 74 ENE Itampolo 25.ii.2002 Fisher *at al.* (2); P.N. Isalo, Ambovo Springs, 29.3 km 4 N Ranohira 9–14.ii.2003 Fisher *et al.* (1♀); Réserve Berenty, 10.xii.1992 B.L. Fisher (2☿) Rés. Berenty, Forêt Malaza, 8.6 km 314 NW Amboasary 6.ii.2002 Fisher *et al.* (9♂).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye large, eye width 1.5× greater than greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set anteriad of midline of head capsule, or, set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 11; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on dorsum of promesonotum. Metanotal groove weakly impressed, with faint costulae or costulae lacking. Propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered to conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole between 4:3 and 1:1; height-length ratio of postpetiole about 4:3; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color dark reddish-brown to almost black. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.08 HL 0.42 HW 0.37 CeI 87 SL 0.30 SI 82 PW 0.25.

OTHER WORKER MEASUREMENTS: HML 1.00–1.12 HL 0.39–0.44 HW 0.34–0.38 CeI 84–90 SL 0.29–0.33 SI 82–89 PW 0.22–0.25 (n=19).

MALE DESCRIPTION.— HEAD: (In full-face view) head width–mesosoma width ratio between 4:3 and 1:1; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 2:3 and 1:2. Maximum number of mandibular teeth and denticles three.

MESOSOMA: Mesoscutum broadly convex; pronotum and mesoscutum shining and microreticulate throughout; parapsidal furrows vestigial or absent; notauli absent; axillae widely separated (i.e., by width of at least one axilla), axilla fused with scutellum.

WING: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 3:4; height–length ratio of postpetiole between 2:1 and 3:2; postpetiole shining and microreticulate.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color chocolate.

MALE MEASUREMENTS: HML 1.73–2.07 HL 0.45–0.55 HW 0.53–0.65 CeI 102–118 SL 0.12–0.18 SI 21–33 PW 0.53–0.73 (n=20).

REMARKS.— This smallish species, the only Malagasy *Monomorium* apart from *Monomorium exiguum* that has an 11-segmented antenna, appears to be confined to Toliara Province, where it is not uncommon in spiny forest. Several workers and males have also been collected in gallery and tropical dry forests. The profile of the worker mesosoma of *Monomorium nigricans* is not unlike that of the African *Monomorium bequaerti* Forel (Fig. 92 in Bolton 1987), but the postpetiole is more rounded and the color is much darker than in *bequaerti*. The relationship of this species to other small African and Malagasy *Monomorium* is uncertain, but the appearance of the worker and the male suggests it may belong to the *M. exiguum* complex. Workers have been collected in sifted litter or from beating low vegetation, or as ground foragers, and ground nests and nests in dead twigs have also produced worker specimens. Males have been taken in malaise traps.

Monomorium platynodis Heterick, sp. nov.

Figs. 22, 63–64.

ETYMOLOGY.— Greek '*platys*' (flat) + pl. of masc. '*nodus*'

Material examined.— Holotype: ☿, **Prov. Toamasina**, Mont Anjanaharibe, 18.0 km 21 NNE Ambinanitelo 470 m 15°11′3″S, 49°36′9″E, 8–12.iii.2003 Fisher *et al.* BLF 8002/sifted litter tropical dry forest/CASENT 0026538 8002(24) (CAS). Paratypes: **Prov. Toamasina** (all specimens with same collection data as holotype): 13☿ (ANIC); 13☿ (BMNH); 13♂ + 13☿ (MCZ).

Other material examined: **Prov. Antsiranana:** Ampasindava, Ambilanivy, 3.9 km 181 S Ambaliha 4–9.iii.2001 Fisher *et al.* (1☿, 1♂). **Prov. Mahajanga:** P.N. Namoroka, 17.8 km 329 WNW Vilanandro, 8–12.xi.2002 Fisher *et al.* (2☿). **Prov. Toamasina:** F.C. Didy, 16–23.xii.1998 H.J. Ratsirarson (1☿). **Prov. Toliara:** 6 km SSW Eminiminy, Rés. Andohahela 4.ii.1993 (3☿, 3♂) (MCZ); 11 km NW Enakara, Rés. Andohahela 17.xi.1992 B.L. Fisher (3☿).

Worker description.— Head: Head rectangular; vertex weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye large, eye width 1.5× greater than greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule to set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin, or, elongate, eye narrowed to point anteriad; Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Mandibular with three evenly sized teeth; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t2 (three teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex; promesonotal setae seven to greater than twelve; standing promesonotal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; propodeum always smoothly rounded; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle laterodorsal and situated slightly anteriad of petiolar node, or, lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height-length ratio of postpetiole about 3:2; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color bright yellow-orange. Worker caste monomorphic.

Holotype measurements: HML 1.15 HL 0.42 HW 0.34 CeI 81 SL 0.29 SI 85 PW 0.24.

Other worker measurements: HML 1.18–1.33 HL 0.44–0.50 HW 0.36–0.39 CeI 75–84 SL 0.31–0.35 SI 84–91 PW 0.25–0.27 (n=18).

Male description.— Head: Head width-mesosoma width ratio between 1:1 and 3:4; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment about 1:1. Maximum number of mandibular teeth and denticles three.

Mesosoma: Mesoscutum broadly convex; pronotum and mesoscutum shining, with dorsum of mesoscutum faintly striolate. Parapsidal furrows vestigial or absent; notauli absent. Axillae separated by width of at least one axilla.

Wing: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node. Node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3. Anteroventral petiolar process absent or vestigial. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae.

General characters: Color brown.

Male measurements: HML 1.31–1.44; HL 0.40–0.41; HW 0.35–0.38; CeI 88–93; SL 0.14–0.17; SI 39–46; PW 0.42–0.44 (n=3).

Remarks.— *Monomorium platynodis* is a rather rare species, which, nonetheless, ranges throughout the entire island of Madagascar. Recorded material comes from Antsiranana, Mahajanga, Toamasina and Toliara provinces. The uniformly orange workers are immediately identifiable through their truncated clypeus, three-toothed mandibles and high nodes. The very small males (the queen is not known) resemble those of *M. exiguum*. The mandible of the male also has three strong teeth, and the entire anterior clypeal margin is straight and well-separated from the basal margin of the mandible. The male node seen in full-face view is bimodal. Specimens of *M. platynodis* have been collected from sifted litter and by hand from a rotten log in tropical dry forest and rainforest.

Monomorium sakalavum Santschi

Figs. 23. 1–11.

Monomorium sakalavum Santschi, 1928:196. Syntype ☿s (lectotype here designated), Madagascar: Nosi be (NHMB) [examined].

Material examined.— Lectotype: ☿, Madagascar, Nosi be [= Nosy be], Decarpentries (NHMB – Reg. No. 210). The lectotype fixes the name of the taxon for the typical, reddish form of the species with scapes that exceed the vertex of the head. The carded lectotype is the ant on the top rectangle on a pin holding three ants, each occupying one card rectangle. Paralectotypes: Two workers, data the same as for the lectotype (NHMB). The two workers occupy the second and third rectangles, respectively, on the pin mentioned above.

Other material examined: **Prov. Antsiranana:** B.L. Fisher; Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (16☿, 1♀); Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (17☿, 3♀); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (1☿); Rés. Spéc. Ankarana, 13.6 km 192 SSW Anivorano Nord 16–21.ii.2001 Fisher *et al.* (10☿, 1♀); **Prov. Mahajanga:** Forêt de Tsimembo 11.0 km 346 NNW Soatana 21–25.xi.2001 Fisher *et* al. (27☿); P.N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (100☿, 1♀); P.N. Tsingy de Bemaraha, 2.5 km 62 ENE Bekopaka 11–15.xi.2001 Fisher *et al.* (4☿, 2♂); **Prov. Toliara:** Andohahela, 7.ii.1993 E. Hajeriarison (MCZ) (1☿, 1♂); Cap Sainte Marie, 12.3 km 262 W Marovato

11–15.ii.2002 Fisher *et al.* (1☿); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (1☿); Kirindy, 15.5 km 64 ENE Marofandilia 28.xi–3.xii.2001 Fisher *et al.* (22☿); P.N. Andohahela, Manantalinjo, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (17☿); P.N. Andohahela, 1.7 km 61 ENE Tsimelahy 16–20.i.2002 Fisher *et al.* (11☿, 1♀); Ranobe, Frontier Project 5–9.ii.2003, MGFO56 (1☿); southern Isoky-Vohimena Forest, 21.i.1996 B.L. Fisher (4☿).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 1,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, entire lower mesopleuron usually distinctly striolate, striolae may be weak in smaller specimens; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove weakly to strongly impressed, with distinct transverse costulae which are typically broad. Propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeal dorsum flat throughout most of its length; propodeum always smoothly rounded; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct; propodeal lobes present as rounded flanges. Petiolar spiracle lateral and situated within anterior sector of petiolar node.

PETIOLE AND POSTPETIOLE: Node (viewed in profile) cuneate, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole about 4:3; postpetiole shining and smooth; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina, or without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color variable: head brown or reddish brown, mesosoma reddish-brown to orange, gaster chocolate, appendages yellowish-brown. Worker caste monomorphic.

LECTOTYPE WORKER MEASUREMENTS: HML 1.35 HL 0.51 HW 0.41 CeI 81 SL 0.47 SI 115 PW 0.26.

Other worker measurements: HML 1.38–1.50 HL 0.52–0.56 HW 0.42–0.46 CeI 81–86 SL 0.47–0.50 SI 106–114 PW 0.28–0.31 (n=20).

Queen description.— Head: Head square; vertex always planar; frons shining and smooth except for piliferous pits and a few striolae around antennal sockets and frontal carinae; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, margin sometimes shallowly concave; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining, uniformly weakly striolate; propodeum always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Propodeal lobes present as vestigial flanges only, or absent.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle lateroventral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node strongly rugose; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:2 and 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 7:3 and 2:1; postpetiole strongly rugose; postpetiolar sternite not depressed, its anterior end an inconspicuous lip or small carina.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color blackish-red. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 2.17–2.46 HL 0.64–0.70 HW 0.63–0.66 CeI 93–102 SL 0.58–0.61 SI 90–96 PW 0.51–0.60 (n=6).

Male description.— Head: (In full-face view) head width-mesosoma width ratio between 1:1 and 3:4; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 2:3 and 1:2. Maximum number of mandibular teeth and denticles three.

Mesosoma: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; parapsidal furrows vestigial or absent; notauli absent; axillae separated by width of at least one axilla.

Wing: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered, bimodal in full-face view; appearance of node shining, with or without longitudinal striolae; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole dorsal sector shining and smooth, basal sector microreticulate.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color chocolate, tibiae and tarsi pale brown to off-white.

MALE MEASUREMENTS: HML 1.75–2.02 HL 0.49–0.52 HW 0.51–0.54 CeI 104–106 SL 0.16–0.18 SI 30–33 PW 0.54–0.62 (n=3).

REMARKS.— *Monomorium sakalavum* is part of a complex of very common and taxonomically difficult Malagasy ants that are also well-represented in southern and east Africa (the *rhopalocerum* complex). Typically, this species can be distinguished from its relatives by its distinctive glassy, brick-red mesosoma that contrasts with the light chocolate head and brown gaster. The mesosoma in profile is straight, the mesopleuron has weak to strong sculpture, and the propodeum is vaguely angulate. The petiolar node is cuneate. However, smaller, paler specimens have a more rounded mesosoma and may be mistaken for *M. termitobium* ('*imerinense*') and *M. xuthosoma*. In such cases the reddish to orange color of the mesosoma will help differentiate *M. sakalavum* from the former and its relatively much longer antennal scape will separate it from the latter. *Monomorium sakalavum* has been collected by a variety of methods in drier forested areas, mainly in western parts of Madagascar. Nest series have been collected from rotted twigs, sticks and logs on the ground as well as above ground.

Monomorium termitobium Forel

Figs. 24, 93–99.

Monomorium termitobium Forel, 1892b:522. Syntype ☿ (lectotype here designated), MADAGASCAR: (?)Mangaroafa (MHNG) [examined].

Monomorium minutum r. *imerinense* Forel, 1892c:257. Syntype ♀s, ♂ (lectotype ♀ here designated), MADAGASCAR: Andrangoloaka (MHNG) [examined]. Syn. nov.

Monomorium minutum subsp. *imerinense* Wheeler, W.M. 1922:1027.

Monomorium imerinense Dalla Torre, 1893:67.

Monomorium exchao Santschi, 1926: 235 Syntype ☿s (lectotype here designated), SOUTH AFRICA: Paradise Kloof, Graham Town, Cape Colony (NHMB) [examined]. Syn. nov.

Monomorium binatu Bolton, 1987: 380, fig. 78 (☿). Holotype ☿, ZIMBABWE: Vumba Mts., nr. Umtali (NHMB) [examined]. Syn. nov.

MATERIAL EXAMINED.— ***M. termitobium***: LECTOTYPE: ☿, Madagascar, (?)Mangoroafa (MHNG). (Published locality Amparafaravantsiv.) The publication implies this species was collected by P. Sikora, though his name does not appear on any of the labels. The length is given as a range, indicating that more than one specimen was examined by Forel. This species is taxonomically confusing: the lectotype fixes the name for populations with yellow, biconvex workers with rather hairy mesosomas. Lectotype measurements have not been taken as the lectotype lacks a head. ***M. imerinense***: LECTOTYPE: ♀, Madagascar, Andrangoloaka, [P.] Sikora (MHNG). The lectotype fixes the taxon name for populations with uniformly brown queens (with *M. termitobium s. str.* the queens have lighter-colored mesosomas). PARALECTOTYPES: (i) Two queens, same data as above (MHNG). (The two queens occupied the same pin as the lectotype: they have been repinned, along with photocopies of the original labels). (ii) One male, Andrangoloaka, [P.] Sikora (MHNG). ***M. exchao***: LECTOTYPE: ☿, South Africa, Paradise Kloof, Graham Town, Cape Colony (NMHB Reg. No. 203). The lectotype (worker on LHS when seen from rear) fixes the name for populations with yellow workers whose gasters are often diffusely infuscated, particularly on the sides of the first gastral tergite. PARALECTOTYPE: One damaged worker mounted on same rectangle as lectotype (RHS), and with same data (NMHB). ***M. binatu***: HOLOTYPE: ☿, Zimbabwe ('Rhodesia') Vumba Mts, nr Umtali, 11.iii.[19]69 W.L. Brown, (MCZ). PARATYPES:

Six workers, with same data as the holotype (MCZ). (Relevant measurements of the holotype and paratypes are provided in Bolton 1987).

Other material examined: **Prov. Antananarivo:** 3 km 41 NE Andranomay, 11.5 km 147 SSE Anjozorobe 5–13.xii.2000 Fisher *et al.* (44☿, 5♀, 24♂); Rés Ambohitantely, 20.9 km 72 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (38☿, 3♀); Rés Ambohitantely, 24.1 km 59 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (16☿). **Prov. Antsiranana:** Ampasindava, Ambilanivy, 3.9 km 181 S Ambaliha 4–9.iii.2001 Fisher *et al.* (31☿, 2♀, 17♂); 12.2 km WSW Befingotra, Res. Anjanaharibe-Sud, 25.xi.1994 (11☿), 26.xi.1994 (5☿, 2♀): B.L. Fisher; Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (25☿, 1♀); Forêt Orangea, 3.6 km 128 SE Remena 22–28.ii.2001 Fisher *et al.* (42☿, 6♀, 2♂); Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (3☿); Nosy Be, Rés. Lokobe, 6.3 km 112 ESE Hellville 19–24.iii.2001 Fisher *et al.* (29☿, 1♀, 1♂); Nosy Be, P.N. Lokobe, 5 km 125 ESE Hellville 13–16.ii.2003 Fisher *et al.* (2☿); P.N. Montagne Ambre, 3.6 km 235 SW Joffreville 20–26.i.2001 Fisher *et al.* (11☿, 1♂); P.N. Montagne Ambre. 12.2 km 211 SSW Joffreville 2–7.ii.2001 Fisher *et al.* (76☿, 10♀, 1♂); Résérve Spéciale Ambre. 3.5 km 235 SW Sakaramy 26–31.i.2001 Fisher *et al.* (60☿, 5♀); Rés. Spéc. Ankarana. 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (46☿, 4 ergatoids, 5♀); Rés. Spéc. Ankarana. 13.6 km 192 SSW Anivorano Nord 16–21.ii.2001 Fisher *et al.* (34☿, 8♀); R.S. Manongarivo, 14.5 km 220 SW Antanambao 20.x.1998 (2☿), 21.x.1998 (11☿) B.L. Fisher; R.S. Manongarivo, 17.3 km 218 SW Antanambao 27.x.1998 B.L. Fisher (1☿); R.S. Manongarivo, 10.8 km 229 SW Antanambao 8.xi.1998 B.L. Fisher (51☿, 1♀); 1 km W Sakalava Beach 23–27.i.2001 R. Harin Hala (1♂). **Prov. Fianarantsoa:** 38 km S Ambalavao. Res Andringitra 23.x.1993 B.L. Fisher (6☿, 1♀); 29 km SSW Ambositra, Ankazomivady, 7.i.1998 B.L. Fisher (6☿); 28 km SSW Ambositra, Ankazomivady, 8.i.1998 (2☿, 1♀), 14.i.1998 (1☿) B.L. Fisher; 29 km SSW Ambositra, Ankazomivady 14.i.1998 B.L. Fisher (1☿); 27.4 km SSW Ambositra, 15.i.1998 B.L. Fisher (6☿); Forêt Analalava, 29.6 km 280 W Ranohira 1–5.ii.2003 Fisher *et al.* (28☿, 11♀); Forêt Antsirakambiaty. 7.6 km 285 WNW Itremo 22–26.i.2003 Fisher *et al.* (19☿, 2♀); Ivohibe, 8.0 km E Ivohibe, 15–21.x.1997 B.L. Fisher (3☿); P.N. Andringitra, Forêt Ravaro, 12.5 km SW Antanitotsy 10–15.i.2000 S. Razafimanimby (30☿); P.N. Isalo, 9.1 km 354 N Ranohira 27–31.i.2003 Fisher *et al.* (3☿, 4♀); P.N. Isalo, 9.1 km 354 N Ranohira 27–31.i.2003 Fisher *et al.* (16☿, 1♀); P.N. Isalo, Sahanafa Riv., 29.2 km 351 N Ranohira R. S. 10–13.ii.2003 Fisher *et al.* (11☿, 1♀); P.N. Ranomafana, Vatoharanana 4.1 km 231 SW Ranomafana 27–31.iii.2003 Fisher *et* al. (1☿, 1♀); P.N. Ranomafana, Sahamalaotra, 6.6 km 310 31.iii.2003 Fisher *et al.* (6☿); 4.1 km 231 SW Ranomafana 27–31.iii.2003 Fisher *et* al. (1☿); Rés. Andringitra, Plateau d'Andohariana, base of Pic d'Ivangomena 3–9.ix.1995 Goodman (1☿, 1♀); Rés. Andringitra, Plateau d'Andohariana, cuvette du Pic Boby, 9–15.ix.1995 Goodman (1☿, 1♀); Rés. Andringitra, 8.5 km SE Antanitotsy 6.iii.1997 B.L. Fisher (12☿, 5♂); R.S. Ivohibe, 6.5 km ESE Ivohibe, 24–30.x.1997 B.L. Fisher (1☿). **Prov. Mahajanga:** Forêt de Tsimembo 11.0 km 346 NNW Soatana 21–25.xi.2001 Fisher *et* al. (17☿, 1♀); Forêt de Tsimembo 8.7 km 336 NNW Soatana 21–25.xi.2001 Fisher *et* al. (11☿); Mahavavy River, 6.2 km 145 SE Mitsinjo 1–5.xii.2002 Fisher *et al.* (2☿, 3♀); P.N. Ankarafantsika, Ampijoroa, 40 km 306 NW Andranofasika 26–31.iii.2001 Fisher *et al.* (4☿); P.N. Ankarafantsika, Ampijoroa, 5.4 km 331 NW Andranofasika 30.iii.2001 Rabeson *et al.* (80☿, 21♀); P.N. Ankarafantsika, Ankoririka, 9–14.iv.2001 10.6 km 13 NE Tsaramandroso Rabeson *et al.* (4☿); P.N. Ankarafantsika, Tsimaloto, 2–8.iv.2001 18.3 km 46 NE Tsaramandroso Rabeson *et al.* (21☿, 3♀); P.N. Baie de Baly, 12.4 km 337 NNW Soalala 26–30.xi.2002 Fisher *et* al. (7☿, 1♀); P.N. Namoroka, 9.8 km 300 WNW Vilanandro, 4–8.xi.2002 Fisher *et al.* (1☿, 1♀); P.N. Namoroka, 17.8 km 329 WNW Vilanandro, 8–12.xi.2002 Fisher *et al.* (6☿); P.N. Namoroka, 16.9 km 117 NW Vilanandro, 12–16.xi.2002 Fisher *et al.* (3☿); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (61☿, 7♀); P.N. Tsingy de Bemaraha, 2.5 km 62 ENE Bekopaka 11–15.xi.2001 Fisher *et al.* (39☿,1♀); P.N. Tsingy de Bemaraha, 10.6 km 123 ESE Antsalova 16–20.xi.2001 Fisher *et al.* (129☿, 1♀); Rés Ambohitantely, 20.9 km 72 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (1☿, 13♀); Res. Bemarivo, 23.8 km 223 SW Besalampy 19–21.xi.2002 (4☿), 19–23.xi.2002 (17☿); Fisher *et al.* **Prov. Toamasina:** 6.9 km NE Ambanizana 2.xii.1993 B.L. Fisher (6☿, 1♀); F. C. Andriantantely 4–7.xii.1998 (2☿) 7–10.xii.1998 (2☿) H.J. Ratsirarson; F. C. Didy, 16–23.xii.1998 H.J. Ratsirarson (4☿, 2♂); F. C. Sandranantitra 18–21.i.1999 H.J. Ratsirarson (6☿, 1♀); Mont Anjanaharibe, 18.0 km 21 NNE Ambinanitelo 8–12.iii.2003 Fisher *et* al. (3☿, 3♀); Mont Anjanaharibe, 19.5 km 27 NNE Ambinanitelo 12–16.iii.2003 Fisher *et al.* (2☿, 1♀); Mont. Akirindro, 7.6 km 341 NNW Ambinanitelo 17–21.iii.2003 Fisher *et* al. (2☿, 2♀); P.N. Mantadia, 28.xi–1.xii.1998 (4☿), 4–10.xii.1998 (1♂) H.J. Ratsirarson; P.N. Masoala, 39.4 km 150 SSE Maroantsetra 28.xi–3.xii.2001 Fisher *et al.* (1☿). **Prov. Toliara:** Cap Sainte Marie, 12.3 km 262 W Marovato 11–15.ii.2002 Fisher *et al.* (9☿); Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (12☿, 3♀, 1♂); 11 km NW Enakara, Rés. Andohahela 17.xi.1992 B.L. Fisher (2☿); Forêt Analavelona, 33.2 km 344 NNW Mahaboboka 12–26.ii.2003 Fisher *et* al. (19☿, 4♀); Forêt Analavelona, 29.2 km 343 NNW Mahaboboka 18–22.ii.2003 Fisher *et* al. (11☿); Forêt Analavelona, 29.4 km 343 NNW Mahaboboka 21.ii.2003 Fisher *et* al. (8☿); Forêt Beroboka, 5.9 km 131 SE Ankidranoka 12–16.iii.2002 Fisher *et al.* (28☿, 12♀); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i–1.ii.2002 Fisher *et al.* (6☿, 4♀); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (68☿, 9♀); Forêt Mite, 20.7 km 29 WNW Tongobory 27.ii–3.iii.2002 Fisher *et al.* (37☿, 10♀); Forêt de Petriky, 12.5 km W 272 Tolagnaro 22.xi.1998 B.L. Fisher (67☿, 15♀); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* 1(1☿, 8♀); southern Isoky-Vohimena Forest, 21.i.1996 B.L. Fisher (1☿); Kirindy, 15.5 km 64 ENE Marofandilia 28.xi–3.xii.2001 Fisher *et al.* (20☿); "MAD99/001" (Lakata Zafera) 30.vi.1999 H. Steiner (1☿); Mahafaly Plateau, 6.2 km 74 ENE Itampolo 25.ii.2002 Fisher *at al.* (2☿); 6.1 km 182 S Marovato 14.ii.2002 Fisher *et al.* (7☿); P.N. Andohahela, 3.8 km 113 ESE Mahamavo 21–25.i.2002 (23☿, 5♀, 3♂) 24.i.2002 (3☿) B.L. Fisher *et al.*; P.N. Andohahela, Manantalinjo, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (6☿, 4♀); P.N. Andohahela, 1.7 km 61 ENE Tsimelahy 16–20.i.2002 Fisher *et al.* (51☿, 6♀, 3?); P.N. Kirindy Mite, 16.3 km 127 SE Belo sur Mer 6–10.xii.2001 Fisher *et al.* (8☿, 2♀); P.N. Tsimanampetsotsa, Bemanateza, 6.7 km 130 SE Efoetse 18–22.iii.2002 Fisher *et al.* (37☿, 11♀); P.N. Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka 22–26.iii.2002 Fisher *et al.* (2☿); P.N. Tsimanampetsotsa, Mitoho, 6.4 km 77 ENE Efoetse 18–22.iii.2002 Fisher *et al.* (28☿, 9♂); P.N. Zombitse, 19.8 km 84 E Sakaraha 5–9.ii. 2003. Fisher *et al.* (13☿, 3♀); P.N. Zombitse, 17.7 km 98 E Sakaraha 8.ii. 2003 Fisher *et al.* (3☿); Rés. Ambohijanahary, 35.2 km 312 NW Ambaravaranala 13–17.i.2003 Fisher *et al.* (7♀); Rés. Ambohijanahary, 34.6 km 314 NW Ambaravaranala 16.i.2003 Fisher *et al.* (4☿, 1♀); Rés. Berenty, Forêt Anjapolo, 21.4 km 325 NW Amboasary 7.ii.2002 Fisher *et al.* (1☿); Rés. Berenty, Forêt Bealoka, 14.6 km 329 NNW Amboasary 3–8.ii.2002 Fisher *et al.* (22☿, 2♀); Rés. Berenty, Forêt Bealoka, 8.6 km 314 NNW Amboasary 6.ii.2002 Fisher *et al.* (31☿, 10♀); S. F. Mandena, 8.4 km NNE 30 Tolagnaro 20.xi.1998 B.L. Fisher (17☿); 2.7 km WNW 302 Ste Luce, 9–11.xii.1998 B.L. Fisher (34☿, 1♀).

WORKER DESCRIPTION.— HEAD: Head square, or, rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate (rarely, small), eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eye set around midline of head capsule, or, set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae well-defined, weakly defined, or indistinct; anteromedian clypeal margin of variable appearance, ranging from broadly convex, or, narrowly convex between weakly ridged clypeal carinae, to straight, or, straight between strongly divergent clypeal carinae with clypeus descending almost vertically to horizontal arc of mandibles and sometimes transversely carinate below level of antennal insertions. Clypeus may also be emarginate, clypeal carinae indistinct or present and terminating in blunt angles. Paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four, with basal tooth only slightly smaller than preceding three teeth, or, three, plus minute, apical denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique, to strongly oblique; basal tooth approximately same size as t3 (four teeth present), or, a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and either completely smooth, or, with faint punctation or striolae on lower anterior mesopleuron; (viewed in profile) promesonotal outline ranging from broadly convex to anterior promesonotum smoothly rounded, thereafter more-or-less flattened, with promesonotum on same plane as propodeum; promesonotal setae very variable, from seven or eight to more than a dozen; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove strongly impressed, with distinct transverse costulae or weakly impressed, with faint costulae or costulae lacking. Propodeum shining and smooth, metapleuron with a few weak to strongly defined, longitudinal, hair-like striolae; propodeal dorsum convex to flat throughout most of its length; smoothly rounded or with indistinct angle; standing propodeal setae either (i) consisting of one prominent pair anteriad, with other shorter setae very sparse or absent, or, (ii) consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum, or, (iii) consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum, or, equidistant from metanotal groove and declivitous face of propodeum; vestibule of propodeal spiracle absent or not visible; propodeal lobes either present as rounded flanges, or, present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral or laterodorsal and situated within anterior sector of petiolar node. Node (viewed in profile) cuneate with vertex tapered or rounded, or, conical with vertex tapered or rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4. Anteroventral petiolar process either present as a thin flange tapering posteriad, or, absent or vestigial; ventral petiolar lobe present. Height ratio of petiole to postpetiole between 3:2 and 1:1; height–length ratio of postpetiole between 3:2 and 1:1; postpetiole shining and smooth; postpetiolar sternite not depressed at midpoint, its anterior end either an inconspicuous lip or small carina, or, this structure lacking or vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae, or, consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color of foreparts yellow to chocolate, gaster of same color or darker, appendages yellowish to brown or bicolored (but not darker than mesosoma). Worker caste monomorphic.

LECTOTYPE MEASUREMENTS (*M. termitobium*): Not taken, as the lectotype is headless.

LECTOTYPE MEASUREMENTS (*M. exchao*): HML 1.22 HL 0.48 HW 0.37 CeI 77 SL 0.34 SI 92 PW 0.24.

WORKER MEASUREMENTS (non-types): HML 0.86–1.54 HL 0.32–0.59 HW 0.25–0.50 CeI 74–90 SL 0.22–0.44 SI 76–109 PW 0.15–0.32 (n=200)

QUEEN DESCRIPTION.— HEAD: Head square to rectangular; vertex weakly concave or planar; frons either completely shining and smooth except for piliferous pits, or, shining and smooth with a few striolae around antennal sockets and frontal carinae; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye either more-or-less circular, or, elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint to below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule to set posteriad of midline of head capsule.

MESOSOMA: Pronotum and anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 7:3 and 3:2. Axillae variable, separation of axillae can range from width of at least one axilla to axillae contiguous, or nearly so. Standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, with multiple hair like striolae on metapleuron; propodeum smoothly rounded, with indistinct angle, or, angulate, propodeal angle blunt; propodeal dorsum either convex, or, flat throughout most of its length, or, slightly elevated anteriad and sloping away posteriad, propodeal angles not raised; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum, or, equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges, or, present as vestigial flanges only, or absent.

WING: Wing veins predominantly depigmented (wing membrane itself may have smoky tinge), with distal segments reduced to vestigial lines; vein m–cu always absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node, or, lateroventral and situated within anterior sector of petiolar node; node, in profile, very variable, ranging from cuneate, vertex tapered or rounded, or, cuneate, vertex rounded and node inclined posteriad, to conical, vertex tapered or rounded; appearance of node shining and smooth, or, shining, with vestigial sculpture, or, shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:2 and 1:1. Anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; height ratio of petiole to postpetiole between 3:2 and1:1; height–length ratio of postpetiole between 3:2 and1:1; postpetiole shining and smooth, or, shining, with vestigial sculpture, or, shining and weakly striolate posteriad; postpetiolar sternite not depressed, its anterior end an inconspicuous lip or small carina or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae, or, consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color of head and mesosoma yellow to chocolate, gaster yellowish to chocolate, sometimes with variable lighter bands or pale patches or maculae near base of first gastral tergite. Brachypterous alates not seen. Ergatoid or worker-female intercastes seen.

LECTOTYPE MEASUREMENTS (*M. imerinense*): HML 2.36 HL 0.68 HW 0.67 CeI 99 SL 0.53 SI 79 PW 0.54.

OTHER QUEEN MEASUREMENTS: HML 1.61–2.53 HL 0.49–0.72 HW 0.42–0.65 CeI 83–98 SL 0.36–0.65 SI 77–94 PW 0.32–0.73 (n=62).

MALE DESCRIPTION.— HEAD: Head width–mesosoma width ratio between 1:1 and 3:4; frons smooth to finely striolate, or, vestigial, consisting of micropunctation and fine striolae, or, finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 1:1 and 1:2. Maximum number of mandibular teeth and denticles four.

MESOSOMA: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron, or, shining and faintly striolate throughout, striolae becoming more deeply impressed on posterior mesopleuron, or, shining, with dorsum faintly striolate. Parapsidal furrows distinct to vestigial or absent; notauli denoted by a central groove, or, absent. Axillae separated by width of at least one axilla to narrowly separated (i.e., less than width of one axilla).

WING: Wing veins predominantly depigmented (though wing membrane itself may have a smoky tinge), with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node. Node (viewed in profile) highly variable, being either conical, with vertex tapered or rounded, or, evenly tumular to roundly conical, to tumular, inclined posteriad, with vertex also tapered posteriad; appearance of node also variable, from shining and smooth to completely shagreenate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 3:4. Anteroventral petiolar process absent or vestigial. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 7:3 and 1:1; postpetiole shining, with vestigial sculpture, or, shining and smooth anteriad, micropuncate posteriad.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae, or, consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color yellowish-brown to chocolate, legs paler in some specimens.

MALE MEASUREMENTS: HML 1.50–2.36; HL 0.39–0.60; HW 0.38–0.72; CeI 88–120; SL 0.12–0.24; SI 28–44; PW 0.43–0.78 (n=63).

REMARKS.— *Monomorium termitobium*, as it is here understood, is not only the most abundant *Monomorium* species on Madagascar, often representing 80–90% of the *Monomorium* specimens in a given sample, but one that is almost intractable to taxonomic analysis based purely on morphology. What I recognize here is the best that I can currently make of the available material, which includes hundreds of queens and many males, as well as thousands of workers. While the amount of CAS material available for study has been daunting, most specimens, unfortunately, have been taken by bulk sampling methods (especially pitfall trapping and from sifted litter) rather than directly from colonies. Collection of nest series is vitally important for taxonomically difficult species (or species complexes) such as this one, to enable the researcher to associate workers with reproductives. In the case of taxa whose workers are without distinctive physical features (such as many small *Monomorium*), such reproductives may provide valuable additional characters as well as being significant in their own right for a good understanding of the taxonomy of a species. Undoubtedly, a more definitive diagnosis of *M. termitobium* will require molecular analysis.

However the species may finally be interpreted, *Monomorium termitobium* is unquestionably highly variable in appearance, and the provisional synonyms here include two African forms currently described as good species. Workers that can be associated together on the basis of shared morphological features often vary in their color, which ranges from bright yellow to deep chocolate. In many cases involving brown specimens, or specimens with a yellow mesosoma and a brown head, the antenna has a brown scape and a yellow funiculus. In workers with light colored foreparts the gaster can be completely yellow, infuscated to varying degrees, or completely black. The clypeal carinae can be strongly defined and parallel or subparallel, weakly defined or completely lacking, the anteromedian sector of the clypeus in the latter being somewhat bulging in appearance (as in *M. micrommaton*). The anteromedian clypeal margin is mostly emarginate in workers with strongly defined clypeal carinae and in a few bicolored workers with dark heads, but without strongly defined clypeal carinae, and straight or convex in the others. The promesonotum, viewed in profile, ranges from roundly convex to quite straight. The propodeum, also viewed in profile, may be rounded, roughly square or elongate. The petiolar node is most commonly broadly conical and tending to circular in cross-section, but may be narrowly cuneate or low, conical and tapered. Pilosity varies, the number of pairs of erect promesonotal setae ranging from three, e.g., brown and yellow specimens of '*binatu*' from Toliara Province, to seven or more (the additional setae often being simply shorter and appressed rather than actually absent in the less 'shaggy' forms). Clinal patterns of color and morphology may exist but are difficult to anatomize, in view of the overwhelming number of specimens that have to be considered (around half-a-dozen packed drawers of pinned specimens, and much wet material besides).

This array of diverse forms has a few worker characters that separate them from similar but more easily recognized species. The mandible always has four teeth, and the basal tooth is usually about the same size as or slightly smaller than the preceding tooth, rarely being reduced to a minute denticle (unlike *M. flavimembra*). The diameter of the eye is between one and one-and-a-half times the greatest width of the antennal scape and has 10 or more ommatidia in all except a tiny handful of specimens with a brownish cast to their head capsules (distinguishing workers of this species from those of *M. micrommaton*). Commonly, there is a peripheral ring of ommatidia with a central row of two or three ommatidia, but two or more rows may be present. Workers with a light-colored head and mesosoma and dark gaster always have narrowly separated and well-defined clypeal carinae, setting them apart from *M. lepidum*.

The material I have examined clusters around about half-a-dozen forms, which I consider most likely to constitute good species if a future revision involving molecular analysis should indicate that *M. termitobium* is a complex. As far as I can see, however, the characters that distinguish clusters of these specimens are not fixed for the entire gene pool, and intermediate forms occur. The most salient morphotypes are:

Monomorium termitobium sensu stricto. Workers conforming closely to the lectotype are bright lemon yellow to a dusky brownish-yellow, often without any gastral infuscation whatever. In some populations the sides of the first gastral tergite have black markings, which may give the gaster a bimaculate appearance in dorsal view (*Monomorium termitobium* form '*exchao*'), or the entire gaster may be a pale, shiny brown, almost iridescent in some lights. Several long series from Antsiranana are light brown with very pale, depigmented tibiae and tarsi. The head of pale '*termitobium*' is often of darker hue than the mesosoma in dorsal view. The clypeal carinae are highly variable in form, being well-defined in some individuals and completely absent in others. The promesonotum, in profile, varies from broadly convex to rather flattened. Standing setae number at least four pairs, often more. The infrahumeral setae are usually well-developed and longer than half the length of the humeral setae, but can be shorter, tending to appressed. The petiolar node is conical and well-rounded, and the preceding peduncle is short and sculptured just before the node. Overall size is very variable, from about 1.3mm to at least 2 mm (i.e., HML 1.00–1.65mm). This form is dispersed throughout the island.

The queen is pale orange or yellow with a brownish gaster (rarely, variegated light brown and orange) and hairy in appearance, with many semi-erect and decumbent setae on the frons and promesonotum. The first gastral tergite may have two small, pale, oval areas near its base. The mesosoma is relatively small in relation to the head and seen to be laterally compressed when viewed dorsally. The male is usually of a light brown and conspicuously hairy. The wings are always brown, and densely covered with small setae. The wing veins are relatively well-developed and sector Rs of the radial vein and the cross-vein connecting it to the pterostigma may have a silvery sheen.

Monomorium termitobium form '*imerinense*'. Workers are more streamlined in appearance than the former morphotype, and typically light- to yellowish-brown with a darker head and gaster. They can, however, be yellow, though the head usually has a brownish tint. The clypeal carinae are usually distinct, but weak, and the head capsule in full-face view has decidedly convex sides. Also included under this head are very many series of mainly much smaller, brown to chocolate workers with distinct clypeal carinae between which the median sector of the clypeus is shallowly excavate so as to form a groove. In these workers, the clypeal carinae tend not to be complete, with the result that the groove also does not reach the anterior clypeal margin, which is narrowly rounded. The head capsule usually has straight sides. Both groups are connected by a few specimens of intermediate size and morphology. In large workers the mesosoma is more flattened than in typical '*termitobium*', and the conical node, which is often broad and low, is more narrowly rounded dorsally. Small workers have a slightly convex to distinctly flattened mesosoma, and a node similar to '*termitobium*'. The pilosity is like that of *termitobium*. The appearance of large '*imerinense*' workers is very suggestive of *M. flavimembra*, but the basal tooth is well-developed in '*imerinense*', and the anteromedian clypeal margin is less depressed. The HML of larger specimens, i.e., the 'typical form', ranges from 1.29 mm to 1.54 mm, and the HML of small, compact specimens of similar appearance is 0.93 mm to 1.13 mm. A smaller number of nondescript brown workers are of intermediate size.

The queen associated with larger workers is brown and the male is glossy and deep reddish-brown, almost black. Both queen and male are distinctly less hairy than the corresponding reproductives of '*termitobium*'. The wings have well-defined veins whose outlines are often brown, but the wings are only lightly to moderately pilose. Queens associated with smaller workers are similar, but reduced in size. Nb. *Monomorium imerinense* was described from Andrangoloaka in Province Antananarivo from a queen and a male. These correspond well to queens and males recently collected from Antsiranana.

Monomorium termitobium form '*binatu*'. With a very elongate mesosoma, a straight propodeum, long antennal scape (SI mostly > 100) and frequent count of only three pairs of erect promesonotal setae, worker samples of this morphotype (here defined as a distinctive form of a taxon) from the south of Madagascar in Toliara Province appear at first glance sufficiently distinctive to warrant separate species status. The situation is complicated by the fact that slightly more northern populations from Fianarantsoa Province are less elongate, often have four or more pairs or erect promesonotal setae, and tend to merge in morphology with the smaller, yellow '*termitobium*'. The color of '*binatu*' is also variable throughout its range, concolored specimens being yellow or brown with other workers being yellow with an infuscated or even black gaster. A large series of brown workers from St Luce, Toliara Province, have the three erect pairs of setae, but in terms of shape of node, etc., seem to form an intermediate cluster between the yellow '*binatu*' (HML 1.05–1.30 mm) and larger '*imerinense*'.

Most collections of this morphotype have been taken from Toliara Province, and the further south they have been collected, in general, the more their appearance conforms to that of the Zimbabwean holotype of *M. binatu*. The queen is relatively large with orange foreparts and a dark brown to black gaster. The petiolar node is thin, tending to squamiform, and wide, contrasting with the thick, dorsally rounded node of '*imerinense*'. The node of '*termitobium*' is intermediate. The male of '*binatu*' has not been recognized among the CAS material.

Monomorium termitobium dark-headed form. Differences between this morphotype and the quite distinct species *Monomorium floricola* are noted above. Workers in which the chocolate head contrasts with a pale yellow mesosoma, nodes and gaster are among the most spectacular small *Monomorium* on Madagascar. If the color is ignored, however, it will be seen that the morphology of these workers is the same as that of brown or yellow workers of sympatric populations of '*termitobium*' or '*imerinense*', and varies as they vary. Also, if an array of workers of increasingly dark mesosoma color is placed together, they will be found to merge into '*imerinense*'. Distinct within this morphotype is a small number of workers and queens in which the anteromedian clypeal margin is emarginate, though the clypeal carinae are not developed. This character is variable, appears to relate purely to the individual or to a particular nest, and to be without taxonomic significance. The intensification of color in the head capsule appears to be a variable feature throughout all populations of *M. termitobium*, and the strikingly bicolored form may represent a different allele or alleles, or the result of a different mix of the proteins that control this expression of color in the worker. The queen is brown with yellow bands on the gaster, and has pale wings and brownish wing veins, but otherwise is similar in appearance to '*termitobium*. No male has been associated with this form.

Monomorium termitobium small yellow form. The worker is pale yellow, minute (HML 0.75–0.94mm) with a very long antennal scape (SI 91–103). The appearance and morphology are those of a very small *binatu*, and, as with that morphotype, this form usually has appressed or very short erect infrahumeral setae. The clypeal carinae are sharply defined, the node is always low, conical and the queen is visibly smaller than, though morphologically similar to, the queen of other morphotypes of *M. termitobium*. The male is unknown. This form has some claims to being a separate, cryptic species, since it does not vary in its appearance in its wide range through the island. However, in Mahajanga Province, where it is most abundant, the appearance of the worker is convergent with that of the very small '*termitobium*' that occurs there. The small '*termitobium*' generally has more weakly defined clypeal carinae, four or more prominent pairs of erect promesonotal setae and a more robust petiolar node. However, workers of both morphotypes often have a fleck of brown pigment on the gena between eye and mandibular insertion. The pattern of infuscation on the sides of the gaster in the small yellow form, moreover, matches that found in most '*termitobium*'.

Known from a few series from Tsimanampetsotsa, Toliara Province, is a handsome morphotype in which the workers are bright orange with a very flat promesonotum. The gaster has distinct brown bands, and the petiolar peduncle is very short. The male, but not the queen, is known. That insect is light brown and smooth with minimal pilosity. The wings are of a milky, pale appearance, the veins being almost invisible against a pale background. This morphotype tends to merge with surrounding populations of '*binatu*'.

The impression I am left with, after many hours of examination of these specimens, is that a single founder species of African origin has given rise to branches in which speciation at this point of time is almost, but not quite complete. Although some worker and queen morphotypes include distinctive individuals or populations of individuals, this does not hold true for the members of all populations of that morphotype, and the distinctions therefore cannot be expressed in a taxonomic key. Differences between the known males, however, are greater and may be significant. With all of the preceding aspects in mind, I am provisionally synonymizing *Monomorium binatu* Bolton, *Monomorium exchao* Santschi and *Monomorium imerinense* Forel under the earliest name, *Monomorium termitobium* Forel. The affinities of *M. termitobium* in its various incarnations seem to lie with the *M. rhopalocerum* group, but I am ascribing to the latter a greater degree of morphological variability than expressed by Bolton (1987). The species is ubiquitous in all situations and has been collected by all the methods commonly used by myrmecologists and their teams.

Monomorium versicolor Heterick, sp. nov.

Figs. 25, 67–68.

ETYMOLOGY.— Latin 'of various colors'.

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Toliara**, Rés. Berenty, Forêt Malaza, 8.6 km 314 NW Amboasary 25°00'S, 46°18'E 40m, 6.ii.2002 Fisher *et al* BLF #/ex rotten log, gallery forest/CASENT 0042524 5434 (CAS). PARATYPES: **Prov. Toliara** (all specimens with same collection data as holotype): 2☿, 1♂ (ANIC); 12☿ + 2♀ + 12♂ (BMNH); 3☿, 1♂ (CAS); 22☿ + 1♀ + 13☿ (MCZ).

Other material examined: **Prov. Antsiranana:** Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (10☿); Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (3☿); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (3☿). **Prov. Fianarantsoa:** P.N. Isalo, Sahanafa Riv., 29.2 km 351 N Ranohira R. S. 10–13.ii.2003 Fisher *et al.* (5☿); Res. Andringitra 8.5 km SE Antanitotsy 6.iii.1997 B.L. Fisher (8☿, 1♀). **Prov. Mahajanga:** Forêt Analalava, 29.6 km 280 W Ranohira 1–5.ii.2003 Fisher *et al.* (19☿, 1♀) P.N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (1☿); N. Ankarafantsika, Tsimaloto, 18.3 km 46 NE Tsaramandroso 2–8.iv.2001 Rabeson *et al.* (66☿); P.N. Namoroka, 9.8 km 300 WNW Vilanandro 4–8.xi.2002 B.L. Fisher (3♀); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 B.L. Fisher (18☿); P.N. Tsingy de Bemaraha, 2.5 km 62 ENE Bekopaka 11–15.xi.2001 (1♀); Res. Bemarivo, 23.8 km 223 SW Besalampy, 19–23.xi.2002 Fisher *et al* (1☿). **Prov. Toliara:** P.N. Andohahela, Manantalinjo, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (28☿); P.N. Andohahela, 1.7 km 61 ENE Tsimelahy 16–20.i.2002 Fisher *et al.* (12☿); Rés. Berenty, Forêt Malaza, 8.6 km 314 NW Amboasary 6.ii.2002 Fisher *et al.* (2☿); southern Isoky-Vohimena Forest, 21.i.1996 B.L. Fisher (2☿) Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka, 22–26.iii.2002 B.L. Fisher (1☿).

Worker description.— Head: Head oval; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule to set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae indistinct; anteromedian clypeal margin straight, or, emarginate, clypeal carinae indistinct; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandible with three evenly sized teeth; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t2 (three teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex; promesonotal setae greater than twelve; promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove weakly impressed, with faint costulae or costulae lacking. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 3:4; anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

GENERAL CHARACTERS: Color variable: from concolorous dark reddish-brown to orange-and-brown, or orange, gaster chocolate, antenna always darker than head in lighter-colored specimens. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.50 HL 0.58 HW 0.51 CeI 89 SL 0.48 SI 93 PW 0.32.

OTHER WORKER MEASUREMENTS: HML 1.21–1.63 HL 0.49–0.62 HW 0.41–0.55 CeI 82–89 SL 0.38–0.52 SI 85–101 PW 0.25–0.36 (n=20).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; (viewed dorsally), occipital angles of head capsule conspicuous, lobate; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron; Propodeum shining and smooth, with a few weak striolae on metapleuron. Propodeum oblique, more-or-less straight; propodeal dorsum flat throughout most of its length; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Propodeal lobes present as well-developed, rounded flanges.

WING: Wing not seen (queens dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered. Appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 2:1 and 3:2; anteroventral petiolar process present as a thin flange tapering posteriad; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 7:3 and 2:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color dark chocolate, mandibles orange. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 1.81–1.94 HL 0.58–0.64 HW 0.49–0.53 CeI 80–84 SL 0.45–0.54 SI 90–102 PW 0.37–0.38 (n=5).

MALE DESCRIPTION.— HEAD: (In full-face view) head width–mesosoma width ratio between 4:3 and 1:1; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 2:3 and 1:2. Maximum number of mandibular teeth and denticles three.

MESOSOMA: Mesoscutum broadly convex; pronotum and mesoscutum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; parapsidal furrows distinct; notauli absent; axillae separated by width of at least one axilla.

WING: Wing veins predominantly depigmented, with distal segments reduced to vestigial lines; vein m–cu absent; vein cu–a absent.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 2:1 and 3:2; postpetiole shining, with vestigial sculpture.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color chocolate.

MALE MEASUREMENTS: HML 1.63–1.86 HL 0.49–0.54 HW 0.47–0.53 CeI 94–102 SL 0.15–0.18 SI 31–35 PW 0.45–0.65 (n=10).

REMARKS.— This fairly large (worker HML 1.21–1.63 mm), handsome species is readily recognized, principally through its three-toothed mandible and high, vertically attenuate petiolar node. The postpetiole is also high and somewhat compressed, resembling that of *M. platynodis*. The different color pattern and the shape of the clypeus distinguish it from that species. The body color of workers varies from a light brownish-orange with darker gaster to uniform blackish-red, and in many workers the propodeum in dorsal view is distinctly darker than the promesonotum. In lighter colored workers the brown antennal scapes are always slightly to distinctly darker than the head capsule. The anteromedian clypeal margin is broadly depressed, as in other members of the *M. flavimembra* complex. The queen and male are equally distinctive, with three strong teeth on each mandible. The occipital angles in queens and males are produced to form a small lobe or sharp angle, which is best seen in dorsal view. The wings of reproductives are pale and the veins are weak, becoming obsolete distally.

Monomorium versicolor is distributed throughout Madagascar, with most collections coming from southern and western regions. Like many other Malagasy *Monomorium* this species prefers a wood substrate for its nests, while individual workers have been collected by such means as beating of low vegetation and sifting of litter. *Monomorium versicolor* does not appear to be limited by habitat, being found in a diverse number of vegetation communities including spiny forest, dry tropical forest, montane rainforest and gallery forest.

Monomorium xuthosoma Heterick, sp. nov.

Figs. 25, 69.

ETYMOLOGY.— Greek '*xouthos*' (yellowish-brown) + '*soma*' (neut. 'body')

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Toliara**, Tsimanampetsotsa, 6.7 km 130 SE Efoetse, 24°06′S, 43°46′E 25 m, 18–22.iii.2002 B.L. Fisher *et al.* BLF 6160/sifted litter, spiny forest/thicket/CASENT 0020507 6160(17) (CAS). PARATYPES: **Prov. Toliara** (all specimens with same collection data as holotype): 3☿ (ANIC); 2☿, 1♀ (BMNH); 2☿ (CAS); 2☿, 1♀ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Toliara:** Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* (19☿, 1♀); Ifaly, 17.ix.1993 W. E. Steiner & R. Andriamasimanana (2☿) (MCZ); Mahafaly ['Mahafely'] Plateau 6.2 km 74 ENE Itampolo, 21–25.ii.2002, Fisher *et al.* (18☿); Madarano ['Manderano'], 10.iv.2002, Frontier Project MG030 (1☿); Ranobe, Frontier Project 5–28.i.2003, MGFO54 (2☿); Ranobe, Frontier Project 25–28.iv.2003, MGFO64 (2☿); Res. Berenty, 10.ii.1993 P. S. Ward (1☿)

(MCZ); Tsimanampetsotsa, 6.7 km 130 SE Efoetse, 18–22.iii.2002 B.L. Fisher (15☿, 6♀); Tsimanampetsotsa, Bemanateza, 23.0 km 131 SE Beheloka, 22–26.iii.2002 B.L. Fisher (18☿, 2♀).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set below midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth three, plus minute, basal denticle or angle; mandibles with sub-parallel inner and outer margins, smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth a small to minute denticle or angle, much smaller than t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) promesonotum broadly convex anteriad, convexity reduced posteriad; promesonotal setae seven to twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum convex; Propodeum always smoothly rounded; standing propodeal setae consisting of one prominent pair anteriad, with other shorter setae very sparse or absent; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; petiolar node, in profile, cuneate, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color foreparts tawny-yellow to orange (postpetiole sometimes darker), antenna brown, gaster chocolate. Worker caste monomorphic: HML 1.14 HL 0.44 HE 0.35 CeI 80 SL 0.33 SI 94 PW 0.24

Other worker measurements: HML 1.13–1.32 HL 0.43–0.5 HW 0.35–0.42 CeI 79-84 SL 0.32–0.39 SI 90–93 PW 0.23–0.28 (n=20).

Queen description.— Head: Head square; vertex always planar; frons shining and longitudinally striolate, with some smooth areas; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye ovoid, narrowed posteriad; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule.

Mesosoma: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined about 2:1; axillae separated by width of at least one axilla to narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of well-spaced, incurved, erect and semi-erect setae only; appressed pronotal, mescoscutal and mesopleural setulae very sparse or absent. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeum always smoothly rounded; propodeal dorsum convex; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges.

Wing: Wing not seen (queen dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 1:1; postpetiole shining and weakly striolate posteriad; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color foreparts dark yellowish-brown, gaster and antennal scape brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 2.27–2.43 HL 0.63–0.66 HW 0.58–0.61 CeI 91–95 SL 0.49–0.52 SI 83–86 PW 0.50–0.54 (n=9).

Remarks.— *Monomorium xuthosoma* strongly resembles *M. termitobium* form '*binatu*' but can be distinguished from that form by its larger propodeal spiracle, the slightly different shape of the propodeum, its higher postpetiole and the pilosity of the promesonotum (at least four prominent pairs of erect setae present, including the infrahumeral pair). The queen is similar in form to that of '*binatu*', but the frons is markedly longitudinally striolate. The male is unknown. This unobtrusive member of the *M. rhopalocerum* complex is confined to Toliara province, where almost all specimens seen have come from the southwestern corner. One slightly aberrant worker (MCZ) was taken from Berenty Reserve, in the south-east. The species appears to be confined to spiny forest, where individuals have been taken from sifted litter and members of a colony were found in a rotten log.

THE *HANNELI*-GROUP

Monomorium hanneli Forel

Figs. 26, 70–71.

Monomorium hanneli Forel, 1907a:18. Holotype ☿, Kenya: Mto-ya-Kifaru (Katona) (MHNG) [examined].

Monomorium moestum Santschi, 1914a:74, fig. 7. Syntype ☿ (lectotype here designated), Kenya: Naivasha (NHMB) [examined].

M. (*Notomyrmex*) *moestum* Emery, 1922:170. Syn. under *M. hanneli* Bolton, 1987: 426.

Monomorium valtinum Bolton, 1987:428. Holotype ☿, Kenya: Kilifi District, (MHNG) [examined]. syn. nov.

Material examined.— ***M. hanneli***: Holotype: ☿, Kenya, Mto-ya-Kifaru (Katona) (MHNG). This worker was designated a 'holotype' by Bolton (1987), and since the length is given as a single measurement, it seems clear no other specimens were examined. Holotype status based on monotypy (Code 73.1.2) is here assumed. ***M. moestum***: LECTOTYPE: ☿, Kenya ('British East Africa'), Naivasha, Dec. 1911, Alluaud and Jeannel, 1900 m st. no. 14 (NHMB – Reg. No. 205a). Although described as a 'holotype' by Bolton (1987), Santschi gives a range of lengths for *M. moestum*, indicating more than one specimen was examined. The lectotype fixes the name for populations of *M. hanneli* with very large, dark workers. ***M. valtinum***: HOLOTYPE: ☿, Kenya, Kilifi District, Mahnert, V. & Perret, J-L., 29.x.1977 (MHNG) (See Bolton 1987 for measurements).

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** Ampasindava, Ambilanivy, 3.9 km 181 S Ambaliha 4–9.iii.2001 Fisher *et al.* (7☿, 1♀, 11♂); Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (1☿); Nosy Be, Rés. Lokobe, 6.3 km 112 ESE Hellville 19–24.iii.2001 Fisher *et al.* (6☿, 1♀); R.S. Manongarivo, 12.8 km 228 SW Antanambao 11.x.1998 B.L. Fisher (13☿). **Prov. Fianarantsoa:** R. S. Ivohibe, 6.5 km ESE Ivohibe, 24–30.x.1997 B.L. Fisher (1☿). **Prov. Mahajanga:** Forêt de Tsimembo 11.0 km 346 NNW Soatana 21–25.xi.2001 Fisher *et* al. (1☿); P.N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (2☿); P.N. Ankarafantsika, Tsimaloto, 2–8.iv.2001 18.3 km 46 NE Tsaramandroso Rabeson *et al.* (7☿); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (1♀, 4♂); P.N. Tsingy de Bemaraha, 2.5 km 62 ENE Bekopaka 11–15.xi.2001 Fisher *et al.* (1☿); Res. Bemarivo, 23.8 km 223 SW Besalampy Fisher *et al* 19–23.xi.2002 (1☿, 1♀). **Prov. Toamasina:** F. C. Andriantantely 4–7.xii.1998 (13☿, 1♀) 7–10.xii.1998 (27☿) H.J. Ratsirarson; F. C. Sandranantitra 18–21.i.1999 (15☿) 21–24.x.1999 (15☿) H.J. Ratsirarson; Mont. Akirindro, 7.6 km 341 NNW Ambinanitelo 17–21.iii.2003 Fisher *et* al. (1☿); Mont Anjanaharibe, 18.0 km 21 NNE Ambinanitelo 8–12.iii.2003 Fisher *et al.* (2☿). **Prov. Toliara:** Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (7☿, 3♀); 10 km NW Enakara, Rés. Andohahela 24.xi.1992 B.L. Fisher (3☿); Rés. Berenty, Forêt Bealoka, 14.6 km 329 NNW Amboasary 3–8.ii.2002 Fisher *et al.* (1♀); Forêt de Petriky, 12.5 km W 272 Tolagnaro 22.xi.1998 B.L. Fisher (18☿, 2♀); P.N. Zombitse, 19.8 km 84 E Sakaraha 5–9.ii. 2003. Fisher *et al.* (10☿); P.N. Zombitse, 17.7 km 98 E Sakaraha 8.ii. 2003 Fisher *et al.* (12☿); Rés. Ambohijanahary, 35.2 km 312 NW Ambaravaranala 13–17.i.2003 Fisher *et al.* (1♀); R.S. Manongarivo, 10.8 km 229 SW Antanambao 8.xI.1998 B.L. Fisher (34☿, 11♀); S. F. Mandena, 8.4 km NNE 30 Tolagnaro 20.xi.1998 B.L. Fisher (26☿, 3♀); 2.7 km WNW 302 Ste Luce, 9–11.xii.1998 B.L. Fisher (2♀).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye small, eye width less than 1× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions; Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised; propodeum distinctly angulate, propodeal angle sharp; length ratio of propodeal dorsum to its declivity about 3:2; standing propodeal setae consisting of one prominent pair anteriad. with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Vestibule of propodeal spiracle distinct in some specimens; propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:4 and 1:2; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90, or, not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color yellowish to tawny orange. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS (*M. hanneli*): HML 1.43 HL 0.51 HW 0.43 CeI 84 SL 0.35 SI 81 PW 0.31.

LECTOTYPE MEASUREMENTS (*M. moestum*): HML 1.60 HL 0.56 HW 0.49 CeI 88 SL 0.38 SI 78 PW 0.34.

OTHER WORKER MEASUREMENTS (non-types): HML 1.22–1.49 HL 0.45–0.54 HW 0.38–0.45 CeI 82–87 SL 0.31–0.38 SI 82–86 PW 0.28–0.33 (n=20).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits and a few striolae around antennal sockets and frontal carinae; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 3:2 and 4:3; axillae contiguous, or nearly so; standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, metapleuron with a few distinct striolae; propodeum angulate, propodeal angle blunt, or, distinctly angulate, propodeal angle sharp; propodeal dorsum flat throughout most of its length, or, sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of one pair of prominent setae anteriad, with a few smaller, erect to decumbent setae on and around dorsal and declivitous faces; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present in some individuals; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node, or, lateroventral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:2 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90°, or, not depressed, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color yellow-orange, gaster may have brownish tint. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 1.40–1.71 HL 0.47–0.57 HW 0.41–0.48 CeI 84–89 SL 0.34–0.41 SI 80–85 PW 0.31–0.44 (n=20).

MALE DESCRIPTION.— HEAD: (In full-face view) head width–mesosoma width ratio between 1:1 and 3:4; frons finely micropunctate. Compound eyes protuberant and elliptical; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 2:3 and 1:2. Maximum number of mandibular teeth and denticles two.

MESOSOMA: Mesoscutum broadly convex; a few vestigial striolae on dorsum of mesoscutum, otherwise smooth and shining; parapsidal furrows vestigial or absent; notauli absent; axillae separated by width of at least one axilla.

WING: Wing veins with vein M indistinct distally, otherwise tubular and sclerotised; vein m–cu absent; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) cuneate, vertex tapered, or, conical, vertex tapered; appearance of node shining and smooth; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:2 and 4:3, or, between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 3:2; postpetiole shining and smooth.

GASTER: Pilosity of first gastral tergite consisting of well-spaced, semi-erect setae.

GENERAL CHARACTERS: Color brown, head darker, appendages light brown.

MALE MEASUREMENTS: HML 1.34–1.61 HL 0.44–0.48 HW 0.39–0.44 CeI 88–98 SL 0.11–0.13 SI 28–31 PW 0.44–0.52 (n=11).

REMARKS.— *Monomorium hanneli* is distinctive throughout its range, being the only member of its species group in Madagascar. The main variation is a pale worker morphotype that has been found in most of the major collection localities, usually in the same transects, as the normal, darker morphotype. Since it has occasionally been collected in the same pitfall trap or in a pitfall trap adjacent to one in which the darker morphotype has been captured, it may conceivably occur within the same nests. This, however, cannot be established with certainty, as only one CAS nest series of just eight workers of this small species is known. The normal worker is usually yellow-orange to tawny orange, with a distinct metanotal groove and angulate propodeum. Well-spaced, erect setae are the usual pilosity pattern on the gaster and the antennal scape, the latter also possessing decumbent setae. The pale yellow or orange form has a much more rounded mesosoma profile, almost crescentic, with a less angulate propodeum. The head in profile is rather fuller than the normal morphotype, which, together with the rounded mesosoma, gives the ant somewhat of a bloated appearance. The gastral setae are abundant and decumbent, the setae on the scape decumbent or appressed. The appearance is reminiscent of a larger *M. chnodes*. Whatever the reason for these differences, the pale workers are not simply tenerals, since their morphology differs from that of other workers. Queens of the pale morphotype also exist, and the same differences in pilosity noted above are the major distinction between these and the normal, darker form. The queen is a bright orange. The distinction between the two forms, however, is not clear-cut and individuals with an intermediate appearance occasionally occur.

Bolton (1987) separated two ostensibly different Kenyan forms, the smaller *Monomorium valtinum* and the larger *M. hanneli*, principally on the basis of the smaller eye in *M. valtinum*. This researcher had relatively few specimens available to him and these excluded queens and males. In Madagascar, by contrast, what I take to be *M. hanneli* is very common and I have been able to examine hundreds of specimens, including over twenty queens and around a dozen males (my descriptions being based on 20 of the former and 11 of the latter). The size of the eye is clearly variable: the number of ommatidia in workers examined ranges from six, in paired rows of three, to at least sixteen with three transverse rows of four ommatidia. On one pin holding three workers of a nest series, the middle worker had 16 ommatidia visible under a stereomicroscope, the other two 11. The body size of Malagasy workers also overlaps the parameters of the morphometric measurements given by Bolton for the two taxa. For this reason, I consider *M. valtinum* and *M. hanneli* to be representatives of the same species, and *M. valtinum* becomes a junior synonym in this work. The queens and males generally have lightly-sclerotized wing veins, with vein M indistinct distally in the male. Vein m–cu has been absent from the wings of all males examined thus far, but is occasionally present in alate queens.

The types described from African worker material differ from Malagasy material in being slightly (*Monomorium hanneli*, *M. valtinum*) to considerably (*M. moestum*) darker with a more brownish or reddish tinge to the cuticle, and in having very small but sharp clypeal denticles. Malagasy populations of this ant range from yellow to tawny orange, and the anteromedian clypeal margin is either straight or weakly emarginate with blunt to sharp angles rather than denticles. I understand these to be non-significant differences, *M. hanneli* revealing considerable variation in color and morphology among both African and Malagasy populations.

Monomorium hanneli has been collected throughout the island of Madagascar, most frequently near the coast. The usual habitat is rainforest, though it also occurs in dry tropical forest and spiny forest. Sifted leaf litter has been the usual collection method, but the nest series was taken from under a stone.

THE *HILDEBRANDTI*-GROUP

Monomorium adiastolon **Heterick, sp. nov.**

Figs. 27, 72.

ETYMOLOGY.— Greek '*adiastolos*' ('confused') [i.e., with two other very similar species]

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Antsiranana**, R.S. Manongarivo, 17.8 km 218 SW Antanambao, 1580 m 14°01′3″S, 48°25′1″E 27.x.1998 B.L. Fisher 1972/beating low vegetation, montane rainforest/1972(17)–3 (CAS). PARATYPES: **Prov. Antsiranana** (specimens with same collection data as holotype): One ergatoid (BMNH); 2☿ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Antsiranana:** 11.0 km WSW Befingotra, Res. Anjanaharibe-Sud, 16.xi.1994 B. (2☿) 18.xi.1994 (4☿, 5♀) 20.xi.1994 (3☿, 2♀) L. Fisher; R.S. Manongarivo, 12.8 km 228 SW Antanambao 11.x.1998 B.L. Fisher (2☿); R.S. Manongarivo, 14.5 km 220 SW Antanambao 20.x.1998 B.L. Fisher (1☿).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer, erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined, anteromedian clypeal margin straight or emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

Mesosoma: Promesonotum shining and smooth on dorsum, entire lower mesopleuron distinctly striolate; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove vestigial. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised propodeum smoothly rounded or with indistinct angle; standing propodeal setae numerous, wholly or mainly erect or sub-erect, without conspicuous paired setae evident; appressed propodeal setulae abundant, particularly on dorsum of propodeum; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle distinct; Propodeal lobes present as blunt-angled flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) tumular, inclined posteriad, with vertex also tapered posteriad, or, subcuboidal, inclined posteriad; appearance of node faintly striolate, striolae becoming costulate on rear face of node; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining, with vestigial sculpture; postpetiolar sternite not, or, only slightly depressed at midpoint, anterior process prominent.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

General characters: Color yellowish to yellowish-brown, gaster darker brown. Worker caste monomorphic.

Holotype measurements: HML 2.39 HL 0.82 HW O.64 CeI 78 SL 0.64 SI 100 PW 0.48.

Other worker measurements: HML 2.17–2.41 HL 0.75–0.84 HW 0.63–0.70 CeI 81–89 SL 0.58–0.68 SI 88–97 PW 0.45–0.52 (n=14).

Queen description.— Head: Head square; vertex weakly concave or planar; frons shining and smooth except for piliferous pits, or, shining and smooth except for piliferous pits and a few striolae around antennal sockets and frontal carinae; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye semi-circular; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum length-width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae separated by width of at least one axilla; standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeum distinctly angulate, propodeal angle sharp, or, distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum flat throughout most of its length, or, sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of a few decumbent setae only; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges, or, present as vestigial flanges only, or absent.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle laterodorsal and situated slightly anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

General characters: Color tawny-orange. Brachypterous alates not seen. Ergatoid or worker-female intercastes seen.

Queen measurements: HML 2.70–3.16 HL 0.85–0.96 HW 0.77–0.88 CeI 91–98 SL 0.62–0.74 SI 78–88 PW 0.68–0.85 (n=2).

remarks.— The taxonomic position of *M. adiastolon* is rather unsatisfactory, as it has more of the appearance of a hybrid between two other taxonomically difficult taxa (namely, *M. fisheri* and *M. hildebrandti*) than of a good species in its own right. I have tentatively identified two morphotypes or forms of this species. Workers from Manongarivo, in Antsiranana Province, have relatively large eyes (15 ommatidia >) for *M. hildebrandti* group workers, and a broad, asymmetrical petiolar node that is longitudinally striolate and similar in appearance to the node of a distinctive coastal population of *M. hildebrandti*. This form has been collected on the same transect as an apparently monomorphic, finely sculptured, small-eyed form of *M. fisheri*. The two ants are visibly distinct taxa. The other form has been collected at Befingotra, in a more eastern region of the Province, where it is adjacent to or sympatric with a population of a different morphotype of *M. fisheri*. In the latter form, the workers are extremely smooth and shiny and the promesonotum is flattened and protrudes laterally at the humeri. Nonetheless, the Befingotra *adiastolon* and *fisheri* workers are much more similar than their counterparts at Manongarivo. At Befingotra *M. adiastolon* also has a striolate node, but this structure is thinner and more like that of the local *M. fisheri*, and the brown coloration, though not the rounded promesonotum, is also similar. The eye, in this population of *M. adiastolon*, is smaller and nearer to that of typical *M. fisheri* belonging to the shiny morphotype. Several samples of the queen of *M. adiastolon* and one ergatoid are known. Queens from Befingotra are of a somewhat smaller average size than *M. fisheri* queens, but otherwise there is no physical difference between the two taxa. All known workers and queens of *M. adiastolon* have a maximum of four mandibular teeth and denticles, whereas at least some members of all the *M. fisheri* morphotypes have five or more, but as this character is variable and the amount of available *M. adiastolon* material is very limited, this fact signifies little.

For the moment, *M. adiastolon* can be separated from *M. hildebrandti* and *M. fisheri* by the characters noted in the key. However, this is provisional, and a better knowledge of the *Monomorium* fauna in the Antsiranana Province, including information from more nest series, could well change the current situation. Both forms have been collected from rotten wood and sifted leaf litter in montane rainforest. The ergatoid and two workers from the Manongarivo population were collected by beating from low vegetation.

Monomorium aureorugosum Heterick, sp. nov.

Figs. 28, 73–74.

Etymology.— Latin '*aureus*' ('golden') + '*rugosus*' ('wrinkled')

Material examined.— Holotype: ☿, **Prov. Toamasina**, 6.9 km NE Ambanizana, 15°34′S, 50°00′E 825m 2.xii.1993 B.L. Fisher #976(41)–19/sifted litter (leaf mold, rotten wood) rainforest (CAS). Paratypes: **Prov. Toamasina** (specimens with same collection data as holotype): 1☿ (ANIC) 12☿ (BMNH); 1☿ (CAS) 23☿ (MCZ).

Other material examined: **Prov. Antsiranana:** RNI Marojejy, 20.xi.1993 Alpert *et* al. (4☿) (MCZ); RNI Marojejy, 10 km NW Manantenina 15–22.x.1996 (1☿). **Prov. Toamasina:** P.N. Masoala, 26.ii–2.iii.2003 D. Silva *et al.* (1☿); 1 km W Sahafary, along Onive River, Masoala Peninsula 25.iv.1996 Alpert *et al.* (16☿) (MCZ).

Worker description.— Head: Head oval; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set anteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club not clearly defined. Clypeal carinae indicated by multiple weak ridges; anteromedian clypeal margin broadly convex; paraclypeal setae short and thickened, not reaching basal margin of closed mandibles; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth five; mandibles triangular and smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present), or, smaller than t4 (five teeth present).

Mesosoma: Promesonotum shining, with whorls of rugae on sides of promesonotum, these becoming longitudinal on dorsum; (viewed in profile) promesonotum broadly convex; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove absent. Propodeum shining, with strong, transverse rugae dorsally, laterally and on declivitous face; propodeal dorsum flat throughout most of its length; propodeum always smoothly rounded; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as blunt-angled flanges; Petiolar spiracle laterodorsal and situated slightly anteriad of petiolar node; node (viewed in profile) broad and thick, with short vertex anteriad, node sloping posteriad; appearance of node transversely rugose, shining between sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1.

Petiole and postpetiole: Anteroventral petiolar process present as a thin flange tapering posteriad to absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 1:1; postpetiole strongly rugose; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color head, gaster and appendages yellow, mesosoma reddish-orange. Worker caste monomorphic.

Holotype measurements: HML 3.61 HL 1.12 HW 1.02 CeI 91 SL 1.02 SI 100 PW 0.75.

Other worker measurements: HML 3.52–3.90 HL 1.10–1.20 HW 1.00–1.09 CeI 89–93 SL 1.02–1.07 SI 98–103 PW 0.74–0.82 (n=13).

Remarks.— *Monomorium aureorugosum* is one of two very large members of the *M. hildebrandti* group with a restricted range in far north-eastern Madagascar. This ant, along with *M. infuscum*, is known only from a small number of workers. Because their ranges overlap, and they are clearly closely related, it is tempting to combine the two forms. However, they appear to represent distinct species, not only because there exist no examples of intermediate color, but because there are subtle but consistent differences in the morphometrics pertaining to the antennal scape (i.e., the SL for *M. aureorugosum* is 1.02–1.10mm, while that for *M. infuscum* is 0.86–1.00mm, and their respective SI's are 98–103 and 92–99).

Monomorium aureorugosum is known from Antsiranana and Toamasina provinces, where it appears to be confined to rainforest. A nest series has been collected from soil below tree roots by researchers from MCZ. Individual workers have been taken from sifted leaf litter, and in pitfall, Winkler and yellow pan traps.

Monomorium cryptobium Santschi

Figs. 29. 75–76.

Syllophopsis cryptobia Santschi, 1921b: 119, fig. 2 (☿). Holotype: ☿, Democratic Republic of Congo (NHMB) [examined].

Monomorium cryptobium Bolton, 1987: 421.

Material examined.— Holotype: ☿, Congo, La Moult (NHMB – Reg. No. 202). In his publication Santschi indicates he examined just the one worker. The label does not mention that it is a type, but the details on the labels are consistent with type status, as is the fact that the specimen lacks a left antennal funiculus. The funiculus of the left antenna is mounted between two cover slips that are held on a separate pin. The identification label on this pin mentions that the funiculus comes from a type specimen.

Other material examined: **Prov. Antsiranana:** Nosy Be, Rés. Lokobe, 6.3 km 112 ESE Hellville 19–24.iii.2001 Fisher *et al.* (5☿, 2♀); Résérve Spéciale Ambre, 3.6 km 235 SW Sakaramy 20–26.i.2001 Fisher *et al.* (3☿); Résérve Spéciale Ambre, 3.5 km 235 SW Sakaramy 26–31.i.2001 Fisher *et al.* (7☿); R.S. Manongarivo, 12.8 km 228 SW Antanambao 11.x.1998 B.L. Fisher (18☿, 10♀); R. S. Manongarivo, 14.5 km 220 SW Antanambao 20.x.1998 B.L. Fisher (14☿, 2♀); R. S. Manongarivo, 10.8 km 229 SW Antanambao 8.xi.1998 B.L. Fisher (12☿, 4♀). **Prov. Mahajanga:** P.N. Ankarafantsika, Ampijoroa, 5.4 km 331 NW Andranofasika 30.iii.2001 Rabeson *et al.* (61☿, 20♀); P.N. Tsingy de Bemaraha, 10.6 km 123 ENE Bekopaka 16–20.xi.2001 Fisher *et al.* (14☿). **Prov. Toliara:** Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (8☿); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (1☿, 1♀); Forêt de Petriky, 12.5 km W 272 Tolagnaro 22.xi.1998 B.L. Fisher (1♀).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye minute, eyes consisting of one or two ommatidia only; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule. Antennal segments 12; Antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin not distinct in specimens seen. Anterior tentorial pits situated nearer mandibular insertions than antennal fossae. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present), or, a small to minute denticle or angle, much smaller than t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, with a few weak striolae on metapleuron; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; propodeum distinctly angulate, propodeal angle sharp; length ratio of propodeal dorsum to its declivity about 1:1; standing propodeal setae consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex tapered, or, conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process absent or vestigial; ventral petiolar lobe present; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole about 4:3; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color pale yellow. Worker caste monomorphic.

HOLOTYPE WORKER MEASUREMENTS: HML 0.99 HL 0.38 HW 0.32 CeI 84 SL 0.30 SI 92 PW 0.21.

OTHER WORKER MEASUREMENTS: HML 0.91–1.04 HL 0.34–0.39 HW 0.27–0.30 CeI 76–85 SL 0.27–0.30 SI 92–100 PW 0.19–0.22 (n=20).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; Eye elliptical, margin sometimes shallowly concave; (in full-face view) eyes set at about midpoint of head capsule: (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Anterior mesoscutum smoothly rounded, thereafter more-or-less flattened; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum length–width ratio of mesoscutum and scutellum combined between 3:2 and 4:3; axillae narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining and smooth, with a few distinct striolae on metapleuron; propodeum distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised, or, sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of one pair of prominent setae anteriad, with a few smaller, erect to decumbent setae on and around dorsal and declivitous faces; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer declivitous face of propodeum than metanotal groove; propodeal lobes present as well-developed, rounded flanges.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing first discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining, with vestigial sculpture; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color head light brown, mesosoma and gaster brownish-yellow, legs pale. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 1.27–1.40 HL 0.36–0.40 HW 0.33–0.36 CeI 88–92 SL 0.30–0.33 SI 86–94 PW 0.29–0.33 (n=20).

REMARKS.— *Monomorium cryptobium* was first described as *Syllophopsis cryptobium* by Santschi (1921), but the genus *Syllophopsis* was reduced to a synonym of *Monomorium* by Bolton (1987). Along with *M. hildebrandti*, this species is the most abundant of the *M. hildebrandti* group *Monomorium* in Madagascar. *Monomorium cryptobium* is one of three Malagasy members of this group in which the compound eye of the worker is reduced to one or two ommatidia. Workers can be separated from those of *M. sechellense* by their unsculptured mesopleuron, and from *M. modestum* by the distinctly angulate nature of the propodeum when seen in profile and by their generally smaller size (HW 0.33–0.36mm compared with 0.36–0.41mm).

Monomorium cryptobium is one of the few west and central African species to be found in Madagascar, whose *Monomorium* fauna is much more representative of eastern and southern Africa. As well as the holotype. I have inspected samples of *M. cryptobium* from these tropical African regions and they are identical with the Malagasy material. Despite its abundance and the presence of many of the small *M. cryptobium* queens among the CAS material, the male is unknown, and does not appear to have been collected by CAS teams (nearly all of the unassigned males in the CAS Collection clearly belong to members of the *M. monomorium* group). In fact, males of all the *M. hildebrandti* group species are very rare in the CAS collection. Possibly this is because they are not only cryptic, but their release during nuptial flights (assuming these occur) is very infrequent and of short duration. *Monomorium cryptobium* is widespread throughout all the forest habitats sampled by the B. Fisher team. Most specimens have been taken from sifted litter.

Monomorium ferodens Heterick, sp. nov.

Figs. 27, 77, 100.

ETYMOLOGY.— Latin '*ferox*' ('fierce') + '*dens*'

MATERIAL EXAMINED.— HOLOTYPE: ☿, 40 km S Ambalavao, Res. Andringitra, 22°13′S, 46°58′E 1275m 15.x.1993 B.L. Fisher #793(8)–13/sifted litter (leaf mold, rotten wood), montane rainforest (CAS). PARATYPES: **Prov. Fianarantsoa** (specimens with same collection data as holotype): 2☿ (ANIC) 12☿ (BMNH); 2☿ (CAS); 12☿ + 1☿ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Fianarantsoa:** 38 km S Ambalavao, Res. Andringitra, 23.x.1993 B.L. Fisher (3☿); R. S. Ivohibe, 6.5 km ESE Ivohibe, 24–30.x.1997 B.L. Fisher (3☿). **Prov. Toliara:** 13 km NW Enakara, Rés. Andohahela, 30.xi.192 B.L. Fisher (5☿); P.N. Andohahela, 3.8 km 113 ESE Mahamavo 21–25.i.2002 Fisher *et al.* (5☿).

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye small, eye width less than 1× greatest width of antennal scape; eyes set above midpoint of head capsule; set posteriad of midline of head capsule; more-or-less circular to semi-circular. Antennal segments 12; club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin straight; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits equidistant from antennal fossae and mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 3,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth distinctly larger than t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to anterior of lower mesopleuron, or, shining and smooth on dorsum, entire lower mesopleuron distinctly striolate; in profile broadly convex; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining and smooth, metapleuron with multiple hair-like striolae; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; angulate, propodeal angle blunt; length ratio of propodeal dorsum to its declivity about 1:1; standing propodeal setae consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer declivitous face of propodeum than metanotal groove; vestibule of propodeal spiracle distinct; propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle laterodorsal and situated slightly anteriad of petiolar node. Petiolar node, in profile, subcuboidal, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and1:1. Anteroventral petiolar process absent or vestigial; ventral petiolar lobe present. Height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining and smooth; postpetiolar sternite not, or, only slightly depressed at midpoint, anterior process prominent.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color pale, depigmented yellow. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.43 HL 0.51 HW 0.44 CeI 86 SL 0.40 SI 91 PW 0.31.

OTHER WORKER MEASUREMENTS: HML 1.21–1.57 HL 0.45–0.57 HW 0.37–0.47 CeI 80–87 SL

0.35–0.44 SI 87–97 PW 0.26–0.32 (n=20).

Remarks.— The worker (queens and males are unknown) of this unobtrusive, but interesting species can easily be confused with a small, pale worker of *M. hildebrandti*. However, it can readily be distinguished by its PF of 3,2 and the enlarged, down-curved basal tooth. In profile, the clypeal protuberance tends to form a blunter angle than is the case with *M. hildebrandti*, its configuration more closely resembling that found in *M. sechellense*. The species is comparatively rare, being known from four sites in Fianarantsoa and Toliara Provinces. All have been taken in sifted litter (leaf mold and rotten wood) in rainforest.

Monomorium fisheri **Heterick, sp. nov.**

Figs. 12, 30–31, 78–79.

Etymology.— In honour of Dr. Brian Fisher (California Academy of Sciences).

Material examined.— Holotype: ☿, **Prov. Toliara**, P.N. Andohahela, Manantalinjo, 3.8 km 113 ESE Mahamavo 900m, Sedro, 24°46′S 46°45′E 21–25.i.2002 Fisher *et al* BLF#/ex rotten log montane rainforest/CASENT0430841 5087 (CAS). Paratypes: **Prov. Toliara** (locality details as for holotype, but collected ex root mat, ground layer, montane rainforest/ collection code 5147): 12♀ (ANIC); 13☿ (BMNH); 1☿2♀ (CAS); 13☿ + 12♀ (MCZ).

Other material examined: **Prov. Antananarivo:** Rés Ambohitantely, 20.9 km 72 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (45☿); Rés Ambohitantely, 24.1 km 59 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (2☿); 3 km 41 NE Andranomay, 11.5 km 147 SSE Anjozorobe 5–13.xii.2000 Fisher *et al.* (57☿, 5♀). **Prov. Antsiranana:** R. S. Manongarivo, 20.4 km 219 SW Antanambao 3.xi.1998 B.L. Fisher (7☿). **Prov. Fianarantsoa:** Forêt Antsirakambiaty, 7.6 km 285 WNW Itremo 22–26.i.2003 Fisher *et al.* (30☿, 8♀, 12♂); P.N. Ranomafana. Vatoharanana 4.1 km 231 SW Ranomafana 27–31.iii.2003 Fisher *et* al. (13☿). **Prov. Toamasina:** F.C. Didy, 16–23.xii.1998 H.J. Ratsirarson (3☿); Mont Anjanaharibe, 19.5 km 27 NNE Ambinanitelo 12–16.iii.2003 Fisher *et al.* (6☿). **Prov. Toliara:** P.N. Andohahela, Manantalinjo, 3.8 km 113 ESE Mahamavo 21–25.i.2002 Fisher *et al.* (106☿).

Worker description.— Head: Head rectangular, oval, or, quadrate (i.e., heart-shaped); vertex planar to strongly concave; frons (i) shining and smooth except for piliferous pits, or, (ii) shining and smooth except for a few striolae around antennal sockets and front carinae and piliferous pits. or, (iii) shining and finely striolate and microreticulate; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye moderate, eye width 1–1.5× greatest width of antennal scape to small, eye width less than 1× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule to set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eyes more-or-less circular, or, elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12: antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin highly variable in appearance, being either: (i) narrowly convex between weakly ridged clypeal carinae, or, (ii) straight, or, (iii) straight between strongly divergent clypeal carinae, with clypeus descending almost vertically to horizontal arc of mandibles and sometimes transversely carinate below level of antennal insertions, or, (iv) emarginate, clypeal carinae indistinct, or, (v) emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae to approximately level with antennal fossae. Anterior tentorial pits equidistant from antennal fossae and mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth either five, or, four and one or two denticles, or, four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t4 (five teeth present), or, smaller than t4 (five teeth present), or, approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, with entire lower mesopleuron distinctly striolate, or, promesonotum shining and faintly striolate dorsally, with striolae becoming more distinct posteriad, and entire mesopleuron distinctly striolate; in profile promesonotum (i) broadly convex, or, (ii) with anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum, or, (iii) promesonotum gently convex or distinctly flattened, humeri with vestigial to strongly accentuated dorsolateral flange; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae very sparse or absent. Metanotal groove variable, from strongly impressed, with distinct transverse costulae to absent. Propodeum varying from shining, with dorsum and sides of propodeum mainly smooth with weak to strong striolae on declivitous face and on metapleuron, to uniformly finely striolate; propodeal dorsum either slightly elevated anteriad and sloping away posteriad, propodeal angles not raised, or, propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; propodeum either (i) smoothly rounded or (ii) with indistinct angle, or, (iii) angulate, propodeal angle blunt, or, (iv) distinctly angulate, propodeal angle sharp; if angulate, length ratio of propodeal dorsum to its declivity is between 3:2 and 4:3; standing propodeal setae consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum, or, consisting of two or more prominent pairs of setae anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae well-spaced and sparse to very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum, or, nearer declivitous face of propodeum than metanotal groove; vestibule of propodeal spiracle distinct in some specimens; propodeal lobes present as blunt-angled flanges, or, present as rounded flanges.

PETIOLE AND POSTPETIOLE: Position of petiolar spiracle varying from lateral and situated well anteriad of petiolar node to lateral and situated within anterior sector of petiolar node. In profile, petiolar node shape ranging from subcuboidal, vertex rounded, to subcuboidal, inclined posteriad; appearance of node shining and smooth throughout, or, shining and faintly striolate and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 3:4. Anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; ventral petiolar lobe absent. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:2; postpetiole shining and smooth; postpetiolar sternite either (i) depressed near its junction with gaster, and sloping anteriad at angle of 45–60 to form large conspicuous lip at its anterior end, or, (ii) not, or, only slightly depressed at midpoint, anterior process prominent, or, (iii) petiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color usually yellow to reddish-brown, some specimens with yellow head and gaster and reddish mesosoma, dark brown specimens with pale legs. Worker caste monomorphic, or, monophasically allometric, i.e., with variable size, but not morphology among workers from same nest, or, polymorphic.

HOLOTYPE MEASUREMENTS: HML 2.25 HL 0.76 HW 0.66 CeI 86 SL 0.64 SI 98 PW 0.46.

OTHER WORKER MEASUREMENTS: HML 1.78–3.58; HL 0.64–1.23; HW 0.50–1.26; CeI 76–103; SL 0.42–0.96; SI 75–107; PW 0.34–0.80 (n=60).

QUEEN DESCRIPTION.— HEAD: Head rectangular; vertex weakly concave or planar; either (i) frons shining and longitudinally striolate, with some smooth areas, or, (ii) frons longitudinally finely striolate; pilosity of frons with a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex, or, with a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex, or, broadly convex anteriad, with convexity reduced posteriad; mesoscutum and mesopleuron either shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum, or, faintly longitudinally striolate on sides of pronotum and mesoscutum, dorsum of mesoscutum mainly smooth; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2. Axillae separated by width of at least one axilla. Standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum either (i) longitudinally striolate, except for posterior sector of propodeum, which is smooth, or, (ii) shining and densely striolate over whole surface, or, (iii) shining, with strong, transverse rugae dorsally, laterally and on declivitous face; propodeum angulate, propodeal angle blunt, or, distinctly angulate, propodeal angle sharp, or, distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle ranging from nearer metanotal groove than declivitous face of propodeum to equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as bluntly angled flanges.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing first discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle either lateral and situated well anteriad of petiolar node, or, lateral and situated slightly anteriad of petiolar node, or, laterodorsal and situated slightly anteriad of petiolar node; node, in profile cuneate, vertex tapered; appearance of node shining and weakly striolate posteriad, or, shining, rugose posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1. Anteroventral petiolar process either present as a thin flange tapering posteriad, or, absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 1:1; postpetiole smooth anteriad, rugose posteriad to strongly rugose; postpetiolar sternite depressed near its junction with gaster, and sloping anteriad at angle of 45–60 to form large conspicuous lip at its anterior end.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color brownish-yellow, through orange to brown with lighter areas. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

QUEEN MEASUREMENTS: HML 3.13–4.92; HL 0.90–1.24; HW 0.83–1.34; CeI 87–111; SL 0.76–1.02; SI 76–95; PW 0.79–1.50 (n=29).

MALE DESCRIPTION.— HEAD: Head width-mesosoma width ratio between 4:3 and 3:4; frons finely micropunctate. Compound eyes protuberant and elliptical, or, protuberant and circular or subcircular; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 1:2 and 1:3. Maximum number of mandibular teeth and denticles four.

MESOSOMA: Mesoscutum broadly convex; either lower pronotum and mesoscutum finely striolate, otherwise smooth and shining, or, shining and faintly striolate throughout, striolae becoming more deeply impressed on posterior mesopleuron. Parapsidal furrows distinct, vestigial or absent; notauli absent. Axillae separated by width of at least one axilla.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing entire discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node. Node (viewed in profile) conical, vertex rounded, or, evenly tumular to roundly conical; appearance of node shining and smooth, or, shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1. Anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial. Height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 3:4; postpetiole shining and smooth, or, shining, with vestigial sculpture.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color head chocolate, gaster, mesosoma brown, legs yellowish-brown.

MALE MEASUREMENTS: HML 2.37–2.99; HL 0.68–0.79; HW 0.66–0.80; CeI 99–102; SL 0.17–0.20; SI 23–29; PW 0.76–0.84 Male (n=7).

REMARKS.— *Monomorium fisheri* and its close ally, *Monomorium hildebrandti* pose the same problems within the *M. hildebrandti* group that *M. termitobium* does for the *M. monomorium* group. Workers within *M. fisheri* cluster around three morphotypes.

(a) Workers of this form exhibit only a slight variation in worker size. They are uniformly pale yellow to orange and, in the northernmost population, finely microstriolate over much of the head and mesosoma. The eye is very small, with about five or six ommatidia, its diameter much narrower than the thickest length of the antennal scape. The mandible most commonly has four teeth, rarely three teeth and two denticles or four teeth and a small denticle. All workers have smoothly rounded humeri. The node is regularly shaped and not particularly thick, and the postpetiole is evenly rounded. Most specimens come from a fairly large series from Ambohitantely Reserve, Antananarivo Province, with three additional workers having been collected from Manongarivo, Antsiranana Province. No queens or males have been identified for this morphotype, whose representatives have been taken from sifted litter and leaf mould.

(b) The second morphotype is very similar, and may well simply represent a southward continuation of form (a). The eye is similarly small and the color is the same. This form has a smoother exoskeleton, and the postpetiole in smaller specimens is attenuated anteriad. Many workers have a slight promesonotal shelf, but in others the humeri are rounded. Allometric variation is apparent between workers of the same nest, and in the southernmost populations the variation becomes a genuine polymorphism, with the largest workers rivaling *M. aureorugosum* and *M. infuscum* in size. These very large workers (HW = 1mm) have massive, quadrate head capsules and proportionately very small eyes. They also have a mandibular count of five or six mandibular teeth and denticles, contrasting with a usual count of four in the smaller workers. The mesonotal sector is sculptured in the large worker as is the mesopleuron, with strong lateral striae and striolae. The petiolar node is 'blocky' and subcuboidal. The queens are reasonably large ants, over half a centimeter in total length, with a massive, rounded mesosoma and small tubercles or denticles at the propodeal angles. Seen in full-face view, a number of these queens have paired setae straddling the mid point of the anterior clypeal margin, rather than one seta. Queens and males (which are as large as most workers of *M. fisheri*) have the full complement of wing veins. The CAS has several long series of this morphotype, collected from montane rainforest in Fianarantsoa and Toliara Provinces. These tend to be nest series, which is unsurprising as *M. fisheri* is larger and, hence, more conspicuous than most *Monomorium* species. Most collections have come from sifted litter, root mats and rotten wood.

(c) Workers of the third morphotype are very smooth and shining, and the predominant base color of the head and mesosoma is a russet-brown with some smaller workers tending to ochraceous. All workers have pale legs. The promesonotum mostly has a distinctly flattened humeral shelf, which projects over the sides when the ant is seen in full-face view. The metanotal groove is weak to absent, but the postpetiole is attenuate, as with smaller workers of morphotype (b). Where present, sculpture is confined to a few dull striolae on the mesopleuron and metanotum. While workers of this form have relatively the longest scapes (SI to 107), scape length shows the same variability as that of the other morphotype. When plotted on a scattergram (Fig. 31), moreover, the relationship between HML and SL in all morphotypes shows the same slope ($r^2 = 0.95$). Morphotype (c) exhibits weak monophasic allometry. The queen is smaller and brown rather than dull orange-yellow, but its appearance otherwise agrees with that of morphotype (b), and there is no significant difference between the males. Collections have been made along Madagascar's eastern half, most samples being associated with rotten wood, though a few have come from sifted litter.

In my opinion, the variation seen in *M. fisheri* is infraspecific, as workers of all three morphotypes show convergence of form in at least some localities and all possess a basic underlying similarity. The tendency of populations of a *Monomorium* species living in very moist conditions to produce a worker morphotype that is smooth and glassy with minimal sculpture and a flattened promesonotum has been previously noted in the case of the Australian species, *Monomorium leae* Forel (Heterick 2001). This appears to have occurred with *M. fisheri*, whose distribution is confined to montane rainforest. Possibly, individual microhabitats experience greater precipitation or are otherwise damper than others, over long time periods imposing selection pressure on isolated populations of individual species to produce the sort of phenotypic variation noted above. The smooth, waxy cuticle may be an adaptation to prevent pathogenic fungi from growing on the ant, or, it may prevent waterlogging. The holotype selected is a medium-sized worker of morphotype (b), which is probably the form most commonly encountered.

Monomorium gongromos Heterick, sp. nov.

Figs. 27, 80.

ETYMOLOGY.— Greek '*gongros*' (masc. 'excrescence') + '*omos*' (masc. 'shoulder')

MATERIAL EXAMINED.— HOLOTYPE: ☿, **Prov. Toamasina**, F. C. Sandranantitra 18°02′9″S, 49°05′5″E 450 m 18–21.i.1999 H.J. Ratsirarson 101(11)–51/sifted litter rainforest (CAS). PARATYPES: **Prov. Toamasina** (specimens with same collection data as holotype): 3☿ (ANIC) 12☿ + 3☿ (BMNH); 4☿ (CAS); 22☿ + 12♀ + 1☿ (MCZ).

OTHER MATERIAL EXAMINED: **Prov. Toamasina:** F. C. Andriantantely 4–7.xii.1998 H.J. Ratsirarson (1☿); F. C. Andriantantely 7–10.xii.1998 H.J. Ratsirarson (7☿); F.C. Sandranantitra 18–24.i.1999 (3☿) 21–24.i.1999 (1☿) H.J. Ratsirarson.

WORKER DESCRIPTION.— HEAD: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; Eye small, eye width less than 1× greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles, or, emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and smooth on dorsum, entire lower mesopleuron distinctly striolate; (viewed in profile) curve of anterior promesonotum abrupt, flattened or gently convex thereafter, promesonotal humeri with small tubercle or rugosity when seen in full-face view; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove absent. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; propodeum distinctly angulate, propodeal angle sharp; length ratio of propodeal dorsum to its declivity about 3:2; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer declivitous face of propodeum than metanotal groove. Vestibule of propodeal spiracle distinct in some specimens. Propodeal lobes present as blunt-angled flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node, or, lateral and situated within anterior sector of petiolar node; node (viewed in profile) subcuboidal, inclined posteriad; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present, but weakly developed to vestigial; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color of head, appendages and node yellow, mesosoma light orange to brick red, gaster yellowish-brown. Worker caste monomorphic.

HOLOTYPE MEASUREMENTS: HML 1.55 HL 0.56 HW 0.47 CeI 84 SL 0.40 SI 85 PW 0.36.

OTHER WORKER MEASUREMENTS: HML 1.36–1.67 HL 0.51–0.58 HW 0.41–0.50 CeI 80–86 SL 0.36–0.42 SI 84–90 PW 0.30–0.39 (n=20).

QUEEN DESCRIPTION.— HEAD: Head square; vertex weakly concave or planar; frons longitudinally striolate medially, sides of head capsule shining and smooth; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye ovoid, narrowed posteriad; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae separated by width of at least one axilla; standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron.

Propodeum shining and densely striolate over whole surface; propodeum distinctly angulate, propodeal angle sharp; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae well-spaced and sparse; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as bluntly angled flanges.

Wing: Wing not seen (queens dealated).

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 3:2 and 4:3; anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole about 4:3; postpetiole smooth anteriad, rugose posteriad; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

Gaster: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

General characters: Color variegated brown and orange. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 2.26–2.29 HL 0.65 HW 0.62–0.63 CeI 95–97 SL 0.49–50 SI 78–79 PW 0.59–0.64 (n=2).

Remarks.— The small red-and-yellow workers of *M. gongromos* closely resemble those of some populations of *M. hildebrandti*, but are distinguished by the presence of humeral angles (evident as small protuberances or rugosities in full-face view) and by numerous, fine, transverse striolae on the dorsum and upper sides of the propodeum. The dorsum of the mesosoma in dorsal view is subcarinate transversely between the humeri with a broken and vestigial lateral carina also arising from each humeral angle and proceeding to about the position normally occupied by the metanotal groove (here absent). The species has been collected at just two sites on the east coast of Madagascar in Toamasina Province. The queens of this species are similar to small queens of *M. hildebrandti*, but the propodeum is uniformly striolate and the mesoscutum is low and flat, so that the pronotum is clearly visible in dorsal view. All specimens have been collected from sifted litter or a rotten log in rainforest.

Monomorium hildebrandti Forel

Figs. 32–33, 101–105.

Monomorium minutum r. *hildebrandti* Forel, 1892c:256. Holotype ♀, Madagascar: 'central Madagascar' (MHNG) [examined].

Monomorium minutum subsp. *hildebrandti* Wheeler, W.M. 1922:1027.

Monomorium hildebrandti Dalla Torre, 1893:67.

Material examined.— Holotype: (See comments under *M. shuckardi*, though, due to its damaged condition, this specimen could not be measured.) ♀, Madagascar, central Madagascar (MHNG). The published description of the queen mentions that a Mr. Hildebrand was the collector. The type specimen lacks head, postpetiole and gaster. A 'type' from Madagascar described by Santschi (1926) (NHMB) as the worker of *M. hildebrandti* is actually a specimen of *Monomorium madecassum* Forel.

Other material examined: **Prov. Antananarivo:** 3 km 41 NE Andranomay, 11.5 km 147 SSE Anjozorobe 5–13.xii.2000 Fisher *et al.* (9☿, 2♀); Rés Ambohitantely, 20.9 km 72 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (15☿, 5♀); Rés Ambohitantely, 24.1 km 59 NE Ankazobe 17–22.iv.2001 Rabeson *et al.* (7☿).

Prov. Antsiranana: 2.2 km WSW Befingotra, Res. Anjanaharibe–Sud, 9.xi.1994 B.L. Fisher (12☿, 1♀); Forêt Anabohazo, 21.6 km 247 WSW Maromandia 11–16.iii.2001 Fisher *et al.* (5☿); Forêt Orangea, 3.6 km 128 SE Remena 22–28.ii.2001 Fisher *et al.* (5☿); Montagne Français, 7.2 km 142 SE Diego Suarez 22–28.ii.2001 Fisher *et al.* (3☿); Nosy Be, Rés. Lokobe, 6 3 km 112 ESE Hellville 19–24.iii.2001 Fisher *et al.* (13☿, 1♀); P.N. Montagne Ambre, 12.2 km 211 SSW Joffreville 2–7.ii.2001 Fisher *et al.* (26☿, 1♀); Résérve Spéciale Ambre, 3.5 km 235 SW Sakaramy 26–31.i.2001 Fisher *et al.* (10☿); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (3☿); Rés. Spéc. Ankarana, 22.9 km 224 SW Anivorano Nord 10–16.ii.2001 Fisher *et al.* (1☿); Rés. Spéc. Ankarana, 13.6 km 192 SSW Anivorano Nord 16–21.ii.2001 Fisher *et al.* (3☿); R.S. Manongarivo, 14.5 km 220 SW Antanambao 20.x.1998 B.L. Fisher (3☿, 2 ergatoids); R.S. Manongarivo, 17.3 km 218 SW Antanambao 27.x.1998 B.L. Fisher (6☿, 1♀); R. S. Manongarivo, 20.4 km 219 SW Antanambao 3.xi.1998 B.L. Fisher (3☿, 1♀); R. S. Manongarivo, 10.8 km 229 SW Antanambao 8.xi.1998 B.L. Fisher (3☿, 1♀). **Prov. Fianarantsoa:** 45 km S Ambalavao 25.ix.1992 B.L. Fisher (3☿, 32♂); 43km S Ambalavao, Res Andringitra, 5.x.1993 B.L. Fisher (3☿, 4♀, 2♂); 40 km S Ambalavao, Res Andringitra 15.x.1993 B.L. Fisher (4☿); 38 km S Ambalavao, Res Andringitra 23.x.1993 B.L. Fisher (12☿, 2♀); R.S. Ivohibe, 7.5 km ENE Ivohibe, 7–12.xi.1997 B.L. Fisher (6☿). **Prov. Mahajanga:** P.N. Ankarafantsika, Ampijoroa, 40 km 306 NW Andranofasika 26–31.iii.2001 Fisher *et al.* (3☿); P.N. Ankarafantsika, Ampijoroa, 5.4 km 331 NW Andranofasika 30.iii.2001 Rabeson *et al.* (128☿, 1 ergatoid, 5♀); P.N. Ankarafantsika, Ankoririka, 10.6 km 13 NE Tsaramandroso 9–14.iv.2001 Rabeson *et al.* (1☿); P.N. Baie de Baly, 12.4 km 337 NNW Soalala 26–30.xi.2002 Fisher *et* al. (3☿); P.N. Namoroka, 17.8 km 329 WNW Vilanandro, 8–12.xi.2002 Fisher *et al.* (23☿, 8 ergatoids); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (3♂); P.N. Tsingy de Bemaraha, 10.6 km 123 ESE Antsalova 16–20.xi.2001 Fisher *et al.* (5☿); Res. Bemarivo, 23.8 km 223 SW Besalampy, 19–23.xi.2002 Fisher *et al* (7☿). **Prov. Toamasina:** 5.3 km SSE Ambanizana, Andranobe, 21.xi.1993 B.L. Fisher (5☿, 1♀); 6.9 km NE Ambanizana, Andranobe, 2.xii.1993 (9☿, 1♀) 9.xii.1993 (3☿) B.L. Fisher; F.C. Andriantantely 4–7.xii.1998 H.J. Ratsirarson (4☿, 1♀); F. C. Sandranantitra 21–24.i.1999 H.J. Ratsirarson (5☿); P.N. Mantadia, 25–28.xi.1998 H.J. Ratsirarson (3☿); SF Tampolo, 10 km NNE Fenoarivo Atn. 10.iv.1997 B.L. Fisher (2☿). **Prov. Toliara:** Cap Sainte Marie, 12.3 km 262 W Marovato 11–15.ii.2002 Fisher *et al.* (4☿); Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (12☿); 11 km NW Enakara, Rés. Andohahela 17.xi.1992 B.L. Fisher (2☿); 10 km NW Enakara, Rés. Andohahela 24.xi.1992 B.L. Fisher (3☿); Forêt Mahavelo, Isantoria Riv., 5.2 km 44 NE Ifotaka 28.i–1.ii. 2002 Fisher *et al.* (1☿); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (3☿); Forêt Tsinjoriaka ['Tsinjoriaky'], 6.2 km 84 E Tsifota 6–10.iii.2002 Fisher *et al.* (1☿); Mahafaly Plateau, 6.2 km 74 ENE Itampolo 21–25.ii.2002 Fisher *at al.* (1♂); P.N. Andohahela, 7.6 km 99 E Hazofotsy 12–16.i.2002 Fisher *et al.* (19☿, 2 ergatoids); P.N. Andohahela, Manantalinjo, 3.8 km 113 ESE Mahamavo 21–25.i.2002 Fisher *et al.* (6☿); P.N. Kirindy Mite, 16.3 km 127 SE Belo sur Mer 6–10.xii.2001 Fisher *et al.* (2♂).

Worker description.— Head: Head oval; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye moderate, eye width 1–1.5× greatest width of antennal scape to small, eye width less than 1× greatest width of antennal scape; (in full-face view) eyes set at about midpoint of head capsule to set below midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; Antennal segments 12; antennal club three-segmented. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits equidistant from antennal fossae and mandibular insertions. Frontal lobes straight, parallel. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

Mesosoma: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron, or, shining and smooth on dorsum, entire lower mesopleuron distinctly striolate; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on dorsum of promesonotum. Metanotal groove absent. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeal dorsum slightly elevated anteriad and sloping away posteriad, propodeal angles not raised, or, sloping posteriad, and depressed between raised propodeal angles; propodeum smoothly rounded or with indistinct angle, or, angulate, propodeal angle blunt; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum to nearer declivitous face of propodeum than metanotal groove. Vestibule of propodeal spiracle distinct. Propodeal lobes present as blunt-angled flanges, or, present as rounded flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated well anteriad of petiolar node, or, lateral and situated slightly anteriad of petiolar node; node (viewed in profile) cuneate, vertex rounded, or, conical, vertex rounded, or, tumular, inclined posteriad, with vertex also tapered posteriad, or, subcuboidal, vertex rounded; appearance of node shining and smooth throughout, or, shining and longitudinally striolate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad, or, absent or vestigial; ventral petiolar lobe present, or, present, but weakly developed to vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth, or, shining and weakly striolate posteriad; postpetiolar sternite depressed near its junction with gaster, and sloping anteriad at angle of 45–60 to form large conspicuous lip at its anterior end, or, depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90, or, not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color highly variable; from uniform pale yellow to light brown, often with yellow or yellowish-brown head and appendages and yellowish-brown to brown gaster, contrasting with reddish-orange mesosoma and nodes. Worker caste monomorphic within nests, but with large internidal and inter-population variation in size and sculpture.

Other worker characters: HML 1.18–2.12 HL 0.44–0.73 HW 0.36–0.61 CeI 75–86 SL 0.30–0.54 SI 82–102 PW 0.25–0.47 (n=40).

Queen description.— Head: Head square, or, rectangular; vertex weakly concave or planar; frons shining and smooth except for piliferous pits and a few striolae around antennal sockets and frontal carinae, or, shining and longitudinally striolate in left and right sectors and medially smooth; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter setae or setulae, which are decumbent or appressed, longer setae thickest on vertex. Eye ovoid, narrowed posteriad; (in full-face view) eyes set above midpoint of head capsule, or, set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

Mesosoma: Mesoscutum broadly convex, or, broadly convex anteriad, convexity reduced posteriad; pronotum, mesoscutum and mesopleuron shining and mainly smooth, vestigial striolae, if present, confined to anterior katepisternum; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2 to between 3:2 and 4:3; axillae separated by width of at least one axilla, or, narrowly separated (i.e., less than width of one axilla); standing pronotal/mesoscutal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae few, mainly on sides of pronotum and mesopleuron. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeum distinctly angulate, propodeal angle sharp to distinctly angulate, propodeal angles produced as short denticles; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae variable, from absent to up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae well-spaced and sparse, or, very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges, or, present as bluntly angled flanges.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing first discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node, or, lateral and situated slightly anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and weakly striolate posteriad; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 4:3 and 1:1; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 3:2 and 4:3; postpetiole shining, smooth anteriad, weakly to strongly striate posteriad; postpetiolar sternite depressed at about its centre, anterior carina usually inconspicuous.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color of smaller specimens usually yellowish or brown, larger specimens variegated yellowish-brown/brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes seen.

HOLOTYPE QUEEN MEASUREMENTS: Not taken, as the queen lacks crucial body parts, including the head.

QUEEN MEASUREMENTS (non-types): HML 3.21–4.13 HL 0.96–1.06 HW 0.92–1.06 CeI 92–101 SL 0.82–0.96 SI 84–99 PW 0.92–1.11 (n=19).

MALE DESCRIPTION.— HEAD: (In full-face view) head width–mesosoma width ratio between 1:1 and 3:4; frons finely micropunctate. Compound eyes protuberant and weakly ovoid; margin of compound eye clearly separated from posterior margin of clypeus. Ocelli not turreted. Ratio of length of first funicular segment of antenna to second funicular segment between 3:4 and 2:3. Maximum number of mandibular teeth and denticles four.

MESOSOMA: Mesoscutum broadly convex with a few vestigial striolae on its dorsum, otherwise pronotum and mesoscutum smooth and shining; parapsidal furrows distinct; notauli absent; axillae separated by width of at least one axilla.

WING: Wing veins tubular and strongly sclerotised; vein m–cu present as an entire vein enclosing entire discoidal cell; vein cu–a present.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node to laterodorsal and situated well anteriad of petiolar node; node (viewed in profile) conical, vertex tapered; appearance of node shining, with vestigial sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

General characters: Color reddish brown, head chocolate.

Male measurements: HML 1.44–1.75 HL 0.43–0.54 HW 0.41–0.53 CeI 83–104 SL 0.07–0.13 SI 13–28 PW 0.37–0.56 (n=12).

Remarks.— By far the most abundant member of the *M. hildebrandti* group on Madagascar, this species varies more than any other Malagasy *Monomorium*. Fortunately, the pattern of variation shows a clinal pattern, unlike that in *M. termitobium*, making its analysis somewhat easier. The species, as it is understood here, is closely related to the very similar *M. fisheri*, and may occasionally hybridize with that species (see 'Remarks' under *M. adiastolon*). The petiolar node, although it varies greatly, is still the best means of separating workers of *M. hildebrandti* from those of *M. fisheri*, but in doubtful cases the other features mentioned in the key should be carefully examined. In the former the node has a posterior face that is rarely vertical, and its dorsum usually retains some degree of asymmetry. The latter species has a symmetrical node with a vertical posterior face. Thick, tapering nodes in some populations of *M. hildebrandti* tend to possess faint longitudinal striolae absent in *M. fisheri*. Workers of *M. hildebrandti* have a maximum of four mandibular teeth, and that will help to distinguish them from those *M. fisheri* workers that have a five-toothed mandible.

Several of the more conspicuous morphotypes of *M. hildebrandti* have a well-defined range. A form whose large, robust, reddish workers possess a longitudinally striolate petiolar node is perhaps the most distinctive. The eye can be relatively large in workers of this morphotype, with up to 30 or more ommatidia. Unlike the similarly large-eyed *M. adiastolon*, this morphotype has a narrow, high postpetiole. This ant is found along the entire western and southern coast of Madagascar, excluding only the extreme north-west. The queen has a distinctive postpetiole that is vertically strongly attenuate and produced laterally, and is otherwise more heavily sculptured than the typical *M. hildebrandti* queen. Some individual workers of this form show actual physical convergence with the smaller yellow worker of the common morphotype, the head and pronotal sector being that of the smaller morphotype, while the propodeum and nodes are those of the robust red morphotype! In the extreme north of Antsiranana Province and on Nosy Be Island, is another, yellow morphotype in which the anteroventral postpetiolar process is very large and terminates in a conspicuous carina. Further south in Antsiranana and parts of Toamasina is a similar form, whose workers are very smooth and have an elongate peduncle. The workers lack the large anteroventral petiolar process of the more northern populations. In some cases the petiolar node of individual workers from both groups is strongly asymmetrical and very low. Colonies with red-and-yellow workers, similar in appearance to *M. gongromos*, occur in Fianarantsoa Province among colonies with more unobtrusive yellow workers. The CAS has a number of queens and males for this morphotype, and the holotype queen, from "Central Madagascar", belongs to the same population. Ergatoids may be paler than fully developed queens. The large workers of yet another morphotype in Antananarivo and Antsiranana Provinces are very similar to workers of morphotype (b) of *M. fisheri* and have a similar node, which, however, usually has a slightly asymmetrical dorsum and a few weak striolae on the sides. The most commonly seen worker of *M. hildebrandti* is a small, depigmented yellow, through bright yellow to yellowish-brown ant with very small eyes (as few as five ommatidia) and a petiolar node that varies from rounded and smooth to more attenuate and sculptured. In brownish specimens the head may be darker than the mesosoma in dorsal view. Workers with this appearance are found in many parts of inland Madagascar.

Despite the variable morphology and color of *M. hildebrandti*, the pattern of distribution to be found among the various morphotypes and the high number of workers of intermediate morphology strongly suggests the divergence in appearance is due to different selection pressures operating on the one species. As with *M. fisheri*, the relationship between HML and SL is very similar for all morphotypes ($r^2 = 0.97$) (Fig. 33). Molecular analysis (i.e., DNA sequencing) may be helpful in elucidating the relationship between this species, *M. fisheri* and *M. adiastolon*, which cannot be fully resolved by morphological examination. *Monomorium hildebrandti* is found in all native habitats. Sifting of litter appears to be the most effective sampling method. Nest series have been taken from rotted tree stumps and other wood substrates, and from under stones.

Monomorium infuscum **Heterick, sp. nov.**

Fig. 28.

Etymology.— Latin '*infuscus*' ('dusky' 'dark brown' 'blackish')

Material examined.— Holotype: ☿, **Prov. Toamasina**, 5.3 km SSE Ambanizana, Andranobe, 15°40′S, 49°58′E 425 m 21.xi.1993 B.L. Fisher #926(43)–12/sifted litter (leaf mold, rotten wood) rainforest (CAS). Paratypes: **Prov. Toamasina** (all specimens with same collection data as holotype): 1☿ (ANIC); 12☿ (BMNH); 12☿ (MCZ).

Other material examined: **Prov. Toamasina:** 6.9 km NE Ambanizana, Andranobe, 2.xii.1993 (3☿) 8.xii.1993 (3☿) 9.xii.1993 (3☿) B.L. Fisher; Ambanisana, P.N. Masoala 2–6.iii.2003 Silva *et al.* (1☿).

Worker description.— Head: Head oval; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of well-spaced, distinctly longer erect and semi-erect setae interspersed with shorter decumbent setae or setulae. Eye moderate, eye width 1–1.5× greatest width of antennal scape; (in full-face view) eyes set above midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule; eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin. Antennal segments 12; antennal club not clearly defined. Clypeal carinae always well-defined; anteromedian clypeal margin emarginate, clypeal carinae terminating in blunt angles, or, emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin approximately level with antennal fossae. Anterior tentorial pits situated nearer antennal fossae than mandibular insertions. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth five; mandibles triangular and smooth (except for piliferous pits); masticatory margin of mandibles approximately vertical or weakly oblique; basal tooth approximately same size as t4 (five teeth present).

Mesosoma: Promesonotum shining, with whorls of rugae on sides of promesonotum, these becoming longitudinal on dorsum; (viewed in profile) promesonotum broadly convex; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove absent; propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face and on metapleuron; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of two or more prominent pairs anteriad, often with another pair of prominent setae posteriad, and other smaller setae on/around dorsal and declivitous surfaces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as sharp, acute angled flanges.

Petiole and postpetiole: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) broad and thick, with short vertex anteriad, node sloping posteriad; appearance of node transversely rugose, shining between sculpture; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) between 1:1 and 3:4; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe absent; height ratio of petiole to postpetiole about 4:3; height–length ratio of postpetiole between 1:1 and 3:4; postpetiole strongly rugose; postpetiolar sternite not depressed at midpoint, its anterior end an inconspicuous lip or small carina.

Gaster: Pilosity of first gastral tergite consisting of well-spaced, erect and semi-erect setae interspersed with a few appressed setulae.

General characters: Color dark reddish- or yellowish-brown. Worker caste monomorphic.

Holotype measurements: HML 3.22 HL 1.04 HW 0.98 CeI 94 SL 0.94 SI 96 PW 0.72.

Other worker measurements: HML 2.87–3.63 HL 0.96–1.16 HW 0.86–1.07 CeI 89–96 SL 0.86–1 00 SI 92–99 PW 0.63–0.78 (n=15).

Remarks.— *Monomorium infuscum* is known only from a few workers from three sites near Ambanizana, Toamasina Province. Samples have been collected from rotten wood, sifted leaf litter and pitfall trap, in rainforest. Differences between this species and the very similar *M. aureorugosum* are provided in '*Remarks*' under the latter species.

Monomorium modestum Santschi

Figs. 34, 81– 82.

Monomorium modestum Santschi, 1914b:17. Syntype ☿s South Africa: Natal, Stamford Hill (NHMB) [type material misplaced in NMHB].

Monomorium (*Syllophopsis*) *modestum* Santschi, 1915:259.

Monomorium modestum Bolton, 1987:423.

Monomorium (*Syllophopsis*) *modestum* var. *boerorum* Santschi 1915:260, fig. 9 (☿). [Junior primary homonym of *Monomorium minutum* var. *boerorum* Forel, 1910b:442.]. Syntype ☿, South Africa: Transvaal, Pretoria (NHMB) [examined].

Monomorium (*Syllophopsis*) *modestum* var. *transwaalensis* [*sic*] Emery, 1922:175 [Replacement name for *boerorum*.]. Syn. under *Monomorium modestum* Santschi: Bolton, 1987:423.

Monomorium modestum var. *smutsi* Wheeler, W.M. 1922: 867 [Unnecessary second replacement name for *boerorum*.]. Syn. under *Monomorium modestum* Santschi: Bolton, 1987:423.

Material examined.— *M. modestum transwaalense* (corrected ending): Syntype: ☿, South Africa (Transvaal), Pretoria (NHMB – Reg. No. 207). The syntype examined is headless. Other, more complete syntypes may be in existence, hence this specimen has not been designated a lectotype.

Other material examined: **Prov. Antananarivo:** 3 km 41 NE Andranomay, 11.5 km 147 SSE Anjozorobe 5–13.xii.2000 Fisher *et al.* (22☿). **Prov. Fianarantsoa:** 45 km S Ambalavao 25.ix.1992 B.L. Fisher (4☿); 43 km S Ambalavao Res., Andringitra 5.x.1993 B.L. Fisher (3☿); P.N. Ranomafana, Vatoharanana 4.1 km 231 SW Ranomafana 27–31.iii.2003 Fisher *et* al. (4☿). **Prov. Toamasina:** 6.9 km NE Ambanizana, 2.xii.1993 B.L. Fisher (4☿); F. C. Sandranantitra 18–21.i.1999 (14☿) 21–24.x.1999 (3☿) H.J. Ratsirarson. **Prov. Toliara:** P.N. Andohahela, 3.8 km 113 ESE Mahamavo 21–25.i.2002 Fisher *et al.* (2☿); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (1☿).

Worker description.— Head: Head rectangular; vertex planar; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye minute, eyes consisting of one or two ommatidia only; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set around midline of head capsule, or, set posteriad of midline of head capsule; Antennal segments 12; antennal club three-segmented. Clypeal carinae weakly to strongly defined; anteromedian clypeal margin emarginate, clypeal carinae indistinct, or, emarginate, clypeal carinae terminating in blunt angles, or, emarginate, clypeal carinae terminating in small denticles; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer mandibular insertions than antennal fossae. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four;

mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

MESOSOMA: Promesonotum shining and mainly smooth, vestigial striolae, if present, confined to lower anterior mesopleuron; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae, or vestigial. Propodeum shining and smooth, metapleuron with a few weak striolae; propodeal dorsum flat throughout most of its length; propodeum smoothly rounded or with indistinct angle; standing propodeal setae consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as rounded flanges.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated within anterior sector of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 1:1; anteroventral petiolar process present as a thin flange tapering posteriad; ventral petiolar lobe present; height ratio of petiole to postpetiole between 3:2 and 4:3; height–length ratio of postpetiole about 1:1; postpetiole shining and smooth; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color depigmented creamy yellow. Worker caste monomorphic.

SYNTYPE WORKER MEASUREMENTS: Measurements not taken as syntype is headless.

OTHER WORKER MEASUREMENTS: HML 1.21–1.44 HL 0.46–0.52 HW 0.36–0.41 CeI 77–80 SL 0.33–0.39 SI 90–97 PW 0.22–0.30 (n=20).

REMARKS.— At the time of writing, type material for *Monomorium modestum* is missing (per Dr. D. Burckhardt, NHMB, pers. commun.), and the syntype of *Monomorium modestum transwaalense* (i.e., previously *M. modestum boerorum*) available to me for examination is headless, hence the identification of the Malagasy material as *Monomorium modestum* is provisional. Bolton (1987) uses the morphology of the propodeum and the nature of the metanotal groove to distinguish *M. modestum* from other African ants in that species group. The *transwaalense* syntype, however, clearly has an angulate propodeum that approximates to what can be found in many *Monomorium cryptobium* specimens. In workers of these small ants propodeal denticles are not always present. Moreover, the *transwaalense* syntype has quite a distinct metanotal impression, not the 'simple indentation' that Bolton mentions. The Malagasy material, on the other hand, *does* have a much more rounded propodeum and the metanotal groove is indeed simply a weak impression. In fact, Malagasy workers have much more of the appearance of Fig. 95 in Bolton's monograph than the *transwaalense* syntype. Electronic images of worker material collected many years ago in Natal and identified (probably by Arnold: H. Robertson pers. commun.) as *M. modestum* have been sent to me by Dr. Hamish Robertson (South African Museum), and these appear to be identical with the Malagasy workers. This raises the possibility that *Monomorium modestum* and *Monomorium modestum transwaalense* may not be conspecific. The general appearance of the *transwaalense* syntype suggests *M. sechellense*, but in that species the propodeum is distinctly dentate and the mesopleuron is sculptured, whereas this is not the case with *transwaalense*.

On Madagascar *Monomorium modestum* has a known distribution that is exactly complementary to that of *M. sechellense*, the latter occupying the drier west coast of Madagascar and the former the more humid east coast. Populations of these two species converge in the south near the Isantoria River (Toliara Province). The workers of *M. modestum* are nearly identical in appearance to small, depigmented yellow workers of *M. hildebrandti,* from which they differ only in the form of the compound eye. The weakly angulate to rounded propodeum enables Malagasy workers of the species to be separated from those of *Monomorium cryptobium* and *M. sechellense*. Queens and males are not represented in the CAS collection. With the exception of one worker taken in a pitfall trap, the universal collection method for this species has been sifted litter. All specimens have been collected in rainforest.

Monomorium sechellense Emery

Figs. 34, 83–84.

Monomorium fossulatum subsp. *sechellense* Emery, 1894a: 69, fig. (☿). Syntype's (lectotype here designated). Seychelles: Marianne (MCSN) [examined]. Syn. under *Monomorium fossulatum* Wilson and Taylor, 1967:64. Syn. under *Monomorium sechellense* Bolton, 1995: 267 [*sechellense* has priority over *fossulatum* as senior synonym].

Material examined.— Lectotype: ☿, Seychelles, Marianne, C. Alluaud, 1892 (MCSN). The erection of the lectotype fixes the name of this widespread taxon, whose populations vary chiefly in the degree of cephalic punctation. Paralectotype: ☿, same data as above (MCSN). (Carded specimen removed from same pin as lectotype above and repinned, together with new labels.)

Other material examined: **Prov. Mahajanga:** P.N. Ankarafantsika, Ampijoroa, 5.4 km 331 NW Andranofasika 30.iii.2001 Rabeson *et al.* (1☿); P.N. Namoroka, 9.8 km 300 WNW Vilanandro, 4–8.xi.2002 Fisher *et al.* (18☿, 6♀); P.N. Namoroka, 17.8 km 329 WNW Vilanandro, 8–12.xi.2002 Fisher *et al.* (11☿, 3♀); P.N. Tsingy de Bemaraha, 3.4 km 93 E Bekopaka 6–10.xi.2001 Fisher *et al.* (8☿). **Prov. Toliara:** Cap Sainte Marie, 14.9 km 261 W Marovato 13–19.ii.2002 Fisher *et al.* (6☿); Fiherenana, Frontier Project 21–24.x.2002 MGF040 (7☿); Forêt Mahavelo, Isantoria Riv., 5.5 km 37 NE Ifotaka 31.i.2002 Fisher *et al.* (1☿); 28 km NNW Ranohira, Isalo N. P., 16.xii.1993 G. D. Alpert (6☿) (MCZ).

Worker description.— Head: Head rectangular; vertex planar or weakly concave; frons shining and smooth except for piliferous pits; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye minute, eyes consisting of one or two ommatidia only; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule. Antennal segments 12; antennal club three-segmented. Clypeal carinae always weakly defined; anteromedian clypeal margin straight between strongly divergent clypeal carinae, clypeus descending almost vertically to horizontal arc of mandibles and sometimes transversely carinate below level of antennal insertions; paraclypeal setae moderately long and fine, curved; posteromedian clypeal margin extending slightly beyond level of posterior margin of antennal fossae. Anterior tentorial pits situated nearer mandibular insertions than antennal fossae. Frontal lobes sinuate, divergent posteriad. Psammophore absent. Palp formula 2,2. Mandibular teeth four; mandibles linear-triangular and smooth (except for piliferous pits); masticatory margin of mandibles strongly oblique; basal tooth approximately same size as t3 (four teeth present).

Mesosoma: Promesonotum shining and smooth on dorsum, lower mesopleuron strongly punctate; (viewed in profile) anterior promesonotum smoothly rounded, thereafter more-or-less flattened, promesonotum on same plane as propodeum; promesonotal setae greater than twelve; standing promesonotal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally and often paired, interspersed with much shorter, incurved, decumbent setae; appressed promesonotal setulae few, mainly on sides of promesonotum. Metanotal groove strongly impressed, with distinct transverse costulae. Propodeum shining, dorsum and sides of propodeum mainly smooth, with weak to strong striolae on declivitous face, metapleuron also with weak to strong striolae; propodeal dorsum flat throughout most of its length; propodeum distinctly angulate, propodeal angles produced as short denticles; length ratio of propodeal dorsum to its declivity about 1:1; standing propodeal setae consisting of one prominent pair anteriad, with a few to many erect to decumbent setae on/around dorsal and declivitous faces of propodeum; appressed propodeal setulae very sparse or absent; propodeal spiracle equidistant from metanotal groove and declivitous face of propodeum. Vestibule of propodeal spiracle absent or not visible. Propodeal lobes present as vestigial flanges or small strips of cuticle only.

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated slightly anteriad of petiolar node; node (viewed in profile) conical, vertex rounded; appearance of node shining and smooth throughout; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; ventral petiolar lobe absent; height ratio of petiole to postpetiole between 4:3 and 1:1; height–length ratio of postpetiole between 4:3 and 1:1; postpetiole shining and smooth; postpetiolar sternite without anterior lip or carina, or this structure vestigial.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, semi-erect setae and slightly shorter decumbent setae.

GENERAL CHARACTERS: Color pale, depigmented yellow. Worker caste monomorphic.

LECTOTYPE MEASUREMENTS: HML 1.12 HL 0.41 HW 0.34 CeI 83 SL 0.31 SI 91 PW 0.23.

OTHER WORKER MEASUREMENTS (non-types): HML 1.07–1.24 HL 0.40–0.45 HW 0.33–0.36 CeI 78–84 SL 0.31–0.35 SI 94–100 PW 0.22–0.25 (n=20).

QUEEN DESCRIPTION.— HEAD: Head square; vertex weakly concave or planar; frons shining and finely longitudinally striolate and microreticulate; pilosity of frons a mixture of incurved, semi-erect setae and slightly shorter decumbent setae. Eye elliptical, curvature of inner eye margin may be more pronounced than that of its outer margin; (in full-face view) eyes set at about midpoint of head capsule; (viewed in profile) eyes set posteriad of midline of head capsule.

MESOSOMA: Mesoscutum broadly convex anteriad, convexity reduced posteriad; pronotum, especially, also mesoscutum and mesopleuron shining with scattered punctation, otherwise smooth; length–width ratio of mesoscutum and scutellum combined between 2:1 and 3:2; axillae separated by width of at least one axilla; standing pronotal/mesoscutal setae a mixture of well-spaced, distinctly longer, erect and semi-erect setae which are curved distally, interspersed with much shorter, incurved, decumbent setae; appressed pronotal, mescoscutal and mesopleural setulae very sparse or absent; propodeum shining, uniformly weakly striolate; propodeum distinctly angulate, propodeal angle sharp; propodeal dorsum sloping posteriad, and depressed between raised propodeal angles; standing propodeal setae consisting of up to a dozen or more longer erect and shorter sub-erect setae; appressed propodeal setulae very sparse or absent; propodeal spiracle nearer metanotal groove than declivitous face of propodeum; propodeal lobes present as well-developed, rounded flanges.

WING: Wing not seen (queens dealated).

PETIOLE AND POSTPETIOLE: Petiolar spiracle lateral and situated well anteriad of petiolar node; node (viewed in profile) cuneate, vertex tapered; appearance of node shining and microreticulate; ratio of greatest node breadth (viewed from front) to greatest node width (viewed in profile) about 4:3; anteroventral petiolar process absent or vestigial; height ratio of petiole to postpetiole about 1:1; height–length ratio of postpetiole about 4:3; postpetiole shining and microreticulate; postpetiolar sternite depressed at about its center, with anterior process developed as a short, conspicuous spur angled at 45–90.

GASTER: Pilosity of first gastral tergite consisting of a mixture of incurved, erect and semi-erect setae and slightly shorter decumbent setae.

General characters: Color brown. Brachypterous alates not seen. Ergatoid or worker-female intercastes not seen.

Queen measurements: HML 1.68–1.78 HL 0.48–0.51 HW 0.45–0.46 CeI 90–96 SL 0.42–0.43 SI 91–93 PW 0.41–0.43 (n=9).

Remarks.— Its sculptured mesopleuron immediately enables the *Monomorium sechellense* worker to be distinguished from the worker of *M. cryptobium* and *M. modestum*. Queens are larger, darker and more heavily sculptured than those of *M. cryptobium*. As has been the case with *M. modestum*, sifted litter has been the most effective collection method for individual workers of *M. sechellense*, though one small nest series was taken from a rotten log. The species is found in dry tropical forest and gallery forest habitats in Antsiranana, Mahajanga and Toliara Provinces. Outside of Madagascar, this species has a wide distribution in the Indo-Pacific region (e.g., Bolton 1987; Wetterer 2002) and probably also occurs in Australia (Heterick 2001).

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Illustrations

Figures 14–30, 32, 34: Distribution maps;
Figures 31 and 33: Scatter diagrams;
Figures 35–105: Automontage images
of specimens examined

FIGURE 14. Distribution of *M. clarinodis*(△), *M. notorthotenes* (□), *M. robertsoni* (▲), and *M. shuckardi* (■) specimens examined during this study

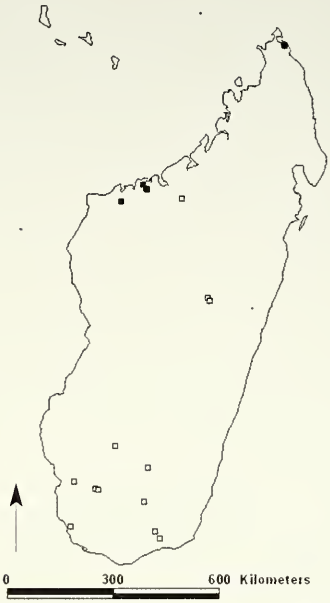


FIGURE 15. Distribution of *M. destructor* (■) and *M. robustior* (□) specimens examined during this study.

FIGURE 16. Distribution of *M. pharaonis* (△), *M. subopacum* (□), *M. willowmorense* (▲), and *M. latinode* (■) specimens examined during this study.

FIGURE 17. Distribution of *M. bifidoclypeatum* (■), *M. clinodes* (□), and *M. denticulus* (▲) specimens examined during this study.

FIGURE 18. Distribution of *M. exiguum* (■) specimens examined during this study.

FIGURE 19. Distribution of *M. flavimembra* (■) and *M. floricola* (□) specimens examined during this study.

FIGURE 20. Distribution of *M.nigricans* (■) and *M. lepidum* (□) specimens examined during this study.

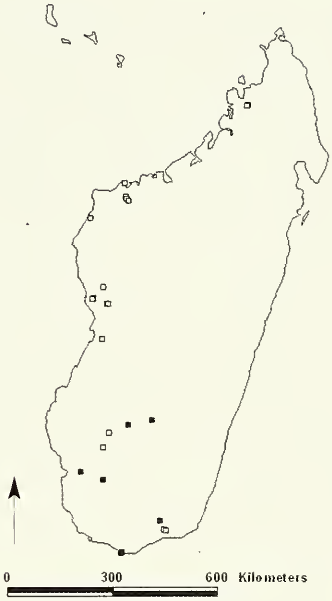


FIGURE 21. Distribution of *M. madecassum* (■) specimens examined during this study.

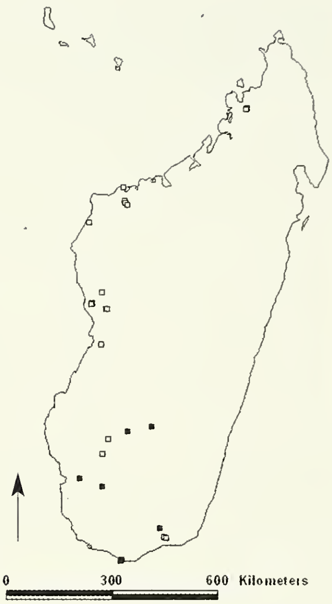


FIGURE 22. Distribution of *M. micrommaton* (□) and *M. platynodis* (■) specimens examined during this study.

FIGURE 23. Distribution of *M. sakalavum* (■) specimens examined during this study.

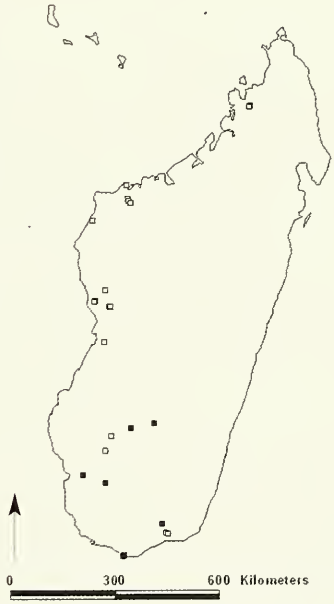


FIGURE 24. Distribution of *M. termitobium* (■) specimens examined during this study.

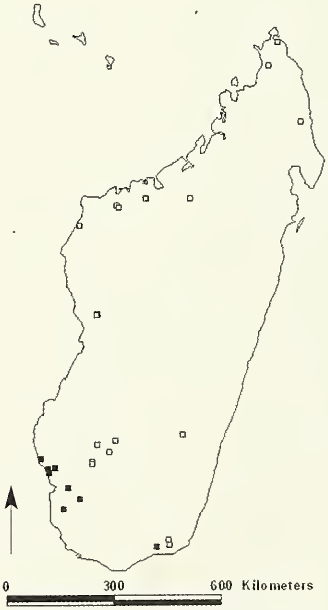


FIGURE 25. Distribution of *M. versicolor* (□) and *M. xuthosoma* (■) specimens examined during this study.

FIGURE 26. Distribution of *M. hanneli* (■) specimens examined during this study.

FIGURE 27. Distribution of *M. adiastolon* (□), *M. ferodens* (●), and *M. gongromos* (▲) specimens examined during this study.

FIGURE 28. Distribution of *M. aureorugosum* (□) and *M. infuscum* (■) specimens examined during this study.

FIGURE 29. Distribution of *M. cryptobium* (■) specimens ex-amined during this study.

FIGURE 30. Distribution of *M. fisheri* (■) specimens examined during this study.

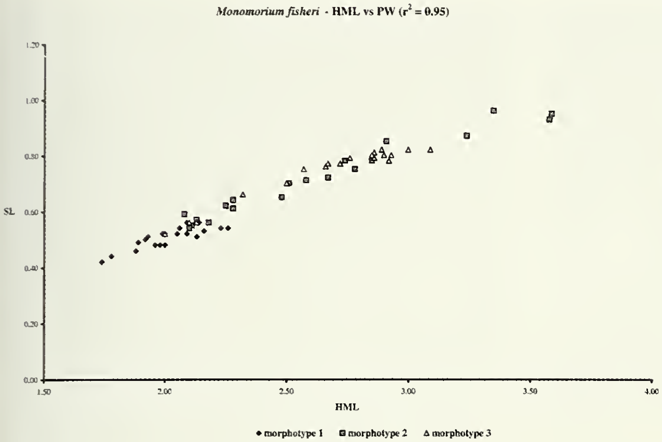


FIGURE 31. Scattegram showing relationship between head-mesosoma length (HML) and scape length (SL) for different morphotypes of *M. fisheri* sp. nov.

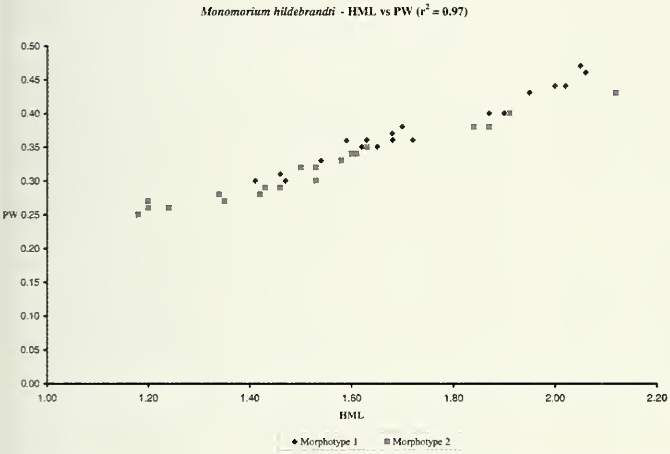


FIGURE 33. Scattegram showing relationship between head-mesosoma length (HML) and scape length (SL) for different morphotypes of *M. hildebrandti* sp. nov.

FIGURE 32. Distribution of *M. hildebrandti* (■) specimens examined during this study.

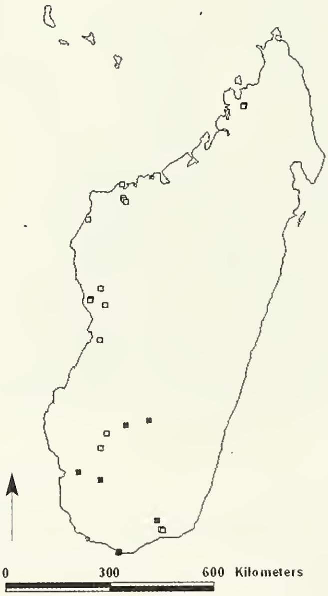
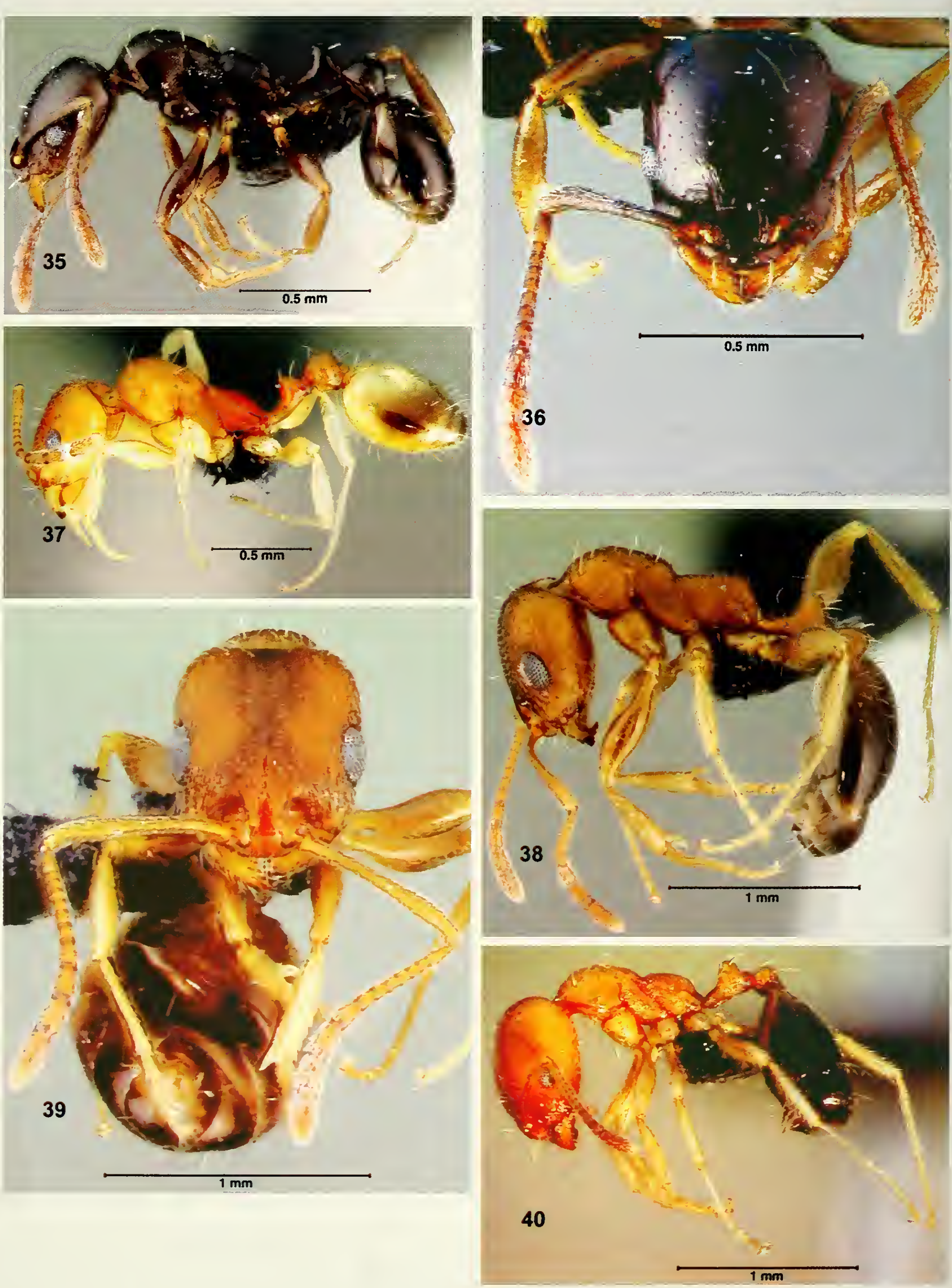
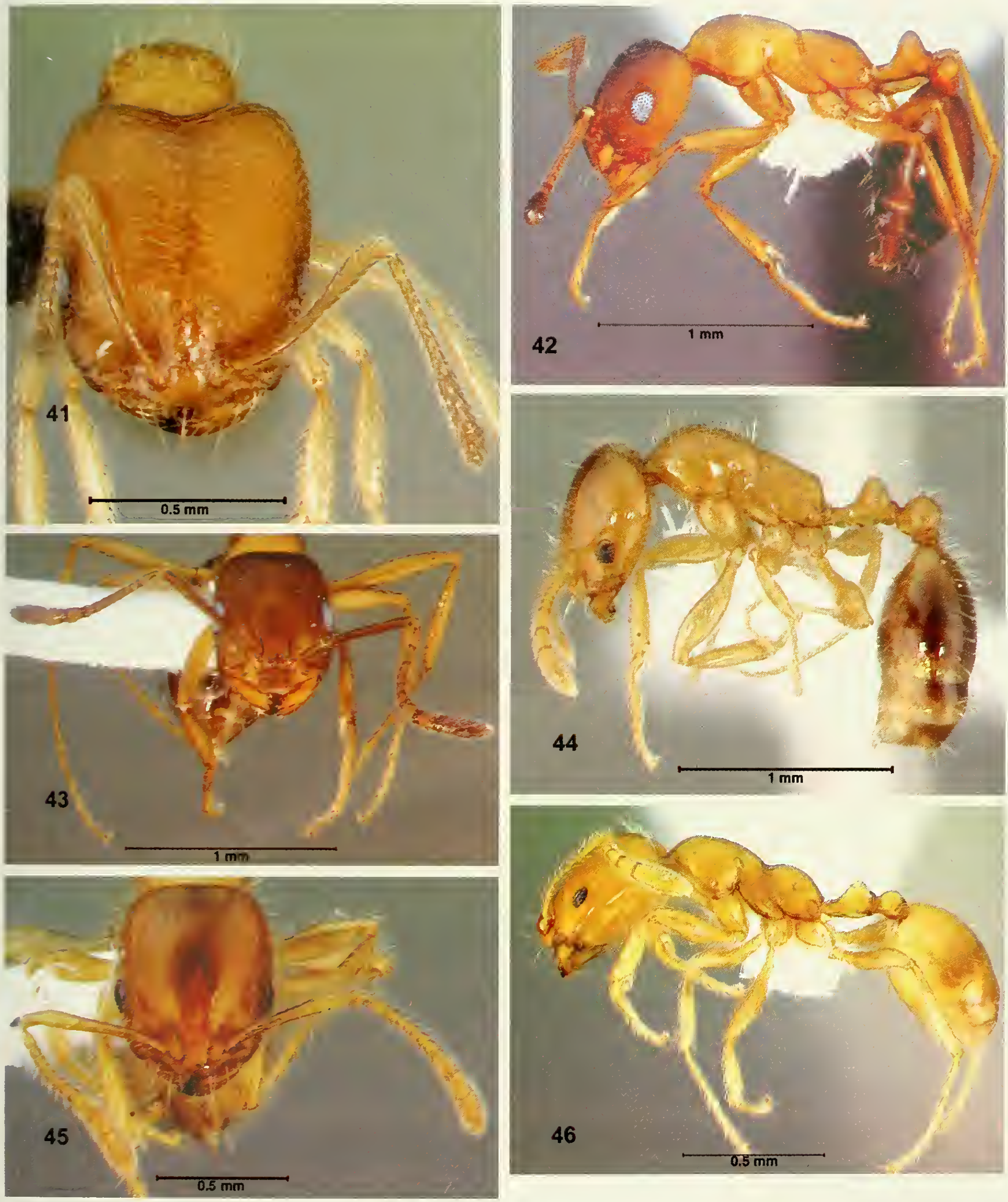


FIGURE 34. Distribution of *M. sechellense* (□) and *M. modestum* (■) specimens examined during this study.



FIGURES 35–40. *Monomorium* workers: 35, profile of *M. clarinodis*; 36, full-face view of *M. clarinodis*; 37, profile of *M. robertsoni*; 38, profile of *M. shuckardi*; 39, full-face view of *M. shuckardi*; 40, profile of *M. destructor* ('*vexator*' lectotype).



FIGURES 41–46. *Monomorium* workers: 41, full-face view of *M. destructor* ('*vexator*' lectotype); 42, profile of *M. subopacum*; 43, full-face view of *M. subopacum*; 44, profile of *M. latinode*; 45, full-face view of *M. latinode*; 46, profile of *M. bifidoclypeatum*.

FIGURES 47–53. *Monomorium* workers: 47, full-face view of *M. bifidoclypeatum*; 48, profile of *M. chnodes*; 49. full-face view of *M. chnodes;* 50, full-face view of *M. denticulus*; 51, profile of *M. exiguum* (lectotype) 52, full-face view of *M. exiguum* (lectotype) 53, profile of *M. flavimembra*.

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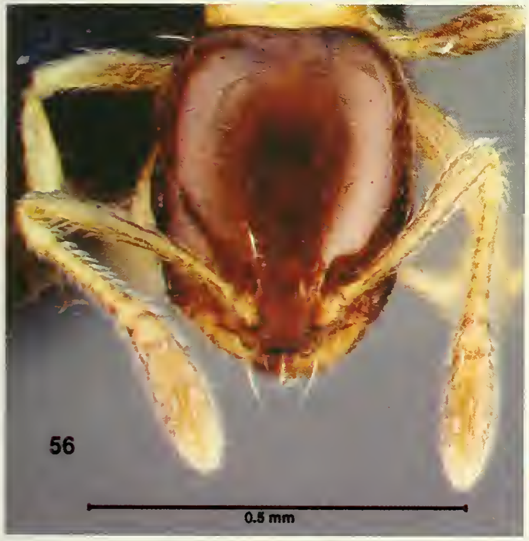

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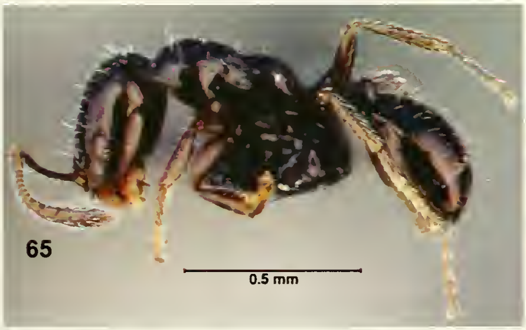
FIGURES 54–59. *Monomorium* workers: 54, full-face view of *M. flavimembra*; 55, profile of *M. floricola*; 56, full-face view of *M. floricola;* 57, profile of *M. lepidum*; 58, full-face view of *M. lepidum*; 59, profile of *M. madecassum*.

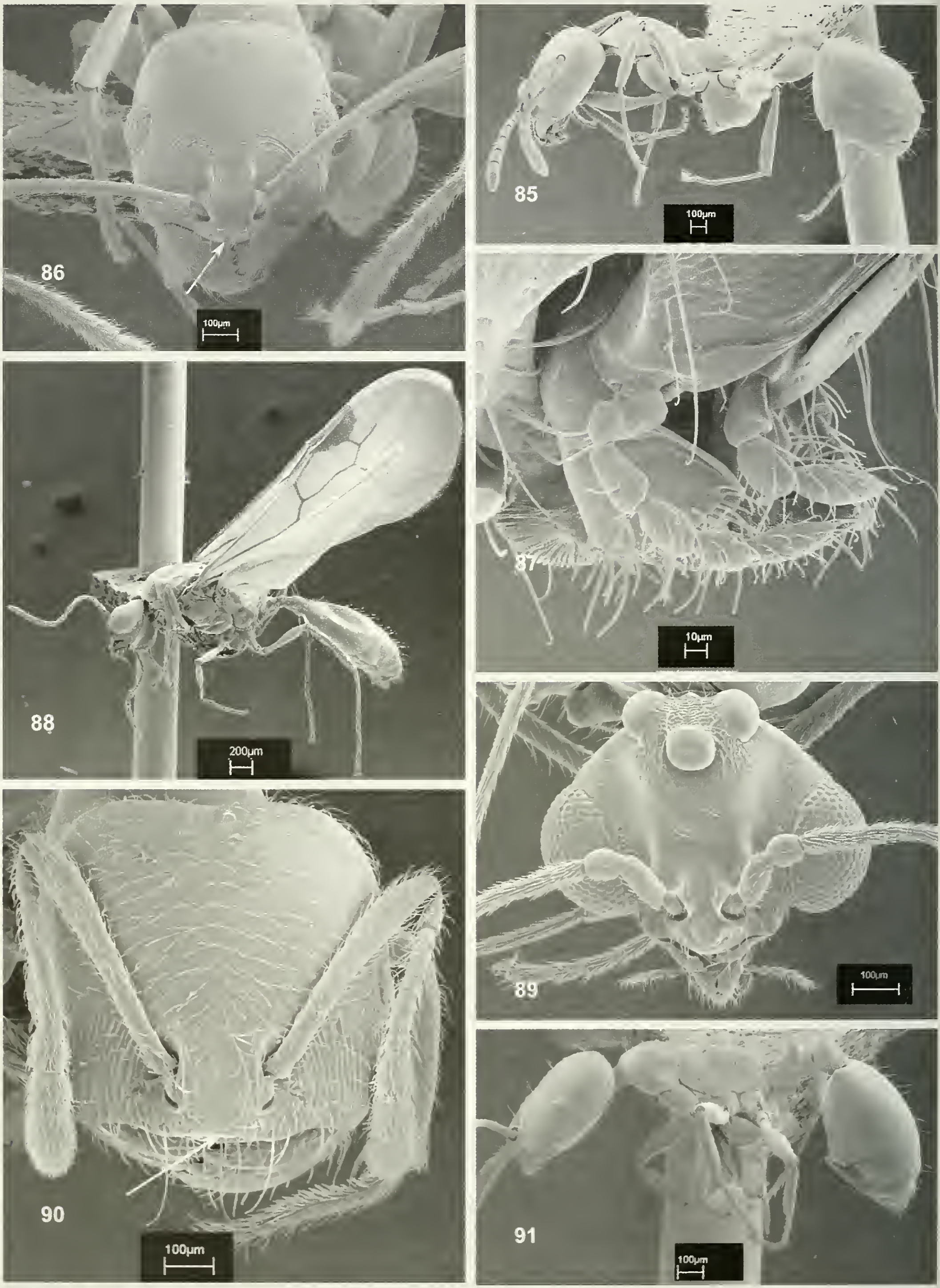


FIGURES 60–65. *Monomorium* workers: 60, full-face view of *M. madecassum*; 61, profile of *M. micrommaton*; 62, full-face view of *M. micrommaton*; 63, profile of *M. platynodis*; 64, full-face view of *M. platynodis*; 65, profile of *M. nigricans*.

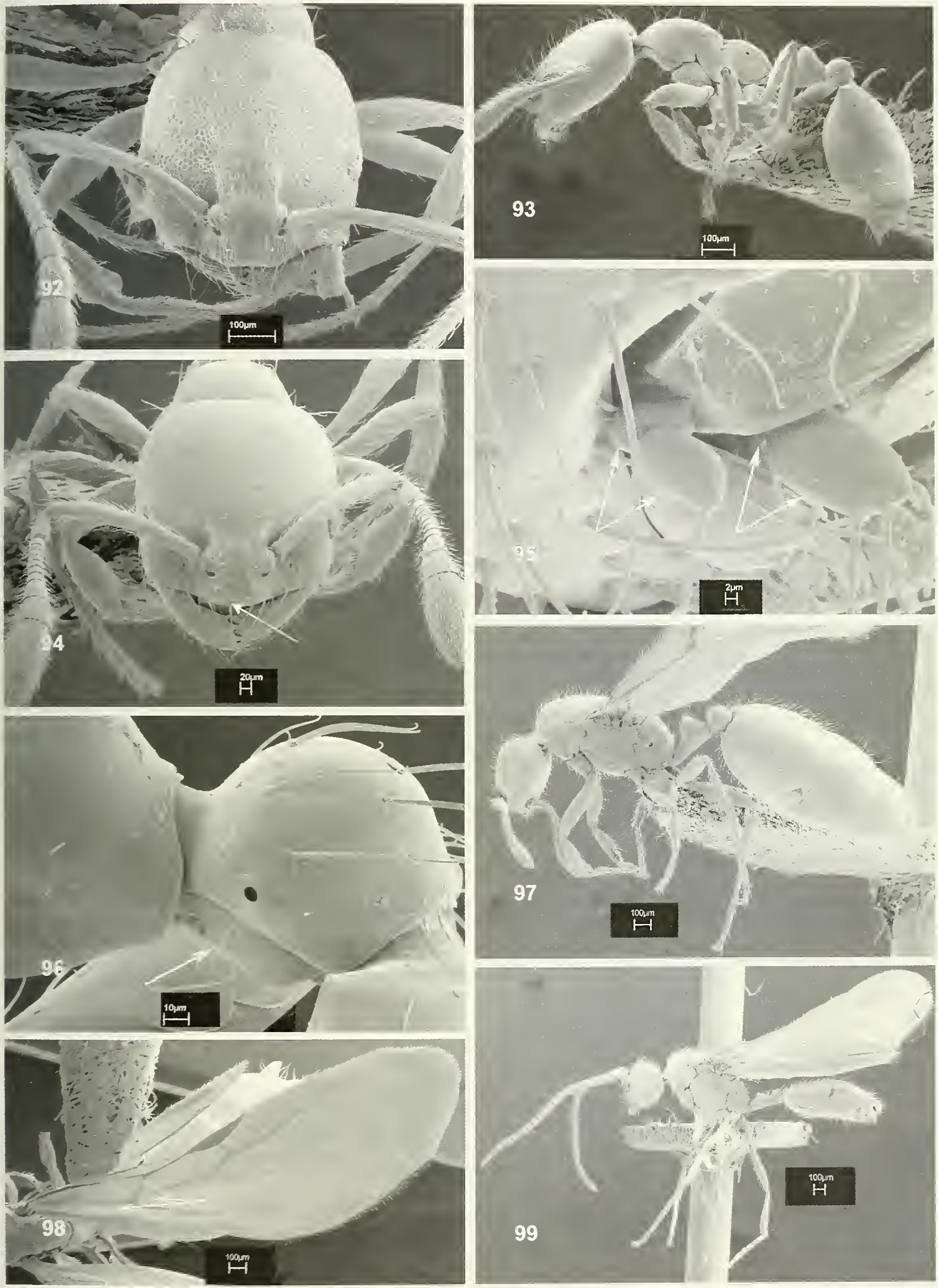
FIGURES 66–72. *Monomorium* workers: 66, full-face view of *M. nigricans*; 67, profile of *M. versicolor*; 68, full-face view of *M. versicolor*; 69, full-face view of *M. xuthosoma*; 70, profile of *M. hanneli* ('*valtinum*' holotype); 71, full-face view of *M. hanneli* ('*valtinum*' holotype); 72, profile of *M. adiastolon*.

FIGURES 73–79. *Monomorium* workers: 73, profile of *M. aureorugosum*; 74, full-face view of *M. aureorugosum*; 75, profile of *M. cryptobium*; 76, full-face view of *M. cryptobium*; 77, full-face view of *M. ferodens*; 78, profile of *M. fisheri*; 79, full-face view of *M. fisheri*.

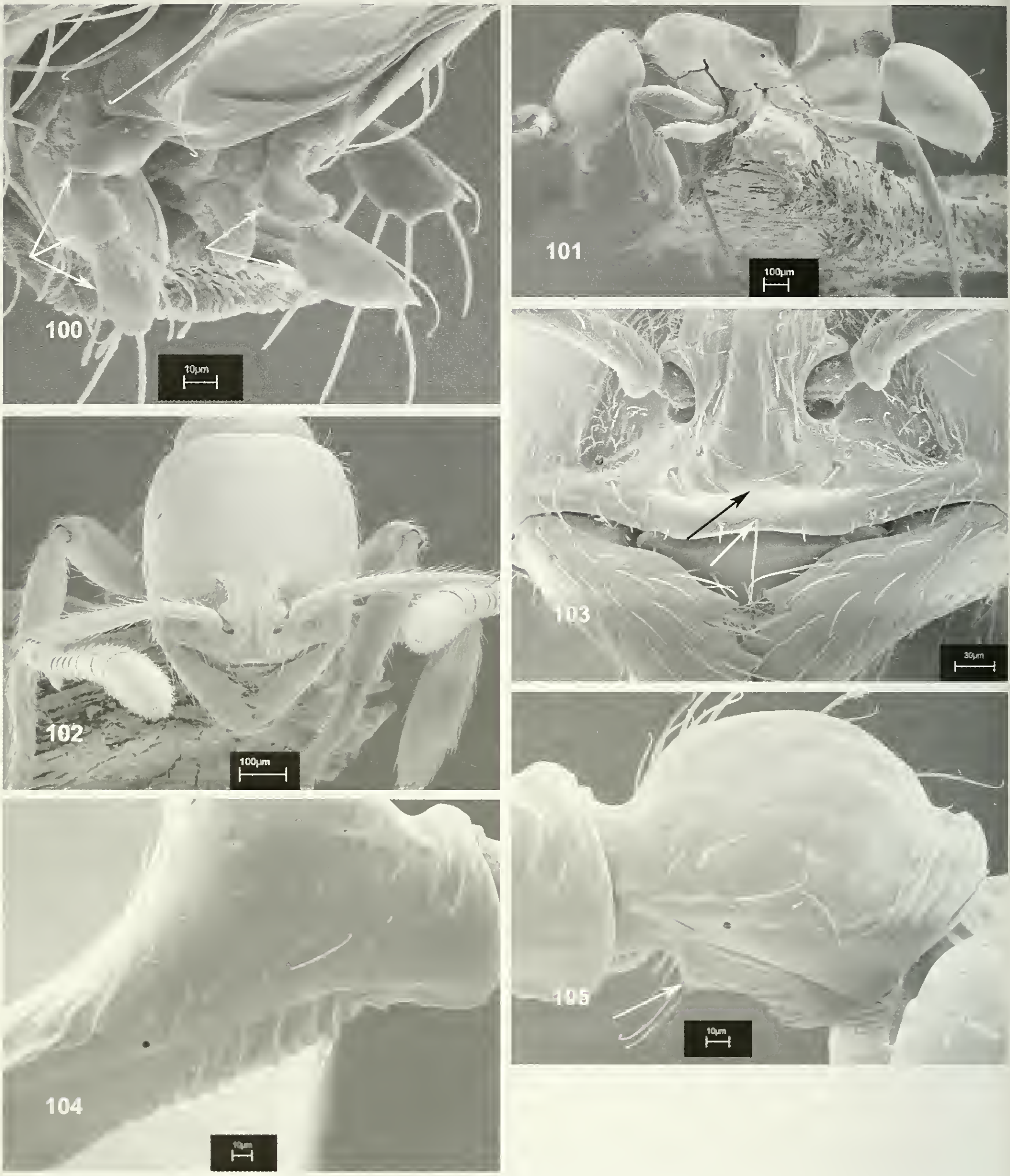
FIGURES 80–84. *Monomorium* workers: 80, full-face view of *M. gongromos* showing humeral excrescences; 81, profile of *M. modestum*; 82, full-face view of *M. modestum*; 83, profile of *M. sechellense*; 84, full-face view of *M. sechellese.*



FIGURES 85–91. *Monomorium* (SEM): 85, profile of *M. notorthotenes* worker; 86, full-face view of *M. notorthotenes* worker; 87, *M. notorthotenes* worker palps; 88, profile of *M. notorthotenes* male; 89, full-face view of *M. notorthotenes* male; 90, full-face view of *M. robustior* worker; 91, profile of *M. pharaonis* worker.



FIGURES 92–99 (left). *Monomorium* (SEM): 92, full-face view of *M. pharaonis* worker; 93, profile of *M. termitobium* worker; 94, full-face view of *M. termitobium* worker; 95, *M. termitobium* worker palps; 96, postpetiolar sternite of M. *termitobium* worker (anteroventral process is absent here); 97, profile of *M. termitobium* queen; 98, forewing of *M. termitobium* queen showing absence of cross-veins m-cu and cu-a; 99, *M. termitobium* male.



Figures 100–105 (above). *Monomorium* (SEM): 100, *M. ferodens* worker palps; 101, profile of *M. hildebrandti* worker; 102, full-face view of *M. hildebrandti* worker; 103, anterior margin of clypeus of *M. hildebrandti* worker showing placement of median seta (black arrow denotes clypeal protuberance); 104, underside of node of *M. hildebrandti* showing transverse rugulae; 105, postpetiolar sternite of M. *hildebrandti* worker showing anteroventral process.

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Pterostichus lattini LaBonte, a New Species of Carabid Beetle (Coleoptera: Carabidae: Pterostichini) from Oregon

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A new species of carabid beetle, *Pterostichus lattini* LaBonte, is described from Oregon (Type locality: Marys Peak, Benton Co., Oregon). Diagnostic characters include the distinctive shape of the pronotum and of the apex and shaft of the median lobe of the male genitalia. Features distinguishing *P. lattini* from species of *P.* (*Hypherpes*) found in Oregon are discussed. Although this species can be extremely abundant where it occurs, it is known only from north and central western Oregon. Habitat and phenological data are provided.

Species in the carabid genus *Pterostichus* Bonelli are among the most familiar beetles of forested habitats in the western United States. This is particularly true of members of the *amethystinus* species group (*sensu* Lindroth 1966 and Bousquet and Larochelle 1993). Charactistics in common among these species include fused elytra, extremely brachypterous hind wings, and the absence of discal dorsal elytral setae. Most of these species (about 70) can be placed in the subgenus *Hypherpes* Chaudoir.

Adult members of typical *Pterostichus* (*Hypherpes*) species are rather consistent in appearance: black or brown medium-sized (circa 10–20 mm in length) beetles that are slightly flattened, with large heads and rather large and broad pronota. This uniform appearance, combined with considerable intraspecific variation, renders identification of many members of *P.* (*Hypherpes*) *sensu stricto* challenging. Examination of male genitalia is often necessary to confirm identification. Compounding this problem is the plethora of Casey names, many of which may be synonyms. The most recent North American species of *P.* (*Hypherpes*) to be described was *P. neobrunneus* Lindroth 1966 (Bousquet and Larochelle 1993).

The Oregon carabid fauna, comprising roughly 500 species, is well known, due in large part to Hatch (1953) and Lindroth (1961–1969), as well as subsequent researchers, e.g., Bousquet (1985) and Kavanaugh (1984). Consequently, it was surprising to detect an undescribed, locally abundant, species of *P.* (*Hypherpes*) in western Oregon. The purpose of this paper is to describe the adults of this new species, to discuss features that distinguish it from other species of *P.* (*Hypherpes*) found in Oregon, and to provide data on the known distribution, habitat, and phenology.

MATERIALS AND METHODS

I examined the types of the *P. amethystinus* group, particularly those of *P.* (*Hypherpes*) species, available at the California Academy of Sciences (CAS), San Francisco, CA and the National Museum of Natural History (USNM), Washington, D.C.. Reliably determined examples of most

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species not represented by types were also examined where possible. Yves Bousquet and Serge Laplante (Agriculture and Agri-Food Canada) very kindly examined specimens of *P. lattini* and concluded they were not conspecific with those species for which I had not seen examples.

Specimens were examined under a stereoscopic microscope with a maximum magnification of 160×. Absolute and relative measurements were obtained via an ocular micrometer used with a stereomicroscope. Total length included the left elytron from apex to humerus, the midline of the pronotum, and the midline of the head from the occiput to the apices of the mandibles. Specimens in my personal collection (JRLC) and the Oregon State Arthropod Collections (OSAC) at Oregon State University (Corvallis, OR) were used for length measurements. Images of pronota and male genitalia were acquired via the Oregon Department of Agriculture's digital imaging system, comprised of a Leica MZ16 stereomicroscope, a Spot Insight digital camera (model 3.2.0, Diagnostic Instruments, Inc., Sterling Heights, MI), and Image-Pro 5.0 image acqusition and analysis software (Media Cybernetics, Silver Spring, MD).

Description of new Taxon

Pterostichus lattini LaBonte, sp. nov.

Holotype.— Male. Label data "OR, Benton Co., Marys Peak, Elev. 1092 m, J.R. LaBonte, 14 Aug. 1996, T12S R7W Sec20. SW1/4 of NE1/4 of SE1/4, N face". Deposited at the California Academy of Sciences, CAS Type no. 18122.

Habitus.— General color black without metallic highlights; palpi, antennomeres 5–11, and tarsi brown. Overall luster shiny. Total body length 15.7 mm. **Head**: Large (typical of *P.* [*Hypherpes*] species). Microsculpture at center of frons isodiametric. **Pronotum** (Fig. 1a): More or less quadrate, about 0.75 times as wide as long, widest at anterior one-quarter of pronotal length; margin between anterior angles 0.75 times as wide as margin between posterior angles. Anterior margin evenly arcuate, with slightly protruding anterior angles. Lateral margins slightly obliquely convergent posterior to anterior lateral setiferous punctures, very slightly sinuate at posterior third; lateral beads distinct. broadening at posterior one-third and broadest at posterior angles, with a few crenulations present just anterior to posterior angles. Bases of anterior lateral setae within deep foveae, just mediad of and adjacent to lateral marginal grooves. Posterior margin more or less truncate, slightly concave medially; lateroposterior beads distinct to just mediad of inner boundaries of inner basal depressions and clearly connected with lateral beads at posterior angles. Posterior angles slightly obtuse and slightly denticulate. Outer basal depressions deep, elongate-oval, and approximately linear, with inscribed line at bottom, each depression terminated distinctly anterior to posterior margin, separated from posterior marginal bead by a distinct convexity, bounded externally and separated from lateral bead by distinct, obtuse linear convexity, with this convexity extended anteriorly to about the posterior one-seventh of pronotum and terminated just anterior to posterior bead. Inner posterior depressions about twice as long as outer depressions, oblong-linear, deep, incised at bottom, extended to posterior bead. Convexities between outer and inner depressions distinct, slightly flattened adjacent to inner margin of outer depressions, extended to posterior bead. Median depression and inner posterior depressions with evanescent horizontal wrinkles extended laterally. Extreme posterior of pronotum between inner depressions with faint longitudinal incisions. Meshes of microsculpture elongate-rectangular or oblong, in irregular horizontal rows. **Elytra**: Fused along suture, without dorsal setae (typical of *P.* [*Hypherpes*] species). Hind wings extremely brachypterous, reduced to small stubs (typical of *P.* [*Hypherpes*] species). Meshes of microsculpture irregularly pentagonal, in irregular horizontal rows; rows more or less imbricate, with posterior margins of meshes in a given row raised above anterior margins of meshes in the following row. **Legs**: Tarsomeres 1–3 of protarsi expanded, with two longitudinal rows of squamose setae ventrally; tarsomeres 4 expanded, without such setae. Fifth tarsomeres of all tarsi asetose ventrally. Dorsolateral margins of crenulae on inner faces of meso- and metatibiae only faintly tuberculate. **Venter**: Mesepisterna densely and shallowly punctate in anterior one-third, with only evanescent stria connecting the punctures (best seen in oblique light). Apical margin of last visible abdominal sternite simple, without carina, tubercle, or lobe, with one pair of long setae. **Aedeagus** (Figs. 2a, 3a, 4a): Median lobe simple: in lateral views, bend between base and shaft approximately 90°, shaft without ventral swelling or lobe, base of apex ventrally produced and apex thin and sinuate; in dorsal view, apex symmetrically narrowed toward the very slightly asymmetrically expanded tip.

PARATYPES.— Paratypes have been placed or are located in the following institutions or collections (codens follow the "Insect and Spider Collections of the World" website at the Bishop Museum <*www.bishopmuseum.org/bishop/ento/codens-r-us.html*> as of September 2005): CAS (64), CIDA (2), CMNH (2), CNC (2), CUIC (2), EMEC (2), JRLC (42), LACM (2), MCZ (2), MSUC (2), ODAC (2), OSAC (331), UASM (2), UCDC (2), USNM (2), WFBM (2), WSU (2).

VARIATION.— The venter of late teneral adults is brown, as are the lateral margins of the pronota and elytra. The legs are paler than in fully pigmented specimens.

Females have more pronounced microsculpture and slightly duller sheen. Protarsomeres 1-4 are not expanded and lack squamose setae ventrally. The crenulae on the inner faces of the meso- and metatibiae are extremely faint, almost absent, and the dorsolateral margins are not tuberculate. The apical margin of the last visible abdominal sternite has two pairs of long setae.

One male specimen (from the H.J. Andrews Experimental Forest) has a single pair of very short ventral setae on the fifth tarsomeres. This specimen otherwise appears to be a typical *P. lattini*.

There is considerable variation in the form of the pronotum among specimens examined. The posterior angles varied from slightly obtuse to rectangular. The lateral pronotal margins in the posterior half range from slightly sinuate, in most specimens, to completely oblique in a few individuals. Some specimens have shallower and more oviform outer posterior depressions with less pronounced lateral convexities. Such variation is most evident in a series from the H.J. Andrews Experimental Forest. In some of these specimens, the outer posterior depressions are almost entirely effaced. The medial development of the posterior bead ranges from extended just mediad of the inner posterior impressions (in most specimens) to extended across the entire posterior margin. The posterior lateral crenulations are almost absent from many specimens. The fine linear grooves at the posterior of the pronotum between the inner depressions range from evanescent to deeply incised. Some specimens with pronounced lateral convexities have the posterior area between the outer and inner depressions flattened.

There appears to be relatively little size variation in this species. Total lengths of specimens selected for a full range of size ($N = 50$) ranged from 13.0 to 15.5 mm, with a mean of 14.2 mm ± 0.5 mm. Males ($n = 25$) averaged slightly smaller than females ($n = 25$), with means of 14.1 mm and 14.4 mm, respectively.

ETYMOLOGY.— I take great pleasure in naming this species in honor of my friend, colleague, and mentor, John D. Lattin (Emeritus Professor, Botany and Plant Pathology Department, Oregon State University). Among his many accomplishments were his tireless efforts promoting an understanding and appreciation of the insect fauna of the H.J. Andrews Experimental Forest, where *P. lattini* is among the most commonly collected carabids. The species epithet is a noun in apposition.

DISTINGUISHING *P. LATTINI* FROM OTHER PACIFIC NORTHWESTERN SPECIES OF *PTEROSTICHUS*.— There are several Pacific Northwestern *P.* (*Hypherpes*) species whose adults are somewhat similar externally to those of *P. lattini*. The species most apt to be confused with *P. lat-*

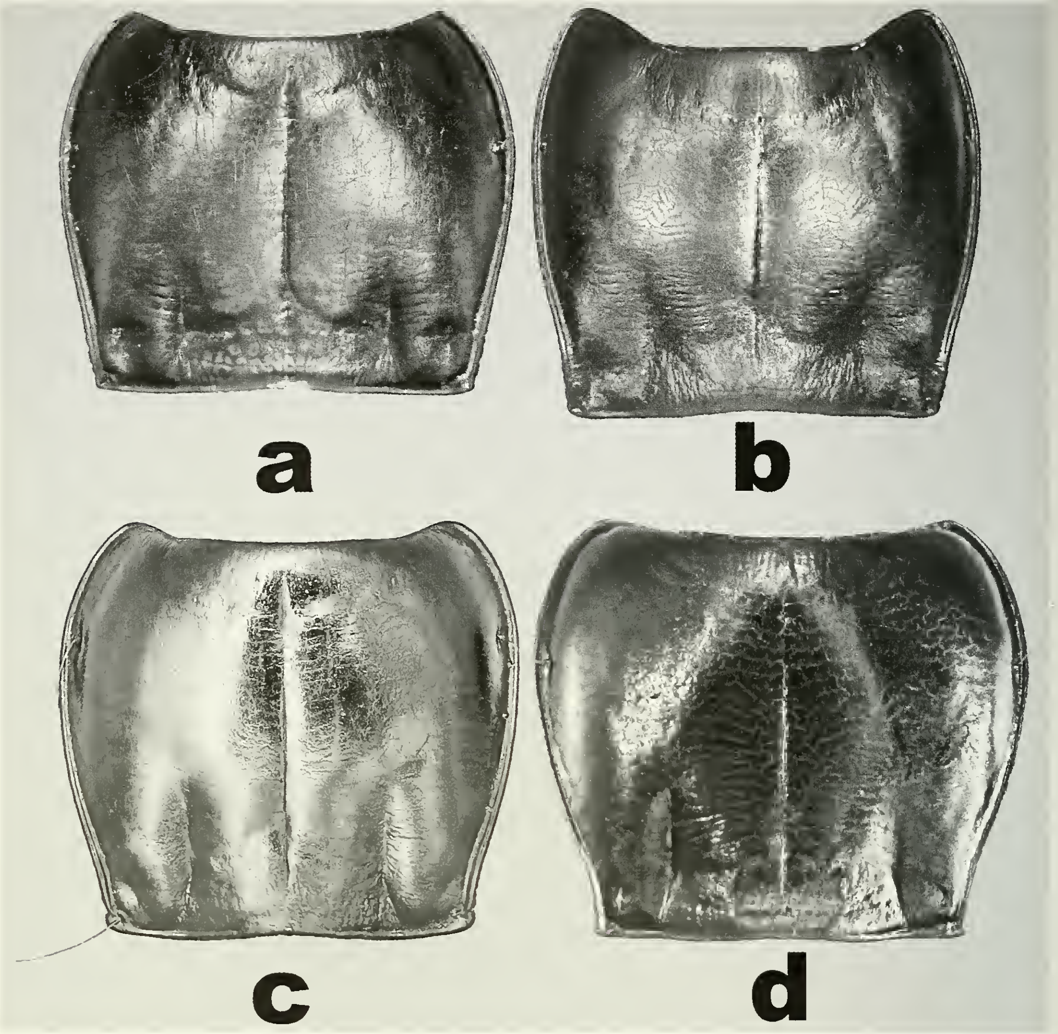

FIGURE 1. Dorsal aspect of pronotum (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

tini, at least based on existing keys, is *P. herculaneus* Mannerheim. These two species often occur sympatrically, increasing the opportunity for confusing them. I have seen specimens of *P. herculaneus* from most *P. lattini* sites.

The pronotum of *P. herculaneus* (Fig. 1b) has distinct linear convexities that form the lateral boundaries of the outer posterior depressions, as in *P. lattini* adults. However, the pronotum of *P. herculaneus* differs in the following characters: the anterior angles are very strongly produced, forming distinct obtuse angles with the medioanterior margin; the outer posterior depressions extend to the posterior margin; the outer and inner posterior depressions are indistinctly separate, forming a flattened area between the posteriolateral convexities and the inner margins of the inner depressions; the posteriolateral convexities are generally more sharply delineated medially and are continuous posteriorly with the posterior marginal bead; strong horizontal wrinkles extend laterally from the median depression and laterally and medially from the inner posterior depressions;

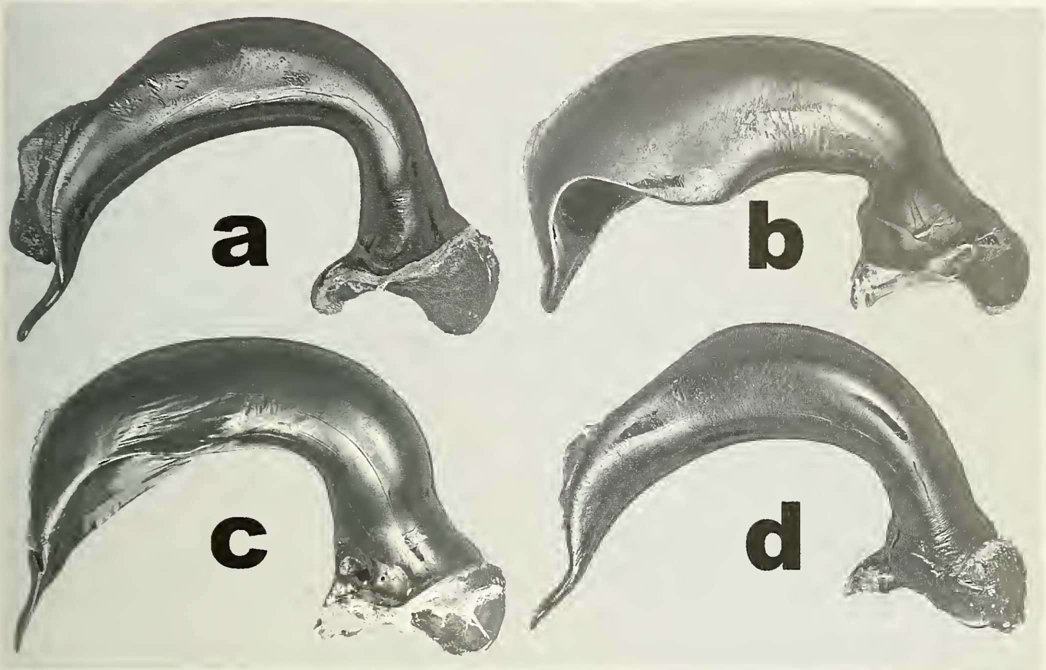

FIGURE 2. Right lateral aspect of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

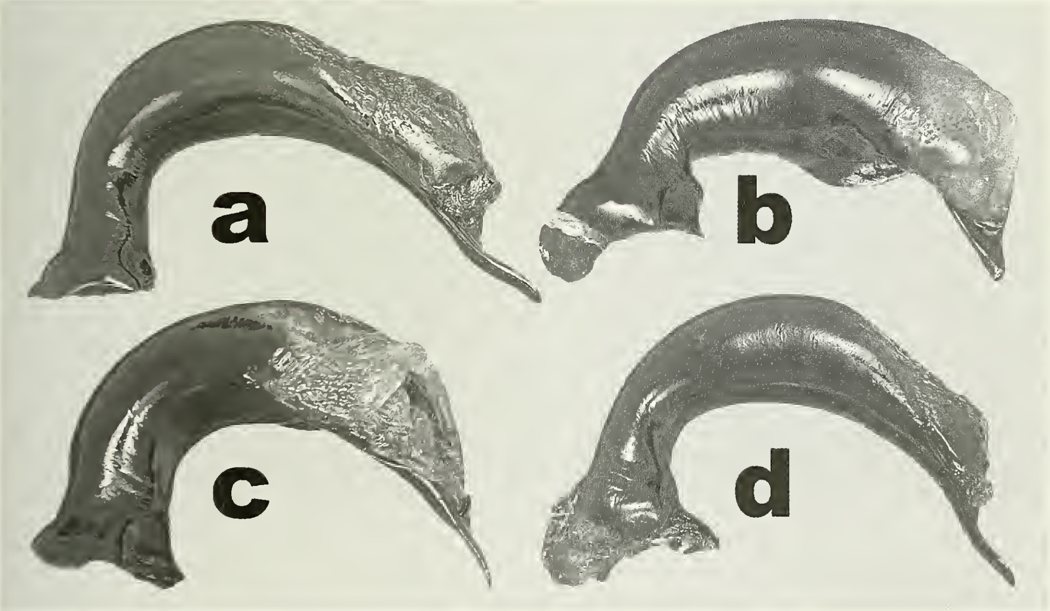

FIGURE 3. Left lateral aspect of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

strong longitudinal incisions along the medioposterior margin between the inner depressions extend

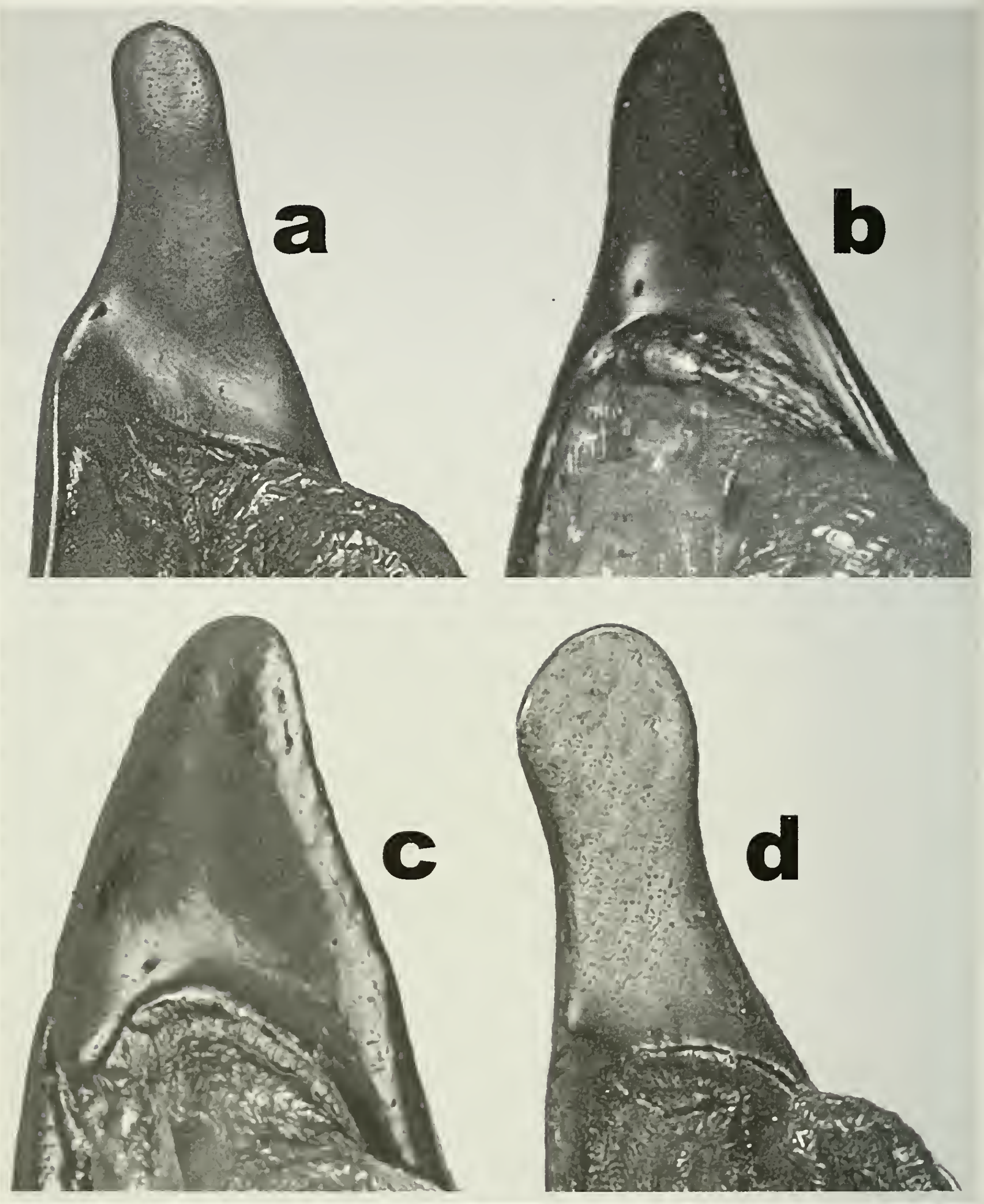

FIGURE 4. Dorsal aspect of apex of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

anteriorly to about half the length of those depressions.

There are also several non-pronotal characters distinguishing the two species. The mesepisterna of *P. herculaneus* are densely, deeply punctate over at least the anterior one-third to one-half, with distinct striae between the punctures (best seen with oblique lighting). The dorsolateral margins of the crenulae on the inner faces of the meso- and metatibiae of *P. herculaneus* males are distinctly tuberculate. The median lobe of the aedeagus of *P. herculaneus* bears no resemblance to that of *P. lattini* as it is much broader overall and has a blunt, broad apex in dorsal view (Figs. 2b, 3b, 4b).

Pterostichus lattini specimens with poorly developed posteriolateral pronotal convexities could be confused with adults of *P. algidus* LeConte. The following characters easily distinguish *P. algidus* from *P. lattini*: the outer posterior pronotal depressions are shallow and round, with the outer margins in contact with the lateral beads (Fig. 1c), not separated from the margins by the lateral convexities, as in *P. lattini*; three pairs of long ventral setae on the fifth tarsomeres; males have dorsolateral tubercles on the inner faces of the meso- and metatibiae, although these are less pronounced than in *P. herculaneus* males; the median lobe of the aedeagus bears no resemblance to that of *P. lattini*—among other differences, a large right ventrolateral lobe extends from about the middle of the shaft and the apex in dorsal view is broad and triangular (Figs. 2c, 3c, 4c). *Pterostichus algidus* is widespread and eurytopic in Oregon, but is known to be sympatric with *P. lattini* only at Marys Peak.

Pterostichus lattini specimens with poorly developed posteriolateral pronotal convexities could conceivably be confused with *P. setosus* Hatch. The following characters most easily distinguish *P. setosus* adults from those of *P. lattini*: two pairs of short, ventral, setae on the fifth tarsomeres; males have two pairs of long setae on the apical margin of the last abdominal sternite; males have dorsolateral tubercles on the inner faces of the meso- and metatibiae, although these are less pronounced than in *P. herculaneus* males. The general conformation of the pronotum is also quite different (Fig. 1d): the pronotum is not quadrate; appears distinctly broader at the anterior margin than at the posterior margin; the lateral margins are strongly and evenly arcuate from the anterior angles to just before the hind angles; the outer posterior depressions are small and round. The elytra are elongate-oviform, narrowest at the humeri, and the humeri are evenly arcuate in dorsal view (versus obtusely angulate in *P. lattini*). The overall habitus of *P. setosus* is also more gracile than that of *P. lattini*. *Pterostichus setosus* is known only from southwestern Oregon (Hatch 1953; LaBonte, unpublished data), where *P. lattini* is not known to occur.

Whereas most Pacific Northwestern species of *P.* (*Hypherpes*) can be readily distinguished by the form of the male genitalia alone, this is not true for *P. setosus* and *P. lattini*. The median lobe of the aedeagus of *P. setosus* males, in either left or right lateral views, is remarkably similar to that of *P. lattini* males (Figs. 2d, 3d); however, the tip of the apex in dorsal view is symmetrically and more apically expanded (Fig. 4d) and the base of the apex is symmetrical in dorsal view in *P. setosus* males (Fig. 4d), whereas it is more swollen on the left side than on the right in *P. lattini* (Fig. 4a).

Distribution.— Despite being one of the most commonly collected carabids on Marys Peak and at the H.J. Andrews Experimental Forest, I have seen specimens of *P. lattini* from only a limited portion of the north-central Oregon Cascades and two sites in the northern Oregon Coast Range (Fig. 5). All the Cascadian sites are on the western slope of the range, although several are near the Cascade Crest. The Coast Range sites are along the eastern flank of that range. I have examined specimens, most of which are paratypes (some specimens examined earlier were not available for paratype designation), from the following localities: Oregon: **Benton County**: Grass Mountain, 44.426°N, 123.664°W, elev. 951 m; Marys Peak (many localities, e.g., 44.497°N, 123.543°W, elev. 796 m; 44.512°N, 123.543°W, elev. 845 m; 44.512°N, 123.563°W, elev. 1,002 m; 44.513°N, 123.550°W, elev. 1,130 m). **Clackamas County**: 24 km NE Mills City, 44.918°N, 122.202°W, elev. 885 m. **Douglas County**: Dog Prairie, 43.187°N, 122.300°W, elev. 1,483 m; Watson Falls, 48.242°N, 122.389°W, elev. 842 m. **Lane County**: 29 km N Oakridge, Christy Flats, 43.911°N, 122.333°W, elev. 900 m; H.J. Andrews Experimental Forest, ~3 km N Mackenzie Bridge (many localities, e.g., 44.212°N, 122.237°W, elev. 631 m; 44.218°N, 122.157°W, elev. 1,109 m; 44.218°N, 122.177°W, elev. 950 m; 44.218°N, 122.217°W, elev. 838 m; 44.218°N, 122.257°W, elev. 593 m; 44.233°N, 122.197°W, elev. 610 m; 44.247°N, 122.157°W, elev. 1,083 m; 44.262°N, 122.177°W, elev. 884 m; 44.277°N, 122.137°W, elev. 1,348 m; 44.277°N, 122.157°W, elev. 1,400 m); Twin Springs Campground, 43.962°N, 122.112°W, elev. 792 m. **Linn County**: ~16 km ESE Cascadia (44.326°N, 122.259°W, elev. 1,269 m; 44.351°N, 122.304°W, elev. 1,147 m; 44.367°N, 122.293°W, elev. 1,147 m); Green Peter Mountain, 44.501°N, 121.301°W, elev. 821 m; Iron Mountain, 44.395°N, 122.157°W, elev. 1,266 m; Marion Forks Guard Station, 44.604°N, 121.961°W, elev. 773 m; 2.4 km NE Middle Santiam Wilderness, 44.564°N, 122.163°W, elev. 1074 m; 1.6 km NE Upper Soda, 44.411°N, 122.258°W, elev. 638 m.

The known distribution of *P. lattini* extends over only about 210 km north to south and 145 km east to west (Fig. 5). The only species of Oregon *P.* (*Hypherpes*) *sensu stricto* with a smaller known range is *P. setosus*, with a known distribution limited to southernmost Oregon and extending 16 km north to south and 68 km east to west (LaBonte, unpublished data). There are no obvious biogeographical factors to account for such limited ranges for either species. I am confident that *P. setosus* is present in the Siskiyou region of northern California adjacent to the Oregon border. With regard to *P. lattini*, I would be surprised if it is not found to be more widely distributed along the western flanks of the Oregon Cascades. In both cases, it seems most likely that these very small overall ranges are at least in part artifacts of collecting or confusion with other species.

The apparently disjunct Coast Range populations of *P. lattini* are on the highest peaks of that range. However, this species is not restricted to the summits but has been found at lower elevations as well, as low as *circa* 730 m. Thus, there appears to be no reason to expect this species to be found in the Coast Range only in the vicinity of the highest peaks. For example, another presumably predominantly Cascadian species of *P.* (*Hypherpes*) *s. str.*, *P. tuberculofemoratus* Hatch, is not only abundant on Marys Peak but also has been collected at sea level along the Oregon Coast (LaBonte, unpublished data).

Whether *P. lattini* will be found in northern California or southern Washington remains uncertain. There are several species of *Pterostichus* known only from northwestern Oregon or with reliable records only from that area. These include *P. campbelli* Bousquet (Bousquet 1985), as well as *P. lanei* Hatch and *P. rothi* Hatch (LaBonte 1994 and unpublished data). Of course, inadequate collecting or misidentification can always be invoked as possible explanations for such distributions. However, these are all flightless species found in cool and moist habitats (Bousquet 1985, LaBonte 1994 and unpublished data). Dispersal of such species could have been constrained by the Columbia River to the north, while past or present climatic conditions further south could either have limited expansion from the north or caused range contraction. Further collecting or examination of museum material could help ascertain whether this may the case for *P. lattini*.

HABITAT DATA.— This species has been found at elevations ranging from 593–1,483 meters. Specimens examined were all from coniferous forests and forest margins, or clear cuts therein. Stands ranged in age from new plantings to old growth. Dominant conifers, depending upon the specific site, aspect, and elevation, included Douglas fir (*Pseudotsuga menziesii* Franco), noble fir (*Abies procera* Lindl.), and western hemlock (*Tsuga heterophylla* Sargent). Understory development and composition varied among sites.

Associated species of Carabidae and Trachypachidae at elevations above 1,000 m on Marys Peak in the Coast Range included *Harpalus cordifer* Notman, *Leistus ferruginosus* Mannerheim, *Notiophilus sylvaticus* Eschscholtz, *Pterostichus algidus*, *P. lanei*, *P. infernalis* Hatch, *P. lama* (Menetries), *P. rothi*, *P. tuberculofemoratus*, *Scaphinotus angulatus* (Harris), *S. angusticollis* (Fischer), *S. marginatus* (Fischer), *S. rugiceps* (Horn), *S. velutinus* (Menetries), *Tanystoma sulcata*

FIGURE 5. Known distribution of *Pterostichus lattini* LaBonte. Map prepared by the Oregon Department of Agriculture. Data source(s): Oregon Geospatial Data Clearinghouse, USGS, ESRI, Oregon Department of Agriculture.

(Dejean), *Trachypachus holmbergi* Motschulsky, and *Zacotus matthewsii* LeConte. Species found with *P. lattini* at a moderate elevation (885 m) Cascade site included *Amara sinuosa* (Casey), *Bembidion farrarae* Hatch, *Cychrus tuberculatus* Harris, *Harpalus cordifer*, *H. somnulentus* Dejean, *Omus dejeani* Reiche, *Promecognathus crassus* LeConte, *Pterostichus crenicollis* LeConte, *P. herculaneus*, *P. lama*, *P. neobrunneus*, *Scaphinotus angulatus*, *S. angusticollis*, *S. marginatus*, and *Trachypachus holmbergi* (LaBonte 1996). Most of these species are typical elements of mid-elevation coniferous forests west of the Cascade Crest in Oregon.

PHENOLOGICAL OBSERVATIONS.— Specimens of *P. lattini* were collected during every month from April through October. Adults no doubt can be found throughout the year, as is true for some related species. The majority of specimens examined were collected in May or June. This pattern may not reflect the true abundance phenology of this species because available (i.e., collected, mounted, and curated) specimens represent only a subset of the total number of individuals present at a given site at the time of collection.

I have seen late teneral adults, recognized by their soft or pale aedeagi, collected in May and from July through September. I have seen early teneral adults, recognized by their entirely pale bodies, only from July and August. Although summer teneral adults suggest that *P. lattini* is a "spring-breeder" with new generation adults breeding after eclosion and with overwintering larvae (Thiele 1977), more data are needed to verify the reproductive pattern of this species.

Phylogenetic considerations.— Although *P. lattini* superficially resembles several other Oregon species of *Pterostichus*, it is not clear as to which of the Oregon species it is most closely related. The phylogenetic position of this species relative to species of *P.* (*Hypherpes*) *s. str.* in general is also uncertain on the basis of morphological features. Recent analyses of molecular data, based on nearly 100 terminal taxa and three different DNA markers, suggest that *P. lattini* is sister to a clade including *P. herculaneus, P. protractus* Le Conte, *P. neobrunneus* Lindroth, and an undescribed species near *P. parens* Casey (K.W. Will, pers. commun.)

Acknowledgements

The following institutions and individuals generously enabled me to examine holotypes and other North American material for comparative purposes: David H. Kavanaugh and the California Academy of Sciences; Terry L. Erwin, Gloria House, and Warren Steiner and the National Museum of Natural History, Smithsonian Institution. A generous loan of material from Oregon State University's Oregon State Arthropod Collections enabled me to examine large series of *P. lattini* from the H.J. Andrews Experimental Forest. Jessica Rykken and Hoonbok Yi graciously allowed me to examine specimens of *P. lattini* and provided locality data from their studies while at Oregon State University. Yves Bousquet and Serge LaPlante of Agriculture and Agri-Food Canada (Ottawa, Ontario, Canada) kindly examined several specimens and confirmed my diagnosis that they represent an undescribed species. Special thanks are due two of my colleagues at the ODA: Kerri A. Schwarz prepared the distribution map for *P. lattini* and Steven A. Valley acquired the excellent images of *Pterostichus* spp. genitalia and pronota. My appreciation is also due the ODA for use of the imaging acquisition equipment for this project. The manuscript was significantly improved by the recommendations of several reviewers.

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Pterostichus brachylobus Kavanaugh and LaBonte, A New Species of the Carabid Beetle Subgenus *Hypherpes* Chaudoir, 1838, from the Central Coast of Oregon (Insecta: Coleoptera: Carabidae: Pterostichini)

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A new species of *Pterostichus*, subgenus *Hypherpes* Chaudoir, *Pterostichus brachylobus* Kavanaugh and LaBonte sp. nov., is described from the central coastal region of Oregon (type locality: Neskowin Creek at Neskowin Campground, 45.0587°N/ 123.9401°W, Tillamook County, Oregon). Features distinguishing adults of *P. brachylobus* from those of other species of *P.* (*Hypherpes*) found in the region are discussed. The known geographical range of *P. brachylobus* is quite limited and completely within the range of *P. nigrocaeruleus* Van Dyke, its apparent closest relative.

Adults of species referable to subgenus *Hypherpes* Chaudoir, 1838, of genus *Pterostichus* Bonelli (the *amethystinus* and *sphodrinus* species groups of Lindroth 1966 and the *amethystinus* species group of Bousquet and Larochelle 1993) are among the most diverse, conspicuous and, arguably, the most frequently encountered carabid beetles on the west coast of North America. Several species, such as *Pterostichus algidus* LeConte and *Pterostichus amethystinus* Mannerheim, occupy broad latitudinal ranges (e.g., from southeastern Alaska to northern California) and live in habitats and exhibit behaviors that bring them into frequent contact with humans (e.g., *P. algidus* are frequently found in gardens and ecotonal areas created by human activity). Many other species, however, occupy small, restricted geographical ranges and occur mainly in undisturbed habitats in which they are seldom encountered.

The basic pattern of presently known species diversity and endemism within the subgenus is one of dramatic increase in both diversity and endemism from north to south along the coast. Among described species, five (none endemic) occur in Alaska, nine (none endemic) in British Columbia, 12 (none endemic) in Washington, 28 (eight endemic) in Oregon, and at least 75 (57 endemic) in California (data mainly from Bousquet and Larochelle 1993). More than 100 different species are already described and dozens of additional species remain to be described (K.W. Will, personal communication).

Due mainly to the landmark works of Hatch (1953) and Lindroth (1966), the pterostichine faunas of Alaska, British Columbia, and Washington are very well known, whereas the large pterostichine fauna of California, which includes most of the presently known but undescribed species and, no doubt, more species yet undiscovered, is still poorly known. The fauna of western Oregon also

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had been considered well-known following the work of Hatch (1953) and Hacker (1968); but with renewed interest in faunal inventory work in that region, new and unexpected discoveries have been made recently. Most recently, LaBonte (2006) described a locally abundant new species, *Pterostichus lattini* LaBonte, recorded from two sites at higher elevations on the eastern flank of the Coast Range and from sites on the western slope of the Cascade Range in westcentral Oregon. This species simply had gone unrecognized as distinct, and LaBonte found many specimens of this taxon mixed in among those of several other species in collections.

On May 1, 2002, while collecting together in a deeply shaded spruce bog formed behind the coastal dunes at the mouth of Moolack Creek in Lincoln County, Oregon, we found a few specimens of what we first believed to be *Pterostichus nigrocaeruleus* Van Dyke. The geographical range of *P. nigrocaeruleus* (Fig. 15) is known to extend narrowly along the coast from southern British Columbia, where it is restricted to forested sites on Vancouver Island, through the Olympic Peninsula in western Washington, along the coast and slopes of the Coast Range in Oregon, south to coastal Humboldt County in northern California. Adults of this species typically are found "along the gravelly margins of the small densely shaded streams which come down from the hills" (Van Dyke 1925:70). In contrast, the beetles encountered at Moolack Creek were found under fallen and rotting spruce branches lying on the moss-covered floor of the forested bog, and not at the nearby graveled stream margin. These beetles also appeared to lack the distinct metallic reflection typical of most *P. nigrocaeruleus* adults.

Intrigued by the possibility that these newly collected pterostichine specimens might represent a new and distinct species, we examined the genitalia of several males immediately after our return from the field. Our suspicions were confirmed when we found a distinct difference in the shape of the apical lamella of the median lobe between these new specimens and specimens of typical *P. nigrocaeruleus*. Subsequent detailed examination of external features in these and additional specimens from previous collections confirmed consistent differences between both males and females of this putative new species and those of *P. nigrocaeruleus*. The purpose of this paper is to describe this unexpected new species, identify the features which distinguish its members from those of other most similar species, and report on its known distribution.

MATERIALS AND METHODS

This study is based on the examination of more than 500 adult specimens of *Pterostichus (Hypherpes)* species, including 20 specimens of the new species and more than 300 specimens of *P. nigrocaeruleus* Van Dyke in collections at the Oregon Department of Agriculture, Salem, Oregon State University, Corvallis, and the California Academy of Sciences, San Francisco (CAS) and in the J.R. LaBonte (JRL) and Robert E. Nelson (REN) collections, as well as representatives of all the other *Hypherpes* species occurring in the region that have adults of comparable size (i.e., excluding species formerly included in subgenera *Leptoferonia* Casey and *Anilloferonia* Van Dyke). Measurements were made with the aid of an ocular micrometer in a Leitz stereoscopic dissecting microscope. Total body length was measured along the midline from the apex of the labrum to the apex of the fused elytra. Visualization and study of female genitalic structures were enhanced by staining dissections with Chlorozol Black E. Digital color images of specimens and selected structures and dissections were created using an Automontage imaging system from Synchroscopy. Distribution maps were prepared using Arcview® software.

Pterostichus brachylobus Kavanaugh and LaBonte, sp. nov.

Figs. 1–2, 4, 6, 8, 10, 12, and 14.

Types.— Holotype, a male, deposited in CAS, labeled: "U.S.A., Oregon, Tillamook County, Neskowin Creek at Neskowin Campground, 120m, 27 June 1986, Stop #86-3A, D.H. Kavanaugh collector"/ "D.H. Kavanaugh Collection" [orange label]/ "Holotype *Pterostichus brachylobus* Kavanaugh & LaBonte sp. nov. des. by D.H. Kavanaugh 2005" [red label]/ "California Academy of Sciences Type No. 18121". A total of 19 paratypes (12 males and 7 females) are deposited in CAS, JRL, and REN (see specimen data below, under Geographical distribution).

Type locality.— Neskowin Creek at Neskowin Campground, 45.0587°N/ 123.9401°W, Tillamook County, Oregon, U.S.A.

Etymology.— The species epithet, *brachylobus*, is a combination of the Greek words *brachys*, meaning short, and *lobos*, meaning a rounded projection or protuberance, in reference to the shape of the apical lamella of the median lobe of male genitalia, which, in dorsal view, is very short and bluntly and broadly rounded (Fig. 12).

Diagnosis.— Adults of this species (Fig. 1) are distinguished from those of all other known *Pterostichus* (*Hypherpes*) species by the following combination of character states: size moderate, total body length males = 10.4 to 12.5 mm, females = 10.5 to 12.7 mm; body color black, elytra with faint to distinct violaceous metallic reflection; head with eyes moderate in size, their diameter about 1.7 times length of tempora, frons smooth, impunctate; pronotum (Fig. 2) slightly cordate, slightly narrowed basally, with lateral margins smooth, not crenulate, smoothly arcuate in anterior four-fifths and slightly but distinctly sinuate toward base, anterior angles slightly and narrowly projected anteriorly and narrowly rounded apically, posterior angles very slightly obtuse, bluntly dentate apicolaterally, inner basal longitudinal impression present, sharply defined, and slightly arcuate (concave laterally), outer basal impression absent, area between inner impression and lateral margin (Fig. 4) slightly but distinctly convex, this convexity with slight depressions on its anterolateral and posterolateral flanks and with a faint ridge between these depressions and extended toward lateral margin, pronotal base without distinct margination (at most with very faint margination laterally); prosternal intercoxal process without margination apically or laterally; elytra with humeri distinctly dentate or tuberculate (at point where basal margin sharply elevated above and slightly extended over lateral margin); abdomen with last visible sternum with one pair of apical setae in males, three pairs in females (Fig. 6); hind femur of males (Fig. 8) without distinct tubercle on posterior (eudorsal) ventral margin; hind tarsomere I with an external, narrowly and sharply-defined longitudinal ridge, ridge also present but successively less distinctly defined on tarsomeres II and III, all tarsi with tarsomere V asetose ven-

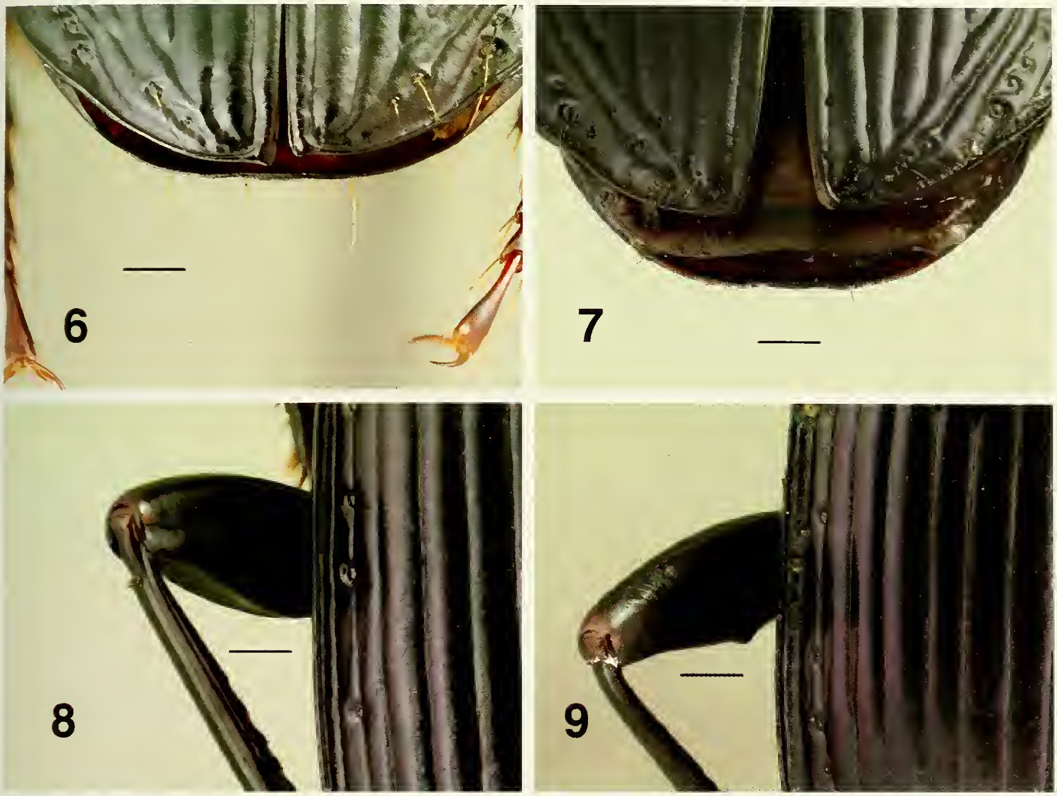
Figure 1. Digital image of holotype, *Pterostichus brachylobus* Kavanaugh & LaBonte sp. nov., dorsal aspect; scale line = 1.0 mm.

FIGURES 2–5. Digital images of pronota. Figs. 2–3. Full pronotum, dorsal aspect, viewed from the vertical; scale lines = 1.0 mm; 2. *Pterostichus brachylobus* Kavanaugh & LaBonte sp.nov.; 3. *Pterostichus nigrocaeruleus* Van Dyke. Figs. 4–5. Left posterior quadrant of pronotum, dorsal aspect, viewed from about 30° oblique right; scale lines = 0.5 mm; 4. *P. brachylobus*; 5. *P. nigrocaeruleus.*

trally; median lobe of male genitalia (Figs. 10 and 12) with apical lamella short, broadly and roundly truncate.

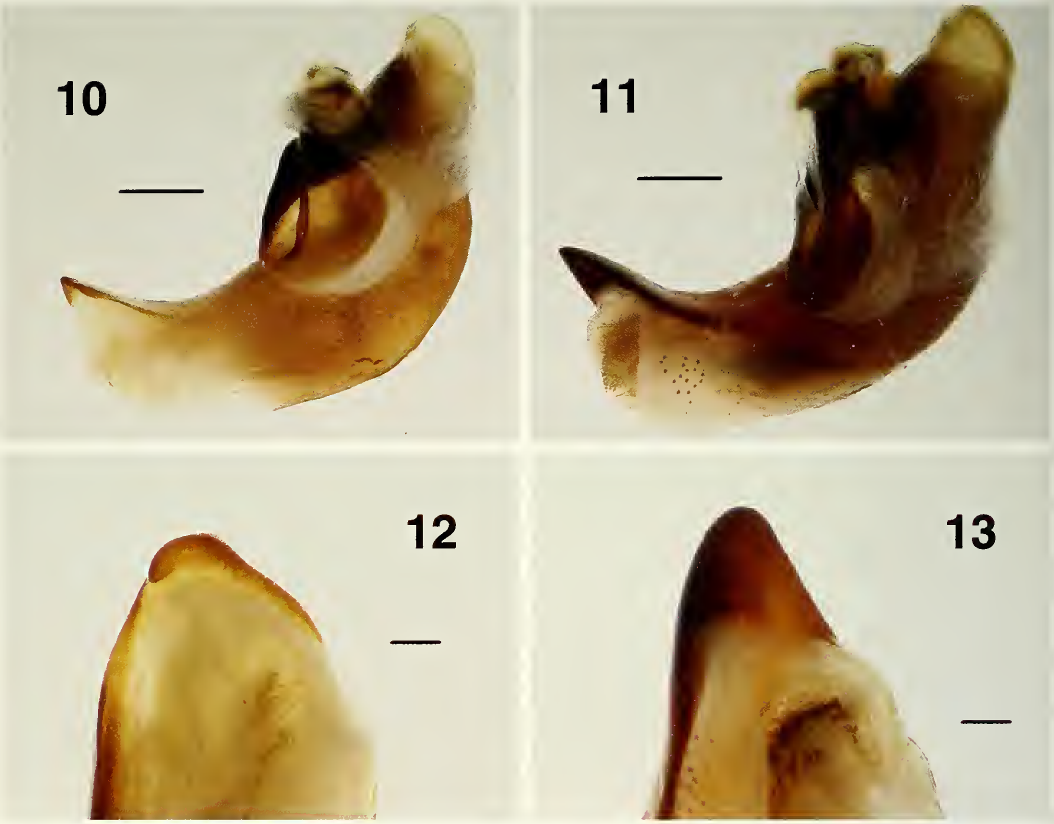
COMPARISONS.— Using Hatch's (1953) key to species of subgenus *Hypherpes*, *P. brachylobus* males are identified (in couplet 3') as *Pterostichus contractus* LeConte (= *Pterostichus castanipes* [Ménétriés]); however, *P. castanipes* males have the prosternal intercoxal process margined apically, elytra without violaceous metallic reflection, and the apical lamella of the genital median lobe more elongate and triangular (compare Hatch 1953, Pl. XXI, Fig. 8c with our Fig. 12). Female specimens of *P. brachylobus* cannot be identified using Hatch's key: the combination of smooth, non-crenulate lateral pronotal margin and last visible abdominal sternum with three pairs of apical setae confounds couplet 1.

Using Lindroth's (1966) key, both males and females of *P. brachylobus* are identified as *P. nigrocaeruleus*. Adults of these two species are indeed very similar and, undoubtedly, are very closely related [preliminary molecular evidence suggests sister species status for this pair; K. W. Will, personal communication]. However, males of *P. nigrocaeruleus* have a distinct tubercle (Fig. 9) on the posterior (eudorsal) ventral margin of the hind femur near its mid-length (absent from *P.*



FIGURES 6–9. Digital images of abdominal apices and left hind femora; all scale lines = 0.5 mm. Figs. 6–7. Abdominal apex of females, viewed from about 45° oblique posterior of vertical; 6. *Pterostichus brachylobus* Kavanaugh & LaBonte sp.nov.; 7. *Pterostichus nigrocaeruleus* Van Dyke. Figs. 8–9. Left hind femur, view of posterior (eudorsal) aspect, viewed from about 20° oblique right of vertical; 8. *P. brachylobus*; 9. *P. nigrocaeruleus*.

brachylobus males [Fig. 8]) and the apical lamella of the genital median lobe (Fig. 11) is more elongate and triangular in dorsal aspect (Fig. 13) (short and bluntly rounded in *P. brachylobus* males [Fig. 12]). Females of *P. nigrocaeruleus* have two pairs of apical setae (Fig. 7) on the last visible abdominal sternum (only two out of more than 120 specimens examined had a third setae on one side only), whereas *P. brachylobus* females (Fig. 6) have three pairs of apical setae (one of the seven females examined had four setae on one side). Both males and females of these two species also differ in several more or less subtle features of their pronota. In *P. brachylobus* adults, the pronotum (Fig. 2) is relatively shorter and broader than in *P. nigrocaeruleus* adults, the anterior angles are slightly shorter and broader, the lateral margin is more smoothly arcuate and slightly more abruptly sinuate, the inner basal longitudinal impression is slightly shorter and more arcuate (concave laterally). The region between the inner longitudinal basal impression and the lateral margin (Fig. 4) is more distinctly convex, and slight depressions in the anterolateral and posteriolateral flanks of this convexity define a faint ridge extended laterally toward the lateral margin. In pronota of most *P. nigrocaeruleus* adults, the anterior angles are slightly longer and more narrowly projected anteriorly, the lateral margin (Fig. 3) is less evenly arcuate, with relatively straighter sections posterior to the anterior angle and anterior to the basal sinuation, which itself is slightly less distinct than in *P. brachylobus* adults. The region between the inner longitudinal basal impression and the lateral margin (Fig. 5) is flat or only faintly convex in *P. nigrocaeruleus* pronota; and a trace of outer



Figures 10–13. Digital images of median lobe of male genitalia. Figs. 10–11. Median lobe, left lateral aspect; scale lines = 0.5 mm; 10. *Pterostichus brachylobus* Kavanaugh & LaBonte sp.nov.; 11. *Pterostichus nigrocaeruleus* Van Dyke. Figs. 12–13. Apical lamella of median lobe, dorsal aspect; scale line = 0.1 mm; 12. *P. brachylobus*; 13. *P. nigrocaeruleus*.

basal longitudinal impression is seen in a few specimens.

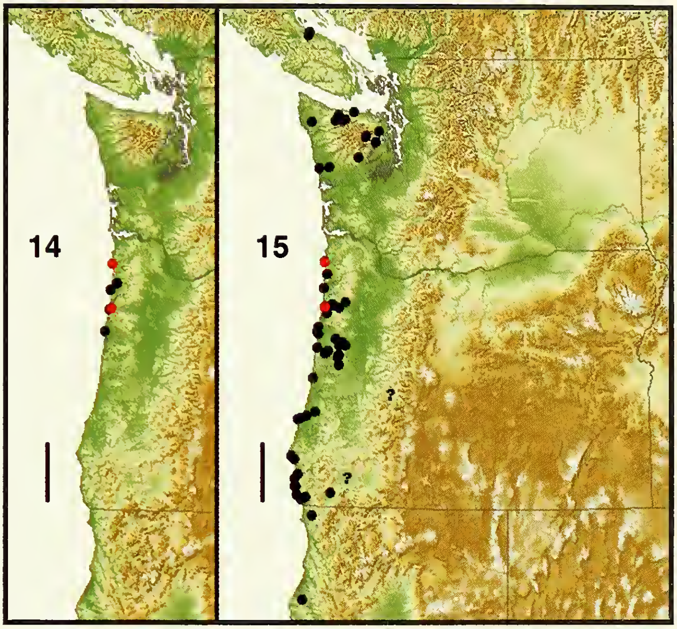
Adults of *P. brachylobus* are easily distinguished from those of *Pterostichus lattini* LaBonte, which was not represented in either Hatch's or Lindroth's key, by the violaceous metallic reflection of the elytra (absent from *P. lattini* adults) and many differences in pronotal shape. In *P. lattini*, the pronotum is more quadrate, relatively broader basally, the base is distinctly margined laterally, and a deep, foveate, outer basal longitudinal impression is distinctly present.

Description.— Size medium (Fig. 1; see Diagnosis for range in body length). Body color piceous to black, except lateral explanations of mandibles, maxillary and labial palpi, antennomeres V to XI, and all tarsi rufous. Elytra with distinct metallic purple reflection (very faint in a few individuals). Head and pronotum shiny, elytra slightly duller, slightly alutaceous in some individuals. Dorsal microsculpture of head comprised of isodiametric meshes, very faintly impressed on frons, slightly more deeply impressed on vertex laterally; pronotal microsculpture comprised of slightly transverse meshes arranged in irregular transverse rows, faintly impressed; elytral microsculpture comprised of deeply impressed isodiametric meshes.

Head large, moderately broad; eyes distinctly convex; antennae relatively short, extended only to basal one-sixth of elytra. Pronotum (Figs. 2, 4) with basal region impunctate. Elytra subquadrate, slightly narrowed basally, slightly convex, fused along medial margin, without setiferous punctures on disk, but parascutellar setiferous puncture present; striae complete, uninterrupted, and deeply impressed; intervals slightly convex, odd and even numbered intervals similar to each other in width; basal elytral margination complete, distinctly elevated above plane of remainder of elytral surface; elytral internal plica distinctly visible externally in lateral view. Hindwings reduced to short stubs. Abdomen with visible sternites III to V each with one pair of posterior paramedial setae, visible sternite VI of male with symmetrically arcuate apical margin, surface without grooves, tubercles, or any distinct macrosculpture. Male genitalia as in Figs. 10 and 12. Female ovipositor with gonocoxite I (basal) with three to five setae arranged in a diagonal row from basolateral to apicomedial apicoventrally; gonocoxite 2 (apical) moderate in length, arcuate laterally and gradually narrowed to a narrowly rounded apex, with two dorsolateral and one dorsomedial ensiform setae.

Sexual dimorphism.— Males and females of *P. brachylobus* are more similar in size than in most carabid species, with the smallest males only slightly smaller than the smallest females and the largest females only slightly larger than the largest males. In males, anterior tarsomeres I through III are distinctly broader than in females and bear two longitudinal rows of squamose adhesive setae ventrally (absent from these tarsomeres in females). Also, males have a single pair of apical paramedial setae on visible sternite VI while females have three pairs of these setae (Fig. 6).

Geographical distribution.— Fig. 14; known only from a few sites on the northcentral coast of Oregon, all within 6 kilometers of the coast itself. We have examined a total of 20 specimens (13 males and 7 females), including the holotype male and 19 paratypes, from the following localities: United States: **Oregon**: Lincoln County, Moolack Creek (just E of Highway 101 [44.70274°N/ 124.06064°W, 15 m]) [May] (4; CAS, JRL); Tillamook County, Cape Lookout ([45.34°N/ 123.992°W]) [March] (2; CAS), Cascade Head (Teal Creek [45.0512°N/ 123.9985°W, 90 m]) [June] (1; JRL), Nes-kowin Creek (at Neskowin Campground [45.0587°N/ 123.9401°W, 120 m]) [June] (10; CAS), Oswald West State Park [October] (2; REN), Tillamook ([45.4557°N/ 123.8461°W]) [May] (1; CAS).



Figures 14–15. Maps of the west coast of North America, from southern British Columbia to northern California (California Albers projection), showing the geographical location of samples examined for each species; red dots = sites where both species have been found together; ? = doubtful records; scale lines = 100 km. 14. *Pterostichus brachylobus* Kavanaugh & LaBonte sp.nov.; 15. *Pterostichus nigrocaeruleus* Van Dyke.

Geographical relationships with related species.—The known geographical range of *P. brachylobus* is restricted to a small portion of the range of its apparent closest relative, *P. nigrocaeruleus* (Fig. 15) To date, members of these two species have been found together at two sites: (1) at the Neskowin Creek site, the type locality of *P. brachylobus*, where a single specimen of *P. nigrocaeruleus* was collected along with 10 specimens of *P. brachylobus*; and (2) at Oswald West State Park, where two specimens of *P. brachylobus* were collected along with seven *P. nigrocaeruleus* specimens.

HABITAT DISTRIBUTION.— As noted in the introduction, one of our first clues to the existence of *P. brachylobus* as a distinct species was the fact that the specimens collected at the Moolack Creek site were found under rotting spruce branches on the mossy floor of the deeply shaded forested bog, rather than under stones at the gravelly margin of the adjacent shaded stream, a habitat more typical of *P. nigrocaeruleus* adults. While both of us recall having collected *P. nigrocaeruleus* specimens in very wet places away from stream margins in the past, neither of us can recall whether these were found under stones or logs or on organic or inorganic substrate. Field notes [dhk] from the Neskowin Creek site, where adults of both species were collected on the same day, note simply that specimens were "collected under rocks along the shaded stream...forest of mixed alder, willows streamside, Douglas fir and hemlock." All of the specimens collected at that time were thought to be of *P. nigrocaeruleus*, hence there was no reason to be looking for specific differences in habitat selection among them. Field notes from the Teal Creek site [jrl] describe the area as consisting of predominantly old-growth Sitka spruce with smaller western hemlock and some red alder, with a shrub understory varying from absent to dense. No specific comments were recorded as to the precise habitat from which the single specimen of *P. brachylobus* was collected. Consequently, our collective experience with adults of both of these species remains inadequate to establish whether or not any significant difference in habitat preference exists. What is clear is that members of both species appear to require cool, moist, deeply shaded sites. Now that the existence of two distinct species is known, biologists can begin to look for differences in habitat preference.

LIFE HISTORY.— Adults of *P. brachylobus* have been collected in March, May, June, and October, and all specimens studied have been fully pigmented (non-teneral). Nothing else is known at present about the life history of this species.

ADDITIONAL COMMENTS.— Among carabid beetles species in western North America for which phylogenetic relationships have been hypothesized, it is unusual to find sympatry among sister taxa (Kavanaugh 1979); so the co-occurrence of *P. brachylobus* with *P. nigrocaeruleus*, presumed sister species, as reported here is noteworthy. Adults of both species are very similar in general body size, form, and appearance, and we have no evidence to suggest differences in life cycle timing, food preference, or behavior. Any actual difference in habitat preference also remains unsubstantiated. So how do these two species co-exist? Why is the geographical range of *P. brachylobus* restricted to only a small part of the range of *P. nigrocaeruleus* and why that particular area along the Oregon coast? These are some of the questions to be addressed now that the existence of these two distinct species is known. Answers to these and other questions will come only from additional study.

ACKNOWLEDGMENTS

We thank Robert E. Nelson (Colby College, Waterville, ME) and Christopher J. Marshall (Oregon State Arthropod Collection at Oregon State University, Corvallis) for the loan of specimens in support of this study. Michelle Koo assisted with the preparation of the distribution maps. Arcview® software used to create these maps was donated by The Environmental Conservation Program, headed by Charles Convis, of the Environmental Systems Research Institute (ESRI).

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Comments on the Status of the Sardinian-Corsican Lacertid Lizard *Podarcis tiliguerta*

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Podarcis tiliguerta **is a lacertid lizard endemic to Corsica, Sardinia and many of their satellite islands. The purpose of this study was to assess the relationships among the various island populations using morphological characters, to assess the usefulness of these characters in phylogenetic studies, and to test the concordance of morphological and earlier genetical studies. Snout-vent length and 11 pholidotic characters have been studied on 2783 specimens from localities on the two main islands and the majority of their respective satellite islands. Data for males and females are analyzed separately using uni- and multivariate statistical methods; the results are compared to previous genetical analyses. With few exceptions, the two populations, one on Corsica, the second on Sardinia (and their satellite islands), are readily distinguishable. We argue that the few exceptions may be due to a founder effect and/or genetic drift. The male sample from northern Corsica and both sex samples from southern Corsica present unresolved problems because they group with the Sardinian clade. Our results, for the most part, are in accord with those obtained with genetical analyses, but further studies are needed to clarify the unresolved questions.**

Riassunto

Podarcis tiliguerta **è una specie endemica di Corsica, Sardegna e molte delle loro isole satelliti. Nel presente lavoro sono stati analizzati la lunghezza testa-cloaca e 11 caratteri della folidosi di 2783 esemplari provenienti da varie località delle isole principali e la maggior parte delle loro isole satelliti. Lo scopo è stato quello di analizzare da un punto di vista morfologico le relazioni tra le varie popolazioni, di verificare l'utilità di questi caratteri negli studi filogenetici e di testare la concordanza tra risultati morfologici e genetici. I dati sono stati analizzati, separatamente per maschi e femmine, con metodi di statistica univariata e multivariata, e i risultati sono stati confrontati con precedenti studi genetici. Le due popolazioni di Corsica e Sardegna (e rispettive isole satelliti) risultano piuttosto ben distinguibili, con poche eccezioni dovute probabilmente a fenomeni di effetto fondatore e deriva genetica. Il campione di maschi del nord della Corsica e i due campioni di maschi e femmine del sud della Corsica occupano una posizione problematica, risultando inclusi nella popolazione sarda. In generale i risultati concordano in larga parte con quelli ottenuti dalle analisi genetiche, ma ulteriori studi sono ritenuti necessari per chiarire alcune delle que-stioni rimaste aperte.**

KEY WORDS: Reptiles, Lacertidae, *Podarcis*, morphology, phylogeny, biogeography, Sardinia, Corsica.

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Podarcis tiliguerta is a lacertid lizard that is endemic to the islands of Corsica and Sardinia and their respective satellite islets. These islands, as a group, have been isolated from the mainland since the last glacial-eustatic marine regression (Ulzega 1995). It is uncertain when the ancestor of *P. tiliguerta* entered the area; although it could have been present before the detachment of the Sardinian-Corsican microplate in the Miocene, there is as good a chance that it arrived during the late Miocene Messinian sea-regression (Lanza 1983). The uncertainty exists because to this day the species' phylogenetic affinities remain unclear. For instance, in one recent study, *P. tiliguerta* has been related to *P. raffonei* (Oliverio et al. 2000), whereas in another study, its affinities are posited with the "Western Islands group," which also includes *P. filfolensis, P. lilfordi,* and *P. pityusensis* (Harris and Arnold 1999).

As do many other of its congeneric species, *P. tiliguerta* shows considerable intraspecific variability in both color pattern and coloration, with even some melanic and concolor populations (Lanza 1972, 1976; Lanza and Brizzi 1974. 1977; Brizzi and Lanza 1975; Lanza and Poggesi 1986; Arnold and Ovenden 2002). The fact is that a number of subspecies have been described for populations occurring on different satellite islands (Lanza and Corti 1996); these nominal taxa have been based mainly on colour pattern and some morphological traits (Corti and Lo Cascio 2002). Inasmuch as recent studies using genetic markers have indicated a high degree of variability and population sub-structuring within previously recognized *Podarcis* species, some authors have come to consider them either as separate species or as species complexes (e.g., Capula 1994 [*P. wagleriana*]; Harris and Sá-Sousa 2001, 2002 and Sá-Sousa and Harris 2002 [Iberian *Podarcis*]; Poulakakis et al. 2003 [*P. erhardii*]). *Podarcis tiliguerta* seems not to be an exception. Electrophoresis studies by Capula (1996) showed that the species' genetic variation was distributed within two and possibly three main groups, one Corsican and a second Sardinian, with the Cerbicale-Lavezzi Archipelago populations having differentiated from both, although seemingly closer to the one on Corsica. Indeed, genetic distances among the three groups were considered higher than those ordinarily found within other *Podarcis* species. More recently, several studies based on mtDNA have partly supported Capula's results. Pinho et al. (2004) and Harris et al. (2005) detected deep genetic divergence between the Corsican and Sardinian clades, but at that time no samples from the Cerbicale-Lavezzi Archipelago were analysed. Almost simultaneously, Podnar and Mayer (2005) detected three mtDNA lineages: Corsica, northern + central + western Sardinia, and eastern Sardina, but they rejected the hypothesis of a species complex. Finally, Vasconcelos et al. (in press) reanalysed all previously published mtDNA sequences to which they added several new samples, including one from the Cerbicale Islands. Their results confirmed the strong genetic divergence between Corsican and Sardinian populations and the Cerbicale population, which, nonetheless, appears to nest with the Corsican clade. However, without additional samples from the eastern Sardinian clade, this form is still known from only one sample.

In lacertid lizards, as in other groups, morphological and molecular studies are proving most useful in supplying complementary information, and both have been used for the reconstruction of phylogenies (see, for instance, Arnold 1989; Harris et al. 1998; Malhotra and Thorpe 2004a and 2004b, these latter two on Asian pitvipers of the genus *Trimeresurus*). At this point, the aim of our work is to test the *P. tiliguerta* "species complex hypothesis" using morphological data, that focuses on pholidosis, an aspect that has never been extensively studied in this species. Our goal is to assess the usefulness of the characters in phylogenetic studies and to test the concordance of morphological and genetical results.

FIGURES 1–4. *Podarcis tiliguerta.* (1) Four adult ♂♂, Leg. Paolo Malenotti, 1980. Mount Spada, m 1400-1500 a.s.l., northern slope of the Gennargentu Mountains (central eastern Sardinia). Photo Benedetto Lanza; (2) Two ♂♂ (left) and two ♀♀ (right), data otherwise as in Fig. 1; (3). Six adult ♂♂, Leg. Benedetto Lanza, 25.VII.1972. Between Giannuccio and Omo di Cagna (S. Corsica). Photo B. Lanza; (4). Four adult ♀♀, data otherwise as in Fig. 3.

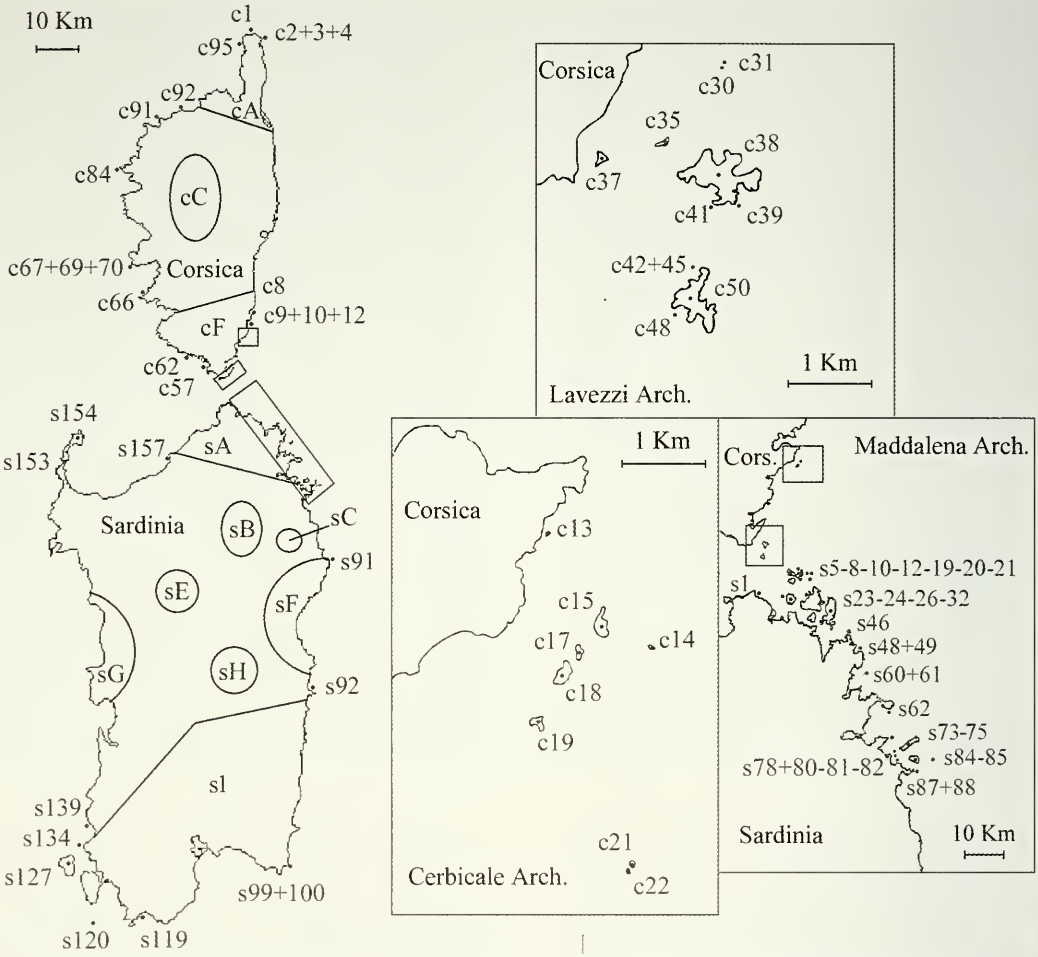

FIGURE 5. Islands and localities studied. The numbering used for the Sardinian satellite islands is the same as in Poggesi et al. (1995) and Lanza & Poggesi (1986) for those around Corsica. c1: Giraglia Island; c2: Di Mezzo Islet; c4: Finocchiarola Islet; c8: Pinarello Island; c9: Cornuta Islet; c10: San Cipriano Island; c12: Scoglio Ziglione; c13 Farina Islet; c14: La Vacca Islet; c15: Forana Island; c17: Maestro Maria Island; c18: Piana delle Cerbicali Island; c19: Pietricaggiosa Island; c21 Toro Grande Island; c22: Toro Piccolo Island; c30: Poraggia Piccola Islet; c31: Poraggia Grande Islet; c35: Ratino Island; c037: Piana di Cavallo Island; c38: Cavallo Island; c39: Camaro Canto Islet; c41: San Bainzo Islet; c42: Luigi Giaffieri Islet; c45: Giacinto Paoli Islet; c48: Semillante Islet; c50: Lavezzi Island; c57: Northern Tonnara Islet; c62: Bruzzi Grande Islet; c66: Piana di Portigliolo Island; c67: Mezzomare Island; c69: Locca Islet; c70: Porro Islet; c84: Gargalu Island; c91: Spano Islet; c92: Rossa Island; c95: Centuri Island; s1: Marmorata Northern Island; s5: Razzoli Island; s8: Capicciolu Islet; s10: S. Maria Island; s12: Paduleddi Northern Islet; s19: Corcelli Islet; s20: Piana della Maddalena Island; s21: Barrettini Island; s23: Spargiotto Islet; s24: Spargi Island; s26: Abbatoggia Islet; s32: Caprera Island; s46: Le Bisce Island; s48: Li Nibani Northern Island; s49: Li Nibani Western Island; s60: Camere Western Island; s61: Soffi Island; s62: Figarolo Island; s73: Barca Sconcia Island; s75: Tavolara Island; s78: Piana di Tavolara Island; s80: Cavalli Island; s81: Reulino Island; s82: Cana Island; s84: Molara Island; s85: Molarotto Islet; s87: Proratora Island; s88: Brandinchi Island; s91: Ruia Island; s92: Ogliastra Island; s99: Southern Varaglione of Serpentara; s100: Serpentara Island; s119: Rossa di Punta Niedda Island; s120: Toro Island; s127: S. Pietro Island; s134: Meli Islet; s139: Pan di Zucchero Island; s153: Piana dell'Asinara Island; s154: Asinara Island; s157: Rossa di Trinità d'Agulto Island. Female's samples are missing from islands: c84, c91, s1, s10, s19, s24, s46, s48, s49, s60, s61, s82, s99, s119, s139, s157.

MATERIALS AND METHODS

A total of 2783 specimens were studied (1812 ♂♂ and 971 ♀♀). Nearly all specimens were collected between the end of the 1960s and the first half of the 1990s primarily by B. Lanza and collaborators (M. Borri, B. Conti, C. Corti, M. Poggesi, and others) from three Corsican and eight Sardinian localities and many of their respective satellite islands (Fig. 5). Most of the specimens are preserved in the Zoological Section "La Specola" of the Natural History Museum, University of Florence (MZUF); additional material in the herpetological collections of the California Academy of Sciences (CAS) San Francisco, USA was also examined.

A total of 12 variables have been studied: snout-vent length (SVL), measured to the nearest 1 mm using callipers, and 11 pholidosis characters (Fig. 6). For bilateral characters, only the right side was considered, although the left side was examined in the case of the ventral scales, for handling reasons. In those instances where the right side was damaged, we did take data from the left side. Furthermore, where either unilateral and/or bilateral characters could not be assessed because damage to both sides of a specimen, those specimens have not been included in the multivariate analyses. Measurements and counts were done mainly by S. Bruschi, B. Lanza, and C. Corti.

Pholidotic characters have been analysed with both uni- and multivariate methods. AN(C)OVA and MAN(C)OVA were used to test variation between localities and island groups for each variable and for all of them, respectively. SVL was used as covariate. Discriminant function analysis on the raw data or on the regression residuals against SVL were performed to distinguish the most relevant island groups. The subsequent matrix of Mahalanobis distances among populations was used to construct both a UPGMA tree and a MDS (Multidimentional Scaling) bidimensional plot.

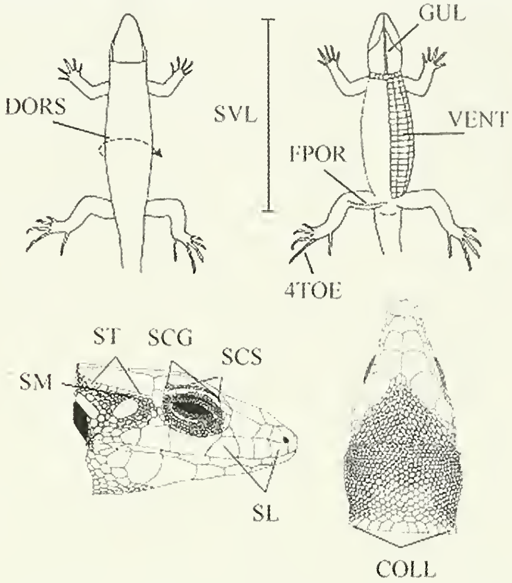

FIGURE 6. Characters analysed (above: by Cheylan, 1988, modified; below: original). SVL: snout-vent length; DORS: dorsal scales along a transversal line at the middle of the body; VENT: ventral scales along the midline on the left side of the body; COLL: collar shields; GUL: gular scales on the midline (from the confluence of the inframaxillary scales to the collar shields); FPOR: femoral pores; 4TOE: scales under the 4th toe; SCS: supraciliar scales; SCG: supraciliar granules; ST: supra-temporal scales; SL: supra-labial scales preceding the eye; SM: scales on the shortest line connecting the masseteric shield and the supratemporal scales.

RESULTS

ANOVAs conducted prior to the other statistical analysis indicate that males and females of the species are dimorphic in many of the studied characters (SVL, DORS, VENT, COLL, GUL, FPOR, 4TOE) with no interaction effects between sexes and sites. Consequently, all statistical analyses have been conducted keeping the sexes separated. ANOVA and MANOVA also showed a highly significant variability among localities for the different variables. For more detailed results, see Table 1. For descriptive statistics, see the Appendix, Tables 2 and 3.

Discriminant function analysis using forward stepwise procedure showed that the 11 pholidotic variables were highly significant in discriminating among the groups, so all were included. In

TABLE 1. ANOVA and MANOVA comparisons between sites and sexes for localities from which samples of both sexes were available. Numbers indicate F (ANOVA) or Wilk's λ (MANOVA), df and P.

ANOVA	*Site*	*Sex*	*Site*sex*
dors	20.33	229.97	0.78
	71, 2378	1, 2378	71, 2378
	<0.0001	<0.0001	0.91
vent	7.54	1308.47	1.15
	71, 2378	1, 2378	71, 2378
	<0.0001	<0.0001	0.19
coll	10.8	12.23	0.95
	71, 2378	1, 2378	71, 2378
	<0.0001	<0.0001	0.6
gul	16.19	34.47	1.18
	71, 2378	1, 2378	71, 2378
	<0.0001	<0.0001	0.14
fpor	17.73	32.01	1.24
	71, 2378	1, 2378	71, 2378
	<0.0001	<0.0001	0.09
4toe	12.64	13.91	0.74
	71, 2378	1, 2378	71, 2378
	<0.0001	0.0002	0.95
scs	5.05	2.65	1
	71, 2378	1, 2378	71, 2378
	<0.0001	0.1	0.48
scg	10.07	2.93	1.1
	71, 2378	1, 2378	71, 2378
	<0.0001	0.09	0.26
st	12.9	1.05	0.92
	71, 2378	1, 2378	71, 2378
	<0.0001	0.3	0.66
sl	2.27	0.47	1.14
	71, 2378	1, 2378	71, 2378
	<0.0001	0.49	0.21
sm	11.06	2.94	1.21
	71, 2378	1, 2378	71, 2378
	<0.0001	0.09	0.12
MANOVA	9.74	147.35	1.01
	781, 25793	11, 2368	781, 25793
	<0.0001	<0.0001	0.0001

UPGMA trees for males and females (Figs. 7 and 8), two clades grouping Corsican and Sardinian samples, respectively, easily could be distinguished. Nevertheless, some islands and islets did not group within either of these two geographic groups: among these were Corsican males, c91 (Spano), and Corsican females, c13 (Farina). This also happened with males from the circum-Sardinian islands s19 (Corcelli), s82 (Cana), and s99 (Faraglione di Serpentara), from where no female samples were available, males from s85 (Molarotto), whose females grouped with the Sardinian clade, and females from s12 (Northern Paduleddi), whose males grouped in the Sardinian clade. Finally, both males and females of c14 (La Vacca Islet), c21 (Toro Piccolo Islet), and c22 (Toro Grande Islet), belonging to the Cerbicale Islands, as well as c30 (Poraggia Piccola), s20 (Piana della Maddalena), and s134 (Meli Islet), did not group with either one of the two clades, nor did they coalesce to form a third clade; rather they appeared as independent entities in our trees.

In a like manner, some samples from the islands bordering Sardinia on the north and northeastern nested within the Corsican clade: males, s48 (Northern Li Nibani), s61 (Soffi), s153 (Piana dell'Asinara) and s157 (Rossa di Trinità d'Agulto). Interestingly, females, which were available only from island s153, nested within the Sardinian clade, whereas samples from s8 (Capicciolu) and s26 (Abbatoggia) fitted into the Corsican clade. Males of the latter two islands fell within the Sardinian clade as did both sexes of c39 (Camaro Canto, SE Corsica).

With regard to the two main islands, all populations were allocated into the two main clades. The only exception were males from cA and both sexes of cF (N and S Corsica, respectively), which fell into the Sardinian clade, and females of sC (surroundings of Torpé, NE Sardinia), which did not fit in either clade.

The existence of the Corsican and Sardinian groups was also graphically supported by the MDS plots (Figs. 3 and 4). The 95% confidence ellipses overlapped, slightly more in males than in females, but the separation between them was in any case evident. Those populations previously ungrouped with any of the clades in the trees were those plotted apart from the others in the MDS: for both sexes c14 (La Vacca) and c22 (Toro Piccolo) from the Cerbicale Islands; for males s82 (Cana), s49 (Western Li Nibani), and s99 (Varaglione di Serpentara) (note that s82 [Cana] fell into the Corsican ellipse [female samples were lacking for the same localities]); for females s20 (Piana della Maddalena), s12 (Northern Paduleddi), and s134 (Meli) (note that s20

[Piana della Maddalena] also fell into the Corsican ellipse).

Inasmuch as all these multivariate analyses showed a clear separation between the Corsican and Sardinian populations, discriminant function analysis considering these two geographic groups was performed. Results indicated high, not absolute, percentages of correct classification for both males (82% for Corsica and 75% for Sardinia, total 79%) and females (86% for Corsica and 75% for Sardinia, total 81%). Such analyses were repeated considering different population groups. Every attempt to separate La Vacca, Toro Grande, and Toro Piccolo Islets resulted in a general slight decrease in those values, both considering them as a third group (males: Corsica 82%, Sardinia 77%, islets 66%, total 79%; females: Corsica 84%, Sardinia 76%, islets 70%, total 80%) or deleting them from the analyses (males: Corsica 82%, Sardinia 77%, total 79%; females: Corsica 84%, Sardinia 76%, total 80%). The same applied when islets were forced to segregate from the main islands within each clade, considering them as a third and fourth group (males: Corsica 21%, Sardinia 0%, Corsican islands 83%, Sardinian islands 79%, total 61%; females: Corsica 22%, Sardinia 12%. Corsican islands 84%, Sardinian islands 74%, total 60%). On the other hand, when considering the sample of S Corsica integrated in the Sardinian sample, the percentages showed little variation with an improvement for Corsica and a decrease for Sardinia (males: Corsica 77% and Sardinia 83%, total 81%; females: Corsica 81%,. Sardinia 79%, total 80%). Separating southern Corsican from the Corsican and the Sardinian samples resulted in a slight improvement in the classification percentages of the two former clades (males: Corsica 84%, Sardinia 83%; females: Corsica 85%, Sardinia 79%), but it also led to a decrease in totals (males 76% and females 77%) because the third and fourth groups could not be correctly classified (males 1% and females 0%). Finally, the classification of single individuals, at least within S Corsica, did not show clear microgeographical separation from specimens classified as "Sardinian" or "Corsican."

Considering the three groups of Corsica, Sardinia, and southern Corsica, MANOVA detected significant variation (males: Wilk's $\lambda_{22,3242} = 0.57$, $p<0.0001$; females Wilk's $\lambda_{22,1828} = 0.54$, $p<0.0001$). Almost all variables were different among localities with the one exception of SL (both sexes) and SM (females). Many subsequent ANOVA comparisons were significant: between Corsica and Sardinia DORS, COLL, GUL, FPOR, SCG and ST for both sexes, SCS, SL, and SM for males, 4TOE for females; between southern Corsica and Corsica DORS, VENT, GUL, FPOR, SCS, SCG, and ST for both sexes, COLL for males; between southern Corsica and Sardinia DORS, VENT, COLL, GUL, 4TOE, SCS, ST, and SM for both sexes, FPOR for females (Scheffe's test $p<0.05$). In both sexes and for the significant variables, Sardinian animals had more scales than those from Corsica, except in the case of ST, in which the reverse is true. The southern Corsican sample occupies an intermediate position with respect to DORS, COLL, GUL, FPOR, SCG, ST, and SL, but more scales are present for 4TOE and SCS and fewer scales for VENT and SM than in either Corsican or Sardinian samples.

In addition to meristic characters, in body size, Sardinian lizards were longer than Corsican ones ($p<0.00001$ in both sexes). Furthermore, a correlation analysis among SVL and several pholidotic characters detected positive, significant relations: in males, DORS ($R^2=0.14$ $p=0.0004$), GUL ($R^2=0.07$ $p=0.02$), FPOR ($R^2=0.05$ $p=0.04$), 4TOE ($R^2=0.11$ $p<0.002$), and ST ($R^2=0.06$ $p=0.02$; in females, DORS ($R^2=0.16$ $p=0.0005$), VENT ($R^2=0.16$ $p=0.0005$), and 4TOE ($R^2=0.08$ $p=0.01$). Therefore, all the analyses were repeated correcting for body size. Discriminant function analyses performed on the regression residuals of the variables against SVL produced similar UPGMA trees, MDS plots and percentage of correct classification of cases. Similarly, the same results were obtained performing MANCOVA and ANCOVAs calculated using SVL as a covariate.

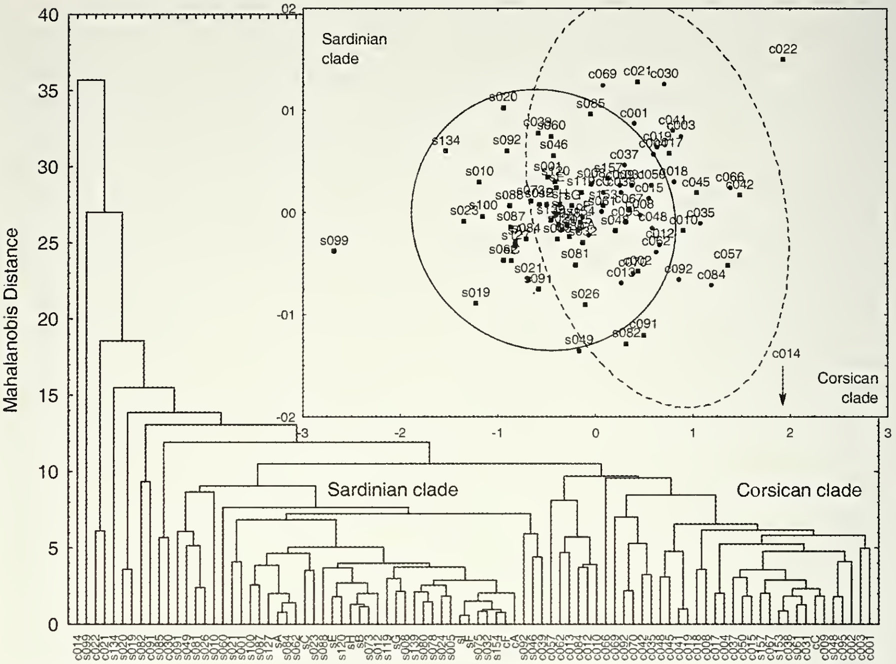

FIGURE 7. UPGMA tree and MDS scatterplot for males.

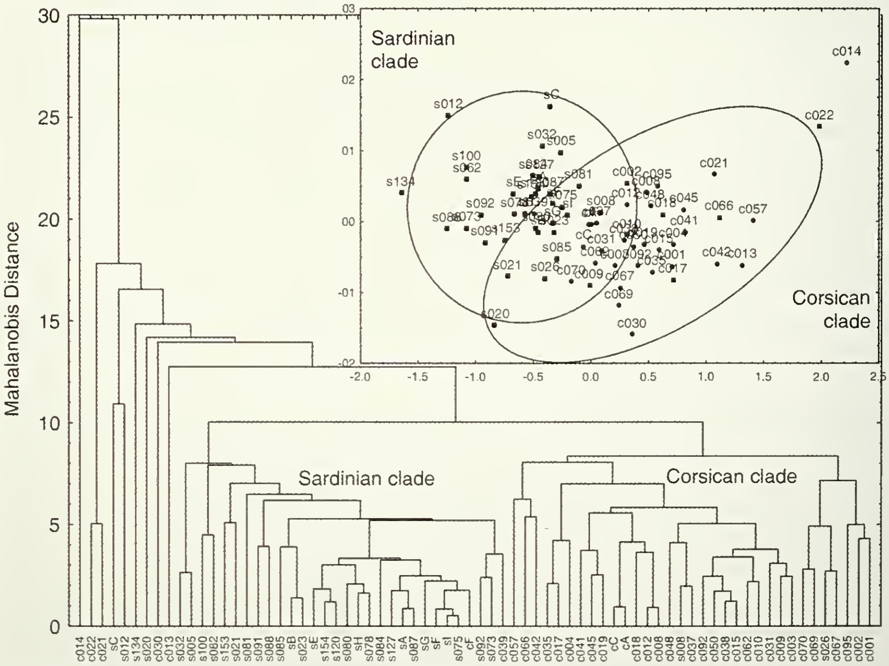

FIGURE 8. UPGMA tree and MDS scatterplot for females.

DISCUSSION

Discriminant function analysis of pholidotic characters of *Podarcis tiliguerta* shows that there is a good differentiation between Corsican and Sardinian populations. No north-south geographical gradient could be detected, and it is possible to exclude even possible effects of insularization: % of correct classification of main islands' specimens did not increase considering Sardinian and Corsican islands as third and fourth groups, and these two last groups had very low levels of correct classification. Thus, it is not possible to discriminate among satellite islands and their respective main islands.

In stepwise discriminant function analysis, all pholidotic variables proven useful in discriminating among the groups. ANOVAs show that most of the variables are significantly different between Corsican and Sardinian clades (excluding from consideration southern and northern Corsican sample): Sardinian specimens have more dorsal, collar, and gular scales, more femoral pores, supracilar granules and scales between the masseteric shield and the supratemporal scales (the last in males). On the other hand, Corsican specimens have more supratemporal scales. Many, if not all the characters are thus important in distinguishing between the two groups of animals, even though the ranges of scale counts largely overlap as in all *Podarcis* species (Arnold and Ovenden 2002).

It must be noted that Sardinian animals are also longer (snout-vent length) than Corsican ones, and a correlation between some pholidotic variables and snout-vent length has been detected between populations. Correlation was not detected within populations and corrections for length did not change the results in either discriminant function analysis or ANOVAs. This suggests that at least part of the variation in scale counts between the two groups is due not to differences in size but rather to phylogeny. This conclusion is further supported by the fact that the number of supratemporal scales decreases, rather than increases, with increasing snout-vent length.

The present work then agrees with the results of the genetics analyses conducted by Harris et al. (2005) and Vasconcelos et al. (in press). The existence of a third clade, represented by specimens from the Cerbicali Islands (Capula 1996), is not supported by morphological data inasmuch as the populations from this archipelago do not group into a uniform clade. Noteworthy is that the "archipelago's" islands and islets include Toro Grande, Toro Piccolo, and La Vacca. Toro Grande and Toro Piccolo are located at the greatest distance from the coast of Corsica and are the only Corsican islands for which the depth of the sea strait separating them from the main island is more than 50 m. (see Figs. 5 and 9). Based on these values and the known oscillations of the sea level during the past 20,000 years, it has been estimated that these islands have been isolated since about 11,000–12,000 years ago. In a like manner, La Vacca became isolated between 8,000 and 8,500 years ago (Lanza and Poggesi 1986). Thus, the deviations noted in their populations may be attributed to both founder effect and genetic drift on islands of ancient origin. We have been unable to detect multiple lineages on Sardinia itself, despite the apparent existence of two divergent mtDNA lineages (Podnar and Mayer 2005). The female sample sC from the surroundings of Torpé (NE Sardinia) cannot be aligned with any clade; this may be attributed to the small sample size that was available for study and analysis.

None of the previously mentioned molecular studies on *P. tiliguerta* included specimens from southern Corsica. From a morphological point of view, these specimens clade with Sardinia and have intermediate scale counts with respect to dorsal, collar, gular, and supratemporal scales, femoral pores, and supraciliar granules, more lamellae and supraciliar scales, fewer ventral scales and scales between the masseteric shield and the supratemporal. We suggest the possibility of hybridization between Corsican and introduced Sardinian specimens. For instance, the city of

Bonifacio, which is located on the southern coast of Corsica, has an active harbour that daily receives commerce from N Sardinia. Inasmuch as introductions of Sardinian animals have already been detected, for example, *Podarcis sicula cettii* (Delaugerre and Cheylan 1992), it seems reasonable to expect that *P. tiliguerta*, a species often found close to human settlements (Corti and Lo Cascio 2002), should also be among the introductions.

Similar problems of misclassification are encountered with northern Corsican males. In this case, the present results do not coincide with the general ones and further study is needed.

From both historical and evolutionary perspectives, whereas the history of the detachment of the Corsican and Sardinian microplate has been extensively studied (see for example Bellon et al. 1977 and related literature), little is known about contacts that the two main islands may have had in the past. Surely they were in contact during the late Miocene and again on and off during the Pleistocene, and almost certainly during the latter part of the Würm Glaciation up to at least about 10,000 ybp (see Fig. 9 in which the shallow submarine platform connecting the islands is clearly shown). On the other hand, the length of time during which Sardinia and Corsica were isolated from one another must have been long enough to permit speciation, as indicated by the presence of *Euproctus montanus* in Corsica and *E. platicephalus* in Sardinia (Delaugerre and Cheylan 1992).

FIGURE 9. Submarine topography showing the Sardinia-Corsica submarine platform and its relation to coastal shelf topography of northwest Italy and of North Africa in the vicinity of coastal Algeria and Tunisia. Map generated using the AGI, USGS, ESRI, *Global GIS DVD* 2003. (USGS DDS-62H).

More studies, both molecular and morphological, are needed to understand the status of *Podarcis tiliguerta*, with particular emphasis on both southern and northern Corsican areas and the Cerbicali Islands. The latter promises to be an excellent region for calibrating molecular clocks and for other comparative phylogeographic studies (see Vasconcelos et al., in press). Lastly, as we noted earlier, the range of scale counts among *Podarcis* species largely overlap, so that the morphological traits seen by different populations, as for instance extreme northern Corsican males, could follow some adaptive pattern, which has yet to be explored. It is obvious that only the integration of genetical and morphological studies can help us understand the evolutionary history of this interesting group of lizards.

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Appendix

TABLE 2: descriptive statistics for the males. Numbers indicate average ± ES and range. The number in parentheses following the range statement indicates the number of data points that were not reported for that variable in the sample of the population studied.

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
c001	28	52.50±0.61	62.21±0.58	25.17±0.24	10.96±0.23	27.29±0.36	20.46±0.32	29.39±0.29	5.75±0.10	9.88±0.31	5.44±0.15	4.04±0.04	1.36±0.09
		44-57	57-70	22-28	9-13 (1)	24-32	17-25	27-33	5-7	7-13 (2)	4-7 (1)	4-5	1-2
c002	11	55.09±0.80	60.09±1.25	24.45±0.41	10.45±0.28	30.91±0.69	21.00±0.49	28.89±0.45	5.27±0.14	10.82±0.58	5.91±0.21	4.00±0.00	1.55±0.21
		51-60	52-66	22-26	9-12	27-34	17-23	28-32 (2)	5-6	8-13	5-7	4	1-3
c003	8	50.88±0.99	62.25±1.82	25.75±0.49	11.00±0.00	28.25±0.62	20.50±0.42	28.88±0.44	6.00±0.19	10.50±0.68	7.13±0.30	4.13±0.13	0.50±0.27
		47-55	56-71	23-28	11	26-32	19-22	28-31	5-7	8-13	6-8	4-5	0-2
c004	26	52.19±0.67	64.27±0.67	26.58±0.19	10.38±0.24	30.58±0.44	20.88±0.32	28.76±0.31	5.50±0.13	10.23±0.23	6.96±0.23	4.04±0.04	1.23±0.14
		46-59	59-71	25-28	9-13	24-34	18-24	25-31	4-6	8-13	5-10	4-5	0-3
c008	22	56.27±0.42	62.86±0.93	25.32±0.20	9.82±0.23	29.86±0.49	23.41±0.34	30.91±0.61	5.68±0.17	13.27±0.55	5.50±0.25	4.14±0.04	0.91±0.17
		52-60	55-72	23-27	8-12	27-34	20-26	27-40	4-7	10-20	3-7	4-5	0-3
c009	19	52.26±0.69	62.89±1.00	25.42±0.16	10.05±0.28	28.63±0.48	20.42±0.29	27.27±0.28	5.63±0.23	12.05±0.56	5.74±0.28	4.00±0.00	1.00±0.17
		45-58	58-73	24-26	8-12	24-32	18-32	25-29 (4)	3-7	8-16	3-8	4	0-2
c010	13	54.54±0.46	65.85±0.90	25.54±0.39	9.46±0.31	31.69±0.67	21.92±0.35	29.38±0.57	6.00±0.11	14.15±0.56	7.69±0.33	4.08±0.08	0.69±0.17
		51-58	60-71	24-28	9-13	28-35	19-24	27-33	5-7	11-17	6-10	4-5	0-2
c012	14	59.71±1.15	66.68±0.88	25.21±0.38	9.36±0.31	31.21±0.75	24.07±0.30	31.15±0.48	5.92±0.18	12.62±0.51	6.57±0.33	4.00±0.00	0.64±0.13
		49-67	62-72	23-28	8-11	26-25	22-26	28-33 (1)	4-7 (1)	10-17 (1)	4-9	4	0-1
c013	14	53.07±0.71	66.36±1.27	25.14±0.23	0.29±0.27	31.79±0.55	22.79±0.43	28.93±0.55	6.00±0.15	14.50±1.04	6.57±0.36	3.64±0.17	1.36±0.23
		49-57	58-73	24-27	7-11	28-35	21-26	25-33	5-7	10-25	2-8	2-4	0-3
c014	11	58.55±1.11	64.09±0.96	25.36±0.15	8.91±0.16	33.18±0.66	22.09±0.28	32.30±0.37	5.36±0.28	11.91±0.58	7.00±0.23	4.00±0.00	14.55±0.21
		52-63	58-70	25-26	8-10	30-37	21-24	31-34 (1)	4-6	9-16	6-8	4	4-6
c015	21	55.00±0.38	64.00±0.55	25.38±0.25	9.38±0.18	29.67±0.51	21.38±0.40	30.20±0.40	6.00±0.17	11.24±0.40	5.95±0.19	4.00±0.00	0.95±0.15
		52-58	59-68	23-28	8-11	26-36	18-24	27-36	5-8	6-14	4-8	4	0-2
c017	15	53.73±0.59	60.53±0.75	26.20±0.22	10.13±0.22	30.33±0.80	19.73±0.57	28.07±0.40	5.33±0.16	10.53±0.27	6.33±0.25	3.93±0.07	1.20±0.14
		49-57	56-66	25-28	9-11	24-35	18-27	25-31	4-6	9-13	4-8	3-4	1-3
c018	10	55.20±1.06	61.10±1.46	26.40±0.34	10.40±0.34	31.60±0.62	22.70±0.62	31.90±0.53	5.80±0.13	11.90±0.41	5.90±0.35	4.00±0.00	1.00±0.21
		50-60	55-69	25-28	9-13	29-36	20-26	29-35	5-6	10-14	4-8	4	0-2
c019	12	54.58±0.62	63.25±1.00	26.17±0.30	9.25±0.37	27.50±0.44	20.17±0.32	28.10±0.38	5.42±0.29	11.67±0.36	5.42±0.23	4.00±0.00	0.67±0.19
		50-57	57-69	24-28	7-11	25-30	19-22	26-30 (2)	3-7	10-14	4-7	4	0-2
c021	38	65.18±0.57	69.13±0.50	26.53±0.20	10.53±0.18	31.96±0.38	22.92±0.25	32.28±0.32	4.95±0.15	12.78±0.29	6.95±0.21	3.97±0.03	1.37±0.10
		57-71	63-75	23-28	9-14	26-36	20-27	29-36 (2)	3-7 (1)	10-17 (1)	3-9	3-4	0-3
c022	17	66.82±0.91	67.24±0.82	27.71±0.35	10.18±0.20	29.71±0.39	21.53±0.41	33.35±0.40	5.06±0.11	10.31±0.47	7.41±0.19	4.06±0.06	1.94±0.16
		60-73	63-75	25-30	9-12	26-32	19-24	30-36	4-6 (1)	7-14 (1)	6-8	4-5	1-3
c030	16	56.00±0.94	64.63±0.80	25.69±0.28	10.75±0.17	28.63±0.47	17.81±0.29	28.53±0.26	5.63±0.15	9.33±0.35	5.88±0.24	4.00±0.00	0.69±0.20
		49-63	59-70	24-28	9-12	25-33	26-20	26-30 (1)	5-7	7-12	4-8	4	0-2
c031	30	58.07±0.68	63.33±0.53	26.27±0.19	9.70±0.24	29.40±0.52	21.60±0.34	29.13±0.31	6.03±0.09	12.23±0.28	5.50±0.19	4.00±0.00	0.50±0.10
		50-63	59-73	24-28	7-12	24-35	19-26	26-33	5-7	10-17	3-7	4	0-2
c035	9	53.44±0.96	59.89±0.81	25.33±0.29	9.11±0.20	29.33±0.67	19.89±0.42	27.00±0.68	6.11±0.26	12.44±1.08	6.56±0.44	4.11±0.11	0.56±0.18
		49-57	57-64	24-27	8-10	26-32	18-22	24-30	5-7	5-16	4-8	4-5	0-1
c037	45	50.44±0.57	63.60±0.54	25.91±0.16	10.76±0.19	29.84±0.31	23.02±0.28	28.52±0.18	5.80±0.08	10.31±0.24	6.40±0.19	4.00±0.03	0.067±0.08
		43-58	55-72	24-29	8-13	25-34	19-26	26-31 (1)	4-7	7-14	4-9	3-5	0-2
c038	18	54.50±0.74	64.11±0.48	25.83±0.32	10.33±0.28	30.50±0.51	21.39±0.38	28.72±0.29	5.83±0.15	11.39±0.37	5.28±0.27	4.00±0.08	0.94±0,15
		50-62	61-68	24-28	8-12	27-34	28-24	27-31	5-7	7-14	5-9	3-5	0-2

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
c039	4	58.00±0.71	68.00±2.12	25.75±0.25	11.25±0.63	29.50±0.87	23.00±0.58	27.00±0.41	5.75±0.25	10.00±1.35	5.50±0.87	4.00±0.00	0.50±0.50
		56-59	62-71	25-26	10-13	28-32	22-24	26-28	5-6	8-14	3-7	4	0-2
c041	22	56.36±0.52	63.00±1.11	26.77±0.25	9.14±0.34	26.64±0.50	20.95±0.47	27.86±0.43	5.27±0.16	10.82±0.32	5.77±0.23	4.00±0.00	0.86±0.15
		51-50	53-78	25-29	6-12	22-32	17-27	24-32	4-6	9-14	4-8	4	0-3
c042	7	59.00±0.69	61.29±0.99	24.86±0.14	8.71±0.18	28.00±0.90	19.29±0.36	28.50±0.56	6.43±0.20	12.00±0.49	6.57±0.37	4.00±0.00	0.43±0.30
		56-61	59-66	24-25	8-9	25-31	18-21	26-30 (1)	6-7	10-14	5-8	4	0-2
c045	11	59.55±0.59	62,64±0.62	26.55±0.21	8.36±0.24	28.73±0.43	22.09±0.62	29.70±0.30	5.64±0.15	12.09±0.92	6.36±0.24	4.09±0.09	1.09±0.21
		57-63	60-66	25-27	7-10	26-31	19-25	28-31 (1)	5-6	8-19	5-7	4-5	0-2
c048	14	52.86±1.03	64.50±0.56	25.79±0.26	8.57±0.27	30.07±0.46	23.71±0.38	28.92±0.47	5.86±0.18	11.79±0.67	5.57±0.23	4.07±0.07	0.64±0.17
		47-59	61-68	24-27	7-10	26-32	21-26	27-32 (1)	5-7	9-17	4-7	4-5	0-2
c050	63	57.24±0.25	64.95±0.44	25.54±0.12	9.38±0.13	29.10±0.33	21.97±0.24	28.57±0.21	5.63±0.10	10.17±0.33	6.48±0.19	4.02±0.03	0.78±0.08
		53-63	57-72	24-28	7-12	22-35	18-37	24-32	4-8 (1)	5-19 (3)	4-11	3-5	0-2
c057	18	58.83±0.68	65.17±0.63	26.44±0.18	8.53±0.38	31.22±0.75	22.00±0.42	30.35±0.38	6.17±0.19	14.89±1.00	7.61±0.27	4.17±0.09	2.00±0.16
		53-63	59-72	25-27	6-12 (1)	26-38	19-25	27-33 (1)	4-7	11-24	5-10	4-5	1-3
c062	26	55.85±0.76	67.12±0.59	24.46±0.22	8.69±0.17	29.23±0.35	21.96±0.33	28.65±0.42	6.15±0.16	13.23±0.48	5.85±0.25	3.96±0.04	0.73±0.15
		43-60	62-75	23-27	7-10	26-32	18-25	24-32	3-7	9-18	4-9	3-4	0-3
c066	12	60.92±0.66	65.58±0.74	25.25±0.22	8.58±0.19	28.50±0.40	19.50±0.45	30.92±0.31	6.25±0.13	13.00±0.66	5.75±0.41	4.17±0.11	0.83±0.11
		57-64	62-69	24-27	8-10	27-31	17-23	29-33	6-7	10-17 (1)	4-8	4-5	0-1
c067	15	52.53±0.61	62.40±0.86	24.53±0.22	9.93±0.34	29.20±0.57	21.13±0.35	29.60±0.48	5.73±0.21	12.47±0.53	5.27±0.21	3.87±0.09	0.93±0.18
		48-56	57-69	23-26	8-13	26-34	19-24	27-33	4-7	9-17	4-7	3-4	0-2
c069	6	52.50±0.92	60.00±1.73	24.00±0.26	9.50±0.43	27.17±0.98	18.67±0.71	27.17±0.60	5.50±0.22	12.33±0.56	4.33±0.21	4.00±0.00	0.33±0.21
		49-56	56-66	23-25	8-11	26-32	16-21	26-30	5-6	10-14	4-5	4	0-1
c070	13	52.31±0.56	61.08±0.47	24.08±0.26	9.15±'0.19	30.15±0.49	21.38±0.46	27.69±0.38	6.23±0.17	11.69±0.40	5.23±0.26	4.00±0.00	0.85±0.10
		49-56	57-63	22-25	8-10	27-33	19-25	26-30	5-7	9-14	4-7	4	0-1
c084	6	53.67±0.71	67.67±0.76	26.00±0.45	8.33±0.21	31.67±0.95	24.17±0.79	30.33±0.61	6.00±0.00	15.67±1.20	7.33±0.49	4.17±0.17	1.00±0.45
		51-55	65-70	25-27	8-9	29-34	21-26	28-32	6	13-21	6-9	4-5	0-2
c091	10	55.10±0.48	64.40±0.79	24.70±0.30	8.90±0.31	28.30±0.67	21.00±0.45	28.13±0.35	6.20±0.20	15.30±1.30	5.90±0.31	3.80±0.13	2.10±0.23
		52-57	60-68	23-26	8-11	25-31	19-24	26-29 (2)	5-7	9-25	5-7	3-4	1-3
c092	12	55.25±0.63	62.17±1.41	24.17±0.21	8.25±0.22	30.25±0.60	20.83±0.52	28.25±0.28	6.33±0.14	12.50±0.56	5.75±0.28	4.25±0.13	1.08±0.19
		52-59	57-72	23-36	7-9	26-33	18-24	26-29	6-7	9-16	4-7	4-5	0-2
c095	27	52.67±0.84	62.85±0.61	25.15±0.17	9.67±0.20	31.30±0.34	22.59±0.51	29.78±0.39	5.41±0.13	11.44±0.45	5.81±0.20	4.00±0.05	1.15±0.15
		38-59	57-69	23-27	7-11	29-37	18-31	25-34	4-7	4-15	4-8	3-5	0-3
cA	47	54.11±0,64	63.19±0.62	24.89±0.17	10.77±0.17	31.49±0.51	22.94±0.31	29.09±0.32	6.06±0.09	13.49±0.44	5.57±0.18	4.04±0.04	1.34±0.11
		43-62	54-73	23-27	9-13	24-41	19-28	24-34	5-8	8-21	3-9	3-5	0-3
cC	85	57.71±0.49	61.32±0.45	25.72±0.14	10.60±0.14	29.84±0.31	21.09±0.18	28.52±0.21	5.91±0.08	12.34±0.23	5.15±0.13	4.06±0.03	1.06±0.08
		45-66	51-72	22-29	8-13	24-36	17-25	24-34 (1)	4-8	7-17	3-8	3-5	0-3
cF	137	56.72±0.31	66.19±0.32	25.06±0.09	10.49±0.11	31.75±0.25	22.77±0.18	29.59±0.18	5.99±0.05	13.09±0.22	5.37±0.10	4.05±0.03	0.95±0.07
		45-64	58-76	22-28	7-14 (1)	26-41	18-35	24-37	4-8	5-20	2-9 (1)	3-5	0-3
s001	7	60.57±0.84	66.57±1.11	26.00±0.62	10.00±0.53	32.00±0.76	22.57±0.37	19.00±0.53	5.00±0.38	13.43±1.46	4.57±0.43	4.14±0.14	0.71±0.18
		57-64	64-72	24-28	8-12	28-34	21-24	27-31	4-7	10-21	3-6	4-5	0-1
s005	11	55.18±0.38	65.73±1.20	26.00±0.30	11.00±0.43	33.55±0.98	22.36-0.47	29.20±0.53	5.91±0.09	14.27±0.78	5.55±0.47	4.36±0.15	1.64±0.20
		53-57	61-74	24-27	9-13	29-38	20-25	26-31 (1)	5-6	10-18	3-8	4-5	1-3
s008	21	54.24±0.75	63.90±0.94	26.14±0.26	11.00±0.23	30.24±0.65	21.90±0.24	29.43±0.51	5.81±0.19	12.71±0.50	5.48±0.33	4.00±0.00	1.81±0.18
		46-60	58-75	24-28	9-13	22-35	20-24	25-36	4-7	8-17	3-9	4	1-4
s010	5	53.80±0.97	61.60±1.60	25.40±0.75	12.40±.024	33.20±1.24	23.20±0.86	28.20±0.37	5.80±0.37	12.60±1.12	5.80±0.58	4.00±0.00	1.60±0.40
		52-57	58-67	23-27	12-13	29-36	21-26	27-29	5-7	10-15	4-7	4	1-3
s012	6	57.17±1.33	70.33±1.63	26.00±0.26	11.00±0.63	33.33±1.23	22.83±0.79	29.75±1.18	6.17±0.17	12.83±0.54	4.83±0.60	4.17±0.17	1.00±0.26
		52-61	65-75	25-27	9-13	30-37	20-25	28-33 (2)	6-7	11-14	3-7	4-5	0-2
s019	5	57.20±0.97	65.20±0.97	25.00±0.71	10.80±0.49	30.20±0.37	21.00±0.84	27.40±0.51	6.00±0.00	16.80±0.66	4.60±0.40	4.60±0.24	1.20±0.20

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
		55-60	62-68	23-27	9-12	29-31	19-23	26-29	6	15-19	4-6	4-5	1-2
s020	14	54.71±0.55	63.50±0.81	25.93±0.27	11.07±0.38	29.21±0.71	20.79±0.32	26.33±0.48	5.21±0.15	13.71±0.51	4.85±0.44	4.43±0.14	1.00±0.26
		50-58	59-69	25-28	9-14	23-33	18-22	24-30 (2)	4-6	11-16	2-7 (1)	2-5	0-3
s021	24	54.33±0.67	65.29±0.61	26.21±0.21	10.29±0.23	31.50±0.42	20.17±0.30	26.29±0.34	5.13±0.16	13.50±0.49	4.71±0.24	4.21±0.08	0.83±0.14
		47-59	59-72	24-28	8-14	29-36	18-23	22-30 (3)	3-6	9-19	3-8	2-5	0-3
s023	10	59.80±0.80	69.60±1.16	26.70±0.37	12.20±0.51	34.20±0.90	22.90±0.72	29.30±0.54	6.00±0.00	15.10±1.06	4.60±0.40	4.10±0.10	1.40±0.27
		54-63	64-75	25-28	10-15	30-39	19-28	27-32	6	11-23	2-7	4-5	0-3
s024	6	54.00±0.93	65.83±1.85	25.50±0.22	11.17±0.31	32.67±0.49	21.67±0.49	29.50±0.76	5.83±0.31	14.50±0.76	5.33±0.56	4.00±0.00	1.50±0.50
		52-58	61-72	25-26	10-12	32-35	20-23	27-32	5-7	12-17	4-7	4	0-3
s026	7	51.43±1.51	64.71±1.91	25.29±0.29	10.71±0.42	32.71±1.46	20.86±0.14	27.67±0.56	6.14±0.14	12.29±0.97	5.71±0.36	4.14±0.14	2.14±0.40
		45-56	59-73	24-26	10-13	27-38	20-21	26-30 (1)	6-7	9-16	4-7	4-5	1-4
s032	6	58.67±10.9	67.00±2.05	25.17±0.83	10.33±0.33	33.83±1.11	23.50±1.31	30.33±0.99	6.17±0.17	12.33±0.42	5.67±0.49	4.00±0.00	1.33±0.21
		56-62	60-72	22-28	9-11	30-37	19-29	28-34	6-7	11-14	4-7	4	1-23
s046	8	55.38±0.78	64.50±1.63	25.88±0.44	11.75±0.37	29.63±0.68	21.75±0.56	28.00±0.65	5.25±0.31	10.88±1.04	4.25±0.45	4.00±0.00	0.75±0.25
		53-59	56-68	24-28	10-13	26-32	20-25	26-30 (1)	4-6	6-24	2-6	4	0-2
s048	7	55.71±0.52	61.71±1.15	25.86±0.40	10.00±0.44	31.86±0.91	23.57±0.69	28.80±0.97	5.29±0.29	10.57±0.57	5.14±0.34	3.86±0.14	0.86±0.14
		54-57	56-66	24-27	9-12	29-35	21-26	26-31 (2)	4-6	9-13	4-6	3-4	0-1
s049	10	54.10±0.74	60.70±1.21	26.70±0.30	9.90±0.31	32.70±1.05	20.40±0.45	26.78±0.32	5.60±0.22	9.30±0.65	4.80±0.33	3.80±0.13	1.80±0.25
		50-57	56-68	25-28	8-11	28-37	17-22	25-28 (1)	5-7	5-12	3-7	3-4	0-3
s060	5	50.40±2.73	68.00±0.84	26.40±0.40	10.40±0.51	31.00±0.63	22.40±0.51	27.50±2.50	5.60±0.24	14.60±0.87	6.00±0.45	4.00±0.00	1.20±0.20
		44-58	65-70	25-27	9-12	30-33	21-24	25-30 (3)	5-6	13-18	5-7	4	1-2
s061	9	50.78±1.00	64.67±1.64	25.33±0.41	10.11±0.35	30.22±0.72	21.67±0.78	28.57±0.75	6.11±0.20	13.00±0.76	5.67±0.33	4.00±0.00	1.00±0.29
		46-56	59-73	23-27	8-11	27-34	19-25	26-32 (2)	5-7	10-17	4-7	4	0-2
s062	10	53.20±0.66	71.40±0.64	25.00±0.37	10.50±0.45	35.80±1.08	24.40±0.85	30.33±1.26	5.90±0.10	14.10±0.75	4.60±0.43	4.10±0.10	1.50±0.17
		49-56	67-74	23-27	8-13	32-43	21-29	21-34 (1)	5-6	9-17	1-6	4-5	1-2
s073	27	55.74±0.64	70.85±0.63	25.70±0.21	10.59±0.22	31.81±0.41	22.00±0.38	28.28±0.39	5.93±0.18	12.70±0.57	4.44±0.18	4.11±0.06	0.96±0.12
		43-61	65-77	24-28	8-13	27-36	18-26	25-32 (2)	4-8	7-21	2-6	4-5	0-2
s075	52	56.02±0.51	66.54±0.60	25.17±0.17	10.48±0.21	32.90±0.40	23.37±0.26	29.41±0.28	5.81±0.12	12.63±0.48	5.38±0.25	4.10±0.06	1.40±0.11
		45-62	58-78 (2)	22-29	7-14 (2)	26-39 (2)	19-27 (1)	26-34 (1)	3-8	4-23	2-10	3-6	0-3
s078	41	55.54±0.57	66.88±0.51	25.56±0.16	10.71±0.21	33.54±0.45	22.18±0.26	28.03±0.35	5.80±0.12	14.03±0.36	5.46±0.20	3.95±0.03	0.83±0.12
		46-62	60-76	23-29	9-14	29-40 (4)	18-25 (1)	25-33 (6)	3-7 (1)	8-19 (1)	3-8	3-4 (1)	0-3
s080	13	56.08±0.87	67.69±1.28	26.00±0.25	10.62±0.33	34.46±0.75	22.69±0.40	28.67±0.63	6.00±0.20	13.31±0.76	5.85±0.32	4.08±0.08	1.46±0.14
		47-60	60.79	25-27	9-12	29-38	21-26	26-33 (1)	5-7	8-17	4-7	4-5	1-2
s081	34	58.44±0.52	66.21±0.60	26.32±0.21	10.62±0.22	34.00±0.51	22.00±0.28	28.42±0.31	6.00±0.14	11.91±0.52	5.79±0.16	3.97±0.03	1.91±0.17
		50-64	60-73	24-29	8-13	28-41	19-25	25-32 (1)	4-8	7-19	4-8	3-4	0-4
s082	5	60.40±0.68	66.80±1.98	24.80±0.49	9.40±0.40	33.80±0.58	22.60±0.51	32.40±0.40	5.60±0.24	15.40±0.51	5.80±0.58	3.60±0.24	1.80±0.66
		59-62	60-72	23-26	9-11	33-36	21-24	31-33	5-6	14-17	5-8	3-4	0-4
s084	105	53.82±0.54	70.80±0.45	25.43±0.12	10.96±0.13	34.31±0.28	24.37±0.21	30.43±0.19	5.95±0.06	15.20±0.25	5.47±0.13	4.08±0.03	1.30±0.08
		38-62 (1)	57-87	22-29	8-15 (6)	29-43 (3)	21-30 (3)	25-35 (3)	3-7 (1)	10-24 (2)	2-9 (1)	3-5 (1)	0-4 (1)
s085	52	65.79±0.63	71.08±0.54	25.92±0.15	10.63±0.14	29.56±0.30	19.82±0.20	29.40±0.16	5.33±0.09	12.52±0.37	5.47±0.15	3.96±0.03	1.12±0.08
		48-73	60-79	23-38 (1)	11-13 (3)	23-34 (2)	16-22 (1)	27-31 (4)	4-7	7-22	3-9 (3)	3-4 (1)	0-3 (2)
s087	19	60.32±0.68	70.79±0.99	25.32±0.20	11.00±0.44	31.68±0.54	23.21±0.16	30.63±0.49	6.00±0.17	15.95±0.61	4.63±0.19	4.11±0.07	1.63±0.16
		53-66	62-78	24-27	8-14	28-36	22-25	28-35	5-7	13-24	3-6	4-5	0-3
s088	10	58.80±0.85	67.40±1.54	25.60±0.31	11.70±0.37	32.90±0.53	22.70±0.62	27.56±0.50	6.00±0.37	11.10±0.77	4.60±0.58	4.00±0.00	1.20±0.39
		54-62	61-75	24-27	10-14	30-36	19-25	26-30 (1)	5-9	9-16	2-8	4	0-4
s091	13	54.85±1.32	66.62±1.07	25.85±0.25	9.92±0.42	31.77±0.52	22.62±0.31	25.92±0.42	6.00±0.16	12.62±0.70	4.54±0.35	4.00±0.00	1.77±0.26
		42-61	61-75	25-28	8-13	29-35	21-24	23-28 (1)	5-7	10-20	2-7	4	1-4
s092	4	56.50±1.94	71.50±2.06	25.50±0.50	11.50±0.65	29.50±1.85	22.50±1.32	28.25±0.95	6.25±0.25	13.25±1.70	5.00±1.15	3.75±0.25	0.75±0.48
		51-60	67-75	25-27	11-13	25-33	19-25	27-31	6-7	10-18	3-7	3-4	0-2

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
s099	8	57.25±1.59	79.13±2.40	25.13±0.35	12.50±0.50	36.75±0.62	25.38±0.80	28.75±0.65	6.50±0.19	14.63±0.60	4.00±0.42	4.00±0.00	1.25±0.37
		49-64	70-88	24-26	12-15	35-40	23-30	26-31	6-7	12-17	2-6	4	0-3
s100	19	55.89±0.73	71.47±10.1	25.05±0.30	11.26±0.30	31.63±0.62	23.89±0.39	29.89±0.48	6.11±0.13	13.68±0.54	3.79±0.26	4.05±0.05	0.79±0.14
		51-61	66-81	22-27	9-14	26-37	21-27	26-34	5-7	10-19	1-5	4-5	0-2
s119	5	60.60±0.51	66.00±1.14	27.00±0.32	10.60±0.51	32.20±1.85	22.40±0.40	29.00±0.32	5.80±0.20	13.40±1.91	5.60±0.75	4.20±0.20	1.20±0.49
		59-62	63-69	26-28	9-12	26-36	21-23	28-30	5-6	9-20	4-8	4-5	0-3
s120	24	62.04±0.81	68.54±0.98	25.63±0.27	10.00±0.18	30.88±0.44	23.63±0.40	28.71±0.37	5.55±0.18	10.64±0.48	4.57±0.22	4.04±0.04	0.87±0.14
		52-67	60-81	23-30	8-12	28-37	20-27	25-31 (3)	3-7 (2)	5-14 (2)	3-6 (1)	4-5 (1)	0-2 (1)
s127	20	56.40±0.79	68.45±0.69	25.05±0.20	10.60±0.27	34.30±0.50	24.70±0.45	30.40±0.57	5.80±0.16	15.00±0.79	5.05±0.26	4.10±0.10	0.50±0.11
		48-63	64-74	23-27	9-13	29-38	21-30	24-35	4-7	10-22	3-8	3-5	0-1
s134	13	62.69±0.49	62.92±10.5	25.77±0.47	10.92±0.33	34.15±0.61	25.46±0.71	29.78±0.95	5.46±0.22	9.69±0.38	3.08±0.26	4.00±0.00	0.15±0.10
		59-66	57-69	22-29	9-13	30-37	22-32	27-36 (4)	4-7	7-12	1-4	4	0-1
s139	10	61.20±1.24	67.70±0.37	26.10±0.41	11.30±0.33	34.50±0.67	21.50±0.45	28.80±0.59	5.80±0.20	11.30±0.40	5.50±0.56	4.00±0.00	1.10±0.18
		53-66	66-70	24-28	9-13	30-37	20-24	26-32	4-6	10-14	3-9	4	0-2
s153	9	61.44±0.84	65.56±1.16	25.33±0.24	10.44±0.38	31.44±0.63	21.11±0.51	28.33±0.71	6.00±0.17	11.56±0.60	5.89±0.51	4.00±0	0.78±0.28
		58-66	61-72	24-26	9-12	28-34	19-24	25-31	5-7	9-15	4-9	4	0-2
s154	15	58.73±0.62	67.47±0.79	25.40±0.35	10.60±0.25	33.60±0.99	13.13±0.42	30.00±0.56	5.80±0.14	12.60±0.58	5.73±0.48	4.00±0.00	0.93±0.23
		53-62	63-74	24-28	9-12	26-40	20-26	26-35	5-7	8-16	3-9	4	0-3
s157	5	49.20±1.93	64.00±2.66	24.80±0.37	10.00±0.55	28.00±0.32	20.80±0.20	28.40±0.81	6.00±0.00	11.40±0.68	4.60±0.40	4.00±0.00	0.60±0.24
		44-56	57-72	24-26	8-11	27-29	20-21	26-30	6	9-13	3-5	4	0-1
sA	26	58.65±0.80	69.92±0.63	25.54±0.20	10.96±0.23	34.96±0.54	24.54±0.43	29.42±0.36	5.85±0.07	15.12±0.67	5.08±0.24	4.08±0.05	10.04±0.14
		52-59	64-81	23-27	9-15	29-42	20-28	25-34	5-6	10-25	3-7	4-5	0-2
sB	39	60.54±0.51	67.64±0.79	26.21±0.20	10.82±0.20	32.10±0.42	22.64±0.31	28.50±0.38	5.79±0.10	13.31±0.42	4.33±0.22	4.13±0.05	0.92±0.11
		53-69	57-81	24-29	8-14	27-39	20-28	24-34 (1)	4-7	8-20	2-8	4-5	0-3
sC	10	58.60±1.20	70.30±1.37	26.11±0.54	11.00±0.21	34.50±0.99	23.70±0.70	29.90±0.62	6.30±0.33	15.70±0.97	5.50±0.22	4.20±0.13	1.80±0.29
		49-63	60-75	24-29 (1)	10-12	30-40	21-28	28-34	5-9	13-22	5-7	4-5	0-3
sE	12	61.50±2.45	67.75±0.86	25.92±0.40	10.33±0.36	30.25±0.91	22.58±0.51	29.42±0.66	5.75±0.25	12.58±1.10	4.00±0.37	3.92±0.08	0.75±0.22
		41-68	65-76	23-28	7-11	24-35	19-25	27-33	4-7	4-19	2-6	3-4	0-2
sF	42	59.33±0.61	67.95±0.75	25.79±0.19	10.74±0.20	32.83±0.53	23.40±0.27	29.55±0.34	6.07±0.12	14.69±0.57	5.17±0.16	4.00±0.05	1.19±0.15
		50-65	54-78	23-28	8-13	25-40	18-26	25-34	4-8	3-25	3-8	3-5	0-4
sG	5	59.20±2.08	69.00±1.82	26.20±0.20	11.20±0.20	32.20±0.80	23.20±0.49	29.80±0.73	6.00±0.32	12.80±0.58	6.20±0.92	4.00±0.00	1.80±0.49
		54-65	63-74	26-27	11-12	30-34	22-24	28-32	5-7	11-14	3-8	4	1-3
sH	37	61.84±1.10	68.24±0.91	25.81±0.21	10.95±0.17	31.54±0.52	22.22±0.34	28.53±0.40	5.97±0.12	12.51±0.34	4.81±0.19	4.00±0.04	1.38±0.16
		50-79	59-80	23-29	9-13	25-36	18-26	22-36 (1)	4-7	7-17	3-8	3-5	0-4
sI	34	59.21±0.66	67.56±0.77	25.35±0.23	11.06±0.18	32.29±0.60	23.68±0.34	29.88±0.41	5.94±0.13	13.56±0.41	4.97±0.20	4.00±0.06	0.94±0.11
		46-67	60-78	22-28	11-13	26-43	20-28 (3)	24-37	4-7	7-18	2-7	3-5	0-2
Corsican	930	56.05±0.16	64.12±0.14	25.54±0.04	9.95±0.04	30.15±0.09	21.83±0.07	29.31±0.07	5.79±0.02	12.07±0.09	5.95±0.04	4.02±0.01	1.05±0.03
clade		38-73	51-78	22-30	6-14 (3)	22-41	16-35	24-40 (13)	3-8 (4)	4-25 (10)	2-11 (2)	2-5	0-6
Sardinian	880	57.67±0.18	68.05±0.16	25.68±0.04	10.77±0.04	32.59±0.11	22.78±0.08	29.12±0.08	5.82±0.02	13.39±0.10	5.08±0.05	4.05±0.01	1.19±0.03
clade		38-79 (1)	54-88 (2)	22-30 (2)	7-15 (11)	22-43 (9)	16-32 (9)	21-37 (49)	3-9 (4)	3-25 (5)	1-10 (6)	3-6 (4)	0-4 (4)

TABLE 3: Descriptive statistics for the females. Numbers indicate average ± ES and range. The number in parentheses following the range statement indicates the number of data points that awere not reported for that variable in the sample of the population studied.

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
c001	16	48.44±1.03 39-54	58.31±0.73 54-63	27.19±0.37 24-30	10.81±0.26 9-12	27.00±0.29 24-28	19.50±0.45 17-23	28.81±0.39 27-32	5.38±0.18 4-6	9.94±0.32 8-11	5.69±0.24 4-7	4.06±0.06 4-5	1.44±0.22 0-3
c002	15	48.60±0.97 40-54	59.67±0.96 52-65	27.13±0.13 26-28	10.93±0.30 9-13	31.07±0.55 25-34	20.87±0.52 17-25	29.71±0.47 27-33 (1)	5.27±0.12 5-6	10.07±0.38 8-13	5.73±0.18 5-7	3.93±0.07 3-4	1.33±0.16 0-2
c003	5	47.00±0.84 45-50	60.80±1.74 57-67	27.40±0.40 26-28	10.00±0.32 9-11	28.00±1.14 25-31	19.80±0.66 18-22	27.80±0.58 27-30	5.60±0.24 5-6	10.20±0.37 9-11	6.00±0.32 5-7	4.20±0.20 4-5	0.60±0.24 0-1
c004	11	48.82±0.70 44-52	59.91±0.59 56-63	29.18±0.26 28-30	10.18±0.26 9-11	30.00±0.60 27-33	19.82±0.42 17-22	28.36±0.65 24-32	5.27±0.27 3-6	9.64±0.43 8-12	6.18±0.30 5-8	4.00±0.00 4	1.27±0.14 1-2
c008	9	51.33±0.78 48-55	60.00±1.59 54-66	27.89±0.48 25-30	9.22±0.28 8-11	30.33±0.62 28-33	23.11±0.77 20-28	30.67±0.58 28-33	5.67±0.17 5-6	12.44±0.99 8-18	5.89±0.31 5-7	4.11±0.11 4-5	1.22±0.15 1-2
c009	10	50.20±0.95 46-55	60.20±1.20 55-66	27.30±0.30 28-29	9.50±0.27 8-11	27.50±0.52 25-31	19.70±0.47 17-22	26.57±0.20 26-27 (3)	5.90±0.23 5-7	11.40-0.70 7-15	4.90±0.23 4-6	4.20±0.13 4-5	0.90±0.10 0-1
c010	12	51.58±0.63 48-56	63.17±0.89 57-69	27.08±0.31 26-29	9.50±0.15 9-10	29.67±0.43 26-31	21.42±0.42 19-23	28.67±0.50 25-31	5.92±0.08 5-6	13.17±0.71 9-16	6.75±0.30 5-8	4.17±0.11 4-5	0.75±0.28 0-3
c012	7	53.86±2.19 47-61	62.00±1.09 58-65	27.57±0.37 26-29	9.43±0.37 8-11	30.00±1.15 27-36	23.14±0.40 22-24	30.00±0.53 27-31	5.57±0.20 5-6	12.57±1.21 9-17	6.14±0.51 4-8	4.14±0.14 4-5	1.00±0.31 0-2
c013	8	50.38±0.53 48-52	62.38±1.38 58-68	27.25±0.25 26-28	8.75±0.31 7-10	28.00±1.10 21-32	20.50±0.57 18-23	28.25±0.77 25-31	6.50±0.19 6-7	16.50±1.52 10-23	6.75±0.25 6-8	4.00±0.00 4	1.63±0.18 1-2
c014	7	53.43±1.80 43-57	61.43±1.41 57-68	27.29±0.29 26-28	8.71±0.42 7-10	32.43±0.97 28-26	21.86±0.34 21-23	31.14±0.46 30-33	5.14±0.46 4-7	11.29±0.89 9-15	7.00±0.44 6-9	3.86±0.14 3-4	3.86±0.26 3-5
c015	9	52.33±0.91 49-57	60.11±0.70 58-64	27.33±0.24 26-28	9.22±0.36 8-11	28.11±1.02 24-34	20.33±0.47 18-22	29.00±0.53 26-31	6.33±0.24 5-7	11.11±0.48 41883.00	6.33±0.24 6-8	4.00±0.00 4	0.89±0.26 0-2
c017	13	49.69±0.87 42-55	57.46±0.63 53-61	27.92±0.42 24-30	9.46±0.22 8-11	30.46±0.42 28-34	18.69±0.40 16-21	28.38±0.50 25-32	5.38±0.18 4-6	10.92±0.52 8-15	6.31±0.29 5-8	3.92±0.08 3-4	1.15±0.25 0-3
c018	10	50.10±0.92 45-55	59.20±1.46 53-67	28.50±0.34 27-30	10.40±0.31 9-12	28.30±0.82 26-35	21.20±0.49 19-23	30.60±0.64 27-33	5.90±0.28 4-7	12.80±1.10 9-21	6.00±0.45 4-9	4.00±0.00 4	0.90±0.10 0-1
c019	9	48.89±0.73 44-51	59.56±1.06 53-65	28.44±0.47 25-30	8.56±0.29 7-10	28.78±1.13 24-36	20.56±0.67 19-24	28.11±0.45 25-29	5.89±0.20 5-7	11.33±0.67 8-14	5.56±0.38 4-7	4.00±0.00 4	1.11±0.20 0-2
c021	26	60.46±0.63 53-64	65.31±0.61 56-73	28.58±0.24 25-31	9.92±0.17 9-12	30.00±0.39 26-35	21.46±0.30 18-25	31.23±0.31 27-34	5.04±0.10 4-6	11.31±0.29 8-14	7.00±0.19 5-9	3.88±0.06 3-4	1.31±0.09 1-2
c022	11	60.91±1.13 51-64	66.64±0.47 65-70	29.64±0.36 28-32	10.09±0.28 9-12	29.55±0.73 26-34	21.18±0.54 19-25	33.55±0.53 31-36	5.27±0.27 4-7	11.91±0.56 9-15	7.18±0.33 6-9	4.09±0.09 4-5	2.18±0.18 1-3
c030	6	50.67±1.02 48-55	60.67±0.80 58-63	27.00±0.26 26-28	11.33±0.33 10-12	27.33±0.49 26-29	17.67±0.56 16-20	28.50±0.62 26-30	5.33±0.21 5-6	9.00±0.45 8-10	5.83±0.48 4-7	4.00±0.00 4	0.33±0.21 0-1
c031	22	53.45±0.94 47-60	61.23±0.74 54-67	27.73±0.27 25-30	9.59±0.25 7-12	27.55±0.52 23-34	20.59±0.31 18-24	28.59±0.35 24-31	5.68±0.15 4-7	12.18±0.33 9-15	5.14±0.14 4-6	4.00±0.00 4	0.50±0.11 0-1
c035	10	51.50±0.40 49-53	57.50±1.21 54-66	28.30±0.26 27-30	9.10±0.41 7-11	31.30±1.13 27-37	19.70±0.37 18-22	28.78±0.40 27-31 (1)	6.20±0.33 5-8	11.60±0.451 9-14	6.20±0.13 6-7	4.10±0.10 4-5	0.80±0.20 0-2
c037	22	48.77±0.74 41-55	62.55±0.60 57-67	28.23±0.25 25-30	10.50±0.28 8-13	29.64±0.46 25-33	21.91±0.46 16-25	28.32±0.37 26-32	5.77±0.11 5-7	10.82±0.38 8-15	6.23±0.19 5-8	3.95±0.08 3-5	0.82±0.16 0-2
c038	6	50.17±1.05 47-54	60.67±.33 60-62	27.17±0.31 26-28	9.50±0.50 8-11	29.00±0.86 26-31	20.33±0.56 18-22	28.67±0.33 28-30	5.67±0.33 5-7	10.83±0.75 9-13	6.00±0.52 4-7	4.00±0.00 4	1.00±0.00 1
c039	6	54.83±1.19 50-59	67.00±0.73 64-69	27.83±0.17 27-28	10.50±0.43 9-12	29.33±1.15 26-32	22.83±1.54 19-28	28.50±0.89 25-31	5.83±0.17 5-6	12.33±0.88 10-16	5.83±0.31 5-7	4.17±0.17 4-5	0.83±0.31 0-2

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
c041	14	52.64±0.93	60.86±0.82	29.14±0.33	9.36±0.40	26.36±0.46	21.43±0.48	27.93±0.41	5.57±0.20	10.93±0.51	5.79±0.19	4.07±0.07	1.00±0.15
		46-58	56-69	27-31	8-14	24-30	19-25	25-30	4-7	8-15	5-7	4-5	0-2
c042	4	54.50±1.32	59.50±0.96	27.50±0.29	8.75±0.25	26.25±1.11	19.25±0.63	29.00±0.00	6.25±0.25	12.00±0.41	6.25±0.25	4.25±0.25	1.50±0.29
		51-57	58-62	27-28	8-9	23-28	18-21	29	6-7	11-13	6-7	4-5	1-2
c045	7	56.00±1.07	59.29±1.60	28.57±0.30	9.00±0.44	28.29±0.68	21.57±0.57	29.86±0.40	5.71±0.18	10.29±0.84	5.86±0.26	4.00±0.00	1.57±0.20
		53-62	54-65	28-30	8-11	25-30	20-24	29-32	5-6	7-13	5-7	4	1-2
c048	5	50.40±0.68	61.40±1.25	27.20±0.20	9.00±0.55	29.00±1.64	23.00±0.45	29.00±0.45	6.00±0.32	10.20±0.37	6.00±0.71	3.80±0.20	0.80±0.37
		48-52	59-66	27-28	7-10	23-33	22-24	28-30	5-7	9-11	4-8	3-4	0-2
c050	29	52.28±0.59	61.90±0.62	27.59±0.27	9.10±0.17	28.00±0.40	21.03±0.28	27.69±0.36	6.14±0.36	11.31±0.39	6.41±0.14	3.93±0.05	0.86±0.10
		46-61	55-71	24-30	8-12	24-34	18-24	23-32	5-16	8-17	5-9	3-4	0-2
c057	13	54.00±1.17	60.00±0.82	27.92±0.29	8.08±0.40	30.85±0.52	21.23±0.32	29.77±0.48	6.08±0.24	12.62±0.51	7.38±0.29	4.23±0.12	1.69±0.26
		45-58	56-65	26-29	6-11	27-34	19-23	27-33	4-8	9-16	6-9	4-5	0-4
c062	7	54.43±0.97	65-86±1-37	27.43±0.20	8.86±0.26	29.14±0.86	20.71±0.61	28.43±0.20	5.86±0.14	13.14±0.70	6.00±0.22	4.14±0.14	0.71±0.29
		49-57	62-71	27-28	8-10	26-33	19-23	28-29	5-6	11-16	5-7	4-5	0-2
c066	9	55.11±1.31	62.11±0.65	27.78±0.22	8.33±0.17	29.33±0.62	19.78±0.40	31.22±0.60	5.56±0.24	11.44±0.84	5.33±0.17	4.11±0.11	1.44±0.18
		47-60	58-64	27-29	8-9	26-32	18-22	29-34	5-7	7-15	5-6	4-5	1-2
c067	7	50.14±1.24	59.86±1.24	27.14±0.14	9.43±0.48	29.43±0.61	18.71±0.61	29.29±0.47	5.29±0.29	13.71±0.64	5.00±0.22	4.00±0.00	1.14±0.26
		45-53	57-65	27-28	8-11	27-32	17-21	27-31	4-6	12-17	4-6	4	0-2
c069	7	48.29±0.92	57.14±1.47	26.29±0.52	9.14±0.14	27.14±0.96	18.57±0.30	27.86±0.46	5.57±0.20	11.57±0.37	4.57±0.43	4.00±0.00	0.86±0.14
		44-50	53-63	24-28	9-10	25-32	17-19	26-30	5-6	10-13	3-6	4	0-1
c070	7	48.57±0.72	57.29±0.89	26.86±0.26	9.71±0.26	28.57±0.65	19.86±0.74	26.86±0.67	6.00±0.22	10.71±0.78	4.83±0.17	4.00±0.00	1.14±0.14
		46-52	53-60	26-28	9-11	26-31	18-24	24-29	5-7	8-13	4-5	4	1-2
c092	9	53.33±1.20	59.22±1.12	27.11±0.20	8.67±0.37	29.78±0.86	20.33±0.69	27.56±0.41	5.78±0.22	12.11±0.51	6.33±0.33	4.00±0.00	0.78±0.22
		47-59	55-64	26-28	7-10	25-34	18-25	25-29	5-7	10-14	4-7	4	0-2
c095	6	49.17±2.27	60.00±0.45	27.17±0.31	9.67±0.33	30.33±0.80	21.50±0.67	29.80±0.66	5.33±0.21	11.83±0.95	5.83±0.60	3.83±0.40	2.00±0.45
		41-56	58-61	26-28	9-11	28-33	19-24	28-32	5-6	8-15	4-8	2-5	1-4
cA	34	50.88±0.78	59.82±0.74	27.68±0.18	10.12±0.17	30.24±0.48	21.82±0.47	28.53±0.29	5.88±0.10	12.21±0.35	5.56±0.16	4.09±0.05	1.15±0.10
		41-60	50-71	25-30	9-13	25-37	17-32	23-32	5-7	7-18	3-7	4-5	0-2
cC	53	52.72±0.75	57.13±0.56	27.96±0.16	10.17±0.15	29.49±0.35	20.94±0.28	28.04±0.34	6.00±0.09	12.60±0.42	5.38±0.14	4.09±0.05	1.21±0.11
		41-64	50-65	25-31	7-12	22-35	18-26	20-32	5-8	6-27	4-8	3-5	0-3
cF	58	52.29±0.44	62.52±0.62	27.34±0.17	9.95±0.16	30.03±0.36	21.53±0.28	29.33±0.24	6.05±0.07	12.71±0.35	5.53±0.17	4.05±0.04	0.98±0.10
		46-59	50-70	25-30	8-13	23-38	18-31	25-33 (1)	5-8	8-21	3-9	3-5	0-3
s005	5	52.60±10.03	63.60±1.72	28.40±0.24	11.40±0.60	30.60±1.08	23.60±0.51	29.00±0.77	5.60±0.40	13.00±0.45	5.60±0.81	4.00±0.00	2.20±0.37
		49-55	59-68	28-29	10-13	28-34	22-25	28-32	4-6	12-14	4-8	4	1-3
s008	5	48.80±0.97	62.60±2.01	27.40±0.40	10.80±0.49	29.80±0.86	21.60±0.51	28.80±0.92	5.80±0.20	11.80±0.73	6.20±0.80	3.80±0.20	1.40±0.24
		45-50	58-69	26-28	9-12	27-32	20-23	27-32	5-6	10-14	5-9	3-4	1-2
s012	7	53.43±1.00	69.29±1.13	29.86±0.26	11.00±0.44	33.14±0.40	24.57±0.37	31.50±0.81	6.00±0.38	15.86±1.28	5.14±0.26	4.14±0.14	1.29±0.18
		50-57	63-72	29-31	9-12	31-34	23-26 (1)	29-35	4-7	11-21	4-6	4-5	1-2
s020	5	52.40±1.25	58.40±0.93	29.00±0.45	9.80±0.37	28.40±0.51	20.20±0.58	24.75±0.48	5.80±0.20	16.60±1.78	5.20±0.37	4.40±0.24	1.00±0.32
		50-57	55-60	28-30	9-11	27-30	19-22	24-26 (1)	5-6	12-22	4-6	4-5	0-2
s021	8	50.25±0.92	62.50±0.68	28.63±0.38	10.50±0.50	30.75±0.53	20.00±0.27	25.83±0.31	5.63±0.18	12.63±0.84	5.75±0.25	4.25±0.16	0.88±0.13
		46-55	59-65	28-31	8-13	28-33	19-21	25-27	5-6	10-18	5-7	4-5	0-1
s023	5	55.00±1.10	65.20±1.39	28.20±0.37	10.00±0.95	31.80±0.37	20.40±0.75	28.80±1.02	5.80±0.49	13.00±0.95	5.00±0.77	4.00±0.00	1.60±0.24
		52-58	62-69	27-29	8-13	31-33	18-22	26-32	4-7	10-16	4-8	4	1-2
s026	5	52.00±1.64	60.60±1.44	27.20±0.37	10.00±0.55	30.40±0.93	19.00±0.55	27.50±0.96	5.40±0.24	14.20±0.58	4.80±0.58	4.00±0.00	1.40±0.24
		48-58	56-65	26-28	8-11	28-33	18-21	25-29 (1)	5-6	12-15	3-6	4	1-2
s032	5	51.60±1.72	66.20±2.46	28.20±0.58	11.40±0.81	31.20±2.13	23.60±1.21	28.80±0.86	6.00±0.00	14.00±1.64	6.20±0.37	4.40±0.24	2.20±0.37
		47-55	60-75	27-30	9-14	24-36	21-28	26-31	6	11-20	5-7	4-5	1-3
s062	4	49.00±0.91	65.25±2.29	27.00±0.41	10.00±0.41	31.50±1.44	23.00±0.41	28.75±0.75	6.00±0.00	12.75±1.11	3.75±0.95	4.25±0.25	2.00±0.71

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
		47-51	60-70	26-28	9-11	29-34	22-24	27-30	6	10-15	1-5	4-5	1-4
s073	7	51.86±1.03	67.57±1.57	27.43±0.43	11.00±0.38	30.86±0.34	22.00±0.72	26.43±0.61	5.86±0.14	12.57±0.37	4.86±0.26	4.00±0.00	1.00±0.31
		47-55	61-72	26-29	10-13	30-32	19-25	24-29	5-6	11-14	4-6	4	0-2
s075	32	52.03±0.58	63.16±0.61	27.16±0.20	10.20±0.26	31.89±0.58	23.23±0.34	28.68±0.35	5.94±0.10	12.56±0.41	5.72±0.27	4.03±0.06	1.26±0.12
		44-56	57-71 (1)	25-29 (1)	8-13 (2)	23-37 (5)	20-26 (1)	25-33 (1)	4-7	8-17	3-8	3-5 (1)	0-3 (1)
s078	13	52.23±0.93	64.15±1.40	27.38±0.31	10.75±0.55	32.00±0.73	22.62±0.65	27.91±0.55	5.85±0.10	11.92±0.80	5.62±0.33	4.00±0.00	1.15±0.27
		46-57	53-70	26-29	9-14 (1)	27-37 (1)	19-26	25-32 (2)	5-6	7-17	3-8	4 (1)	0-4
s080	8	53.63±1.28	63.63±1.18	28.50±0.53	10.63±0.46	32.63±0.56	21.38±0.38	27.88±0.30	5.88±0.13	11.63±0.94	5.25±0.45	4.13±0.13	0.88±0.30
		47-58	58-68	27-31	9-13	31-35	20-23	27-29	5-6	6-15	3-7	4-5	0-2
s081	21	54.52±0.69	62.48±0.61	28.43±0.32	10.33±0.17	33.67±0.56	21.52±0.35	27.19±0.44	6.00±0.17	12.43±0.43	6.05±0.23	4.05±0.05	2.10±0.22
		48-60	57-67	25-31	9-12	29-40	19-25	21-30	4-8	10-17	5-9	4-5	0-4
s084	52	48.73±0.66	68.12±0.61	27.33±0.14	11.02±0.25	33.98±0.42	24.04±0.27	29.74±0.27	5.92±0.07	15.08±0.47	5.96±0.19	4.20±0.06	1.56±0.12
		38-60 (1)	58-74 (2)	25-30	8-18 (2)	29-40 (2)	20-29	25-34 (2)	4-7 (2)	10-24 (2)	3-10	4-5 (2)	0-4
s085	44	59.64±0.84	67.23±0.43	27.86±0.16	10.44±0.15	28.82±0.27	19.66±0.23	28.57±0.20	5.23±0.10	11.93±0.34	5.32±0.14	4.00±0.00	1.20±0.10
		40-69	61-73 (1)	25-30	9-13 (1)	25-33	17-24	26-32 (2)	4-6	4-15	4-7	4	0-4
s087	9	55.33±0.90	64.44±1.77	27.00±0.47	10.44±0.44	31.78±0.36	22.44±0.69	29.89±0.59	5.89±0.20	14.22±10.01	4.22±0.32	4.00±0.00	1.33±0.29
		51-60	57-72	25-29	8-13	30-33	19-26	27-32	5-7	11-21	3-6	4	0-3
s088	5	52.20±2.44	65.40±0.68	28.20±0.86	10.40±0.60	33.40±0.51	22.40±0.51	26.60±0.51	6.00±0.00	11.40±0.40	4.00±0.55	4.00±0.00	0.60±0.24
		45-57	63-67	26-31	9-12	32-35	21-24	25-28	6	10-12	3-6	4	0-1
s091	20	53.15±0.66	61.75±0.95	28.60±0.21	9.50±0.24	30.75±0.50	22.35±0.50	26.20±0.46	5.55±0.14	11.10±0.45	3.90±0.19	4.00±0.00	1.25±0.20
		48-59	54-70	27-31	8-11	27-35	20-25	21-30	4-6	7-16	3-6	4	0-3
s092	7	53.86±1.35	69.86±1.83	27.29±0.29	10.43±0.48	29.14±1.01	22.29±1.29	27.86±1.10	5.86±0.14	13.24±1.34	4.43±0.37	4.14±0.14	1.14±0.26
		49-58	61-75	26-28	9-12	25-33	19-29	23-32	5-6	7-17	3-6	4-5	0-2
s100	9	50.11±0.96	68.11±1.56	27.11±0.26	10.89±0.31	30.33±0.90	23.56±0.65	30.11±0.39	6.56±0.24	13.11±0.87	3.87±0.28	4.22±0.15	1.00±0.24
		45-53	60-77	26-28	9-12	26-34	20-27	28-32	6-8	9-18	3-5	4-5	0-2
s120	12	56.67±1.80	66.33±1.39	27.58±0.23	9.83±0.37	32.17±0.58	24.08±0.54	29.00±0.63	5.83±0.11	11.83±0.47	5.00±0.39	4.00±0.00	0.83±0.21
		41-64	57-73	26-29	8-12	29-36	21-28	27-34	5-6	9-14	3-8	4	0-2
s127	6	49.33±0.92	65.17±1.49	28.00±0.52	10.67±0.67	33.00±0.63	24.17±0.60	30.50±0.72	6.17±0.31	14.67±0.61	5.00±0.37	4.00±0.26	1.17±0.48
		45-51	62-72	27-30	8-13	31-35	23-26	28-33	5-7	12-16	4-6	3-5	0-3
s134	14	57.50±0.91	59.50±0.82	28.64±0.25	11.07±0.35	33.64±0.71	24.14±0.38	28.67±0.38	5.43±0.17	9.14±0.36	3.71±0.38	4.00±0.00	0.57±0.14
		53-64	53-64	27-30	9-13	30-39	22-27	27-31 (2)	5-7	7-12	1-6	4-4	0-1
s153	5	57.00±0.84	64.20±1.53	28.60±0.51	10.20±0.58	32.00±1.14	22.40±1.54	27.60±1.40	5.40±0.24	11.80±2.18	5.80±1.20	4.20±0.20	0.20±0.20
		55-59	59-68	27-30	8-11	29-35	19-28	23-31	5-6	7-20	4-10	4-5	0-1
s154	8	54.63±0.98	66.50±0.98	28.13±0.40	10.25±0.37	34.00±0.63	23.38±0.50	28.86±0.59	6.00±0.00	11.63±0.56	5.50±0.46	4.00±0.00	0.88±0.23
		50-58	63-70	27-30	9-12	31-36	21-25	27-31 (1)	6	10-14	4-8	4	0-2
sA	15	53.33±1.49	64.14±1.25	27.64±0.39	10.67±0.41	32.87±0.95	23.07±0.30	29.93±0.56	5.80±0.14	14.73±0.45	4.47±0.26	4.00±0.00	1.00±0.17
		40-61	59-76 (1)	24-30 (1)	8-13	26-38	20-25	27-33	4-6	12-19	2-6	4	0-2
sB	23	54.04±0.91	64.57±1.04	28.57±0.40	10.39±0.27	31.35±0.52	21.00±0.28	28.09±0.47	5.91±0.12	13.17±0.48	4.48±0.23	4.00±0.06	1.00±0.15
		46-62	56-77	25-32	8-13	26-37	18-25	24-32	5-7	9-17	3-6	3-5	0-2
sC	4	52.25±1.03	65.75±2.90	26.25±1.11	11.00±0.41	33.50±2.90	25.50±0.65	31.75±0.95	6.00±0.00	16.50±3.48	6.50±0.29	4.25±0.25	1.50±0.50
		50-55	58-72	23-28	10-12	26-40	24-27	29-33	6	10-26	6-7	4-5	1-3
sE	10	52.50±2.35	67.70±1.53	28.10±0.31	10.50±0.58	32.30±1.18	23.40±0.54	29.50±0.98	5.70±0.21	12.30±1.00	4.20±0.29	4.00±0.00	1.00±0.15
		41-60	62-76	26-29	8-14	26-37	21-26	26-35	4-6	7-17	3-6	4	0-2
sF	31	55.26±0.80	66.29±0.97	27.55±0.26	10.48±0.22	32.32±0.66	22.97±0.37	29.23±0.50	5.97±0.10	13.61±0.37	5.06±0.27	4.00±0.00	1.32±0.13
		41-62	55-79	24-31	8-13	27-47	19-27	24-34 (1)	4-7	8-17	2-8	4	0-3
sG	4	55.00±0.91	61.75±0.91	27.75±0.25	10.00±1.00	32.75±1.65	22.00±1.08	28.50±1.19	5.50±0.50	12.75±1.03	4.75±0.48	4.00±0.00	0.75±0.25
		53-57	56-67	27-28	7-11	29-36	20-25	26-31	4-6	10-15	4-6	4	0-1
sH	24	56.67±1.23	66.21±1.30	28.38±0.27	11.29±0.21	32.04±0.65	22.17±0.47	27.92±0.26	5.75±0.14	13.42±0.72	5.33±0.25	4.00±0.06	1.29±0.23
		42-65	58-80	24-30	10-13	27-39	18-28	26-31	4-7	7-20	3-7	3-5	0-5

sample	n	svl	dors	ventr	coll	gul	fpor	4toe	scs	scg	st	sl	sm
sl	20	51.45±0.99	63.89±1.12	27.68±0.40	10.25±0.23	31.74±0.67	22.40±0.41	28.68±0.34	5.85±0.11	12.70±0.70	5.15±0.23	4.00±0.00	0.90±0.20
		42-56	55-74 (1)	24-30 (1)	9-12	26-37 (1)	17-25	25-32 (1)	5-7	9-21	3-8	4	0-3
Corsican	517	52.08±0.21	60.75±0.19	27.78±0.05	9.70±0.05	29.27±0.12	20.92±0.09	28.97±0.09	5.77±0.04	11.80±0.11	5.91±0.05	4.03±0.01	1.13±0.03
clade		26-64	50-73	24-32	6-14	21-38	16-32 (1)	20-36 (6)	3-16	6-27	3-9 (1)	2-5	0-5
Sardinian	452	53.61±0.25	65.13±0.23	27.86±0.06	10.53±0.06	31.87±0.14	22.43±0.11	28.59±0.11	5.79±0.03	12.98±0.14	5.15±0.06	4.06±0.01	1.23±0.04
clade		38-69 (1)	53-80 (6)	23-32 (3)	7-18 (6)	23-47 (9)	17-29 (1)	21-35 (17)	4-8 (2)	4-26 (2)	1-10	3-5 (4)	0-5 (2)

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Vascular Flora of Isla del Coco, Costa Rica

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Isla del Coco (Cocos Island) is a small volcanic island located 500 km off the Pacific coast of Costa Rica. The flora of this remote island had been studied sporadically, and historical plant collections are scattered in herbaria throughout Europe, Central and North America. Since the island's discovery in 1526, no fewer than fifteen major historical collecting trips have been made to it. The resulting collections have provided the basis of our floristic knowledge of the island. For the current study, three collecting trips, in addition to herbarium research, were undertaken in order to assess the floristic diversity of the island. Two hundred and sixty-three plant species were identified of which 37 are endemic to Isla del Coco. Furthermore, as a result of this study, we now report an addition of 51 species as new to the island.

Seven vegetation types are identified on the island: bayshore, coastal cliff, riparian, low elevation humid forest, high elevation cloud forest, landslide and islet. The island is unique among OCEANIC islands WORLDWIDE in that it receives nearly 7 m of rain each year. This rainfall supports the island's high fern diversity. Forty-two percent of the native vascular plants are pteridophytes and 50% of the endemic species are ferns. This high number of endemic pteridophytes is not known on any other oceanic island. Like many islands, Isla del Coco has been impacted by contact with humans. In this study, we consider 71 species (27%) as introduced by humans to the island. In addition, five potentially invasive plant species are identified. Isla del Coco is both a national park and a UNESCO World Heritage Site. This current level of official protection can provide a legal framework for the future preservation of its unique plant biodiversity.

Resumen

La Isla del Coco es una pequeña isla oceánica del Océano Pacífico situada a unos 500 km de Costa Rica. La flora de esta isla remota ha sido estudiada de forma muy esporádica y sus colecciones históricas se encuentran dispersas en varios herbarios de Europa, Centro- y Norte-América. Desde el descubrimiento de esta isla, en el año de 1526, la misma ha sido el objetivo de quince expediciones botánicas de importancia. Las colecciones de estas expediciones han proporcionado la base para su conocimiento florístico. En el trabajo que se presenta hacemos una investigación de la diversidad florística de la Isla del Coco. Esta investigación se basa en material recientemente recolectado por nosotros en tres expediciones botánicas y en la revisión de material depositado en varios herbarios. La Isla del Coco contiene 263 especies vegetales, de las cuales 37 son endémicas. Se dan 51 especies como nuevas registras para la flora

de la isla. Se identifican siete tipos diferente de vegetación: litoral costera, litoral rupícula, higrófila, bosque húmedo a baja altitud, bosque nubaldo a gran altitud, derrubios, e islotes. La cantidad de lluvia que recibe la isla anualmente llega a los 7 m. Esta alta e inusual precipitación favorece una gran diversidad en pteridófitos. Cuarenta y dos por ciento de la flora vascular nativa de Isla del Coco está formada por helechos y el 50% de las especies endémicas de esta isla pertenecen a este grupo de plantas. Esta alta proporción de helechos no es conocida en ninguna otra isla oceánica. Al igual que otras islas, la Isla del Coco ha recibido el impacto de la intervención humana. En este estudio se considera que 71 especies (27% de la flora) son el resultado de introducciones por humanos. Consideramos que cinco de estas especies tienen un gran peligro de convertirse en especies invasoras y se recomienda su erradicación de la isla. La Isla de Coco tiene categoría de Parque Nacional y de Patrimonio Mundial de la Humanidad UNESCO. Este nivel de protección oficial puede proporcionar el marco legal para la conservación futura de la biodiversidad vegetal única de esta isla.

INTRODUCTION

LOCATION (Fig. 1): Isla del Coco, also known as Cocos Island, is a small, 24 km^2 volcanic island located at 5°32′57″N latitude and 86°59′17″W longitude in the Pacific Ocean. The island is approximately 500 km (300 miles) west of Costa Rica and 680 km (350 miles) northeast of the Galápagos Islands. The highest point on the island is 630 m (2275 ft) at Cerro Iglesias. Although the island was claimed by Costa Rica in 1869, it remains nearly uninhabited to this day. The name Isla del Coco arose as a misnomer from the original map in 1542 where the island was called "Ysle de Coques" or Seed Island (Anonymous 1920).

NATIONAL AND INTERNATIONAL CONSERVATION STATUS: Isla del Coco was designated as a Costa Rican National Park by Executive Decree in 1978. In 1991 the Park's limits were extended to include the marine ecosystems up to a distance of 15 km around the island. At this time, the entire park was declared a zone of absolute protection, and no resources can be extracted. In 1995, both the marine and terrestrial regions were designated as National Conservation Areas, and in 1997 Isla del Coco was inscribed on the World Natural Heritage List by UNESCO. In addition, in 1998 Cocos Island was designated as a Wetland of International Importance by the Ramsar Convention.

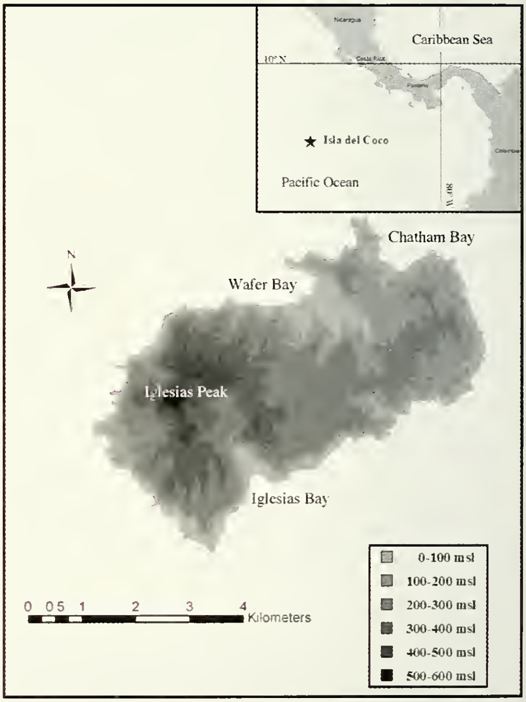

FIGURE 1. Isla del Coco. Map prepared by author.

The island is world-renowned for its unique marine life and heralded for its location as a marine bird breeding ground. Unfortunately, little has been mentioned about the floristic composition and diversity of Isla del Coco. This work hopes to bring attention to Isla del Coco as one of the true botanical treasures of Costa Rica.

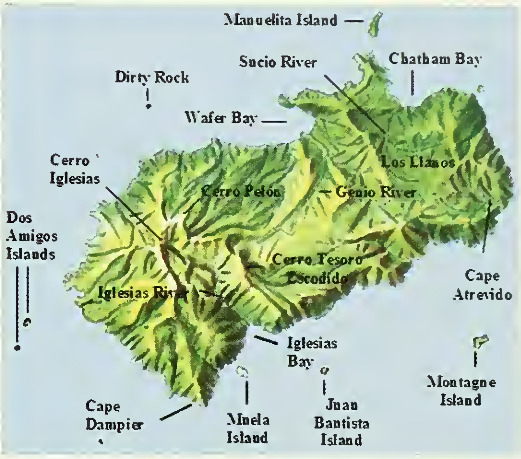

FIGURE 2. Map of Isla del Coco including collection localities. Map prepared by author.

MAP AND LOCATIONS: The names of the locations used in this paper can be found on the map shown in Figure 2. The location of French Point, listed in the collection information for *Cyperus tenuis*, was not found; we believe it corresponds to Cape Dampier.

Geology

Isla del Coco is the only portion of the submarine Cocos Ridge that rises above sea level. The island is volcanic in origin and is a product of the active and dynamic tectonics of the Cocos and Nazca plates. The Cocos Ridge was formed in the Miocene as the Galápagos hotspot alternated between the Cocos and Nazca plates across the zone of active plate tectonics known as the Galápagos Spreading Center (Castillo et al. 1988). Geological dates based on K/Ar and paleomagnetic data indicate that the island is between 1.9 and 2.4 Ma, much younger than the age of the Cocos Ridge (Bellon et al. 1984). Castillo et al. (1988) determined that Isla del Coco is the result of seamount volcanism superimposed upon this earlier hot-spot volcanism. In fact, the northern portion of the island is suggested to be the remains of the summit of the old Cocos seamount (Castillo et al. 1988). Isotopic analysis of the Cocos Island rock series indicates that the Cocos and Galápagos volcanic rocks share a common although heterogeneous mantel reservoir and that the young Cocos volcano is still a part of the Galápagos hot-spot signal (Castillo et al. 1988; Werner and Hoernle 2003). The island is composed mainly of basaltic rock and pyroclastic breccia in addition to a tracheyte dome at the northern end of the island (Chubb 1933; Castillo et al. 1988). The soils are very acidic entisols with low Ca, Mg, P and Na content (Brenes and Gonzalez 1995).

Werner and Hoernle (2003) have shown that many of the underwater seamounts that make up the Cocos, Nazca and Carnegie Ridge systems may have been above water during the last 17 million years. These "islands," thus, may have effectively formed an archipelago that could have served as "stepping-stones" for the flora and fauna of the Galápagos Islands and Isla del Coco.

Climate

Isla del Coco is the only humid oceanic island in the eastern Pacific Ocean (Costa Rica, Government of 1996). Like many tropical areas and oceanic islands, temperature varies little. The average recorded temperature is 25.5°C whereas the minimum is 23.1°C and the maximum is 27.6°C (Herrera 1984). Stewart (1912) reports the low temperature as 20°C and the high temperature as 33.3°C. In contrast, the high average yearly rainfall of 5000–7000 mm is not spread equally throughout the year. May and June receive the greatest rainfall with over 1000 mm whereas January through March receive around 200 mm (Herrera 1986). This rainfall maintains a positive hydrologic balance in the island and there is no true dry season (Montoya 1990).

The climate and seasonality of Isla del Coco are a product of its unique location within the Intertropical Convergence Zone (ITCZ). The ITCZ moves from 2–4° North latitude in February or April to 11–15° North latitude in August or September (Montoya 1990). During most of the year there is an eastward flowing equatorial counter current bringing clouds, rain and a persistent southeast wind. In contrast, when the ITCZ is at its meridian in February or March, this current becomes a westward current bringing drier air.

Vegetation

Upon the first view of Isla del Coco, the rugged relief of the island is apparent. The coastline is irregular with cliffs rising almost vertically out of the sea to heights of up to 200 m. Beyond the narrow shore, green mountain ranges, separated by steep ravines, rise up in all directions. Pittier (1898) wrote "I believe that it would be difficult to find in all of the interior [of the island] a flat and horizontal space of half a kilometer". This imposing geography has protected the island from the impact of human colonization and provides a home to its unique flora and fauna.

There are seven major vegetation types on Isla del Coco: bayshore, coastal cliff, riparian, low elevation humid forest, high elevation cloud forest, landslide and islet. These vegetation types are subjectively identified by the authors from the interactions of elevation, topography, and hydrologic conditions. The main floristic elements of these plant communities and the degree of human disturbance in each of them are discussed below.

BAYSHORE COMMUNITIES: There are three natural bays on Isla del Coco: Chatham and Wafer Bays on the northwest side of the island offer protected anchorage for boats and are the traditional entrance points onto the island; Iglesias Bay on the southeast side of the island is much smaller and is affected by strong winds, waves, and currents. Chatham and Wafer Bays are home to the two park ranger stations and the original beach communities of these bays have been modified due to human activities. Wafer Bay has a small strip of sandy beach backed by a large grove of the trees, *Talipariti tiliaceum* var. *pernambucense* mixed with *Annona glabra, Terminalia catappa,* and a few large *Erythrina fusca* and *Ochroma pyramidale*. The vines *Mucuna sloanei*, *M. mutisiana,* and *Canavalia maritima* are found growing on these shoreline trees and shrubs. There is a small section of beach near the original ranger's station that has coconut palms (*Cocos nucifera*) and an understory of the herbs *Setaria geniculata*, *Sphagneticola trilobata,* and *Hydrocotyle umbellata.* Chatham Bay has a small area of sandy beach that is exposed only at high tide. The shoreline is steep behind the beach except for the small area near the mouth of the Chatham River. The river edge is mainly a grove of *Talipariti tiliaceum* var. *pernambucense*. Despite its name, there are relatively few coconut palms left on Isla del Coco. These are found in small isolated pockets of beach and at Iglesias Bay. Iglesias Bay is similar to Chatham Bay as it has no permanent sandy beach area. Wave action has pushed a wall of rocks up protecting a small area of beach vegetation from the wind and waves. The small grove of *Cocos nucifera* is formed along the floodplain area of the Iglesias River behind this natural seawall. In addition, beach morning glory, *Ipomoea pes-caprae* is found growing on rocks along with the fern *Blechnum occidentale*. There are no mangrove communities on Isla del Coco although the mangrove associate *Cassipourea guianensis* is occasionally found.

COASTAL CLIFF COMMUNITIES: The steep slopes of Chatham Bay are representative of the cliff vegetation around the island. The open overstory is primarily the endemic *Cecropia pittieri* (Cecropiaceae) mixed with *Clusia rosea*. The overwhelming majority of the vegetation is a mixture of *Ipomoea* spp. vines forming a nearly vertical green wall. The sedge, *Rhynchospora polyphylla,* stinging nettle, *Laportea aestuans,* and red-flowered *Kohleria spicata* are some of the few herbaceous plants that are common on the cliffs near the shoreline. In less steep areas, the closed-canopy forest vegetation reaches to the shore. Here it is possible to find a canopy of the endemic tree *Sacoglottis holdridgei* (Humiriaceae) along with tree species *Ocotea insularis* and *Clusia rosea.* The understory is composed of melastome shrubs such as *Ossaea macrophylla* and *O. bracteata*. A unique feature of this vegetation is the presence of the endemic tree fern *Cyathea nesiotica*

(Cyatheaceae) which is restricted to these moderately steep areas that receive more sunlight. Many waterfalls cascade from these cliffs into the sea.

RIPARIAN AREAS: The unusually high rainfall and steep terrain of Isla del Coco support many streams and rivers. The largest and most permanent of these rivers are those leading into the three bays at Chatham, Wafer and Iglesias. The overstory of the riparian areas is the same as the rest of the island with an abundance of *Sacoglottis holdridgei*, *Ocotea insularis*, and *Clusia rosea* trees. The sedge, *Calyptrocarya glomerulata*, the aroid *Spathiphyllum laeve*, and the fern *Danaea nodosa* are abundant along river and stream banks throughout the island. At the lower elevations (0–50 m) of Wafer Bay, the Genio River and its tributary streams are home to *Rustia occidentalis* and *Pilea gomeziana*. The endemic *Hoffmannia piratarum* (Rubiaceae) is restricted to the Genio River riparian area.

The Iglesias River on the southwestern side of the island is only accessible for a short section from the waterfall to the sea. This area is home to a small grove of the endemic tree *Eugenia cocosensis* (Myrtaceae) and an understory including the shrub *Psychotria gracilenta*. The Chatham River leading to Chatham Bay is much steeper and has large boulder outcrops along the edges. The endemic shrub *Ardisia cuspidata* (Myrsinaceae) is common along the banks of this river.

LOW ELEVATION HUMID FOREST. The majority of the island is classified as premontane rain forest in the Holdridge life zone system (Holdridge 1974). Tree diversity is extremely low. Only five species of canopy trees were recorded in a study of all tree species over 10 cm diameter at breast height (dbh) in ten 400 m^2 plots along an east-west elevational transect from 30 m to the highest elevation at 630 msl on the north-eastern slope of Cerro Iglesias. These are *Sacoglottis holdridgei, Clusia rosea, Ocotea insularis, Henriettella fascicularis* and *Miconia dodecandra*. *Ficus pertusa, Eugenia cocosensis,* and *Brosimum* sp. are also found sporadically along the north side of the island. The shrub layer in this vegetation zone is dense and diverse with many melastomes and two common endemic tree fern species, *Cyathea alfonsiana* and *C. notabilis*. The sole forest palm is *Euterpe precatoria* var. *longevaginata*. The herbaceous layer consists mostly of fern species and the large sedge species *Hypolytrum amplum*. Thick lianas of *Schlegelia brachyantha* and *Entada gigas* wind through the trees. A notable aspect of this forest is the density and diversity of epiphytic species. The forest appears a mixture of green and red from the abundance of the bromeliad *Guzmania sanguinea* that covers nearly every tree. In addition, four orchid species are commonly found including the endemics *Epidendrum cocoënse* and *E. insulanum*. There are many epiphytic ferns and two endemic pendent epiphytes, *Huperzia brachiata* and *H. pittieri*.

HIGH ELEVATION CLOUD FOREST: The cloud forest on Cocos Island begins around 450 m elevation and is restricted to the two highest peaks on the island, Cerro Iglesias and Cerro Pelon. The canopy of this forest is exclusively *Sacoglottis holdridgei* with an understory largely dominated by the tree fern *Cyathea alfonsiana*. These large trees and tree ferns are completely covered in a thick layer of mosses and the whole forest constantly drips as the clouds roll over the peak. *Freziera calophylla, Hedyosmum racemosum* and the endemic fern *Elaphoglossum reptans* are known on Isla del Coco only from these cloud forests.

LANDSLIDES: Due to the abundance of rain and its rugged terrain, Cocos Island has many landslides both near the coast and inland (Fournier 1966). These open areas are quickly covered with the vining ferns *Dicranopteris flexuosa, D. pectinata* and *Sticherus remotus* and vines of several species of *Ipomoea*. These species are joined by *Cecropia pittieri*. These successional areas caused by landslides are common and probably constant features of the Cocos Island vegetation.

ISLETS: There are more than ten small islets surrounding Isla del Coco and three of them (Isla Manuelita, Isla Ulloa and Isla Muela) were visited during our research. These small islets do not contain much soil as a result of constant weathering by the wind and sea. Only two species of plants, *Clusia rosea* and the endemic grass *Chloris paniculata* were recorded on these islets. The overwhelming majority of the plants of *Chloris paniculata* are found on these small islets although a few small sub-populations are found on the coastal cliffs of Isla del Coco near the islets.

Human Impacts

The biota of oceanic islands is unique and fragile. The paucity of species in island habitats increases the importance of the native species in ecosystem function and dynamics. The biological equilibrium of oceanic islands is very sensitive to any external alteration. The impact of humans and their introduced animals and plants on the biota of oceanic islands is well known (Moulton and Pimm 1986; Quammen 1996; Haberle 2003). There have been many examples of extinctions produced by the intentional or accidental intervention of man in fragile ecosystems such as islands. Isla del Coco is not excluded from this list. In the nearly 500 years since the island was discovered, man has impacted its ecosystems.

HUMAN INHABITANTS: Isla del Coco has not had extensive human inhabitation. The island functioned as a prison colony between 1874 and 1877 in Chatham Bay (Alfaro 1898). The longest tenure any human has had living on the island was by August Gissler and his wife who spent 16 years from 1889 to 1905 in Wafer Bay. Gissler brought 13 German families to work in the Cocos Island Agricultural Company (Jinesta 1937), but very few families stayed for a second year. Today, the park has two stations, one in Chatham Bay that houses four people and the other in Wafer Bay that houses up to 30 people. The majority of the island has remained uninhabited. Recently, there has been a hydroelectric facility installed on the Genio River in Wafer Bay that provides power to the ranger station.

INTRODUCED ANIMALS: In July of 1793 James Colnett, captain of the English whaler *Rather*, introduced pigs and goats onto the island (Lievre 1893). Today, the feral pig (*Sus scrofa*) is abundant and is one of the main threats for the native plants of Cocos Island. Although this introduction has had the greatest negative environmental impact on the island, it is not the only animal introduction. Paca (*Agouti paca*), white-faced monkeys (*Cebus capucinus*), domestic dogs (*Canis familiaris*), domestic rabbits (*Oryclolagus cuniculus*) and guinea hens (*Numida meleagris*) have all been introduced (Madrigal 1954; Rojas 1964). However, none of these introduced vertebrates have prospered, and they do not occur on the island today. The current introduced fauna of the island consists of feral pigs, feral cats (*Felis domesticus*), goats (*Capra hircus*), white-tailed deer (*Odocoileus virginianus*) and two species of rats (*Rattus rattus* and *Rattus norvegicus*) (Montoya 1990; Gómez 2004).

An estimated 400–500 feral pigs occur on Isla del Coco (Sierra 2001a). Research has shown that areas rooted by the feral pig population have a rate of soil erosion nearly 100 times greater than unrooted areas and that 10–20% of the total island surface is rooted annually by these animals (Sierra 2001b). Rooting is a major soil disturbance and can increases the loss of soil nutrients (Singer et al 1984). Rooting diminishes the abundance of soil arthropods (Vtorov 1993) and reduces and/or modifies the structure of the herbaceous vegetation (Bratton 1974; Diong 1982). In addition, Sierra (2001a) found that 88% of the stomach contents of the feral pigs is vegetable matter, with 63% fruits of Moraceae spp., *Annona glabra*, and *Ocotea insularis*. Sierra (2001a) did not find that the pigs were dispersing the seeds of any exotic species. Park officials have approved the eradication of feral pigs (Montoya 1990) but are awaiting funding.

Studies of the rat populations of Isla del Coco have added to our knowledge of their impacts on the island. Gómez (2004) found that rat densities on the island range from 45 rats/ha in the cloud forest of the island to a high of 156 rats/ha near the inhabited area of Wafer Bay. Rats are also found on many of the islets near the island. Gómez (2004) also found that 70% of the stomach contents of these animals is vegetable matter. In addition, he found that 68% of seeds of the endemic tree *Sacoglottis holdridgei* were gnawed on by rats (Gómez (2004).

Introduced plants: The first account of exotic plant species on Isla del Coco was by Don Francisco Bernardo de Quiroz in 1546 who wrote, " I planted some plants and fruits brought from Peru" (Sierra 1998). This early account was only 20 years after the discovery of the island. Passmore (1895) recorded pumpkins and grapes on the island, while Pittier (1898) recorded jocote (*Spondias lutea*), achiote (*Bixa orellana*), and marañones (*Anacardium occidentale*). August Gissler (1889–1905) and his Cocos Island Agricultural Company cultivated a large area in Wafer Bay with bananas, beans, cacao, coffee, corn, avocado, achiote, sugar cane, oranges, limes, pineapples, tobacco, cherimola, almonds and yuca (Jinesta 1937). Today, avocado, bananas, cacao and coffee remain from Gissler's fields. In addition, the park service personnel maintain several tropical fruits and vegetables in cultivation for their own consumption. The only cultivated plant that has managed to escape into at least two known forested areas of the island is the shade-loving coffee plant.

It is uncertain to what extent the species with extensive, worldwide or pantropical distributions have reached the island because of human intervention. Drift disseminated species such as *Cocos nucifera*, *Mucuna sloanei*, and *Ipomoea pes-caprae* have seeds that can survive and germinate after long periods floating at sea (Guppy 1906). The propagules of weedy species such as *Rolandra fruticosa*, *Urena lobata* and *Drymaria cordata* are small and can be moved by wind or can be easily dispersed by migrating birds (Ridley 1930; Carlquist 1970). In contrast, a number of plant species are commonly associated with humans. Species such as *Sida acuta*, *Phyllanthus urinaria*, *Hydrocotyle umbellata* and many grass and sedge species are usually found only in human disturbed areas or around dwellings. It is likely that these species were accidentally introduced by humans. Unfortunately, due to the lack of early plant collections, knowing whether a plant is native but widely distributed or whether it has been accidentally introduced is a difficult distinction to make. For this publication, any ruderal species first found after 1905 is considered accidentally introduced by humans unless there is evidence to the contrary. This date was chosen because it is the date of the first fairly complete plant collection for the island published by Stewart (1912). By these criteria, we consider 71 species to have been intentionally or accidentally introduced to Isla del Coco by humans in the last 100 years.

Deforestation: The most apparent impact man has made on the vegetation of Isla del Coco is through deforestation. Many mariners cut wood or collected coconuts from the islands throughout its history. Lievre (1893) stated that many coconuts were collected by felling the coconut palms. This activity led to the 1895 account that there were no coconut palms on Isla del Coco (McCartney 1895). Despite this extensive harvesting, coconuts can still be found in isolated coastal locations. The deforested areas of Isla del Coco are limited to the areas near Chatham and Wafer Bays. The area near Chatham Bay was deforested for agriculture in 1874 by the penal colony and despite the cessation of agriculture for the past 125 years, remains deforested to this day (Alfaro 1898; Sierra 1998).

Previous Botanical Research

Although the island had been known to mariners since the sixteenth century (Hertlein 1963) the first known plant collections from Isla del Coco were made in 1838 by George W. Barclay during the voyage of H.M.S. *Sulfur* (Belcher 1843). Fifty years after these initial collections, Alexander Agassiz of Harvard University collected a number of plants in 1888 and 1891 during expeditions of the United States Fish Commission (Agassiz 1891–1892). Agassiz, like many of the subsequent plant collectors, spent a few days on Isla del Coco as a stop during his trip to the Galápagos Islands. Six years after Agassiz' expedition, the Costa Rican government funded Anastasio Alfaro, Henri

Pittier and Paul Biolley to visit in 1898 and 1902 in the interest of re-instating the use of the island as a penal colony (Pittier 1898). The three naturalists suggested that the island should be conserved as a protected area instead. Pittier's plant collections are the basis of nine species endemic to Cocos Island (Pittier 1898). Robert E. Snodgrass and Edmund Heller, naturalists aboard the Hopkins-Stanford Expedition in 1899, also collected on Cocos Island (Robinson 1902). One of the most complete early botanical expeditions to Cocos Island was accomplished by Alban Stewart who collected in 1905 for the California Academy of Sciences (Stewart 1912).

Interest in plant collecting on Isla del Coco was renewed in the 1930s with the Vincent Astor expedition of 1930 with botanist Henry K. Svenson (Svenson 1935, 1938) and during the Templeton-Crocker Expedition sponsored by the California Academy of Sciences in 1932 with the plant collections of John T. Howell. The Presidential Cruise of the United States stopped on Cocos Island in 1935, 1937 and 1940 and collections were made and sent to the United States National Herbarium. In 1964, W.L. Klawe collected Isla del Coco plants as part of the Galápagos Islands International Scientific Project (Fournier 1966; Fosberg and Klawe 1966).

Plant collecting on Cocos Island has greatly increased in the last decades due to the establishment of Isla del Coco National Park and the availability of transportation to the island. The majority of this work has been conducted by Costa Rican botanists from the Universidad de Costa Rica, Universidad Nacional de Costa Rica and the Instituto Nacional de Biodiversidad. Collectors include Gregorio Dauphin, Robin Foster, Luis Diego Gómez, Jorge Gómez-Laurito, Jose González, Leslie R. Holdridge, Alfonso Jiménez, Eduardo Lépiz, Luís Poveda, Francisco Quesada, Alexander Rojas, Pablo Sánchez, Ricardo Soto, and Manuel Valerio. Table 1 (See Appendix) gives a summary of the most important historical botanical collections from Isla del Coco with details on the dates, institutions/countries which organized these expeditions, and the locations of the specimens collected.

Despite the number of collectors who have visited the island, there are relatively few published works on the plants of Isla del Coco and no complete flora has been assembled. The earliest published records of vascular plants for Isla del Coco are those of Bentham (1844–1846), Rose (1892), Pittier (1898), Robinson (1902), Stewart (1912) and Svenson (1935, 1938). It was not until 1966 when Fosberg and Klawe published the "Preliminary List of Plants from Cocos Island" that this information was assembled for the island (Fosberg and Klawe 1966). Many new collections have been made since this checklist was published and better taxonomic and floristic treatments have aided in the identification of previous collections and in the description of new species (e.g., Gómez 1971; Burger 1975; Gómez 1975; Gómez 1976; Hamilton 1988; Rojas-Alvarado 2003; Rojas-Alvarado and Trusty 2004). The present work, synthesizes over 150 years of collection data along with data from recent expeditions, stands as the first complete flora for this island.

BOTANICAL WORK THAT MAKES UP THIS VOLUME: We have compiled a list of all the species previously collected or currently present on Isla del Coco and have updated the taxonomy and nomenclature for these species. This research is based both on the study of herbarium specimens and also on material collected by us during our recent expeditions to Cocos Island. Three collecting trips were made between 2001 and 2002: Trusty (July 2001), Trusty and Kesler (January–March 2002) and Trusty and Kesler (November–December 2002). A total of 497 numbers was collected during these three trips. Complete sets of these collections can be found in the Museo Nacional de Costa Rica (CR) and Fairchild Tropical Botanic Garden (FTG); partial sets are located in the California Academy of Sciences (CAS), the Instituto Nacional de Biodiversidad (INB), and Universidad de Costa Rica (USJ). In addition, the original plant collections of all published species were reviewed in CR, USJ, INB, the Gray Herbarium at Harvard (GH), and the Smithsonian Institution (US). Loans were obtained of collections from Isla del Coco housed at the California Academy of Sciences (CAS), the Brooklyn Botanic Garden (BKL) and US. More than 1800 specimens were studied including historical and type collections. These collections were verified and annotated. On the basis of these specimens and current taxonomic treatments, we recognize 263 species on Isla del Coco. Fifty-one species are new records for the island. Twenty-eight of these were collected by J. Trusty. Eleven previously published species are either excluded from the flora or are considered as doubtful occurrences. In addition, information about species' abundance and distribution on the island is provided. The abundance designations are: rare, infrequent, frequent, locally common, common and very common. These are subjective assessments made by the authors based on the frequency of encounter from least to greatest. The List of Exiccatae provides a summary of the herbarium specimens that are the basis for this flora.

PLANT BIOGEOGRAPHY

The known native vascular flora of Isla del Coco now stands at 263 species. One of these is identified only to genus (*Brosimum* sp.) due to lack of adequate material. Of the 262 identified species, 37 are endemic to the island and 154 are considered native. Seventy-one species are considered introduced by humans. A summary is given in Appendix Table 2.

ENDEMIC SPECIES: Isla del Coco is home to 33 endemic plant species and four endemic varieties representing 24% of the native flora. This rate is relatively low when compared to other islands or archipelagos in the Pacific. The nearby Galápagos Island flora boasts an endemism rate of 43%, the Juan Fernandez Islands have 60%, while Hawaii boasts 97% (Wagner et al. 1990; Lavergne et al. 1999, Baeza et al 2002). Single islands such as Rodriques, La Réunion and Mauritius have endemism ranges between 29–45% (Lavergne et al. 1999). The small size and young age of Isla del Coco may influence the low rate of endemism on this island.

Six genera on Isla del Coco have more than one endemic species on the island (*Cyathea,* 3 spp.; *Elaphoglossum,* 3 spp.; *Epidendrum,* 3 spp.; *Eugenia,* 2 spp.; *Hoffmannia,* 2 spp. and *Miconia,* 2 spp.). Preliminary molecular evidence for *Epidendrum* and *Miconia* (J. Trusty et al., in prep.) and morphological assessments for *Cyathea* do not suggest the endemic species to be sister taxa (M. Turner, pers. commun.). This evidence suggests that although a moderate number of new species has evolved on the island, a radiation event has not occurred. Most endemic species on Isla del Coco are the result of separate introductions from the mainland.

The endemic flora of Isla del Coco is unique in that 50% of the endemics are fern species. In no other island flora does the number of fern endemic species equal that of flowering plant endemics (Smith 1972; Given 1993). In addition, the total fern diversity is high, with 80 species making up 30% of the total flora of Isla del Coco. In comparison, ferns in continental areas represent a much smaller proportion of the flora. For example, ferns constitute only 9% of the vascular plant diversity of Costa Rica (Moran 1993).

ORIGIN OF THE FLORA: The majority of the species on Isla del Coco are considered to be Central or South American in origin due to the proximity of the island (500 km) to mainland Costa Rica. The distributional ranges of the native species are listed in the Species Descriptions and a summary is given in Appendix Table 3. The floristic affinities of the endemic species based on the distribution of putative sister species are compiled in Appendix Table 4. The close relationship of the Isla del Coco flora with the Caribbean Islands and Central America is shown with 66.8% of all Cocos Island native taxa present on at least one island in the Caribbean and 95.7% present in Central America. This biogeographic relationship was suggested by Croizat (1958) who considered Isla del Coco to be a part of a biogeographical track that joins the Caribbean, Central America and the Galápagos Islands. This biogeographical track has been confirmed by the geological and tectonic history of the region (Rosen 1976; Haug and Tiedemann 1998). To date, no floristic links have been found between Isla del Coco and the Galápagos Islands and they only have 26 plant species in common (Trusty et al., in prep.). Approximately 30% of plants native to Cocos Island are pantropical in distribution.

Using the guidelines proposed by Carlquist (1974), the most likely dispersal mode was determined for each species found on Isla del Coco based on seed size, palatability for birds, presence/absence of appendages or glands, ability to float and/or published dispersal mode (Carlquist 1974; Croat 1978; STRI 2004; NYBG 2004; data available from J. Trusty on request). The results of this analysis are shown in Appendix Table 5. Approximately 47.1% of native species are considered dispersed by wind, 11.5% by water, 26.7% internally by birds and 14.7% externally by birds.

WIND PATTERNS: The climate of Isla del Coco is determined by the northern and southern migration of the Inter-Tropical Convergence Zone (ITCZ). The ITCZ is an air current that moves from 2–4° North latitude between February and April to 11–15° North latitude between August and September. During most of the year there is an eastward flowing equatorial counter current bringing clouds, rain and a persistent southeast wind. In contrast, when the ITCZ is closest to Isla del Coco in February or March, the equatorial current becomes a westward current bringing drier air (Montoya 1990).

The majority of wind-dispersed plants is fern or orchid species due to their minute spores and seeds. Ferns and orchids are predisposed to the colonization of insular environments due to their incredible dispersal abilities. Fern spores are microscopic with nearly 80% of pteridophyte species within a range of 20 to 60 micra in diameter (Tryon 1970). The small size of fern spores allows them to be easily transported by air currents, and it has been said that distances of 800 km is not a significant barrier (Tryon 1970).

Orchid seeds are often described as "dust-like" and range in size from 150 to 6000 micra in diameter (Molvray and Kores 1995). The seeds also have large internal air spaces that allow them to float on air for long periods of time, facilitating long distance transport (Arditti and Ghani 2000). In addition to the ease of transport, fern spores and orchid seeds are particularly numerous; a single plant can produce thousands of propagules at one time and many millions in a lifetime (Carlquist 1965; Arditti and Ghani 2000). Once the propagules have arrived, the wet, tropical environment on Isla del Coco is beneficial to the establishment and survival of fern and orchid species. Although air currents flow westward from the mainland of Central America/northern South America for only a small part of the year, many fern and orchid species have successfully made the voyage to Isla del Coco as evidenced by the high proportion of these plants in the total flora.

Due to the remarkable dispersal ability of ferns and orchids, it is surprising that these air dispersed groups make up the majority (56.8%) of endemic species on Isla del Coco. If large numbers of orchid seeds and fern spores were continuously colonizing the island, the genetic input of these mainland populations would prevent the Isla del Coco populations from diverging into new species via genetic drift or selection. Unless the island populations had developed a method of reproductive isolation via mutation or chromosome rearrangement, the influx of mainland genes would reunite the island population with the mainland species and likely swamp out the traits under selection in the island environment (Templeton 1982, Futuyma 1998). The presence of 18 endemic fern taxa and three endemic orchid species indicates that although ferns and orchid propagules are able to survive the long journey to Isla del Coco, this event is rare for many species.

OCEAN CURRENTS: Isla del Coco is situated in the eastern Pacific where a complex series of marine currents join. The system of ocean currents that influences the island is made up of three main components: strong eastern circulating currents that transport warm tropical water along (and slightly north) of the equator two western circulating cold currents that parallel the warm equatorial current on each side a complex of minor currents that originate on the coast of Central and South America and influence ocean patterns up to 800 km from that coast.

The interplay and influence of any one of these currents are variable within each year and from year to year (Montoya 1990). In addition, each current also responds to patterns of atmospheric circulation. The warm eastern flowing Northern Equatorial Countercurrent (NECC) circulates between 4–10 degrees N latitude and is particularly influenced by the northern and southern migrations of the ITCZ. The two cold currents do not directly affect the island but act on the range and movement of the NECC. Finally, the warm Costa Rican, Colombian and Peruvian coastal currents influence the development and occurrence of the El Niño Southern Oscillation (ENSO), which can provoke catastrophic disequilibria in marine and terrestrial environments of the region through increased ocean temperatures.

Overseas flotation is the least common mode of dispersal to Isla del Coco for plant species. Only a small and specialized group of beach strand species commonly uses flotation as a dispersal route. These species are often extremely widespread throughout tropical areas as a result of the effectiveness of flotation as a dispersal method. A number of common coastal, drift-seeded species such as *Ipomoea pes-caprae*, *Cocos nucifera*, *Mucuna* spp. and *Caesalpinia bonduc* are present on the island. Mangrove species, which are common drift fruits, are not found on Isla del Coco but this may be due to the lack of protected beachfront. Due to the frequent input of propagules to Isla del Coco, most drift dispersed species are not reproductively isolated from conspecific mainland populations and are prevented from diverging into new species. In fact, only a single endemic species, *Sacoglottis holdridgei,* on Isla del Coco is considered related to a plant whose propagules can be dispersed by water. Interestingly, *S. holdridgei* and its putative sister species, *S. ovicarpa*, are closed-canopy forest species and not common in beach strand ecosystems. It is likely that the ecological preferences of these species help to maintain the genetic and morphological distinctness of each taxon.

BIRD VISITATION: Isla del Coco is home to three endemic species of birds but is visited by many other bird taxa. A compiled checklist of bird species lists 97 taxa with the majority of these as nonbreeding visitors (Slud 1967; Sherry and Werner 1984; Costa Rica, Government of 1996). These visiting birds are able to move plant propagules in a number of different ways. The most common form of bird dispersal is internal (Carlquist 1974). Many birds are frugivorous and eat a wide variety of fruits and seeds. Proctor (1968) and De Vlaming and Proctor (1968) have shown that shorebirds can retain seeds in their digestive system for up to 300 hrs. Birds may also move seeds on external portions of their bodies. Morphological adaptations of externally-dispersed seeds include the presence of bristles and/or barbs or viscid glands which aid the seeds in sticking to the bird's feathers and legs. Other seeds dispersed by birds, such as many grass and sedge species, are small and common in muddy areas. It is thought that these species are often moved in the mud stuck to the legs and feet of migrating birds.

Bird dispersal of plant propagules, internally and/or externally, is common on Isla del Coco. Forty-one percent of all native plant species on the island are presumed to have been dispersed by birds. Internal bird dispersal is the only explanation for many large or fleshy-fruited plant species such as many taxa in the families Rubiaceae, Melastomataceae and Myrtaceae. The apparent frequency of internal bird dispersal to Isla del Coco is surprising. Of the 52 plants that are believed to have been internally dispersed to the island, only 12 are endemic species. This implies that the majority of these native plants are internally bird-dispersed to the island with enough regularity to prevent these species from diverging via genetic drift or selection and becoming reproductively isolated from mainland populations. In addition, internal bird dispersal is more common than external bird dispersal for Cocos Island plants (27.2% vs. 14.1%).

Three endemic species are considered to be externally bird-dispersed species (*Chloris paniculata, Kyllinga nudiceps*, and *Pilea gomeziana*). These taxa have small seeds (often with appendages to aid in attachment) and are found in muddy and/or coastal habitats. The progenitors of these species, which presumably shared these seed dispersal characteristics, were most likely picked up on the body or feet of a bird and carried to the island.

INTRODUCED SPECIES: A total of 71 plant species has been introduced by humans to the island, representing 27% of the flora of Isla del Coco. In comparison with other island systems in the Pacific, this is a remarkably low figure. Lavergne et al. (1999) found that introduced species outnumber the native species in all of the Pacific Islands they studied except for the Galápagos where 45% of the flora is introduced. Lonsdale (1999) in his study of worldwide plant invasions found that on average 13% of introduced species become invasive. Invasive species can rapidly alter island ecosystems. Many islands have encountered the extinction of native plant and animal species due to invasive exotics (Baeza et al. 2002; Leon de la Luz et al. 2003). Eradication of exotic species that have become naturalized can be extremely time-consuming and costly (Cronk and Fuller 1995; Pimental et al. 2000).

The majority of Isla del Coco has not been impacted by invasive exotic species but as visitation and tourism increase, it is likely that the number of introduced or exotic species on Isla del Coco will grow. Quick and decisive removal of introduced plant species on the island will be imperative to the continued success of the native flora. In addition, inspection and monitoring of goods brought to the island are some of the mechanisms that should be implemented in order to minimize the accidental introduction of exotics to this island. We have noted in the remarks (see List of Vascular Plants) those species introduced to Isla del Coco that are invasive in other island ecosystems. We recommend their timely removal to prevent these species from becoming naturalized within the island.

DESCRIPTION OF TERMS

The families used are those currently accepted by the publication "Plant Systematics" by Judd et al. (2002). This work recognizes a broad Malvaceae that includes Sterculiaceae, Tiliaceae, and Bombacaceae. In addition, the Apocynaceae includes species previously included in Asclepiadaceae. *Chrysobalanus* is recognized in the Chrysobalanaceae and not Rosaceae. *Muntingia* is included in the Muntingiaceae not Elaeocarpaceae and *Scoparia* is included the Plantaginaceae not Scrophulariaceae. Finally, *Schlegelia* is included in the Schlegeliaceae and not Bignoniaceae.

Synonyms are listed after the species names. This list of synonyms does not include all possible nomenclatural synonyms but only synonyms for those species that have been published in the previous floristic treatments of the island by Rose (1892), Pittier (1898), Robinson (1902), Stewart (1912), Svenson (1935, 1938) and Gómez (1975, 1976). The list of pteridophytes is based on the publication by Rojas-Alvarado and Trusty (2004). All author abbreviations follow Brummitt and Powell (1992). Species descriptions are provided for the endemic species. The endemic species are highlighted in bold type while species introduced by humans are marked with an asterisk.

CATALOG OF SPECIES

Key to the Families of Pteridophytes on Isla del Coco

1. Plants with no leaves or roots; stems dichotomously branching; sporangia trilocular . . . . Psilotaceae
1. Plants with leaves; sporangia unilocular. 2
  2. Leaves with a single unbranched vein. 3
    3. Fertile cones 4-sided; leaves oblong to ovate; heterosporous. . . . . .Selaginellaceae
    3. Fertile cones round in cross-section or sporangia in axils of unmodified leaves; leaves sharp-pointed, usually linear; homosporous . . . . .Lycopodiaceae
  2. Leaves complex, veins branched. 4
    4. Sporangia born on erect spikes or panicles from near the base of the blade . . . . .Ophioglossaceae
    4. Sporangia on back of blade or sometimes born on modified fronds or parts of fronds 5
      5. Stems tree-like. . . . . .Cyatheaceae
      5. Stems not tree-like 6
        6. Petiole with one vascular bundle 7
          7. Vascular bundles of petiole U-shaped or Ω-shaped (with the open end of the "U" or omega oriented adaxially) when viewed in cross-section . . . 8
            8. Leaves forked; petiolar vascular bundle with enrolled arms . . . . Gleicheniaceae
            8. Leaves not forked; petiolar vascular bundle without enrolled arms . . . . Dennstaedtiaceae (in part)
          7. Vascular bundles of the petiole terete 9
            9. Lamina one cell thick between the veins, translucent . . . . Hymenophyllaceae
            9. Lamina more than one cell thick between the veins, opaque 10
              10. Plants epiphytic; fronds pendulous, simple, entire; rhizome scales clathrate. . . . . Vittariaceae
              10. Plants epiphytic or not; fronds various; rhizome scales clathrate or not. 11
              11. Leaves jointed to phyllopodia, arranged in two rows on the dorsal side of the stem . . . . Polypodiaceae
              11. Leaves not jointed to phyllopodia; arranged radially on the stem 12
                12. Rhizome scales peltate; sori indusiate . . . Oleandraceae
                12. Rhizome scales basifixed or absent; sori exindusiate . . . . Grammitidaceae
        6. Petiole with two or more vascular bundles 13
          13. Petioles with two vascular bundles. 14
            14. Vascular bundles terete . . . . Pteridaceae
            14. Vascular bundles elongated or strap-shaped 15
              15. Vascular bundles free in the distal part of the petiole; lamina often 1-pinnate-pinnatifid; trichomes unicellular, acicular, bifurcate or stellate . . . . Thelypteridaceae
              15. Vascular bundles united in the distal portion of the petiole; tri-

chomes multicellular 16
16. Scales generally clathrate; sori thinly elongate to linear . . . . Aspleniaceae
16. Scales not clathrate; sori rounded or if elongate or linear, paired back to back on the same nerve . . . . . . Woodsiaceae
13. Petioles with three or more vascular bundles 17
17. Petiolar vascular bundles arranged in concentric circles. 18
18. Blades 1-pinnate; veins netted; rachis without pulvinus-like thickening at junctures with costae; fleshy, ear-like stipules absent at petiole base .·. . . . . Pteridaceae (*Acrostichum*)
18. Blades 2-5-pinnate; veins free; rachis with pulvinus-like thickening at junctures with costae; fleshy, ear-like stipules present at petiole base . . . . Marattiaceae
17. Petiolar vascular bundles arranged in one circle 19
19. Rhizome and petiole base hairy . . . . Dennstaedtiaceae (in part)
19. Rhizome and petiole base scaly 20
20. Blades 1-pinnate, with a small fiddlehead at the tip; pinnae jointed to the rachis; hydathodes conspicuous; plants stoloniferous . . . . Oleandraceae (*Nephrolepis*)
20. Plants not as above 21
21. Sporangia completely covering the back of the leaf, not in sori 22
22. Rhizome creeping, in cross-section with a broad, ventral vascular bundle . . . . Lomariopsidaceae
22. Rhizome creeping to erect, in cross-section with a ventral vascular bundle the same size and shape as the dorsal bundles . . . . Dryopteridaceae
21. Sporangia grouped in sori of diverse types 23
23. Rachis and costae pubescent on the upper surface; sori dorsal between the costa and the margins of the lamina . . . . Tectariaceae
23. Rachis and costae glabrous on the upper surface; sori elongated to linear and parallel along the costae . . . . Blechnaceae

ASPLENIACEAE

1. Rhizome creeping; leaves proximal to remote . . . . *Asplenium dissectum*
1. Rhizome erect to curved-ascendant or sometimes procumbent; leaves grouped 2
2. Pinnae conspicuously pedicellate, at least the basal and medial portions, 2 mm or longer . . . . *Asplenium delicatulum* var. *cocosensis*
2. Pinnae sessile, subsessile or briefly pedicellate up to 1 mm. 3
3. Rachis with thin green margins proximally . . . .*Asplenium abscissum*
3. Rachis with green wings . . . .*Asplenium barclayanum*

1. *Asplenium abscissum* Willd., Sp. Pl. 5:321. 1810.

DISTRIBUTION.— Rare; collected once on Cerro Tesoro Escondido on Isla del Coco. Distributed from southern Florida and Mexico to Brazil and Uruguay; also found in the Greater and Lesser

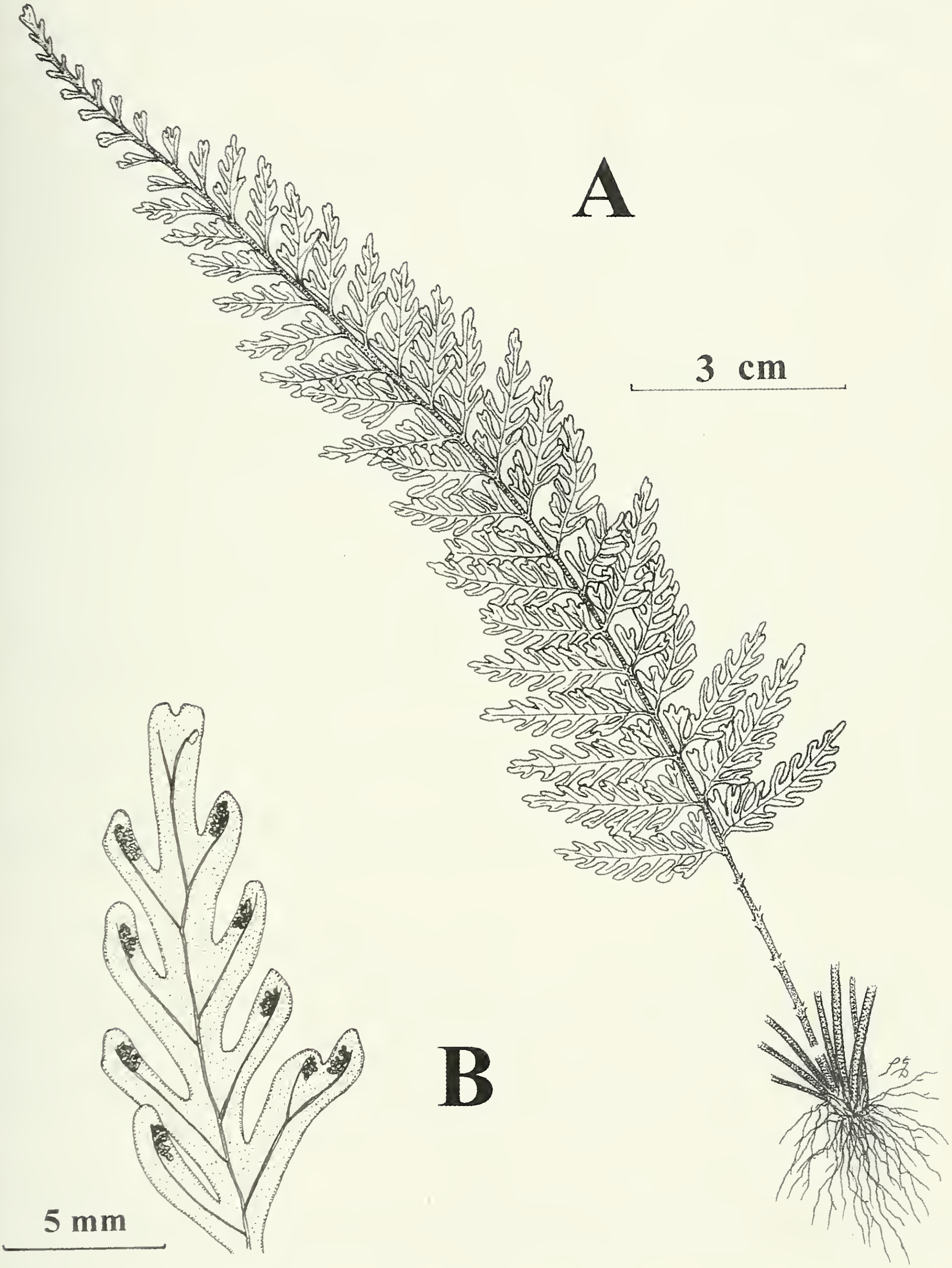

FIGURE 3. *Asplenium barclayanum* (drawn from *Trusty 126*). A. Habit of plant showing a single frond. B. Abaxial view of frond showing sori.

Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Gómez 3333*; *Gómez 3334*; US: *Gómez 3333*.

2. ***Asplenium barclayanum*** C.D. Adams, Novon 2:290. 1992. (Fig. 3)

TYPE: *Barclay 2196* (holotype: BM).

Rhizome 1–3 × 0.2–0.4 cm, suberect or shortly creeping; scales 1–5 × 0.2–0.8 mm, elongate-deltate from a rounded auriculate base, tapered to a short hair tip, remotely denticulate, flat or slightly crispate, clathrate, dark brown or blackish with narrow paler margins, slightly lustrous, eventually reniform, clustered over rhizome apex and extending to base of petiole only; leaves 11-38 cm long, tufted or closely approximate; petiole 2–8 cm long, purplish or grayish brown, narrowly green-winged from near base, brittle with residual vascular shreds; blade 9–30 × 2–2.5 cm, 2-pinnate-pinnatifid, lanceolate, gradually narrowed to base, with apex shortly accuminate, nonconform; rachis green-winged adaxially, widening at pinna bases and laterally to ca. 1 mm or more overall below the tip, confluent with pinna-bases on the basiscopic side, rounded and purplish brown abaxially, becoming stramineous or green distally, with a few short glandular hairs near junctions with pinnae; pinnae 0.5–3 × 0.4–1.2 cm, the longest submedial, stalked to less than 1 mm long, 15–30 pairs, obliquely deltate to lanceolate in outline, with a distinct 2–4-lobed pinnule proximally on the acroscopic side and up to 6 uniform pairs of simple or shortly forked lobules; costae prominent adaxially, winged throughout; proximal pinnules 3–5 × 2–4 mm, subflabellate; terminal segment linear, ascending-lobulate; ultimate segments to ca. 4 × 1 mm, linear or oblong, obtuse or emarginate, herbaceous, glabrescent, scarcely discolorous; veinlets simple or 1-forked in the lobed segments, evident, ending in linear hydathodes well short of the margins; sori 0.5–3 mm, solitary or double and sometimes continous around the veinlet-tip; indusia 0.4–0.5 mm wide, hyaline, colorless or light brown with broadly rounded entire or shortly erose margin, gaping and pocketlike at maturity; spores ca. 42 × 30 mm, light brown, reniform-ellipsoid with a loose, unsculptured, sparsely rugose perispore.

DISTRIBUTION.— Locally frequent; found on the cliffs near the pools of the two large waterfalls near Wafer Bay. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 3337*; *Gómez 4536*; *Gómez 6561*; *Quesada 1060*; *Rojas 3777*; FTG: *Trusty 126*; *Trusty 390*; *Trusty 469*; *Trusty 490*; GH: *Svenson 339*; INB: *Quesada 1060*; *Rojas 3777*; NY: *Rojas 3777*; US: *Gómez 6561*; *Pittier 16235*; *Snodgrass and Heller 954*; *Stewart 228*; *Svenson 339*.

3. ***Asplenium delicatulum*** C. Presl var. ***cocosensis*** A. Rojas & Trusty, Brenesia 62: 3. 2004.

TYPE: *Rojas 3777* (holotype: INB; isotypes: CR, MO, NY, UC, US).

Differs from the type variety by its terrestrial or epiphytic habit (vs. epiphytic), more developed leaves (7–15 cm long vs 3.3.–9 cm) and is 1-pinnate-pinnatifid vs. 2-pinnate-pinnatifid. It is included in *A. delicatulum* for the size of the petiole, the form of the lamina, and the proliferous roots.

DISTRIBUTION.— Rare; found only near the waterfall in Iglesias Bay. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 6555*; *Gómez 6562* (not seen).

4. *Asplenium dissectum* Sw., Podr. 130. 1788

DISTRIBUTION.— Rare; found on Cerro Iglesias above 300 msl on Isla del Coco. Distributed throughout Mesoamerica to Brazil; including the Greater Antilles (except Puerto Rico).

SPECIMENS EXAMINED.— CR: *Rojas 3619*; FTG: *Trusty 183*; *Trusty 287*; INB: *Rojas 3619*.

BLECHNACEAE

5. *Blechnum occidentale* L., Sp. Pl. 1077. 1753.

DISTRIBUTION.— Rare; found near the Pittier River in Iglesias Bay on Isla del Coco. Distributed from the United States to northern Argentina and Chile; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Rojas 3776*; FTG: *Trusty 398*; INB: *Rojas 3776*.

CYATHEACEAE

1. Petioles and costae covered with short, fine hairs . . . . *Cyathea nesiotica*
1. Petioles and costae lacking hairs 2
    2. Nerves of pinnae bifid . . . . *Cyathea alfonsiana*
    2. Nerves of pinnae simple . . . . *Cyathea notabilis*

6. ***Cyathea alfonsiana*** L.D. Gómez, Amer. Fern J. 61:166. 1971. (Fig. 4)

TYPE: *Gómez 3349* (holotype: CR; isotypes: F, GH, US!).

Trunk up to 3 m tall, ca. 50 cm diameter, apex in petiole basally dense paleaceous, palea oblong-lanceolate, bicolored, middle reddish brown, margins cream-white; leaf scars obvious, stipes occasionally persistant, the upper side of the rachis canaliculate and pilose, lower side of rachis glabrous, spines sparse, small, apex nearly round; pneumatophores not obvious; primary costae pilose above, glabrous below, secondary costae pilose above, paleaceous below, paleas numerous nearly appressed lemon-yellow hyaline, membranes bulliform; petiolar hairs on upper side of rachis, costa, and costule multicellular, ferruginous, attenuate, thick, rigid, apex obviously curved; foliar lamina oblong-lanceolate, 1.4 m long, 80–90 cm wide, bipinnate-pinnatifid; basal pinnae abruptly reduced, apex pinnatisect; pinnae 12–15 (21) pairs, alternate to subalternate, 6–8 cm long, 2 cm wide, nearly divided to the costa, segments up to 14 pairs, alternate, oblong, basal pinnae somewhat constricted, 7–9 mm long, 4–5 mm wide, smooth lobate, apex subcrenulate, veins 7–8 pairs, 1–3 times furcate; sori inframedial, indusiate. Indusium squamiform, small.

DISTRIBUTION.— Common throughout the island from 50–630 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 4504*; *Gómez 4517*; *Gómez 18045*; *González 1164*; *González 1169*; *González 1208*; *Quesada 1016*; *Quesada 1089*; *Rojas 3635*; FTG: *Trusty 30*; *Trusty 152*; *Trusty 192*; *Trusty 322*; *Trusty 528*; *Trusty 529*; INB: *González 1164*; *González 1169*; *González 1208*; *Quesada 1016*; *Quesada 1089*; *Rojas 3635*; US: *Gómez 3349*; *Schmitt 129*; *Schmitt 130*; *Schmitt 131*.

7. ***Cyathea nesiotica*** (Maxon) Domin, Acta Bot. Bohem. 9:140. 1930.

TYPE: *Pittier 16229* (holotype: US!).

Stem to 8 m tall; petiole with hairs and spines, pale, the tricomes 1–3 mm long, the scales not visible, bicolored, clear brown with white borders, without dark denticulations; lamina 2-pinnate-pinnatifid, the apex uniformly attenuate, pinnatifid; pinnae sessile; pinnules 6–10 × 1.5–2.3 cm, sessile; final segments 20–28 pairs per pinnule, 2–3 mm wide, pinnatifid, the lobes less retuse than the apex; rachis, costa and costules with hairs, apparently without scales, the tricomes 1–3 mm, white, acicular; nerves 8–11 pairs per segment, 1–2-bifurcate, with sparse hairs; lamminar tissue between the nerves glabrous; sori inframedial; paraphyses inconspicuous, shorter than the sporangia, red-brown, turgid; indusium absent.

DISTRIBUTION.— Frequent along the rocky shoreline and in partially open habitats from 0–200 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 3317*; *Gómez 4507*; *Gómez 4519*; *Jiménez 3143*; *Quesada 1102*; *Rojas 3680*; FTG: *Trusty 164*; *Trusty 263*; *Trusty 491*; *Trusty 527*; INB: *Quesada 1102*; *Rojas 3680*; US: *Barclay 2208*; *Fisher s.n.*; *Gómez 3317*; *Gómez 4507*; *Jiménez 3143*; *Pittier 16229*; *Snodgrass and Heller 964*.

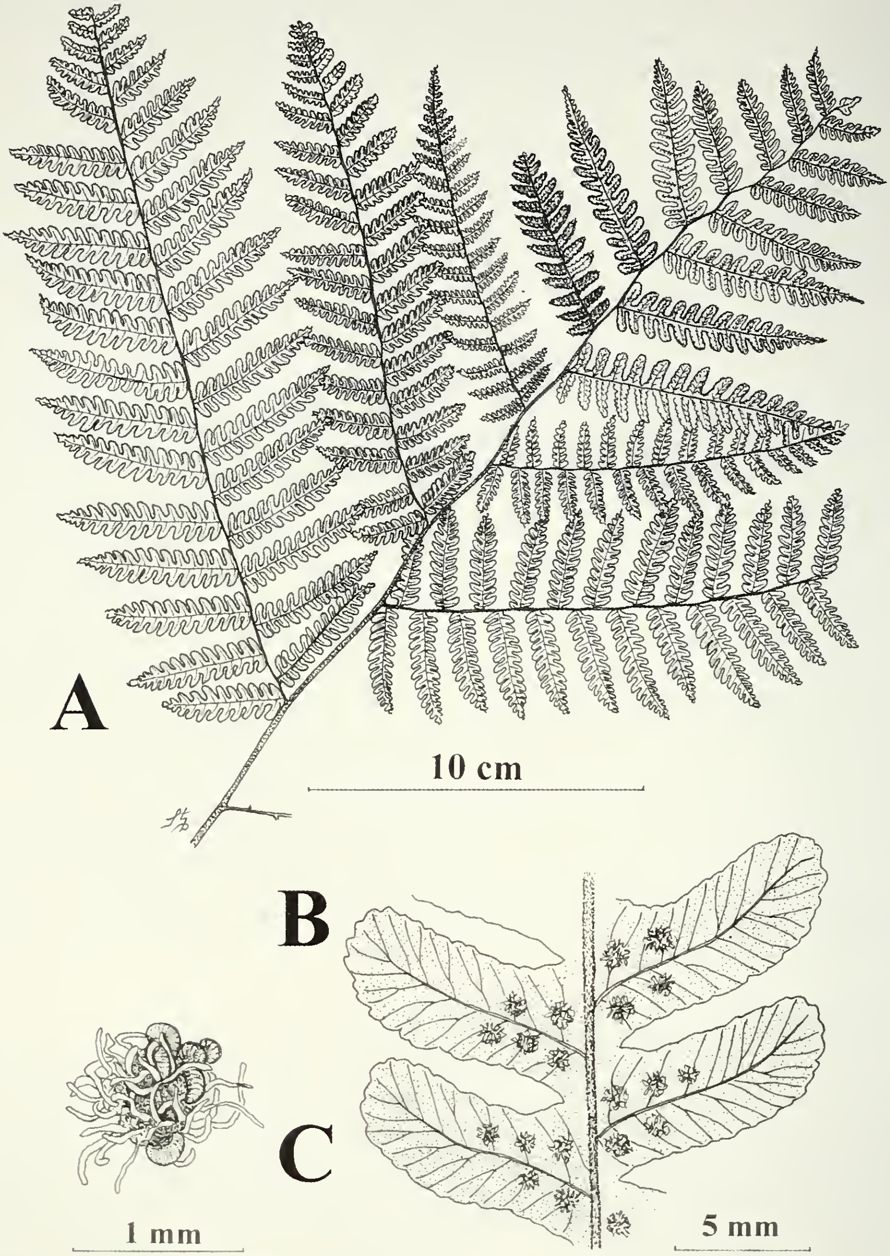

FIGURE 4. *Cyathea alfonsiana* (drawn from *Trusty 152*). A.Terminal portion of frond. B. Close up of pinna showing sori. C. Close up of sorus.

8. ***Cyathea notabilis*** Domin, Acta Bot. Bohem. 9:141. 1930.

TYPE: *Pittier 12355* (holotype: US!).

Stem to 2 m tall; petiole straw colored, with remote raised dots, scales 10–20 × 2.5–5 mm, lanceolate to ovate, bicolorous, light brown to yellowish with a lighter border; lamina 2-pinnate-pinnatifid, the apex pinnatifid; pinnae sessile or pedicellate, the pedicel up to 1 cm; pinnules 3–4 × 0.8–1 cm, sessile, the final segments 8–13 pairs per pinnule, 2–4 mm wide, serrate; rachis and costa with hairs, the trichomes 0.3–0.5 mm, cylindrical, erect; costules with scales, the scales golden or brown, bulliform, entire; nerves 5–7 per segment, not bifurcate, with hairs, the trichomes erect, white; the laminar tissue between the nerves glabrous; sori medial; paraphysis 3–4 times longer then the sporangia, very enlarged basally, not colored; indusium squamiform, small, adpressed to the lamina, sometimes obscured below the sporangia and paraphyses.

DISTRIBUTION.— Common throughout the island from 50–200 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Barclay s.n.*; *Dauphin 1118*; *Fournier 331*; *Gómez 3330*; *González 1163*; *Jiménez 3146*; *Klawe s.n.*; *Rojas 3590*; *Rojas 3774*; FTG: *Trusty 31*; *Trusty 153*; *Trusty 190*; *Trusty 191*; *Trusty 334*; *Trusty 476*; *Trusty 533*; GH: *Gómez 3330*; INB: *González 1163*; *Rojas 3590*; *Rojas 3774*; NY: *Fournier 331*; *Gómez 3330*; US: *Barclay s.n.*; *Gómez 3330*; *Klawe s.n.*; *Pittier 12355*; *Pittier 16228*; *Schmitt 128*.

DENNSTAEDTIACEAE

1. Sori 1-nerved 2
  2. Indusium simple, formed only by the recurved margin and the lamina; spores monolete . . . . *Hypolepis lellingeri*
  2. Indusium double, formed by an internal and external portion of the lamina; spores trilete 3
    3. Rhizome erect or decumbent, covered by the old petiole bases, squamous . . . . *Saccoloma elegans* var. *spinosa*
    3. Rhizome short to long creeping, not covered by the old bases of the petiole, hairy . . . . *Dennstaedtia dissecta*
1. Sori 2- to multinerved 4
  4. Ultimate segments diminished in size . . . . *Lindsaea lancea* var. *lancea*
  4. Ultimate segments not diminished . . . . *Pteridium feei*

9. *Dennstaedtia dissecta* (Sw.) T. Moore, Index Fil. 305. 1861.

DISTRIBUTION.— Found in closed canopy forest throughout Isla del Coco. Distributed from southern Mexico to Peru and southern Brazil; also found in the Greater Antilles and Trinidad.

SPECIMENS EXAMINED.— FTG: *Trusty 47*; *Trusty 123*; *Trusty 305*; *Trusty 409*; GH: *Svenson 343*; INB: *González 1190*; *Rojas 3650*; US: *Barclay 2207*; *Gómez 3357*; *Klawe 1540*; *Pittier 12358*; *Pittier 12358*; USJ: *Soto s.n.*

10. ***Hypolepis lellingeri*** A. Rojas, Rev. Biol. Trop. 49: 439–441. 2001. (Fig. 5)

TYPE: *A. Rojas 3617* (holotype: INB!; isotypes: CR, MO).

Terrestrial; rhizome 3–5 mm diameter, creeping, dark brown to black, densely covered by trichomes 1.0–2.5 mm long, dark brown to dark purple; leaves 120–160 cm long, with determinate growth, erect; petiole 40–70 cm long, 40 mm diameter, generally dark brown to black at the base, clear brown to pale yellow distally, densely spiney, with spines commonly 0.5–1 mm long (also small buds) with the apex black and in the form of a cup upon which grows a glandular hair, the trichomes 0.5–2.5 mm long, brown to pale yellow, dense and 0.2–0.5 mm long, not glandular, pale

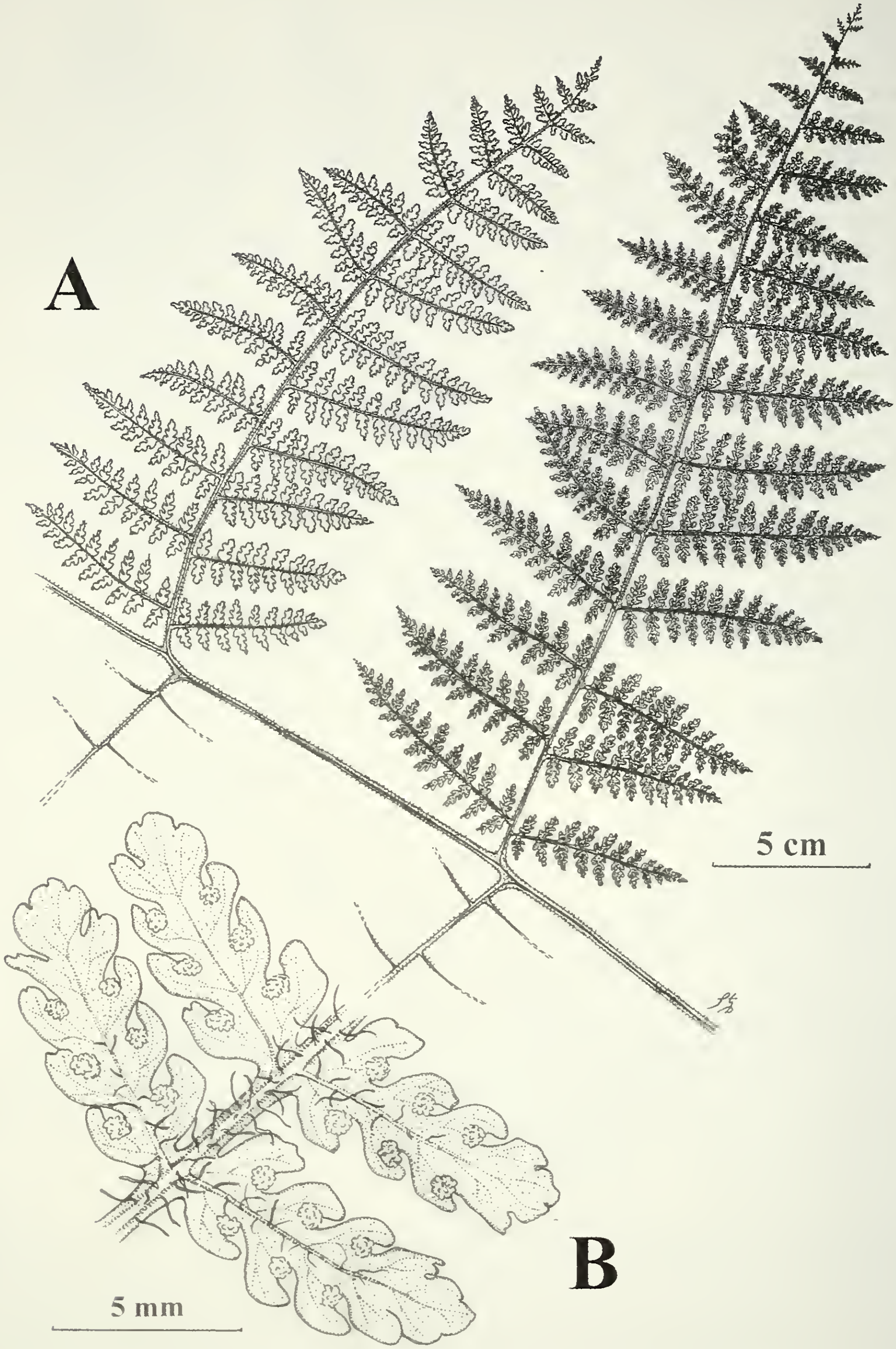

FIGURE 5. *Hypolepis lellingeri* (drawn from *Trusty 42*). A. Portion of frond showing two pinnae. B. Close up of pinnule showing marginal sori.

yellow, scarce, cateniform; lamina 75–90 × 80–100 cm, deltate, 3-pinnate-pinnatifid for the total extension; rachis brown yellow to pale green, erect (not flexuose), spiny-strigose, spines and buds as in the petiole but less dense and smaller towards the apex, pilose, the trichomes as on the petiole, dense, brown to pale yellow, cateniform; 10–15 pairs of pinnae, opposite to subopposite, the basal pinnae 30–45 × 20–30 cm, lanceolate; costae strigose, pale green to green yellow, densely pilose on both sides, the trichomes 0.5–1.0 (1.5) mm, glandular, cateniform, clear brown to pale green, mixed with smaller non-glandular trichomes; pinnules commonly 5–10 (15) × 1.5–2.5 (5.5) cm, lanceolate to linear, 10–20 pairs; costules pale yellow to yellow-green, winged (except in the basal pinnae), densely pilose on both surfaces, the trichomes 0.2–1.0 mm, glandular and eglandular, cateniform, pale; segments of the third order 0.7–1.0 (2.0) × 0.24–0.4 (0.8) cm, pinnate in the basal pinnae, not bordered adaxially by perpendicular and decurrent herbaceous wings; segments crenulate to pinnatified, pilose along the length of the central vein, the trichomes similar to those of the costules, cateniform, occasionally with glands at the tip (also on the secondary veins of the basal pinnae), glabrous on the laminar tissue, the margin glabrous; sori round, submarginal; indusium 0.2–0.5 mm wide, entire, scarious; paraphyses absent.

DISTRIBUTION.— Infrequent but locally common, in forest gaps and trail edges from 0–250 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Barclay 2201*; *Gómez 4514*; *Gómez 18090*; *González 1221*; *Rojas 3617*; FTG: *Trusty 250*; *Trusty 326*; *Trusty 42*; *Trusty 499*; INB: *González 1221*; *Quesada 1085*; *Rojas 3617*; US: *Barclay s.n.*; *Svenson 341.*

11. *Lindsaea lancea* var. *lancea* (L.) Bedd., Suppl. Ferns S. Ind. 6. 1876.

DISTRIBUTION.— Extremely common throughout Isla del Coco. Distributed from Mexico to Peru and Brazil; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Holdridge 5146*; *Jiménez 3158*; *Klawe s.n.*; *Lépiz 355*; *Quesada 1017*; *Soto s.n.*; FTG: *Trusty 149*; *Trusty 229*; *Trusty 302*; *Trusty 365*; GH: *Svenson 433*; INB: *Lépiz 355*; *Quesada 1017*; USJ: *Soto s.n.*

12. *Pteridium feei* (W. Schaffn. ex Fée) Faull, Contr. Arnold Arbor. 11:87. 1938.

DISTRIBUTION.— Rare; in Wafer Bay and along the trail to Chatham Bay on Isla del Coco. Distributed from central Mexico to Panama.

SPECIMENS EXAMINED.— INB: *Rojas 3685.*

13. ***Saccoloma elegans*** Kaulf. var. ***spinosa*** A. Rojas & Trusty, Bresenia 62:3. 2004.

TYPE: F. *Quesada 1082* (holotype: INB!; isotypes: CR, MO).

Differs from the continental material by the dark brown rhizome scales (vs. brown-yellow); the base of the stipe has dispersed spines vs. densely spiny; the pinnas are wider [1.7–2.5 (–3.0) cm wide vs. 2.5–4.5 cm] and the basal pinnae have the base widely cuneate to truncate (vs. narrowly cuneate) and are more irregularly shaped (the basiocopic side is more concave).

DISTRIBUTION.— Frequent, locally common from 0–250 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— INB: *González 1172*; *Quesada 1082*; *Rojas 3612*; USJ: *Soto s.n.*; FTG: *Trusty 150*; *Trusty 249*; *Trusty 325.*

DRYOPTERIDACEAE

1. Lamina with an apical pinna similar in form to the lateral pinnae; vascular bundles placed irregularly, not surrounded by a dark sclerified vein . . . . *Olfersia cervina*
1. Lamina with a pinnatifid apex; vascular bundles placed in concentric rings, each one surrounded by a dark sclerified vein 2

2. Sterile lamina 1-pinnate . . . . *Polybotrya polybotryoides*
2. Sterile lamina 2-pinnate pinnatifid . . . . *Polybotrya osmundacea*

14. *Olfersia cervina* (L.) Kunze, Flora 7:312. 1824.

DISTRIBUTION.— Common throughout the closed canopy forest of Isla del Coco. Distributed throughout the Neotropics.

SPECIMENS EXAMINED.— CR: *Dauphin 1129*; *Gómez 3351*; *Jiménez 3157*; *Lépiz 341*; *Sánchez 36*; *Quesada 1008*; *Rojas 3585*; *Rojas 3585*; *Valerio 1084*; FTG: Trusty 99; *Trusty 379*; *Trusty 487*; INB: *Lépiz 341*; *Quesada 1008*; *Rojas 3585.*

15. *Polybotrya osmundacea* Humb. & Bonpl. ex Willd., Sp. Pl. 5:99. 1810.

DISTRIBUTION.— Extremely common throughout the closed canopy forest of Isla del Coco. Distributed from Mesoamerica to Peru and northern Brazil; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Gómez 4535*; *Gómez 4537*; *Valerio 2225*; FTG: *Trusty 151*; *Trusty 246*; *Trusty 314*; *Trusty 503*; INB: *González 1188*; *Rojas 3591*; USJ: *Soto s.n.*

16. *Polybotrya polybotryoides* (Baker) H. Christ, Bull. Herb. Boissier ser. 2, 1:70. 1901

DISTRIBUTION.— Frequent in closed canopy forest of Isla del Coco from 0-400 msl. Distributed from southern Mexico to Ecuador and Peru.

SPECIMENS EXAMINED.— CR: *Gómez 4541B*; *Jiménez 3209*; FTG: *Trusty 488*; INB: *Rojas 3578*; *Rojas 3581*; *Rojas 3669* USJ: *Soto s.n.*

GLEICHENIACEAE

1. Rhizome and axillary buds hairy; sporangia 6-20 per sorus; nerves 2-4 bifurcate 2
    2. Accessory pinnae present in all of the bifurcations except terminal . *Dicranopteris flexuosa*
    2. Accessory pinnae absent . . . . *Dicranopteris pectinata*
1. Rhizome and axillary buds with scales; sporangia 2-5(6) per sorus; nerves simple or 1-bifurcate 3
    3. Second to the last segments 1.2-2.5(3) cm wide . . . . *Sticherus rubiginosus*
    3. Second to the last segments (2.5)4-9 cm wide 4
        4. Scales of the bud pale orange to brown-orange, ciliate, the cilia lax, pale . . . .*Sticherus palmatus*
        4. Scales of the bud brown to blackish, erose-ciliate to setose, the bristles erect, dark . . . .*Sticherus remotus*

17. *Dicranopteris flexuosa* (Schrad.) Underw., Bull. Torrey Bot. Club 34:254. 1907.

DISTRIBUTION.— Common in disturbed areas and landslides on Isla del Coco. Distributed from the southeastern Unites States and Mexico to Brazil and Paraguay; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Rojas 3627*; INB: *Rojas 3627.*

18. *Dicranopteris pectinata* (Willd.) Underw., Bull. Torrey Bot. Club 34:260. 1907.

DISTRIBUTION.— Extremely common in disturbed areas and landslides throughout Isla del Coco. Distributed from Southern Mexico to Peru and Brazil; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Gómez 4523*; *Rojas 3622*; FTG: *Trusty 155*; *Trusty 266*; GH: *Holdridge 5152*; *Svenson 332*; INB: *Rojas 3622.*

19. *Sticherus palmatus* (W. Schaffn. ex E. Fourn.) Copel., Gen. Fil. (Ann. Cryptog. Phytopathol.) 5:28. 1947.

DISTRIBUTION.— Common in disturbed areas and landslides above 400 msl on Isla del Coco. Distributed from Mexico to Panama; also found in Jamaica and Cuba.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 268.*

20. *Sticherus remotus* (Kaulf.) Chrysler, Amer. J. Bot. 31:483. 1944.

DISTRIBUTION.— Locally common near Cerro Pelón on Isla del Coco. Distributed from Costa Rica to Brazil; also found in Cuba and Trinidad.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Rojas 3605*; FTG: *Trusty 294*; INB: *Rojas 3605.*

21. *Sticherus rubiginosus* (Mett.) Nakai, Bull. Natl. Sci. Mus. 29:28. 1950.

DISTRIBUTION.— Locally common along the trail from Wafer Bay to Chatham Bay on Isla del Coco. Distributed from Costa Rica to Peru and Bolivia; also found in Trinidad.

SPECIMENS EXAMINED.— CR: *Rojas 3628.*

GRAMMITIDACEAE

1. Lamina simple, entire, with the border sclerified, black or brown-black. . . *Grammitis bryophila*
1. Lamina simple, lobate or pinnate, without a sclerified border, black not brown-black. 2
    2. Hydathodes absent or inconspicuous. 3
        3. Lamina simple, differentiated into sterile and fertile parts, the sterile leaves and often the sterile portion of the fertile leaves serrate-dentate . . . . *Cochlidium serrulatum*
        3. Lamina simple or pinnate, not sub-dimorphic nor differentiated into sterile and fertile portions . . . . *Ceradenia pruinosa*
    2. Hydathodes present adaxially at the termination of the nerves. 4
        4. Nerves of the pinnae simple or with a single acroscopic nervule; lamina less than 1 cm wide, narrowly linear . . . . *Micropolypodium taenifolium*
        4. Nerves of the pinnae with more than one ramification; lamina more than 1 cm wide, linear to narrowly ovate . . . . *Terpsichore cocosensis*

22. *Ceradenia pruinosa* (Morton) L.E. Bishop, Amer. Fern J. 78:5. 1988.

DISTRIBUTION.— Rare on Isla del Coco, collected on Cerro Pelón. Distributed from southern Mexico to southern Venezuela and Brazil.

SPECIMENS EXAMINED.— INB: *Rojas 3602*; *Rojas 3718.*

23. *Cochlidium serrulatum* (Sw.) L.E.Bishop, Amer. Fern. J. 68:80. 1978.

DISTRIBUTION.— Infrequent epiphyte on *Sacoglottis holdridgei* above 300 msl on Isla del Coco. Distributed from southern Mexico to Peru and Brazil; also found in the Antilles, Africa, Madagascar, Maritius and Amsterdam Island.

SPECIMENS EXAMINED.— CR: *Gómez 3340*; *Klawe s.n.*; *Lellinger and de la Sota 773*; FTG: *Trusty 129*; *Trusty 171*; *Trusty 269*; *Trusty 377*; GH: *Holdridge 5138*; *Howell 10189*; INB: *Quesada 1030*; *Rojas 3600.*

24. *Grammitis bryophila* (Maxon) F. Seym., Phytologia 31:172. 1975.

DISTRIBUTION.— Infrequent; found in the cloud forest above 400 msl on Isla del Coco. Distributed from Costa Rica to Peru and Bolivia.

SPECIMENS EXAMINED.— FTG: *Trusty 267*; *Trusty 378*; INB: *Rojas 3604.*

25. *Micropolypodium taenifolium* (Jenman) A. R. Sm., Novon 2:423. 1992.

Distribution.— Rare; found in the cloud forest above 400 msl on Isla del Coco. Distributed from southern Mexico to Ecuador and the Guianas; also found in the Antilles and Trinidad.

Specimens examined.— FTG: *Trusty 248*; *Trusty 291*; INB: *Quesada 1078.1*; *Rojas 3603*.

26. ***Terpsichore cocosensis*** A. Rojas, Brenesia 45-46:47-49. 1996.

Type: *Lépiz 337* (holotype: INB!; isotypes: CR, MO, UC).

Epiphyte; rhizome 1–2 mm in diameter, short creeping to ascendent; rhizome scales absent; fronds from 25–45 (50) cm long, 1.3–2.0 cm wide, linear, decumbent; stipe 1–3 cm long, 0.5 mm diameter, pilose, the hairs 1–3 mm long, gold-red; lamina 6–10 mm long, 3–5 mm wide, 1-pinnate, linear lanceolate, pinnae basifixed and a little reduced at the base, apex acute to obtuse; lamina hairs on both surfaces, the abaxial face 0.5–1 mm long, golden, hairs of the adaxial face, rachis and costa 2–4 mm long, the margin of the pinnae stellate basally, golden-red; sori rounded, on the apical half of the pinnae, 3–7 sori per pinna; paraphyses absent; sporangia setose.

Distribution.— Common in the closed canopy forest from 100–400 msl. Endemic to Isla del Coco.

Specimens examined.— CR: *Fournier 332*; *Rojas 3616*; FTG: *Trusty 55*; Trusty *143*; *Trusty 407*; *Trusty 537*; GH: *Holdridge 5136*; *Pittier 12353*; INB: *Lépiz 337*; *Rojas 3616*; NY: *Fournier 332*; *Rojas 3616*.

HYMENOPHYLLACEAE

1. Indusium 2-valved; receptacle generally not prolonged more than the border of the indusium . 2
    2. Lamina glabrous . . . . *Hymenophyllum polyanthos*
    2. Lamina pelose, the trichomes on the nerves, the margins and the laminar tissue . . . . *Hymenophyllum cocosense*
1. Indusium tubular, sometimes two-labiate but not 2-valvate; receptacle prolonged more than the border of the indusium 3
    3. Nervation anadromous, pinnate; lamina 1–4 pinnate-pinnatifid 4
        4. Rhizome long creeping with leaves distant; plants epiphytic or rupicolous 5
            5. Rhizome 1–2 mm in diameter or more; petiole winged . . . .*Trichomanes collariatum* var. *alvaradoi*
            5. Rhizome 0.1–1 mm in diameter; petiole not winged . . . .*Trichomanes capillaceum* var. *cocos*
        4. Rhizome decumbent to erect with fasciculate leaves; plants terrestrial 6
            6. Petiole and rachis not winged . . . .*Trichomanes rigidum*
            6. Petiole and rachis winged . . . .*Trichomanes elegans*
    3. Nervation catadromous or flabellate; lamina simple to 1-pinnate pinnatifid 7
        7. Margins of the lamina with paired suborbicular scales . .*Trichomanes membranaceum*
        7. Margins of the lamina glabrous or with bifurcate or stellate trichomes 8
            8. Leaves 0.2–3 cm; rhizome creeping 9
                9. Leaves with a false submarginal nerve, the margins glabrous; indusium immersed, the margins without dark cells . . . . *Trichomanes kapplerianum*
                9. Leaves without a false sugmarginal nerve, the margins with bifurcate or stellate trichomes; indusium exerted or immersed, the margins of the indusium generally with one or more rows of dark cells . . . . *Trichomanes angustifrons*
            8. Leaves 4–70 cm; rhizome decumbent to erect, sometimes creeping 10

10. False nerves absent. . . . . *Trichomanes galeotii*
10. False nerves present 11
  11. Rhizome erect or suberect; leaves fasciculate, not adherent to the substrate; false nerves abundant, perpendicular to the true nerves
  . . . . *Trichomanes pinnatum*
  11. Rhizome creeping; leaves distant, adhering to the substrate; false nerves scarce, near the margins and parallel to the true nerves
  . . . . *Trichomanes ankersii*

27. ***Hymenophyllum cocosense*** A. Rojas, Brenesia 45–46:37. 1996.

Type: F. *Quesada 1015* (holotype: INB!; isotypes: CR, MO, NY).

Epiphyte or terrestrial; rhizome creeping, 0.3–0.4 mm in diameter; rhizome hairs ca. 0.5 mm long; fronds 5.5–11 cm long, determinant growth, erect to slightly pendulous, rigid, commonly separated by (0.8) 1.5–3.5 cm; stipe 0.6–4.3 cm long, 0.3–0.4 mm in diameter, not winged, rachis linear to a little flexuose, slightly winged to not winged, the wing from 0.1 (0.2) mm, with stellate hairs with 3–4 rays; lamina 3.5–7.5 cm long, 1.5–2 cm wide, pinnate-pinnatisect, elliptic to linear-elliptic, with the basal pinnae reduced and the apex acute on fertile fronds and obtuse in sterile fronds; pinnae 0.3–1.5 cm long, flat, with hairs on the margins and the veins, the hairs ca. 0.2 mm long, bifurcate to stellate with 3–4 rays (rarely simple or twice-bifurcate); segments commonly (2) 3–5 mm long and 0.5–1 (1.5) wide, 1–4 pairs per pinna, simple or bifurcate; indusium rounded, 0.6–0.8 mm in diameter, inbedded in the lamina, slightly wider than the segment, found on the terminal half of the frond, 1–12 per pinna; receptacle not exerted.

Distribution.— Common from 100–630 msl throughout the island. Endemic to Isla del Coco.

Specimens examined.— CR: *Gómez 18063*; *Gómez 18068*; *Quesada 1015*; *Rojas 3601*; FTG: *Trusty 180*; *Trusty 270*; *Trusty 274*; *Trusty 328*; *Trusty 376*; *Trusty 411*; GH: *Holdridge 5139*; INB: *Quesada 1015*; *Rojas 3601*; US: *Holdridge 5139*; *Stewart 253*; USJ: *Dauphin 1167.*

28. *Hymenophyllum polyanthos* (Sw.) Sw., J. Bot. (Schrader) 1800(2):102. 1801.

Distribution.— Extremely common throughout the closed canopy forest on Isla del Coco. Distributed from central Mexico to Peru, Bolivia and southern Brazil; also found in the Antilles, East Asia and Africa.

Specimens examined.— CR: *Gómez 3329*; *Gómez 4553*; *Gómez 18058*; *Gómez 18067*; *Gómez 18070*; *Gómez 18094; Klawe s.n.*; FTG: *Trusty 137*; *Trusty 54*; *Trusty 179*; *Trusty 330*; GH: *Holdridge 5137*; *Svenson 345*; INB: *Rojas 3615*; US: *Gómez 3329*; *Holdridge 5137*; *Stewart 252*; *Svenson 345.*

29. *Trichomanes angustifrons* (Fée) Wess. Boer, Fl. Netherl. Antilles 1(Pterid.):17. 1962.

Distribution.—Frequently found in Wafer Bay and along the trail from Wafer Bay to Cerro Iglesias on Isla del Coco. Distributed from Mesoamerica to Peru, Brazil and Paraguay; also found in the Antilles.

Specimens examined.— CR: *Gómez 4545*; *Gómez 6565*; *Gómez 18062*; *Rojas 3679*; *Rojas 3719*; INB: *Rojas 3679*; *Rojas 3719*; US: *Gómez 6565*; *Klawe s.n.*

30. *Trichomanes ankersii* C. Parker ex Hook. & Grev., Icon. Filic. 2:t.201. 1831.

Distribution.—Infrequently collected along the trail from Wafer Bay to Cerro Iglesias on Isla del Coco. Distributed from Mesoamerica to Peru, Bolivia and Brazil.

Specimens examined.— CR: *Holdridge 5143*; *Rojas 3664*; FTG: *Trusty 327*; INB: *Rojas 3664*; US: *Klawe s.n.*

31. ***Trichomanes capillaceum*** L. var. ***cocos*** (H. Christ) L.D. Gómez, Brenesia 6:37. 1975.
Type: *Pittier 12390* (holotype: US!).

Differs from the type variety by the length of the ultimate segments 10–25 mm long (vs. 2–5 mm).

Distribution.— Common epiphyte on *Cyathea* sp. throughout the island. Endemic to Isla del Coco.

Specimens examined.— CR: *Dressler 4462*; *Gómez 3214A*; *Gómez 18069*; *Jiménez 3164*; *Klawe s.n.*; *Rojas 3636*; FTG*: Trusty 144*; *Trusty 293*; GH: *Holdridge 5135*; INB: *Rojas 3636*; US: *Foster 4165*; *Gómez 3314A*; *Pittier 12393*; *Svenson 349*; *Svenson 349*; USJ: *Soto s.n.*

32. ***Trichomanes collariatum*** Bosch var. ***alvaradoi*** A. Rojas, Lankesteriana 4(2):145–147. f.2. 2004.

Differs from var. *collariatum* by the shorter >20 cm (vs. 40 cm) and ovate (vs. elliptical) fronds.

Distribution.— Common near stream edges and on wet rocks from 0–300 msl. Endemic to Isla del Coco.

Specimens examined.— CR: *Gómez 3318A*; *Gómez 3345A*; *Gómez 4543*; *Gómez 4547*; *Gómez 6557*; *Gómez 18093*; *Jiménez 3208*; *Sánchez 29*; *Quesada 1116*; *Valerio 30417*; FTG: *Trusty 225*; *Trusty 299*; *Trusty 517*; INB: *Rojas 3651*; US: *Fricke s.n.*; *Gómez 3318A*; *Gómez 3345A*; *Klawe s.n.*; *Stewart 233*; *Svenson 338*.

33. *Trichomanes elegans* Rich., Actes Soc. Hist. Nat. Paris 1:114. 1792.

Distribution.— Frequent; found near small streams from 0–300 msl on Isla del Coco. Distributed from Mesoamerica to Peru, Bolivia and Brazil; also found in the Lesser Antilles and Trinidad.

Specimens examined.— CR: *Gómez 3319*; *Gómez 3328*; *Gómez 4527*; *Gómez 4527A*; *Gómez 18038*; *Gómez 18073*; *Klawe s.n.*; *Lépiz 331*; *Quesada 1010*; *Soto s.n.*; FTG: *Trusty 473*; INB: *González 1198*; *Lépiz 331*; *Quesada 1010*; *Rojas 3610*; US: *Barclay 2206*; *Gómez 3319*; USJ: *Lépiz 331*; *Soto s.n.*

34. *Trichomanes galeottii* E. Fourn., Bull. Soc. Bot. France 15 :147. 1868.

Distribution.— Common in closed canopy forest from 0–450 msl on Isla del Coco. Distributed from southern Mexico to western Columbia; also found in Cuba.

Specimens examined.— CR: *Gómez 4548*; *Gómez 18060*; *Gómez 18071*; *Gómez 18080*; *Jiménez 3162*; *Klawe s.n.*; *Lépiz 338*; *Quesada 1014*; *Rojas 3662*; FTG: *Trusty 34*; *Trusty 105*; *Trusty 227*; *Trusty 292*; *Trusty 323*; *Trusty 368*; *Trusty 372*; INB: *Lépiz 338*; *Quesada 1014*; *Rojas 3559*; *Rojas 3662*; US: *Foster 4161*; *Gómez 3343*; *Jiménez s.n.*; *Klawe s.n.*; USJ: *Dauphin 1166*; *Soto s.n.*

35. *Trichomanes kapplerianum* J. W. Sturm in Mart., Fl. Bras. 1(2):276. 1859.

Distribution.— Frequent on wet boulders near the Chatham River in Chatham Bay on Isla del Coco. Distributed from Costa Rica to Peru and Brazil; also found in the Lesser Antilles.

Specimens examined.— CR: *Gómez 6566*; *Gómez 6568*; *Gómez 18098*; FTG: *Trusty 474*; INB: *Rojas 3663*; US: *Svenson 344*.

36. *Trichomanes membranaceum* L., Sp. Pl. 1097. 1753.

Distribution.— Infrequent on Isla del Coco; found near Iglesias Bay. Distributed from southern Mexico, to Peru and Boliva; also found in the Antilles and Trinidad.

Specimens examined.— CR: *Gómez 3332*; *Gómez 4541A*; *Gómez 4546*; *Rojas 3775*; INB: *Rojas 3775*; US: *Gómez 3332*; USJ: *Dauphin 1012*; *Dauphin 1138*.

37. *Trichomanes pinnatum* Hedw., Fil. Gen. Sp. t.4, f. 1. 1799.

Distribution.— Infrequent on Isla del Coco; found between Iglesias Bay and Cerro Tesoro Escondido. Distributed from Mexico to Peru, Bolivia and southern Brazil; also found in the Antilles and Trinidad.

Specimens examined.— CR: *Quesada 1123*; INB: *Quesada 1123*; *Rojas 3773*; FTG: *Trusty 289*; *Trusty 369*; *Trusty 381*; *Trusty 382*; INB: *Rojas 3611*; US: *Gómez 6567*.

38. *Trichomanes rigidum* Sw., Podr. 137. 1788.

Distribution.— Infrequent in closed canopy forest above 250 msl on Isla del Coco. Distributed from southern Mexico to Peru, Boliva and southern Brazil; also found in the Antilles and the Old World tropics.

Specimens examined.—CR: *Gómez 6567*; INB: *Rojas 3611*; FTG: *Trusty 289*; *Trusty 369*; *Trusty 381*; *Trusty 382*.

LOMARIOPSIDACEAE

1. Sterile leaves with linear-lanceolate scales generally enrolled to appear to be subulate trichomes, at least on the petiole, but in general on all of the leaf 2
    2. Lamina 10–22 cm wide, widely oblong, the apex obtuse; nerves reticulate . . . . *Elaphoglossum crinitum*
    2. Lamina 2–10 cm wide, lanceolate, narrowlly elliptic to oblanceolate, the apex acuminate to rounded; nerves free . . . . *Elaphoglossum auripilum* var. *longipilosum*
1. Sterile leaves densely squamose to nearly glabrous; scales diverse but not subulate;. 3
    3. Leaves pendent. 4
        4. Scales of the lamina limited to the margins and the costa, the rest of the laminar surface without scales . . . .*Elaphoglossum decoratum*
        4. Scales of the lamina not limited to the margins and the costa, with some types of scales in one or both surfaces of the lamina . . . .*Elaphoglossum cocosense*
    3. Leaves erect 5
        5. Leaves separated by 20–30 mm along rhizome . . . .*Elaphoglossum reptans*
        5. Leaves separated by 3–7 mm along rhizome . . . .*Elaphoglossum incognitum*

39. *Elaphoglossum auripilum* H. Christ var. *longipilosum* Atehortúa, Novon 2:369. 1992.

Distribution.— Common throughout Isla del Coco. This variety is also found in Costa Rica.

Specimens examined.— CR: *Gómez 18042*; *Lépiz 351*; FTG: *Trusty 120*; *Trusty 185*; *Trusty 264*; *Trusty 385*; *Trusty 477*; INB: *González 1196*; *González 1209*; *Lépiz 351*; *Quesada 1087*; *Quesada 1125*; *Rojas 3620*.

40. ***Elaphoglossum cocosense*** Mickel, Novon 2:372. 1992. (Fig. 6)

Type: *Pittier 12359* (holotype: US).

Epiphytic; rhizome ca. 5 mm diameter, compact; rhizome scales 7–12 mm long, linear-lanceolate, orange-tan to blackish, thin, margin with sparse, very long (to 1 mm long) hair-teeth; leaves 37–65 cm long, approximate; phyllopodia present; petiole $\frac{1}{10}$–$\frac{1}{5}$ the sterile leaf length, orange-tan, densely covered with orange-tan scales 4–8 mm long, sparsely long-hair-toothed; sterile lamina 36–50 cm long, (2.4) 3.0–4.0 cm wide, narrowly oblanceolate, chartaceous, base gradually long-attenuate, apex cuspidate; veins obscure, ca. 1 mm apart, at ca. 70° angle to costa; hydathodes lack-

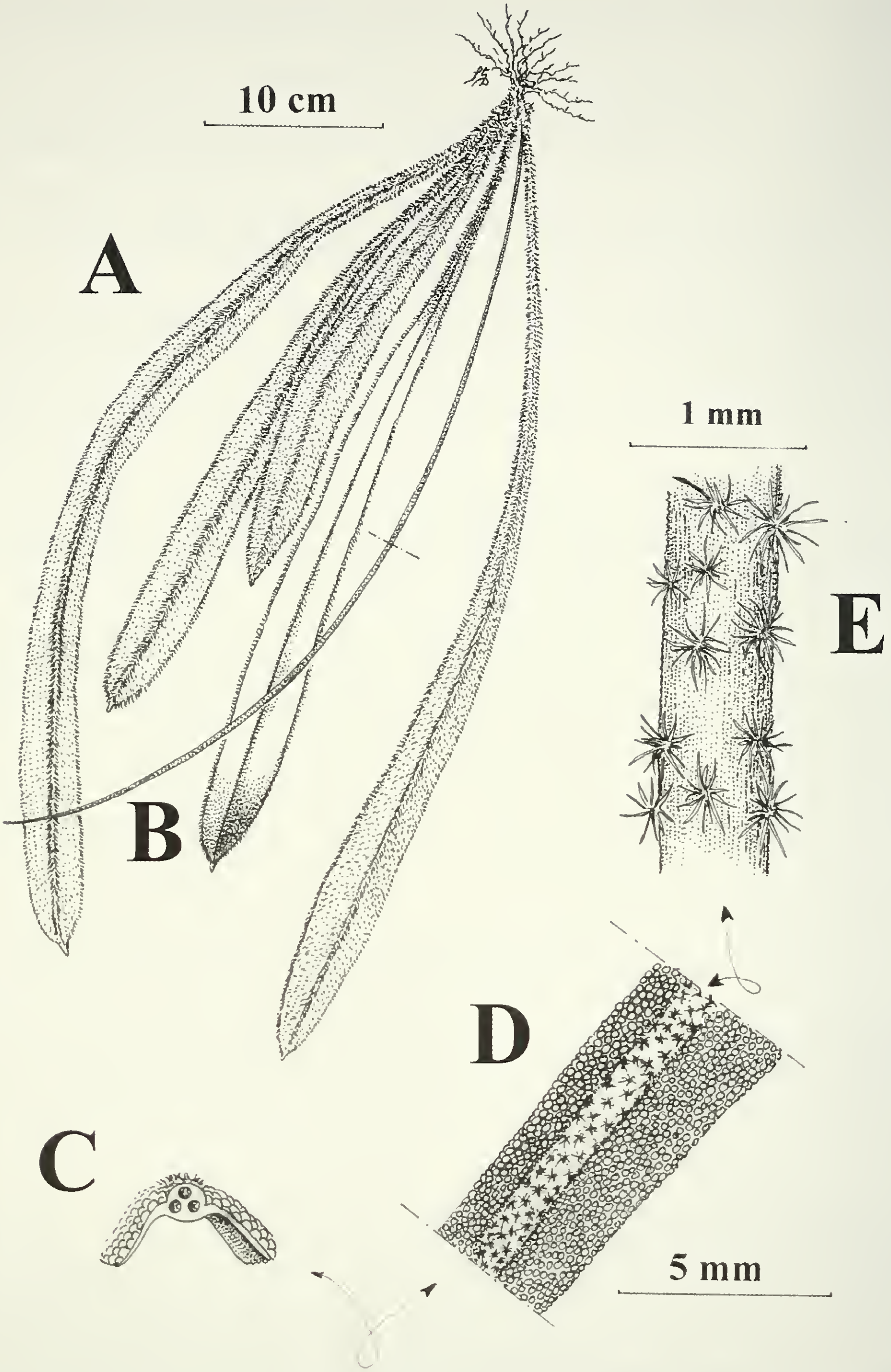

FIGURE 6. *Elaphoglossum cocosensis* (drawn from *Trusty 67*). A. Habit of plant showing sterile and fertile fronds. B. Fertile frond. C. Cross-section of fertile frond showing vein traces. D. Abaxial view of a portion of a fertile frond showing midvein. E. Close up of midvein showing stellate hairs.

ing; lamina scales abaxially 3–6 mm long, abundant, imbricate, linear-lanceolate, long hair-toothed, adaxially mostly 2–3 mm long, to glabrescent; fertile frond much longer and thinner than sterile fronds, 37–45 cm × 3–7 mm, petiole 5–8.5 cm long, equal or longer than those of sterile fronds, fertile lamina linear, the base long attenuate, the apex acuminate, scales of the costa and abaxial side of lamina small, brown, ciliate, 0.2–0.4 mm long, intersporangial scales absent.

Distribution.— Frequent in the closed canopy forest from 200–630 msl. Endemic to Isla del Coco.

Specimens examined.— CR: *Gómez 3327*; *Gómez 3362*; *Gómez 4502*; *Rojas 3580*; *Rojas 3642*; *Soto s.n.*; *Valerio s.n.*; FTG: *Trusty 67*; *Trusty 109*; *Trusty 535*; INB: *Rojas 3580*; *Rojas 3642*; NY: *Gómez 3362*; *Rojas 3580*; *Rojas 3642*; USJ: *Soto s.n.*

41. *Elaphoglossum crinitum* (L.) H. Christ, Nue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36(1):102. 1899.

Distribution.— Frequent in the closed canopy forest from 200–630 msl on Isla del Coco. Distributed from Mesoamerica to Venezuela and Guiana; also found in the Antilles and Trinidad.

Specimens examined.— CR: *Gómez 4508*; *Lépiz 343*; *Quesada 1001*; *Rojas 3608*; FTG: *Trusty 386*; *Trusty 513*; *Trusty 70*; INB: *Lépiz 343*; *Quesada 1001*; *Rojas 3608.*

42. *Elaphoglossum decoratum* (Kunze) T. Moore, Index Fil. 8. 1857.

Distribution.— Rare; in the cloud forest above 400 msl of Isla del Coco. Distributed from Mesoamerica to Peru and Bolivia; also found in the Antilles.

Specimens examined.— CR: *Quesada 1002*; FTG: *Trusty 281*; *Trusty 374*; INB: *Quesada 1002*; *Rojas 3609.*

43. ***Elaphoglossum incognitum*** A. Rojas, Rev. Biol. Trop. 51:7. 2004.

Type: *Rojas 3613* (holotype: INB; isotypes: CR, MO, NY, UC, US).

Epiphytic or terrestrial; rhizomes 3–5 mm diameter, short-creeping; rhizome scales 7–12 × 0.8–1.0 mm, linear-lanceolate, orange-yellowish, marginally entire to occasionally long ciliate; phyllopodia present, 10–15 mm long; fronds 27–43 cm long, 2–7 mm wide, stipes ⅒–⅕ (¼) of frond length; stipe scales 3–7 × 0.7–1.0 mm, ovate lanceolate to linear-lanceolate, orange-yellowish, marginally long-ciliate; blade scales 0.1–0.3 mm wide, stellate, orange-yellowish, dispersed, marginally long-ciliate; present only on abaxial surface; veins evident, 1–2-forked, 1.0–1.5 mm apart, diverging at 75–85° from costa; hydathodes absent; fertile fronds smaller than sterile, petiole 7–10 cm long, equal or longer than those of sterile fronds, petiole scales sparse, linear 3–5 mm long, lamina linear-lanceolate, base attenuate, apex acuminate, completely glabrous, intersporangial scales absent.

Distribution.— Frequent in closed canopy forest from 100–300 msl. Endemic to Isla del Coco.

Specimens examined.— FTG: *Trusty 139*; *Trusty 295*; *Trusty 324*; *Trusty 462*; *Trusty 463.*

44. ***Elaphoglossum reptans*** A. Rojas, Rev. Biol. Trop. 51:13. 2004.

Type: *Rojas 3621* (holotype: INB; isotypes: CR, F, K, MEXU, MO, NY, UC, US).

Terrestrial, rhizomes 1.5–2.0 mm diameter, long-creeping; rhizome scales 1–1.5 × 0.3–0.6 mm, ovate to ovate-lanceolate, blackish, deciduous, marginally entire to denticulate; phyllpodia present, 15–30 mm wide; fronds 23–27 cm long, 20–30 mm wide; stipes ca. ⅓ of frond length; basal stipe scales 2–3.5 × 0.4–0.8 mm, linear-lanceolate, brown with paler margin, marginally entire to denticulate, dense; medial stipe scales 3–5 × 1.0–1.5 mm, lanceolate, bicolorous with brown central line and yellowish to pale brown margin, dispersed, marginally entire to dentate; blades 16–18 × 5–6.5 cm, ovate to elliptic-lanceolate, coriaceous, basally cuneate, apically obtuse to rounded; blade scales 0.1–0.3 mm wide, stellate, orange-yellowish, dispersed, marginally long-ciliate, present only on abaxial surface; veins evident, simple to 1-forked, 1.0–1.5 mm apart, diverging at 70–85° from costa; hydathodes absent; fertile fronds 22.5 cm long; stipes ca. ½ of frond length; fertile blades 1–.5 × 2.6 cm, elliptic-lanceolate, basally obtuse, apically obtuse; intersporangial scales absent.

DISTRIBUTION.— Infrequent but locally common in cloud forest above 400 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 117*; *Trusty 273*; *Trusty 383*; *Trusty 558*; INB: *Quesada 1009*.

LYCOPODIACEAE

1. Plants terrestrial . . . . *Lycopodium cernuum*
1. Plants epiphytic 2
    2. Plants delicate; longest leaves less than 7 mm, acicular, less than 0.7 mm wide; stems generally less than 1 mm wide at the base (excluding the leaves) . . . . *Huperzia brachiata*
    2. Plants robust; leaves of the basal divisions longer than 8 mm; leaves 1–5 mm wide, linear subulate to lanceolate; stems 0.3–5 mm wide . . . . *Huperzia pittieri*

45. ***Huperzia brachiata*** (Maxon) Holub, Folia Geobot. Phytotax. 20:71. 1985.

TYPE: *Agassiz s.n.* (holotype: US!).

Pendent epiphyte, 15–40 cm long, 3 to 5 times dichotomous, the branches 6–9 mm wide (including the leaves) spreading, widely divaricate (60°–90°), the tips (if fertile) almost continuously sporangiate for a distance of 2–6 cm. Stems very slender, 0.5 mm in diameter, wholly concealed by the appressed imbricate bases of the very numerous closely set leaves; leaves 5–6 × 0.3–0.5 mm, in 4 (5) ranks, not twisted at the base, all alike slightly ascending, somewhat secund, membranous, 5–6 mm long, acicular to linear-subulate from a linear-lanceolate base ca. 0.5 mm wide, subcapillary at the tips, entire, the upper surface usually somewhate concave in drying, often deeply so near the base, the basal portion of the leaf sometimes plicate, the apical portion often irregularly tortuous; costa percurrent, relatively prominent, readily visible by transmitted light, distinctly elevated below, the base of the leaf strongly carinate; sporophylls scarce, like the sterile leaves, not reduced in size; sporangia reniform to obtusely cordate-reniform, ca. 0.8 mm broad, the sinus very deep.

DISTRIBUTION.— Rare; in closed canopy forest. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 6558*; *Gómez 6560*; *Rojas 3720*; INB: *Rojas 3720*; US: *Agassiz s.n.*

46. ***Huperzia pittieri*** (H. Christ) Holub, Folia Geobot. Phytotax. 20:76. 1985. (Fig. 7)

TYPE: *Pittier 12357* (holotype: US!).

Epiphyte; plants up to 60 cm long, flaccidly pendulous, sparsely ramified; branches 10–20 mm wide (including the leaves), nearly the same width throughout the plant, often scarcely attenuate, homophyllous or nearly homophyllous; stems ca. 1 mm wide (excluding the leaves); leaves 10–15 × 1–1.5 mm, in irregular verticillations alternating 3 or 4, linear-lanceolate to linear, spreading to ascendent, the base generally torcid, the apex prolongedly filiform; leaves of the distal portions equal or shorter; nerves slender, sporangia ca. 1 mm wide, yellow.

DISTRIBUTION.— Frequent in the closed canopy forest above 200 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Dauphin 1088*; *Dressler 4457*; *Gómez 6564*; *Gómez 6931*; *Gómez 6945*; *Gómez 18047*; *Klawe s.n.*; *Rojas 3618*; *Sánchez 9*; *Valerio 1592*; *Valerio 2227*; *Valerio 31048*; *Valerio 31049*; FTG: *Trusty 102*; *Trusty 142*; *Trusty 181*; *Trusty 182*; *Trusty 245*;

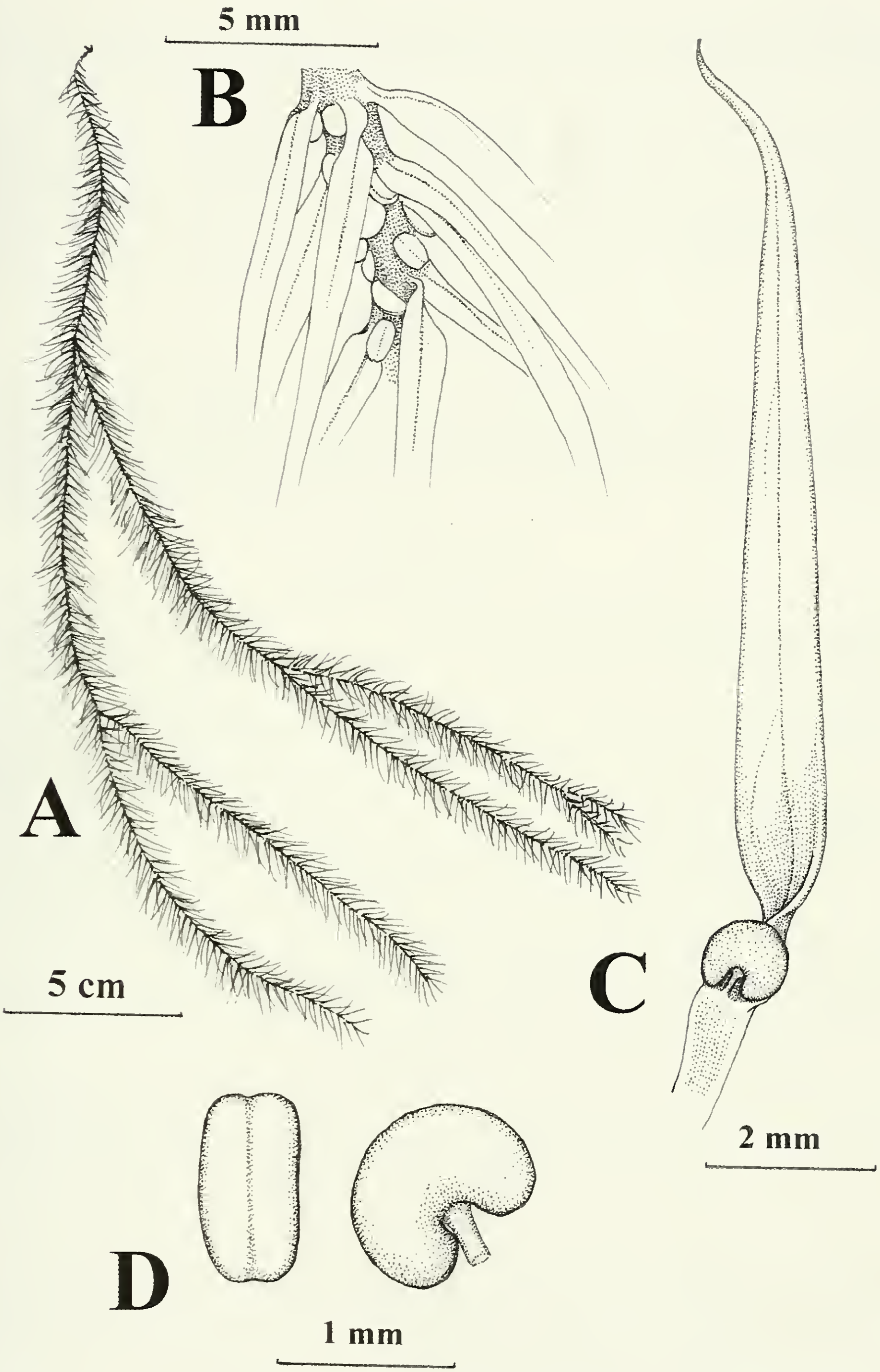

FIGURE 7. *Huperzia pittieri* (drawn from *Trusty 245*). A. Habit of plant showing bifurcating stems. B. Close up of fertile portion of stem showing sporophylls and sporangia. C. Close up of sporophyll and associated sporangium. D. Ventral and lateral view of sporangium.

Trusty 460; *Trusty 480*; *Trusty 498*; *Trusty 545*; GH: *Holdridge 5144*; *Holdridge 5154*; *Howell 10179*; *Snodgrass and Heller 971*; *Svenson 324*; INB: *Rojas 3618*; US: *Barclay 2211*; *Pittier 12357*; *Svenson s.n.*; *Valerio 1592*; *Valerio 2227*.

47. *Lycopodiella cernua* (L.) Pic. Serm., Webbia 23:166. 1968.

DISTRIBUTION.— Locally common in the cloud forest above 350 msl on Isla del Coco. Distributed from the United States to Peru, Brazil and Paraguay; also found in the Antilles, Trinidad and the Old World tropics.

SPECIMENS EXAMINED.— FTG: *Trusty 58*; INB: *González 1176*; *Lépiz 334*; *Quesada 1074*; *Rojas 3626*.

MARATTIACEAE

48. *Danaea nodosa* (L.) Sm., Mém. Acad. Roy. Sci. (Turin) 5. 1790–1791.

DISTRIBUTION.— Common along river and stream edges throughout Isla del Coco. Distributed from southern Mexico to Peru and southern Brazil; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— FTG: *Trusty 165*; *Trusty 475*; INB: *Rojas 3644*; USJ: *Soto s.n.*

OLEANDRACEAE

1. Lamina simple, entire; petiole articulate to the phyllopodia; rhizome long creeping; sori along the medial or proximal portion of the nerves . . . . *Oleandra articulata*
1. Lamina 1-pinnate; petiole continuous with the rhizome; rhizome short creeping; sori at the apex of the nerves 2
    2. Base of the mature petioles with adpressed dark brown scales with narrow pale margins . . . . *Nephrolepis multiflora*
    2. Base of the mature petioles often with a few lax scales, reddish to clear brown, or without scales 3
        3. Pinnae of the distal half of the the frond equilateral . . . .*Nephrolepis biserrata*
        3. Pinnae of the distal half of the frond not equilateral . . . .*Nephrolepis rivularis*

49. *Nephrolepis biserrata* (Sw.) Schott, Gen. Fil. t. 3. 1834.

DISTRIBUTION.— Extremely common in full sun and disturbed areas along trails on Isla del Coco. Distributed from Florida and southern Mexico to Peru, Bolivia and southern Brazil; also found in the Antilles, Trinidad and the Old World tropics.

SPECIMENS EXAMINED.— CR: *Quesada 1093*; *Quesada 1094*: *Quesada 1112*: *Rojas 3599*; *Soto s.n.*; FTG: *Trusty 275*; *Trusty 41*; INB: *González 1145*; *González 1192*; *Quesada 1093*: *Quesada 1094*; *Quesada 1112*; *Rojas 3599*; US: *Agassiz s.n.*; *Foster 4152*; *Gómez 3352*; *Klawe 1498*; *Klawe 1555*; *Pittier 12361*; *Schmitt 133*; *Stewart 234*; *Stewart 235*; *Stewart 236*; USJ: *Soto s.n.*

50. *Nephrolepis multiflora* (Roxb.) F. M. Jarret ex C. V. Morton. Contr. U.S. Natl. Herb. 38:309. 1974.

Distribution.—Infrequent on Isla del Coco; found in Wafer Bay and along the trail from Wafer to Chatham Bay. Distributed from Florida and southern Mexico to Peru, Bolivia and Brazil; also found in the Antilles, Bahamas and the Old World tropics.

SPECIMENS EXAMINED.— CR: *Rojas 3687*; INB: *Rojas 3687*; USJ: *Soto s.n.*

51. *Nephrolepis rivularis* (Vahl) Mett. Ex Krug, Bot. Jarhrb. Syst. 24:122. 1897.

DISTRIBUTION.— Found only in the cloud forest areas above 400 msl on Isla del Coco.

Distributed from southern Mexico to Peru, Bolivia and Brazil; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Rojas 3607*; FTG: *Trusty 318*; *Trusty 366*; INB: *Rojas 3607.*

52. *Oleandra articulata* (Sw.) C. Presl, Tent. Pterid. 78. 1836.

DISTRIBUTION.— Common epiphyte from 0–400 msl on Isla del Coco. Distributed from southern Mexico to Peru, Bolivia and Brazil; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Gómez 3346*; *Holdridge 5132*; *Jiménez 3147*; *Rojas 3579*; FTG: *Trusty 45*; *Trusty 118*; *Trusty 319*; *Trusty 549*; GH: *Gómez 3346*; *Holdridge 5132*; INB: *Quesada 1003*; *Rojas 3579*; US: *Foster 4154*; *Jiménez 3147*; *Schmitt 132*; *Stewart 239*; USJ: *Soto s.n.*

OPHIOGLOSSACEAE

53. *Cheiroglossa palmata* (L.) C. Presl, Suppl. Tent. Pterid. 57. 1845.

DISTRIBUTION.— Rare; found in closed canopy forest above 200 msl on Isla del Coco. Distributed from Florida and southern Mexico to Peru, Boliva and Brazil; also found in the Antilles, Cuba, Vietnam, the Democratic Republic of the Congo, Madagascar, Réunion and the Seychelles.

SPECIMENS EXAMINED.— FTG: *Trusty 216.*

POLYPODIACEAE

1. Lamina simple, entire 2
    2. Fronds 25–140 cm long . . . . *Campyloneurum phyllitidis*
    2. Fronds 6–20 cm long 3
        3. Scales of the rhizome clathrate . . . . *Pleopeltis astrolepis*
        3. Scales of the rhizome not clathrate . . . . *Microgramma nitida*
1. Lamina pinnatisect to 3-pinnate 4
    4. Laminar tissue scaley abaxially . . . . *Polypodium dissimile*
    4. Laminar tissue without scales abaxially . . . . *Phlebodium pseudoaureum*

54. *Campyloneurum phyllitidis* (L.) C. Presl, Tent. Pterid. 190. 1836.

DISTRIBUTION.— Common throughout Isla del Coco. Distributed from southern Florida and Mexico to Argentina; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— FTG: *Trusty 48*; *Trusty 441*; *Trusty 565*; GH: *Svenson 311*; INB: *González 1148*; *González 1193*; *Rojas 3597*; USJ: *Soto s.n.*

55. *Microgramma nitida* (J. Sm. & Hook.) A. R. Sm., Proc. Calif. Acad. Sci. ser. 4, 40:230. 1975.

DISTRIBUTION.— Rare on Isla del Coco; only one location known near the ranger station in Chatham Bay. Distributed from Mexico to Panama; also found in Jamaica and Barbados.

SPECIMENS EXAMINED.— FTG: *Trusty 443.*

56. *Phlebodium pseudoaureum* (Cav.) Lellinger, Amer. Fern J. 77:101. 1987.

DISTRIBUTION.— Common throughout Isla del Coco from 0–400 msl. Distributed from Florida and Mexico to Argentina; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Gómez 3355*; *Lépiz 342*; FTG: *Trusty 121*; *Trusty 532*; GH: *Holdridge 5157*; *Pittier 16236*; *Snodgrass and Heller 969*; INB: *Lépiz 342*; *Quesada 1004*; *Rojas 3595*; US: *Holdridge 5157*; *Pittier 16236*; *Snodgrass and Heller 969*; USJ: *Soto s.n.*

57. *Pleopeltis astrolepis* (Liebm.) E. Fourn., Mexic. Pl. 1:87. 1872.

Distribution.— Infrequent on Isla del Coco; usually found growing together with bryophyte species. Distributed from southern Mexico to Peru, Bolivia and Brazil; also found in the Antilles.

Specimens examined.— FTG: *Trusty 145*; *Trusty 170*; GH: *Snodgrass and Heller 958*; *Svenson 321*; INB: *Rojas 3665*; *Rojas 3780*; US: *Agassiz s.n.*; *Gómez 3363*; *Svenson 321.*

58. *Polypodium dissimile* L., Syst. Nat. ed. 10, 2:1325. 1759.

Distribution.— Frequent at mid elevations (200–400 msl) on Isla del Coco. Distributed from southern Mexico to Venezuela and Ecuador; also found in the Antilles and Trinidad.

Specimens examined.— CR: *Gómez 3341*; *Gómez 3364*; *Gómez 18044*; *Lépiz 353*; FTG: *Trusty 127*; *Trusty 136*; *Trusty 497*; INB: *Lépiz 353*; *Rojas 3614.*

PSILOTACEAE

59. *Psilotum nudum* (L.) P. Beauv., Podr. Aethéogam. 106, 112. 1805.

Distribution.— Rare on Isla del Coco; found near the ranger station in Wafer Bay. Distributed from the southern United States and Mexico to Argentina; also found in the Antilles and the Old World tropics and subtropics.

Specimens examined.— CR: *Dauphin 1180*; *Rojas 3596*; FTG: *Trusty 76*; INB: *Dauphin 1180*; *Quesada 1024*; *Rojas 3596*; USJ: *Dauphin 1180.*

PTERIDACEAE

1. Margins of the fertile segments not recurved, generally herbaceous like the rest of the lamina, sori acrostichoid 2
    2. Nerves free . . . . *Acrostichum aureum*
    2. Nerves areolate . . . . *Pityrogramma calomelanos*
1. Margins of the fertile segments recurved, generally scarious, sori not acrostichoid 3
    3. Sportangia above the reflexed margins of the lamina (false indusium); petiole black to brown, generally shiny, terete . . . . *Adiantum latifolium*
    3. Sporangia under the reflexed margins on the lamina, petiole variously colored, shiny or opaque, terete or sulcate 4
        4. Basal pinnae 1-pinnate pinnatifid past the basal acroscopic pinnula . . .*Pteris tripartita*
        4. Basal pinnae pinnatifid past the basal basiscopic pinnula . . . .*Pteris biaurita*

60. *Acrostichum aureum* L., Sp. Pl. 1069. 1753.

Distribution.— Common along the coasts of Isla del Coco. Distributed from southern Florida and Mexico to Ecuador, Brazil and Paraguay; also found in the Antilles, Trinidad and the Old World tropics.

Specimens examined.— FTG: *Trusty 125*; INB: *González 1195*; *Rojas 3652.*

61. *Adiantum latifolium* Lam., Encycl. 1:43. 1783.

Distribution.— Infrequent; found in closed canopy forest of Isla del Coco from 0–250 msl. Distributed from Mexico to Peru. Brazil and Paraguay; also found in the Antilles and Trinidad.

Specimens examined.— BKL: *Stewart 226*; CR: *González 1202*; FTG: *Trusty 40*; INB: *González 1202*; *Lépiz 371*; *Quesada 1104*; *Rojas 3582.*

62. *Pityrogramma calomelanos* (L.) Link, Handbuch 3:20. 1833.

Distribution.— Frequent in full sun between 0–100 msl on Isla del Coco. Distributed from southern Florida and Mexico to Argentina; also found in the Antilles and widely introduced in the Old World tropics.

SPECIMENS EXAMINED.— FTG: *Trusty 255*; *Trusty 395*; INB: *González 1216*; *Rojas 3648*; USJ: *Soto s.n.*

63. *Pteris biaurita* L., Sp. Pl. 1076. 1753.

DISTRIBUTION.— Infrequent; found in canopy gaps or near streams 0–200 msl on Isla del Coco. Distributed from southern Mexico to Peru and southern Brazil; also found in the Antilles and the Old World tropics.

SPECIMENS EXAMINED.— FTG: *Trusty 159*; *Trusty 337*; INB: *Quesada 1097*; *Rojas 3594*; US: *Jiménez 3175*; *Klawe 1542*.

64. *Pteris tripartita* Sw., J. Bot. (Schrader) 1800(2):67. 1801.

DISTRIBUTION.— Rare on Isla del Coco; collected along the trail from Wafer Bay to Cerro Iglesias. Distributed from Costa Rica to Peru and the Guianas; also found in the Antilles and the Old World tropics.

SPECIMENS EXAMINED.— INB: *Rojas 3645*.

SELAGINELLACEAE

1. Stems not articulate; leaves entire or merely short-toothed, not ciliate. . . . *Selaginella flagellata*
1. Stems articulate; leaves conspicuously ciliate (at least the base of the lateral leaves) . . . . *Selaginella horizontalis*

65. *Selaginella flagellata* Spring, Bull. Acad. Roy. Sci. Bruxelles 10(1):228. 1843.

DISTRIBUTION.— Common in disturbed areas of Isla del Coco near Wafer Bay and along trails. Distributed from Mexico to Peru, Bolivia and Brazil; also found in Trinidad and Tobago.

SPECIMENS EXAMINED.— FTG: *Trusty 85*; GH: *Snodgrass and Heller 942*; INB: *Rojas 3588*.

66. Selaginella horizontalis (C. Presl) Spring, Bull. Acad. Roy. Sci. Bruxelles 10(1):226. 1843.

DISTRIBUTION.— Common in disturbed areas of Isla del Coco near Wafer Bay and along trails. Distributed from Costa Rica to Peru and Venezuela.

SPECIMENS EXAMINED.— FTG: *Trusty 169*; *Trusty 458*; INB: *Rojas 3586*; USJ: *Gómez-Laurito s.n.*; *Soto s.n.*

TECTARIACEAE

1. Nerves anastomosing 2
    2. Pinnae or lobes pinnatifid or pinnate for the majority of their length. . . . *Tectaria mexicana*
    2. Pinnae or lobes entire or undulate for the majority of their length . . . . *Tectaria incisa*
1. Nerves free 3
    3. Trichomes of the adaxial face of the rachis, costae and costulae generally more than 0.5 mm, whitish, with acute apices . . . . *Megalastrum subincisum*
    3. Trichomes of the adaxial face of the rachis, costae and costulae generally less then 0.5 mm, reddish, with obtuse apices. . . . . *Ctenitis sloanei*

67. *Ctenitis sloanei* (Poepp. ex Spreng.) C.V. Morton, Amer. Fern J. 59:66. 1969.

DISTRIBUTION.— Infrequent on Isla del Coco; collected along the trail from Wafer Bay to Cerro Iglesias. Distributed from Florida and southern Mexico to Peru and Venezuela; also found in the Antilles and Trinidad.

Specimens examined.— CR: *Gómez 3356*; *Gómez 3360*; *Gómez 4516*; *Rojas 3646*; INB: *Rojas 3646*.

68. *Megalastrum subincisum* (Willd.) A.R. Sm. & R.C. Moran, Amer. Fern. J. 77:129. 1987.

Distribution.— Infrequent in closed canopy forest on Isla del Coco between 200–400 msl. Distributed from southern Mexico to Peru and Bolivia; also found in the Antilles.

Specimens examined.— CR: *Rojas 3649*; FTG: *Trusty 146*; INB: *Rojas 3649*.

69. *Tectaria incisa* Cav., Descr. Pl. 249. 1802.

Distribution.— Infrequent; found in open areas from 0–150 msl on Isla del Coco. Distributed from southern Florida and southern Mexico to northern Argentina; also found in the Antilles.

Specimens examined.— CR: *Holdridge 5156*; FTG: *Trusty 256*; *Trusty 315*; INB: *González 1150*; *González 1217*; *Rojas 3647*; US: *Carrasquilla 360*; *Gómez 3358*; USJ: *Soto s.n.*

70. *Tectaria mexicana* (Fée) C. V. Morton, Amer. Fern J. 56:133. 1966.

Distribution.— Rare; found near the Genio River in Wafer Bay and in Iglesias Bay on Isla del Coco. Distributed from southwestern Mexico to western Ecuador.

Specimens examined.— CR: *Rojas 3782*; GH: *Gómez 3336*; *Gómez 4529*; INB: Rojas *3782*; US: *Gómez 3336*.

Thelypteridaceae

1. Lamina simple to 1-pinnate pinnatifid; petiole adaxially sulcate. 2
1. Lamina 2-pinnate-pinnatifid; petiole not sulcate adaxially . . . . *Macrothelypteris torresiana*
2. At least some of the trichomes of the rachis and costae bifurcate. . . . . . *Thelypteris calypso*
2. All trichomes acicular, unicellular or mulitcellular, rarely absent 3
3. Lamina pinnate, the pinnae entire or with undulate or serrate margins; nerves united, forming areolas . . . .*Thelypteris serrata*
3. Lamina pinnate-pinnatifid, the pinnae generally incised half their width or more; nerves free, joining the sinus 4
4. Lamina without proximally reduced pinnae, or if reduced pinnae present, then the nerves uniting below the sinus 5
5. Bacilliar or squamiform aerophores present at the base of the pinnae 6
5. Aerophores absent at the base of the pinnae . . . . *Thelypteris hispidula*
6. Nerves joining the margin above the sinus; nerves 25 pairs or more per segment . . . . *Thelypteris decussata* var. *costaricensis*
6. Nerves joining at or below the sinus, up to 22 pairs of nerves per segment . . . . *Thelypteris leprieurii* var. *subcostalis*
4. Lamina with one or more various pair of proximally reduced pinnae, nerves free, joining the margin above the sinus 7
7. Laminar tissue with numerous trichomes on both surfaces. . *Thelypteris cocos*
7. Laminar tissue glabrous . . . . *Thelypteris balbisii*

71. *Macrothelypteris torresiana* (Gaudich.) Ching, Acta Phytotax. Sin. 8:310. 1963.

Distribution.— Common along the beach edges on Isla del Coco. Distributed from the southeastern United States to northern Argentina; also found the Antilles, Asia, Africa and the Pacific Islands.

Remarks.— First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 262*; *Trusty 298*.

72. *Thelypteris balbisii* (Spreng.) Ching, Bull. Fan Mem. Inst. Biol., Bot. 10:250. 1941.

DISTRIBUTION.— Infrequently found in closed forest throughout Isla del Coco. Distributed from Mexico to Panama; also found in the West Indies.

SPECIMENS EXAMINED.— CR: *Gómez 18072*; FTG: *Trusty 240*; *Trusty 402*; US: *Gómez 3359*; *Klawe 1506*.

73. ***Thelypteris calypso*** L. D. Gómez, Brenesia 8:98. 1976.

TYPE: *Gómez 4534* (holotype: UC; isotype: CR!).

Rhizome suberect; leaves 40–50 cm; petiole 15–25 cm × 2–3 mm; lamina 20–25 cm, the apex confluent and pinnatifid; bulbils with small plants in the axils of the distal pinnae; pinnae 8–12 pairs, up to 10 × 2.3 cm, incised ca. 3/4 of their width; segments 3–4 mm wide, rounded at the apex; nerves 7–9 pairs per segment, the proximal pair of adjacent segments connecting at the margin of the sinus; indumentum of the underside of trichomes, 0.1–0.2 mm long, bifurcate, stipitate, stellate, above the axils and the nerves, also with trichomes up to 0.5 mm, acicular, dispersed, the margins of the segments with trichomes 0.3–0.4 mm, acicular, simple, the laminar tissue without trichomes, frequently ferruginous; indumentum of the back absent, the laminar tissue glabrous; sori indusiate; indusium persistent, with trichomes 0.2–0.2 mm, bifurcate; sporangia glabrous.

DISTRIBUTION.— Infrequent in open areas and trail edges from 0–100 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 4534*; FTG: *Trusty 193*.

74. ***Thelypteris cocos*** A.R. Sm. & Lellinger, Proc. Biol. Soc. Wash. 98:918. 1985. (Fig. 8)

TYPE: Klawe *1480a* (holotype: US).

Rhizome suberect, the caudex 1.5–2 cm diameter; leaves 20–60 cm; petiole up to 4 cm × 2–3 mm, proximally with sparse ciliate or glabrous scales, brown; lamina up to 55 cm, proximally with 5–10 pairs of gradually reduced pinnae, the inferior pairs 2–5 mm, ariculiform; pinnae up to 30 pairs, up to 7 x1.4 cm, the majority opposite or subopposite, incised up to 1 mm from the costa; aerophores absent; segments 2–3 mm wide; nerves 5–9 pairs per segment; indumentum of the back of trichomes 0.2–1 mm, dense, also of the rachis and costa, the laminar tissue with numerous trichomes 0.1–0.2 mm on both surfaces, also with sessile orange glands on the back; sori indusiate; indusium 0.2–0.4 mm diameter, persistent, with trichomes ca. 0.2 mm and some with sessile glands.

DISTRIBUTION.— Common throughout the island from 0–400 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 18089*; *Gómez s.n.*; *González 1199*; FTG: *Trusty 46*; *Trusty 303*; *Trusty 347*; *Trusty 375*; *Trusty 392*; *Trusty 530*; *Trusty 559*; INB: *González 1199*; *Rojas 3593*; *Rojas 3681*; US: *Fisher s.n.*

75. *Thelypteris decussata* (L.) Proctor var. *costaricensis* A.R. Sm., Univ. Calif. Publ. Bot. 76:16. 1980.

DISTRIBUTION.— Extremely common in closed canopy forest of Isla del Coco from 0–400 msl. This variety is also found in Costa Rica.

SPECIMENS EXAMINED.— CR: *Foster 4158*; *Foster 4158*; *Gómez 4513*; *Gómez 18092*; *Holdridge 5149*; *Rojas 3577*; *Soto s.n.*; *Valerio 38490*; FTG: *Trusty 98*; *Trusty 320*; INB: *González 1189*; *Rojas 3577*; US: *Klawe s.n.*; *Stewart 232*; USJ: *Soto s.n.*

76. *Thelypteris hispidula* (Decne.) C.F. Reed, Phytologia 17:283. 1968.

DISTRIBUTION.— Frequent along trail between Chatham and Wafer Bays of Isla del Coco. Distributed from the southeastern United States to northern Argentina; also found in the Antilles and the Old World tropics and subtropics.

SPECIMENS EXAMINED.— CR: *Gómez 3350; Gómez 4533*; *Gómez 4538*; *Gómez 4539*; *Gómez*

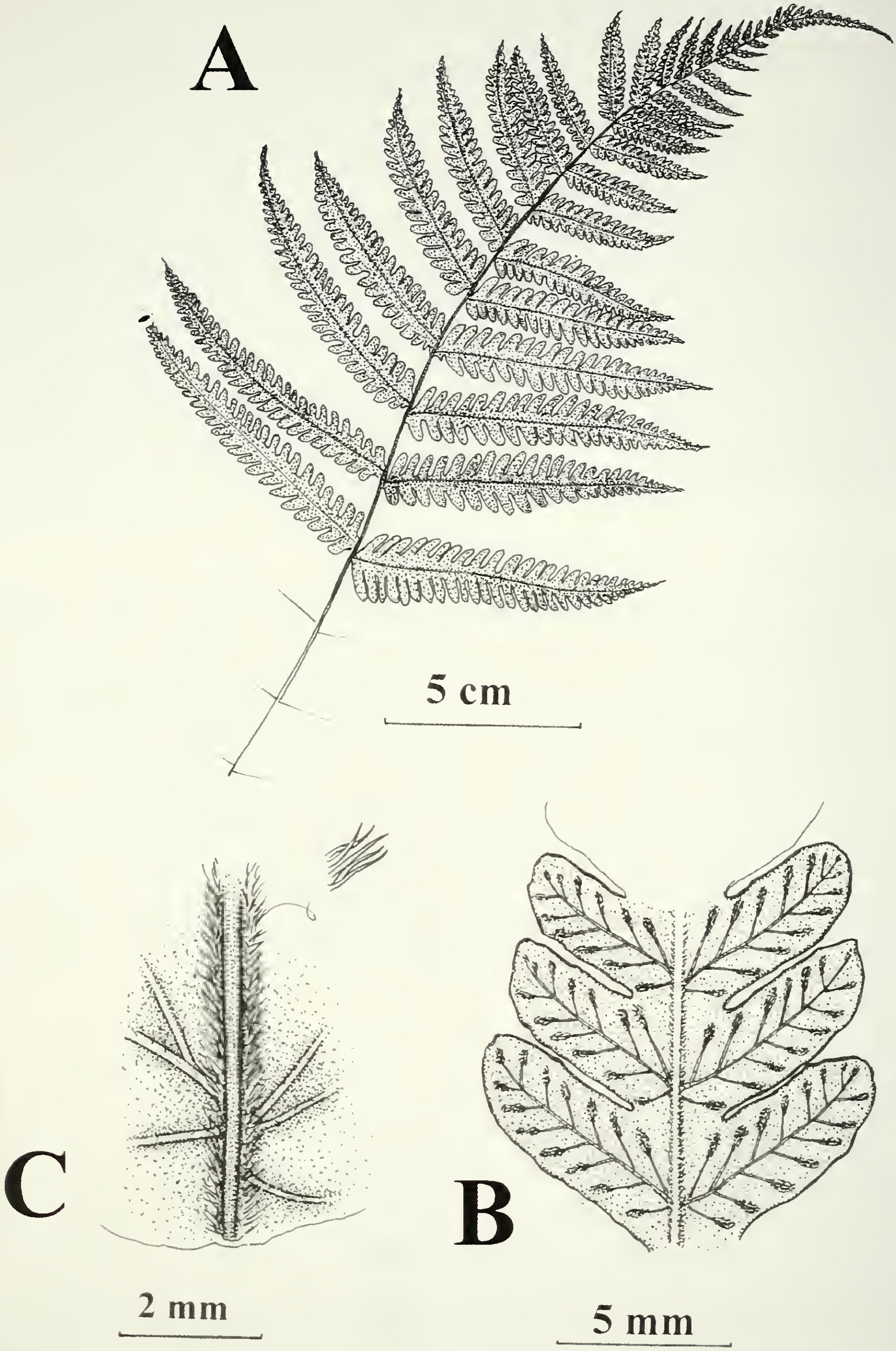

FIGURE 8. *Thelypteris cocos* (drawn from *Trusty 347*). A. Terminal section of frond. B. Close up of pinna showing immature sori. C. Close up of pinna venation showing dense hairs.

18096; *Gómez 18097*; *Klawe s.n.*; *Rojas 3583*; FTG: *Trusty 49*; *Trusty 258*; *Trusty 308*; *Trusty 524*; *Trusty 554*; INB: *Rojas 3583*; US: *Gómez 3361.*

77. *Thelypteris leprieurii* (Hook.) R.M. Tryon var. *subcostalis* A.R. Sm., Univ. Calif. Publ. Bot. 76:26. 1980.

DISTRIBUTION.— Infrequent on Isla del Coco; collected near the Genio River in Wafer Bay and along the trail between Wafer and Chatham Bays on Isla del Coco. Distributed from Guatemala and Belize to Columbia.

SPECIMENS EXAMINED.— CR: *Gómez 18053*; *González 1201*; *Rojas 3592*; INB: *González 1201*; *Rojas 3592.*

78. *Thelypteris serrata* (Cav.) Alston, Bull. Misc. Inform. Kew. 1932:309. 1932.

DISTRIBUTION.— Infrequent; found in full sun along trail edges on trail between Chatham and Wafer Bays on Isla del Coco. Distributed from Florida and southern Mexico to northern Argentina; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Jiménez 3201*; FTG: *Trusty 523*; INB: *González 1218*; *Rojas 3686.*

VITTARIACEAE

1. Leaves elliptical; sori subacrostichoid. . . . . *Anetium citrifolium*
1. Leaves linear; sori linear or elongate. . . . . *Vittaria graminifolia*

79. *Anetium citrifolium* (L.) Splitg., Tijdschr. Natuuri. Gesch. Physiol. 7:395. 1840.

DISTRIBUTION.— Rare on Isla del Coco, found near the waterfall in Wafer Bay. Distributed from Guatemala and Belize to Peru, Bolivia and Brazil; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED. — GH: *Gómez 3331.*

80. *Vittaria graminifolia* Kaulf., Enum. Filic. 192. 1824.

DISTRIBUTION.— Common in closed canopy forest on Isla del Coco from 0–300 msl. Distributed from Mexico to Peru, Uruguay and southern Brazil; also found in the Antilles and Trinidad.

SPECIMENS EXAMINED.— CR: *Soto s.n.; FTG: Trusty 97; Trusty 279; Trusty 489; INB: Quesada 1029; Rojas 3643; US: Foster 4118; Gómez 3342; Klawe 1479; Klawe s.n.; Svenson 330.*

WOODSIACEAE

81. *Diplazium lechleri* (Mett.) T. Moore, Index Fil. 141. 1859.

DISTRIBUTION.— Extremely common in the cloud forest above 400 msl on Isla del Coco. Distributed from Costa Rica to Peru and Brazil.

SPECIMENS EXAMINED.— FTG: *Trusty 72; INB: Lépiz 336; Quesada 1007; Rojas 3634.*

Key to the Families of Spermatophytes on Isla del Coco

1. Plants vines climbing by tendrils 2
    2. Tendrils simple . . . . Passifloraceae
    2. Tendrils branched . . . . Cucurbitaceae
1. Plants without tendrils. 3
    3. Plants parasitic or saprophytic 4

4. Plants attached to branches of living shrubs or trees . . . . .Loranthaceae
4. Plants not attached to branches of living shrubs or trees 5
5. Plants leafless, composed of a single yellow flower . . . . .Gentianaceae
5. Plants with bract-like leaves, composed of a panicle of cream-white flowers . . . . .Burmanniaceae
3. Plants not parasitic or saprophytic. 6
6. Inflorescence a dense head subtended by an involucre; sepals dry scales, bristles or absent, white to brown . . . . .Asteraceae
6. Inflorescence various, but not an involucrate head; sepals usually green 7
7. Plants conspicuously woody; lianas, shrubs or trees 8
8. Leaves compound . . . . GROUP A
8. Leaves simple. 9
9. Leaves opposite . . . . GROUP B
9. Leaves alternate . . . . GROUP C
7. Plants herbaceous or with a slightly woody base 10
10. Plants vining . . . . GROUP D
10. Plants not vining. 11
11. Flowers lacking petals, or complete perianth 12
12. Flowers in compact spikes; leaves pellucid punctate. . . . Piperaceae
12. Flowers not in spikes, leaves without pellucid punctations 13
13. Leaves opposite. . . . . Euphorbiaceae (*Chamaesyce*)
13. Leaves alternate . . . . Phyllanthaceae
11. Flowers with developed perianth (sepals and petals) 14
14. Leaves with parallel venation, alternate; blades often sheathing at the base . . . . GROUP E
14. Leaves without parallel venation, alternate, opposite or whorled; blades not sheathing at the base . . . . GROUP F

Group A: Shrubs, trees or lianas with compound leaves

1. Plants palm-like; venation parallel. . . . . Arecaceae
1. Plants not palm-like; venation pinnate 2
2. Ovary 1-carpellate, 1-locular; fruits samaras; stamens free . . . . Fabaceae
2. Ovary with 2 or more carpels and locules, fruits capsular with 4 or more valves; attached to a gynophore . . . . Meliaceae

Group B: Shrubs, trees or lianas with simple, opposite leaves

1. Plant dioecious; leaves lemon-scented. . . . . Chloranthaceae
1. Plants bisexual; leaves without lemon scent. 2
2. Ovary inferior. 3
3. Flowers with corolla tubular; interpetiolar stipules . . . . .Rubiaceae
3. Flowers with the petals free; stipules lacking 4
4. Leaves palmately veined, lacking pellucid punctations . . . . .Melastomataceae
4. Leaves pinnately veined, with pellucid punctations . . . . .Myrtaceae
2. Ovary superior 5
5. Petals united at least at the base; perianth differentiated into calyx and corolla 6

        6. Hemiepiphytic liana; corolla actinomorphic . . . . .Schlegeliaceae
        6. Shrub or small tree; corolla zygomorphic . . . . .Verbenaceae
    5. Petals free or lacking 7
        7. Styles or stigmas 3 or more; calyx present; colored sap present . . . . . . .Clusiaceae
        7. Styles or stigmas 1; flowers lacking calyx; colored sap absent . . .Rhizophoraceae

Group C: Shrubs or Trees with simple, alternate leaves

1. Branches producing aerial roots that may reach the ground to from secondary trunks; flowers borne on the inside of a globose, fleshy receptacle . . . . Moraceae
1. Branches not producing aerial roots; flowers variously arranged, not inside a receptacle 2
  2. Leaves not entire (toothed or lobed) 3
    3. Blades lobed, not toothed 4
      4. Leaf blades less than 20 cm long . . . . .Euphorbiaceae (Manihot, *Ricinus*)
      4. Leaf blades greater than 20 cm long 5
        5. Blades deeply pinnately divided . . . . Arecaceae
        5. Blades not pinnately divided 6
          6. Flowers many, minute in axillary spikes. . . . . Cecropiaceae
          6. Flowers solitary or multiple, not minute, cauliflorous . . . . Caricaceae
    3. Blades not lobed, toothed 7
      7. Teeth rare, inconspicous 8
        8. Ramiflorous; leaves with black punctations . . . . Aquifoliaceae
        8. Flowers axillary; leaves lacking black punctations . . . . Theaceae
      7. Teeth common, obvious 9
        9. Leaves stellate pubescent 10
        9. Leaves not stellate pubescent . . . . Euphorbiaceae (*Acalypha*)
          10. Stamens fused by their filaments; anthers free . . . . . Malvaceae (in part)
          10. Stamens free, anthers free . . . . Muntingiaceae
  2. Leaves entire 11
    11. Colored sap present; red peltate scales on leaf undersurface . . . . .Bixaceae
    11. Colored sap not present; red peltate scales lacking on leaves 12
      12. Venation parallel; conspicuous colored bracts subtending the flowers . .Musaceae
      12. Venation pinnate; lacking colored bracts 13
        13. Ovary inferior . . . . Combretaceae
        13. Ovary superior 14
          14. Leaves with punctations 15
            15. Plants with spines; petiole winged . . . . Rutaceae
            15. Plants lacking spines; petiole not winged . . . . Myrsinaceae
          14. Leaves lacking punctations 16
            16. Anthers opening by valves . . . . Lauraceae
            16. Anthers not opening by valves. 17
              17. Flowers with a single fertile stamen . . . . Anacardiaceae
              17. Flowers with more than one fertile stamen 18
                18. Fruits single seeded . . . . Chrysobalanaceae
                18. Fruits with more than one seed 19
                  19. Fruit aggregate . . . . Annonaceae
                  19. Fruit simple 20

20. Canopy tree; venation brochididromous . . . . Humiriaceae
20. Shrub; venation palmate at the base . . . . Malvaceae (*Theobroma*)

Group D: Herbaceous vines

1. Leaves compound. . . . . Fabaceae
1. Leaves simple 2
    2. Plants with copious milky sap . . . . Apocynaceae (*Tassadia*)
    2. Plants without milky sap 3
        3. Venation parallel . . . . .Araceae
        3. Venation pinnate or palmate, not parallel 4
            4. Inflorescence umbelliform; corolla zygomorphic . . . . .Marcgraviaceae
            4. Inflorescence of single or multiple flowers, not umbelliform; corolla radial . . . . .Convolvulaceae

Group E: Herbs; Monocotyledons

1. Flowers inconspicuous. less than 1cm 2
    2. Flowers without sepals or petals 3
        3. Leaves two-ranked . . . . .Poaceae
        3. Leaves three-ranked . . . . .Cyperaceae
    2. Flowers with sepals and petals . . . . Araceae (*Spathiphyllum*)
1. Flowers conspicuous; greater than 1 cm. 4
    4. Leaves basal forming a tank-like rosette; flowers hidden between old leaf bases . . . . Bromeliaceae
    4. Leaves cauline not forming a tank; flowers not hidden 5
        5. Plants epiphytic . . . . .Orchidaceae
        5. Plants terrestrial 6
            6. Stem decumbent, creeping . . . . .Commelinaceae
            6. Stem erect . . . . .Musaceae

Group F: Herbs; Dicotyledons

1. Leaves trifoliolate. . . . . Fabaceae
1. Leaves simple 2
    2. Flowers unisexual . . . . Urticaceae
    2. Flowers bisexual 3
        3. Leaves alternate 4
        3. Leaves opposite 5
            4. Petals free 6
            4. Petals fused 7
                5. Milky sap present . . . . Apocynaceae (*Catharanthus*)
                5. Milky sap absent 8
                    6. Flowers in heads or umbels: petals white . . . . Apiaceae
                    6. Flowers solitary. not in heads or umbels; petals yellow . . . . . Onagraceae
                        7. Stamens more than 10. fused by the filaments. . . . . Malvaceae
                        7. Stamens 5. free. . . . . Solanaceae

8. Leaves peltate . . . . Caryophyllaceae
8. Leaves not peltate 9
9. Stipule present, interpetiolar . . . . Rubiaceae
9. Stipule present or absent; not interpetiolar 10
10. Inflorescence a raceme, fruits purple berries . . . . Phytolaccaceae
10. Inflorescence not a raceme, solitary or in compact heads, fruits otherwise 11
11. Plants aromatic; fruit a 4-seeded nutlet . . . . Lamiaceae
11. Plants not aromatic; fruit a capsule 12
12. Corolla red; anthers fused . . . . Gesneriaceae
12. Corolla white; anthers free 13
13. Corolla 5-parted . . . . .Scrophulariaceae
13. Corolla 4-parted 14
14. Winged hypanthium present . . . . .Melastomataceae (*Schwackaea*)
14. Winged hypanthium absent . . . . .Plantaginaceae

ANACARDIACEAE

1. Blades acute or acuminate at the apex . . . . *Mangifera indica*
1. Blades blades obtuse to rounded at the apex . . . . *Campnosperma panamense*

82. *Campnosperma panamense* Standl., J. Arnold Arbor. 2:111–112. 1920.

DISTRIBUTION.— Rare on Isla del Coco; collected between Iglesias Bay and Cerro Tesoro Escondido. Distributed from Honduras to Colombia and coastal Ecuador.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— INB: *Quesada 1127.*

83. **Mangifera indica* L., Sp. Pl. 200. 1753.

DISTRIBUTION.— Cultivated on Isla del Coco near the Wafer Bay ranger station. This species is native to Asia and is cultivated throughout the tropics.

REMARKS.— The trees appear to be young and did not have flowers or fruit during any of our research trips to the island.

SPECIMENS EXAMINED.— CR: *Quesada 1105.*

ANNONACEAE

1. Leaves densely pubescent beneath . . . . *Annona cherimola*
1. Leaves glabrous . . . . *Annona glabra*

84. **Annona cherimola* Mill., Gard. Dict. ed. 8. no. 5. 1768.

DISTRIBUTION.— Cultivated on Isla del Coco in Wafer Bay. Stewart (1912) states that these trees are "in gardens and probably introduced". Distributed throughout Mesoamerica to Peru and Bolivia; also cultivated widely in the New World.

REMARKS.— This species was reported by Stewart (1912) but no collections were located.

SPECIMENS EXAMINED.— No collections located.

85. *Annona glabra* L., Sp. Pl. 537. 1753.

DISTRIBUTION.— Found throughout Isla del Coco near the shoreline from 0–200m. Distributed from Mexico to Ecuador and Brazil; also found in the West Indies and western Africa.

Remarks.— Sierra (2001a) found that this was one of most commonly eaten fruits by the feral pigs on the island.

Specimens examined.— CR: *Dauphin 1053*; *Gómez-Laurito 6913*; *Lépiz 365*; *Quesada 1021*; FTG: *Trusty 35*; GH: *Jiménez s.n.*; INB: *González 1168*; *Lépiz 365*; *Quesada 1021*; *Rojas 3683*; USJ: *Soto 3854.*

APIACEAE

1. Leaves orbicular, peltate. . . . . *Hydrocotyle umbellata*
1. Leaves elliptical, not peltate. . . . . *Eryngium foetidum*

86. **Eryngium foetidum* L., Sp. Pl. 232. 1753.

Distribution.— Cultivated on Isla del Coco near the Wafer Bay ranger station. This species is commonly cultivated throughout the tropics of the New World and has been introduced into tropical Africa.

Remarks.— The plants have not escaped from cultivation but these should be monitored as *E. foeditum* is found in clearings and weedy places in Panama (Croat 1978). First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 201.*

87. **Hydrocotyle umbellata* L., Sp. Pl. 234. 1753.

Distribution.— Forms mats in the cleared areas near the shore in Wafer Bay. Native to the tropical areas of the New World and has been introduced into tropical southern Africa.

Remarks.— This is probably a very recent introduction by humans to Isla del Coco due to its recent collection by us and the restricted distribution on the island near human settlements. First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 210*; INB: *Rojas 3710.*

APOCYNACEAE

1. Cultivated herb; flowers pink or white . . . . *Catharanthus roseus*
1. Forest vine; flowers white. . . . . *Tassadia obovata*

88. **Catharanthus roseus* (L.) G. Don, Gen. Hist. Dichl. Pl. 4:95. 1837 (1838).

Distribution.— Cultivated on Isla del Coco near the Wafer Bay ranger station. Native to Madagascar but cultivated and escaped throughout the tropics.

Remarks.— This species is an invasive exotic in many island ecosystems (Swarbrick 1997, Space et al. 2003), and we recommend its removal.

Specimens examined.— FTG: *Trusty 198.*

89. *Tassadia obovata* Decne., Prodr. 8:579–580. 1844.

Distribution.— Common in the closed forest throughout Isla del Coco from 50–450 msl. Distributed from Mexico south to Ecuador and the Guianas; including Trinidad.

Remarks.— Although the plants are common in the understory of the forest, they do not appear to flower and fruit until they reach the canopy or a light gap is formed. This species was previously published under the name *T. colubrina* Descne. in Stewart (1912).

Specimens examined.— CR: *Gómez 3295*; *Quesada 1083*; FTG: *Trusty 110*; *Trusty 507*; *Trusty 551*; INB: *Quesada 1083.*

AQUIFOLIACEAE

90. *Ilex yurumanguinis* Cuatrec., Lloydia 11(3):210–212, f. 3. 1948.

DISTRIBUTION.— Infrequent throughout Isla del Coco but more common in the northern part of the island near Cabo Atrevido. Distributed from Nicaragua to Colombia and Ecuador.

REMARKS.— This plant has been confused with *Rapanea guianensis* (Myrsinaceae) when in fruit due to the presence of ramiflorous fruits and the dark pellucid dots on the leaves.

SPECIMENS EXAMINED.— CAS: *Stewart 320*; CR: *González 1187*; *Rojas 3696*; FTG: *Trusty 505*; GH: *Foster 4115*; *Foster 4156*; INB: *González 1187*; *Rojas 3696*; USJ: *Soto 3863*.

ARACEAE

1. Plants terrestrial; stems erect 2
    2. Plants cultivated; leave blades lobed . . . . *Xanthosoma sagittifolium*
    2. Plants not cultivated; leaf blades simple and entire . . . . *Spathiphyllum laeve*
1. Plants epiphytic or climbing; stems vining. 3
    3. Blades with without basal lobes; collecting vein present. . . . . *Anthurium scandens*
    3. Blades with prominent basal lobes; collecting vein absent . . . . . *Philodendron hederaceum*

91. *Anthurium scandens* (Aubl.) Engl. in Mart., Fl. Brasil. 3(2):78. 1878.

DISTRIBUTION.— Infrequent in the forest of Isla del Coco between 200–400 msl. This species is found from Mexico throughout Central America to the Guianas and southern Brazil; also Trinidad and the Greater Antilles.

SPECIMENS EXAMINED.— CR: *Quesada 1084*; *Rojas 3630*; FTG: *Trusty 211*; INB: *Quesada 1084*; *Rojas 3630*.

92. *Philodendron hederaceum* (Jacq.) Schott, Wiener Z. Kunst 3:780. 1829.

DISTRIBUTION.— Frequent in the forest of Isla del Coco from 200–600 msl. Found from Mexico to Colombia, Venezuela and the Guianas.

REMARKS.— This plant is extremely difficult to find in flower or fruit but is conspicuous in the Cocos Island flora and is recognized by its large leaves with cordate blades. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 148*; *Trusty 296*; INB: *Quesada 1075*; *Quesada 1126*.

93. *Spathiphyllum laeve* Engl., Bot. Jahrb. Syst. 37:120. 1905.

DISTRIBUTION.—Common near rivers and streams throughout Isla del Coco. Distributed from Nicaragua to Colombia.

REMARKS.— Previously published under the name *S. wendlandii* Schott in Stewart (1912) and *S. atrovirens* Schott in Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— CR: *Dauphin 1130*; *Gómez 3286*; *Lépiz 380*; *Sánchez 18*; FTG: *Trusty 71*; *Trusty 486*; GH: *Pittier 16244*; INB: *Lépiz 352*; *Lépiz 380*; *Rojas 3632*; US: *Dressler 4465*; *Holdridge 5165*; *Lépiz 380*; *Pittier 12370*; *Pittier 16244*; *Stewart 278*.

94. **Xanthosoma sagittifolium* (L.) Schott & Endl., Melet. Bot 19. 1832.

DISTRIBUTION.— Cultivated on Isla del Coco at the Wafer Bay ranger station. Native to the American tropics but cultivated worldwide.

REMARKS.— This plant is currently being removed from the island as it is able to spread rapidly in the cleared areas. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 134*.

ARECACEAE

1. Fruits up to 5 cm long, turning purple when ripe . . . . *Euterpe precatoria* var. *longevaginata*
1. Fruits 20–30 cm long turning yellow when ripe . . . . *Cocos nucifera*

95. *Cocos nucifera* L., Sp. Pl. 1188. 1753.

Distribution.— Frequent along the shore and cultivated near the Wafer Bay ranger station. Pantropical in cultivation and abundant in tropical coastal areas.

Remarks.— Coconuts are apparently making a come-back on Isla del Coco from the extensive harvesting that occurred in the late 1800's.

Specimens examined.— Not collected.

96. *Euterpe precatoria* Mart. var. *longevaginata* (Mart.) A.J. Hend., Palms Amazon 111. 1995. *Rooseveltia frankliniana* O.F. Cook; *E. macrospadix* Oerst.

Distribution.— Common both within the forest and along the steep areas near the coast of Isla del Coco. Distributed from Belize to Ecuador and Peru.

Remarks.— This palm species was originally described as an endemic genus named for the U. S. President Franklin D. Roosevelt (Cook 1940).

Specimens examined.— CR: *Poveda 817*; *Valerio s.n.*; FTG: *Trusty 154*; INB: *González 1173*; USJ: *Poveda 817.*

ASTERACEAE

1. Leaves alternate. 2
2. Leaves white tomentose below . . . . *Rolandra fruticosa*
2. Leaves not white tomentose below . . . . *Pseudoelephantopus spicatus*
1. Leaves opposite. 3
3. Pappus of numerous bristles or plumose bristle-like scales 4
4. Shrub; flowers white . . . .*Clibadium acuminatum*
4. Herb; flowers not white 5
5. Plants with milky sap, flowers yellow . . . .*Youngia japonica*
5. No milky sap present, flowers lavender . . . .*Chromolaena odorata*
3. Pappus not as above. 6
6. Heads axillary, sessile or short-pedunculate . . . .*Synedrella nodiflora*
6. Heads terminal, the peduncles greater than 1 cm long . . . .*Sphagneticola trilobata*

97. **Chromolaena odorata* (L.) King & H. Rob., Phytologia 20:204. 1970.

Distribution.— Rare on Isla del Coco; near the Chatham Bay ranger station along the trail between Chatham and Wafer Bays. This species is widespread throughout tropical, subtropical and warm temperate America.

Remarks.— This species has recently arrived to Cocos Island and is found only in one disturbed area near Chatham Bay ranger station.

Specimens examined.— FTG: *Trusty 252*.

98. *Clibadium acuminatum* Benth., Bot. Voy. Sulphur 114. 1844.

Distribution.— Rare; collected on Isla del Coco only near Wafer Bay and along the trail from Wafer to Cerro Iglesias. Distributed in Colombia and Venezuela.

Remarks.— This species was considered a common understory shrub by Stewart (1912) but is currently rare on the island. There has been only one collection of this species since the early 1900s.

This species was originally described from Isla del Coco collections and later found on the mainland.

SPECIMENS EXAMINED.— GH: *Stewart 326*; INB: *Rojas 3637*; US: *Barclay 2179*; *Hinds s.n.*

99. **Pseudoelephantopus spicatus* (Juss.) C. F. Baker, Trans. Acad. Sci. St. Louis 12:45,55. 1902.

DISTRIBUTION.— Infrequent on Isla del Coco; found in disturbed areas near the boat landing at Wafer Bay. Distributed in continental tropical America, the West Indies and introduced in Africa and eastern Asia.

REMARKS.— This is probably a very recent introduction by humans to Isla del Coco due to the recent collection by us and its restricted distribution on the island near human settlements. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 353.*

100. *Rolandra fruticosa* (L.) Kuntze, Rev. Gen. Pl. 1:360. 1891.

R. argentea Rottb.

DISTRIBUTION.— Common in disturbed areas near habitations and trails on Isla del Coco. Distributed from Honduras to the Guianas, Peru, Brazil and the West Indies.

REMARKS.— *R. fruticosa* is considered native here due to the early collections, but it may represent an introduction to the island by humans.

SPECIMENS EXAMINED.— CR: *Gómez 3265*; *Gómez s.n.*; *Gómez-Laurito 6904*; *González 1142*; *Jiménez 3151*; *Rojas 3639*; *Valerio 1098*; FTG: *Trusty 88*; *Trusty 112*; GH: *Gómez 3265*; *Howell 10167*; *Pittier 16262*; *Snodgrass and Heller 947*; *Svenson 308*; INB: *González 1142*; *Lépiz 354*; *Quesada 1098*; *Rojas 3639*; US: *Pittier 16262*; USJ: *Soto s.n.*

101. *Sphagneticola trilobata* (L.) Pruski, Mem. New York Bot. Gard. 87:114. 1996.

Wedelia trilobata (L.) Hitchc.; *W. paludosa* DC.

DISTRIBUTION.— Locally abundant near the shoreline of Isla del Coco. Distributed in Florida, Central and South America, the West Indies and West Africa.

SPECIMENS EXAMINED.— CR: *Dauphin 1132*; *Gómez 3287*; *Quesada 1065*; *Rojas 3678*; *Valerio 1111*; FTG: *Trusty 36*; *Trusty 111*; INB: *Lépiz 366*; *Quesada 1065*; *Rojas 3678*; USJ: *Soto 3856.*

102. *Synedrella nodiflora* (L.) Gaertn., Fruct. & Sem. Pl. 2:456. 1791.

DISTRIBUTION.— Common in cleared areas of Isla del Coco. *S. nodiflora* is widespread throughout the tropics.

REMARKS.— *S. nodiflora* is considered native here due to the early collections but is probably introduced to the island by humans. This species was published under the name *Blainvillea biaristata* DC. in Stewart (1912) and Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— FTG: *Trusty 277*; *Trusty 354*; *Trusty 555*; GH: *Pittier 16249*; INB: *Quesada 1036*; US: *Stewart 319*; USJ: *Soto s.n.*

103. **Youngia japonica* (L.) DC., Prodr. 7:194. 1838.

DISTRIBUTION.— Common in the lawn area of the Wafer Bay ranger station on Isla del Coco. A cosmopolitan weed.

REMARKS.— This is probably a very recent introduction by humans to Isla del Coco due to the recent collection by us and restricted distribution on the island near human settlements. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 200.*

BIXACEAE

104. *_Bixa orellana_ L., Sp. Pl. 512. 1753.

DISTRIBUTION.— No longer found. Previously cultivated on Isla del Coco in Wafer Bay. Native to tropical America but cultivated throughout the tropics and subtropics.

REMARKS.— Pittier (1898) cited this species for the island and it has not been collected since.

SPECIMENS EXAMINED.— No collections located.

BROMELIACEAE

1. Epiphyte; flowers sessile . . . . _Guzmania sanguinea_
1. Terrestrial; flowers pedunculate . . . . _Ananas comosus_

105. *_Ananas comosus_ (L.) Merr., Interpr. Herb. Amboin. 133. 1917.

DISTRIBUTION.— Cultivated on Isla del Coco at the Chatham Bay ranger station. Native to Brazil but widely cultivated throughout the tropics.

SPECIMENS EXAMINED.— Not collected.

106. _Guzmania sanguinea_ (André) André ex Mez in C. DC., Monogr. Phan. 9:901. 1896.

DISTRIBUTION.— Extremely abundant throughout Isla del Coco. Distributed from Costa Rica to Ecuador.

REMARKS.— This species was published under the name _G. crateriflora_ Mez & Wercklé in Svenson (1935), _Catopsis aloides_ Baker in Robinson (1902) and _Tillandsia_ sp. in Stewart (1912).

SPECIMENS EXAMINED.— CR: _Gómez 3272_; _Lépiz 350_; _Lépiz 364_; _Rojas 3656_; FTG: _Trusty 128_; INB: _Lépiz 350_; _Lépiz 364_; _Quesada 1091_; _Rojas 3656_; US: _Foster 4172_; _Gómez 3272_; _Klawe 1517_; _Svenson 322_; _Svenson 436_.

BURMANNIACEAE

107. _Gymnosiphon panamensis_ Jonker, Monogr. Burmmann. 199, f. 18. 1938.

DISTRIBUTION.— Rare on Isla del Coco; found only along one section of the ridge on the research trail from Wafer Bay to Los Llanos. Distributed from Mexico to Panama.

SPECIMENS EXAMINED.— FTG: _Trusty 212_; _Trusty 539_.

CARICACEAE

108. *_Carica papaya_ L., Sp. Pl. 1466. 1753.

DISTRIBUTION.— Cultivated on Isla del Coco at the Chatham and Wafer Bay ranger stations. Native to the American tropics but widespread in cultivation.

REMARKS.— Papaya has not escaped from cultivation on Cocos Island, however, this species is considered an invasive exotic in island ecosystems (Space et al. 2000), and we recommend its removal.

SPECIMENS EXAMINED.— Not collected.

CARYOPHYLLACEAE

109. *_Drymaria cordata_ (L.) Willd., Syst. Veg. 5:406. 1819.

DISTRIBUTION.— Extremely common along open-canopy trails and in cleared areas on Isla del Coco. Pantropical in distribution.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 91*; *Trusty 336*; *Trusty 466*; INB: *González 1219*.

CECROPIACEAE

110. ***Cecropia pittieri*** B.L. Rob., Proc. Calif. Acad. Sci., ser. 4, 1:389. 1912. (Fig. 9)

TYPE: *Pittier 16237* (holotype: GH).

Tree; branches 3–4 cm thick, hollow with septate cavity, leaves orbicular, large, 50 cm in diameter, briefly peltate, 10-lobate, sparsely pilose above, glabrate, green, below intensely white, nerves reticulate and patently hirsute; lobes widely orbiculate, margins undulate, apex rounded or short acuminate, sinuses rounded; petioles 40 cm long, 1 cm in diameter, terete, white-arachnoid, base thickened, dingy hirsute; stipules oblong-lanceolate, acute 16 cm long, 6 cm wide, hirsute on both sides, except for glabrisculous margins, margins absolutely entire; male spathes rounded, apex longly attenuate, 14 cm long, grey pubescent on the outside, peduncle robust, 8 cm long; male spikes ca. 19, sessile, 10 × 3 cm; female spikes unknown.

DISTRIBUTION.— Common in full sun, especially in the steep cliffs of the coast from 0–300msl. Appears as a successional species. Endemic to Isla del Coco.

REMARKS.— Alfaro (1898) stated that these plants house ants of the genus *Camponotis*.

SPECIMENS EXAMINED.— CR: *Dressler 4460*; *Gómez-Laurito 6943*; *Gómez-Laurito 6943*; *Jiménez 3184*: *Poveda 810*; *Rojas 3672*; *Sánchez 20*; FTG: *Trusty 161*; *Trusty 237*; *Trusty 404*; INB: *González 1213*; *Quesada 1064*; *Rojas 3672*; NY: *Dressler 4460*; *Fournier 311*; US: *Carrasquilla 362*; *Dressler 4460*; *Fournier 311*; USJ: *Gómez-Laurito 6943*; *Poveda 810*; *Quesada 1064*.

CHLORANTHACEAE

111. *Hedyosmum racemosum* (Ruiz & Pav.) G. Don, Gen. Hist. 3:434. 1834.

DISTRIBUTION.— Frequent on Isla del Coco above 400 msl on Cerro Iglesias. Distributed from northern Colombia to to Bolivia, the Guayana highlands of Venezuela and Guiana.

REMARKS.— *Hedyosum* is a typical species of the cloud forests of the Americas. The shrinking of climatic zones found on mountainous islands allows this species, which is commonly found above 1000 msl on the continent, to survive at 400 msl. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 61*; *Trusty 276*; *Trusty 562*; INB: *Quesada 1077*; *Rojas 3625*.

CHRYSOBALANACEAE

1. Cultivated tree; leaves 10–30 cm long. . . . . *Licania platypus*
1. Shrub, not cultivated; leaves up to 8 cm long . . . . *Chrysobalanus icaco*

112. *Chrysobalanus icaco* L., Sp. Pl. 513. 1753.

DISTRIBUTION.— Infrequent along the coast of Isla del Coco. Distributed from Florida and Mexico through Central America and the West Indies to northern South America; also in West Africa.

SPECIMENS EXAMINED.— CR: *Gómez 3275*; FTG: *Trusty 452*.

113. **Licania platypus* (Hemsl.) Fritsch, Ann. K.K. Naturhist. Hofmus. 4:53. 1889.

DISTRIBUTION.— Only one individual found on Isla del Coco near the Genio River in Wafer Bay. Distributed from southern Mexico south to Colombia.

REMARKS.— This large tree appears to be vestigial from the Gissler settlement. Rats and pigs

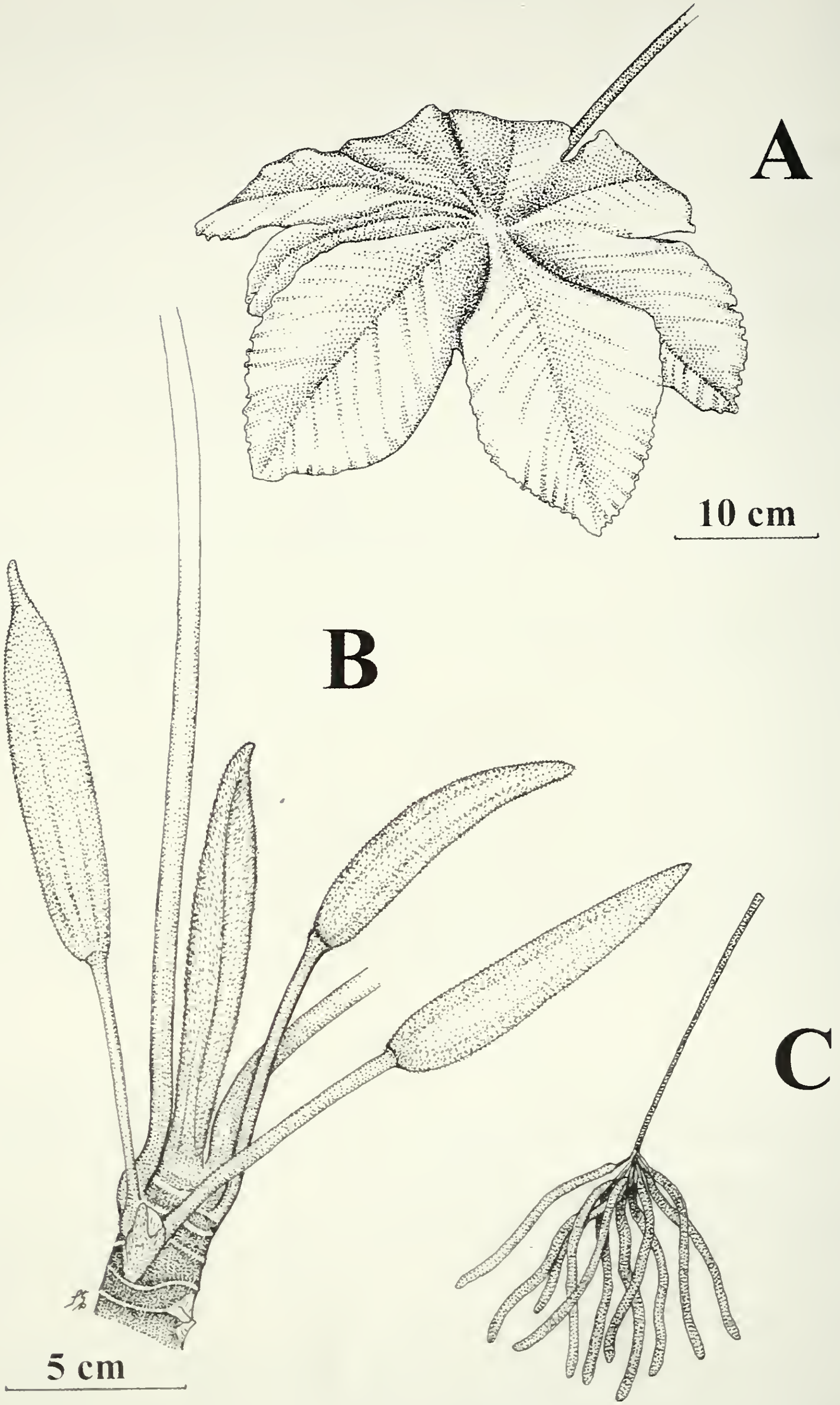

FIGURE 9. *Cecropia pittieri* (drawn from *Trusty 414*). A. Single palmate leaf. B. Fertile branch showing spathes enclosing inflorescences. C. Staminate inflorescence.

eat the fallen fruits (J. Trusty, pers. obs.). Seedlings have established under the parent tree. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 230*; *Trusty 492*.

CLUSIACEAE

1. Tree producing aerial roots, veins arcuate to the midrib; flowers pink . . . . *Clusia rosea*
1. Shrub or tree not producing aerial roots; veins perpendicular to the midrib; flowers white . . . . *Calophyllum inophyllum*

114. *Calophyllum inophyllum* L., Sp. Pl. 513–514. 1753.

DISTRIBUTION.— Frequent on Isla del Coco along the shore in Wafer and Chatham Bays. Native to Africa and the South Pacific but commonly cultivated in tropical America.

REMARKS.— First report for Isla del Coco. This species is listed as native due to the fact that it is a littoral species that has reached the island through oceanic drift.

SPECIMENS EXAMINED.— CR: *Quesada 1027*; *Rojas 3666*; FTG: *Trusty 133*; *Trusty 219*; INB: *Quesada 1027*; *Rojas 3666*.

115. *Clusia rosea* Jacq., Enum. Syst. Pl. 34. 1760.

DISTRIBUTION.— Common throughout Isla del Coco below 400 msl. Also found on many of the islets surrounding the island. Distributed from southern Florida to northern South America and the Antilles.

REMARKS.— *Clusia rosea* is an important nesting site for the brown and red-footed boobies (*Sula sula* and *S. melanogaster*) on the islets and cliffs of the island. In addition, the authors have seen the seeds eaten by the Cocos Island Finch (*Pinaroloxias inornata*).

SPECIMENS EXAMINED.— CR: *Dressler 4459*; *Gómez-Laurito 6940*; *Lépiz 381*; *Quesada 1051*; FTG: *Trusty 160*; *Trusty 340*; INB: *Lépiz 381*; *Quesada 1051*; USJ: *Gómez-Laurito 6940*; *Soto s.n.*

COMBRETACEAE

1. Leaves narrowly elliptical; fruits aggregated into a cone-like structure . . . . *Conocarpus erectus*
1. Leave obovate; fruits solitary, not aggregated. . . . . *Terminalia catappa*

116. *Conocarpus erectus* L., Sp. Pl. 176. 1753.

DISTRIBUTION.— Infrequent on Isla del Coco; found near the Genio River in Wafer Bay. Distributed in tropical and subtropical America and Africa.

REMARKS.— Although the island has no true mangroves, this is an important mangrove associate of tidal swamps on the mainland.

SPECIMENS EXAMINED.— CR: *Sánchez 24*; *Sánchez 25*; INB: *Quesada 1052*; USJ: *Soto 3855*.

117. *Terminalia catappa* L., Mant. 1:128. 1767.

DISTRIBUTION.— Common on Isla del Coco along the shorefront in Wafer and Chatham Bays. Native to the Old World but now widely distributed throughout the Americas.

SPECIMENS EXAMINED.— CR: *Jiménez s.n.*; *Quesada 1026*; *Quesada 1109*; *Rojas 3697*; *Sánchez 6*: *Valerio 1093*; FTG: *Trusty 38*; INB: *Quesada 1026*; *Quesada 1109*; *Rojas 3697*.

COMMELINACEAE

118. *Commelina diffusa* Burm. f., Flora Indica 18, pl. 7, f. 2. 1768.

DISTRIBUTION.— Common in the clearings near the Wafer Bay ranger station on Isla del Coco.

Distributed in subtropical and tropical regions of the world.

REMARKS.— *C. diffusa* is considered native here due to the early collection by Stewart (1912) but was probably introduced to the island by humans.

SPECIMENS EXAMINED.— FTG: *Trusty 130.*

CONVOLVULACEAE

1. Fruits indehiscent . . . . *Stictocardia tiliifolia*
1. Fruits dehiscent 2
    2. Flowers white . . . . *Ipomoea alba*
    2. Flowers blue or purple 3
        3. Plants not scandent not climbing . . . . *Ipomoea pes-caprae*
        3. Plants climbing 4
            4. Sepals herbaceous; stigma lobes 3 . . . . *Ipomoea indica*
            4. Sepals coriaceous; stigma lobes 2 . . . . *Ipomoea philomega*

119. *Ipomoea alba* L., Sp. Pl. 161. 1753.

Ipomoea bona-nox L.

DISTRIBUTION.— Frequent in human created disturbed areas and steep areas that undergo landslides on Isla del Coco. Native to the tropics and subtropics of the New World but pantropical through cultivation.

SPECIMENS EXAMINED.— CR: *Quesada 1063*; FTG: *Trusty 204*; *Trusty 450*; INB: *Quesada 1063.*

120. *Ipomoea indica* (Burm.) Merr., Interp. Herb. Amboin. 445. 1917.

I. acuminata (Vahl) Roem. & Schult.; *I. learii* Pax

DISTRIBUTION.— Frequent in successional areas created by landslides on Isla del Coco. Pantropical in distribution.

REMARKS.— This species was published under the name *I. cathartica* Poir. in Stewart (1912).

SPECIMENS EXAMINED.— GH: *Pittier 16277.*

121. *Ipomoea pes-caprae* (L.) R. Br. in Tuckey, Narr. Exped. Zaire 477. 1818.

DISTRIBUTION.— Rare on Isla del Coco; found only along the shore at Iglesias Bay. Pantropical in distribution.

REMARKS.— Stewart (1912) collected this species from the beachfront at Wafer Bay where it was reported as common. This population no longer occurs at this location.

SPECIMENS EXAMINED.— CR: *Quesada 1131*; FTG: *Trusty 394*; USJ: *Soto 3860.*

122. *Ipomoea philomega* (Vell.) House, Ann. New York Acad. Sci. 18:246. 1908.

DISTRIBUTION.— Extremely common in human created disturbed areas and steep areas that undergo landslides on Isla del Coco. Distributed from Guatemala to Guiana and Peru, also found in the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 447*; INB: *Quesada 1056.*

123. *Stictocardia tiliifolia* (Desr.) Hallier f., Bot. Jahrb. Syst. 18(1–2):159. 1893.

DISTRIBUTION.— Extremely common in human created disturbed areas and steep areas that undergo landslides on Isla del Coco. Native to Africa through Malaysia, naturalized from south Florida to Guyana, Peru and Ecuador, and also the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Quesada 1103*; *Sánchez 11*; FTG: *Trusty 205*; *Trusty 449*; INB: *Quesada 1103*.

CUCURBITACEAE

124. **Momordica charantia* L., Sp. Pl. 1009. 1753.

DISTRIBUTION.— Escaped from cultivation on forest edge near the Wafer Bay ranger station on Isla del Coco. Found in the tropics and subtropics worldwide.

REMARKS.— This species is considered an invasive exotic in many island ecosystems (Swarbrick 1997, Space and Falanruw 1999), and we recommend its removal. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 83*.

CYPERACEAE

1. Inflorescence simple and unbranched 2
2. Culms three-angled . . . . *Eleocharis acutangula*
2. Culms terete 3
3. Inferior veins of the stem without laminas; inflorescence bracts less than 4 cm long . . . . *Kyllinga nudiceps*
3. Inferior veins of the stem with developed laminas; inflorescence bracts greater than 4 cm long . . . . *Kyllinga brevifolia*
1. Inflorescence compound 4
4. Spikelets compound . . . . *Hypolytrum amplum*
4. Spikelets simple 5
5. Florets unisexual 6
6. Plant erect to .7 m tall . . . . *Calyptrocarya glomerulata*
6. Plant scandent, stems 3–10 long . . . . *Scleria secans*
5. Florets bisexual 7
7. Fertile scales spiraled 8
8. Achene lacking tubercle . . . . *Fimbristylis dichotoma*
8. Achene with tubercle 9
9. Spikelets pedicellate and arranged in panicles . . . . *Rhynchospora polyphylla*
9. Spikelets all sessile and arranged in heads 10
10. Bracts adjacent to the head white basally . . . *Rhynchospora nervosa*
10. Bracts adjacent to the head green . . . . *Rhynchospora pubera* var. *parvula*
7. Fertile scales distichous 11
11. Spikelets in a solitary head, glomerulate . . . . *Cyperus tenerrimus*
11. Spikelets in spikes along a conspicuous rachis 12
12. Rachilla articulated at the base of each scale, the mature spikelets disarticulating in segments formed by a scale, an internode and the wings of the raquilla . . . . *Cyperus odorata*
12. Rachilla continuous or articulated only at the base of the spikelet . . . 13
13. Scales smooth; spikelets flattened 14
14. Stolons lacking tubercles; mature fruit commonly formed . . . . *Cyperus sphacelatus*

14. Stolons with tubercles present; mature fruit generally not formed 15
    15. Scales brown; base of the culm soft . . . *Cyperus esculentus*
    15. Scales brown with a green midvein; base of the culm hardened . . . . *Cyperus rotundus*
13. Scales plicate; spikelets quadrangular or subterete 16
    16. Culms, rays and leaf lamina papillose; leaves asperously scabrous on the margins and the medial nerves . . . . *Cyperus ligularis*
    16. Culms, rays and leaf lamina not papillose; leaves scaberulose or smooth on the margins and the medial nerves 17
        17. Scales green; spikes densely ovoid . . . . *Cyperus tenuis*
        17. Scales brown; spikes cylindrical . . . . *Cyperus hermaphroditus*

125. *Calyptrocarya glomerulata* (Brongn.) Urb., Symb. Ant. 2:169. 1900.

C. longifolia (Rudge) Kunth; *C. palmetto* Nees

Distribution.— Common along rivers and streams throughout Isla del Coco. Native from Mexico to Brazil.

Specimens examined.— CR: *Dauphin 1168*; *Gómez-Laurito 6920*; *Jiménez 3176*; *Murawski 307*; *Pittier 16274*; *Quesada 1018*; *Soto s.n.*; FTG: *Trusty 84*; *Trusty 286*; GH: *Pittier 16274*; INB: *Quesada 1018*; US: *Barclay 2189*; *Gómez 3263*; *Howell 10188*; *Pittier 12376*; *Pittier 16274*; USJ: *Castaing s.n.*; *Dauphin 1168*; *Gómez-Laurito 6957*; *Gómez-Laurito s.n.*; *Soto s.n.*

126. *Cyperus hermaphroditus* (Jacq.) Standl., Contr. U.S. Natl. Herb. 18:88. 1916.

Distribution.— Frequently found in the lawn area of the Wafer Bay ranger station on Isla del Coco. Distributed from Texas to northern Argentina; also found in the Antilles.

Remarks.— *C. hermaphroditus* is considered native here due to the early collections but may have been introduced to the island by humans.

Specimens examined.— CAS: *Stewart 269*; CR: *Gómez-Laurito 6958*; FTG: *Trusty 86*; *Trusty 388*; *Trusty 448*; GH: *Snodgrass and Heller 946A*; USJ: *Soto s.n.*

127. **Cyperus ligularis* L., Syst. Nat. ed. 10, 2:867. 1759.

Distribution.— Infrequent on Isla del Coco; found near drainage ditch near Wafer Bay ranger station. Distributed in subtropical and tropical areas throughout the world.

Specimens examined.— CR: *Gómez-Laurito 6927*; *Sánchez 21*; FTG: *Trusty 135*.

128. *Cyperus odoratus* L., Sp. Pl. 46. 1753.

Distribution.— Frequent in clearings and near drainage areas near the Wafer Bay ranger station on Isla del Coco. Found in the tropics and subtropics throughout the world.

Remarks. — This species was published under the name *C. prolixus* Kunth in Stewart (1912).

Specimens examined.— BKL: *Svenson 310*; CAS: *Stewart 266*; CR: *Pittier 16271*; FTG: *Trusty 468*; US: *Klawe 1503*.

129. **Cyperus rotundus* L., Sp. Pl. 45. 1753.

Distribution.— Rare; found in Wafer Bay on Isla del Coco. Distributed in the tropics and subtropics throughout the world.

Remarks.— First report for Isla del Coco.

Specimens examined.— CR: *Gómez 3386* (not seen).

130. *Cyperus sphacelatus* Rottb., Descr. Pl. Rar. 21. 1772.

DISTRIBUTION.— Frequent in the lawn area of the Wafer Bay ranger station and on the banks of the Genio River on Isla del Coco. Distributed from Honduras to northern South America and the Antilles; also in tropical Africa.

REMARKS.— *C. sphacelatus* is considered native here due to the early collections but is probably introduced to the island by humans. This species was published under the name *C. esculentus* L. in Svenson (1935).

SPECIMENS EXAMINED.— CAS: *Stewart 267*; *Stewart 268*; GH: *Snodgrass and Heller 946B*.

131. **Cyperus tenerrimus* J. Presl & C. Presl in C. Presl, Reliq. Haenk. 1(3):166. 1828.

DISTRIBUTION.— Rare; found in Wafer Bay on Isla del Coco. Distributed from southern Mexico to Costa Rica.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Murawski 365* (not seen).

132. **Cyperus tenuis* Sw., Prodr. 20. 1788.

DISTRIBUTION.— Rare; found in the thickets at French Point on Isla del Coco. Distributed from Mexico to Brazil; also found in the West Indies and tropical Africa.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 3281* (not seen).

133. **Eleocharis acutangula* (Roxb.) Schult., Mant. 2:91. 1824.

E. fistulosa Schult.

DISTRIBUTION.— Infrequent in Wafer Bay on Isla del Coco. Pantropical in distribution.

SPECIMENS EXAMINED.— CR: *Gómez-Laurito 6915* (not seen).

134. **Fimbristylis dichotoma* (L.) Vahl, Enum. Pl. 2: 287. 1805.

DISTRIBUTION.— Frequent in the lawn area of the Wafer Bay ranger station on Isla del Coco. Found at low altitudes in temperate and tropical areas of the world.

SPECIMENS EXAMINED.— CR: *Gómez 3384*; *Soto s.n.*; FTG: *Trusty 90*; *Trusty 355*.

135. *Hypolytrum amplum* Poepp. & Kunth in Kunth, Enum. Pl. 2:272. 1837.

DISTRIBUTION.— Extremely common in the closed canopy forest up to 450 msl throughout the island. Distributed in Costa Rica, Peru, Venezuela, the Guianas and Brazil.

REMARKS.— This species is currently the most common understory component of Isla del Coco. It forms dense stands especially near Cabo Atrevido. This species was published under the name *H. nicaraguense* Liebm. in Stewart (1912) and Svenson (1935).

SPECIMENS EXAMINED.— CR: *Dauphin 1163*; *Dressler 4473*; *Gómez 3313*; *Gómez-Laurito 6921*; *Gómez-Laurito 6936*; *Jiménez 3144*; *Murawski 306*; *Murawski 327*; *Soto s.n.*; *Valerio 1109*; FTG: *Trusty 50*; GH: *Pittier 16273*; *Stewart 271*; INB: *González 1143*; *Quesada 1005*; US: *Klawe 1503*; *Pittier 12380*; *Pittier 16273*; USJ: *Castaing s.n.*; *Dauphin 1163*; *Soto s.n.*

136. **Kyllinga brevifolia* Rottb., Descr. Icon. Rar. Pl. 13, pl. 4, f. 3. 1773.

DISTRIBUTION.— Common in the lawn near the Wafer Bay ranger station on Isla del Coco. Distributed from the southern United States to Argentina.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 87*; *Trusty 356*.

137. ***Kyllinga nudiceps*** C.B. Clarke ex Standl., Publ. Field Columbian Mus., Bot. Ser. 4(8): 199. 1929. (Fig. 10)

TYPE: *Pittier 16272* (holotype: US!; isotypes: F, GH!, LCU, NY!).

Cyperus nudiceps (C.B. Clarke ex Standl.) O'Neill

Tufted perennial, (10) 25–40 (55) cm tall; rhizome short, oblique, 1–3 cm long, (0.5) 2–3 mm thick, closely covered with overlapping reddish-brown, broadly ovate scales 1–3 mm long; roots brownish, finely pubescent especially near the rhizome; leaves bladeless, the base of the culms with about 3 reddish-brown, scarious sheaths (0.6) 2–8 cm long, densely reddish spotted along the apical margins; culms 0.4–0.8 mm thick just above the apex of the longest sheath, 0.4–0.6 (0.9) mm thick just below the inflorescence; inflorescence bracts 2 or 3, rather broadly ovate, 1.3–2.8 (3.5) mm long, the cusp an additional 1–2 mm long, 1.4–2.5 mm wide, light reddish brown to sordid whitish, smooth or often sparsely scabrous along the keel distally, erect to ascendent at anthesis, stiffly erect and clasping the rachis after the spikelets fall; spike loosely hemispherical, 3.5–4.5 mm high, 5–6 mm wide; rachis cylindric, (0.9) 1.3–1.8 mm long, (0.4) 0.6–0.8 mm thick; spikelet pedicels rather densely packed, separated by less than their own width, 0.2–0.35 mm long, 0.15–0.2 mm wide, abaxially with a conspicuous toothlike scar from the lowest sterile scale; spikelets 15–45, elliptic, 2–2.8 mm long, 0.7–1.2 mm wide, dull white to light greenish-brown; scales 2–2.4 mm long 1.4–2.1 mm wide, 7–11 nerved, keel green to dull whitish, smooth, the apiculate apex up to 0.1 mm long; stamens 1, 2, or 3; filaments dirty white to light brown, 2–3 mm long; anthers linear oblong, 0.8–1.1 mm long, the connective tip reddish, up to 0.1 mm long. Styles 0.4–1.4 mm long; stigmatic branches 2, 1.4–2 mm long; achenes lenticular, broadly ovate, 1.1–1.2 mm long, 0.75–0.8 mm wide, the apex obtuse, the style persistent, the base cuneate to substipitate, surface essentially smooth, light brown.

DISTRIBUTION.— Restricted to wet, open areas near the Iglesias Bay waterfall. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Holst and Soto s.n.*; *Jiménez 3204*; *Pittier 16272*; *Quesada 1067*; FTG: *Trusty 401*; INB: *Quesada 1067*; NY: *Pittier 16272*; *Tucker s.n.*; US: *Klawe 1501*; *Pittier 16272*; *Snodgrass and Heller 944*.

138. **Rhynchospora nervosa* (Vahl) Boeck., Vidensk. Meddel. Dansk Naturhist. Føren. Kjøbenhavn 143. 1869.

DISTRIBUTION.— Rare; found in Wafer Bay on Isla del Coco. Distributed throughout the Neotropics.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Gómez 3382* (not seen).

139. **Rhynchospora polyphylla* (Vahl) Vahl. Enum. pl. 2:230. 1805.

DISTRIBUTION.— On beachside cliffs and in open areas near Wafer Bay on Isla del Coco. Distributed from southern Mexico to Peru and Brazil; also found in the Antilles.

SPECIMENS EXAMINED.— FTG: *Trusty 238*; *Trusty 400*; *Trusty 534*; INB: *Quesada 1068*; *Quesada 1076*; US: *Gómez 3277*; *Klawe 1495*.

140. **Rhynchospora pubera* (Vahl) Boeck. subsp. *parvula* (Vahl) Boeck., Linnaea 37:528. 1873.

DISTRIBUTION.— Found in open areas along the trail from Wafer Bay to Chatham Bay on Isla del Coco. Distributed from Costa Rica to Colombia and Venezuela.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 408*.

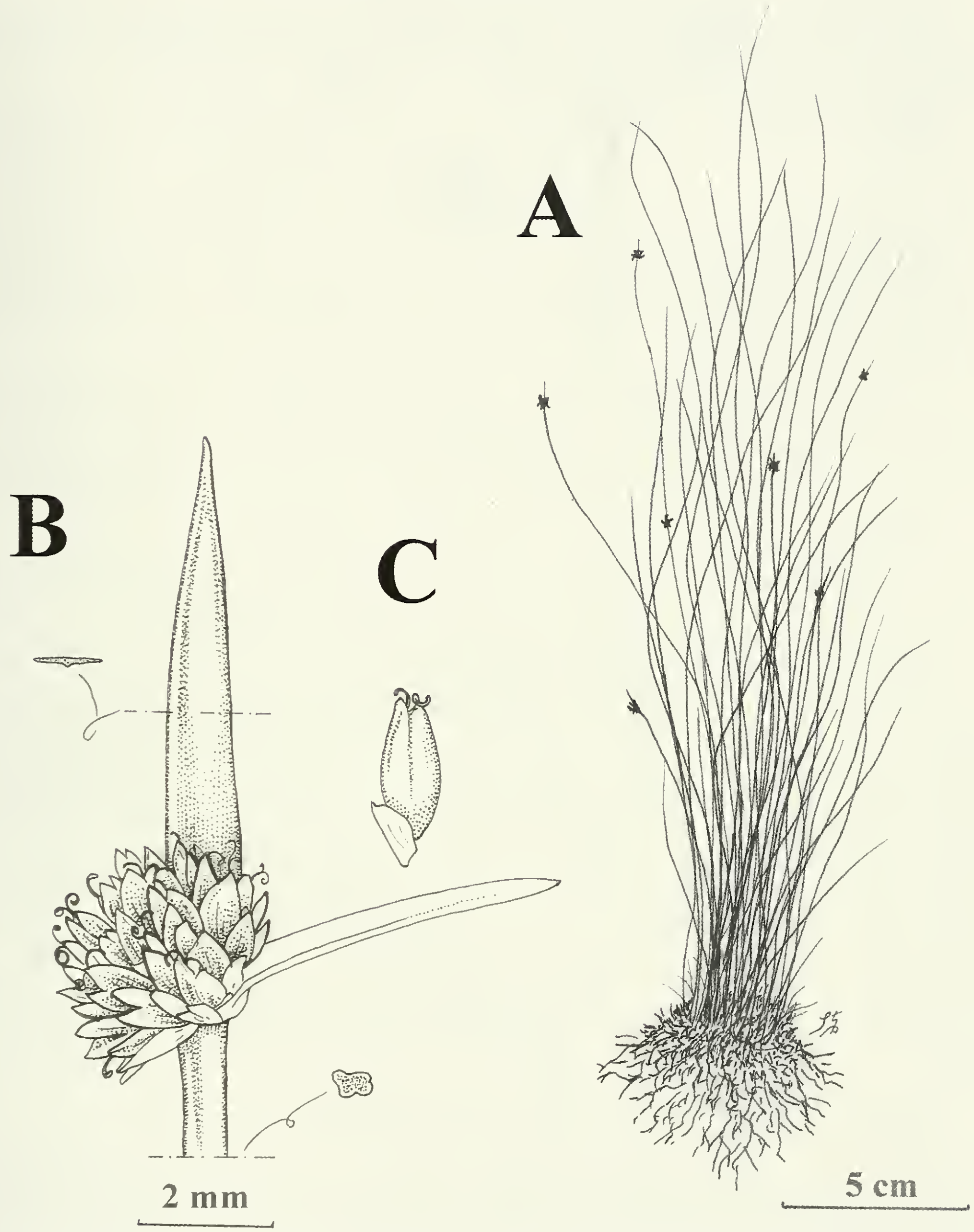

FIGURE 10. *Kyllinga nudiceps* (drawn from *Trusty 401*). A. Habit of fertile plant. B. Close up of inflorescence showing cross-sections of inflorescence bract and culm. C. Close up of single spikelet.

141. *_Scleria secans_ (L.) Urb., Symb. Ant. 2:169. 1900.

Distribution.— Rare on Isla del Coco; found only near the remains of a World War II airplane on Cerro Iglesias. Native from Mexico to Bolivia and Brazil, also in the West Indies.

Remarks.— First report for Isla del Coco.

Specimens examined.— FTG: _Trusty 272._

EUPHORBIACEAE

1. Leaves conspicuously lobed 2
    2. Leaves not peltate; stamens 10 .... _Manihot esculenta_
    2. Leaves peltate; stamens numerous .... _Ricinus communis_
1. Leaves simple and not lobed.. 3
    3. Shrubs or trees 4
        4. Leaves completely green .... _Acalypha pittieri_
        4. Leaves with white, gold or red coloration 5
            5. Leaves linear, margin entire to subulate .... _Cordiaeum variegatum_
            5. Leaves elliptic, margins toothed .... _Acalypha wilkesiana_
    3. Herbs 6
        6. Capsules and stems pubescent .... _Chamaesyce hirta_
        6. Capsules and stems glabrous .... _Chamaesyce hyssopifolia_

142. **_Acalypha pittieri_** Pax & K. Hoffm.. Pflanzenr. IV, 147, 16:18. 1924. (Fig. 11)

Type: _Pittier 16246_ (holotype: US!; isotype: GH!)

Shrub; branches velvety-pubescent; plants monoecious or dioecious; stipules 3–12 mm × 2 mm, ovate-lanceolate and acuminate, scarious, pubescent on the midrib and margins; leaves with petioles 6–14 (23) cm long, densely pubescent, small glands present at the apex; leaf blades elliptic to ovate, 10–20 × 4–8 cm, apex cuspidate-acuminate 1–2.3 mm long, base widely obtuse to slightly cordate, margins serrate with 27–55 teeth/side, upper side of leaf sparsely pubescent on major veins with hairs to 1mm, lower side densely pubescent with hairs 1–2 mm long, without glands, basally palmate to subpalmate, 5-nerved, secondary veins 8–9 on each side; staminate inflorescence unknown; pistillate spike (6) 9–12.5 cm long and 3–6 mm wide, axillary, densely pubescent, extremely delicate, loosely bractate, the bracts small, 1-flowered; female flowers sessile; sepals ovate, white ciliate; ovary 0.5 × 0.5 mm globose, glabrous to verrucose; styles 2–3 mm long, 8–12 laciniate, branches exerted, reddish; fruits not enclosed in bracts, peduncles .5–2 mm long; sepals reflexed, fruits globose 1–1.5 mm in diameter; seeds 0.8 mm, smooth, ovoid-globose, light brown.

Distribution.— Rare; near the coast in Wafer Bay. Endemic to Isla del Coco.

Remarks.— This species was reduced to the synonomy of _A. macrostachya_ Jacq. by Burger and Huft (1995) but upon examination of the type specimen, it is recognized as a distinct species by its thin, delicate inflorescences, sessile flowers and fruits which are not enclosed in enlarged bracts. This species has not been collected from Cocos Island since 1902. This species was published under the name _A. bisetosa_ Bert. in Stewart (1912) and Svenson (1935).

Specimens examined.— CAS: _Stewart 300_; GH: _Pittier 16246_; US: _Pittier 16246_ (photo).

143. *_Acalypha wilkesiana_ Müll. Arg. in DC., Prodr. 15(2):817. 1866.

Distribution.— No longer occurs on Isla del Coco but previously found near habitations Svenson (1935). Native to the Pacific Islands but cultivated throughout the world.

Specimens examined.— BKL: _Svenson 319_; US: _Howell 10172._

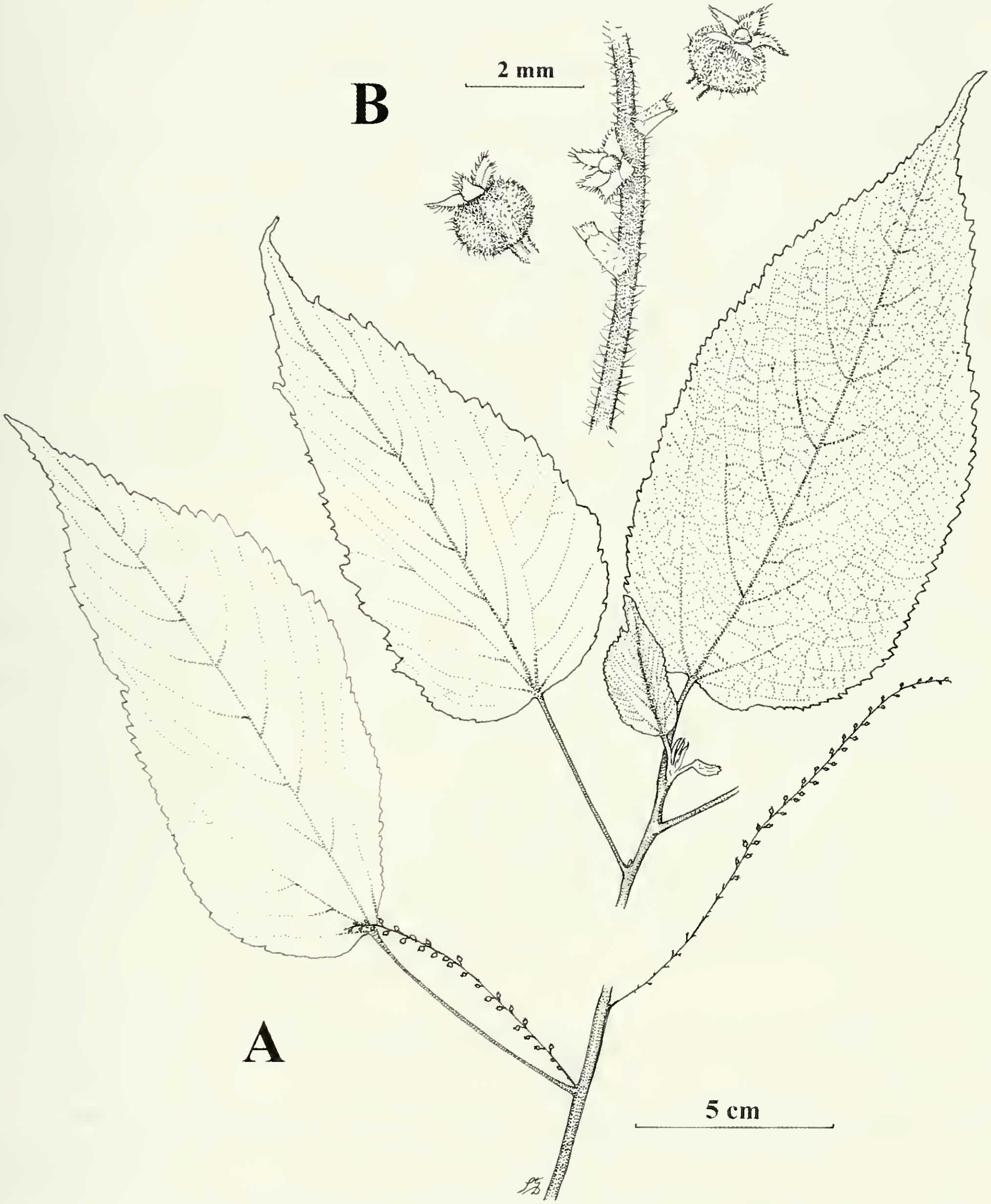

FIGURE 11. *Acalypha pittieri* (drawn from *Stewart 300*). A. Branch of plant including pistillate inflorescences. B. Portion of pistillate branch with young fruits.

144. **Chamaesyce hirta* (L.) Millsp., Publ. Field Columbian Mus. Bot. ser. 2:303. 1909.
Euphorbia hirta L.; *E. pilulifera* L.

Distribution.— Common in disturbed and cleared areas on Isla del Coco. *C. hirta* is a pantropical weed.

Specimens examined.— CR: *Gómez-Laurito 6928*; FTG: *Trusty 89*; INB: *Quesada 1041*; *Rojas 3707*; US: *Foster 4146*; USJ: *Soto s.n.*

145. **Chamaesyce hyssopifolia* (L.) Small, Bull. New York Bot. Gard. 3:429. 1905.

Distribution.— Common in disturbed and cleared areas on Isla del Coco. Found throughout tropical America and adventive in the Old World.

Remarks.— First report for Isla del Coco.

Specimens examined.— CR: *L. González 649*; *Quesada 1038*; *Rojas 3715*; FTG: *Trusty 74*; INB: *Quesada 1038*; *Rojas 3715*; USJ: *Soto s.n.*

146. **Codiaeum variegatum* (L.) Juss., Euphorb. Gen. 80, III, pl. 9, f. 30. 1824.

Distribution.— Cultivated on Isla del Coco near the Wafer Bay ranger station. Native to the Pacific Islands but widely cultivated throughout the world.

Remarks.— First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 305*.

147. **Manihot esculenta* Crantz, Inst. Rei. Herb. 1:167. 1766.

Distribution.— Cultivated on Isla del Coco near the Wafer Bay ranger station. Native to South America but widely cultivated in the tropics.

Remarks.— This species is reported to have become naturalized in Hawaii (Swearingen 2003) and should therefore be monitored closely on Isla del Coco.

Specimens examined.— FTG: *Trusty 82*.

148. **Ricinus communis* L., Sp. Pl. 1007. 1753.

Distribution.— Previously cultivated in Wafer Bay on Isla del Coco. Native to East Africa but now widely distributed throughout the world.

Specimens examined.— USJ: *Gómez s.n.*

FABACEAE

1\. Leaves simple . . . . *Dalbergia brownei*
1\. Leaves compound 2
  2. Vines 3
    3. Leaves trifoliolate 4
      4. Stems and petioles bearing conspicuous, spreading, brownish trichomes . . . . *Vigna vexillata*
      4. Stems and petioles lacking spreading, brown trichomes 5
        5. Inflorescence erect; legumes not covered in irritating trichomes . . . . *Canavalia maritima*
        5. Inflorescence pendent; legumes densely covered in irritating trichomes 6
          6. Flowers yellow . . . . *Mucuna sloanei*
          6. Flowers pinkish . . . . *Mucuna mutisiana*
    3. Leaves bipinnate 7
      7. Spines present . . . . *Caesalpinia bonduc*
      7. Spines absent . . . . *Entada monostachya*

2. Herbs, shrubs or trees 8
8. Shrubs or trees 9
9. Leaves bipinnate .... *Zapoteca tetragona*
9. Leaves pinnate 10
10. Stamens united .... *Erythrina fusca*
10. Stamens free 11
11. Leaflets 8–12; legume compressed and flat 12
11. Leaflets 4–8; legume cylindrical..................................... *Cassia fistula*
12. Foliage and inflorescence densly stellate pubescent
.... *Caesalpinia eriostachys*
12. Foliage and inflorescence without stellate hairs . . . *Senna reticulata*
8. Herbs 13
13. Leaflets often emarginate at the apex .... *Desmodium adscendens*
13. Leaflets not emarginate at the apex 14
14. Leaves strictly trifoliolate .... *Desmodium incanum*
14. Leaves 1–3 foliolate .... *Desmodium procumbens* var. *longipes*

149. *Caesalpinia bonduc* (L.) Roxb., Fl. Ind., ed. 2:362. 1832.

C. bonducella (L.) Fleming

DISTRIBUTION.— Infrequent; found along the rocky beachfront of Isla del Coco. Distributed in the tropics and subtropics of the world.

REMARKS.— This species was published under the name *C. crista* L. in Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— FTG: *Trusty 454*; GH: *Pittier 16281*; INB: *Quesada 1035*; US: *Klawe 1559*; *Pittier 16281*; US: *Klawe 1559*; *Pittier 16281*; USJ: *Soto s.n.*

150. *Caesalpinia eriostachys* Benth., Bot. Voy. Sulphur 88. 1844.

DISTRIBUTION.— Unknown distribution on Isla del Coco.

REMARKS.— This species was reportedly collected by Barclay both on Isla del Coco and the Nicoya peninsula of Costa Rica. It is a typical dry forest species on the mainland and we believe the specimen from Isla del Coco may have been mislabeled. No other collections have been made from the island.

SPECIMENS EXAMINED.— K: *Barclay s.n.* (not seen).

151. *Canavalia maritima* (Aubl.) Thouars, J. Bot. Agric. 1:80–81. 1813.

C. rosea (Sw.) DC.

DISTRIBUTION.— Frequent; found along the rocky beachfront and near the lower part of the Rio Genio in Wafer Bay of Isla del Coco. Widely distributed along beaches in the tropics and warm regions of the world.

SPECIMENS EXAMINED.— FTG: *Trusty 234*; *Trusty 484*; US: *Klawe 1560.*

152. **Cassia fistula* L., Sp. Pl. 377–378. 1753.

DISTRIBUTION.— Cultivated in Wafer Bay on Isla del Coco. Native to Southeast Asia but cultivated in tropical areas throughout the world.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 197.*

153. *Dalbergia monetaria* L. f., Suppl. Pl. 317. 1781 [1782].

DISTRIBUTION.— Collected along the Sucio River in Chatham Bay on Isla del Coco. Distributed from Florida and southern Mexico to Colombia and Peru, also in the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Quesada 1106*; INB: *Quesada 1106.*

154. **Delonix regia* (Bojer ex Hook.) Raf., Fl. Tellur. 2:92. 1836 [1837].

DISTRIBUTION.— Cultivated on Isla del Coco near the Wafer Bay ranger station. Native of Madagascar but planted in most tropical regions of the world. Distributed from Texas and Mexico thoughout the West Indies and Central and South America; introduced and cultivated worldwide.

SPECIMENS EXAMINED.— CR: *Lépiz 363*; *Quesada 1054*; INB: *Lépiz 363*; *Quesada 1054* USJ: *Lépiz 363.*

155. **Desmodium adscendens* (Sw.) DC., Podr. 2: 332. 1825.

DISTRIBUTION.— Common on Isla del Coco in full sun along the disturbed part of the trail between Chatham and Wafer Bays. Distributed from Mexico to South America, the West Indies, and tropical Africa.

SPECIMENS EXAMINED.— CR: *Quesada 1101*; FTG: *Trusty 103*; INB: *Lépiz 368*; *Lépiz 370*; *Quesada 1101.*

156. *Desmodium incanum* DC., Prodr. 2:332. 1825.

Desmodium canum (G.F. Gmel) Shinz & Thellung

DISTRIBUTION.— Common in full sun on Isla del Coco along the disturbed part of the trail between Chatham and Wafer Bays. Distributed throughout the New World tropics and tropical Africa.

SPECIMENS EXAMINED.— CR: *Gómez-Laurito 6952*; *Jiménez s.n.*; *Quesada 1100*; FTG: *Trusty 257*; *Trusty 364*; INB: *González 1153*; *Lépiz 369*; *Quesada 1100*; USJ: *Soto 3857*; *Soto s.n.*

157. **Desmodium procumbens* var. *longipes* (Schindl.) B. G. Schub. Contr. Gray Herb. 129: 8–11. 1940.

DISTRIBUTION.— Common on Isla del Coco in full sun along the disturbed part of the trail between Chatham and Wafer Bays. Distributed from northern Mexico to northern South America; also in the Old World tropics.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 348.*

158. *Entada gigas* (L.) Fawc. & Rendle, Fl. Jamaica 4:124. 1920.

DISTRIBUTION.— Common throughout Isla del Coco forming large lianas in the closed forest. Distributed in Central America and tropical South America, the West Indies, and West Africa.

SPECIMENS EXAMINED.— CR: *Rojas 3690*; FTG: *Trusty 300*; *Trusty 403*; INB: *Lépiz 375*; *Quesada 1107*; *Rojas 3690*; USJ: *Soto s.n.*

159. *Erythrina fusca* Lour., Fl. Cochinch. 427. 1790.

DISTRIBUTION.— Infrequent; found along the shoreline in Wafer Bay in Isla del Coco. Found from Guatemala throughout the Amazon basin, the West Indies and throughout the Old World tropics.

SPECIMENS EXAMINED.— CR: *Quesada 1132*; *Sánchez 3*; FTG: *Trusty 220*; INB: *Quesada 1132.*

160. *Mucuna mutisiana* (Kunth) DC., Prodr. 2:406. 1825.

DISTRIBUTION.— Frequent in Isla del Coco along the beachfront at Wafer Bay. Distributed from Panama to Venezuela.

REMARKS.— R. Soto (Government of Costa Rica 1996) stated that the island populations of this species have undergone a change in floral color compared with mainland populations. He suggested that this may be due to a change in pollinator.

SPECIMENS EXAMINED.— CR: *Quesada 1025*; FTG: *Trusty 175*; INB: *Quesada 1025*.

161. *Mucuna sloanei* Fawc. & Rendle, J. Bot. 55:36. 1917.

M. urens (L.) DC.

DISTRIBUTION.— Frequent in Isla del Coco along the beachfront at Wafer Bay. Distributed in Central and South America, the Antilles and Africa.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 235*; INB: *Soto 1*.

162. *Senna reticulata* (Willd.) H.S. Irwin & Barneby, Mem. New York Bot. Gard. 35:458. 1982.

Cassia reticulata Willd.

DISTRIBUTION.— Cultivated on Isla del Coco near ranger station in Wafer Bay. Native from Mexico to Bolivia and Brazil.

REMARKS.— Although this plant is found in wet areas throughout the American tropics, the Cocos Island specimens appear to be maintained in cultivation. No plants were found in the forest.

SPECIMENS EXAMINED.— FTG: *Trusty 278*.

163. *Vigna vexillata* (L.) A. Rich. in Sagra, Hist. Fis. Cuba, Bot. 10:191. 1845.

DISTRIBUTION.— Near the beach edge at the mouth of the Genio River in Wafer Bay on Isla del Coco. Native to the Old World but pantropical in distribution.

SPECIMENS EXAMINED.— USJ: *Soto 3864*.

164. *Zapoteca tetragona* (Willd.) H. M. Hern., Ann. Missouri Bot. Gard. 73:757. 1986 [1987].

DISTRIBUTION.— Collected once on Isla del Coco near Chatham Bay. Distributed from Mexico to Ecuador.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Quesada 1135*; INB: *Quesada 1135*.

GENTIANACEAE

165. *Voyria aphylla* (Jacq.) Pers., Syn. Pl. 1:284. 1805.

DISTRIBUTION.— Infrequent in the closed canopy forest between 200–450 msl on Isla del Coco. Distributed from throughout tropical America and the West Indies.

SPECIMENS EXAMINED.— FTG: *Trusty 51*; INB: *González 1159*.

GESNERIACEAE

166. *Kohleria spicata* (Kunth) Oerst., Centralamer. Gesner. 27. 1858.

K. longifolia (Lindl.) Hanst. var. *petiolaris* (Benth.) C. V. Morton

DISTRIBUTION.— Frequent along the rocky beachfront around Isla del Coco. Distributed from southern Mexico to northern South America.

SPECIMENS EXAMINED.— CR: *Gómez 3296*; FTG: *Trusty 232*; *Trusty 451*; *Trusty 464*; GH: *Pittier 16256*.

HUMIRIACEAE

167. ***Sacoglottis holdridgei*** Cuatrec., Ciencia (Mexico) 23:138–139. 1964. (Fig. 12)

TYPE: *Holdridge 5164* (holotype: US).

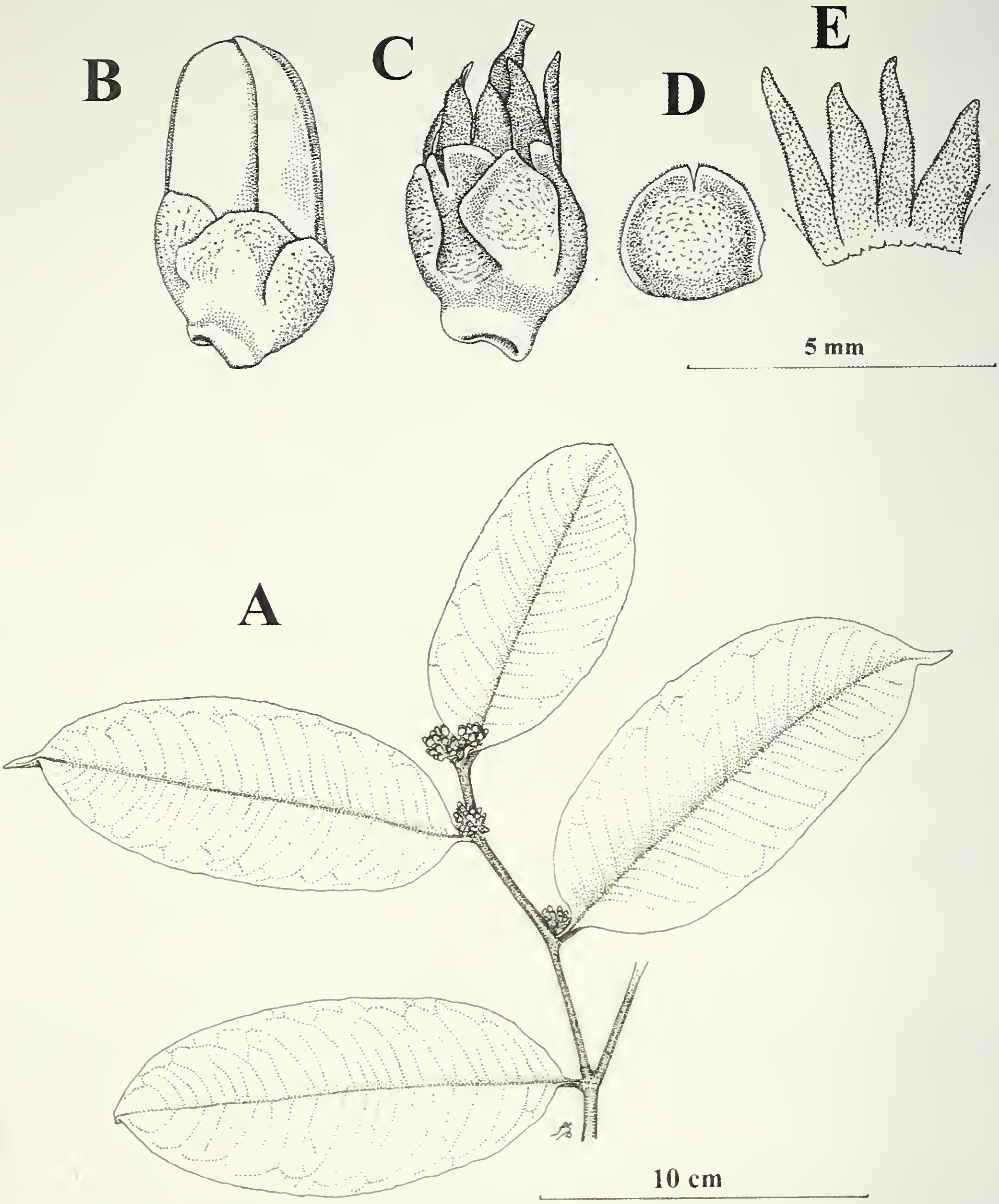

FIGURE 12. *Sacoglottis holdridgei* (drawn from *Trusty 453*). A. Branch of plant showing axillary inflorescences. B. Close up of closed flower bud. C. Close up of flower bud with petals removed. D. Sepal. E. Anther filaments lacking thecae.

Medium to large trees, to 25 m tall and with trunks to 1 m dbh, leafy branchlets with internodes 1–3.5 cm long, 1.5 mm thick, glabrous, subterete; stipules 0.5–1 mm long, caducous. Leaves alternate and distichous, petioles 4–7 mm long, 2–4 mm thick, with adaxial ridges continuous with the lamina margins, glabrous; leaf blades 7–13 (15) cm long, 4.2–6.5 (8) cm borad, oblong-ovate to ovate-elliptic, abruptly short-acuminate at the apex, rounded to truncate at the base, margin entire or slightly sinuate-crenate, minutely glandular punctate at the margin, drying dark grayish brown to almost black above, paler beneath, glabrous above and below, with 8–11 major secondary veins on each side, the sentral secondaries arising at angles of 70–90º, weakly loop-connected near the margin. Inflorescences axillary, 0.5–3 cm long, cymose-paniculate, subsessile or sessile (and appearing as several inflorescences in the leaf axil), peduncle 0–4 mm long, branches dichotomous, 1–4 mm long, sparsely and minutely papillate-puberulent, bracts ca. 2.5 mm long, 1 mm broad, deciduous, pedicels ca. 0.5 mm long. Flowers green to greenish yellow, calyx 1.7–2 mm high, calyx lobes ca. 2 mm broad, broadly rounded and suborbicular, glabrous but minutely ciliolate along the edge; petals ca. 5.5 mm long and 2 mm broad, narrowly oblong; stamens 10, glabrous, the longer filaments 4 mm long and sepal-opposed, the shorter filaments 3 mm long and petal-opposed, anthers ca. 1 mm long, ovate, thecae orange, attached at the base of the connective, annular disc cupulate, ca. 0.8 mm high, with denticulate margin; ovary ca. 1.5 mm long, oviod, style ca. 2.5 mm long, columnar. Fruits 32–40 mm long, 21–32 mm in diameter, oblong-ellipsoid, sepals persisting at the base, exocarp 2–4 mm thick, endocarp woody, irregulary 5 septate, resin vesicles with lustrous interior surfaces; seeds ca. 12 mm long, 4 mm in diameter, oblong.

DISTRIBUTION.— Extremely common throughout the island. Endemic to Isla del Coco.

REMARKS.— The name Isla del Coco is a misnomer from the original map in 1546 where the island was called 'Ile de Cocques" which is French for "seed island." Those seeds are most likely those of *S. holdridgei*, which are abundant along the beach and throughout the island.

SPECIMENS EXAMINED.— CR: *Danphin 1091*; *Dressler 4458*; *Dressler 4467*; *Foster 4126*; *Gómez 3298*; *Gómez 18055*; *Gómez-Laurito 6934*; *Gómez-Laurito 6966*; *González 1149*; *Jiménez 3179*; *Lépiz 328*; *Murawski 348*; *Poveda 813*; *Quesada 1013*; *Rojas 3631*; *Rojas 3654*; FTG: *Trusty 59*; *Trusty 162*; *Trusty 261*; *Trusty 453*; INB: *González 1149*; *Lépiz 328*; *Quesada 1013*; *Rojas 3631*; *Rojas 3654*; NY: *Dressler 4458*; *Dressler 4467*; *Foster 4126*; *Gómez 3298*; *González 1149*; *Rojas 3631*; USJ: *Castaing s.n.*; *Poveda 813*; *Soto 3859*.

LAMIACEAE

1. Flowers in compact heads . . . . *Hyptis capitata*
1. Flowers not in compact heads . . . . *Salvia occidentalis*

168. **Hyptis capitata* Jacq., Coll. 1:102. 1787.

DISTRIBUTION.— Common in open areas along trails on Isla del Coco. Found from Mexico to Colombia, Venezuela, Ecuador, and Peru; also in the West Indies, Asia and Polynesia.

SPECIMENS EXAMINED.— CR: *Gómez 3293*; *Sánchez 19*; *Soto s.n.*; FTG: *Trusty 253*; *Trusty 301*; *Trusty 446*; INB: *Quesada 1059*.

169. **Salvia occidentalis* Sw., Prodr. 14. 1788.

DISTRIBUTION.— Locally common on Isla del Coco near the beachfront in Wafer Bay. Distributed throughout the American tropics.

REMARKS.— This is probably a very recent introduction by humans to Isla del Coco due to the recent collection by us and its restricted distribution on the island near human settlements. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 350.*

LAURACEAE

1. Leaf blades densely pubescent on the lower surface .... *Persea americana*
1. Leaf blades essentially glabrous.. *Ocotea insularis*

170. *Ocotea insularis* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5:271. 1889.

DISTRIBUTION.— Common throughout Isla del Coco from 0–400 msl. Distributed from northern Costa Rica to Ecuador.

REMARKS.— Originally described from Isla del Coco, *O. insularis* has been found in continental Central and South America.

SPECIMENS EXAMINED.— CR: *Dauphin 1052*; *Dauphin 1181*; *Foster 4114*; *Gómez 18041*; *Gómez-Laurito 6938*; *Gómez-Laurito 6946*; *Howell 10185*; *Jiménez 3183*; *Poveda 821*; *Rojas 3676*; *Rojas 3682*; *Sánchez 23*; FTG: *Trusty 173*; *Trusty 312*; *Trusty 339*; *Trusty 502*; INB: *González 1155*; *Lépiz 374*; *Quesada 1020*; *Rojas 3671*; *Rojas 3676*; *Rojas 3682*; USJ: *Gómez-Laurito 6938*; *Gómez-Laurito 6946*; *Poveda 821*; *Soto 3853.*

171. **Persea americana* Mill., Gard. Dict. Ed. 8. 1768.

DISTRIBUTION.— Persisting from cultivation on Isla del Coco in the clearing near the radio tower in Chatham Bay. Native to the Mexico and Central America but cultivated widely in the tropics and subtropics.

SPECIMENS EXAMINED.— CR: *Gómez 18054*; FTG: *Trusty 522*; INB: *González 1144*; USJ: *Soto s.n.*

MALVACEAE

1. Fertile stamens as many as petals .... *Theobroma cacao*
1. Fertile stamens not equal in number to petals 2
  2. Leaf blades not toothed 3
    3. Flowers white; fruit densely woolly within .... *Ochroma pyramidale*
    3. Flowers yellow turning red with age, fruit not woolly within
    .... *Talipariti tilliaceum* var. *pernambucense*
  2. Leaf blades toothed 4
    4. Epicalyx bracteoles exceeding calyx .... *Pavonia paniculata*
    4. Epicalyx bracteoles shorter than calyx or lacking 5
      5. Flowers red; staminal tube long-exerted; cultivated ...... *Hibiscus rosa-sinensis*
      5. Flowers yellow-orange or pink; staminal tube not exerted; not cultivated 6
        6. Leaves simple; narrowly ovate to elliptic..................... *Sida acuta*
        6. Leaves simple to lobed; widely ovate or angulate .... *Urena lobata*

172. **Hibiscus rosa-sinensis* L. var. *rosa-sinensis*, Sp. Pl. 694. 1753.

DISTRIBUTION.— Cultivated on Isla del Coco at the Wafer Bay ranger station. Native to tropical Asia but now widespread as an ornamental.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 199.*

173. *Ochroma pyramidale* (Cav. ex Lam.) Urb., Repert. Spec. Nov. Regni Veg. Beih. 5:123. 120.

O. lagopus Sw.

DISTRIBUTION.— Frequent on the rocky shores of the island. Native to the New World and pantropical in cultivation.

REMARKS.— The Cocos Island finch (*Pinaroloxias inornata*) has been observed drinking nectar from the flowers of *O. pyramidale* by the authors.

SPECIMENS EXAMINED.— CR: *Gómez 3274*; FTG: *Trusty 233.*

174. *Pavonia paniculata* Cav., Diss. 3:135, t. 46, f. 2. 1787.

DISTRIBUTION.— Found in the disturbed areas in Wafer Bay on Isla del Coco. Distributed from Mexico to Argentina and the Greater Antilles.

SPECIMENS EXAMINED.— GH: *Pittier 16243.*

175. **Sida acuta* Burm.f., Fl. Ind. 147. 1768.

DISTRIBUTION.— Infrequently found in cleared areas on Isla del Coco near housing of the Wafer Bay ranger station. Pantropical in distribution.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 81.*

176. *Talipariti tiliaceum* (L.) Fryxell var. *pernambucense* (Arruda) Fryxell, Contr. Univ. Michigan Herb. 23:262. 2001.

Hibiscus tiliaceus L.

DISTRIBUTION.— Forming dense stands on Isla del Coco near the bayshore and in abandoned agricultural areas in Wafer and Chatham Bays. Found from Mexico to Brazil; also the West Indies; occasionally cultivated.

SPECIMENS EXAMINED.— CR: *Gómez 3299*; *Gómez-Laurito 6953*; *Lépiz 361*; *Quesada 1110*; *Rojas 3713*; *Sánchez 7*; FTG: *Trusty 39*; *Trusty 221*; INB: *González 1191*; *Lépiz 361*; *Quesada 1110*; *Rojas 3713*; USJ: *Soto 3852*; *Soto s.n.*

177. **Theobroma cacao* L., Sp. Pl. 782. 1753.

DISTRIBUTION.— Persisting from cultivation on Isla del Coco. Found in the former agricultural area in Wafer Bay. Native to the New World tropics but cultivated worldwide.

REMARKS.— The fruits of *T. cacao* are eaten by the rats on the island (J. Trusty, pers. obs.).

SPECIMENS EXAMINED.— FTG: *Trusty 228*; *Trusty 493.*

178. **Urena lobata* L., Sp. Pl. 692. 1753.

DISTRIBUTION.— Common in disturbed and successional areas throughout Isla del Coco. A pantropical weed.

SPECIMENS EXAMINED.— CR: *Gómez 3303*; *González and Sierra 647*; FTG: *Trusty 131*; *Trusty 223*; *Trusty 442*; INB: *González 1206*; *Quesada 1122*; USJ: *Soto s.n.*

MARCGRAVIACEAE

179. ***Marcgravia waferi*** Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 18:698. 1937. (Fig. 13)

TYPE: *Svenson 327* (holotype: F).

Vine, leaves dimorphic, juvenile leaves small, rotund, appressed to object, adult leaves with short thick petiole, coriaceous, lamina lanceolate-oblong ca. 6.5 × 2.5 cm, apex acute to shortly obtuse acuminate, base obtuse to subrotund, coriaceous, nerves scarcely apparent on either side, costa prominent below; inflorescence short pedunculate, umbelliform, few-flowered, pedicels 1.5–2.5 cm long, flowers obliquely affixed; tubular bracts short sitpulate 1.5 cm long, apex rounded and barely expanded; sepals 3 mm long; fruits bright red, globular 1 cm diameter, apex with a small central depression; seeds minute, numerous.

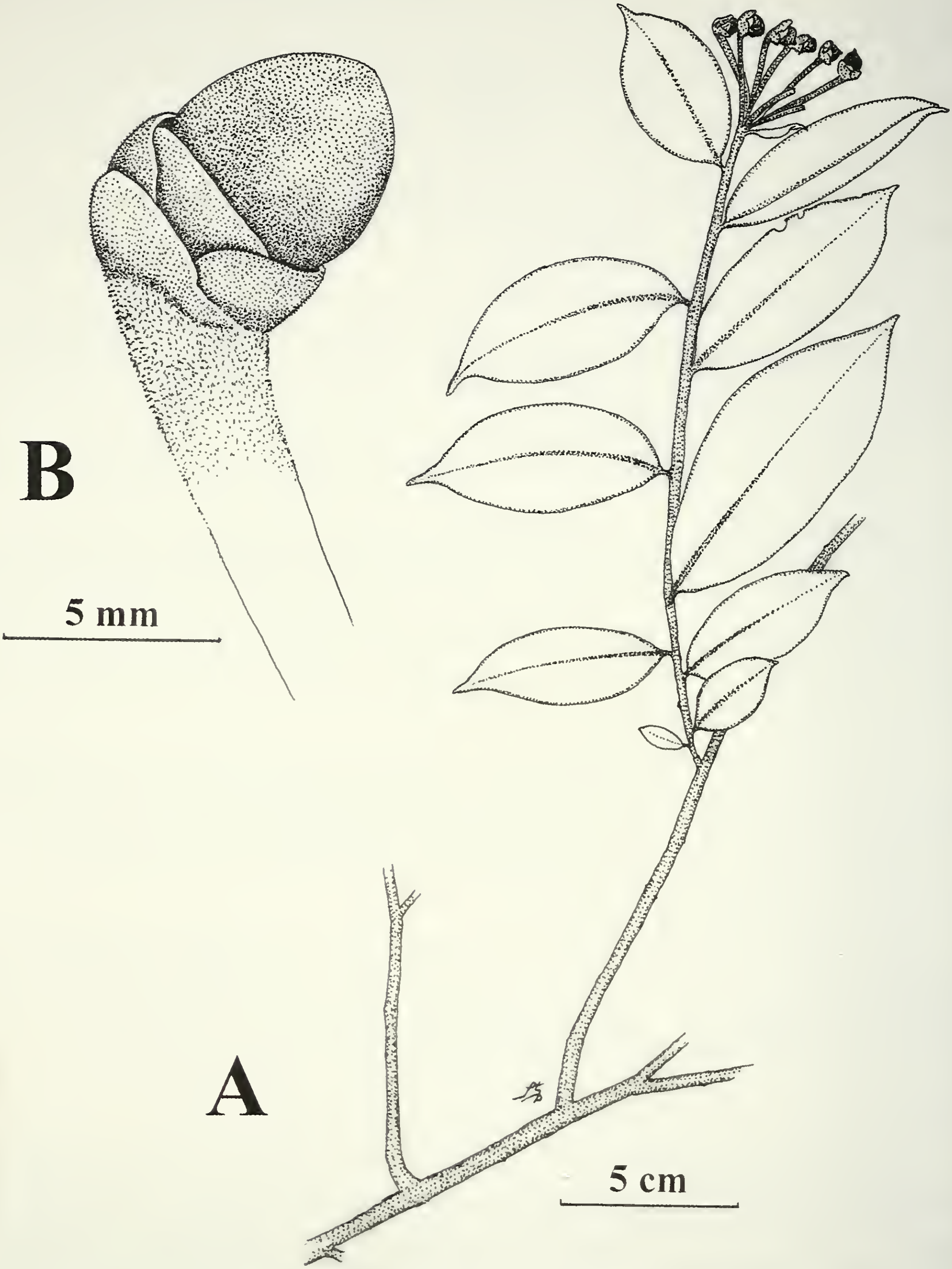

FIGURE 13. *Marcgravia waferi* (drawn from *Trusty 481*). A. Habit of plant showing terminal inflorescence. B. Single flower (stamens lacking) showing ovary.

DISTRIBUTION.— Common liana of the closed canopy forest from 50–600 msl. Endemic to Isla del Coco.

REMARKS.— This species was published under the name *M.* cf. *rectiflora* Triana & Planch. in Svenson (1935).

SPECIMENS EXAMINED.— CR: *Dauphin 1128*; *Foster 4127*; *Gómez 3261*; *Gómez-Laurito 6939*; *Gómez-Laurito 6947*; *González and Sierra 639*; *Jiménez 3190*; *Jiménez s.n.*; *Lépiz 330*; *Murawski 332*; *Murawski 347*; *Poveda s.n.*; *Rojas 3661*; *Sánchez 1*; *Valerio 1105*; FTG: *Trusty 57*; *Trusty 163*; *Trusty 481*; INB: *Dauphin 1128*; *Lépiz 330*; *Quesada 1012*; *Rojas 3661*; NY: *Foster 4127*; *Gómez 3261*; *Jiménez s.n.*; USJ: *Gómez-Laurito 6939*; *Lépiz 330*; *Soto s.n.*

MELASTOMATACEAE

1\. Fruits loculicidal capsules; ovary superior . . . . *Schwackaea cupheoides*
1\. Fruits berries; ovary wholly or partly inferior 2
  2\. Inflorescence lateral or axillary 3
    3\. Hypanthium and calyx lobes together greater than 1.2 cm long 4
      4\. Petals pubescent on both surfaces . . . . *Henriettea succosa*
      4\. Petals glabrous on both surfaces 5
        5\. Mature leaves strigose to setose abaxially . . . . *Henriettella fascicularis*
        5\. Mature leaves glabrous on both surfaces . . . . *Henriettella odorata*
    3\. Hypanthium and calyx lobes together less than 1 cm long 6
      6\. Petals obtuse or rounded 7
        7\. Herb to 0.5 m tall . . . . *Maieta poeppigii*
        7\. Shrub over 1 m tall. 8
          8\. Flowers 4-merous; leaves glabrous . . . . *Clidemia ombrophila*
          8\. Flowers 5-merous; leaves strigose . . . . *Clidemia strigillosa*
      6\. Petals acute or acuminate 9
        9\. Hypanthium densely hirsute . . . . *Ossaea bracteata*
        9\. Hypanthium glabrous . . . . *Ossaea macrophylla*
  2\. Inflorescence terminal 10
    10\. Calyx calyptrate in bud, becoming completely detached by anthesis
     . . . . *Conostegia lasiopoda*
    10\. Calyx open in bud, the lobes present at anthesis 11
      11\. Leaves green adaxially; rufous pubescent abaxially . . . . . . *Miconia dodecandra*
      11\. Leaves green on both sides 12
        12\. Leaf base decurrent onto the petiole . . . . *Miconia prasina*
        12\. Leaf base not decurrent onto the petiole 13
          13\. Shrub less than 0.5 m tall. . . . . *Miconia* sp. B
          13\. Shrub or tree greater than 1 m tall. *Miconia* sp. A

180\. *Clidemia ombrophila* Gleason, Brittonia 3:138–139. 1939.

DISTRIBUTION.— Frequent in the closed canopy forest throughout Isla del Coco from 200–500 msl. Distributed from Nicaragua to Panama.

SPECIMENS EXAMINED.— CR: *Quesada 1114*; FTG: *Trusty 187*; *Trusty 231*; INB: *Quesada 1114*; *Rojas 3779*; US: *Pittier 12373*.

181\. *Clidemia strigillosa* (Sw.) DC., Prodr. 3:159. 1828.
C. umbonata DC.

Distribution.— Common in full sun or in forest openings or edges from 50–450 msl on Isla del Coco. Distributed from southern Mexico to the Brazilian Amazon; also found in the Greater Antilles.

Remarks.— This species was published under the name *C. novemnervia* (DC.) Triana in Svenson (1935) and *C. pustulata* DC. in Fosberg and Klawe (1966).

Specimens examined.— *CR: Gómez 18048*; *Gómez 18057*; *Gómez 3264*; *Gómez-Laurito 6919*; *González 1154*; *Jiménez 3140*; *Jiménez 3149*; *Sánchez 12*; *Valerio 1104*; FTG: *Trusty 43*; *Trusty 284*; *Trusty 321*; *Trusty 445*; *Trusty 509*; GH: *Pittier 12391*; *Svenson 307*; INB: *González 1154*; *Lépiz 360*; *Quesada 1049*; *Quesada 1086*; US: *Gómez 3264*; *Holdridge 5166.*

182. *Conostegia lasiopoda* Benth., Bot. Voy. Sulphur 96. 1844.

Distribution.— Frequent in closed forest riparian areas from 30–450 msl on Isla del Coco. Found in Nicaragua, Costa Rica, Panama, northern Colombia and Ecuador.

Specimens examined.— CR: *Fournier 303*; *Gómez 3306*; *Gómez-Laurito 6923*; *Gómez-Laurito 6933*; *González 1200*; *Jiménez 3141*; *Jiménez 3148*; *Jiménez 3197*; *Lépiz 356*; *Quesada 1033*; *Quesada 1048*; *Rojas s.n.*; *Sánchez 16*; *Soto s.n.*; *Valerio 1103*; FTG: *Trusty 189*; *Trusty 309*; *Trusty 444*; *Trusty 472*; GH: *Howell 10183*; *Pittier 12372*; *Pittier 16221*; *Snodgrass and Heller 963*; INB: *González 1166*; *González 1200*; *Lépiz 356*; *Quesada 1033*; *Quesada 1048*; *Rojas 3576*; USJ: *Soto s.n.*

183. *Henriettea succosa* (Aubl.) DC., Prodr. 3:178. 1828.

Distribution.— Common subcanopy tree in closed canopy forest from 30–250 msl on Isla del Coco. Distributed from southern Mexico to the Guianas and eastern Brazil; also Trinidad and Tobago.

Remarks.— First report for Isla del Coco.

Specimens examined.— CR: *Gómez 18040*; *Gómez-Laurito 6925*; *Gómez-Laurito 6926*; *González 1160*; *Jiménez s.n.*; *Lépiz 373*; *Rojas 3655*; *Soto s.n.;* FTG: *Trusty 140*; *Trusty 172*; *Trusty 311*; *Trusty 566*; INB: *González 1160*; *Lépiz 373*; *Rojas 3655*; USJ: *Lépiz 373.*

184. *Henriettella fascicularis* (Sw.) C. Wright in Sauvalle, Anales Acad. Ci. Med. Habana 5:435. 1869.

Distribution.— Very common subcanopy tree in closed canopy forest from 30–450 msl throughout Isla del Coco. Distributed from Belize to Panama; also found in the Greater Antilles.

Remarks.— First report for Isla del Coco.

Specimens examined.— CR: *Fournier 304*; *González 1204*; *Jiménez 3152*; FTG: *Trusty 349*; INB: *González 1204.*

185. *Henriettella odorata* Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 15(3):380–381. 1941.

Distribution.— Infrequent in riparian areas along the northern part of Isla del Coco. Found in Nicaragua, Costa Rica and Ecuador.

Remarks.— First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 521*; *Trusty 546.*

186. *Maieta poeppigii* Mart. ex Cogn., Mart., Fl. Bras. 14(4):464, pl. 99. 1888.

Distribution.— Common in closed forest from 150–450 msl throughout Isla del Coco. Distributed from Colombia and Venezuela to Peru, Brazil and the Guianas.

Remarks.— This species commonly has ant associations in continental areas. No ant-plant interactions have been studied for the Cocos Island populations.

Specimens examined.— CR: *Dauphin 1174*; *Fournier 353*; *Rojas 3633*; *Soto s.n.*: FTG: *Trusty*

63; *Trusty 506*; GH: *Foster 4122*; *Pittier 12374*; *Pittier 16225*; *Svenson 401*; INB: *González 1170*; *Rojas 3633*; US: *Foster 4122*; *Holdridge s.n.*; *Pittier 12374.*

187. ***Miconia*** **sp. B**

Distribution.— Infrequently found in closed canopy forest from 50–400 msl. Endemic to Isla del Coco.

Remarks.— First report for Isla del Coco. Dr. Frank Almeda and Ricardo Kriebel will be publishing the name and description of this species.

Specimens examined.— FTG: *Trusty 68.*

188. *Miconia dodecandra* Cogn., Mart., Fl. Bras. 14(4):243. 1887.

Distribution.— Very common subcanopy tree species on Isla del Coco from 150–530 msl; forms extensive groves in the area of Cabo Atrevido. Distributed from southern Mexico through Central America to Bolivia and Southern Brazil; also the Greater Antilles, Dominica, and Trinidad.

Specimens examined.— CR: *Dauphin 1160*; *Gómez 18051*; *Quesada 1108*; *Rojas 3624*; FTG: *Trusty 60*; *Trusty 406*; *Trusty 479*; GH: *Foster 4124*; *Pittier 16223*; INB: *González 1185*; *Lépiz 329*; *Quesada 1108*; US: *Holdridge 5179.*

189. *Miconia prasina* (Sw.) DC., Prodr. 3:188. 1828.

M. pteropoda Benth.; *M. attenuata* DC.

Distribution.— Frequent throughout the island from 50–450 msl on Isla del Coco. Distributed from southern Mexico to Bolivia and Paraguay; also in the West Indies.

Specimens examined.— BKL: *Svenson 303*; CR: *Gómez 3262*; FTG: *Trusty 384*; *Trusty 470*; *Trusty 519*; USJ: *Soto s.n.*

190. ***Miconia*** **sp. A**

Distribution.— Rare; found on Cerro Iglesias and also on ridge tops near Iglesias Bay. Endemic to Isla del Coco.

Remarks.— First report for Isla del Coco. Dr. Frank Almeda and Ricardo Kriebel will be publishing the name and description of this species.

Specimens examined.— FTG: *Trusty 270*; *Trusty 557.*

191. *Ossaea bracteata* Triana, Trans. Linn. Soc. London 28:147. 1871.

Distribution.— Common throughout Isla del Coco from 0–550 msl. Found on Isla del Coco and from Panama to Colombia and Ecuador.

Specimens examined.— FTG: *Trusty 66*; *Trusty 119*; *Trusty 285*; *Trusty 331*; *Trusty 384*; GH: *Foster 4168*; INB: *González 1179*; *Quesada 1118*; *Rojas 3694*; US: *Foster 4168.*

192. *Ossaea macrophylla* (Benth.) Cogn in A. & C.DC., Monogr. Phan. 7:1064. 1891.

Distribution.— Common throughout Isla del Coco from 0–550 msl. Distributed from Nicaragua to Colombia and Ecuador.

Remarks.— This taxon was originally described from Isla del Coco.

Specimens examined.— CR: *Dauphin 1165*; *Dressler 4472*; *Fournier 340*; *González 1141*; *González 1182*; *Lépiz 357*; *Quesada 1006*; *Rojas 3575*; *Sánchez 15*; *Soto s.n.*; FTG: *Trusty 33*; *Trusty 122*; *Trusty 251*; *Trusty 316*; *Trusty 367*; GH: *Foster 4128*; *Pittier 12381*; *Pittier 16224*; *Snodgrass and Heller 951*; INB: *González 1141*; *González 1182*; *Lépiz 357*; *Quesada 1006*; *Rojas 3575*; US: *Barclay s.n.*; *Foster 4128*; *Gómez 3302*; *Holdridge 5171*; *Jiménez 3161*; *Klawe 1550*; *Pittier 12381.*

193. *Schwackaea cupheoides* (Benth.) Cogn. in T. Durand, Index. Gen. Phan. 132. 1888.

DISTRIBUTION.— Unknown on Isla del Coco. Distributed from southern Mexico to Panama and Colombia.

REMARKS.— This species may be extinct on Isla del Coco. There is a single collection by Crossland made in 1924.

SPECIMENS EXAMINED.— BM: *Crossland 454* (not seen).

MELIACEAE

194. *Guarea glabra* Vahl, Eclog. Amer., 3:8. 1807.

DISTRIBUTION.— Locally common on Isla del Coco in Los Llanos (200–300 msl). Distributed from Mexico to Colombia, Venezuela and Ecuador; also occurs in the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 208*; *Trusty 242*; *Trusty 547*; INB: *Rojas 3657*.

MORACEAE

1. Leaves lobed . . . . *Artocarpus altilis*
1. Leaves not lobed 2
    2. Stipules scars completely encircling the stem . . . . *Ficus pertusa*
    2. Stipule scars small, linear . . . . *Brosimum* sp.

195. **Artocarpus altilis* (Parkinson ex Z.) Fosberg, J. Wash. Acad. Sci 31:95. 1941.

DISTRIBUTION.— Infrequent along the coast of Isla del Coco. Probably native to Malenesia but widely cultivated throughout the tropics of the world.

REMARKS.— These plants are apparently persisting from an early introduction or have naturalized onto Isla del Coco. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 226*.

196. *Brosimum* sp.

DISTRIBUTION.— Frequent as the largest canopy tree on Isla del Coco. More common in the northern part of the island near Cabo Atrevido.

REMARKS.— The identity of this species could not be determined. Additional collections in flower or fruit are needed to clarify its identity.

SPECIMENS EXAMINED.— BKL: *Svenson 337*.

197. *Ficus pertusa* L.f., Suppl. Pl. 442. 1781 [1782].

DISTRIBUTION.— Infrequently found on Isla del Coco near the Genio River in Wafer Bay. Distributed from Mexico to Paraguay; also occurs in the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Quesada 1069*; INB: *Quesada 1069*.

MUNTINGIACEAE

198. *Muntingia calabura* L. Sp. Pl. 509. 1753.

DISTRIBUTION.— Found near the beach edge in Wafer Bay on Isla del Coco. Widely distributed in tropical America in secondary forests.

SPECIMENS EXAMINED.— USJ: *Gómez-Laurito 6905* (not seen).

MUSACEAE

199. **Musa X paradisiaca* L., Sp. Pl. 1043. 1753.

DISTRIBUTION.— Cultivated on Isla del Coco in Chatham and Wafer Bays. Cultivated in tropical areas around the world.

SPECIMENS EXAMINED.— Not collected.

MYRSINACEAE

1. Flowers terminal, paniculate. . . . . *Ardisia cuspidata*
1. Flowers ramiflorous, simple . . . . *Myrsine pellucidopunctata*

200. ***Ardisia cuspidata*** Benth., Bot. Voy. Sulphur. 123. 1844. (Fig. 14)

TYPE: *Hinds s.n.* (holotype: BM).

Shrub to trees 1–7 m tall; branchlets slender, angulate, 2–4 mm in diam., with densely, minute furfuraceous-lepidote scales at least apically, usually glabrescent with age; leaves: with blades membranaceous, elliptic to obovate, 2.7–11.1 × 2.3–4.5 cm, apically acuminate, with an acumen 5–12 mm, basally obtuse, decurrent on the petiole to the base, conspicuously and prominently punctate and punctate-lineate, essentially glabrous above, scattered to densely, minute furfuraceous-lepidote scales below, denser along the midrib, the secondary veins 18–26 pairs, the margins entire, flat; petioles slender, marginate, 3–8 mm, glabrous above, densely, minute furfuraceous-lepidote scales below; inflorescences lateral and terminal, erect, pinnately to tripinnately paniculate, 3–7 × 3–6 cm, pyramidal, shorter than the leaves, densely, minute furfuraceous-lepidote scales, the branches loosely congested into 3–7-flowered corymbs; peduncles 5–20 mm; inflorescence branch bracts unknown, early caducous; floral bracts caducous, membranaceous, ovate to oblong, 0.5–1.2 × 0.2–0.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous, the margins irregular, minutely erose, hyaline; pedicels slender, 3.5–5 mm, prominently punctate and punctate-lineate, scattered, minute furfuraceous-lepidote scales; flowers 5-merous; calyx 1.4–1.6 mm, the tube 0.1–0.3 mm, the lobes ovate, 1.1–1.3 × 0.8–1 mm, apically acute, conspicuously and prominently punctate and punctate-lineate, glabrous within, sparsely, minute furfuraceous-lepidote scales outside, the margins entire, minutely erose, hyaline; corolla 3.3–3.5 mm, the tube 0.9–1.1 mm, the lobes lanceolate, 2.3–2.6 × 1.1–1.4 mm, apically acute, prominently punctate and punctate-lineate, glabrous, the margins entire; stamens 2.5–2.7 mm, the filaments 1.1–1.3 mm, the staminal tube 0.5–0.6 mm, the apically free portion 0.6–0.8 mm, prominently punctate and punctate-lineate, glabrous, the anthers ovate to lanceolate, 1.4–1.6 × 0.5–0.7 mm, apically apiculate, basally subcordate, the connective conspicuously punctate; pistil 4–4.4 mm, glabrous, the ovary ovate, 1–1.2 mm, the styles 2.9–3.2 mm, prominently punctate and punctate-lineate, the ovules 37–43; fruits globose, 3.5–4.5 mm in diam., conspicuously and prominently punctate and punctate-lineate, glabrous.

DISTRIBUTION.— Common in closed canopy forest and riparian areas throughout the island from 50–450 msl. Endemic to Isla del Coco.

REMARKS.— This species, previously recombined as *Icacorea cuspidata* (Benth.) Lundell, is recognized as a species of *Ardisia* by Rickertson and Pipoly (in prep.). This species was published under the name *A. compressa* Kunth in Svenson (1935) and Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— FTG: *Trusty 64*; *Trusty 177*; *Trusty 209*; *Trusty 247*; *Trusty 304*; *Trusty 313*; *Trusty 373*; *Trusty 405*; *Trusty 478*; *Trusty 516*; *Trusty 540*; INB: *Lépiz 335*; *Lépiz 349*; *Lépiz 378*; *Rojas 3670.*

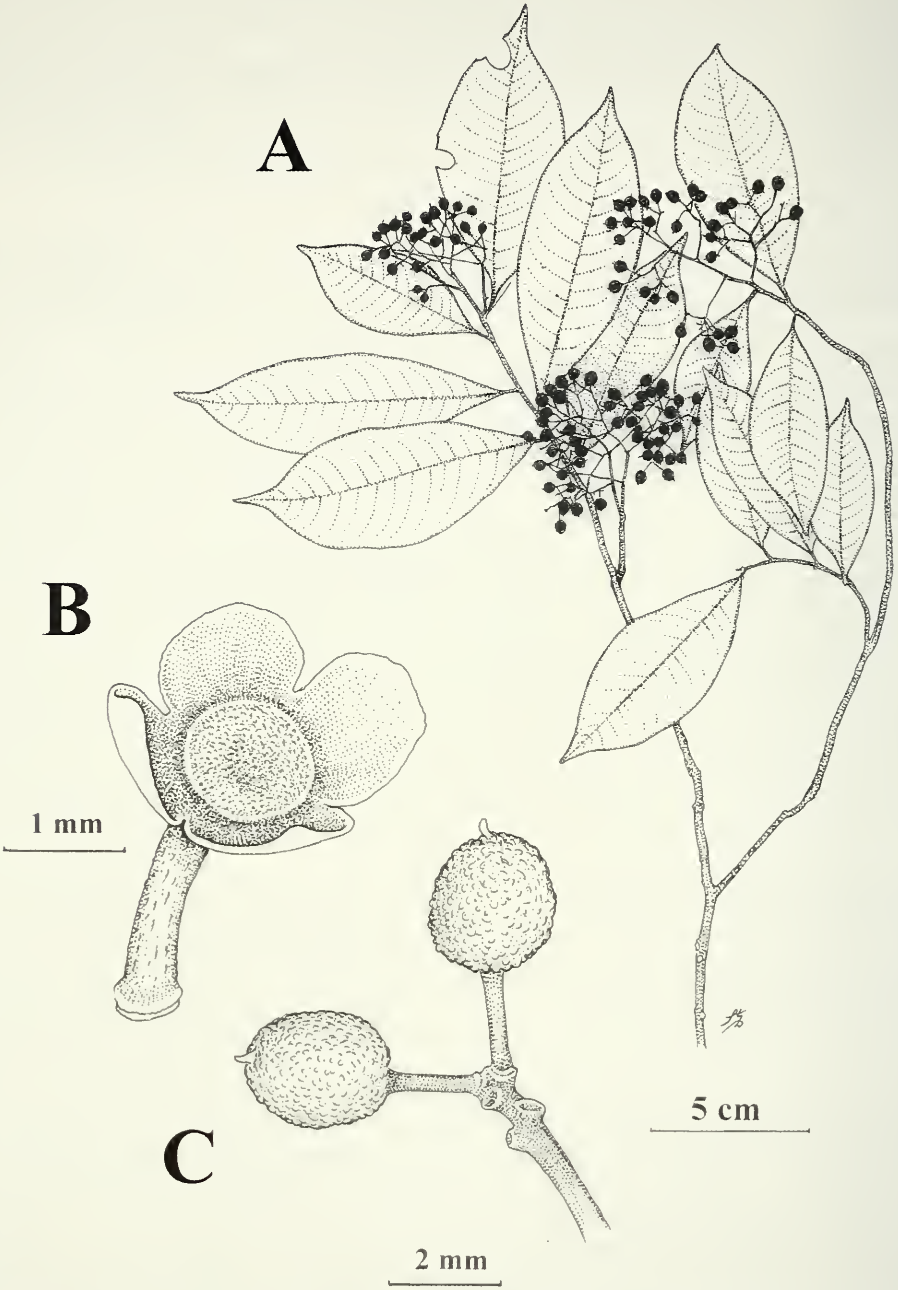

FIGURE 14. *Ardisia cuspidata* (drawn from *Trusty 209*). A. Branch of plant showing infructescences. B. Calyx of flower. C. Fruits showing punctations.

201. *Myrsine pellucidopunctata* Oerst., Vidensk. Meddel. Dansk. Naturhist. Føren. Kjobenhavn 1861:133. 1861.

DISTRIBUTION.— Infrequent in the upper elevations (350–630 msl) of Isla del Coco. Distributed from Costa Rica to Colombia.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Rojas 3693*; FTG: *Trusty 538*; INB: *Rojas 3693*.

MYRTACEAE

1. Ovules numerous, seeds many . . . . *Psidium guajava*
1. Ovules few; seeds 1 or 2 2
    2. Leaves greater than 2.5 cm wide . . . . *Eugenia pacifica*
    2. Leaves less than 2 cm wide . . . . *Eugenia cocosensis*

202. ***Eugenia cocosensis*** Barrie, Novon 15(1):11–12. 2005.

TYPE: *Foster 4129* (holotype: CR; isotypes: CAS, F, MO)

Small trees of shrubs, 4–5 m; buds, inflorescences, and emergent leaves thinly appressed-pubescent with cinereous or pale coppery, dibrachiate hairs, 0.2 mm long; branchlets compressed; bark reddish, glabrate. Leaves lanceloate or ovate, the blades 3.5–5 × 1–2 cm, 2.5–4 times as long as wide, coreiaceous, drying a concolorous olive, the petioles and midveins reddish; midvein impressed above, reased below; lateral veins 4 to 6, straight, obscure on the upper surface; marginal veins similar to the laterals and arched between them, 1–2 mm from the margins; both surfaces glabrate; glands numerous, conspicuous, usually strongly rounded; margins revolute near the base, decurrent into the inner edge of the petiole; apex acuminate; petioles 2–3 mm long, channeled dorsally, glabrate. Inflorescences axillary, racemose, solitary, appressed-pubescent with pale coppery, dibrachiate hairs; axis 1–3 mm long; flowers 2–6; bracts 0.5 mm long, persistent, ovate, the margins scarious, the apex acute; buds 2 mm long, turbinate. Flowers pedicellate, the pedicels 2 mm long, appressed-pubescent; bracteoles fused, forming an involucre 1 mm diam. dilated at anthesis, appressed pubescent on the outer surface only, the margins scarious, the apex rouned; hypanthium 1 mm long, obconic, appressed pubescent; calyx lobes in unequal pairs, 0.5–1 × 1 mm, elliptic, appressed pubescent on the outer surface, the margins scarious-ciliate, the apex rounded; petals 1 × 1 mm, ovate, the margins entire, the apex bluntly acute; disk ca. 1 mm diam., glabrous; stamens 25–30, 1 mm long; style 1.5 mm long, glabrous. Fruits 9–10 × 7–8 mm, widely ellipsoid or obovoid; pericarp think-walled, glabrous, glandular; calyx persistent, erect but inconspicuous; immature fruit orange, maturing to black.

DISTRIBUTION.— Infrequent or locally common in the closed canopy forest throughout Isla del Coco. Endemic to Isla del Coco.

REMARKS.— Barrie (2005) states that the leaf blades of *E. cocosensis* are half the size of *E. pacifica* Benth. with the petioles one third as long, the flowers are half as large and the fruits are shorter and wider. We were able to collect immature fruits of this species which were orange in color, drying black.

Specimens examined.—CR: *Quesada 1071*; FTG: *Trusty 138*; *Trusty 550;* INB: *Lépiz 345*; *Quesada 1071*

203. ***Eugenia pacifica*** Benth., Bot. Voy. Sulphur 98. 1844.

TYPE: *Barclay 2182* (holotype: BM, isotype: K!)

Shrub or tree 8 m tall. Branchlets puberlulent or almost glabrous; leaves short-petiolate, ovate, 5 cm long and 2.5 cm wide, subacuminate, cuneate, subcoriaceaous, glossy above, glabrous; petioles 6–10 mm long; peduncles axillary, very short, few flowered; flowers unknown; berries black, oblong, 10–13 mm long and 4–6 mm wide.

Distribution.— Infrequent in closed canopy forest 50–250 m on the island. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Pittier 16247*; FTG: *Trusty 343*; *Trusty 542*; K: *Barclay 2182*.

204. **Psidium guajava* L., Sp. Pl. 470. 1753.

DISTRIBUTION.— Apparently has not persisted on Isla del Coco. Cultivated throughout the tropics.

REMARKS.— This species is not currently in cultivation on the island. This species should not be cultivated on the island as it is an invasive pest plant in many island ecosystems (Pacific Island Ecosystems at Risk 2002).

SPECIMENS EXAMINED.— GH: *Howell 10184B*; USJ: *Gómez 3383*.

ONAGRACEAE

205. *Ludwigia hyssopifolia* (G. Don) Exell, Garcia de Orta 5:471. 1957.

Jussiaea linifolia Vahl

DISTRIBUTION.— Common on Isla del Coco in disturbed or cleared areas near Chatham and Wafer Bays. Pantropical in distribution.

REMARKS.— *L. hyssopifolia* is considered native here due to the early collections but is probably introduced to the island.

SPECIMENS EXAMINED.— FTG: *Trusty 113*; *Trusty 132*; *Trusty 457*; INB: *Quesada 1057*.

ORCHIDACEAE

1. Pseudobulbs present . . . . *Maxillaria parviflora*
1. Pseudobulbs absent 2
    2. Plants erect; flowers axillary . . . . *Maxillaria adendrobium*
    2. Plants pendent; flowers terminal 3
        3. Leaves greater than 6 cm long, inflorescence of 3–4 flowers . . .*Epidendrum cocoënse*
        3. Leaves less than 6 cm long, inflorescence of 1–2 flowers 4
            4. Leaves 6–8 cm long; flowers white . . . .*Epidendrum jimenezii*
            4. Leaves less than 6 cm; flowers green-yellow . . . . . .*Epidendrum insulanum*

206. ***Epidendrum cocoënse*** Hágsater, Icon. Orchid. (Mexico) 3:pl. 325. 1999.

TYPE: *Svenson 333* (holotype: AMES; isotype: AMES, BKL!)

Pendent, branching epiphytic herb to 80 cm in length. Roots only at base, 1–2 cm in width. Stems successive, produced from a subapical internode of the previous stem, there is no main stem as such, all flowering apically, 15–30 × 0.5–0.7 cm. Leaves alternate, evenly distributed throughout each stem, articulate, narrowly elliptic-lanceolate to ligulate, obtuse, subcoriaceous, up to 2.7 cm in length. Inflorescence apical, flowering only once, 5–6 cm long. Flowers 3–4, apparently successive, distichous, cream colored. Floral bracts slightly longer than the ovary, ovate, conduplicate, imbricate, 19–29 × 15–18 mm. Ovary not inflated, round, 19 × 3 mm. Sepals ovate-elliptic to ovate-lanceolate, acute, 7-veined. Petals narrowly elliptic-oblanceolate, acute, 5-veined, 10–11 × 2.5 mm. Lip entire, cordiform, elongate, 9.5 × 7 mm; callus "Y"-shaped. Column straight, short, 5.5 mm. Clinandrium reduced, erose. Capsule pyriform 28 × 12 mm with an apical neck ca. 7 mm.

DISTRIBUTION.— Common from 0 to 500 msl throughout the island. Endemic to Isla del Coco.

Remarks.— This species was published under the name *E. imbricatum* Lindl. in Svenson (1935) and Fosberg and Klawe (1966).

Specimens examined.— BKL: *Svenson 333*; *Svenson 348*; CR: *Dressler 4471*; *Gómez 3270*; *Gómez-Laurito 6914*; *Valerio 1108*; FTG: *Trusty 101*; *Trusty 167*; *Trusty 176*; *Trusty 184*; *Trusty 194*; *Trusty 195*; *Trusty 363*; *Trusty 387*; *Trusty 461*; *Trusty 483*; *Trusty 494*; *Trusty 496*; *Trusty 501*; *Trusty 510*; *Trusty 511*; *Trusty 512*; *Trusty 520*; *Trusty 544*; *Trusty 548*; *Trusty 560*; *Trusty 561*; INB: *Lépiz 339*; *Rojas 3691*; USJ: *Dressler 4471*; *Gómez 3270*; *Gómez-Laurito 6914*; *Rojas 3691*; *Sánchez 10*.

207. ***Epidendrum insulanum*** Schltr., Beih. Bot. Centralbl. 36:404. 1918. (Fig. 15)

Type: *Pittier 16350* (holotype: CR; isotype: GH!).

Pendent epiphyte, 30–60 cm or more. Stems ramified, 5–15 cm, the secondary stems shorter, Leaves long lanceolate, bilobed, those on the principle stem 4.1–5.4 × 0.7–0.9 cm, more or less equal except the basal leaves are smallest, the leaves of the secondary stems 1.7–4.0 × 0.6–0.7 cm, unequal. Inflorescence terminal, simple, flowering only once for each stem; floral bract shorter than the ovary, ca. 10 mm. Flowers one, carnose, resupinate, greenish-yellow, cerose; sepals spreading, 8–10 × 2.5–3.0 mm, ligulate-obovate, obtuse; petals spreading, 7–9 × 1.7 mm, obovate-ligulate, rounded; lip 6.5 × 4.5 mm, ovate, the base rounded, the apex obtuse; callous triangular; column erect, ca. 4 mm, thick; clinandrium truncate, toothed; ovary subsessile, glabrous ca. 7 mm long.

Distribution.— Frequent throughout the island from 200–500 msl. Endemic to Isla del Coco.

Specimens examined.— BKL: *Svenson 335*; CR: *Gómez-Laurito 6924*; FTG: *Trusty 53*; *Trusty 158*; *Trusty 218*; *Trusty 500*; GH: *Agassiz s.n.*; *Pittier 16350*; *Svenson s.n.*; INB: *Rojas 3660*; US: *Foster 4117*; *Klawe s.n.*; USJ: *Gómez-Laurito 6924*; *Soto s.n.*

208. ***Epidendrum jimenezii*** Hágsater, Icon. Orchid. (Mexico) 3:pl. 341. 1999.

Type: *Jiménez 3178* (holotype: F, isotype: CR, MO, PMA!, SEL, U, USJ!).

Epiphytic, pendent herb to 100 cm or more in length. Roots from the basal nodes of the main stems, 1.5 mm in width. Stems branching, cane-line, straight, somewhat laterally flattened up to 75 cm in lenth, the secondary flowering stems, short to 12 cm lenth, but producing a new extension from the apex. Leaves numerous, distributed throughout the stems, blade narrowly lanceolate 2.1 × 0.5 cm, apex bilobed, subcoreiaceous, those of the main stem similar except for the basal ones which are smaller, those of the branches unequal, progressively larger, except for the last one which is often reduced. Inflorescence apical, from the secondary stems, flowers only once, 3 cm in length, the base enveloped in a foliose sheath which is smaller than the leaves. Floral bract conduplicate, shorter than the ovary 11–21 mm long. Flowers 1–2, white. Ovary slightly inflated ventrally towards the middle, 10–14 mm long. Sepals partly spreading, free, narrowly ligulate-obovate, acute, with a prominent apical keel on the laterals, 11 veined, 8–10 × 2.5–3.0 mm. Petals spreading, ligulate, slightly dilated towards the apical half, obtuse, 3-veined, 9.5–10 × 1.6 mm. Lip entire, cordiform, obtuse, mucronate, 5.5 × 3.6 mm; callus "Y"-shaped, ending in a central keel. Column straight, 5 mm long. Clinandrium reduced, sinuose, with a short tooth on each side. Nectary prominent, penetrating more tha half the ovary, inflated towards the end. Capsule ovoid, 12 × 8 mm pyramidal, without pedicel, with a short apical neck 6 mm long.

Distribution.— Rare; found at below 100 msl near Wafer Bay. Endemic to Isla del Coco.

Remarks.— We were unable to locate an herbarium specimen of this species. From the photos viewed; we were unable to distinguish this species from *E. insulanum*. It is possible that this species is a hybrid between *E. cocoënse* and *E. insulanum*; although the type has white flowers, the collection listed in the protologue (*Dressler 4468*) states that this collection has green flowers, not white as in the species description.

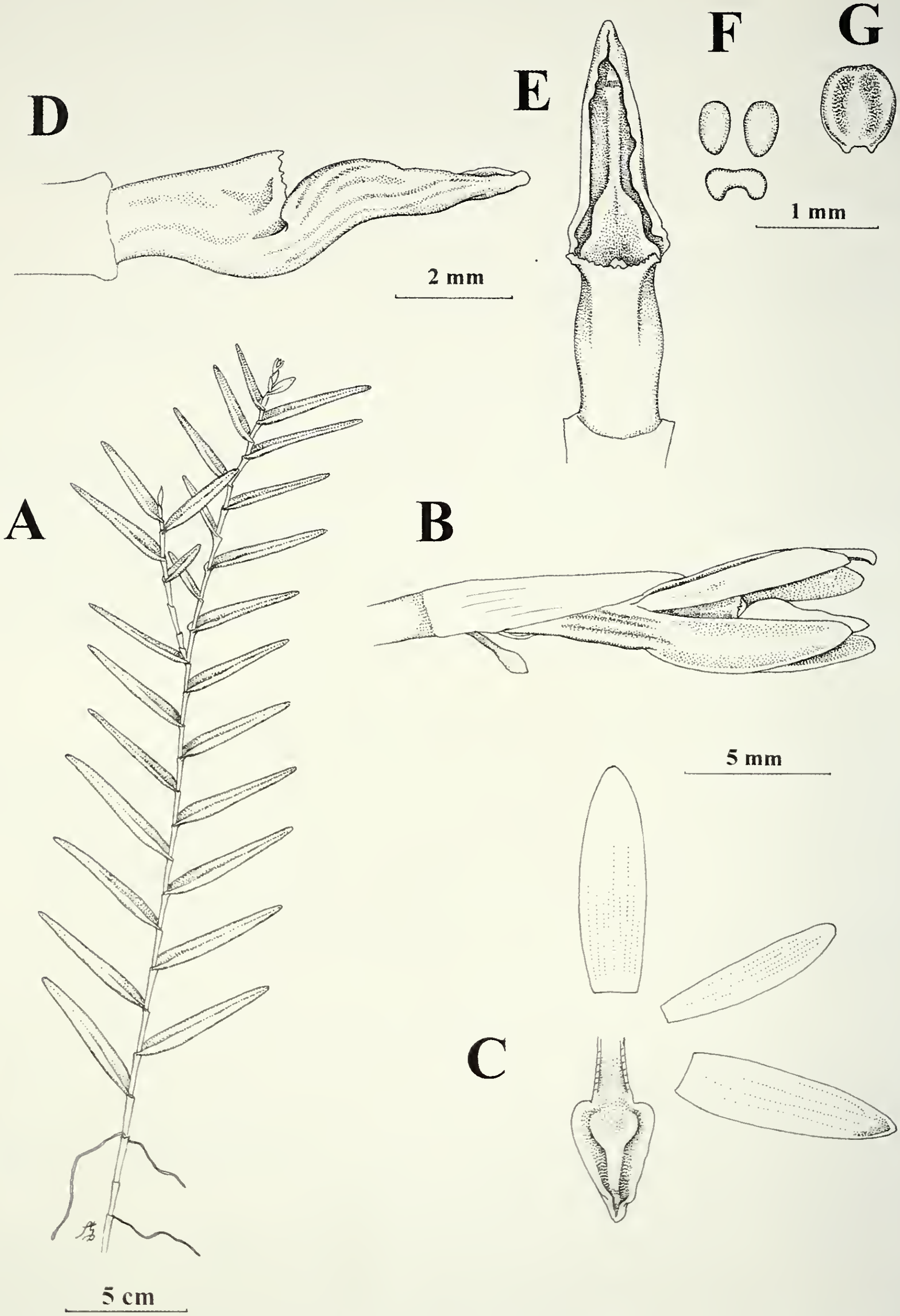

FIGURE 15. *Epidendrum insulanum* (drawn from *Trusty 53*). A. Habit of plant showing terminal inflorescence. B. Lateral view of flower. C. Diagram of flower showing petals, sepals and lip. D. Lateral view of column with attached lip. E. Ventral view of column and lip. F. Pollinia in relation to the stigmatic surface. G. Close up of pollinia.

SPECIMENS EXAMINED.— FLAS: *Dressler 4468* (photo); PMA: *Dressler 4468* (photo); *Jiménez 3178* (photo); USJ: *Jiménez 3178* (photo).

209. *Maxillaria adendrobium* (Rchb. f.) Dressler, Taxon, 13:248–249. 1964.

DISTRIBUTION.— Frequent from 300 to 630 msl throughout Isla del Coco. Distributed in Costa Rica, Panama and Ecuador; also the Dominican Republic.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 52*; *Trusty 100*; *Trusty 157*; *Trusty 495*; *Trusty 515*; *Trusty 556*; *Trusty 564*; INB: *Rojas 3692*.

210. *Maxillaria parviflora* (Poepp. & Endl.) Garay, Bot. Mus. Leafl. 21: 258. 1967.

DISTRIBUTION.— Common from 30–450 msl throughout Isla del Coco. Distributed from southern Florida, southern Mexico and Honduras to Ecuador, Peru and Brazil; also the Antilles.

REMARKS.— First report for Isla del Coco. This species was published under the name *Ornithidium* sp. aff. *stenophyllum* Schltr. in Svenson (1935) and Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— CR: *Dauphin 1175*; *Gómez 18043*; *Valerio 1086*; *Valerio 1106*; FTG: *Trusty 104*; *Trusty 156*; *Trusty 244*; *Trusty 482*; *Trusty 504*; INB: *Quesada 1081*; *Rojas 3659*; USJ: *Dauphin 1175*; *Soto s.n.*

PASSIFLORACEAE

211. **Passiflora edulis* Sims f. *flavicarpa* O. Deg., Fl. Hawaii. 250. 1932.

DISTRIBUTION.— Cultivated on Isla del Coco in Wafer Bay. Native to Brazil but cultivated widely in tropical America.

REMARKS.— This species is considered an invasive exotic in many island ecosystems (Staples et al. 2000, Space et al. 2003), and we recommend its removal. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 485*.

PHYLLANTHACEAE

212. **Phyllanthus urinaria* L., Sp. Pl. 982. 1753.

DISTRIBUTION.— Common in cleared areas on Isla del Coco. Native to tropical Asia but widely introduced throughout tropical America.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 73*; INB: *González 1194*; *Quesada 1039*.

PHYTOLACCACEAE

213. *Phytolacca rivinoides* Kunth & C. D. Bouché, Index Sem. (Berlin) 15. 1849.

DISTRIBUTION.— Frequent in full sun near trails or riparian margins on Isla del Coco. Distributed from Mexico to Boliva and the West Indies.

REMARKS.— This species was published under the name *P. icosandra* L. in Stewart (1912), Svenson (1935) and Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— BKL: *Svenson 405*; CR: *L. Gonzalez 660*; *Quesada 1062*; *Rojas 3675*; FTG: *Trusty 32*; *Trusty 471*; INB: *Quesada 1062*; *Rojas 3675*; USJ: *Soto s.n.*

PIPERACEAE

214. *Peperomia glabella* (Sw.) A. Dietr., Sp. Pl. 1:156. 1831.

P. nigropunctata Miq.

Distribution.— Common throughout Isla del Coco from 50 to 630 msl. Distributed from Guatemala to Colombia, Venezuela, the Guianas and Brazil; also occurs in the West Indies.

Specimens examined.— CR: *Dauphin 1164*; *Gómez 3271*; *Lépiz 362*; *Murawski 301*; *Murawski 325*; *Rojas 3638*; *Valerio s.n.*; FTG: *Trusty 62*; *Trusty 186*; INB: *Lépiz 362*; *Quesada 1028*; *Rojas 3638*; USJ: *Soto 3861.*

Plantaginaceae

215. **Scoparia dulcis* L., Sp. Pl. 116. 1753.

Distribution.— Infrequent on Isla del Coco in the cleared areas along the trail edge between Chatham and Wafer Bays. Distributed from the southern United States throughout subtropical and tropical America; also found in the Old World tropics.

Remarks.— First report for Isla del Coco.

Specimens examined.— CR: *Rojas 3688*; FTG: *Trusty 114*; *Trusty 541*; INB: *González 1215*; *Rojas 3688.*

Poaceae

1. Inflorescence a solitary spike or a solitary spikelike raceme or panicle 2
 2. Inflorescence lacking conspicuous, threadlike awns or bristles . . . . . . *Paspalum decumbens*
 2. Inflorescence with conspicuous, threadlike bristles or awns 3
  3. Spikelet subtended by awns . . . . *Ischaemum rugosum*
  3. Spikelet subtended by bristles 4
   4. Inflorescence a true spike, spikelets sessile, enclosed in burs subtended by a ring of retrorsely barbed bristles . . . . *Cenchrus brownii*
   4. Inflorescence a spikelike panicle; spikelets subtended by a few, antrorsely barbed bristles . . . . *Setaria parviflora*
1. Inflorescence paniculate or more than one raceme 5
 5. Foliar lamina with pseudopetioles, 5 mm long or longer . . . . *Pharus latifolius*
 5. Foliar lamina lacking pseudopetioles 6
  6. Spikelets disarticulating above the glumes, generally breaking into separate florets or remaining intact until the expulsion of the seeds; empty glumes remaining adherent to the pedicel as visible bracts 7
   7. Spikelets with one floret, without additional rudimentary florets . . . . *Sporobolus indicus*
   7. Spikelets with two or more florets 8
    8. Spikelets with 1 basal bisexual floret and 1 reduced rudimentary florets above; found mainly on the islets . . . . *Chloris paniculata*
    8. Spikelets with many similar bisexual florets 9
     9. Spikelets sessile . . . . *Eleusine indica*
     9. Spikelets pedicelate . . . . *Eragrostis ciliaris*
  6. Spikelets disarticulated below the glumes; no glumes remain adherent to the pedicel 10
   10. Spikelets compressed laterally . . . . *Melinis minutiflora*
   10. Spikelets compressed dorsally 11
    11. Inflorescence of paired or digitate spikes or racemes or racemes clustered very near the apex of the peduncle 12
     12. Spikelets 2 or more at each node of the rachis . . . . *Digitaria setigera* var. *setigera*

12. Spikelets solitary at each node of the rachis.................... 13
  13. Spikelets 2 or more times as long as broad, acute at apex .... *Axonopus compressus*
  13. Spikelets less than 2 times as long as broad, usually rounded or blunt .... *Paspalum conjugatum*

11. Inflorescence paniculate or racemose with the racemes not clustered near the apex of the peduncle 14
  14. Inflorescence with primary lateral branches strictly racemose or with slender uniform, raceme-like panicles (appearing 1-pinnate) 15
    15. Plants generally greater than 100 cm tall...... *Paspalum virgatum*
    15. Plants less than 50 cm tall .... *Paspalum nutans*
  14. Inflorescence with branches compounded 2 or more times, diffuse, open, lacking distinctly racemose branches 16
    16. Superior floret rugose or rugulose .... *Panicum maximum*
    16. Superior floret smooth.................................. 17
      17. Inferior palea absent or shorter than the inferior lema .... *Panicum polygonatum*
      17. Inferior palea present and as long as or longer than the inferior lema .... *Panicum laxum*

216. *Axonopus compressus* (Sw.) P. Beauv., Ess. Agrostogr. 12, 154, 167. 1812.

DISTRIBUTION.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Distributed throughout the warm regions of the New and Old Worlds.

REMARKS.— This species was published under the name *Paspalum platycaule* Poir. in Robinson (1902) and as *Digitaria sanguinalis* (L.) Scop. in Stewart (1912).

SPECIMENS EXAMINED.— CR: *Gómez 3278*; FTG: *Trusty 260*; GH: *Howell 10177*; *Snodgrass and Heller 942*; US: *Howell 10177*; *Klawe 1509*; *Stewart 261*; *Svenson 305.*

217. **Cenchrus brownii* Roem. & Schott, Syst. Veg. 2:258. 1817.

DISTRIBUTION.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Distributed from the southern United States through Central America to Bolivia and Brazil; also in the West Indies, Australia and the South Pacific.

SPECIMENS EXAMINED.— CR: *Quesada 1042*; INB: *Quesada 1042*; *Rojas 3702*; USJ: *Soto s.n.*

218. ***Chloris paniculata*** Scribn., Proc. Amer. Acad. Arts 38(4):262. 1902.

TYPE: *Snodgrass and Heller 968* (holotype: GH).

Herb to 70 cm tall; perennial; arising from an upright stout underground stem bearing many rootles and shreds of leaf sheaths; sheaths glabrous; ligule lacking; blades very long and narrow up to 50 cm long and 5 mm wide, arching, glabrous except for the scabrous margins; inflorescence panicle-like, made up of at least 50 spikes racemosely arranged on the upper 10 to 12 cm of the culm; spikes about 5 cm long at lower part of inflorescence, becoming progressively shorter near the tip; glumes narrow to broadly lanceolate, glabrous except for the scabrous midnerve; first glume ca. 1.2 mm × 0.2 mm; second glume ca. 3 × 0.4 mm; fertile lemma ca 2.6 × 0.6 mm, broadly lanceolate, glabrous except for the prominently bearded callus and scabrous keel, apex more or less obtuse. awn 2.5–2.8 mm long; sterile floret one, ca 1.5 × 0.2 mm, glabrous, awn 1.5–1.8 mm.

DISTRIBUTION.— Commonly found on the islets near Isla del Coco and infrequent on the rocky cliffs of the island. Endemic to Isla del Coco.

Specimens examined.— CR: *Dressler 4464*; *Lépiz 382*; FTG: *Trusty 341*; *Trusty 342*; INB: *Lépiz 382*; *Quesada 1113*.

219. *Digitaria setigera* Roth ex Roem. & Schult. var. *setigera*, Syst. Veg. 2:474. 1817.

Distribution.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Native to tropical Asia; introduced in other tropical regions.

Specimens examined.— FTG: *Trusty 79*; *Trusty 410*; *Trusty 467*; *Trusty 526*; GH: *Pittier 16268*; INB: *Rojas 3703*.

220. *Eleusine indica* (L.) Gaertn., Fruct. & Sem. Pl. 1:8. 1788.

Distribution.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Introduced from the Old World and now widely naturalized. Distributed from the southern half of the United States south to northern Argentina and Uruguay; also the West Indies, Galápagos Islands, and the Old World.

Specimens examined.— FTG: *Trusty 78*; *Trusty 358*; GH: *Pittier 16266*; INB: *Rojas 3700*.

221. **Eragrostis ciliaris* (L.) R. Br. in Tuckey, Narr. Exped. Zaire 478. 1818.

Distribution.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Native to the tropics and subtropics of the Old World; naturalized in the tropics and subtropics of the Americas.

Specimens examined.— CR: *Rojas 3705*; FTG: *Trusty 77*; INB: *Quesada 1040*; *Rojas 3705*; USJ: *Soto s.n.*

222. **Ischaemum rugosum* Salisb., Icon. Stirp. Rar. 1:pl. I. 1791.

Distribution.— Infrequent on Isla del Coco in the lawns and cleared areas near the Wafer Bay ranger station. Native to the Old World but introduced throughout the tropics.

Specimens examined.— INB: *Quesada 1050*.

223. **Melinis minutiflora* P. Beauv., Ess. Agrostogr. 54, t. 11, f. 4. 1812.

Distribution.— Unknown distribution on Isla del Coco. Native to Africa but widely cultivated and naturalized in the American tropics.

Remarks.— This species was reported by Fosberg and Klawe (1966), but no specimens were located.

Specimens examined.— No specimens located.

224. **Panicum laxum* Sw., Podr. 23. 1788.

Distribution.— Found near Chatham Bay on Isla del Coco. Native to tropical America but introduced into tropical West Africa.

Specimens examined.— CR: *Dressler 4463*; *Gómez 3280*; *Gómez 3291*; *Valerio s.n.*

225. **Panicum maximum* Jacq., Icon. Pl. Rar. 1:2, t. 13. 1781.

Distribution.— Very common on Isla del Coco in the disturbed area along the trail between Chatham and Wafer Bays. Native to the Old World but introduced throughout the Neotropics.

Remarks.— This species is considered an invasive exotic in many island ecosystems (Swarbrick 1997, Space et al. 2003).

Specimens examined.— CR: *Quesada 1133*; FTG: *Trusty 115*; INB: *Quesada 1133*.

226. **Panicum polygonatum* Schrad. in Schult., Mant. 2:256. 1824.

Distribution.— Common throughout the open areas and trail edges throughout Isla del Coco. Distributed from Mexico to Paraguay; also found in Trinidad and Jamaica.

Specimens examined.— CR: *Gómez 18034*; *Jiménez s.n.*; *Murawski 308*; FTG: *Trusty 168*; *Trusty 202*; *Trusty 241*; *Trusty 310*; *Trusty 344*; INB: *Rojas 3711*; US: *Howell 10173.*

227. *Paspalum conjugatum* P.J. Bergius, Acta Helv. Phys.-Math. 7:129,pl. 8. 1762.
Distribution.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Native to the New World but now widely naturalized in pantropical and subtropical areas worldwide.
Specimens examined.— CR: *Gómez 18035*; *Gómez 18074*; *Jiménez 3132*; *Jiménez 3134*; *Valerio s.n.*; FTG: *Trusty 37*; *Trusty 282*; *Trusty 359*; *Trusty 360*; INB: *Rojas 3698*; US: *Klawe 1489*; USJ: *Soto s.n.*

228. *Paspalum decumbens* Sw., Prodr. 22. 1788.
Distribution.— Common on Isla del Coco in the lawns and the cleared areas near the Wafer Bay ranger station. Distributed from southern Mexico to Brazil and Bolivia; also in the West Indies.
Specimens examined.— FTG: *Trusty 106*; *Trusty 361*; US: *Pittier 16209*; USJ: *Gómez-Laurito 6948.*

229. **Paspalum nutans* Lam., Tabl. Encycl. 1:175. 1791.
Distribution.— Found in the lawn area near the Wafer Bay ranger station and along the trail from Wafer Bay to Cerro Iglesias on Isla del Coco. Distributed from Mexico to Ecuador, the Guianas. Brazil and the Antilles; introduced into the island of Mauritius.
Specimens examined.— CR: *Gómez 3311*; *Jiménez 3169*; INB: *Quesada 1031*; *Rojas 3698.1*; *Rojas 3699*; US: *Gómez 3311*; *Klawe 1536.*

230. **Paspalum virgatum* L., Syst. Nat. ed. 10:855. 1759.
Distribution.— Infrequent along the trail from Chatham Bay to Wafer Bay on Isla del Coco. Distributed from Texas and Mexico to Paraguay and Argentina; also found in the West Indies.
Specimens examined.— CR: *Quesada 1134*; FTG: *Trusty 525*; INB: *Quesada 1134*; *Rojas 3698.*

231. *Pharus latifolius* L., Syst. Nat. ed. 10:1269. 1759.
Distribution.— Infrequent on Isla del Coco near the Genio River in Wafer Bay. Distributed from Mexico to Bolivia and Brazil, the Guianas and the West Indies.
Specimens examined.— CR: *Rojas 3584*; FTG: *Trusty 94*; INB: *Quesada 1046*; *Rojas 3584.*

232. *Setaria parviflora* (Poir.) Kerguélen, Lejeunia, n.s. 120:161. 1987.
S. geniculata (Lam.) P. Beauv.
Distribution.— Common on Isla del Coco in the lawn and cleared areas near the Wafer Bay ranger station. Distributed from the southern United States to Argentina; also found in the West Indies and introduced elsewhere.
Specimens examined.— CR: *Jiménez 3130*; *Soto s.n.*; GH: *Howell 10176*; *Pittier 16267*; FTG: *Trusty 80*; *Trusty 357*; INB: *Quesada 1047*; *Rojas 3704*; US: *Howell 10176*; USJ: *Soto s.n.*

233. **Sporobolus indicus* (L.) R. Br., Prodr. 170. 1810.
Distribution.—Rare; collected in Chatham Bay on Isla del Coco. Distributed from the southeastern United States and Mexico to Argentina and Chile; also found in the West Indies.
Specimens examined.— CR: *Jiménez 3133* (not seen).

RHIZOPHORACEAE

234. *Cassipourea guianensis* Aubl., Pl. Guiane 1:529, t. 211. 1775.

C. elliptica (Sw.) Poir.

DISTRIBUTION.— Infrequent on Isla del Coco along the coast near the mouth of the Genio River in Wafer Bay. Distributed from Mexico to Peru; also found in the Antilles.

SPECIMENS EXAMINED.— CR: *Gómez 3266*; *Sánchez 27*; FTG: *Trusty 236*; INB: *Quesada 1130*; USJ: *Poveda 812*.

RUBIACEAE

1. Herbs 2

2. Stipules fimbriate with 3–15 lobes 3

3. Fruits indehiscent 4

4. Fruits schizocharps with three indehiscent mericarps; corolla lobes 6 . . . .*Richardia scabra*

4. Fruits with simple; corolla lobes 4 . . . .*Diodia sarmentosa*

3. Fruits with one or two dehiscent valves 5

5. Fruits with 2 unequal valves, one dehiscent and the other indehiscent . . . .*Spermacoce exilis*

5. Fruits with 2 equal valves, both dehiscent 6

6. Calyx lobes 4, subequal or equal . . . . *Borreria ocymoides*

6. Calyx lobes 2 or 4; when 4, unequal with one pair half the size of the other . . . . *Borreria prostrata*

2. Stipules not fimbriate, unlobed 7

7. Creeping herb, leaves up to 3 cm long . . . .*Oldenlandia corymbosa*

7. Erect herb to subshrub, leaves 10–20 cm long . . . .*Hoffmannia piratarum*

1. Shrubs or trees. 8

8. Leaves with glandular punctations . . . . *Rustia occidentalis*

8. Leaves without punctations 9

9. Ovules and seeds, one per locule 10

10. Fruits single seeded . . . .*Guettarda crispiflora* subsp. *sabiceoides*

10. Fruits with more than one seed 11

11. Corolla with convolute lobes . . . . *Coffea arabica*

11. Corolla with valvate lobes 12

12. Shrub to 1 m tall; leaves lacking domatia; fruits purple . . . . *Psychotria gracilenta*

12. Shrub or tree greater than 1 m tall; leaves with domatia at axils of secondary veins; fruits red . . . . *Psychotria cocosensis*

9. Ovules and seeds numerous per locule 13

13. Inflorescences axillary . . . .*Hoffmannia nesiota*

13. Inflorescences terminal . . . .*Bertiera angustifolia*

235. ***Bertiera angustifolia*** Benth., Bot. Voy. Sulphur 103. 1845. (Fig. 16)

TYPE: *Barclay s.n.* (holotype: BM!; Isotype: GH!)

Shrubs or trees to 5 m tall, the branchlets terete, smooth, densely pilose, the nodes well spaced. Leaves pellucid punctate, arising as juveniles from a cylindrical bract or pair of bracts, the bract drying brown, puberulent; stipules connate in the sheath, split from the side, the apex bidentate; leaf

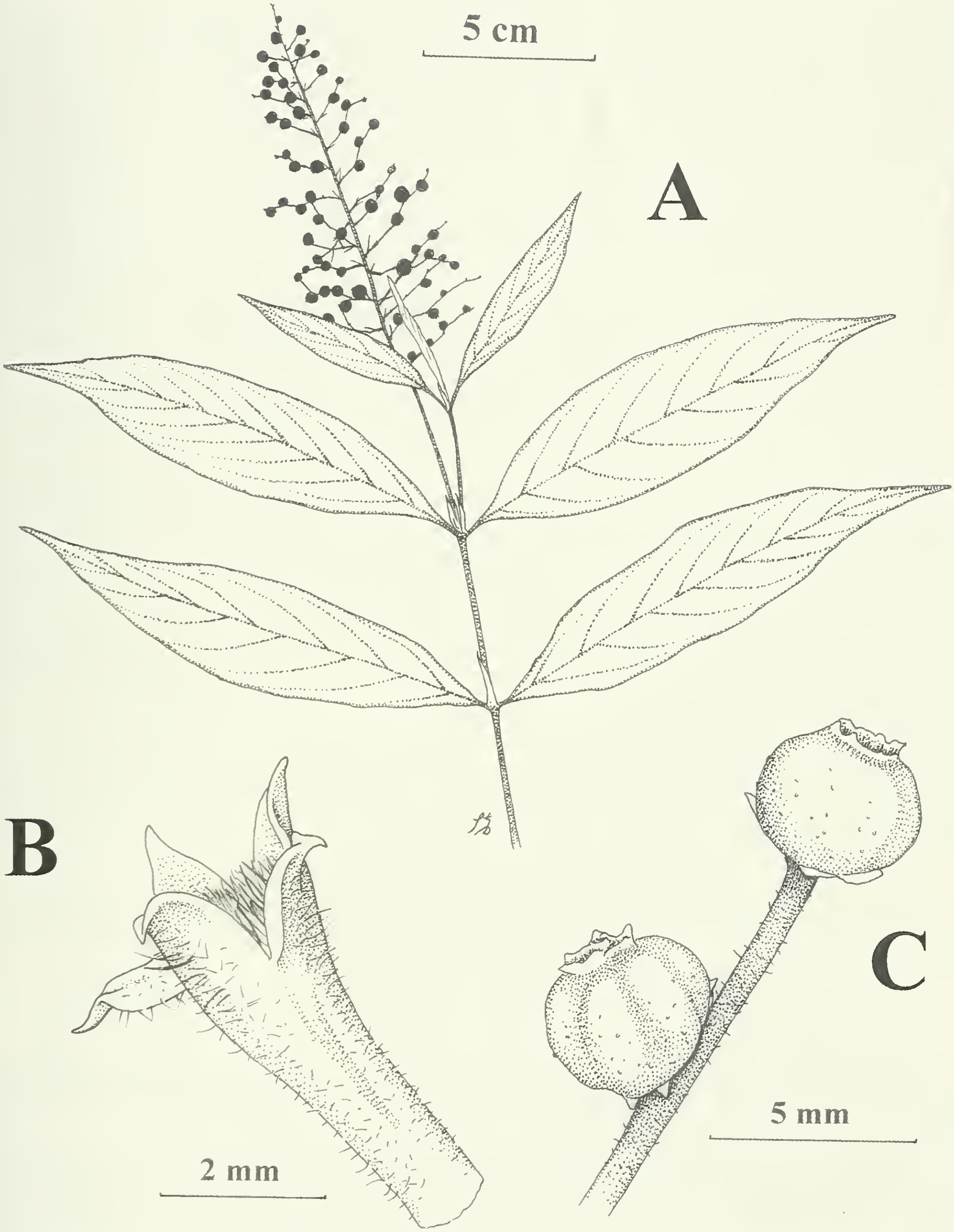

FIGURE 16. *Bertiera angustifolia* (drawn from *Trusty 217*). A. Branch of plant showing terminal inflorescence. B. Lateral view of flower. C. Close up of two fruits.

blades ovate oblong, 9–13 cm long, 1.6–3.2 cm wide, acute towards the apex, acuminate, the acumen conspicuous, cuneate or rounded at the base, the costa prominulous, the lateral veins 5–7 pairs, strongly ascending, sometimes immersed above, leaves papery when dry, rubescent above, glabrous except for the costa and margins, glabrous beneath except for the costa and veins, the hairs simple, appressed, elongate; petioles to 0.7 cm long, pubescent; stipules triangular subulate, puberulent, to 1.5 cm long, ca. 0.5 wide at the base, ultimately appressed to the stem. Inflorescences terminal, solitary, paniculate, puberulent, to 6–12 cm long, to 4 cm wide; peduncle slender, 2.5–4.0 cm long, the rachis somewhat flexuous, the branches alternate or opposite; bracts and bracteoles linear subulate, 6–16 mm long, pubescent; flowers sessile, the calycine cup small, the teeth 5, small, triangular; corolla white, 4.0–5.0 mm long, carnose, glabrous or sparsely puberulent outside, densely villose with orange hairs inside, the lobes deltoid, to 1.5 mm long, acute; stamens 5, the anthers oblong, to 1.5 mm long, short acuminate at the apex, the acumen ca. 0.4 mm long; stigma 5-sided, 2 mm long and 0.5 mm wide; fruits sessile, rotund, 3.0–3.5 mm in diameter, drying black, sparsely pubescent, the hairs short, strigose, the ribs obvious, marginate, the calycine cup vestigial.

Distribution.— Infrequent in the closed canopy forest between 250–450 msl. Endemic to Isla del Coco.

Remarks.— Dwyer (1980) reported this species from Panama but did not see the type specimen collected from Isla del Coco. He stated that although Bentham described the leaves of *B. angustifolia* as pellucid punctate, the Panamanian collections he examined are not. *Bertiera angustifolia* as determined from the type collection has much thinner (1.6–3.2 cm vs 2.7 to 7.5cm), pellucid-punctate leaves with prominent acumen, the secondary veins number 5–7 vs 8–9, and the inflorescences are shorter (up to 12 cm vs up to 17 cm) and thinner (4 cm vs 7 cm).

Specimens examined.— BM: *Barclay s.n.*; CR: *Barclay 2184*; FTG: *Trusty 116*; *Trusty 217*; GH: *Barclay s.n.*; *Foster 4135*; INB: *González 1220*; *Lépiz 346*; *Soto 3862*; *Quesada 1119*; NY: *Barclay 2184*; US: *Barclay 2184*.

236. *Borreria ocimoides* (Burm. f.) DC., Prodr. 4:544. 1830.

Distribution.— Infrequent on Isla del Coco in full sun in cleared areas and near river edges. Widespread from Mexico to Peru and Bolivia.

Specimens examined.— FTG: *Trusty 259*; *Trusty 553*.

237. **Borreria prostrata* (Aubl.) Miq., Stirp. Surinam Select. 177. 1851.

Distribution.— Frequent on Isla del Coco near the edge of the Genio River in Wafer Bay. Distributed from Mexico to Brazil and Bolivia; also found in the West Indies and Africa.

Remarks.— First report for Isla del Coco.

Specimens examined.— FTG: *Trusty 391*.

238. **Coffea arabica* L., Sp. Pl. 172. 1753.

Distribution.— Persisting from cultivation on Isla del Coco. Spreading from Chatham and Wafer Bay cleared areas into forest along the trail to Cerro Iglesias. Native to Ethiopia but widespread in cultivation throughout the world.

Remarks.— This species is one of the greatest potential threats to the native flora of Isla del Coco as it is the only introduced species that is shade tolerant. In addition, this species has been found to be an invasive exotic in many island ecosystems (Space et al. 2003; Pacific Island Ecosystems at Risk 2002), and we recommend its removal.

Specimens examined.— CR: *Lépiz 348*; *Quesada 1096*; *Rojas 3587*; FTG: *Trusty 147*; *Trusty 459*; INB: *González 1146*; *Lépiz 348*; *Quesada 1096*; *Rojas 3587*.

239. **Diodia sarmentosa* Sw., Prodr. 30. 1788.

Hemidiodia ocymifolia (Willd.) K. Schum.

Distribution.— Infrequent on Isla del Coco in open areas along trails and river edges. Distributed from Mexico to eastern Brazil; also found in the Greater Antilles and Africa.

Specimens examined.— CR: *Gómez 3288*; *Gómez 6960*; *González 1156*; *Lépiz 367*; *Quesada 1044*; *Rojas 3689*; FTG: *Trusty 93*; *Trusty 222*; INB: *González 1156*; *Lépiz 367*; *Quesada 1044*; *Rojas 3689*; US: *Klawe 1499*.

240. *Guettarda crispiflora* subsp. *sabiceoides* (Standl.) C.M.Taylor, Novon 11:133, f. 3E, F. 2001.

G. conferta Benth.

Distribution.— Collected once in Chatham Bay on Isla del Coco. This species is found from southern Costa Rica to Bolivia.

Remarks.— This species has not been collected since 1902.

Specimens examined.— GH: *Pittier 16255*; US: *Barclay 2190*; *Pittier 16255*.

241. ***Hoffmannia nesiota*** Donn. Sm., Bot. Gaz. 61:374–375. 1916. (Fig. 17)

Type: *Pittier 12387* (holotype: US!).

Shrub to 2 m tall. Branchlets subterete, glabrous; leaves opposite, the petioles stout, almost three-sided. 7–8 cm long. 2–3 mm thick, pubescent; mature leaf blades broadly elliptic, 18–26 cm long, 10–13 cm wide, elliptic to broadly elliptic-oblong, acuminate, base obtuse and slightly decurrent, stiffly chartaceous and pubescent or glabrescent, secondary veins 12–16 per side; inflorescence cymose. with few or many flowers, lax, the peduncles mostly 1–5 cm long, pubescent or glabrescent, lacking bracts and bracteoles, the pedicels 6–10 mm long, slender; flowers 15–16 mm long, with pyramidal calyx tube, lobes narrowly triangular, 1.5–2 mm long, acute; corolla four-fid, 11 mm long, rotate, puberulent, the linear lobes acute, about equaling the tube; stamens four, attached to the throat of the corolla, anthers subsessile, linear 5.5 mm long, connective brown, elongated toward the apex; disk elevated, strongly convex; ovary at anthesis, oblong-obovoid, twice as long as wide, slightly four-sided, trilocular, style 12 mm long, stigma lobes subconnate, oblong-ovate, 1.5 mm long; fruit globose, bright red when ripe, 1 cm in diameter, toothed calyx not accrescent, crowning; seeds ellipsoid, 0.5 mm long, minutely pitted, reddish.

Distribution.— Rare; found in Wafer and Iglesias Bays. Endemic to Isla del Coco.

Specimens examined.— CR: *L. Gonzalez 661*; FTG: *Trusty 96*; INB: *Quesada 1128*; US: *Barclay 2178*; *Pittier 12387*.

242. ***Hoffmannia piratarum*** Standl., J. Wash. Acad. Sci. 18:180. 1928.

Type: *Pittier 16259* (holotype: US).

Suffrutescent herb to 1 m tall; branches obtusely quadrangular, glabrous, the internodes 1.5–3 cm long; stipules caducous; leaves opposite, the petioles slender, 2.5–4.5 cm long, glabrate; leaf blades elliptic-lanceolate, 10–20 cm long, 5–6 cm wide, long-acuminate, the acumen narrow, long-attenuate, often falcate, the blades membranaceous, deep green above, glabrous, paler below, sparsely short-villous with ferruginous hairs beneath when young but soon glabrate; the costa prominent, rather stout, the secondary veins 8–9 on each side, very slender, strongly ascending, arcuate. irregularily anastomosing close to the margin; inflorescence axillary; inflorescence in leaf axils. cymes solitary or fasciculate, dense, 1–3-flowered, to 3 cm long, the peduncles 1–2.5 cm long, short villous, the bracts caducous; pedicels 2–5 mm long, usually short-villous; flowers puberulent proximally, hypanthium 3 cm long, calyx lobes 4, triangular-oblong, 2–3 mm long, acute or rounded, villous-ciliate; corolla white, glabrous, 1 cm long, glabrous or with a few short hairs at

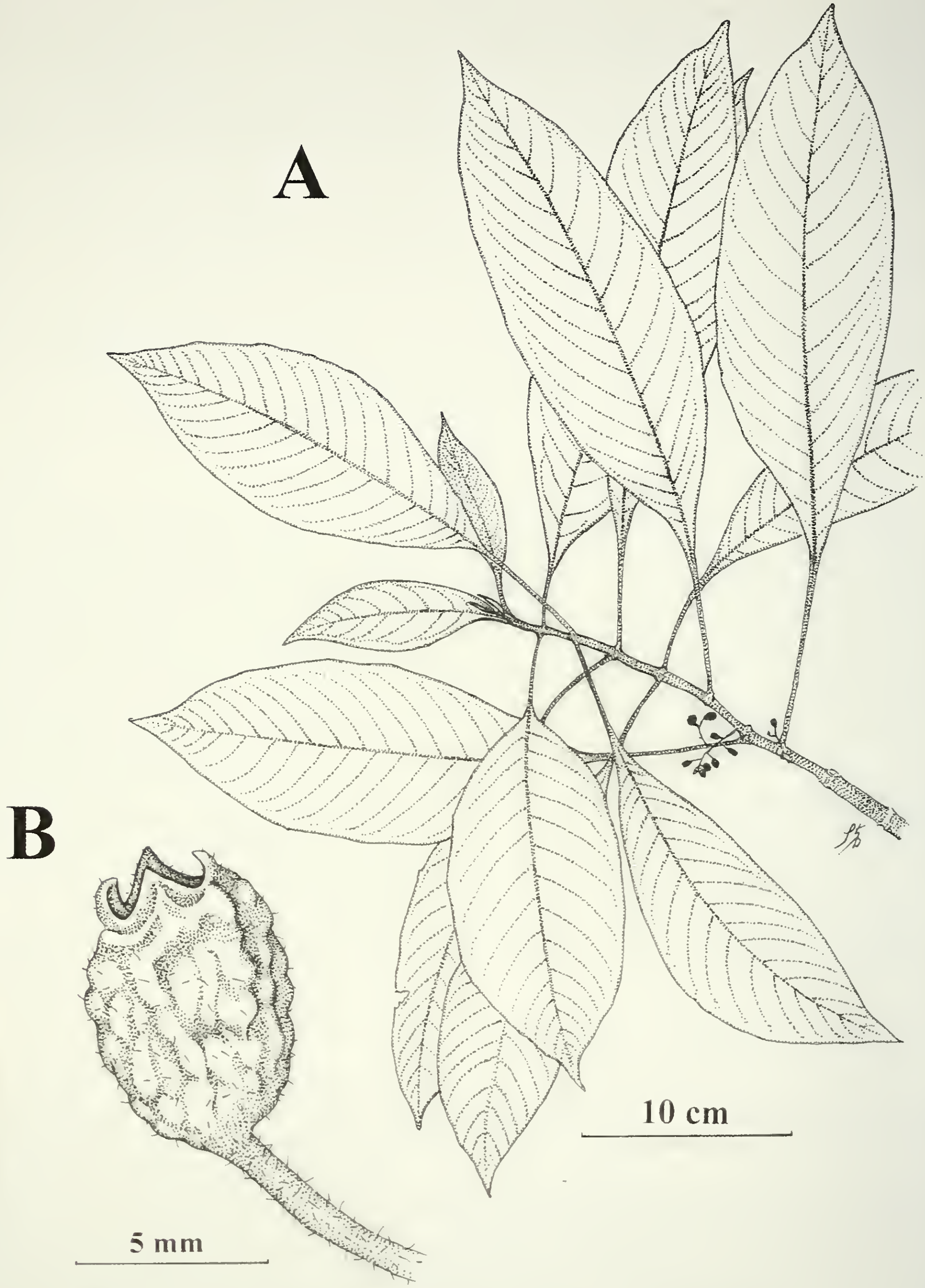

FIGURE 17. *Hoffmannia nesiota* (drawn from *Trusty 96*). A. Branch of plant showing axillary infructesence. B. Close up of dried fruit.

the apex, the tube obconic, 2 mm wide at the base, 5 mm wide at the throat, the lobes oblong-triangular, slightly shorter than the tube; ovary 2-locular; fruit subglobose, 6 mm long, glabrous; seeds minute, subglobose, dark brown, coarsely and deeply pitted.

DISTRIBUTION.— Along the edge and floodplain of the Genio River in Wafer Bay. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 271.*

243. *Oldenlandia corymbosa* L., Sp. Pl. 119. 1753.

DISTRIBUTION.— Common on Isla del Coco in cleared or disturbed areas in Wafer Bay. Native to Africa but widespread in the tropics of the world.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 92*; *Trusty 174*; *Trusty 254*; INB: *Quesada 1043*; *Rojas 3708.*

244. ***Psychotria cocosensis*** C. W. Ham., Phytologia 64:222. 1988. (Fig. 18)

TYPE: *Pittier 12375* (holotype: US).

Shrub; young stems glabrous, the bark furrowed longitudinally; stipules lanceolate, 12–35 × 2–5 mm, glabrous, caducous. Leaves petiolate; petioles 7–14 mm long, glabrous; blades membranous to coriaceous, elliptical, the apex acuminate to subcaudate, the base attenuate, (12) 14–17 × 5.5–7 cm. glabrous above and below, drying red-brown to green-brown; secondary veins (9) 10–12 pairs; diverging 45°–50°, eucamptodromous to brochidodromous, straight then arcuate mear margin, elevated below in less coriaceous leaves, the axils with small domatia below; tertiary veins inconspicuous to evident percurrent to reticulate. Inflorescences terminal, panicles of cymes; panicle branched 2–3 degrees; main axis 1 cm long, the peduncle lacking; secondary axes in 2 ranks, the first rank axes 2, 0.6 cm long, the second rank axes 2, reduced; cymes branched to 1 degree; bracts triangular, 0.7–1.5 mm long, glabrous. Flowers pedicellate, the pedicels 2–3 mm long; calyx cup-shaped, the tube 1 mm long, the lobes 5, broadly triangular to barely evident, glabrous; corolla white, the tube cylindrical, 3 × 3 mm, white pubescent in throat, the lobes 5, linear, 4 × 2 mm; stamens 5, the filaments 7 mm long, the anthers 2 mm long; style 9–10 mm long, the branches minute, linear. Fruit spherical to ellipsoidal, 6 mm long, 5.5–6 mm in diameter, red drying dark red-brown; persistent calyx cuplike, coriaceous, 1.5 mm long; seeds 2, the dorsal surface with 4 shallow irregular longitudinal furrows, the ventral surface with 2 deep irregular longitudinal furrows.

DISTRIBUTION.— Frequent in closed canopy forest from 150–630 msl. Endemic to Isla del Coco.

SPECIMENS EXAMINED.— CR: *Foster 4132*; *L. Gonzalez 637*; *Lépiz 333*; *Quesada 1080*; *Rojas 3623*; *Rojas 3684*; FTG: *Trusty 69*; *Trusty 188*; *Trusty 224*; *Trusty 265*; *Trusty 333*; *Trusty 396*; INB: *González 1167*; *Lépiz 333*; *Rojas 3623*; *Rojas 3684.*

245. *Psychotria gracilenta* Müll. Arg., Flora 59:545. 1876.

P. brachybotrya Müll.Arg.

DISTRIBUTION.— Common on Isla del Coco in the understory of the closed canopy forest from 250–550 msl. Distributed from Nicaragua to the Guianas and Peru.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 65*; *Trusty 543*; INB: *González 1171*; *Lépiz 344*; *Quesada 1032*; *Quesada 1045*; *Rojas 3640.*

246. **Richardia scabra* L., Sp. Pl. 330. 1753.

DISTRIBUTION.— Found in the lawn and disturbed areas near the Wafer Bay ranger station on

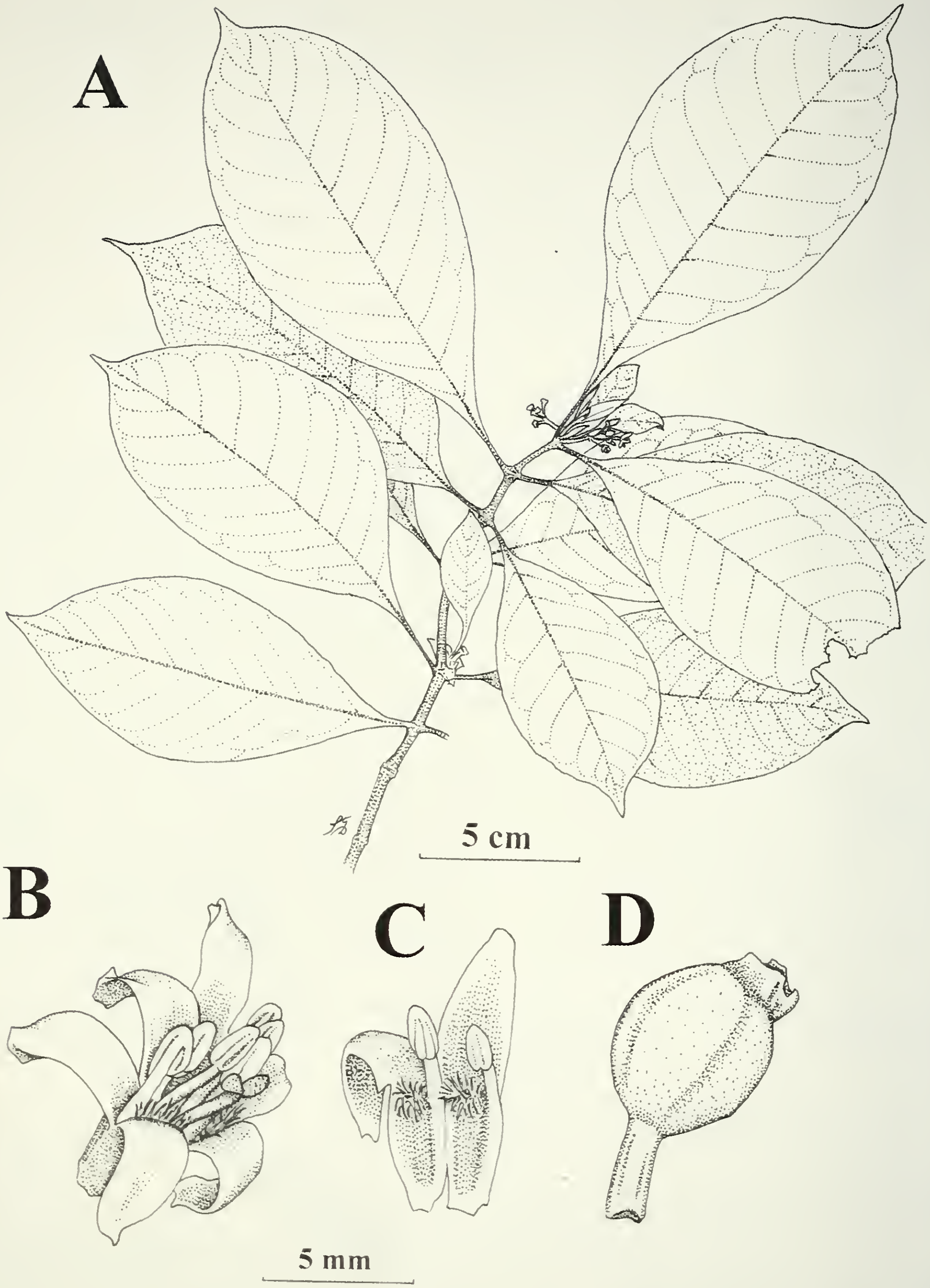

FIGURE 18. *Psychotria cocosensis* (drawn from *Trusty 265*). A. Branch of plant showing axillary inflorescence. B. Close up of flower. C. Longitudinal section of corolla showing pubescence. D. Lateral view of fruit.

Isla del Coco. Distributed from the southern United States to Brazil and the Antilles; also introduced to Africa and Asia.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— CR: *Quesada 1037*; *Rojas 3714*; *Soto s.n.*; FTG: *Trusty 75*; *Trusty 352*; INB: *Quesada 1037*; *Rojas 3714*; USJ: *Soto s.n.*

247. *Rustia occidentalis* (Benth.) Hemsl., Biol. Cent. Amer. Bot. 2:14. 1881.

DISTRIBUTION.— Locally common on Isla del Coco along the banks of the Genio River in Wafer Bay. Distributed from Nicaragua to Colombia.

REMARKS.— Mainland populations of this species are reported to have red/orange flowers while the Isla del Coco plants are a light lavender color.

SPECIMENS EXAMINED.— CR: *Gómez 3307*; *Jiménez 3173*; *Murawski 320*; *Poveda 814*; *Rojas 3653*; *Sánchez 14*; FTG: *Trusty 203*; *Trusty 352*; INB: *González 1177*; *González 1205*; *Rojas 3653*; USJ: *Poveda 814*.

248. **Spermacoce exilis* (L. O. Williams) C. D. Adams, Fieldiana Bot., n.s. 33:316, f. 5. 1993.
Borreria exilis L. O. Williams
B. gracilis L. O. Williams

DISTRIBUTION.— Infrequent in Chatham Bay along the trail from Wafer to Chatham Bay on Isla del Coco. Distributed throughout the Neotropics and the islands of the Pacific Ocean.

REMARKS.— Although the type was collected on Isla del Coco, we have designated this species as introduced due to its widespread mainland distribution, its restriction to disturbed habitats on the island and its late (1939) collection date.

SPECIMENS EXAMINED.— FTG: *Trusty 297*; *Trusty 552*; INB: *González 1151*; *Lépiz 372*.

RUTACEAE

1. Petioles broadly winged, 2–15 mm wide. . . . . *Citrus x aurantifolia*
1. Petioles narrowly winged, up to 2 mm wide . . . . *Citrus x aurantium*

249. **Citrus x aurantifolia* (Christ.) Swingle (pro sp.), J. Wash. Acad. Sci. 3:456. 1913.

DISTRIBUTION.— Cultivated on Isla del Coco in Wafer Bay. Native to the Old World but cultivated in the tropics and subtropics worldwide.

SPECIMENS EXAMINED.— Not collected.

250. **Citrus x aurantium* L. (pro sp.), Sp. Pl. 782–783. 1753.

DISTRIBUTION.— Cultivated on Isla del Coco in Wafer Bay. Native to the Old World but cultivated in the tropics and subtropics worldwide.

SPECIMENS EXAMINED.— Not collected.

SCHLEGELIACEAE

251. *Schlegelia brachyantha* Griseb., Cat. Pl. Cub. 191. 1866.

DISTRIBUTION.— Extremely common throughout the forest area of Isla del Coco from 50–600 msl. Widespread in the Neotropics.

SPECIMENS EXAMINED.— FTG: *Trusty 178*; *Trusty 215*; *Trusty 280*; *Trusty 317*; *Trusty 329*; *Trusty 335*; *Trusty 371*; *Trusty 508*; *Trusty 518*; INB: *González 1162*; *Lépiz 332*; *Quesada 1073*; *Rojas 3674*.

SCROPHULARIACEAE

252. **Capraria biflora* L., Sp. Pl. 628. 1753.

DISTRIBUTION.— Infrequent on Isla del Coco in the disturbed areas near the buildings in Wafer Bay. Distributed throughout suptropical and tropical America, introduced into the Old World.

SPECIMENS EXAMINED.— CR: *Gómez 3297*; *Gómez 3312*; FTG: *Trusty 351*.

SOLANACEAE

1. Corolla lobes not divided to near the base. . . . . *Capsicum annuum* var. *aviculare*
1. Corolla lobes divided nearly to the base. 2
    2. Leaves glabrous, spines absent. . . . . *Solanum americanum*
    2. Leaves densely hirsute, spines present . . . . *Solanum quitoense*

253. **Capsicum annuum* L. var. *aviculare* (Dierb.) D'Arcy & Eshbaugh, Phytologia 25(6): 350. 1973.

DISTRIBUTION.— Cultivated on Isla del Coco at the Chatham Bay ranger station. Native to tropical America.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 531*.

254. *Solanum americanum* Mill., Gard. Dict. ed. 8, Solanum: n. 5. 1768.

DISTRIBUTION.— Infrequent along the rocky beaches around Isla del Coco. Distributed widely throughout the tropics.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 456*.

255. **Solanum quitoense* Lam., Tabl. Encycl. 2:16. 1794.

DISTRIBUTION.— Cultivated on Isla del Coco at the Wafer Bay ranger station. Native to Ecuador and Colombia but cultivated throughout the American tropics.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 95*.

THEACEAE

256. *Freziera calophylla* Triana & Planch., Ann. Sci. Nat., Bot., ser. 4, 18:261. 1862.

DISTRIBUTION.— Rare on Isla del Coco, found only above 350 msl on Cerro Iglesias. Distributed from Panama to Colombia and Ecuador.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 56*; *Trusty 290*; INB: *González 1181*; *Lépiz 376*.

ULMACEAE

257. *Trema micrantha* (L.) Blume, Mus. Bot. 2:58. 1856.

DISTRIBUTION.— Found near the rocky beachfront at the mouth of the Genio River in Wafer Bay on Isla del Coco. Widely distributed in the tropics and subtropics of the Western Hemisphere.

SPECIMENS EXAMINED.— GH: *Pittier 16240*.

URTICACEAE

1. Leaves alternate, urticating hairs present . . . . *Laportea aestuans*
1. Leaves opposite, urticating hairs absent 2

2. Plants decumbent, creeping; leaves less than 1 cm long . . . . *Pilea microphylla*
2. Plants erect; leaves greater than 3 cm long . . . . *Pilea gomeziana*

258. *Laportea aestuans* (L.) Chew. Gard. Bull. Singapore 21:200. 1965.

Fleurya aestuans (L.) Gaudich. ex Miq.

Distribution.— Frequent along the rocky coastline of Isla del Coco. Distributed throughout Central and South America; also found in the West Indies, Arabia, Africa, Madagascar, India to Java and the lesser Sunda Islands.

Specimens examined.— CR: *Gómez 3268*; *Sánchez 13*; FTG: *Trusty 108*; *Trusty 455*; INB: *Quesada 1053*; *Rojas 3716*; USJ: *Soto s.n.*

259. ***Pilea gomeziana*** W. C. Burger, Phytologia 31:269. 1975. (Fig. 19)

Type: *Gómez 3304* (holotype: F; isotype: CR, US).

Herb, bisexual (unisexual in early stages) leafy stems erect and unbranched, 20–50 cm tall, leafy internodes (2) 7–50 mm long, 1–4 mm thick, puberulent with thin curved or crooked whitish hairs 0.3–1 mm long; stipules 4–8 mm long, broad and rounded at the apex, persisting with the leaves; leaves usually subequal and similar in form at each node, usually differing by about ¼ in size but occasionally with the smaller leaf ½ the size of the larger (at the same node), petioles 1–5 cm long, 0.4–2 mm thick, sparsely puberulent, usually sucate above; laminae 3–15 cm long, 2.5–7 cm wide, broadly ovate to elliptic-ovate or elliptic, usually broadest below the middle, short-acuminate at the apex, obtuse to truncate at the base, margins serrate with 2 to 4 prominent teeth per cm, lamina drying very thin chartaceous or membranaceous, upper surface with with evenly spaced slender and transparent hairs about 1 mm long, lower surface with smaller hairs along the veins, venation palmate with 3(5) primary veins, the 5–10 pairs of secondary veins ascending, very short linear cystoliths scattered or in groups above; male inflorescences usually in the uppermost leaf-axils, 1–2 cm long, usually of several small clusters of flowers on an unbranched rachis; male flowers subsessile, the buds about 1 mm in diameter with clavate subapical appendages 1 mm long, perianth usually with a few thin hairs; female inflorescence in lower leaf-axils or at the lower leafless nodes, 2–5 cm long, the primary rachis with 1–4 branches, flower clusters very small and distant along the rachis; female flowers pedicellate, less than 0.5 mm long; fruit about 0.6 mm long, oblong in outline with convex survaces, pale brown, margins outlined by a submarginal ridge or dark-punctate lines.

Distribution.— Frequent in wet areas near secondary rivers or streams below 250 msl throughout the island. Endemic to Isla del Coco.

Specimens examined.— CR: *Dressler 4469*; *Lépiz 379*; FTG: *Trusty 97*; *Trusty 279*; *Trusty 489*; INB: *González 1203*; *Lépiz 379*; NY: *Dressler 4469*; USJ: *Lépiz 379.*

260. **Pilea microphylla* (L.) Liebm., Kongel. Danske Vidensk. Selsk. Skr. Naturvidensk. Math. Afd., ser. 5, 2:296. 1851.

Distribution.— Rare; found in Wafer Bay on Isla del Coco. Distributed from Florida throughout tropical America.

Remarks.— First report for Isla del Coco.

Specimens examined.— USJ: *Gómez 3391.*

VERBENACEAE

1. Leaves elliptic or lanceolate, 1.5–5.5 cm long; flowers capitate. . . . . *Lippia alba*
1. Leaves ovate, 8–28 cm long; flowers paniculate . . . . *Cornutia microcalycina* var. *anomala*

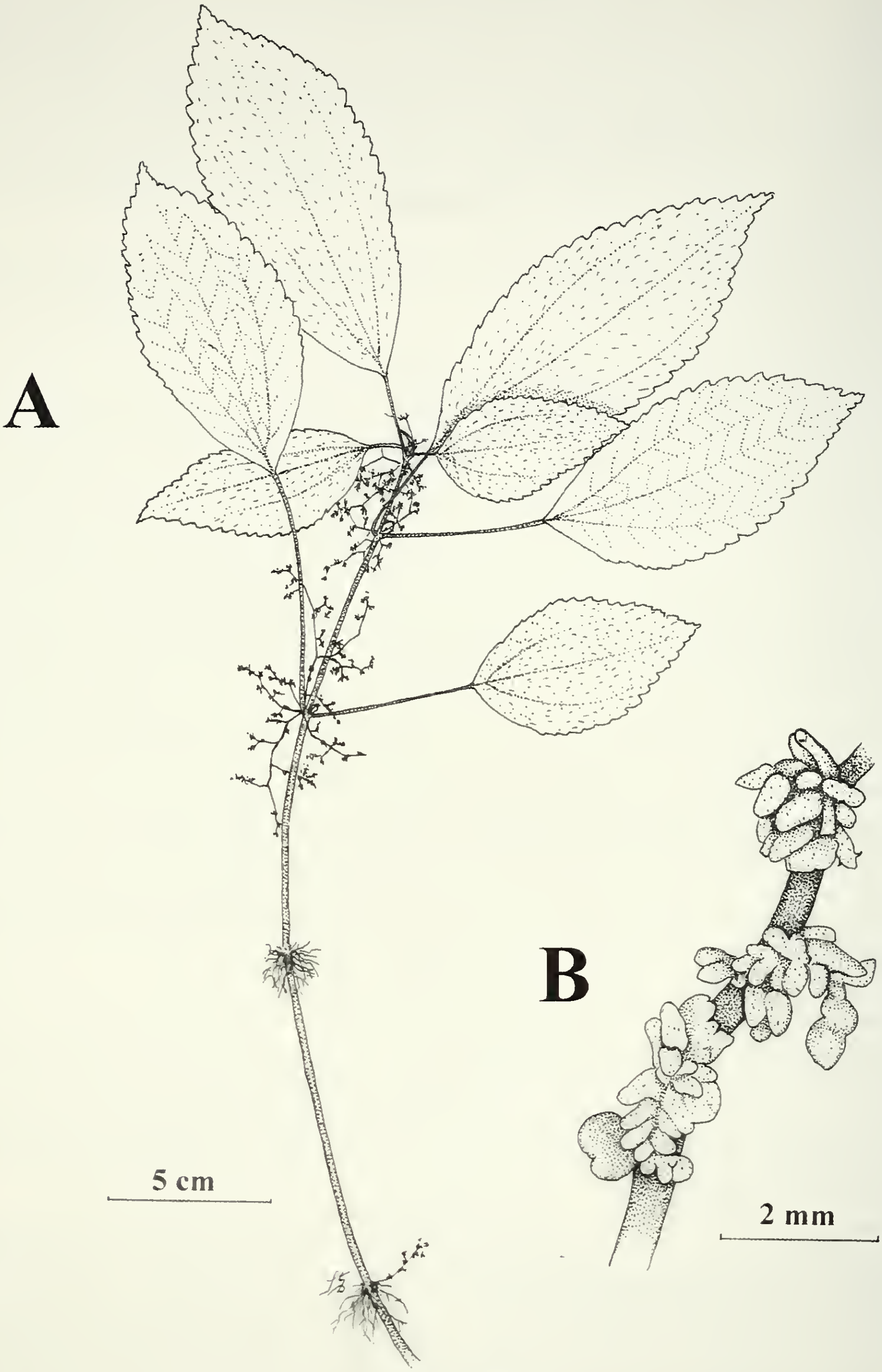

FIGURE 19. *Pilea gomeziana* (drawn from *Trusty 489*). A. Habit of plant showing axillary inflorescences. B. Close up of staminate inflorescence.

261. *Cornutia microcalycina* var. *anomala* Moldenke, Repert. Spec. Nov. Regni Veg. 40(1031/1039):176. 1936.

DISTRIBUTION.— Rare on Isla del Coco; found near the coast in Chatham Bay and also collected between Iglesias Bay and Cerro Tesoro Escondido. Distributed in Colombia, Ecuador and Venezuela.

REMARKS.— This species was published under the name *C. grandifolia* (Schltdl. & Cham.) Schauer in Stewart (1912) and Fosberg and Klawe (1966).

SPECIMENS EXAMINED.— GH: *Pittier 16254*.

262. **Lippia alba* (Mill.) N. E. Br. in Britton & P. Wilson, Bot. Porto Rico 6:141. 1925.

Distribution.—Locally common on Isla del Coco near the housing in Wafer Bay. Distributed from Texas and Mexico throughout the West Indies and Central and South America; introduced and cultivated elsewhere.

REMARKS.— This is probably a very recent introduction by humans to Isla del Coco due to its recent collection and the restricted distribution on the island near human settlements. First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 307*.

VISCACEAE

263. *Phoradendron piperoides* (Kunth) Trel., Phoradendron 145. 1916.

DISTRIBUTION.— Infrequent on Isla del Coco; parasite on *Ocotea insularis* and *Cecropia pittieri*. Distributed from Mexico to Argentina and the West Indies.

REMARKS.— First report for Isla del Coco.

SPECIMENS EXAMINED.— FTG: *Trusty 213*; *Trusty 214*; INB: *Quesada 1055*; *Rojas 3658*.

DOUBTFUL SPECIES

These species have been previously published for Isla del Coco but no specimens with the published names could be found. As there are related species that are common to the island, it is likely that these specimens have been incorrectly identified.

Ardisia humilis Vahl
Clidemia bullosa DC. (now a synonym of *C. condolleana* Cogn.)
Clidemia hirta (L.) D. Don
Ficus tecolutensis (Liebm.) Miq.
Hordeum secalinum Schreb.
Ipomoea batatas (L.) Poir. in Lam.
Nephrolepis pectinata (Willd.) Schott
Ossaea quinquenervia (Mill.) Cogn. (now a synonym of *C. quinquenervia* [Mill.] Almeda)
Paspalum vaginatum Sw.
Polystichum adiantiforme (Forst. f.) J. Sm.
Trichomanes pyxidiferum L.

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Appendix

Tables 1–5
and
List of Exsiccatae

TABLE 1. Botanical expeditions to Isla del Coco. Abbreviations of herbaria as in Holmgren et al. (1990).

Expedition	Country/Institution	Collectors	Date	Principle Herbarium
Voyage of *H. M. S. Sulphur*	England	G. Barclay	April 1838	BM/K
Hopkins-Stanford Expedition to the Galápagos Islands	USA/Stanford University	R. Snodgrass and E. Heller	July 1899	GH/US/DS
Expedition of the US Fishing Commission	USA/United States Fish Commision	A. Agassiz	February 1891	US
Unknown	Costa Rica	H. Pittier	June 1898 January 1902	US/CR
California Academy of Sciences Expedition to the Galápagos	USA/California Academy of Science	A. Stewart	September 4-11, 1905	CAS
Expedition to the South Pacific of the *S. Y. St. George*	England	C. Crossland	April 1924	BM
Unknown	USA	A. K. Fisher	June 11, 1929	US
Vincent Astor Expedition	USA	H. K. Svenson	April 17-19, 1930	BKL
Templeton-Crocker Expedition/CAS	USA	J. Howell	June 28, 1932	CAS
US Presidential Cruise	USA	W. Schmitt	August 2, 1935	US
Unknown	Costa Rica	J. Valerio	May 4-7, 1936; December 1939;March 1940	CR
Galápagos International Scientific Project	USA/California Academy of Sciences	W. Klawe	December 5, 1959 September 3, 1967	CR
	USA	L. Hodridge	February 22-24, 1963	US
	Unknown	L. Fournier	March 8-9, 1964	US/CR/DAV
	Costa Rica	A. Jiménez	April 11-13, 1965	CR
	Costa Rica	L. D. Gómez	March 1970; March 1974; February 1976; December 1981	US/CR
		C. Lellinger and E. De La Sota	March 26, 1971	CR
		L. Carrasquilla and R. Dressler	August 13-17, 1973	US/CR
		L. Poveda	March 1974	CR
		P. Sánchez	July 1980	CR
		D. Murawaski	September 1981	CR
	Costa Rica/Universidad de Costa Rica	R. Soto	June 6-8, 1989	UCR/CR
	Unknown	R. Foster	April 9-11, 1979	US
	Costa Rica/Universidad de Costa Rica	G. Dauphin	January26-February 4, 1994	UCR/CR
	Costa Rica/Instituto Nacional de Biodiversidad	F. Quesada	September 22, 1994	INB
	Costa Rica/Instituto Nacional de Biodiversidad	E. Lépiz	June 13-16, 1994	INB
	Costa Rica/ Instituto Nacional de Biodiversidad	J. González	August 14, 1996	INB
	Costa Rica/Instituto Nacional de Biodiversidad	A. Rojas	June 12-July 9, 1997	INB

TABLE 2. Vascular plant diversity on Isla del Coco.

	Families		Genera		Species	
	Native	Introduced	Native	Introduced	Native	Introduced
Ferns and Fern Allies	22	0	48	0	81	0
Dicotyledons	39	10	71	35	84	47
Monocoytledons	7	1	20	12	26	24
All vascular plants	68	11	139	47	191	71
Total	79		186		262	

TABLE 3. Biogeographical relationships of the endemic plant species of Isla del Coco based on morphological assessment.

Family	Genus	Species	Closest Relative(s)	Distribution of Closest Relative(s)	Citation
Euphorbiaceae	*Acalypha*	*pittieri*	Not listed		Pax and Hoffman 1923
Myrsinaceae	*Ardisia*	*cuspidata*	*A. pseudocuspidata*	Panama	J. Pipoly pers. comm.
Aspleniaceae	*Asplenium*	*barclayanum*	*A. cristatum*	south Florida, Mexico to Peru and Brazil, Galápagos Islands, Antilles, Trinidad and Tobago	Adams (1992)
			A. cladaleptan	southern Mexico to Peru	
			A. myriaphyllum	southern Mexico to Peru and Bolivia, Bermuda, and the Greater Antilles	
Aspleniaceae	*Asplenium*	*delicatulum* var. *cacosensis*	*A. delicatulum*	Mexico to Venezuela	Rojas and Trusty (2004)
Rubiaceae	*Bertiera*	*angustifalia*	*B. guianensis*	southern Mexico to Ecuador and Brazil	Bentham (1844-1846)
Cecropiaceae	*Cecropia*	*pittieri*	*C. peltata*	Mexico to Colombia and Venezuela	Stewart (1912)
			C. obtusa	French Guiana and Suriname to Bolivia	

TABLE 3 (continued)

Family	Genus	Species	Closest Relative(s)	Distribution of Closest Relative(s)	Citation
Lomariopsidaceae	*Elaphoglossum*	*cocosense*	*E. paleaceum*	Mexico to Peru and Brazil, Antilles, Azores Islands and Madeira	Mickel (1992)
Lomariopsidaceae	*Elaphoglossum*	*incognitum*	*E. latifolium*	Mexico to Peru and Brazil, and Antilles	Rojas-Alvarado (2003)
Lomariopsidaceae	*Elaphoglossum*	*reptans*	*E. lingua*	Costa Rica to Chile and Paraguay, and Antilles	Rojas-Alvarado (2003)
Orchidaceae	*Epidendrum*	*cocoense*	*E. santaclarense*	El Salvador to Panama	Hágsater et al. (1999)
			E. rafael-lucasii	Costa Rica	
			E. acunae	Mexico to Costa Rica, Cuba	
Orchidaceae	*Epidendrum*	*insulanum*	*E. repens*	Guatemala and Honduras to Ecuador	Schlecter (1918)
Orchidaceae	*Epidendrum*	*jimenezii*	*E. insulanum*	Cocos Island	Hágsater et al. (1999)
Myrtaceae	*Eugenia*	*cocosensis*	*E. pacifica*	Cocos Island	Barrie (2005)
Myrtaceae	*Eugenia*	*pacifica*	*E. coffeifolia*	Venezuela and Suriname to Peru and Brazil	Bentham (1844-1846)
Rubiaceae	*Hoffmannia*	*nesiota*	*H. pittieri*	Costa Rica to Colombia	Smith (1914)
Rubiaceae	*Hoffmannia*	*piratarum*	*H. nicotianifolia (syn. H. angustifolia)*	Mexico to Colombia	Standley (1928)
			H. psychotriifolia	Mexico to Panama	
Lycopodiaceae	*Huperzia*	*brachiata*	*L. portoricense*	Puerto Rico	Maxon (1913)
			L. wilsonii	southern Mexico to Ecuador, Antilles and Puerto Rico	Gómez (1976b)
Lycopodiaceae	*Huperzia*	*pittieri*	*H. linifolium*	southern Mexico to Peru and Bolivia, Antilles	Christ (1909)
Hymenophyllaceae	*Hymenophyllum*	*cocosense*	*H. hirsutum*	Mexico to Peru and Brazil, Antilles, and Trinidad	Rojas-Alvarado (1996)

TABLE 3 (continued).

Family	Genus	Species	Closest Relative(s)	Distribution of Closest Relative(s)	Citation
Dennstaedtiaceae	*Hypolepis*	*lellingeri*	*H. aspidiodes*	China and Vietnam	Rojas-Alvarado (2001)
Marcgraviaceae	*Marcgravia*	*waferi*	Not listed		Standley 1937
Melastomataceae	*Miconia*	*acanthotheca*	*M. theizens*	Costa Rica to Colombia and Brazil	F. Almeda pers. comm.
			M. brevitheca	Costa Rica, Panama and Ecuador	
Melastomataceae	*Miconia*	*sp. nov.*	Not available		
Urticaceae	*Pilea*	*gomeziana*	*P. pittieri*	Costa Rica to Colombia;	Burger (1975)
			P .pubescens	Mexico to Peru, and Brazil	
Rubiaceae	*Psychotria*	*cocosensis*	*P. panamensis*	Mexico to Panama, Colombia	Hamilton (1988)
Dennstaedtiaceae	*Saccoloma*	*elegans var. spinosa*	*S. elegans*	Mexico to Peru, and northeastern Brazil, Dominican Republic, Greater Antilles, and Trinidad	Rojas and Trusty (in press)
Humiriaceae	*Sacoglottis*	*holdridgei*	*S. ovicarpa*	Panama to Colombia	Burger and Zamora (1991)
			S. amazonica	Colombia to Peru	
Grammitidaceae	*Terpsichore*	*cocosensis*	*T. cultrata*	southern Mexico to Peru and Brazil, Antilles, and Africa	Rojas-Alvarado (1996)
			T. mollissima	southern Mexico to the Guianas and Ecuador, Antilles	
Thelypteridaceae	*Thelypteris*	*calypso*	*T. eggersii*	Costa Rica to Venezuela and Peru	Gómez (1976b)
Thelypteridaceae	*Thelypteris*	*cocos*	*T. nockiana*	Jamaica	Smith and Lellinger (1985)
Hymenophyllaceae	*Trichomanes*	*capillaceum var. cocos*	*T. capillaceum*	Mexico to Venezuela and Peru, Greater Antilles	Christ 1904
Hymenophyllaceae	*Trichomanes*	*collariatum var. alvaradoi*	*T. collariatum*	Mexico to Peru and northern Brazil	Rojas-Alvarado (in review)

TABLE 4. Geographic relationships of the flora of Isla del Coco. Percentages are based on the 154 identified native species and the 30 endemics for which the closest relatives have been suggested. Data for individual species can be found in the List of Vascular Plants.

	Caribbean		*Central America*		*Northern South America*		*Not in Central America or northern South America*	*Old World*	
	Present	Restricted	Present	Restricted	Present	Restricted		Present	Restricted
Native (154 spp.)	110 71.4%	0 0	150 97.4%	3 1.9%	143 92.9%	4 2.6%	0 0	46 29.9%	0 0
Closest relatives of endemics (30 spp.)	13 43.3%	1 3.3%	26 86.6%	3 10.0%	23 77.0%	1 3.3%	2 6.7%	3 10.0%	1 3.3%
Total (184 spp.)	123 66.8%	1 0.5%	176 95.7%	6 3.3%	166 90.2%	5 2.7%	2 1.1%	49 26.6%	1 0.5%

TABLE 5. Dispersal modes utilized by endemic native plants on Isla del Coco.

	Air	*Drift*	*Bird Internal*	*Bird External*
Endemic species (37 spp.)	21 56.8%	1 2.7%	12 32.4%	3 8.1%
Native Species (154 spp.)	69 44.8%	21 13.6%	39 25.3%	25 16.2%
Total (191 spp.)	90 47.1%	22 11.5%	51 26.7%	28 14.7%

List of Exsiccatae

The numbers in parentheses correspond with the species numbers in the present treatment.

Agassiz, A., s.n. (45); s.n. (49); s.n. (57); s.n. (207)

Barclay, G., 2178 (241); 2179 (98); 2182 (203); 2184 (235); 2184 (235); 2189 (125); 2190 (240); 2201 (10); 2206 (33); 2207 (9); 2208 (7); 2211 (46); s.n. (8); s.n. (10); s.n. (192); s.n. (235)

Carrasquilla. L.., 360 (69); 362 (110)

Castaing, A., s.n. (125); s.n. (135); s.n. (167)

Crossland, C., 454 (193)

Dauphin. G., 1052 (170); 1053 (85); 1088 (46); 1091 (167); 1118 (8); 1128 (179); 1129 (14); 1130 (93); 1132 (101); 1138 (36); 1160 (188); 1163 (135); 1164 (214); 1165 (192); 1166 (34); 1168 (125); 1174 (186); 1175 (210); 1180 (59); 1181 (170)

Dressler, R. L., 4457 (46); 4458 (167); 4459 (115); 4460 (110); 4462 (31); 4463 (224); 4464 (218); 4465 (93); 4467 (167); 4468 (208); 4469 (259); 4471 (206); 4472 (192); 4473 (135)

Fisher. A. K., s.n. (7); s.n. (74)

Foster, R. B., 4114 (170); 4115 (90); 4117 (207); 4118 (80); 4122 (186); 4124 (188); 4126 (167); 4127 (179); 4128 (192); 4132 (244); 4135 (235); 4146 (144); 4152 (49); 4154 (52); 4156 (90); 4158 (75); 4161 (34); 4165 (31); 4168 (191); 4172 (106)

Fournier, L. A., 303 (182); 304 (184); 311 (110); 331 (8); 332 (26); 340 (192); 353 (186)

Fricke, R. L., s.n. (32)

Gómez, L. D., 3214A (31); 3261 (179); 3262 (189); 3263 (125); 3264 (181); 3265 (100); 3266 (234); 3268 (258); 3270 (206); 3271 (214); 3272 (106); 3274 (173); 3275 (112); 3277 (139); 3278 (216); 3280 (224); 3281 (132); 3286 (93); 3287 (101); 3288 (239); 3291 (224); 3293 (168); 3295 (89); 3296 (166); 3297 (252); 3298 (167); 3299 (176); 3302 (192); 3303 (176); 3306 (182); 3307 (247); 3311 (229); 3312 (252); 3313 (135); 3314A (31); 3317 (7); 3318A (32); 3319 (33); 3327 (40); 3328 (33); 3329 (28); 3330 (8); 3331 (79); 3332 (36); 3333 (1); 3334 (1); 3336 (70); 3337 (2); 3340 (23); 3341 (58); 3342 (80); 3343 (34); 3345A (32); 3346 (52); 3349 (6); 3350 (76); 3351 (14); 3352 (49); 3355 (56); 3356 (67); 3357 (9); 3358 (69); 3359 (72); 3360 (67); 3361 (76); 3362 (40); 3363 (57); 3364 (58); 3382 (138); 3383 (204); 3384 (134); 3386 (129); 3391 (260); 4502 (40); 4504 (6); 4507 (7); 4508 (41); 4513 (75); 4514 (10); 4516 (67); 4517 (6); 4519 (7); 4523 (18); 4527 (33); 4527A (33); 4529 (70); 4533 (76); 4534 (73); 4535 (15); 4536 (2); 4537 (15); 4538 (76); 4539 (76); 4540 (32); 4541A (36); 4541B (16); 4543 (32); 4545 (29); 4546 (36); 4547 (32); 4548 (34); 4553 (28); 6557 (32); 6558 (45); 6560 (45); 6561 (2); 6564 (46); 6565 (29); 6566 (35); 6567 (38); 6568 (35); 6931 (46); 6945 (46); 6960 (239); 18034 (226); 18035 (227); 18038 (33); 18040 (183); 18041 (170); 18042 (39); 18043 (210); 18044 (58); 18045 (6); 18047 (46); 18048 (181); 18051 (188); 18053 (77); 18054 (171); 18055 (167); 18057 (181); 18058 (28); 18060 (34); 18062 (29); 18063 (27); 18067 (28); 18068 (27); 18069 (31); 18070 (28); 18071 (34); 18072 (72); 18073 (33); 18074 (227); 18080 (34); 18089 (74); 18090 (10); 18092 (75); 18093 (32); 18094 (29); 18096 (76); 18097 (76); 18098 (35); s.n. (74); s.n. (100); s.n. (148)

Gómez-Laurito, J., 6904 (100); 6905 (198); 6913 (85); 6914 (206); 6915 (133); 6919 (181); 6920 (125); 6921 (135); 6923 (182); 6924 (207); 6925 (183); 6926 (183); 6927 (127); 6928 (144); 6930 (126); 6933 (182); 6934 (167); 6936 (135); 6938 (170); 6939 (179); 6940 (115); 6943 (110); 6946 (170); 6947 (179); 6948 (228); 6952 (156); 6953 (176); 6957 (125); 6966 (167); s.n. (66); s.n. (125)

González, J., 1141 (192); 1142 (100); 1143 (135); 1144 (171); 1145 (49); 1146 (238); 1148 (54); 1149 (167); 1150 (69); 1151 (248); 1153 (156); 1154 (181); 1155 (170); 1156 (239); 1159 (165); 1160 (183); 1162 (251); 1163 (8); 1164 (6); 1166 (182); 1167 (244); 1168 (85); 1169 (6); 1170 (186); 1171 (245); 1172 (13); 1173 (96); 1176 (47); 1177 (247); 1179 (191); 1181 (256); 1182 (192); 1185 (188); 1187 (90); 1188 (15); 1189 (75); 1190 (9); 1191 (176); 1192 (49); 1193 (54); 1194 (212); 1195 (60); 1196 (39); 1198 (33); 1199 (74); 1200 (182); 1201 (77); 1202 (61); 1203 (259); 1204 (184); 1205 (247); 1206 (178); 1208 (6); 1209 (39); 1213 (110); 1215 (215); 1216 (62); 1217 (69); 1218 (78); 1219 (109); 1220 (235); 1221 (10)

González, L., 637 (244); 649 (145); 660 (213); 661 (241)

González, J. and Sierra, C., 639 (179); 674 (178)

Hinds, R. B., s.n. (98)

Holdridge. L.., 5132 (52); 5135 (31); 5136 (26); 5137 (28); 5138 (23); 5139 (27); 5143 (30); 5144 (46); 5146 (11); 5149 (75);5152 (18); 5154 (46); 5156 (69); 5157 (56); 5165 (93); 5166 (181); 5171 (192); 5179 (188); s.n. (186)

Holst, I. and Soto, R., s.n. (137)

Howell, J. T., 10167 (100); 10172 (142); 10173 (226); 10176 (232); 10177 (216); 10179 (46); 10183 (182); 10184B (204); 10185 (170); 10188 (125); 10189 (23)

Jiménez, A., 3130 (232); 3132 (227); 3133 (233); 3134 (227); 3140 (181); 3141 (182); 3143 (7); 3144 (135); 3146 (8); 3147 (52); 3148 (182); 3149 (181); 3151 (100); 3152 (184); 3157 (14); 3158 (11); 3161 (192); 3162 (34); 3164 (31); 3169 (229); 3173 (247); 3175 (63); 3176 (125); 3178 (208); 3179 (167); 3183 (170); 3184 (110); 3190 (179); 3197 (182); 3201 (78); 3204 (137); 3208 (32); 3209 (16); s.n. (34); s.n. (85); s.n. (117); s.n. (156); s.n. (179); s.n. (183); s.n. (226)

Klawe, W., 1479 (80); 1489 (227); 1495 (139); 1498 (49); 1499 (239); 1501 (137); 1503 (128); 1506 (72); 1509 (216);

1517 (106); 1536 (229); 1540 (9); 1542 (63); 1550 (192); 1555 (49); 1559 (149); 1560 (151); s.n. (8); s.n. (11); s.n. (23); s.n. (28); s.n. (29); s.n. (30); s.n. (31); s.n. (32); s.n. (33); s.n. (34); s.n. (46); s.n. (75); s.n. (76); s.n. (80); s.n. (207)

Lellinger, D. B., and de la Sota, E. R., 773 (23)

Lépiz, E., 328 (167); 329 (188); 330 (179); 330 (179); 331 (33); 332 (251); 333 (244); 334 (47); 335 (200); 336 (81); 337 (26); 338 (34); 339 (206); 341 (14); 342 (56); 343 (41); 344 (245); 345 (202); 346 (235); 348 (238); 349 (200); 350 (106); 350 (106); 351 (39); 352 (93); 353 (58); 354 (100); 355 (11); 356 (182); 357 (192); 359 (208); 360 (181); 361 (176); 362 (214); 363 (154); 364 (106); 365 (85); 366 (101); 367 (239); 368 (155); 369 (156); 370 (155); 371 (61); 372 (248); 373 (183); 374 (170); 375 (158); 376 (256); 378 (200); 379 (259); 380 (93); 381 (115); 382 (218)

Murawski, D. A., 301 (214); 306 (135); 307 (125); 308 (226); 320 (247); 325 (214); 327 (135); 332 (179); 347 (179); 348 (167); 365 (131)

Pittier, H., 12353 (26); 12355 (8); 12357 (46); 12358 (9); 12361 (49); 12370 (93); 12372 (182); 12373 (180); 12374 (186); 12376 (125); 12380 (135); 12381 (192); 12387 (241); 12390 (31); 12391 (181); 16209 (228); 16221 (182); 16223 (188); 16224 (192); 16225 (186); 16228 (8); 16229 (7); 16235 (2); 16236 (56); 16240 (257); 16243 (174); 16244 (93); 16246 (143); 16247 (203); 16249 (102); 16254 (261); 16255 (240); 16256 (166); 16262 (100); 16266 (220); 16267 (232); 16268 (219); 16271 (128); 16272 (137); 16273 (135); 16274 (125); 16277 (120); 16281 (149); 16350 (207)

Poveda, L. J., 810 (110); 812 (234); 813 (167); 814 (247); 817 (96); 821 (170); s.n. (179)

Quesada, F., 1001 (41); 1002 (42); 1003 (52); 1004 (56); 1005 (135); 1006 (192); 1007 (81); 1008 (14); 1009 (44); 1010 (33); 1012 (179); 1013 (167); 1013 (167); 1014 (34); 1015 (27); 1016 (6); 1017 (11); 1018 (125); 1020 (170); 1021 (85); 1024 (59); 1025 (160); 1026 (117); 1027 (114); 1028 (214); 1029 (80); 1030 (23); 1031 (229); 1032 (245); 1033 (182); 1035 (149); 1036 (102); 1037 (246); 1038 (145); 1039 (212); 1040 (221); 1041 (144); 1042 (217); 1043 (243); 1044 (239); 1045 (245); 1046 (231); 1047 (232); 1048 (182); 1049 (181); 1050 (222); 1051 (115); 1052 (116); 1053 (258); 1054 (154); 1055 (263); 1056 (122); 1057 (205); 1059 (168); 1060 (2); 1062 (213); 1063 (119); 1064 (110); 1064 (110); 1065 (101); 1067 (137); 1068 (139); 1069 (197); 1071 (202); 1073 (251); 1074 (47); 1075 (92); 1076 (139); 1077 (111); 1078.1 (25); 1080 (244); 1081 (210); 1082 (13); 1083 (89); 1084 (91); 1085 (10); 1086 (181); 1087 (39); 1089 (6); 1091 (106); 1093 (49); 1094 (49); 1094 (49); 1096 (238); 1097 (63); 1098 (100); 1100 (156); 1101 (155); 1102 (7); 1102 (7); 1103 (123); 1104 (61); 1105 (83); 1106 (153); 1107 (158); 1108 (188); 1109 (117); 1110 (176); 1112 (49); 1113 (218); 1114 (180); 1116 (32); 1118 (191); 1119 (235); 1122 (178); 1123 (37); 1125 (39); 1126 (92); 1127 (82); 1128 (241); 1130 (234); 1131 (121); 1132 (159); 1133 (225); 1134 (230); 1135 (164)

Rojas, A., 3575 (192); 3576 (182); 3577 (75); 3578 (16); 3579 (52); 3580 (40); 3581 (16); 3582 (61); 3583 (76); 3584 (231); 3585 (14); 3586 (66); 3587 (238); 3588 (65); 3589 (34); 3590 (8); 3591 (15); 3592 (77); 3593 (74); 3594 (63); 3595 (56); 3596 (59); 3597 (54); 3599 (49); 3600 (23); 3601 (27); 3602 (22); 3603 (25); 3604 (24); 3605 (20); 3607 (51); 3608 (41); 3609 (42); 3610 (33); 3611 (38); 3612 (13); 3614 (58); 3615 (28); 3616 (26); 3617 (10); 3618 (46); 3619 (4); 3620 (39); 3622 (18); 3623 (244); 3624 (188); 3625 (111); 3626 (47); 3627 (17); 3628 (21); 3630 (91); 3631 (167); 3632 (93); 3633 (186); 3634 (81); 3635 (6); 3636 (31); 3637 (98); 3638 (214); 3639 (100); 3640 (245); 3642 (40); 3643 (80); 3644 (48); 3645 (64); 3646 (67); 3647 (69); 3648 (62); 3649 (68); 3650 (9); 3651 (32); 3652 (60); 3653 (247); 3654 (167); 3655 (183); 3656 (106); 3657 (194); 3658 (263); 3659 (210); 3660 (207); 3661 (179); 3662 (34); 3663 (35); 3664 (30); 3665 (57); 3666 (114); 3669 (16); 3670 (200); 3671 (170); 3672 (110); 3674 (251); 3675 (213); 3676 (170); 3678 (101); 3679 (29); 3680 (7); 3681 (74); 3682 (170); 3683 (85); 3684 (244); 3685 (12); 3686 (78); 3687 (50); 3688 (215); 3689 (239); 3690 (158); 3691 (206); 3692 (209); 3693 (201); 3694 (191); 3696 (90); 3697 (117); 3698 (230); 3698.1 (229); 3699 (229); 3700 (220); 3702 (217); 3703 (219); 3704 (232); 3705 (221); 3708 (243); 3710 (87); 3711 (226); 3713 (176); 3714 (246); 3715 (145); 3716 (258); 3718 (22); 3719 (29); 3720 (45); 3773 (37); 3774 (8); 3775 (36); 3776 (5); 3777 (2); 3779 (180); 3780 (57); 3782 (70); s.n. (182)

Sánchez, P., 1 (179); 3 (159); 6 (117); 7 (176); 9 (46); 10 (206); 11 (123); 12 (181); 13 (258); 14 (247); 15 (192); 16 (182); 18 (93); 19 (168); 20 (110); 21 (127); 23 (170); 24 (116); 25 (116); 27 (234); 29 (32); 36 (14)

Schmitt, W., 128 (8); 129 (6); 130 (6); 131 (6); 132 (52); 133 (49)

Snodgrass, R. and Heller, E., 942 (216); 944 (137); 946A (126); 946B (130); 947 (100); 951 (192); 954 (2); 958 (57); 963 (182); 964 (7); 969 (56); 971 (46); 972 (65)

Soto, R., 1 (161); 3852 (176); 3853 (170); 3854 (85); 3855 (116); 3856 (101); 3857 (156); 3859 (167); 3860 (121); 3861 (214); 3862 (235); 3863 (90); 3864 (163); s.n. (9); s.n. (11); s.n. (13); s.n. (15); s.n. (16); s.n. (31); s.n. (33); s.n. (34); s.n. (40); s.n. (48); s.n. (49); s.n. (50); s.n. (52); s.n. (54); s.n. (56); s.n. (62); s.n. (66); s.n. (69); s.n. (75); s.n. (80); s.n. (100); s.n. (102); s.n. (115); s.n. (125); s.n. (126); s.n. (134); s.n. (135); s.n. (144); s.n. (145); s.n. (149); s.n. (156); s.n. (158); s.n. (168); s.n. (171); s.n. (176); s.n. (178); s.n. (179); s.n. (182); s.n. (183); s.n. (186); s.n. (189); s.n. (192); s.n. (207); s.n. (210); s.n. (213); s.n. (217); s.n. (221); s.n. (227); s.n. (232); s.n. (246); s.n. (258)

Stewart, A., 226 (61); 228 (2); 232 (75); 233 (32); 234 (49); 235 (49); 236 (49); 239 (52); 252 (28); 253 (27); 261 (216); 266 (128); 267 (130); 268 (130); 269 (126); 271 (135); 278 (93); 300 (143); 319 (102); 320 (90); 326 (98)

Svenson, H. K., 303 (189); 305 (216); 307 (181); 308 (100); 310 (128); 311 (54); 319 (142); 321 (57); 322 (106); 324 (46); 330 (80); 332 (18); 333 (206); 335 (207); 337 (196); 338 (32); 339 (2); 341 (10); 343 (9); 344 (35); 345 (28); 348 (206); 349 (31); 401 (186); 405 (213); 433 (11); 436 (106); s.n. (46); s.n. (207)

Trusty J. L., 30 (6); 31 (8); 32 (213); 33 (192); 34 (34); 35 (85); 36 (101); 37 (227); 38 (117); 39 (176); 40 (61); 41

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A New Species of *Adalaria* (Nudibranchia: Onchidorididae) from the Northeastern Pacific

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A new species of *Adalaria* Bergh, 1878 is described from the northeastern Pacific. It is white, characterized by highly spiculose, rounded tubercles with narrow bases, 4-6 tubercles on the rhinophore sheath, and separate gill leaves inserted in a circlet. This species is known to range from Alaska to Oregon. A comparison is made between this new species and others in the genus.

KEY WORDS: *Adalaria*, *Arctadalaria*, Onchidorididae, phanerobranch, Nudibranchia, Northeastern Pacific

The genus *Adalaria*, in the family Onchidorididae, is composed of small white, off-white, or yellow phanerobranch dorid nudibranchs with a spiculose dorsum and tubercles, an ample mantle margin, lamellate rhinophores and a veil-like head. They are bryozoan feeders and are similar to another bryozoan feeding genus, *Onchidoris*, which are usually white or brown in colour. Both genera have a reduced or absent, rectangular central tooth, a large, flat, beak-like first lateral tooth, which may have a few inner denticles, and small, oval, outer lateral teeth with a small hook. *Adalaria* are distinguished by having more than one outer lateral tooth and by usually having a smooth rather than a papillate lip disk, although *A. jannae* Millen, 1987 has a papillate lip disk. Both genera have a short, wide ampulla, a wide unarmed penis and a correspondingly wide but short vagina (Millen 1985, 1987). An exception is *Onchidoris bilamellata*, which has a longer, narrow, chitinized penis, without spines, and a longer narrower vagina. There are two bursae, the oviduct usually enters near the base of the sessile receptaculum seminis and the insemination duct to the female gland mass is near the base of the bursa copulatrix, as illustrated for *Onchidoris bilamellata* by Thompson (1966:350, Fig. 2). All species in both genera are cold-water northern species. Based on the phylogenetic analysis by Millen and Martynov (2005), the genus *Adalaria* is situated in a clade with *Onchidoris* and the family Corambidae genera *Corambe* and *Loy*. A sister clade includes other Onchidorididae genera *Calycidoris, Diaphorodoris, Acanthodoris* as well as *Goniodoris*. The latter genus had previously been placed in the family Goniodorididae. A more recent analysis by Fahey and Valdés (2005) which did not include the family Corambidae genera, placed *Adalaria* as a sister genus to *Onchidoris* and that clade as basal to *Acanthodoris* and a sister clade containing *Calycidoris Diaphodoris* and two genera of Goniodorididae (*Goniodoris* and *Okenia*). Although the relationship of these three families needs further exploration, it is clear that *Adalaria* and *Onchidoris* are closely related genera.

There are two species of *Adalaria* known to occur in the Atlantic, White, and Barents Seas, *A. loveni* (Alder and Hancock 1862) and *A. proxima* (Alder and Hancock 1854), and three are recorded from the Bering Sea, Sea of Okhotsk and Sea of Japan, but, in this region, the genus is currently being reassessed (Martynov, pers. commun.). *Adalaria proxima s.l.* is rarely found subtidally in all three seas. *Adalaria jannae* is a common intertidal species in Peter the Great Bay in the Sea of Japan and extends to the northern Kurile Islands (Martynov 2005). *Adalaria tschuktschica* Krause, 1885 (sometimes as its junior synonym *Arctadalaria septentrionalis* Roginskaya, 1971) has been reported from the Laptev and Chukchi Seas (Martynov 2001). *Adalaria spiculoides* (Volodchenko, 1941) is a *nomen dubium* according to Martynov (1997). Volodchenko determined two other specimens under this name, which are similar to *Onchidoris muricata* with the radulae absent. *Adalaria beringi* (Volodchenko, 1941) is a *nomen dubium* and other specimens determined by this name by Volodchenko appear to be similar to *Onchidoris muricata* with the radulae absent, according to Martynov (1997). Two additional, apparently undescribed species have been collected from the northern Sea of Japan and Kurile Islands; one is photographed in Nakano (2004:98 #191). In the northeastern Pacific, two species of *Adalaria* are found; *Adalaria proxima* and *A. jannae.* Both species are sympatric with the newly described species (Millen 1987).

A small, white, undescribed dorid nudibranch belonging to the genus *Adalaria* has been collected sporadically in Oregon (Goddard 1984), British Columbia (Millen 1987) and Alaska (Millen 1989; Goddard and Foster 2002). In 1987, a substantial population was discovered near Horseshoe Bay, British Columbia, and specimens were collected over several months. This paper describes the new species and compares it with other species of *Adalaria*.

Subclass Opisthobranchia
Order Nudibranchia
Suborder Doridacea
Superfamily Anadoridoidea
Family Onchidorididae Gray, 1827

Genus *Adalaria* Bergh, 1878

TYPE SPECIES: *Doris loveni* Alder and Hancock, 1862.

Adalaria evincta Millen sp. nov.

Figs. 1–3.

Adalaria sp. Goddard 1984:145, 155–156, 159, Tbls. 1,2,3.
Adalaria sp. Millen 1987:2701.
Adalaria sp. Millen 1989:66.
Adalaria sp. 1. Behrens 1991:50,fig. 67.
Adalaria sp. Goddard et al. 1997: Tble. 1 pg. 294.
Adalaria sp. 1. Goddard, 2005: Tble. 1. pg. 1959.
Adalaria sp. 1, Goddard and Foster 2002:333.
Adalaria sp. 1, Behrens and Hermosillo 2005:58.
Adalaria MC309. Lamb and Hanby 2005:256.

ETYMOLOGY.— The species name *evincta* (L. wreath or crown) refers to the crown of spines found on each tubercle.

MATERIAL EXAMINED.— Holotype: California Academy of Sciences, CASIZ 110799. 20 March 1987, Tyee Pt., Copper Cove, Horseshoe Bay, British Columbia, Canada (49°22′8″N, 123°16′5″W), 2 m depth on the bryozoan *Dendrobenia lichenoides*, rock substrate. S. Millen. Paratypes: Royal British Columbia Museum, RBCM 988-25-1, 5 specimens, collected with the holotype on March 20, 1987 by S. Millen; RBCM 975-230-2, 1 specimen, collected Georgeson Passage, between Maine and Samuel Is., June 27, 1975; RBCM 976-1040-15, 1 specimen, collected Langara Island, Queen Charlotte Islands, Dribrell Bay, March 30, 1976.

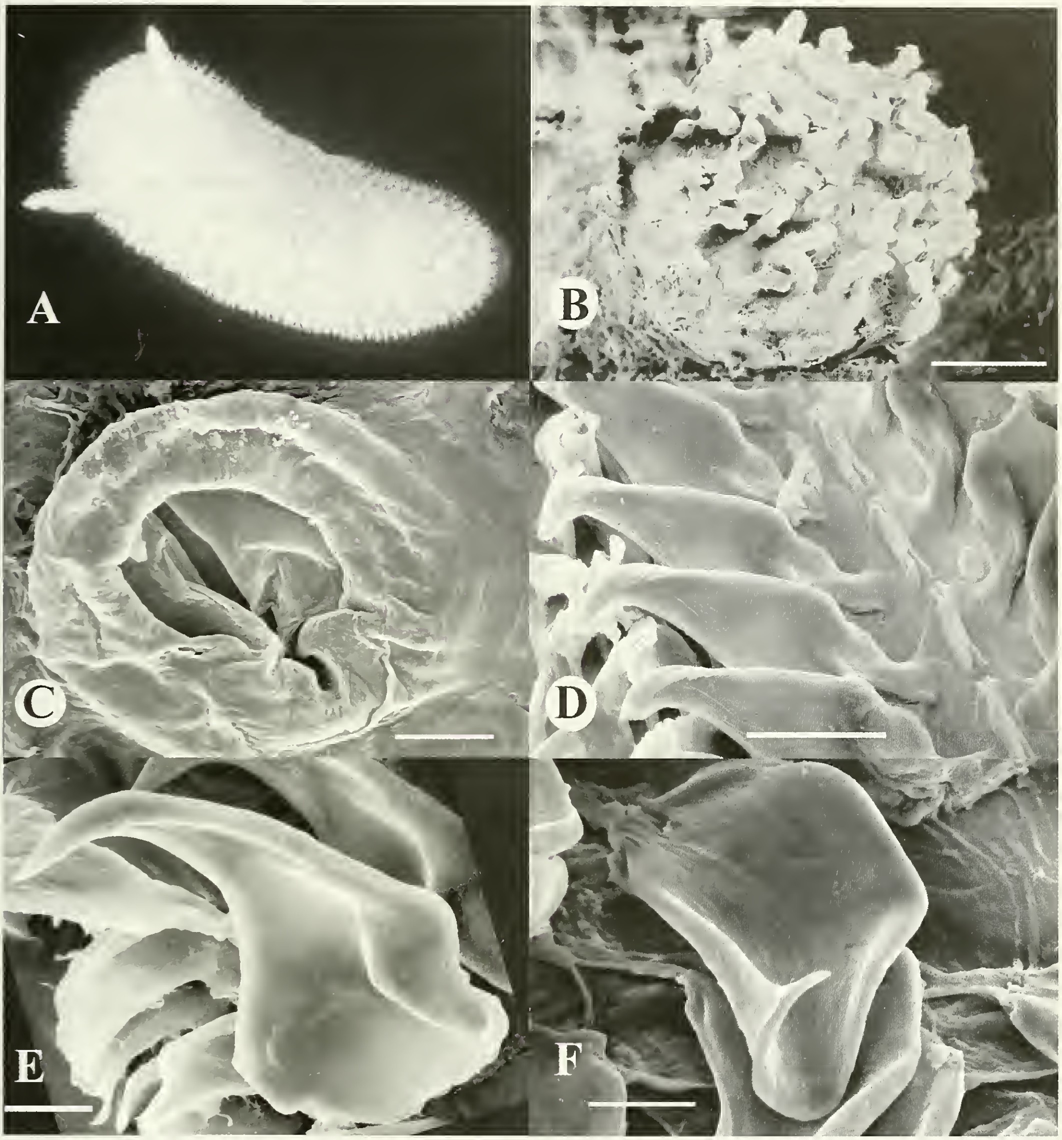

FIGURE 1. *Adalaria evincta* sp. nov. A. Living animal. Specimen from Bowen Island, British Columbia, Canada, March, 1974. Photo by Ron Long. B. SEM of tubercle with spines. Scale bar = 100 µm. C. SEM of lip disk. Scale bar = 100 µm. D. SEM of the radula showing central and lateral teeth. Scale bar =50µm. E. SEM of the first lateral tooth. Scale bar = 20 µm. F. Outer lateral tooth. Scale bar = 10 µm.

EXTERNAL MORPHOLOGY.— The body shape is elongate-oval and tapering, wider in front than behind (Fig. 1A). Specimens range in size from 7–14 mm (preserved lengths) the largest having a live length of 16 mm. The mantle margin is narrow, covering the sides and head but not the flattened tail, which tapers to a rounded tip. The notum bears tubercles with rounded spiculose tops and long narrow stalks (Figs. 1B, 2A). The closely spaced tubercles vary in size with smaller tubercles predominating towards the mantle margin. Larger tubercles are 0.9 mm high and 0.5 mm wide at the top with a stalk diameter of 0.2 mm. The tubercle stalks are densely packed with vertical spicules, which, at the top, radiate out at an angle of approximately 15° from the central axis, creating a spiculose crown. At the bases of the tubercles, spicules extend in a conspicuous radial, star-like pattern throughout the notum. Elsewhere in the notum larger spicules are visible over the dark background of the digestive glands and sperm filled bursa copulatrix, where they can be seen running crosswise to the body axis. In the foot, the spicules form a reticulating network, which is radially arranged towards the outside. The rhinophores contain a central shaft of spicules and small supporting spicules on the lamellae.

The margins of the rhinophores are slightly raised and bear from 4–7 (usually 5) tubercles of various dimensions. The branchial circlet contains 4–9 tubercles of varying sizes within it and tubercles surround the outsides of the gill pockets. There are 6–13 pinnate gill leaves with long irregular side branches. These contract into separate gill depressions arranged in a nearly complete circle. The gill leaves are longer anteriorly, slightly shorter posteriorly (1.9 and 1.2 mm respectively in one live specimen). The rhinophores are long and slender with a rectangular, flat-topped tip. The stalk is short and the clavus bears sloping lamellae. The 11–17 (usually 15) lamellae are attached along a vertical anterior line. The lamellae slope ventrally and the distal most 4–10 meet posteriorly forming a chevron. More proximally the lamellae are progressively more incomplete. The large head (Fig. 2B) is veliform, semi-circular with a ruffled or smooth outer edge. Small notches separate leaf-like tentacles attached at their posterior edge. The mouth is a small vertical oval. The triangular foot is wider and thickened anteriorly, with rounded front corners. It tapers to a slightly protruding, narrow, rounded tail.

Living specimens are white, occasionally pale yellow and semi-translucent. In mature animals the mid-dorsal region appears yellowish due to the creamy gonads underneath. Sometimes there is a brown spot slightly to the right of the midline indicating the location of the sperm filled bursa copulatrix. In immature animals, the small digestive glands, which are dark brown or reddish brown, can be seen dorsally as well as ventrally. The rhinophores are pale yellow. The gill leaves and foot are white or pale yellow. The gill leaves have opaque white glands on their bases. On the midline, posterior to the branchial circlet, a mantle gland is visible as a small circular area of opaque white granulations.

ANATOMY.— The buccal tube is short and broad, internally folded and glandular. Dorsally the buccal bulb has a rounded sucking crop with a broad median muscular band and a short stalk. The posterior radular sac projects ventrally. It is long and narrow, usually bent to one side. The lip disk is smooth, thin and light yellow (Fig. 1C). Two small ventral flaps guard the opening. The radula ranges in length from 34–39 rows. The radula (Figs. 1D– F; 2C) has a formula of 3-6.1.1.1.3-6. The central (rachidian) tooth is a narrow elongate rectangle with thickened sides and rounded ends. Central tooth lengths ranged from 0.03–0.04 mm (x= 0.04 mm, n=19). Each large inner lateral tooth has a triangular base and an elongate hook. The anterior edge of the hook is straight and the tip curves suddenly. The hook is usually smooth but larger specimens had 1–12 tiny denticles along the upper edge, which do not extend to the tip. A large inner, wing-like knob is present. The inner lateral teeth range in height from 0.08–0.10 mm (x=0.09, n=23). The outer lateral teeth are somewhat oblong with rounded edges. The anterior edge is thickened and recurved with a single posteriorly directed hook. The outer lateral teeth are smaller towards the outside of the radula and assume a triangular shape. Outer lateral tooth heights ranged from 0.01–0.04 mm (n=21).

At the posterior end of the buccal bulb is the long, thin esophagus. The salivary glands insert at its base. They are white, S- shaped, with a thicker, fluffy anterior portion. The small stomach is buried in the digestive glands anteriorly but posteriorly it loops up to the surface where a small, cylindrical caecum lies under the loop of the intestine. The digestive glands appear as one elongate oval, dark brown mass, hollowed out on the anterior right due to the reproductive organs. The tubu-

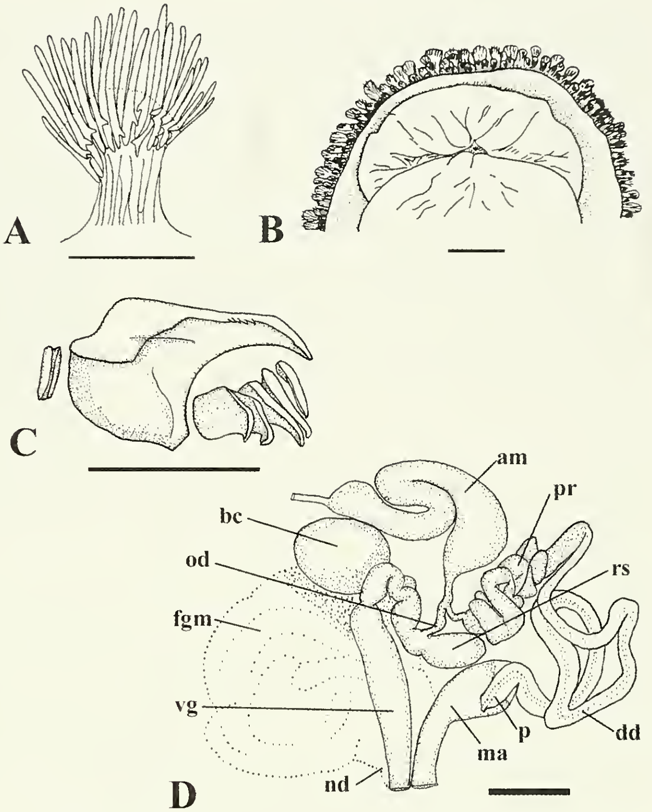

FIGURE 2. *Adalaria evincta* sp. nov., drawn by camera lucida. A. Notal tubercle . Scale bar = 0.5 mm. B. Head. Scale bar = 1 mm. C. Radula. Scale bar = 0.1 mm. D. Reproductive system. Scale bar = 1 mm. Key: am= ampulla, bc=bursa copulatrix, dd=deferent duct, fgm=female gland mass, ma=male atrium, nd=nidamental duct, od=oviduct, p=penis, pr=prostate, rs=receptaculum seminis, vg=vagina.

lar intestine curves to the right over the caecum and runs to the anus located slightly left of center in the branchial circlet. The anal opening is simple and not raised, located at the base of a large posterior tubercle. The renal pore is located slightly to the right at the base of the same large tubercle.

The Circulatory system has a thin walled, triangular auricle and a smaller, slightly thicker walled, diamond shaped ventricle. The aorta ends in large, fluffy, white blood glands appearing as one mass covering the central nervous system.

In the central nervous system, the cerebral and pleural ganglia are partially fused. The cerebral ganglia are oval and connected by a short commissure. The pleurals are oval and lie ventral and lateral to the cerebrals. Dorsally they are separated from the cerebrals by a groove and have larger nerve cells. Ventrally the cerebro-pleurals form an almost indistinguishable mass. The almost separate pedal ganglia are posterior, oval and nearly as large as the combined cerebropleurals. They are connected by a short commissure. The eyes are connected by a short optic nerve. The small olfactory bulbs are unstalked. The paired buccal ganglia adjoin each other and each has a gastro-esophageal ganglia attached by a short stalk.

The ovotestis consists of creamy yellow lobules on the dorsal surface and sides of the digestive glands. The branched gonoducts of the ovotestis merge forming a thin pre-ampullary duct, which widens into a S-shaped ampulla (Fig. 2D). The postampullar duct bifurcates into a short oviduct leading to the buried receptaculum seminis (fertilization chamber) and an extremely long vas deferens. The proximal, prostatic, portion of the vas deferens is highly coiled, soft and glandular. It continues as a less coiled, muscular deferent duct. Near the outer body wall the vas deferens enters an enlarged male atrium with highly folded walls. The penis is cylindrical and unarmed. The oval receptaculum seminis is hidden within the albumen gland and has a wide, muscular duct. The bursa copulatrix has a short duct leading to a large, round sac, which is dark brown when filled with unaligned sperm. The proximal portion of the vagina is free of the female gland mass and has an insemination duct on the inner side. Distally, the vagina is a soft, cylindrical duct, which is open to the female gland mass on the inner side. The female gland mass consists of a granular yellow albumen gland which is anterior, a highly convoluted mucous gland and an elongate, less convoluted, white membrane gland. The latter envelopes the other two glands and forms the nidamental duct that is attached to the inner side of the vagina and opens ventral to the vagina.

The reproductive openings are located under the notum on the right side on a small papilla a short distance posterior to the anterior margin of the foot. The penial opening is round, the common vaginal and oviductual opening forms a crescent shape posterior to the male opening.

Natural history.— *Adalaria evincta* occurs in the low intertidal zone and shallow subtidal to 15 m. Its known range is from Tatitlek, Alaska (60°52.10′N, 146°43.47′W) to North Cove, Cape Argo, Oregon (43°20′N, 124°22′W) (Goddard 1984; Goddard and Foster 2002). According to Goddard (1984) this species eats the white encrusting bryozoan *Hincksina minuscula* (Hincks, 1822) at his study site in Oregon. In British Columbia, this species was consistently found feeding and spawning on the pale brown bryozoan *Dendrobenia lichenoides* (Robertson, 1905). *Adalaria evincta* has been found year round, predominately January to March, although it is never abundant (Fig. 3). Spawning has been observed from late January to May. The egg mass, a white ribbon on edge with 2–3 turns and larval development has been described by Goddard (1984:145, Table 1).

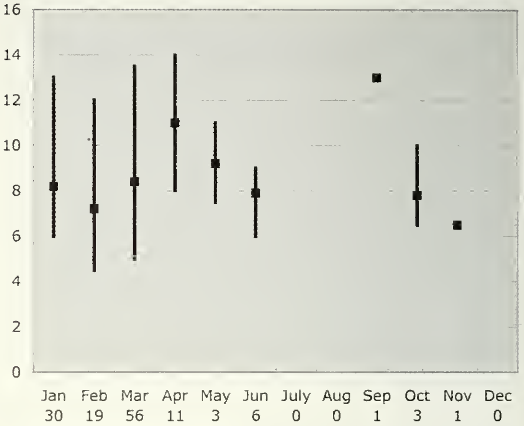

Figure 3. *Adalaria evincta* sp. nov. annual cycle. Preserved length of specimens in mm showing the range and average versus month collected. Number of specimens noted with the month. N=130.

Discussion.— This new species is placed in the genus *Adalaria* because it has pinnate gill leaves inserted into separate notal areas and several outer lateral teeth. Externally it differs from most other *Adalaria* species in having an elongate, tapering shape, tubercles which have projecting spicules, many tubercles around the rhinophores and gill leaves arranged in a circlet rather than a horseshoe. These latter two features were considered sufficient by Roginskaya (1971), to create a new genus, *Arctadalaria*. I consider them insufficient to be considered a generic difference and agree with Martynov (2001) that *Arctadalaria* is a junior synonym of *Adalaria*. Along the northeastern Pacific coast, only *Adalaria albopapillosa* Bergh, 1880 from Sitka, Alaska is like *Adalaria evincta* in having similar sized (1mm long) tubercles with projecting spicules. It differs in having fewer radular tooth rows (29–30 vs. 34–39) and more outer lateral teeth (8 vs. 3–6). The lateral teeth are larger (12 mm vs. 9 mm), with stronger denticulations and a curved anterior edge. In addition, the body shape is oval and there are only 2 tubercles guarding the rhinophores. These features are more consistent with *Adalaria proxima* than with *Adalaria evincta* as poorly preserved specimens of *Adalaria proxima* often show projecting spicules. I therefore continue to consider *Adalaria albopapillosa* as a junior synonym of *Adalaria proxima* (Millen 1987).

In the Bering and Laptev Seas, three species have been described with a similar tooth shape and several tubercles around the rhinophores. *Adalaria tschuktschica* from the Bering Sea has an elongate body form and a similar radular formula 39 (7.1.1.1.7). The teeth differ in that the inner laterals are more strongly denticulate and the tip is straighter. Other differences are the longer (2mm vs. 0.9 mm) cylindrical tubercles and the larger body size (22 mm vs. 14 mm preserved lengths). *Arctadalaria septentrionalis* from the Laptev Sea, was described as having projecting spines along the length of the tubercles, like a pinecone. The gill leaves are arranged in a circlet but they have common rather than separate insertions and the anterior most gills are tripinnate. This species, according to Martynov (2001) is a junior synonym of *Adalaria tschuktschica. Adalaria spiculoides* (Volodchenko, 1941), a *nomen dubium* from the Bering Sea has lateral teeth, which have longer and straighter hooks, the tubercles are cylindrical conical, and the body spicules are more developed. It has an elongate body shape, gill leaves in a circlet, tuberculate rhinophore sheaths and its radula formula of 33 (5.1.1.1.5) overlaps that of *Adalaria evincta. Adalaria beringi* (Volodchenko, 1941), another *nomen dubium* from the Bering Sea has a similar radula formula 39 (5.1.1.1.5). It has a longer, straighter hook on the lateral teeth, and the outer lateral teeth have a serrated margin. Other differences are its oval shape, equally rounded at both ends, with a thin wide mantle margin, small head with pointed tentacles, smooth rhinophore and gill margins and a common gill opening. None of these species have cylindrical spines ending in a round ball with projecting spicules that are so obvious on *Adalaria evincta* and they all have straighter tipped, less abruptly hooked lateral teeth than does *Adalaria evincta*.

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A Review of Our Knowledge of California Mecoptera

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Nine species in eight genera of Mecoptera are probably found in California. More genera of Mecoptera occur in California than in any other state in the country. California representatives of Mecoptera also contain an unusually high number of basal species and their distributions are unusually small.

Mecoptera, or scorpion-flies, hanging-flies, and earwig-flies, are among the oldest holometabolous insects with fossils dating back to the early Permian, 250 million years ago. By the late Permian they were quite abundant (Carpenter 1931; Riek 1980). Fore- and hind wings have very similar venation that has remained little modified over hundreds of millions of years. Most mecopterans have a distinctive long rostrum with mouthparts at the end. Most species are saprophagous or phytophagous, but members of Bittacidae are predaceous. They are found all over the world, but tend to be more common in temperate regions; and some groups, like Boreidae in northern boreal climates and Apteropanorpidae in Tasmania, are highly adapted to colder temperatures.

In the United States, Mecoptera are thought to exist primarily in the eastern part of the country. When Carpenter (1931) wrote his revision of the 54 species of Nearctic Mecoptera, there were only seven species known from the western part of the country and only three species from California. Byers' (1954) report on the Mecoptera of North America included 70 species, 16 of which (mostly *Boreus*) were western and still only three species from California. This seems strange in light of the relictual nature of many faunal elements (Rasnitsyn 1997; Vickery and Sandoval 2001; Wygodzinsky 1961) in the Mediterranean climate of California and the long, rich geological history of Mecoptera (Carpenter 1931, 1992).

The Mecoptera that do exist in the western U.S. were generally thought to be Boreidae (winter scorpion-flies) in the Great Basin and high mountains, two species of *Brachypanorpa* in the Northwest, and two species of Bittacidae (hanging-flies) in coastal California.

However, a more complex picture of mecopteran distribution recently has begun to emerge. Several new species have been discovered with very small distributions (Cooper 1972; Villegas and Byers 1981; Russell 1979; Byers 2005). Today, eight genera are likely found within the boundaries of the state, and with no more than six genera found in any other state, California could arguably be considered to have the most taxonomically diverse fauna in the country.

The purpose of this paper is to draw the attention of the scientific community to the importance and diversity of the fauna of California, in this case with specific reference to the Mecoptera, and to report briefly on what is currently known about the California species and their distributions.

Family Bittacidae (hanging-flies)

These insects look like four-winged crane-flies, hanging by their forelegs from vegetation. Some species rest with their wings open, others with wings closed, and in California there is one species with no wings at all. Despite the common notion that mecopterans are predaceous, Bittacidae is probably the only predaceous family in the order. In this family, the hindleg is modified to include a single enlarged apical claw that is raptorial. The prey is transferred from the hindlegs to the forelegs for feeding, or in some cases is given to a potential mate as a nuptial meal (Bornemissza 1966). Larvae are eruciform and saprophagous, living at the soil surface, and feeding on dead insects and earthworms (Setty 1940).

The family Bittacidae, and notably the genus *Bittacus*, is distributed worldwide. Four bittacid genera have been reported from North America: *Hylobittacus apicalis* (Hagen) has dark wingtips and is found in river bottoms over much of the eastern U.S. (Byers 1979); *Bittacus* is represented by seven species, six of which are found commonly along streams and sometimes in open grasslands throughout the eastern U.S. as far west as eastern Montana (Byers 1973), and one, *Bittacus chlorostigma*, occurs in California; two additional genera, also known from California, are *Apterobittacus apterus* (McLachlan) and *Orobittacus obscurus* Villegas and Byers.

Bittacid species in the eastern U.S. lay eggs in mid-summer and larvae almost immediately hatch and begin development. By late summer the larvae are fully grown and overwinter as prepupae. The two lowland California species of bittacids lay eggs in April and May. Eggs have a pink coating and go through a five to six month aestivation. When the rains begin in the fall, eggs swell to twice their original size and the pink coating is cracked and broken and the eggs hatch. Larvae develop during the late fall and winter. Nothing is known of immature stages of *Orobittacus obscurus*.

Apterobittacus apterus (McLachlan, 1871)

Fig. 1.

This species is found in grasslands of the coastal hills and the Central Valley of California (Map 1). It was originally described from Brooklyn, California. The town once stood near what is now Mills College in the hills behind Oakland. This is one of two wingless species of Bittacidae in the world, the other being *Anomalobittacus gracilipes* Kimmins of South Africa.

Adults climb amongst the grass blades feeding on flies, caterpillars, and other insects that they capture with their raptorial hindlegs. Adults emerge from late March to early June. The larval stages were described by Applegarth (1939).

Because they are wingless, these mecopterans are vulnerable to population extirpation through fragmentation of habitat and subsequent habitat modification. Recolonization is difficult if roads, land cultivation, or other barriers to local dispersal exist.

MAP 1. Distribution of *Bittacus chlorostigma*, *Apterobittacus apterus* and *Orobittacus obscurus* in California.

Bittacus chlorostigma McLachlan, 1881

Fig. 2.

This species of rather large hanging-fly has one unmistakable characteristic—the pterostigma of the wings is bright yellow. They are found in open oak woodlands of the foot-hills of the Sierra Nevada and Sutter Buttes (Map 1), emerging as adults from late March to mid-July. They can be locally abundant at peak emergence. As with *Apterobittacus apterus,* the egg first goes through a long aestivation period before eclosion.

Orobittacus obscurus Villegas and Byers, 1981

These secretive and primitive bittacids are unusual in several respects. They have darkly infuscated wings and live in the shadows below rock overhangs and at the base of protruding tree roots. They are very sensitive to warm temperatures and females do not appear to drop eggs as readily as do other bittacids. Whereas all other North American bittacids are known to occupy ranges that extend for hundreds or even thousands of square kilometers, this species is known from only two small populations along the American River in the Sierra Nevada—at a U.S. Forest Service picnic area about 30 km east of Placerville (El Dorado County), and near Foresthill (Placer County) (Map 1). Adults emerge from early May to early July.

The male genitalia possess several characteristics that are strikingly unique among North American bittacids. The dististyles are enlarged, a characteristic that they have in common with *Tytthobittacus maculpinei* Smithers of Australia and *Anabittacus iridipennis* Kimmins from Chile. As in these other two genera, the cerci are expanded. However, *Orobittacus* is unique in that the ninth tergum has developed into a single median lobe with terminal, claw-like spines (Villegas and Byers 1981). This species must have diverged from other bittacids at a quite early period to have these primitive features in common with species from Chile and Australia, and yet also to have developed such a remarkable and unique character.

FIGURE 1. *Apterobittacus apterus* (McLachlan). Photo by Vincent F. Lee.

FIGURE 2. *Bittacus chlorostigma* McLachlan. Photo by T.W. Davies.

Family Boreidae (winter scorpion-flies)

These insects are among the smallest mecopterans. Adults are about 3–5 mm long, brown to shiny black in color, have highly reduced wings, and emerge during the winter months in the lower 48 states. Females have an ovipositor that can be long (*Boreus*) or vestigial (*Caurinus*). Most species can be recognized as mecopterans by their long rostrum. Adults feed on the foliage of mosses, club mosses, and liverworts. Larvae are white, scarabaeiform and sedentary, and feed upon the rhizoids of the same plants as the adults.

The family is divided into two subfamilies (Russell 1979): Caurininae (*Caurinus*) and Boreinae (*Boreus* and *Hesperoboreus*). All three genera are probably found in California.

Genus *Caurinus* Russell

Caurinus dectes Russell, 1979

This is a very unusual insect. It is almost certainly a boreid, but lacks the elongate rostrum that is characteristic of all other boreids and most mecopterans. Males have reduced, spiniferous, strap-like forewings and females have rounded, short, forewing pads similar to most other boreids. However, unlike other boreids, hindwings are absent. The male has recurved dististyles, but females lack ovipositors. They are smaller than all other boreids, with overall length from 1.4–1.9 mm. Larvae are almost legless (Russell 1979). They are found in moist forests with abundant epiphytes and terrestrial bryophytes. Adults feed on the epiphytic liverwort *Porella navicularis* (L. & L.) Lindb., but they have also been found in terrestrial mosses (Russell 1979). They are distributed in the Coast Range of central Oregon. However, in his Ph.D. thesis Russell mentioned finding feeding damage from *Caurinus* on epiphytic liverworts in northernmost California and he believes that they exist there.

Genus *Boreus* Latreille

Boreus is the most speciose of the three genera of Boreidae. They can be distinguished by the rostrum which has a narrow hypostomal bridge. Males have the ninth tergum modified into a small to large hood to receive the recurved dististyles. Females have a long ovipositor that is about as long as the elongate rostrum. They are Holarctic in distribution (Penny 1977) and in North America are distributed in the cooler regions of the eastern U.S. (2 species), Alaska (2 species), and across the western states (8 species).

Boreus californicus Packard, 1871

Fig. 3.

This species was originally described from 3 males and 4 females from the east (Ft. Bidwell) and west (Goose Lake) sides of the Warner Mountains in Modoc County, California (Map 2). This is the most widely distributed species of boreid in western North America. They are found at high elevations from the Canadian Rockies of British Columbia and Alberta through Wyoming and Montana south to northern Arizona and California (Penny 1977). In California they can be found on tightly compacted *Grimmea* mosses in the Sierra Nevada and White Mountains. They prefer rock surfaces above 4000 feet from Yosemite National Park northwards to the Oregon border. Individuals will occasionally get off of the rocks and wander over the snow surface, but this is uncommon. In California adults emerge from December to March.

Genus *Hesperoboreus* Penny

Hesperoboreus is a genus of rather small boreids (less than 4 mm long) with a broad hypostomal bridge to the rostrum. Males have a ninth tergum with a medial notch and no central hood for receiving the dististyles. Females have an ovipositor about half the length of the rostrum. This genus contains only two species—*H. brevicaudus* from western Oregon and Washington and *H. notoperates* from southern California.

Hesperoboreus brevicaudus (Byers, 1961)

This is a lowland species usually found below 600 m west of the Cascade Range in Oregon and Washington. Individuals have been collected by Berlese funnel extraction from mosses, holding a beating sheet under vertical moss banks and scraping the moss surface, or capturing them walking on the snow surface on warm winter days. Russell (1979) mentions their presence in epiphytic mosses in moist forests. Collection records are from 16 October to 31 December, perhaps indicating a somewhat earlier emergence than other species.

They are not known from California, but can probably be found in the northern coastal regions of the state, as they have been taken southwest of Williams, Oregon only 24 km (15 miles) from the California border (Penny 1977).

MAP 2. Distribution of *Boreus californicus* and *Hesperoboreus notoperates* in California.

FIGURE 3. *Boreus californicus* Packard. Photo by D.D. Wilder.

Hesperoboreus notoperates (Cooper, 1972)

Boreids are known to be cold-adapted insects, and as their name implies, are distributed almost completely in boreal habitats. However, this species is found on Mt. San Jacinto in the Upper Sonoran region of chaparral and yellow pine of southern California at 33.7° north latitude (Map 2), making this the southernmost species of the family (Cooper 1972). Larvae appear to go through four moults during a two year life cycle, metamorphose to pupae in mid-August and September, and emerge as adults from mid-November to mid-March (Cooper 1974). During the long, dry summers when the moss mats are dry and friable, the larva forms a small cell around itself, apparently from salivary secretions. After an occasional summer rain and at the beginning of the fall rainy season they immediately break out of their cells and begin feeding (Cooper 1974). They are found on the northwest slopes of steep canyons in only two places—

at 1210 m elevation in Coldwater Canyon, and at 1645 m elevation in Black Canyon on Mount San Jacinto, Riverside County, California (Cooper 1974).

Family Panorpodidae

This family is thought to be closely related to Panorpidae (true scorpion-flies), but is phytophagous rather than saprophagous. Adults have smooth tarsal claws, rather than the toothed claws of Panorpidae. Also, larvae of *Brachypanorpa* (and by inference *Panorpodes*) are scarabaeiform and subterranean, while larvae of Panorpidae live at the soil surface and are eruciform (Byers 1965). The family contains only two genera, *Brachypanorpa* and *Panorpodes* distributed in North America, Korea, and Japan.

Genus *Brachypanorpa* Carpenter

Brachypanorpa, as the name implies, have brachypterous females that are flightless. The long rostrum that is so characteristic of Mecoptera is much reduced in *Brachypanorpa*. The sedentary larvae live in the soil of moist forests where they are presumed to feed on plant roots, and adults emerge in early summer. Little else is known of their life history. There are five species recognized, 2 in the eastern U.S. and 3 in the West. The western species include *B. montana* Carpenter in Oregon, *B. oregonensis* McLachlan in California, Oregon, Idaho, and Utah, and *B. sacajawea* Byers in Idaho and Montana.

Brachypanorpa oregonensis McLachlan, 1881

This is the most widely distributed species of *Brachypanorpa*, but is known from only a single locality in California, at Patrick's Point State Park in Humboldt County (Map 3). Adults can be found in early June resting on dense beds of false lilies-of-the-valley (*Malanthemum dilatatum* [Alph. Wood] Nelson and J.F. Macbr.) near the campground. This small population is only a few hundred meters from the Pacific Ocean and may exist here only because of the moderating influence of the nearby ocean currents. Because females are flightless, dispersal is extremely limited. Any perturbation, such as a climate shift or expansion of the campground, could easily eliminate this population.

Genus *Panorpodes* McLachlan

Panorpodes, unlike *Brachypanorpa*, have fully winged females. The rostrum is long in *Panorpodes* and they are more robust, rapid fliers. They live in more open habitats, exposed to sun and wind. Until 2005 they were known only from Korea (1 species) and Japan (2 species) when Byers (2005) described a species from the northern Sierra Nevada of California.

Panorpodes colei Byers, 2005

Fig. 4.

At first glance this appears to be a true scorpion-fly found far outside its known generic range. It has the long rostrum and transparent wings with dark spots so commonly associated with *Panorpa*. However, a careful inspection discloses the smooth tarsal claws and rather thick abdomen. The wings and abdomen have an amber tint. Females are fully winged and both sexes are strong fliers, much faster than most panorpids.

Adults can be found between 1815 and 1907 m (5900–6200 ft) along the Pacific Crest Trail near Buck's Lake in the high Sierra Nevada (Map 3). The area is covered with deep snow in the winter and most of the vegetation is low, woody shrubs with a few taller pines. Adults are seen resting on the shrubs in bright sunlight during the early morning, but seem to disappear during the afternoon when temperatures are warmest. For now, they are only known from this one mountainside.

Family Panorpidae (scorpion-flies)

True scorpion-flies (*Panorpa* sp.) are known from eastern North America as far west as southern Manitoba, Canada, eastern Kansas, and central Texas. Although it is highly unlikely that *Panorpa* will ever be found in the state of California, records exist for true scorpion-flies much closer to the state than most people realize. Mexican populations are found as far north as the Sierra Madre Occidental behind Mazatlan, about 1300 km (806 miles) southeast of the California border and records exist for Utah localities less than 900 km (558 miles) east of California.

MAP 3. Distribution of *Paborpodes colei* and *Brachypanorpa oregonensis* in California.

FIGURE 4. *Panorpodes colei* Byers. Photo by Wes Bicha.

In 1937, Ashley Gurney described a new species of *Panorpa* from Uintah Canyon and Whiterocks, Utah. He also included new records for *Panorpa venosa* Westwood (now *P. helena* Byers) from the same localities. These distribution records extended the known range for this genus by about 1210 km (750 miles). Frank Carpenter studied the new species and reidentified the males as *Panorpa submaculosa* Carpenter and the females as *Panorpa maculosa* Hagen. Carpenter also questioned the validity of the collection records. However, the collector Fred Harmston, reported that he believed the locality information was accurate (Gurney 1938). No additional specimens have ever been collected there. George Byers (pers. commun.) has been to the locality and, although he didn't find any *Panorpa* at this spot, said that the locality looked like good *Panorpa* habitat.

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A New Species of Sand Eel, *Yirrkala moorei* (Anguilliformes: Ophichthidae), from the South Pacific

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***Yirrkala moorei*, a new species of sand eel, subfamily Ophichthinae, tribe Sphagebranchini, is described from specimens captured using ichthyocides and trawls in the Marquesas and American Samoa at depths of 25–454 m. It is most similar to the Indo-Pacific *Y. lumbricoides* and *Y. tenuis*, but differs from them and their congeners in a combination of its body proportions, brown-striped coloration, and its vertebral number (162-173).**

KEY WORDS: Ophichthidae; *Yirrkala moorei* sp. nov.; Marquesas Is., American Samoa.

In attempting to distinguish the numerous species of eastern Pacific *Ophichthus*, McCosker and Rosenblatt (1998:423) lamented that "the morphological reduction that is the essence of eelness has resulted in a paucity of characters useful in other fishes for determining species . . . The eel shape presents few landmarks for measurements on the body; gill openings, the anus, and dorsal and anal origins exhaust the list." And, as a result of the often twisted nature of the poorly preserved specimens, they concluded that "In general, it is a fair statement that measurements on eels may be made with great precision but without much accuracy." The Indo-Pacific sand eels of the genus *Yirrkala*, tribe Sphagebranchini (*sensu* McCosker 1977), are even more poorly known and difficult to delineate in that they have also lost their paired fins and are for the most part generally small, mostly unpigmented, and uniform in appearance. The discovery of several well-preserved specimens of a previously unknown striped species of *Yirrkala* has, therefore, provided a welcome opportunity to add to the knowledge of the diversity of these eels.

MATERIALS AND METHODS

Specimens were captured by dredge or by rotenone-based ichthyocides. All specimens deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN), were captured using a Warren Dredge during the MUSORSTOM Campagne 9 survey of the Marquesas Islands.

Measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length, trunk length, and tail length), and recorded to the nearest 0.5 mm, or a 1 m ruler with 1 mm gradations and recorded to the nearest 1 mm. All other measurements are made with dial calipers or dividers and recorded to the nearest 0.1 mm. Body length is head plus trunk length. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; maximum body depth does not include the median fins. The rictus of a paratype was surgically cut on its right side to allow the accurate illustration of its dentition, a necessary procedure. Head pore terminology follows that of McCosker et al.

(1989:257). Vertebral counts (which include the hypural) were taken from radiographs. The mean vertebral formula (MVF) is expressed as the average of predorsal, preanal, and total vertebrae. Type specimens are deposited at the Academy of Natural Sciences, Philadelphia (ANSP); the California Academy of Sciences, San Francisco (CAS), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the National Museum of Natural History (NMNH), Washington DC. Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985).

Genus *Yirrkala* Whitley, 1940

Yirrkala Whitley 1940: 410 (Type species: *Y. chaselingi* Whitley 1940, by original designation).

Yirrkala moorei McCosker, sp. nov.

(Figs. 1–3; Table 1)

Yirrkala sp. McCosker, 1977:16, 69.— Wass, 1984:6.

Material examined.— Holotype: CAS 46677, 434 mm TL, immature male, American Samoa, Aunu'u Id. (14°17′S, 170°34′W), collected using rotenone over a sandy bottom, 24 m, by R.C. Wass, Nov. 1975. Paratypes: All paratypes and nonparatypes are from the Marquesas Islands. BPBM 11857, 289 mm TL, Nuku Hiva Id., Hatuatua Bay (08°51′S, 140°00′W), dredged in 53-59 m by D. Devaney et al., 18 Sept. 1967. BPBM 11858, 307 mm TL, cleared and stained, Nuku Hiva Id., Ua Pou (15°40′S, 146°13′W), dredged in 84–93 m by D. Devaney et al., 18 Sept. 1967. BPBM 36172, 119 mm TL, Eiao Id. (07°59′S, 140°48′W), dredged in 55 m by J. Poupin, 19 Jan. 1991. USNM 306545, 410 mm TL, Nuku Hiva Id., Hatuatua Bay (08°51′S, 140°00′W), dredged in 42-59 m by H. Rehder et al., 18 Sept. 1967. ANSP 165122, 375 mm TL, collected with USNM 306545. MNHN 2001-1075, 259 mm TL, Nuku Hiva Id. (08°56′S, 140°06′W), dredged in 45-64 m by J. Poupin & B. Richer de Forges, 24 Aug. 1997. MNHN 2001–1076, 402 mm TL, Hiva Oa Id. (09°50′S, 139°02′W), dredged in 50 m, 29 Aug. 1997. MNHN 2001-1077, 243? mm TL (specimen severed by dredge), Nuku Hiva Id. (08°49′S, 140°03′W), dredged in 31–33 m by J. Poupin & B. Richer de Forges, 26 Aug. 1997. Nonparatypes: MNHN 2001-1073, 225 mm body length (tail missing, cut by dredge), Moto One Hatutaa Id. (07°47′S, 140°20′W), dredged in 450–454 m, 7 Sept. 1997. MNHN 2001-1074, 181 mm tail length (head and anterior trunk missing, cut by dredge), female with developing ova, Hiva Oa Id. (09°50′S, 139°00′W), dredged in 85 m, 29 Aug. 1997.

Diagnosis.— An elongate species of *Yirrkala* with the unique combination of characters: head 6.3–6.9% of total length (TL); tail 48–52% of TL; dorsal-fin origin in advance of gill openings; eye above middle of upper jaw; teeth conical, minute, uniserial on jaws and vomer; coloration pale, overlain with a broad longitudinal brown stripe above the lateral midline; total vertebrae 162–173; and mean vertebral formula 4-77.5-167.

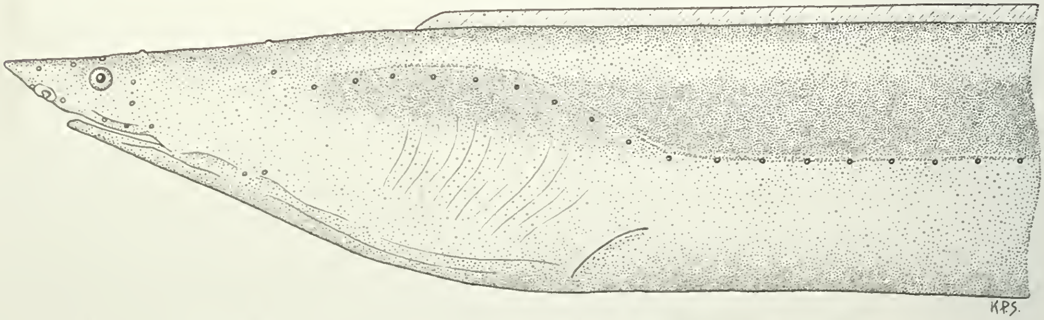

Figure 1. Head of holotype of *Yirrkala moorei* sp. nov., CAS 46677, immature male, 434 mm.

COUNTS AND MEASUREMENTS OF HOLOTYPE (IN MM).— Total length 434; head length 27.4; trunk length 182.6; tail length 224; body depth at gill openings 7.9; body depth at anus 6.2; body width at gill openings 5.6; body width at anus 5.5; origin of dorsal fin 17.6; snout length 4.0; upper jaw length 7.8; isthmus 1.5; left gill opening length 4.0; eye diameter 1.2; interorbital distance 2.2. Total vertebrae 173; predorsal vertebrae 4; preanal vertebrae 81.

TABLE 1. Proportions (in thousandths) and counts of the holotype and 7 paratypes of *Yirrkala moorei*. The smallest paratype, BPBM 37162, is not included. Abbreviations are: TL = total length; HL = head length; DFO = dorsal-fin origin; IO = interorbital width; GO = gill opening length.

	mean	*range*
Total length (in mm)		243-434
Head/TL	65	63-69
Trunk/TL	494	483-517
Tail/TL	506	483-517
Depth/TL	16	14-18
DFO/TL	42	39-47
Snout/HL	161	146-182
Upper jaw/HL	261	257-296
Eye/HL	39	35-44
IO/HL	70	50-82
GO/HL	109	92-146
Vertebrae		
Predorsal	4	4
Preanal	77.5	75-81
Total	167	162-173

DESCRIPTION OF HOLOTYPE AND PARATYPES.— Body very elongate, its depth at gill openings 55–71 times in TL; body and tail nearly cylindrical, tapering posteriorly to an acute finless point. Head and trunk 1.9–2.1 and head 14.5–15.9 in TL. Snout acute at tip, conical from above, flat on underside and split medially nearly to anterior edge of nostril. Lower jaw included, does not reach anterior nostril edge. Anterior nostril nearly flush with snout, surrounded at base by a prominent groove; posterior nostril within inner edge of lip, not visible externally. Center of eye at middle of upper jaw.

Median fins low but obvious. Dorsal arises behind middle of head. Gill openings low, their major axis nearly horizontal, without an anterior lateral membrane or duplication. Isthmus narrow, its width much less than gill opening.

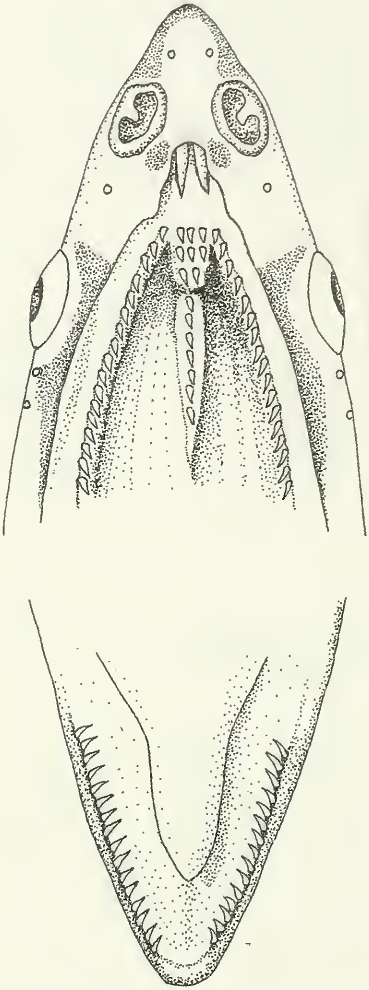

FIGURE 2. Dentition of paratype of *Yirrkala moorei* sp. nov., MNHN 2001-1076, 402 mm TL, an immature male.

Head pores reduced but visible (Fig. 1). Four mandibular, 2 preopercular, 1 ethmoidal + 3 supraorbital, 4 + 2 infraorbital, and single interorbital and supratemporal pores. Lateral-line pores minute, covered with a waxy exudate, and difficult to discern. Total left lateral-line pores of the stained-and-cleared paratype 162; 8 before the gill opening and 80 before the anus.

Teeth (Fig. 2) small and conical, slightly recurved, uniserial in jaws. Intermaxillary teeth the largest, 2–3 as an inverted "V" and partially exposed beneath snout, followed by a short gap and 3–4 pairs of smaller vomerine teeth, followed by 7 even smaller uniserial teeth. Approximately 15–17 uniserial upper jaw teeth and 15–16 lower jaw teeth.

Body coloration in isopropyl alcohol uniform yellowish, overlain with a broad longitudinal dark stripe above the lateral line, extending from the branchial basket nearly to the tail tip. Upper lip behind center of orbit and rictus of jaw darker than surrounding area. Head pores within spots darker than paler surrounding area. A wide pale mid-dorsal stripe, about as wide as the interorbital distance, extending nearly the length of the specimen. Head paler than body, and fins nearly colorless. A color photograph of a living Marquesan specimen taken soon after its capture (Fig. 3; also published in black and white in Rehder, 1974: fig. 5) indicates that the broad dark stripe is chocolate in color and contrasts strongly with the mid-dorsal stripe and lower body coloration.

Size.— The largest known specimen is 434 mm TL.

Etymology.— Named in honor of Gordon E. Moore, in recognition of his interest in fishes, his love of fishing, and his support of biodiversity research and conservation.

Distribution.— Known from Nuku Hiva and Ua Pou islands in the Marquesas and from American Samoa. A single specimen was dredged in 454 m; all others were collected in 25–93 m.

FIGURE 3. Living paratype of *Yirrkala moorei* sp. nov. (either USNM 306545, 410 mm TL, or ANSP 165122, 375 mm TL) captured by dredge in 42–59 m, Nuku Hiva Id., Hatuatua Bay.

Remarks.— The new species is quite similar in its general morphology, dentition, and pore pattern to other species of *Yirrkala*, particularly *Y. lumbricoides* and *Y. tenuis*. It differs from them in its coloration, body proportions and vertebral number. *Yirrkala lumbricoides* is uniform in coloration and has 150–159 vertebrae. *Yirrkala tenuis*, an estuarine species, is nearly uniform in coloration (olive brown dorsally, lighter ventrally) and somewhat stouter (depth 41–45 in TL).

A coloration similar to that of the new species is possessed by other ophichthids of the tribe Callechelyini (*sensu* McCosker 1977) including the Indo-Pacific species *Callechelys catostoma* (Forster, in Bloch and Schneider, 1801), *C. randalli* McCosker (1998), and *Xestochilus nebulosus* (Smith, 1962), and the Atlantic species *Aprognathodon platyventris* Böhlke (1967) and *Letharchus aliculatus* McCosker (1974). It is unlikely that such a similarity in coloration would indicate a mimicry relationship with each other or with other striped marine organisms, but rather it is probably advantageous to such a sand-burrowing species when it leaves the substrate. (The coloration of the smallest specimen [BPBM 37162, 119 mm TL], a recently transformed juvenile, appears to be like that of the adults.) At this time, an explanation for such an advantage is not obvious.

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Paracetonurus flagellicauda (Koefoed, 1927) (Macrouridae, Gadiformes, Teleostei), new records from the Mid-Atlantic Ridge and Madagascar Plateau

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Paracetonurus flagellicauda **is recorded from 41 specimens collected at four sites on the Mid-Atlantic Ridge in the North Atlantic and one specimen from the Madagascar Plateau in the southwestern Indian Ocean. All four previous records of the species were from the North Atlantic: the type specimens from near the recent captures on the Mid-Atlantic Ridge, 24 specimens from the Porcupine Seabight, a specimen from the Rockall Trough, and a small specimen from off the south coast of Portugal. The Indian Ocean specimen suggests a considerable disjunction in the distribution of the species or possible evidence of its ranging along the entire length of the Mid-Atlantic Ridge into the South Atlantic and east into the southwest Indian Ocean.** ***Echinomacrurus occidentalis*** **Iwamoto, 1979 from the eastern Pacific is placed in the genus** ***Paracetonurus*****.**

A workshop was held at the Espegrend Biological Station of the University of Bergen from 22 to 28 February 2005 with the purpose of identifying the demersal fishes collected during Leg 2 of the *R/V G.O. Sars* MAR-ECO Cruise. During that cruise a total of 22 hauls was made with a 29-m otter trawl over the Mid-Atlantic Ridge (MAR) at depths ranging from 826 to 3505 m; only three of the trawls were made shallower than 1000 m, with 13 hauls exceeding 2000 m. Among the more exciting finds from this cruise were 41 specimens of *Paracetonurus flagellicauda,* a little-known species of grenadier that had been recorded only four times before. In 1910 the Norwegian fishery research vessel *Michael Sars* collected four specimens close to the MAR-ECO site; those specimens formed the basis for the original description of *Macrurus flagellicauda* Koefoed, 1927. In 1946, a juvenile of 95+ mm length was taken in 2150 to 2300 m off the south coast of Portugal, west of the Strait of Gibraltar (Nybelin 1948). In 1987, Gordon and Duncan (1987) recorded a 235 mm specimen from 2975 m in the Rockall Trough. Merrett et al. (1991) recorded 24 specimens from nine stations in the Porcupine Seabight southwest of Ireland. Based on those captures, the species was thought to be confined to the higher latitudes of the North Atlantic Ocean. However, in 1988 during a cruise of the former Soviet Union research vessel *Vityaz' II* to the western Indian Ocean, one specimen was collected off the Madagascar Plateau. That specimen was unrecognized as to species until the first author examined the North Atlantic specimens and made the connection between the two. It is the purpose of this paper to record these new specimens and to add to the description of the species.

Methods and Materials

Counts and measurements were taken following Gilbert and Hubbs (1916), later modified by Iwamoto (1970) and Iwamoto and Sazonov (1988). Institutional abbreviations are as follows: CAS—California Academy of Sciences; IORAN (formerly IOAN)—P. P. Shirshov Institute of Oceanology of the Russian Academy of Sciences; NHM (formerly BMNH)—The Natural History Museum, London; SAIAB (formerly RUSI)—South African Institute of Aquatic Biology, Rhodes University, Grahamstown; ZMMGU—Zoological Museum, Moscow State University; ZMUB—Zoological Museum, University of Bergen.

Genus *Paracetonurus* Marshall, 1973

type species: *Macrourus parvipes* Smith and Radcliffe, 1912, by original designation.

Paracetonurus flagellicauda (Koefoed, 1927)

Figs. 1–3

Macrurus flagellicauda Koefoed, 1927:99–100, pl. 5, fig. 8, text-figs. 34, 35 (original description; 4 syntypes, ZMUB 3383).

Grenurus flagellicauda: Nybelin, 1948:69–70, pl. 4, fig. 4 (1 spec., 95+ mm TL; 35°43′N, 8°16′W; 2150~2300 m).

Paracetonurus flagellicauda: Marshall, 1973:616 (in key). Gordon and Duncan, 1987:318, table 4 (1 spec., Rockall Trough, 54°27′N, 12°25′W; 2975 m). Merrett et al., 1991: table 2 (24 specimens listed from Porcupine Seabight; 2486–3098 m).

Specimens examined.— Syntypes: ZMUB 3383 (4 specimens, 55.2~67.8 mm HL, 294+~393+ mm TL); Mid-Atlantic Ridge, 45°26′N, 25°25′W, 3120 m; *Michael Sars* st. 88, 18 July 1910. Other material (44 spec.): ZMUB 16353 (1, 22.2 HL, 131+ TL), ZMUB 16354 (10, 31.5~59.7 HL. 179+~395 TL); Mid-Atlantic Ridge, 42°55′N, 30°20′W, 2670-2660 m; *R/V G.O. Sars* superstation 40, local station 367; 7 July 2004. ZMUB 16355 (1, 16.4 HL, 97+ TL); 42°49′N, 29°38′W, 2107-2063 m; *R/V G.O. Sars* superstation 42, local station 368; 8 July 2004. ZMUB 16356 (9, 37.5~58.3 HL, 205+~375+ TL) and ZMUB 16357 (1, 40.7 HL, 233+ TL); Mid-Atlantic Ridge, 42°46′N, 29°16′W, 3050-3005 m; *R/V G. O. Sars* superstation 46, local station 372; 11 July 2004. ZMUB 16358 (1, 62.0 HL, 379 TL), ZMUB 116359, O-1787, O-1788, O-1789 (7, 37.4~61.6 HL, 270+~392 TL) and ZMUB 16360 (11, 33.4~61.8 HL, 210+~383 TL); Mid-Atlantic Ridge, 42°55′N, 28°08′W, 2979–2973 m; *R/V G.O. Sars* superstation 52, local station 374; 13 July 2004. NHM 1996.8.12.1-2 (2, 28.3~29.1 HL, 142~147+ TL); Porcupine Seabight, 50°27′N, 12°59′W; *Discovery* station 5141101, 2470-2500 m. ZMMGU P-21618 (1, 47.9 HL, 287+TL); Madagascar Plateau, 30°30′S, 46°53′E, 2580–2680 m; R/V *Vityaz' II*, cruise 17, st. 2779; otter trawl; 26 Dec. 1988.

Counts and measurements (from 20 specimens; see also Table 1).— **Counts**. 1D II,7~9 (10 in 1 spec.); P i14~18; V 6 or 7 (8 in 1 spec.); total gill rakers 1st arch (lateral/mesial) 7~10 / 11~13, 2nd arch (8)10~12 / (9)10~12; scales below 1D about 12~15, below 2D 10~15; pyloric caeca 6 (1 spec.). **Measurements:** Head length 33~67.9 mm, total length 187+~393+ mm. The following in percent of head length: snout length 32~37; preoral length 22~29; internasal width 33~42; interorbital width 40~49; orbit diameter 20~26; suborbital width 13~18; postorbital length 47~52; distance orbit to angle of preopercle 41~48; upper jaw length 27~34; barbel length 11~17; length outer gill slit 12~18; preanal length 123~140; distance outer pelvic ray to anal origin 30~42; greatest body depth 65~92; 1D-2D interspace 27~70; height 1D 42~65; length P 51~61; length V 27~42.

Description.— Head broad, rounded, interorbital width almost twice (1.8~2.1 times) orbit diameter in most specimens; head length more than six times in total length in specimens with a complete tail. Body depth about 1.2~1.4 in head length; body tapering gradually to long, slender tail, which is almost string-like posteriorly. Snout broad, greatest width across lateral angles about

FIGURE 1. *Paracetonurus flagellicauda*, ZMUB 16357, from the Mid-Atlantic Ridge in the North Atlantic at a depth of 3050–3005 m.

FIGURE 2. *Paracetonurus flagellicauda*, ZMMGU P-21618 (47.9 mm HL, 287+ mm TL), from the Madagascar Plateau at a depth of 2580–2680 m: (left) dorsal and (right) ventral views of head.

equal to or slightly more than interorbital width; snout high, its tip on a longitudinal line passing through dorsal part of orbit and upper margin of operculum, the nasal fossa mostly above that line. Suborbital region deep; suborbital ridge prominent but not sharply demarcated, connected to leading edge of snout, the two ridges separating head into dorsal and ventral parts. Preopercle large, its diagonal length from orbit to posteroventral margin about two or more times orbit diameter. Opercle and subopercle small, the latter mostly hidden behind preopercle, which is adnate along its ventral margin to the mostly hidden interopercle. Mouth somewhat inferior, jaws relatively short, less than one-third HL, not restricted by lip folds at posterior angle. Chin barbel short and slender, its length about equal to suborbital width, about 0.5 length of upper jaw. Gill opening wide, extending ventrally to point slightly behind vertical through posterior end of mandible; gill membranes narrowly connected to isthmus. Gill rakers all small, tubercular; gill filaments short, fragile. Periproct broad, spanning a length about ⅔ orbit diameter, situated close before anal fin, the anus and urogenital opening surrounded by broad margin of black naked skin. Pyloric caeca fairly short, well devel-

TABLE 1. *Paracetonurus flagellicauda.* Comparison of measurements and counts of four syntypes, 15 Mar-Eco specimens, and one Madagascar Plateau. Figures in parentheses for counts represent peripheral values observed in only one or two specimens.

	Syntypes (4)	**Mar-Eco (15)**	**Madagascar**
Total length (mm)	294+~393+	97+~390	287+
Head length (mm)	55.2~67.8	16.4~62.5	47.9
in percent of HL			
Snout length	32~36	32~36	37
Preoral length	26~28	22~28	29
Internasal width	34~36	33~42	39
Interorbital width	40~42	41~49	44
Orbit diameter	20~25	20~26	22
Suborbital width	15~18	13~18	16
Postorbital length	47~50	48~52	49
Len. Orbit to preopercle	42~46	41~48	42
Len. Upper jaw	27~32	28~34	31
Len. Barbel	13~17	11~17	15
Preanal length	133~136	123~140	132
Outer V to A origin	34~38	30~42	38
Body depth	65~92	70~88	80
1D-2D interspace	42~70	27~48	31
Height 1D	58~64	42~65	40
Length P	51~61	–	–
Length V	27~42	–	–
Counts			
1D	II,7~9	II,(7)8~9(10)	II,9
P	i14~i18	i15~i19	i16
V	6~8	6(7)	6
GR-1 (lateral)	9~10	7~10	9
GR-1 (mesial)	11	11~13	11
GR-II (lateral)	12	(8)10~12	10
GR-II (mesial)	11	(9)10~12	11

oped, six in one female of 54 mm HL from ZMUB 16356.

Premaxillary teeth short, conical, little recurved, slightly larger anteriorly, in tapered band about five or six teeth wide anteriorly, becoming two or three, then one row wide posteriorly, the band spanning about half length of premaxillary. Mandibular tooth band slightly shorter but otherwise similar to that of premaxillary.

Scales on head and body small, densely covered with 5~12 short, erect, needle-like spinules, the bases of each forming low buttresses, as elegantly illustrated in Koefoed's (1927: text-figs. 34 and 35) original description. Almost entire head and body uniformly covered with small thin scales, the exceptions being naked lips, gular and branchiostegal membranes, anterior part of mandibular rami, nasal fossae, fins, cresent-shaped area behind pectoral-fin base, narrow to moderately broad triangular patch of naked skin under snout immediately in front of mouth (extending forward ventromesially to tip of snout in some specimens), and periproct. Head ridges lack modified scute-like scales characteristic of other related genera (e.g., *Nezumia, Sphagemacurus*), and terminal and lateral angles of snout not tipped with coarse, thick tubercles. No enlarged scales along dorsal and anal fins. Grooved lateral line not well developed on trunk, mostly occurring as short interrupted segments, better defined on tail.

First dorsal fin short based, its height about ⅖ to about ⅔ length of head; its spinous second ray with few to many serrations along leading edge in smaller specimens, but almost entirely smooth in some larger specimens. Second dorsal fin low throughout its length. Anal fin well developed and relatively high throughout. Pectoral fin of moderate size, its distal tip extending well beyond origin of anal fin. Pelvic fin small, narrow based and short, its distal tip extending to or slightly beyond anal-fin origin (to about 8th anal ray in 1 specimen). Origins of first dorsal and pelvic fins anterior to pectoral-fin base, the pelvic-fin base under gill cover; anal-fin origin slightly behind vertical through posterior end of first dorsal. Interspace between first and second dorsal fins highly variable, usually less (considerably less in some specimens) than postorbital length of head.

Coloration in adults with pattern of black parts contrasting sharply with pale to white overall color of head, trunk, and anterior part of tail and anal fin. Coal black areas include narrow median strip on underside of snout, jaws (although posteriormost end of lower jaw pale), branchiostegal membranes, posterior part of anal fin, long spine of first dorsal fin and membrane immediately following, oral and gill cavities, gill arches and gill rakers. Blackish areas on chest and abdomen (within triangular area from behind gill cover posteroventrally to immediately behind anal-fin origin, including pectoral-fin base) often obscured by scale covering. Posteriorly, about one head length behind abdominal cavity, tail swarthy to blackish. Pectoral and pelvic fins white in most specimens, but in some, uppermost pectoral ray and outermost pelvic ray blackish. Barbel variably pale to dark. Smaller individuals generally darker overall, and black markings less pronounced as a consequence.

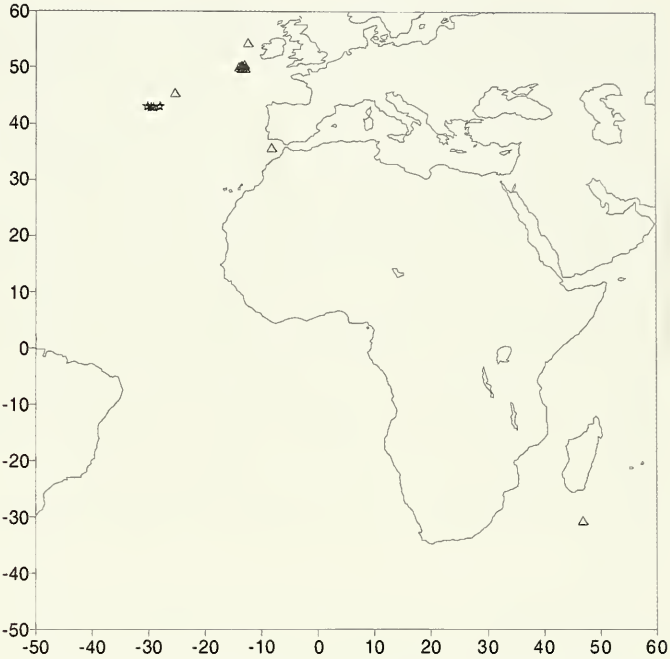

FIGURE 3. Capture localities of *Paracetonurus flagellicauda*. (1) Triangles represent non-Mar-Eco specimens; (2) stars indicate Mar-Eco localities.

SIZE.— The maximum size of specimens examined was more than 393 mm TL and almost 68 mm HL. The longest specimen and another of 335 mm TL (62.4 mm HL) were females with large gonads that appeared to have well-developed oocytes.

DISTRIBUTION.— Known only from the eastern North Atlantic (Mid-Atlantic Ridge, off Portugal, Rockall Trough, and Porcupine Seabight) and on the Madagascar Ridge in the southwestern Indian Ocean (Fig. 3), at mid-sounding depths of 2085–3120 m.

REMARKS.— The genus *Paracetonurus* was erected by Marshall (1973) to include *Macrurus parvipes* Smith and Radcliffe, 1912, *Lionurus cetonuropsis* Gilbert and Hubbs, 1916, and *M. flagellicauda.* Sazonov and Shcherbachev (1982:11), in their revision of genera related to *Cetonurus*, described a new species, *Paracetonurus pusillus*, and shifted *Macrurus fragilis* Garman, 1888, which Iwamoto (1979) had placed in *Paracetonurus*, into their new genus *Asthenomacrurus.* Marshall considered the genus to be most closely related to *Kumba* Marshall, 1973, but Sazonov and Shcherbachev considered it to be closest to *Cetonurus* Günther, 1887 and *Pseudonezumia* Okamura, 1970. More extensive discussions of the relationships within this group of genera were provided by Sazonov and Shcherbachev (1985) in their second paper on this group.

The material for this paper prompted a re-examination of the description of *Echinomacrurus occidentalis* Iwamoto, 1979. That species was distinguished from the only other species of the genus, *E. mollis* Roule, 1916, by a number of characters related to fin-ray counts, proportional measurements, and squamation. In particular, the pelvic fin-ray count was higher (12 vs. 9~10), the orbit was larger (20% HL cf. 10~15%), and the scales on the abdomen were much smaller. Furthermore, the second spinous ray of the first dorsal fin was serrated along the leading edge in *E. occidentalis*, but entirely smooth in *E. mollis.* Almost all these differences are shared with *Paracetonurus flagellicauda*, with only the pelvic fin-ray count differing. It thus appears incontrovertible that *E. occidentalis* belongs in *Paracetonurus* and not in *Echinomacrurus.* The main character distinguishing *P. occidentalis* from all others of the genus is its pelvic fin-ray count of 11 or 12, compared with usually 6 or 7, rarely 8, in the other species.

Nigel R. Merrett (NHM, retired) informed us of the 24 specimens captured in 2486–3098 m in the Porcupine Seabight in the eastern North Atlantic (roughly 50°N and 13°W) and recorded in Merrett et al. (1991: table 2). He provided the following *Discovery* stations (for geographical coordinates and depths, see Merrett et al. 1991: Appendix 1) and number of *P. flagellicauda* specimens (which ranged 22-66 mm HL) from each station: 5051201 (2 spec.); 5071201 (2); 5081401 (2); 5090701 (1); 5101501 (1); 5141101 (2); 5141301 (5); 5161101 (1); 5180401 (8). In addition, five others were taken at three stations using an epibenthic sledge: station 5141201 (1), 50°16.9′N, 13°29.3′W, 2760–2790 m; 5141601 (1), 2780–2770 m; 5141701 (3), 50°10.3′N, 13°22.3′W, 2790-2770 m. Two of these *Discovery* specimens are deposited in the NHM where the second author examined them during a visit in February 2006; the disposition of the remaining specimens is unknown.

Discussion.— It was a propitious coincidence that the MAR-ECO Fish Taxonomy Workshop was held in Bergen, Norway, as it was on a Norwegian vessel that the type specimens of *P. flagellicauda* were taken, and those specimens were deposited in the Bergen Museum, where they were available for examination and comparison with the MAR-ECO material.

The many specimens captured at the three *G.O. Sars* stations and the 11 *Discovery* stations suggest that the species is not uncommon at appropriate depths on trawlable grounds. Mid-depth soundings of the *G.O. Sars* captures spanned 1035 m, while those of *Discovery* spanned only 614 m, suggesting a narrow vertical distribution that Merrett (in litt., Feb. 2006) considers as continental rise. The four *Michael Sars* specimens representing the types were captured about 2.5 degrees latitude farther north than the *G.O. Sars* specimens, and the total area of the MAR captures spanned 2°40′ north to south and 4°55′ east to west. The *Discovery* localities in the Porcupine Seabight spanned an area of only 33.5 minutes N-S and 38.0 minutes E-W. Although the highly restricted areas of capture suggest pockets of abundance, more likely the data are artifacts of collecting efforts.

The single specimen taken on the Madagascar Plateau is an enigma and leads one to wonder if the distribution of the species is continuous across the equator, from north to south along the MAR and then east into the Indian Ocean. Alternatively, the species may have a disjunct distribution, assuming that our calling the single Indian Ocean specimen the same species as our many North Atlantic ones is valid. Nigel Merrett (in litt., Feb. 2006) notes the similarity of the distribution with that of *Macrosmia phalacra* Merrett, Sazonov and Shcherbachev, 1983, which has been taken in the North Atlantic and the eastern Indian Ocean. It is probably safe to assume that the depth distribution of the *P. flagellicauda* lies between approximately 2000 and 3000 m, which coincides with depths of the middle North Atlantic Deep Water. That water mass, which originates in part from subpolar waters north of latitude 40°N, works its way south across the equator well into the South Atlantic where it is "...mixed with Antarctic components of the intermediate and bottom water" (Dietrich 1963:484). Could *P. flagellicauda* have become widely dispersed along the Mid-Atlantic Ridge within this water mass, and found its way into the Indian Ocean? In many stretches of the Ridge, the elevation does not rise above 3000 m—these large gaps could conceivably block demersal fishes that lack means of dispersing across such barriers. If the population of *P. flagellicauda* is continuous along the MAR, how much genetic interchange is taking place at opposite ends of the ridge? It is perhaps too speculative to consider these questions at this time, and only after considerably more collecting along the entire MAR will it be possible to address these thoughts.

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