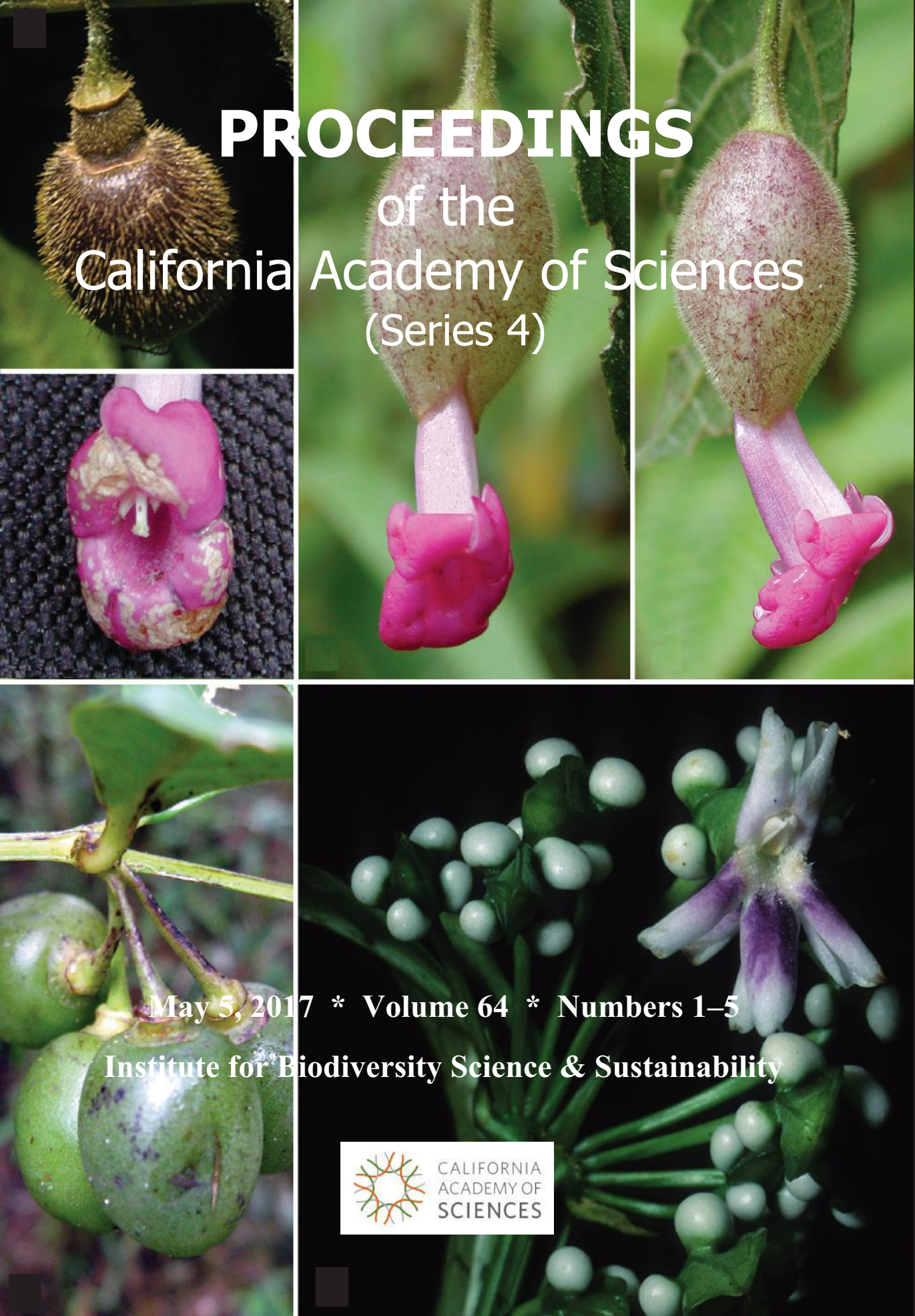

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Figure 11, *Mendoncia cowanii* (upper four images) and *M. flagellaris* (bottom two images). in Emily B. Magnaghi and Thomas F. Daniel, Systematics of *Mendoncia* (Acanthaceae: Thunbergioideae) in the Paleotropics.

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A Revision of the Wasp Genus *Aulacophilinus* Lomholdt, 1980 with Descriptions of Three New Species (Hymenoptera: Crabronidae)

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The genus *Aulacophilinus* Lomholdt, 1980 is revised, and its updated definition is presented. All known species are redescribed, and three new species are added: *Aulacophilinus carinatus*, *A. solitarius*, and *A. tegularis*, all from the island of New Guinea. A key to all species is provided, cladistic analysis performed, important taxonomic characters are illustrated, and maps of geographic distribution included.

Since its descripion in 1980 and until 2016, *Aulacophilinus* included only one species, *A. rennellensis* Lomholdt. Menke (2016), however, demonstrated that *Aulacophilinus* also includes the *caliginosum* species group previously placed in the genus *Pison* Jurine (Naumann 1990b), and he described one new species, provided a key to species determination, and commented on the types of *A. rennellensis* and *A. mandibulatus*. In the present paper, three new species are described and all previously known species are redescribed, including a cladistic analysis, some previously unnoticed characters, variability, and a number of additional specimens that extend the known ranges. A key for species identification is also provided herein.

Methods and Technical Terms

The specimens were examined under a Leica MZ APO stereomicroscope with a fluorescent light illuminator. The illustrations of sternum VIII and genitalia were generated under a Leo 1450VP and a Hitachi SU3500 Scanning Electron Microscopes and those of the remaining body parts through the Automontage software package by Syncroscopy. For each species, I indicate not only the body length, but also the head width, which is a more precise measurement according to Ohl and Thiele (2007). Measurements were made using an ocular micrometer with the scale interval of 0.1 mm. The male genitalia and sternum VIII of *Aulacophilus rennellensis*, missing from the male paratype now, are here reproduced using the original illustration of Lomholdt (1980).

Distribution maps were genertd using ArcMap, version 10.5 program.

Molecular techniques have not been attempted. See caption for Fig. 1 for description of phylogenetic methods.

In the Species Descriptions sections, species are arranged alphabetically. Most of the morphological terms are as in Bohart and Menke (1976). Those not included in their work or needing clarification are defined below:

Acetabular groove: a setiferous, longitudinal groove on the outer surface of the mandible between the acetabular carina and the outer ridge, typically starting near the mandibular acetabulum (= anterior mandibular articulation), but at some distance from it in some species, and separating the anterior and the outer mandibular surfaces (Michener and Fraser, 1978).

Clypeal lamella: the most ventral, unsculptured and asetose part of the middle clypeal lobe, adjacent to lobe free margin.

Condylar groove: a setiferous, longitudinal groove parallel to the posterior mandibular margin, typically starting near the mandibular condyle.

Lower interocular distance: the shortest distance between the eyes adjacent to the clypeus or near the level of the antennal sockets (Menke, 1988).

Ocellocular distance: the shortest distance between the outer margin of a hindocellus and the adjacent orbit.

Scutum: a shortened term for the mesoscutum.

Sternum (plural: **sterna)**: an abbreviated term for the gastral sternum (sterna).

Tergum (plural: **terga)**: an abbreviated term for the gastral tergum (terga).

Upper interocular distance: the shortest distance between the eyes at the vertex, measured behind the ocellar triangle (Menke, 1988).

Origin of Material

This paper is based on the material kindly sent by the institutions listed below (the names of the contact persons are given in parentheses); some specimens were also collected by the author and his wife, Veronica Ahrens, during eight expeditions to Australia (2006–2012) totaling 12 months. Arnold Menke generously transferred to me several specimens he had borrowed earlier for his studies of the genus. The institutions are referred to in the text by their respective capitalized abbreviations preceding the institutions full name below as well as the contact person's name.

AEI: American Entomological Institute, Logan, Utah (through Arnold Menke).

AMS: Australian Museum, Sydney, New South Wales, Australia (Derek Smith).

ANIC: Australian National Insect Collection, Canberra, Australian Capital Territory, Australia (Nicole Fisher).

BISH: The Bernice Pauahi Bishop Museum, Honolulu, Hawaii, USA (mostly through Arnold Menke)

BMNH: The Natural History Museum (formerly British Museum Natural History), London, United Kingdom (David G. Notton).

CAS: California Academy of Sciences, San Francisco, California, USA.

SAM: South Australian Museum, Adelaide, South Australia, Australia (Peter Hudson).

QMB: Queensland Museum, Brisbane, Queensland, Australia (Chris Burwell, Karin Koch, Susan Wright).

UCD: Bohart Museum, University of California Davis, Davis, California, USA (through Arnold Menke).

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (through Arnold Menke).

USU: Utah State University, Logan, Utah, USA (Terry L. Griswold, Frank D. Parker).

WAM: Western Australian Museum, Perth, Australia (Brian Hanich).

ZMUC: Zoological Museum, University of Copenhagen, Copenhagen, Denmark (Lars Vilhelmsen).

Genus *Aulacophilinus* Lomholdt

Aulacophilinus Lomholdt, 1980:27. Type species: *Aulacophilinus rennellensis*, by original designation and monotypy. Synonymized with *Pison* by Antropov, 1999:564, resurrected by Menke, 2016.

Taxonomic History.— Lomholdt (1980) established the genus *Aulacophilinus*, a member of Trypoxylini, for his new species *A. rennellensis* from the Solomon Islands. He pointed out that the new genus has gastral segment I as long as in the Neotropical genus *Aulacophilus* and shares with it the presence of only two submarginal cells and the absence of a carina at the top of the propodeal side, but differs from it by the flagellum filiform (rather than claviform), the occipital carina con-

tinuous (rather than interrupted ventrally), and the mesopleuron non-ridged (rather than horizontally ridged). There are also three additional differences between these genera: in *Aulacophilus* the mandible is acuminate apically (truncate in *Aulacophilinus*, see below for details), the metapleuron is parallel-sided for most of its length (in *Aulacophilinus* the metapleuron is markedly wider above the upper metapleural pit than below it), and tergum I has a pair of longitudinal, admedian carinae (no such carinae are present in *Aulacophilinus*). Antropov (1999) questioned the close relationships of these two genera, claimed that *Aulacophilinus* has not a single autapomorphy within Trypoxylini and that its gaster is just an extreme case of the situation in *Pison*, in which several species have the gaster elongate to a various degree, with the length exceeding the maximum width (*P. difficile* Turner, *P. icarioides* Turner, *P. obliteratum* F. Smith, *P. pistillum* Menke, and *P. woji* Menke; in *P. icarioides* segment I is bulging apically, in *P. woji* the basal portion is approaching the condition of *Aulacophilus*). He concluded that *Aulacophilinus* should be treated as a specialized member of *Pison* and as its junior synonym. Neither Lomholdt nor Antropov, however, paid attention to the specialized, unique mandible and the specialized clypeus of *Aulacophilinus*. Naumann (1990b), on the other hand, recognized the importance of the broadly truncate mandible and revised the four Australian species with this character, calling them the *caliginosum* group of *Pison.* He did not recognize the close relationship of the group to *Aulacophilinus rennellensis.* Menke (2016), however, demonstrated that the *caliginosum* species group should be included into *Aulacophilinus,* resurrected *Aulacophilinus* from synonymy, provided its definition, described one new species (*A. amblygnathus*), provided a key to determination of the species known to him, and commented on the types of *A. rennellensis* and A. *mandibulatus*.

Definition of Genus.— *Aulacophilinus* is characterized by a mandible that is unique within Trypoxylini: both the outer and inner surfaces are punctate and setose throughout (except narrowly impunctate and asetose adjacent to the apical margin), the acetabular and condylar grooves are absent, and the inner portion is broadly expanded preapically, thus forming an apical truncation (the apical margin of the truncation being slightly concave, e.g., Fig. 2). Unlike *Pison*, the clypeus is punctate throughout, without a shiny, medioventral lamella (see below for exception). I agree with Menke (2016) that these striking features justify recognition of *Aulacophilinus* as an independent genus. An undescribed *Pison* from Australia, however, is somewhat intermediate between *Aulacophilinus* and *Pison*: the clypeus without a lamella and the broadened preapically inner mandibular portion are as in *Aulacophilinus*. Unlike *Aulacophilinus*, however, the inner mandibular surface is impunctate and glabrous (as in *Pison*), and the following are unique: two large, preapical teeth on the inner mandibular margin, a broad, shallow condylar groove, and a sharp conspicuous acetabular carina. Also, the setae of tergum I are erect (appressed in *Aulacophilinus*).

The unique mandible of *Aulacophilinus,* clearly an outstanding autapomorphy, may be related to a particular way of nest building. Unfortunately, nothing is known about the nesting habits of the included species.

Description.— In addition to the specialized clypeus and mandible, the species share the following characters: eye asetose, ommatidia about equal in size; inner eye margin convergent above; frons without middle supraantennal carina except carina present in large females of *A. caliginosus*; distance between antennal socket and orbit larger than socket diameter (about equal to socket diameter in female of *A. rennellensis*); clypeus transverse; flagellum cylindrical, not thickened toward apex; mandibular posterior margin straight, neither emarginate nor step-like; labrum not emarginate or minimally emarginate apically; occipital carina continuous ventrally, not joining hypostomal carina, mostly not expanded but expanded in *A. weiri,* in many *A. caliginosus,* and slightly so ventrally in *A. amblygnathus*; hypostomal carina not expanded; gena narrow in dorsal view (e.g., Fig. 31), somewhat thicker in *A. solitarius*; scutum without notauli; scutellum not foveate along

anterior margin except slightly foveate in *A. carinatus* and *A. solitarius*; postspiracular carina present, about as long as midocellar diameter (about twice as long as midocellar diameter in *A. solitarius*); propleuron and forecoxal venter closely punctate; metapleuron not ridged longitudinally between dorsal and ventral metapleural pits except ridged in *A. weiri* and most *A. caliginosus*; metapleural flange narrowly lamelliform; propodeal dorsum with median longitudinal carina; forewing with two or three submarginal cells; first recurrent vein received by submarginal cell I or interstitial with first intersubmarginal vein; marginal cell acuminate; midcoxae separated, hindcoxae contiguous; punctures of tergum I well defined; sterna without graduli, punctate throughout; setae silvery, appressed to suberect on tergum I, at most slightly shorter than midocellar diameter; female tergum VI without pygidial plate; male flagellomeres cylindrical, not emarginate nor expanded, and without tyli except tyli present in *A. rennellensis*; posterior margin of male sternum VIII emarginate.

Geographic Distribution.— Four species of *Aulacophilinus* inhabit Australia (*A. caliginosus*, *A. mandibulatus*, *A. pyrrhicus*, and *A. weiri*), four other occur in New Guinea (*A. amblygnathus*, *A. carinatus*, *A. solitarius*, and *A. tegularis*), and *A. rennellensis* is found on the Rennell Island in the Solomon Archipelago. Of the four Australian species, *A. caliginosus* is known from all parts of the continent including Tasmania, *A. mandibulatum* occurs in the South Australia and Western Australia, and *A. pyrrhicum* and *A. weiri* are found in the Northern Territory and Queensland.

Cladistic Analysis

The following is the list of characters used in the analysis below:

1. Clypeal lamella: 0. present, 1. absent.
2. Mandible surface: 0. partly impunctate, 1. punctate throughout on both inner and outer surface.
3. **Mandible: acetabular and condylar groves**: 1. grooves present, 2. grooves absent.
4. Mandible: apex: 0. acuminate, 1. broadly truncate.
5. Mandible: **color**: 0. black, 1. ferruginous
6. **Width of labrum**: 0. more than one midocellar diameter, 1. less than one midocellar diameter
7. Sculpture of frons, vertex, scutum, and mesopleuron: 0. punctate, 1. areolate.
8. Crenulate sulcus on gena: 0. absent, 1. present.
9. Tegula: 0. impunctate posteriorly, 1. punctate throughout.
10. Omalus: 0. absent, 1. present.
11. Number of submarginal cells: 0. three, 1. two.
12. Gaster: **shape**: 1. sessile, 2. pedunculate.
13. Gaster: **color**: 0. black,1. ferruginous
14. Apical emargination of male sternum VIII: 0. shallow or moderately deep, 1. prominently deep.

Pison atrum Spinola, the type species of *Pison*, was used as the outgroup, and the following data matrix was constructed:

Pison atrum	00000 00000 0000
amblygnathus	11110 00000 0000
caliginosus	11110 10010 1001
carinatus	11110 00000 0000
mandibulatus	11111 10010 0000
pyrrhicus	11110 00100 0010
rennellensis	11110 10000 1100
solitarius	11110 00000 000?
tegularis	11110 00010 000?
weiri	11110 11111 1001

A cladistic analysis was kindly performed by Fernando Alvarez Padilla of the Universidad Nacional Autónoma de México through implicit enumeration, using T.N.T. program by Pablo Goloboff, Steve Farris, and Kevin Nixon (2003). One tree of 16 steps was found (Fig. 1), with the consistency index of 87 and the retention index of 80 (several nodes on the cladogram are without support because there are no characters that can be optimized unambiguously at those nodes).

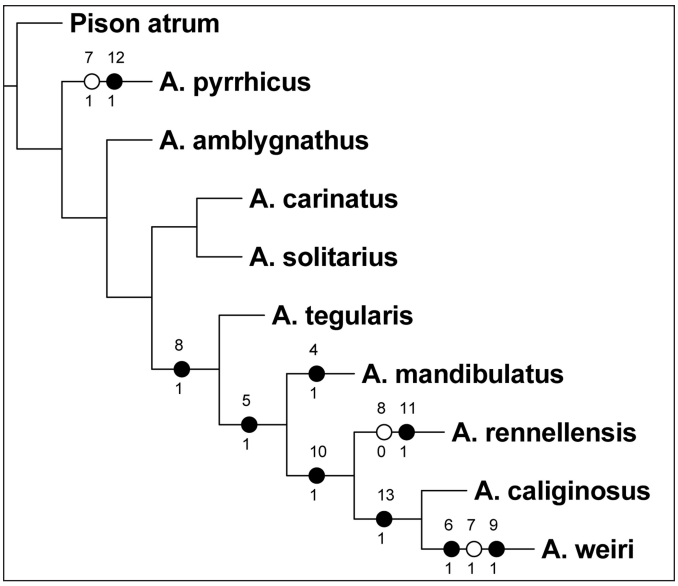


FIGURE 1. Phylogenetic tree of *Aulacophilinus*

Key to Species

1. Forewing with two submarginal cells in each wing (with one submarginal cell in occasional specimens) 2
– Forewing with three submarginal cells 4

2. Gaster conspicuously pedunculate (Figs. 37, 38), its length 3.0–3.5 × its maximum width, conspicuously swollen apically (Fig. 38); tegula impunctate in posterior half; outer surface of hindtibia without spines; dorsal length of flagellomere I 2.5 × its apical length in female, 2.4 × in male. Solomon Islands. . . . . *rennellensis* Lomholdt, p. 00
– Gaster sessile (its length about equal to maximum width), not swollen apically; tegula minutely punctate throughout; outer surface of hindtibia with fine but well-defined spines; dorsal length of flagellomere I 1.4–2.0 × its apical length in female, 1.3–1.9 × in male 3

3. Frons, vertex, scutum, and mesopleuron areolate; gena with well-defined, crenulate sulcus along posterior eye margin, sulcus delimited posteriorly by well-defined carina; pronotal collar with well-defined, crenulate furrow; omalus present. Australia. . . . . *weiri* Naumann, p. 00
– Frons: vertex, scutum, and mesopleuron punctate (mesopleuron rugose in some specimens); gena without sulcus and carina along posterior eye margin; pronotal collar without crenulate furrow; omalus absent. Australia, Norfolk Island. . . . . *caliginosus* Turner, p. 00

4. Gaster and at least tibiae ferruginous; gena with crenulate sulcus along posterior eye margin, sulcus delimited posteriorly by well-defined carina; posterior propodeal surface with several ridges radiating up from gastropropodeal articulation. Australia. . . . . *pyrrhicus* Naumann, p. 00
– Gaster and legs black; gena without crenulate sulcus and carina along posterior eye margin; posterior propodeal surface without ridges radiating up from gastropropodeal articulation 5

5. Mandible ferruginous; tegula finely punctate throughout. Australia. *mandibulatus* Turner, p. 00
Mandible black; tegula punctate throughout or impunctate posteriorly 6

6. Punctures of frons 2–3 diameters apart, on scutum more than one diameter apart at least at center; setae on frons erect, about as long as midocellar diameter, on scutum erect, about 0.5 × as long as midocellar diameter. New Guinea . . . . . *amblygnathus* Menke, p. 00
– Punctures of frons and scutum averaging no more than one diameter apart; setae on frons suberect, about as long as 0.5–0.7 × midocellar diameter, on scutum suberect, about 0.3 × as long as midocellar diameter 7

7. Tegula evenly punctate throughout. New Guinea . . . . . *tegularis* Pulawski, sp. nov., p. 00
– Tegula impunctate posteriorly or with evanescent, microscopic punctures (punctures markedly smaller than those in anterior part) 8

8. Propodeum with well-defined carina between side and dorsum and posterior surface, on dorsum laterally with well-defined, short, transverse ridges meeting carina. New Guinea . . . . . *carinatus* Pulawski, sp. nov., p. 00
– Propodeum without carina between side and dorsum and posterior surface, on dorsum laterally with evanescent ridges. New Guinea . . . . . *solitarius* Pulawski, sp. nov., p. 00

Species Descriptions

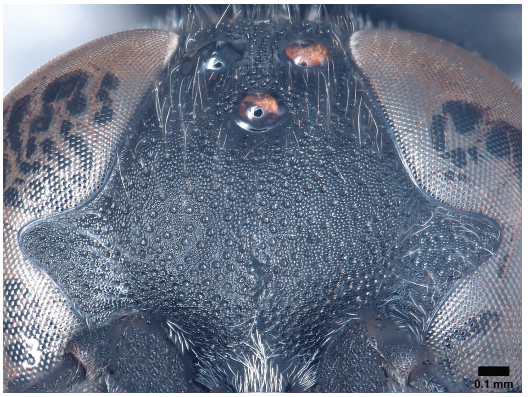
Aulacophilinus amblygnathus Menke

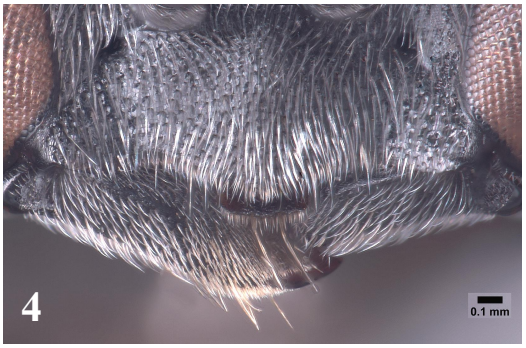
Figures 2–9.

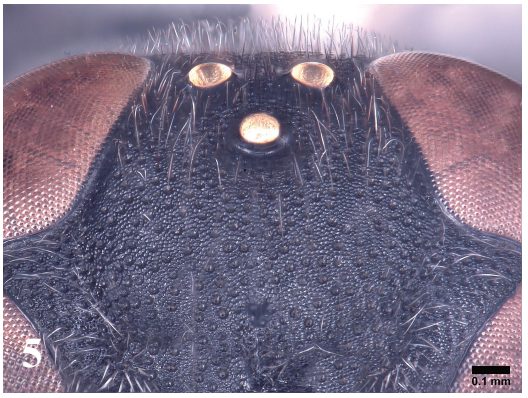
Aulacophilinus amblygnathus Menke, 2016:335, ♀, ♂. Holotype: ♂, New Guinea: Morobe Province: Wau (AEI), examined.

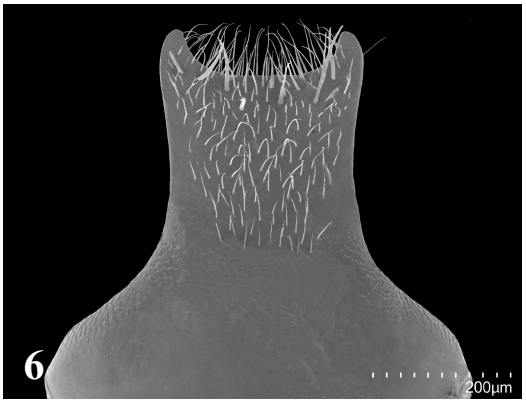
Recognition.— *Aulacophilinus amblygnathus* is an all black endemic of New Guinea with three submarginal cells. It differs from all its congener in having the frontal punctures 2–3 diameters apart (rather than less than one to slightly more than one diameter apart), and also in having the frontal setae about as long as 1.5–2.0 midocellar diameters (while no longer than one midocellar diameter in the other species). The absence of silvery, setal fasciae on terga is a subsidiary recognition feature.

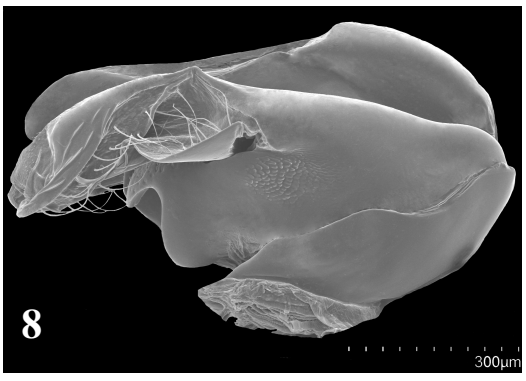
Description.— Frons dull, shallowly punctate, punctures averaging 2–3 diameter apart (Figs. 3, 5). Free margin of clypeal lobe obtusely angulate to rounded (Figs. 2, 4). Occipital carina slightly expanded ventrally. Width of labrum equal to 1.1 × midocellar diameter. Anteromedian pronotal pit transversely elongate, about as long as midocellar diameter. Scutum not foveate along flange, with short longitudinal ridges adjacent to posterior margin; scutal punctures well defined, varying from about one diameter apart on average on disk to less than one diameter apart; interspaces aciculate. Tegula impunctate in posterior half. Mesopleural punctures well defined, less than one diameter apart except about one diameter apart near center. Propodeum in most specimens without longitudinal carina separating side from dorsum and posterior surface, but evanescent carina present in some specimens or replaced by vague linear series of short, transverse rugae; dorsum, side and posterior surface with well-defined punctures; dorsum with punctures slightly more than one diameter apart near midline, less than one diameter apart laterally, with well defined, oblique ridges basally; side with punctures less than one diameter apart except about one diameter apart posterodorsally, with fine ridges visible from certain angles; posterior surface with punctures less than one diameter apart near midline, about one diameter apart laterally, with transverse ridges in ventral half ridges near base Forewing with three submarginal cells. Posteroventral forefemoral surface with fine punctures several diameters apart. Hindcoxal dorsum with outer margin obtusely carinate. Outer surface of hindtibia with several fine spines. Punctures of tergum I averaging about two diameters apart anterior of apical depression.











FIGURES 2–8. *Aulacophilus amblygnathus* Menke. (2) Clypeus and mandibles, female; (3) Upper frons, female; (4) Clypeus and mandibles, male; (5) Upper frons, male; (6) Sternum VIII, ventral surface, male; (7) Genitalia, dorsal view, male; (8) Genitalia, lateral view, male.

Setae silvery, on upper frons erect, sinuous, varying from about 1.5 × to 2.0 × midocellar diameters; on postocellar area erect, straight, shorter than midocellar diameter; on scutum erect, straight, about 0.5 × to 0.8 × midocellar width; on tergum I suberect, slightly shorter than midocellar width; on lower gena suberect, curved apically, slightly longer than midocellar diameter; not concealing integument on clypeus. Apical depressions of terga without silvery, setal fasciae.

Body all black.

♀.– Upper interocular distance equal to 0.58–0.62 × lower interocular distance; ocellocular distance equal to 0.6–0.7 × hindocellar diameter, distance between hindocelli equal to 1.0–1.3 × hindocellar diameter; eye height equal to 0.94–1.00 × distance between eye notches. Dorsal length of flagellomere I 1.9–2.1 × apical width. Length 7.2–7.3 mm; head width 2.1 mm.

♂.– Upper interocular distance equal to 0.7 × lower interocular distance; ocellocular distance equal to 0.7 × hindocellar diameter, distance between hindocelli equal to 1.4 × hindocellar diameter; eye height equal to 1.06 × distance between eye notches. Dorsal length of flagellomere I 1.8 × apical width. Apical margin of sternum VIII emarginate (Fig. 6). Genitalia (Figs. 7, 8): Length 7.0 mm; head width 2.0–2.1 mm.

Geographic Distribution (Fig. 9).— Higher elevations of New Guinea.

Records.— **Indonesia**: **Western Papua**: Paniai Lakes (as Wisselmeren): Enarotadi, elevation 1,850 m (1 ♀, BISH), Top Camp [of 1939 Dutch-American New Guinea Expedition = approximately 122 km SW Jaiapura] (1 ♂, RMNH). **Papua New Guinea**: **Madang Province**: Pandambai 6 air km W Bundi at 5º38′S 145º11′E, elevation 2,330 m (2 ♀, CAS), Teptep at 5°55′S 146°30′E, elevation 1,900 m (1 ♂, CAS). **Morobe Province**: Wau [elevation 1,134 m] (1 ♀, 1 ♂, AEI, holotype and paratype of *A. amblygnathus*; 1 ♀, BISH).

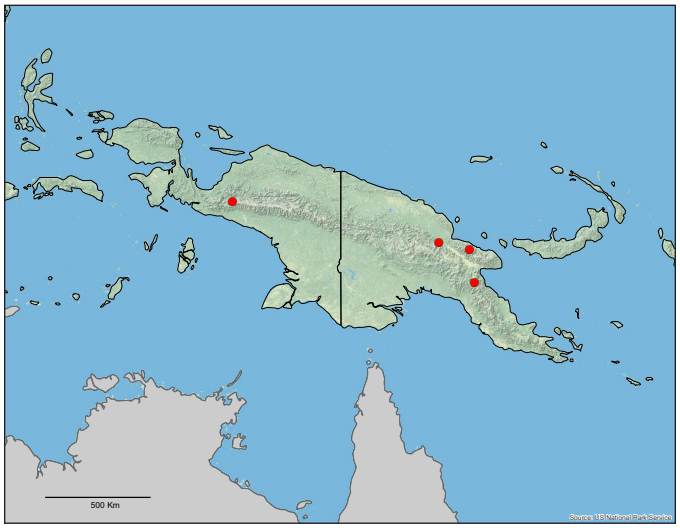


Figure 9. Collecting localities of *Aulacophilinus amblygnathus*.

Aulacophilinus caliginosus (Turner)

Figures 10–17.

Pison caliginosum Turner, 1908:518, ♀. Holotype: ♀, Australia: Queensland: Kuranda near Cairns (BMNH), not examined. – Turner, 1916:596 (in key to Australian *Pison*), 600 (brief description); R. Bohart and Menke, 1976:335 (in checklist of world Sphecidae); Cardale, 1985:258 (in catalog of Australian Sphecidae); Naumann, 1990a:24 (Norfolk Island), 1990b:235 (in revision of *caliginosum* group of *Pison*, descri-

pion of ♂), 1998:185 (Australia: Northwest Queensland: Musselbrook area at approximately 18°40′S 138°23′E).– **As *Aulacophilinus caliginosus***: Menke, 2016:337 (new combination, in key to *Aulacophilinus*).

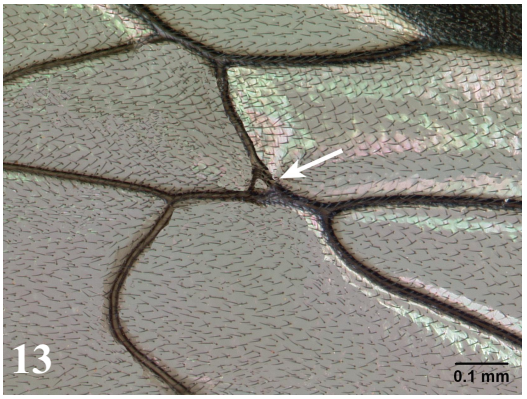
Recognition.— *Aulacophilinus caliginosus* shares with *rennellensis* and *weiri* the presence of only two submarginal cells. Unlike *rennellensis*, its gastral segment I is sessile rather than conspicuously pedunculate; the entirely punctate tegula is a subsidiary recognition feature. Unlike *weiri*, the frons, scutum, and mesopleuron of *caliginosus* are punctate rather than coarsely areolate (although the mesopleuron may be rugose), the gena has no crenulate sulcus along the posterior eye margin, there is no omaulus (omaulus present in *weiri*), and the pronotal collar has no crenulate furrow (crenulate furrow present in *weiri*).

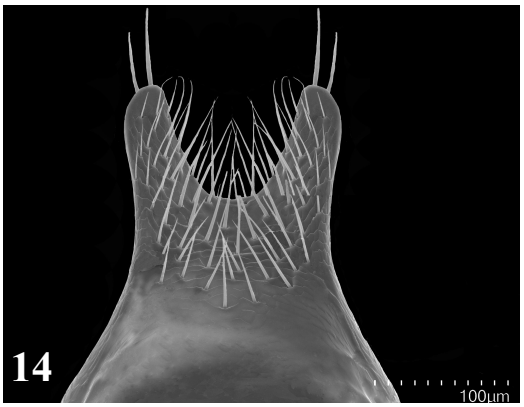
Species Status.— The material I have examined shows significantly more variation than described by Naumann (1990b). Most variants of different characters, however, do not correlate with each other, indicating that one species, and not a number of closely related species, is involved.

Description.— Frons with well defined punctures less than one diameter apart in most specimens (compressed against each other in some), but punctures ill defined, shallow, up to about one diameter apart in females from Taree area, New South Wales; interspaces varying from unsculptured, shiny, to conspicuously microsculptured, dull; middle supraantennal line mostly absent, present in larger females. Free margin of clypeal lobe obtusely triangular (Fig. 10). Occipital carina expanded in many specimens. Width of labrum equal to 0.5 × midocellar diameter. Anteromedian pronotal pit slightly transversely elongate, about as long as midocellar diameter. Pronotal collar with ill-defined transverse furrow next to apical margin (furrow not foveolate). Scutum foveate along flange (only inconspicuously so in smallest specimen), with or without short longitudinal ridges adjacent to posterior margin; scutal punctures less than one diameter apart in most specimens, but some punctures more than one diameter apart in some individuals; interspaces varying from unsculptured and shiny to markedly microsculptured, dull. Tegula punctate throughout. Mesopleuron mostly punctate, but rugose in some specimens from Western Australia; punctures conspicuous, less than one diameter apart, but not conspicuous and more than one diameter apart ventrally in females from Taree area. Metapleuron longitudinally ridged between dorsal and ventral metapleural pits in most specimens, but minutely, sparsely punctate in females from Blundells Creek and from Taree area. Propodeum in most specimens without longitudinal carina separating side from dorsum and posterior surface and extending from gastral socket area toward spiracle, but such carina present (rudimentary to well defined) in some specimens; dorsum obliquely ridged, punctate between ridges (punctures fine in most specimens, but coarse in some males), punctate only in one male from Pilbara Region, Western Australia; side ridged, punctate between ridges in larger specimens, punctate only in small ones; posterior surface densely, coarsely punctured, transversely ridged ventrally in some specimens. Forewing with only two submarginal cells (Fig. 11); in one female from 50 km NW Taree, minuscule additional submarginal cell appears in lower right corner of second cell of left wing, making the wing appear to have three submarginal cells (Figs. 12, 13); length of posterior margin of second cell 1.2–2.4 × its height, second cell triangular in some males from Pilbara Region. Hindcoxal dorsum with outer margin sharply carinate, but carina obsolete basally in many specimens. Outer surface of hindtibia with fine but well-defined spines. Punctures of tergum I averaging about one diameter apart.

Setae nearly appressed on upper frons and scutum, appressed on tergum I, completely concealing integument on clypeus or nearly so; erect (curved apically) on lower gena, about as long as 0.5 × midocellar diameter. Apical depressions of terga with silvery, setal fasciae.

Body all black or mandibular apex ferruginous.

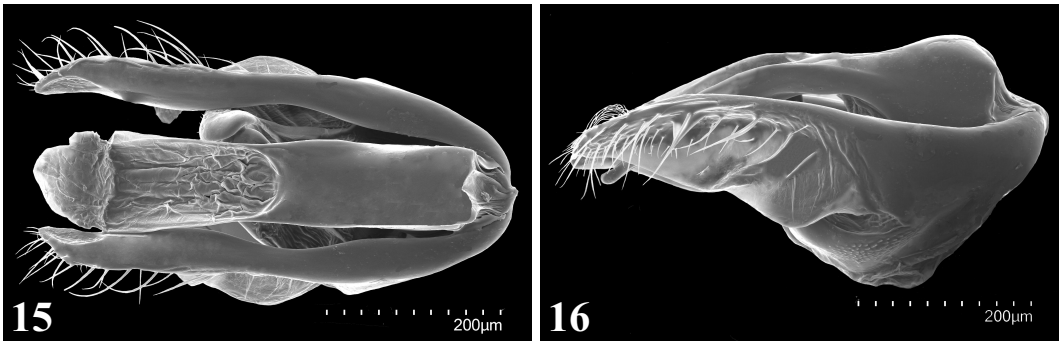




FIGURES 10–14. *Aulacophilinus caliginosus*. (10) Female clypeus and mandibles; (11) Right wing, with normal venation; (12) Left wing of the same individual, venation abnormal (arrow shows additional submarginal cell); (13) Portion of left wing at a higher magnification (arrow shows additional submarginal cell); (14) Male sternum VIII (ventral surface).

♀.– Upper interocular distance equal to 0.68–0.70 × lower interocular distance; ocellocular distance equal to 0.1–0.5 × hindocellar diameter, distance between hindocelli equal to 1.0–1.2 × hindocellar diameter; eye height equal to 0.98–1.04 × distance between eye notches. Dorsal length of flagellomere I 1.8–2.0 × apical width. Length 5.9–6.5 mm; head width 1.8–1.9 mm.

♂.– Upper interocular distance equal to 0.77–0.86 × lower interocular distance; ocellocular distance equal to 0.5–0.6 × hindocellar diameter, distance between hindocelli equal to 1.2 × hindocellar diameter; eye height equal to 0.92–1.04 × distance between eye notches. Dorsal length of fla-



FIGURES 15–16. *Aulacophilinus caliginosus*. (15) Male genitalia dorsally; (16) Male genitalia laterally

gellomere I 1.4–1.9 × apical width. Sternum VIII deeply emarginate (Fig. 14). Genitalia: Figs. 15 and 16. Length 4.7–6.8 mm; head width 1.5–1.7 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 17).— Whole Australia including Tasmania, also Norfolk Island.

RECORDS (N = Naumann, 1990b).— **AUSTRALIA**: **Australian Capital Territory**: Black Mountain at 35°16′S 149°06′E (3 ♀, 2 ♂, ANIC; 1 ♂, BMNH; 1 ♀, 2 ♂, CAS; 1 ♂, UCD), Blundells Creek at 35°22′S 148°50′E (7 ♀, ANIC), Canberra (1 ♀, ANIC), Hume (1 ♀, ANIC). **New South Wales**: 6 km NE Bilpin near Kurrajong (2 ♀, AMS), 100 km SE Broken Hill at 32°51′S 141°37′E (1 ♀, ANIC), Colo Heights (N), Congo Point (1 ♀, BMNH), Cullerin (1 ♂, UCD), Gilgandra (1 ♀, 1 ♂, AMS), Jinki Creek in Blue Mountains (1 ♀, AMS), 0.5 km SE Lansdowne near Taree (1 ♀, AMS), Lindfield at 33°46′S 151°11′E (1 ♀, CAS), Lorien Wildlife Refuge 3 km N and ca 1 km NNW Lansdowne near Taree (2 ♀, AMS), Mount Tomah (1 ♀, 1 ♂, AMS), 15 km SE Nimmitabel (N), Springs Creek 68 km SW Wilcannia at 31°44′S 142°41′E (N), 50 km NW Taree at 31°31′S 152°14′E (2 ♀, 2 ♂, AMS), Whiskers 7 km WNW Hoskinstown at 35°24′S 149°23′E (1 ♂, ANIC), Woodford (N). **Norfolk Island**: Mount Bates (1 ♀, BISH), Rocky Point Reserve at 29°03′S 167°55′E (N), Selwyn Pine Road at 29°01′S 167°57′E (N). **Northern Territory**: Areyonga (N), Roe Creek 12 km WSW Alice Springs (N), Gregory National Park at 16°03′01″S

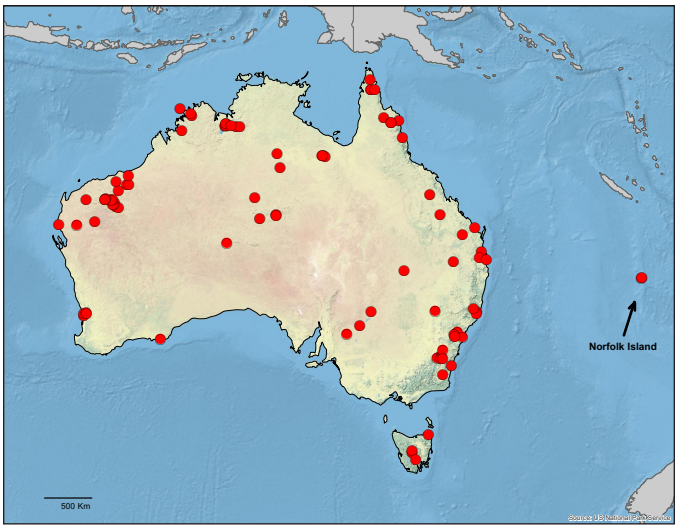


FIGURE 17. Collecting localities of *Aulacophilinus caliginosus*.

130°04′07″E (1 ♂, ANIC), Keep River National Park at 15°44′17″S 129°06′55″E (2 ♂, CAS), at 15°45′42″S 129°06′45″E (1 ♂, USU), at 15°54′55″S 129°04′11″E (1 ♂, USU), at 15°55′22″S 129°03′25″E, at 15°57′55″S 129°01′52″E (1 ♀, ANIC), and at 16°03′01″S 130°24′07”E (1 ♂, ANIC), Tennant Creek (1 ♂, WAM), 131 km N Tennant Creek at 18°28′S 133°52.1′E (1 ♂, CAS), Victoria Highway 109 km WSW Timber Creek at 15°56′11″S 129°35′22″E (1 ♂, USU), Waterhouse Range 19 km SSW Alice Springs (N), Yuendumu (N). **Queensland**: 5 km S Batavia Downs at 12°41′S 142°41′E (3 ♀, ANIC), 3 km W Batavia Downs at 12°40′S 142°39′E (1 ♀, ANIC), Beerwah (1 ♀, QMB), Bundaberg (N), 48 km S Cunnamulla (N), Davies Creek National Park at 17°00.6′S 145°34.9′E (1 ♂, CAS), Hann River at 15°11′S 143°52′E (2 ♀, 1 ♂, ANIC), Heathlands at 11°45′S 142°35′S (1 ♀, ANIC), 2 km S Horseshoe Lookout in Blackdown Tableland (N), Isaacs River 100 km NE Clermont (1 ♂, QMB), Lawn Hill National Park at 18°35′15″S 138°04′28″E (1 ♂, QMB), 18°38′13″S 138°12′29″E (1 ♀, QMB), and 18°40’15″S 138°22’15” (1 ♀, QMB), Moonie (1 ♀, QMB), Mount Cook National Park (N), Mount Nebo (N), 29 km NW Mundubbera (1 ♀, QMB), Musselbrook Camp at 18°36′S 138°08′E (2 ♂, ANIC), North Stradbroke Island (N), Split Rock 14 km SE Laura at 15°39′S 144°31′E (2 ♀, ANIC), 6 km N Taroom at 25°36′S 149°46′E (1 ♂, QMB), 13 km SE Weipa at 12°40′S 143°00′E (4 ♀, 1 ♂, ANIC). **South Australia**: Mount Davies area in Tomkinson Range (N), 79 km NNW Renmark at 33°31′S 140°24′E (2 ♀, ANIC; 3 ♀, CAS). **Tasmania**: 14 km S Bronte Park at 42°15′S 146°29′E (1 ♀, ANIC), 1 km SSE Gladstone (N), Great Pine Tier 13 km NNW Bronte Peak (1 ♂, BMNH), Mount Field National Park (N). **Western Australia**: 48 km NW Carnarvon at 24°35.2′S 113°31.2′E (1 ♀, CAS), Charnley River 2 km SW Rolly Hill (1 ♀, ANIC), Drysdale River at 15°02′S 125°55′E (N), Great Northern Highway at 22°41′36″S 118°42′19″E (2 ♀, 4 ♂, AMS), 23°02.6′S 118°50.2′E (3 ♀, CAS; 1 ♂, USU), and 23°07.3′S 119°05.5′E (1 ♂, ANIC; 1 ♂, USU), Juna Downs road to Packsaddle Bore at 22°51’30″S 118°40’14″E (4 ♀, 4 ♂, AMS) and 22°52′31″S 118°31′49″E (1 ♂, AMS), 14 km SE Kalumburu Mission at 14°25′S 124°50′E (1 ♀, ANIC), Karijini National Park at 22°26.3′S 118°22.9′E (2 ♀, 2 ♂, USU), at 22°28.4′S 118°32.6′E (1 ♂, ANIC), and at 22°30.1′S 118°24.4′E (1 ♂, USU), Kennedy Range National Park at 24°38.7′S 115°10.7′E (1 ♀, USU), 11 km E Marble Bar at 21°09.0′S 119°51.7′E (2 ♂, ANIC; 1 ♂, CAS), 25 km N Marble Bar at 20°56.2′S 118°51.0′E (1 ♂, USU), 30 km E Marble Bar at 21°11.0′S 120°01.7′E (1 ♀, ANIC; 2 ♂, CAS), 133 km SW Marble Bar at 21°41.6′S 119°04.8′E (4 ♀, USU), 4 km SW Mining Camp in Mitchell Plateau at 14°52′S 125°50′E (4 ♀, ANIC), Mount Augustus National Park at 24°21.9′S 116°52.2′E (1 ♂, CAS), Murdoch, southern suburb of Perth (1 ♀, WAM), 65 km E Nanutarra Road House at 22°27.8′S 116°02.6′E (1 ♂, USU), Nanutarra-Wittenoom road at 22°21′21″S 117°54’16” (1 ♂, AMS), 22°26′08″S 117°49′56″E (2 ♀, 2 ♂, SAM), and 22°26’36″S 117°48′23″E (1 ♀, 2 ♂, AMS), 47 km S Pardoo Roadhouse on Shay Gap road at 20°22.7′S 120°01.3′E (2 ♀, 4 ♂, ANIC), Perth (1 ♂, BMNH), Perth: Darling Range (1 ♀, BMNH), Perth: Darlington (1 ♂, WAM), Thomas River 23 km NNW Mount Aridat 33°55′S 123°00′E (N).

Aulacophilinus carinatus Pulawski, species nova

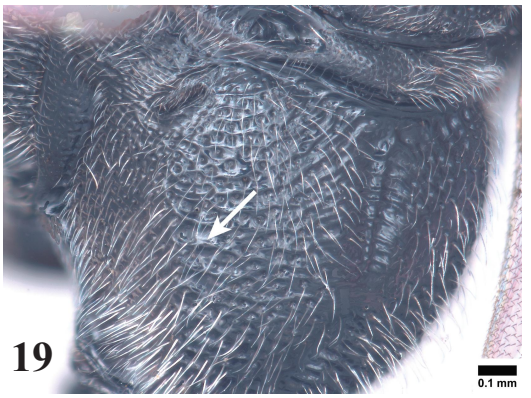
Figures 18–23.

Name derivation.— *Carinatus*, Latin for *carinate*; with reference to the carinate propodeum of his species.

Recognition.— *Aulacophilinus carinatus* is an all black inhabitant of New Guinea with three submarginal cells. It differs from its three other New Guinean congeners with these characters, *A. amblygnathus*, *solitarius*, and *tegularis*, in having the propodeum with a longitudinal carina that separates the side from the dorsum and the posterior surface, and with s series of transverse ridges

meeting the carina on its dorsal side (Fig. 19). In the three other species, the longitudinal carina is absent or evanescent, and the transverse ridges on the sides of the propodeal dorsum are lacking or are evanescent. Unlike *A. amblygnathus*, the punctures of the frons are no more than one diameter apart (rather than 2–3 diameters apart), and unlike *A. tegularis* the tegula is impunctate posteriorly (rather than uniformly punctate throughout).

Description.— Frons dull, punctate, punctures no more than one diameter apart. Free margin of clypeal lobe obtusely angulate to rounded (Fig. 18). Width of labrum equal to 1.3 × midocellar diameter. Scutum not foveate along flange, with short, inconspicuous, longitudinal ridges adjacent to posterior margin; scutal punctures well defined, almost contiguous. Scutellum slightly foveate along anterior margin. Tegula impunctate (only aciculate) in posterior half. Mesopleural punctures well defined, less than one diameter in female, some punctures about one diameter apart in male Propodeum with longitudinal carina separating side from dorsum and posterior surface and extending from gastral socket area toward spiracle (Fig. 19); dorsum obliquely ridged, punctate between ridges (ridges becoming more conspicuous as they meet longitudinal carina); side punctate and somewhat irregularly ridged; posterior surface with well defined punctures, transversely ridged in ventral half. Forewing with three submarginal cells. Posteroventral forefemoral surface minutely punctate, punctures more than one diameter apart. Hindcoxal dorsum with outer margin obtusely carinate. Outer surface of hindtibia with fine but well defined spines. Punctures of tergum I fine in female, well defined in male, several diameters apart anterior of apical depression.



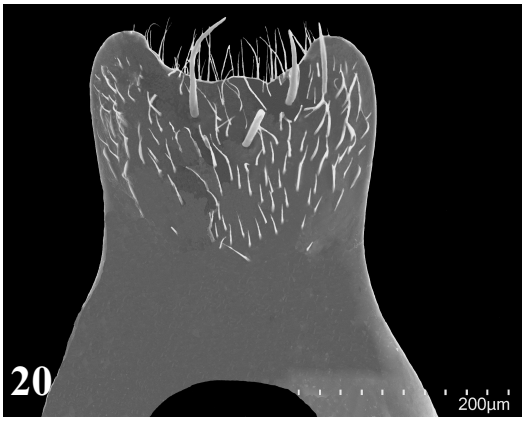
Figures 18–19. *Aulacophilus carinatus*. (18) Female clypeus and mandibles; (19) Propodeal dorsum of female in lateral oblique view (arrow shows longitudinal carina).

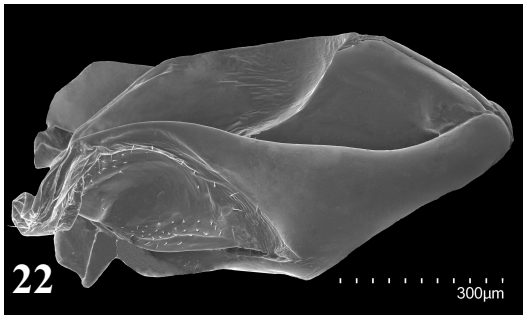
Setae silvery, suberect on frons, about 0.5 × midocellar diameter long in female, up to one diameter in male; appressed on postocellar area, subappressed on scutum and about 0.3 × as long as midocellar diameter in female, as 0.5 × diameter in male; suberect on tergum I and up to about 0.5 × midocellar diameter long; on lower gena erect and up to one midocellar diameter long; not concealing integument on clypeus in female, concealing in male. Apical depressions of terga with silvery, setal fasciae (fasciae ill defined in female).

Body all black.

♀.– Upper interocular distance equal to 0.62 × lower interocular distance; ocellocular distance equal to 0.3 × hindocellar diameter, distance between hindocelli equal to 1.0 × hindocellar diameter; eye height equal to 0.98 × distance between eye notches. Dorsal length of flagellomere I 2.1 × apical width. Length 6.2 mm; head width 1.8 mm.

♂.– Upper interocular distance equal to 0.60 × lower interocular distance; ocellocular distance equal to 0.5 × hindocellar diameter, distance between hindocelli equal to 0.8 × hindocellar diame-





FIGURES 20–22. *Aulacophilus carinatus.* (20) Male sternum VIII (ventral surface); (21) Male genitalia dorsally; (22) Male genitalia laterally.

ter; eye height equal to 1.06 × distance between eye notches. Dorsal length of flagellomere I 2.4 × apical width. Sternum VIII: (Fig. 20). Genitalia: (Figs. 21, 22). Length 6.3 mm; head width 2.0 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 23).— Indonesian part of the island of New Guinea.

RECORDS.— HOLOTYPE: ♀, **INDONESIA**: **Western Papua**: Waris S of Jayapura (as Hollandia), 1–2 Aug 1959, T.C. Maa (BISH). PARATYPE: **INDONESIA**: **Western Papua**: no specific locality, 10 Nov 1944, T. Aaron (1 ♂, CAS, labeled "Neth. New Guinea").

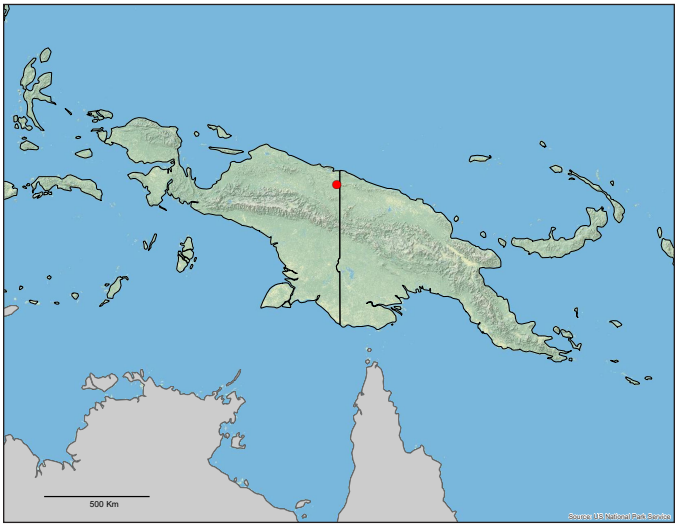


FIGURE 23. Collecting locality of *Aulacophilinus carinatus.*

***Aulacophilinus mandibulatus* (Turner)**
Figures 24–29.

Pison mandibulatum Turner, 1916:605, ♀, ♂. Lectotype: ♀, Australia: Western Australia: Yallingup (BMNH), designated by Naumann, 1990b:242, examined. – Turner, 1916:597 (in key to Australian *Pison*); Bohart and Menke, 1976:336 (in checklist of world Sphecidae); Cardale, 1985:260 (in catalog of Australian Sphecidae); Naumann, 1990b:242 (in revision of *caliginosum* species group of *Pison*). – **As *Aulacophilinus mandibulatus***: Menke, 2016:337 (new combination, in key to *Aulacophilinus*), 338 (discussion of characters).

Recognition.— *Aulacophilinus mandibulatus* is the only species of the genus with the entire mandible ferruginous (the remaining body being black). Subsidiary recognition features are: forewing with three submarginal cells, tegula punctate throughout.

Description.— Frons dull, markedly microsculptured, punctate (punctures less than one diameter apart). Free margin of clypeal lobe obtusely angulate mesally (Fig. 24). Width of labrum equal to 0.7 × midocellar diameter. Anteromedian pronotal pit transversely elongate, smaller than midocellar diameter. Scutum not foveate along flange, without longitudinal ridges adjacent to posterior margin; scutal punctures well defined, interspaces somewhat microsculptured, linear in female, averaging less than one diameter apart in male. Tegula punctate throughout. Mesopleural punctures well defined, compressed against each other; interspaces merging into small ridges. Propodeum with well-defined, irregular carina separating side from dorsum and posterior surface and extending from gastral socket area toward spiracle; dorsum finely, obliquely ridged, punctate between ridges, with middle sulcus triangularly enlarging basally (Fig. 25); side punctate, interspaces merging into fine ridges; posterior surface in female conspicuously punctate (punctures compressed against each other), with well defined transverse ridges in male (punctate between ridges). Forewing with three submarginal cells. Posteroventral forefemoral surface microscopically, closely punctate. Hindcoxal dorsum with outer margin sharply carinate except anteriorly. Outer surface of hindtibia with fine but well-defined spines. Tarsomeres with plantulae. Punctures of tergum I on horizontal part averaging slightly more than one diameter apart mesally.

Setae silvery, nearly appressed on upper frons, straight, suberect on lower gena (setal length about 0.6 × midocellar diameter), suberect but markedly shorter than midocellar diameter on scutum, appressed on tergum I, not concealing integument on clypeus. Apical depressions of terga without silvery, setal fasciae.

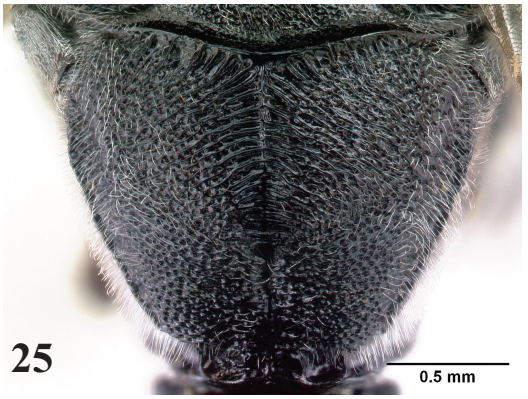
Head, thorax, propodeum, legs, and gaster black, mandible ferruginous, female clypeus ferruginous next to lobe free margin.

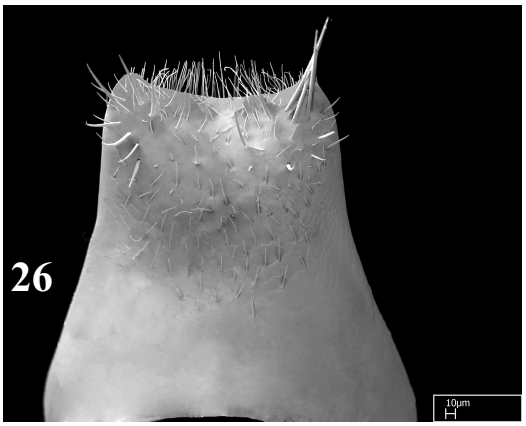
♀.– Upper interocular distance equal to 0.72 × lower interocular distance; ocellocular distance equal to 0.9 × hindocellar diameter, distance between hindocelli equal to 1.3 × hindocellar diameter; eye height equal to 0.92 × distance between eye notches. Dorsal length of flagellomere I 2.1 × apical width. Mandible: trimmal carina with minimal preapical incision. Length 9.2 mm; head width 2.5 mm.

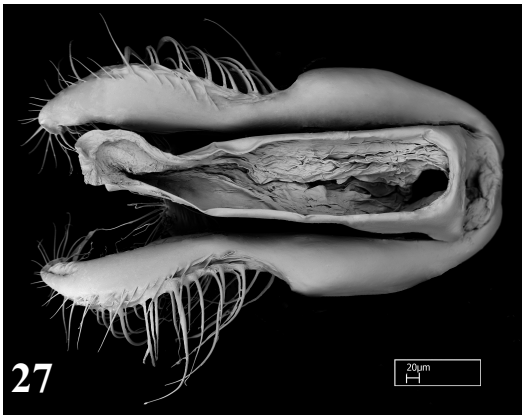
♂.– Upper interocular distance equal to 0.78 × lower interocular distance; ocellocular distance equal to 1.3 × hindocellar diameter, distance between hindocelli equal to 1.5 × hindocellar diameter; eye height equal to 0.96 × distance between eye notches. Dorsal length of flagellomere I 1.9 × apical width. Sternum VIII broadly emarginate apically (Fig. 26). Genitalia: Figs. 27, 28. Length 5.5 mm; head width 1.7 mm.

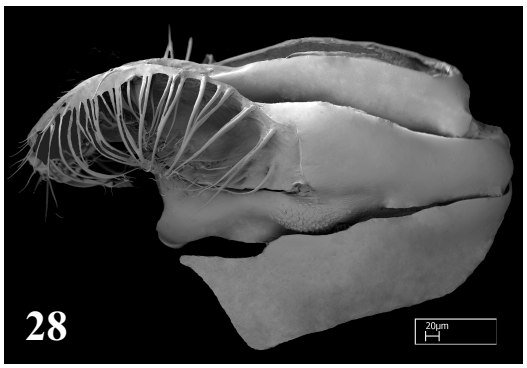
Geographic Distribution (Fig. 29).— South Australia, Western Australia.

Records.— **Australia**: **South Australia**: 44 km NW Lock at 33°31′S 135°16′E (1 ♂, ANIC). **Western Australia**: Yallingup (1 ♀, BMNH, lectotype of *Pison mandibulatum*).









FIGURES 24–28. *Aulacophilinus mandibulatus.* (24) Female clypeus and mandibles; (25) Ppropodeal dorsum of female; (26) Male sternum VIII (ventral surface); (27) Male genitalia dorsally; (28) Male genitalia laterally.

***Aulacophilinus pyrrhicus (*Naumann)**

Figures 30–37.

Pison pyrrhicum Naumann, 1990b:240, ♀, ♂. Holotype: ♀, Australia: Queensland: Kookaburra Cave in Carnarvon National Park (QMB), examined. – **As *Aulacophilinus pyrrhicus***: Menke, 2016:338 (new combination, in key to *Aulacophilinus*).

RECOGNITION.— *Aulacophilinus pyrrhicum* is the only member of the genus with a ferruginous gaster and with the posterior propodeal surface with several ridges radiating up from the gastropropodeal articulation. It shares with *A. weiri* the gena with a crenulate sulcus along the poste-

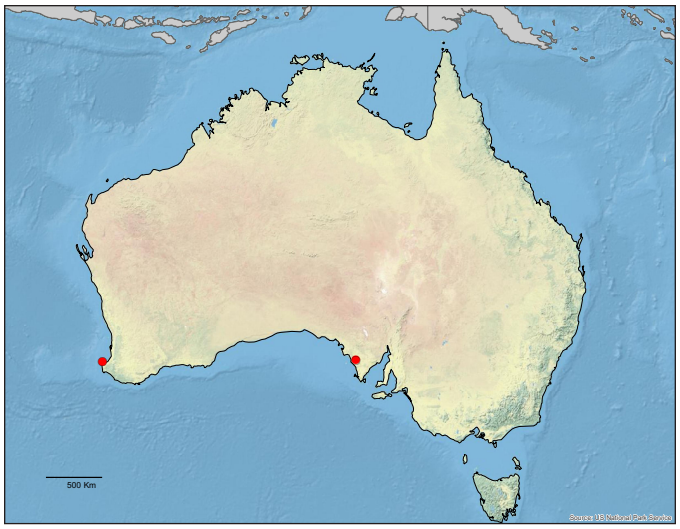


FIGURE 29. Collecting localities of *Aulacophilinus mandibulatus*.

rior eye margin, the sulcus delimited posteriorly by a well-defined carina. The presence of three submarginal cells is a subsidiary recognition feature.

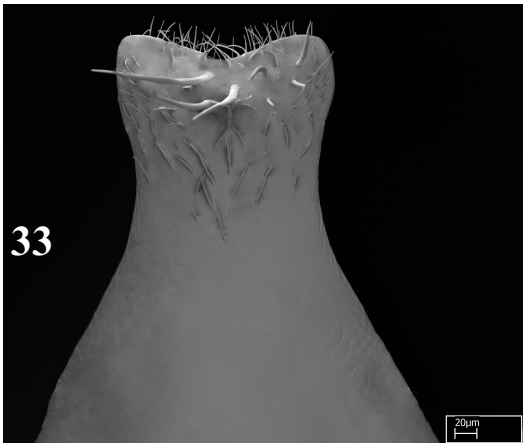
DESCRIPTION.— Frons coarsely punctate or punctatorugose, interspaces shiny, linear. Free margin of clypeal lobe arcuate mesally, with minute apical point (Fig. 30). Occipital carina expanded ventrally. Width of labrum equal to 1.3× midocellar diameter. Anteromedian pronotal pit transversely elongate, about three times as long as midocellar diameter. Scutum not foveate along flange, without longitudinal ridges adjacent to posterior margin; scutum and mesopleuron coarsely punctate or punctatorugose, interspaces linear, unsculptured (Fig. 32). Tegula posterolaterally impunctate or with microscopic, scattered punctures. Propodeum with or without longitudinal carina separating side from dorsum and posterior surface and extending from gastral socket area toward spiracle; dorsum obliquely ridged, rugose laterally; side coarsely punctate, interspaces merging into fine ridges; posterior surface irregularly transversely ridged, coarsely punctate between ridges, with several ridges radiating up from gastropropodeal articulation. Forewing with three submarginal cells. Posteroventral forefemoral surface minutely punctate, punctures averaging about two diameters apart. Hindcoxal dorsum with outer margin sharply carinate. Outer surface of hindtibia with fine but well-defined spines. Punctures of tergum I conspicuous, no more than one diameter apart on horizontal part in female and some males, slightly more in other males.

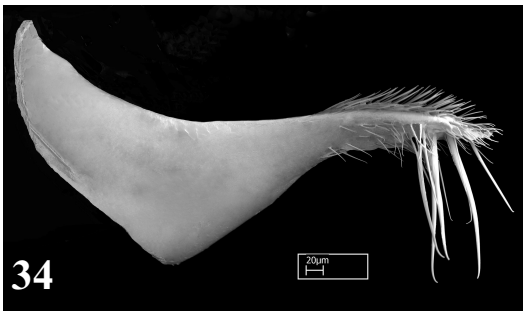
Setae silvery, erect on frons and scutum, up to about as long as midocellar diameter; on lower gena subappressed to suberect, curved or sinuous, about as long as midocellar diameter; appressed on tergum I; not concealing integument on clypeus. Apical depressions of terga without setal fasciae. Apical depressions of terga without silvery, setal fasciae.

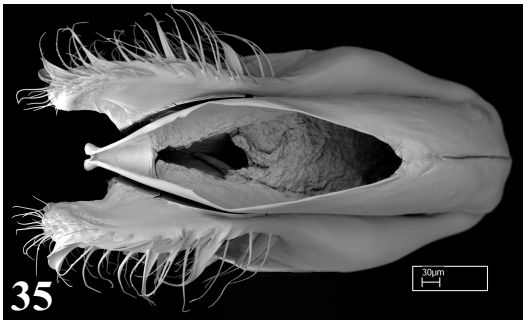
Head, thorax, and propodeum black; flagellum ferruginous (apical flagellomere partly dark). Fore- and midfemora black, ferruginous apically, hindfemur ferruginous in apical third to all ferruginous; tibiae and tarsi ferruginous. Gaster ferruginous.

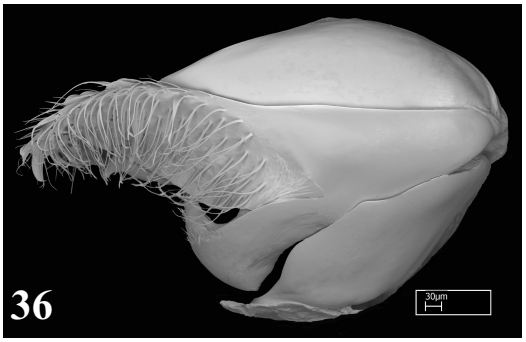
♀.– Upper interocular distance equal to 0.60–0.62 × lower interocular distance; ocellocular distance equal to 0.5–0.6 × hindocellar diameter, distance between hindocelli equal to 1.1 × hindocellar diameter (Fig. 31); eye height equal to 0.94–0.96 × distance between eye notches. Dorsal length of flagellomere I 2.2 × apical width. Length 6.5–7.5 mm; head width 2.1–2.3 mm.

♂.– Upper interocular distance equal to 0.68–0.76 × lower interocular distance; ocellocular









FIGURES 30–36. *Aulacophilus pyrrhicus.* (30) Female clypeus and mandibles; (31) Female head in dorsal view; (32) Female tegula and adjacent portion of scutum; (33) Male sternum VIII (ventral surface); (34) Male sternum VIII in lateral view; (35) Male genitalia dorsally; (36) Male genitalia laterally.

distance equal to 0.7–0.8 × hindocellar diameter, distance between hindocelli equal to 1.1 × hindocellar diameter; eye height equal to 0.92–0.96 × distance between eye notches. Dorsal length of flagellomere I 2.0–2.3 × apical width. Sternum VIII shallowly, broadly emarginate apically (Fig. 33), with long, erect setae apically (Fig. 34. Genitalia: Figs. 35 and 36. Length 5.5–6.0 mm; head width 1.9–2.1 mm.

Geographic Distribution (Fig. 37).— Northern Territory, Queensland.

Records.— **Australia**: **Northern Territory**: Kakadu National Park (1 ♂, CAS), Nourlangie Creek and Obiri Rock in Kakadu National Park (Naumann, 1990). **Queensland**: Arcadia on Magnetic Island (1 ♀, ANIC), Calamvale, a southern suburb of Brisbane (1 ♀, USNM), Fletcher Creek 43 km NW Charters Towers at 19°48.9′S 146°03.3′E (3 ♀, CAS), Kookaburra Cave in Carnarvon National Park (Naumann, 1990), Pendland at 20°31.0′S 145°24.2′E (3 ♀, 1 ♂, CAS), 2 km N Rokeby at 13°39′S 142°40′E (1 ♀, ANIC).

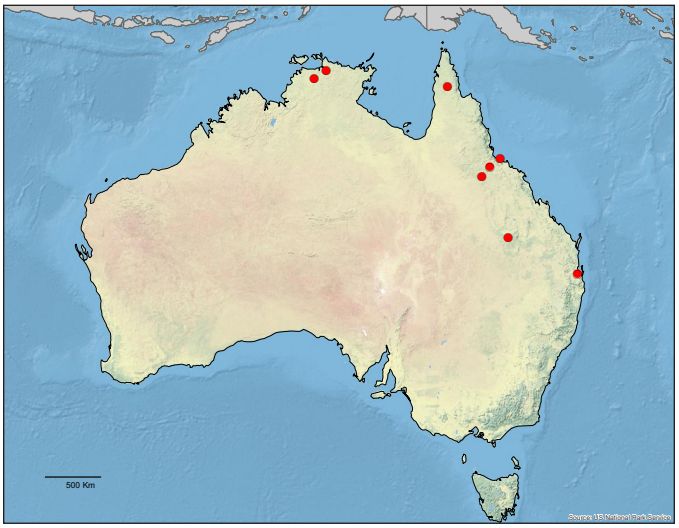


Figure 37. Collecting localities of *Aulacophilinus pyrrhicus*.

Aulacophilinus rennellensis Lomholdt

Figures 38–46.

Aulacophilinus rennellensis Lomholdt, 1980:28, ♀, ♂. Holotype: ♀, Solomon Islands: Rennell Island: Hutuna (ZMUC), examined. – Menke, 2016:337 (in key to *Aulacophilinus*), 338 (discussion of characters). – **As *Pison rennellense***: Antropov, 1999:564 (new combination, analysis of relationships).

Recognition.— *Aulacophilinus rennellensis* differs from all its congeners in having a conspicuously pedunculate gastral segment I (its length is about 3.0 × maximum width in the female and 3.5 × in the male rather than about equal to width) and also conspicuously swollen apically (Figs. 41, 42). The presence of only two submarginal cells is a subsidiary recognition feature.

Description.— Frons dull, microareolate, finely punctate, punctures averaging more than one diameter apart. Distance between antennal socket and orbit about equal to socket diameter in female, slightly greater in male. Free margin of clypeal lobe roundly arcuate (Figs. 38, 39). Occipital carina not expanded. Width of labrum equal to 0.6 × midocellar diameter. Anteromedian pronotal pit transversely elongate, about as long as midocellar diameter. Scutum foveate along flange, with short longitudinal ridges adjacent to posterior margin; scutal punctures minute, several diameters apart. Tegula impunctate in posterior half. Mesopleural punctures of medium size, several diameters apart. Propodeum without longitudinal carina separating side from dorsum and posteri-

FIGURES 38–40. *Aulacophilinus rennellensis.* (38) Female clypeus and mandibles; (39) Male clypeus and mandibles; (40) Female head dorsally.

or surface; dorsum obliquely ridged; side punctate, finely, transversely ridged anteriorly in male; posterior surface punctate. Forewing with two submarginal cells, length of posterior margin of second cell equals 1.8–1.9 × its height. Posteroventral forefemoral surface minutely punctate, punctures several diameters apart. Hindcoxal dorsum with outer margin obtusely carinate. Outer surface of hindtibia without spines. Gastral segment I conspicuously pedunculate (its length about 3.0 × maximum width in female and 3.5 × in male), conspicuously swollen apically (Figs. 42). Apical swelling of tergum I with minute punctures several diameters apart.

Setae silvery, subappressed on upper frons, on postocellar area appressed in female, erect in male, on scutum subappressed in female, suberect in male, appressed on tergum I, on lower gena suberect, straight, up to one midocellar diameter long, partly concealing integument on clypeus. Terga without setal, silvery, fasciae.

Body all black, mandible with ferruginous tint.

♀.– Upper interocular distance equal to 0.4 × lower interocular distance; ocellocular distance equal to 0.2× hindocellar diameter, distance between hindocelli equal to 0.5× hindocellar diameter (Fig. 40); eye height equal to 1.6 × distance between eye notches. Dorsal length of flagellomere I 2.5 × apical width. Length 9.0 mm; head width 2.0 mm.

♂.– Upper interocular distance equal to 0.48 × lower interocular distance; ocellocular distance equal to 0.4 × hindocellar diameter, distance between hindocelli equal to 0.8 × hindocellar diameter; eye height equal to 1.12 × distance between eye notches. Dorsal length of flagellomere I 2.4 × apical width; flagellomeres I-IV with polished, elevated tyli. Sternum VIII and male genitalia missing from the specimens examined, but figured by Lomholdt (1980) and here reproduced as Figs. 43–45); sternum VIII emarginate apically (Fig. 43). Genitalia: (Figs. 44, 45). Length 8.5 mm; head width 1.7 mm.

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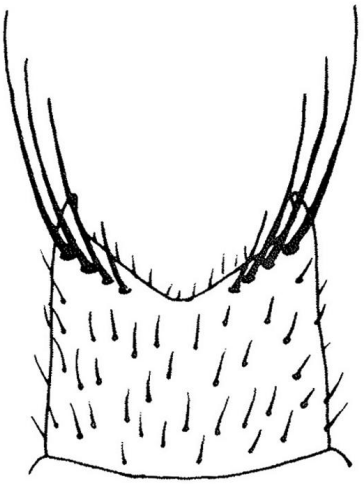

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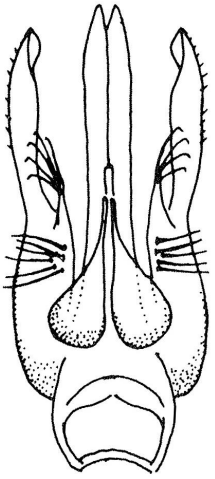

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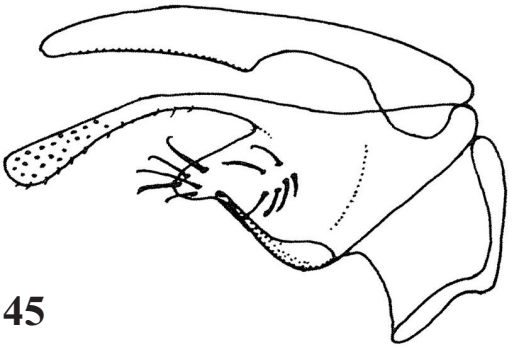

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FIGURES 41–45. *Aulacophilinus rennellensis*. (41) Female tergum I dorsally; (42) Female tergum I laterally; (43) Male sternum VIII (from Lomholdt, 1980); (44) Male genitalia ventrally (from Lomholdt, 1980);.(45) Male genitalia laterally (from Lomholdt, 1980).

Geographic Distribution (Fig. 46).— Rennell Island (Solomon Islands archipelago).

Records.— Solomon Islands: **Rennell Island**: Hutuna (1 ♀, 1 ♂, ZMUC, holotype and paratype of *Aulacophilinus rennellensis*).

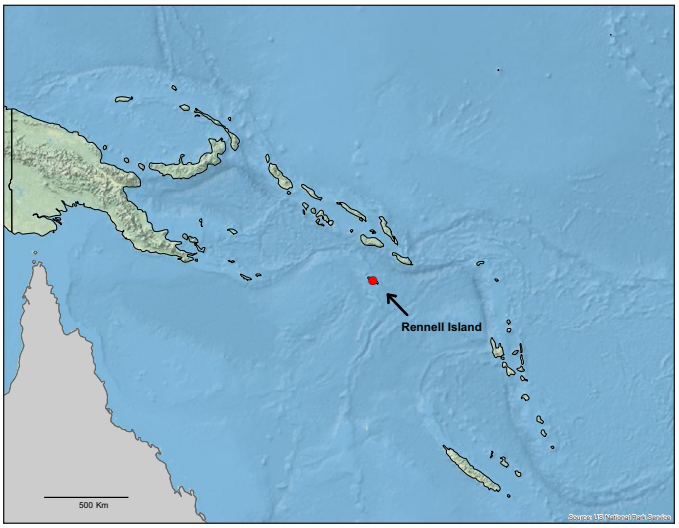


Figure 46. Collecting locality of *Aulacophilinus rennellensis*.

Aulacophilinus solitarius Pulawski, species nova

Figures 47–48.

Name derivation.— *Solitarius* is a Latin adjective meaning *solitary*, *lonely*; with reference to the fact that only one specimen of this species is known.

Recognition.— *Aulacophilinus solitarius* is an all black endemic of New Guinea with three submarginal cells. It differs as follows from this island's congeners: unlike *A. amblygnathus*, the frons punctures are no more than one diameter apart (rather than 2–3 diameters apart); unlike *A. carinatum*, it lacks the longitudinal carina separating the propodeal side from the dorsum and posterior surface and the ridges at the side of the propodeal dorsum are evanescent (carina present *in carinatum*, with well-defined ridges meeting its dorsal side); and unlike *A. tegularis*, the tegula is impunctate posteriorly (rather than punctate throughout).

Description.— Frons dull, markedly microsculptured, with well-defined punctures that average about one diameter apart. Free margin of clypeal lobe obtusely angulate (Fig. 47). Width of labrum equal to 1.5 × midocellar diameter. Gena somewhat thicker in dorsal view than in other *Aulacophilinus*. Anteromedian pronotal pit transversely elongate, about twice as long as midocellar diameter. Scutum foveate along flange, with minute, inconspicuous longitudinal ridges adjacent to posterior margin; scutal punctures well defined, less than one diameter apart. Tegula impunctate in posterior half. Mesopleural punctures well defined, less than one diameter apart except about one diameter apart ventrally. Postspiracular carina about twice as long as midocellar diameter. Propodeum without longitudinal carina separating side from dorsum and posterior surface; dorsum regularly, obliquely ridged (ridges evanescent laterally), with middle carina that is visible only from certain angles; side punctate, interspaces merging into fine, irregular ridges; posterior surface punctate, transversely ridged in ventral half. Forewing with three submarginal cells. Posteroventral forefemoral surface minutely punctate, punctures averaging about 2–3 diameters apart. Hindcoxal dorsum with outer margin obtusely carinate. Outer surface of hindtibia with fine spines. Punctures

of tergum I fine, more than one diameter apart (except on apical depression).

Setae silvery, suberect on frons and about as long as midocellar diameter, appressed on postocellar area, suberect on scutum and tergum I and up to about 0.5 × as long as midocellar diameter; on lower gena curved, about as long as midocellar diameter; not concealing integument on clypeus. Apical depressions of terga with silvery, setal fasciae.

Body all black.

♀.– Upper interocular distance equal to 0.56 × lower interocular distance; ocellocular distance equal to 0.8 × hindocellar diameter, distance between hindocelli equal to 1.2 × hindocellar diameter; eye height equal to 0.96 × distance between eye notches. Both flagella missing. Length 9.0 mm; head width 2.5 mm.

FIGURE 47. *Aulacophilus solitarius*: female clypeus and mandibles.

♂.– Unknown.

GEOGRAPHIC DISTRIBUTION (Fig. 48).— Known from one locality in the Indonesian part of New Guinea.

RECORDS.— HOLOTYPE: ♀, **INDONESIA**: **Western Papua**: Paniai Lakes (as Wisselmeren): Enarotadi, elevation 1,800–1,900 m, 22 Aug 1962, J. Sedlacek (BISH).

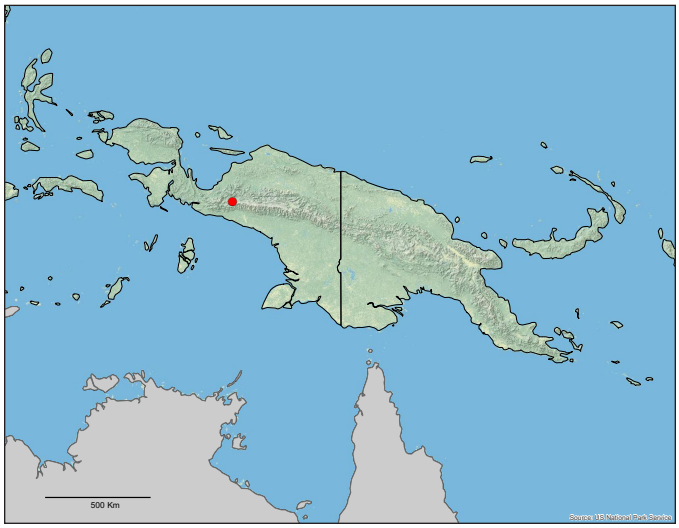


FIGURE 48. Collecting locality of *Aulacophilinus solitarius*.

Aulacophilinus tegularis Pulawski, species nova

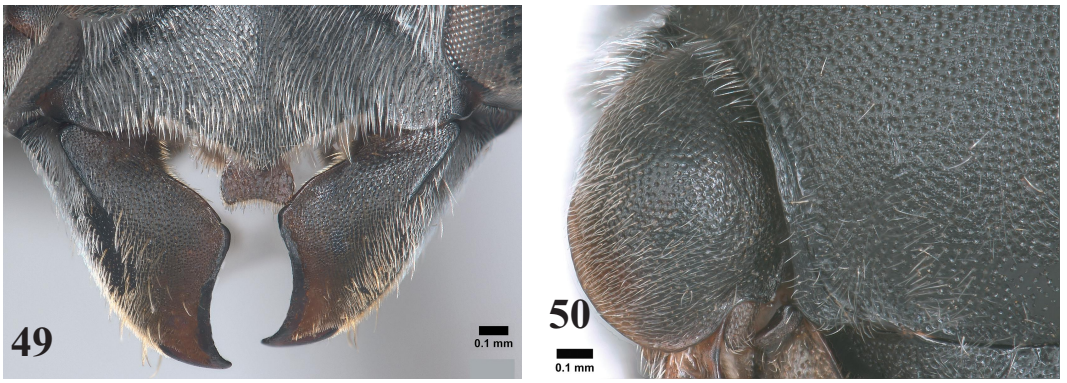
Figures 49–51.

NAME DERIVATION.— *Tegularis* is an adjective derived from *tegula*, Latin for *tile*; with reference to the uniformly punctate tegula of this species.

RECOGNITION.— *Aulacophilinus tegularis* is an all black endemic of New Guinea with three submarginal cells. It differs from the other three New Guinean species with these characters, *A. amblygnathus*, *A. solitarius*, and *A. carinatus*, in having the tegula uniformly punctate through-

out (Fig. 50) rather than impunctate or with evanescent, microscopic punctures posteriorly. Also, unlike *A. amblygnathus*, it has the frontal and scutal punctures less than one diameter apart (rather than more than one diameter apart), and the frontal setae about as long as 0.5 × midocellar diameter (rather than about one diameter long), It differs from *A. carinatum* in lacking the longitudinal carina separating the propodeal side from the dorsum and posterior surface and in lacking ridges on the side of the propodeal dorsum (longitudinal carina and transverse carinae present in *A. carinatum*).

Description.— Frons dull, markedly microsculptured, with well-defined punctures that are less than one diameter apart. Free margin of clypeal lobe obtusely angulate (Fig. 49). Width of labrum equal to 1.4 × midocellar diameter. Anteromedian pronotal pit transversely elongate, almost as long as midocellar diameter. Scutum minutely foveae along flange, with rudimentary longitudinal ridges adjacent to posterior margin; scutal punctures well defined, less than one diameter apart. Tegula uniformly punctate throughout (Fig. 50). Mesopleural punctures well defined, less than one diameter apart, interspaces merging posteriorly into small ridges. Propodeum without longitudinal carina separating side from dorsum and posterior surface; dorsum obliquely ridged, punctate between ridges; side irregularly ridged, punctate between ridges; posterior surface punctate, also transversely ridged in ventral half. Forewing with three submarginal cells. Posteroventral forefemoral surface microscopically, closely punctate. Hindcoxal dorsum with outer margin sharply carinate. Outer surface of hindtibia with fine but well-defined spines. Tarsomeres with plantulae. Punctures of tergum I, on horizontal part, averaging slightly more than one diameter apart.



Figures 49–50. *Aulacophilus tegularis*. (49) Female clypeus and mandibles; (50) Female tegula and adjacent scutum.

Setae silvery, suberect on frons and about 0.5 × as long as midocellar diameter, appressed on postocellar area, on scutum and tergum I suberect and about 0.3 × as long as midocellar diameter; on lower gena partly straight, partly curved, up to one midocellar diameter long; not concealing integument on clypeus. Apical depressions of terga with silvery, setal fasciae.

Body all black, mandible narrowly ferrugineus apicoventrally in paratype.

♀.– Upper interocular distance equal to 0.56–0.58 × lower interocular distance; ocellocular distance equal to 0.5–0.7 × hindocellar diameter, distance between hindocelli equal to 0.5–0.8 × hindocellar diameter; eye height equal to 1.06–12.10 × distance between eye notches. Dorsal length of flagellomere I 2.3–2.5 × apical width. Length 9.4–9.8 mm; head width 2.5 mm.

♂.– Unknown.

Geographic Distribution (Fig. 51).— Known from two localities in the Madang Province of Papua New Guinea.

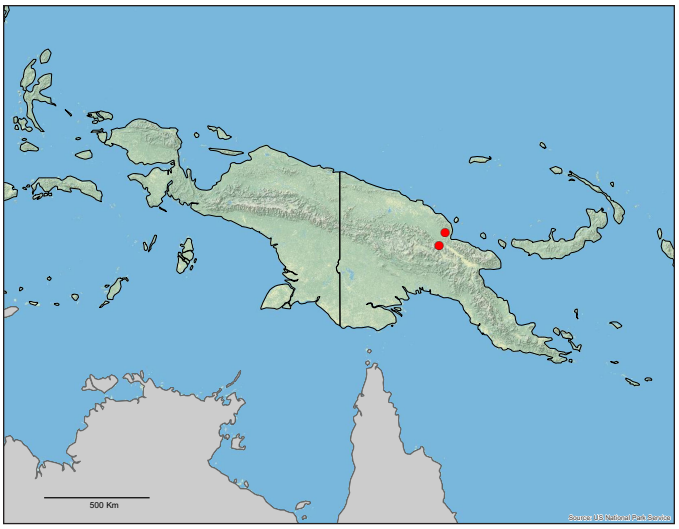


FIGURE 51. Collecting localities of *Aulacophilus tegularis*.

RECORDS.— HOLOTYPE: ♀, **PAPUA NEW GUINEA**: **Madang Province**: Bundi at 5º45′S 145º15′E, 20 May 1988, W.J. Pulawski (CAS). PARATYPE: **PAPUA NEW GUINEA**: **Madang Province**: Sapi Forest Reserve 30 km W Madang at 5º12′S 145º30′E, 10 Feb 1987, W.J. Pulawski (1 ♀, CAS).

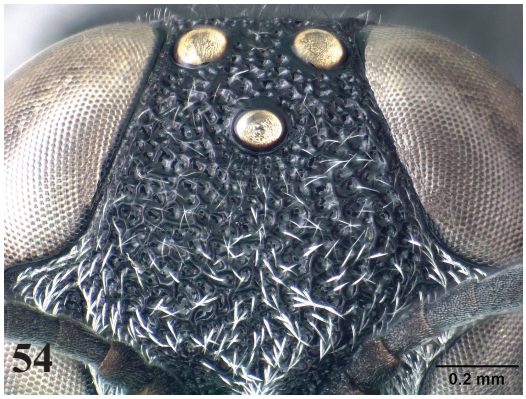
Aulacophilinus weiri (Naumann)

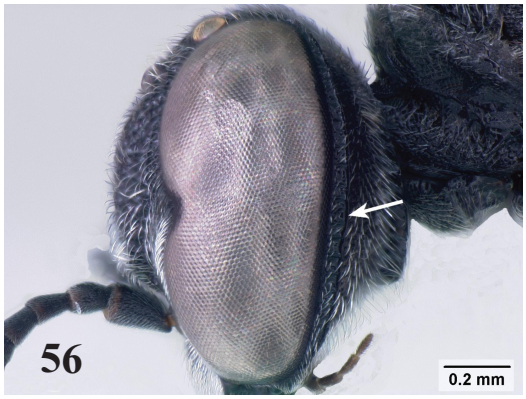
Figures 52–62.

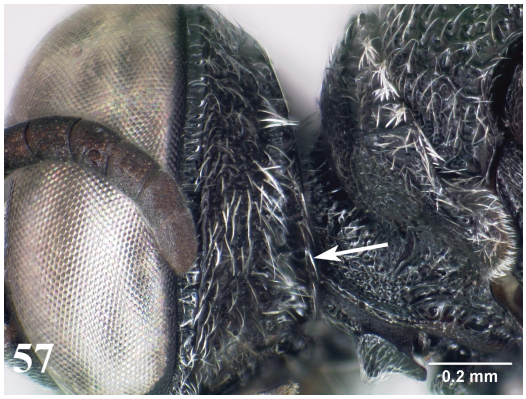
Pison weiri Naumann, 1990b:239, ♀, ♂. Holotype: ♀, Australia: Northern Territory: Island of Rimbija (ANIC), examined. – **As *Aulacophilinus weiri***: Menke, 2016:337 (new combination, in key to *Aulacophilinus*).

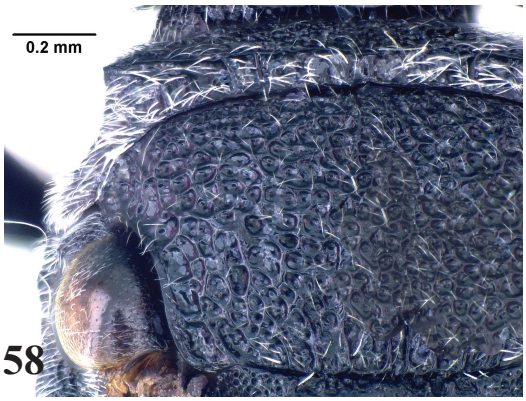
RECOGNITION.— *Aulacophilinus weiri* shares with *A. caliginosus* and *A. rennellensis* the presence of only two submarginal cells. It is unique among its congeners in having the frons (Fig. 54), scutum (Fig. 58), and mesopleuron coarsely areolate (rather than punctate), the pronotal collar with a crenulate furrow posteriorly (no such furrow elsewhere or furrow ill defined), and in having an omalus (no omalus in the other *Aulacophilinus*). It shares with *A. pyrrhicum* the gena with a crenulate sulcus along the posterior eye margin, the sulcus delimited posteriorly by a well-defined carina (Fig. 56). Unlike *A. rennellensis*, its gastral segment I is sessile rather than conspicuously pedunculate. Unlike these two species, the tegula of *A. weiri* is minutely punctate throughout (rather than impunctate posteriorly).

DESCRIPTION.— Frons shiny, coarsely areolate (Fig. 54). Free margin of clypeal lobe widely rounded (Figs. 52, 53). Occipital carina expanded (Fig. 57), as high ventrally as midocellar diameter (less than that in some specimens). Width of labrum equal to 0.9 × midocellar diameter. Gena with crenulate sulcus along posterior eye margin (Fig. 56), sulcus delimited posteriorly by well-defined carina. Anteromedian pronotal pit rounded elongate, smaller than midocellar diameter. Scutum foveate along flange, with short longitudinal ridges adjacent to posterior margin, conspicuously areolate. Tegula microscopically punctate throughout. Mesopleuron conspicuously areolate, with omaulus. Metapleuron longitudinally ridged between dorsal and ventral metapleural pits. Propodeum without longitudinal carina separating side from dorsum and posterior surface and









FIGURES 52–58. *Aulacophilinus weiri.* (52) Female clypeus and mandibles; (53) Male clypeus and mandibles; (54) Upper frons of female; 55) Female head in dorsal view; (56) Female head in lateral view (arrow shows postorbital carina); (57) Female head in lateral oblique view (arrow shows occipital carina); (58) Female tegula and adjacent portion of scutum.

extending from gastral socket area toward spiracle; dorsum rugose, with short, transverse carinae emerging from middle carina; side with well-defined punctures (interspaces in some specimens merging into fine longitudinal ridges); posterior surface areolate, with tendency to form transverse ridges in ventral half. Forewing with two submarginal cells; length of posterior margin of second cell equals 1.3–1.4 × its height. Posteroventral forefemoral surface minutely, closely punctate. Hindcoxal dorsum with outer margin sharply carinate. Outer surface of hindtibia with evanescent spines. Punctures of tergum I well defined, about one diameter apart on horizontal portion.

Setae silvery, appressed on frons, scutum, and tergum I; almost completely concealing integument on clypeus; genal setae suberect, straight, curved apically, longest setae about equal to midocellar diameter. Apical depressions of terga with ill-defined, silvery, setal fasciae.

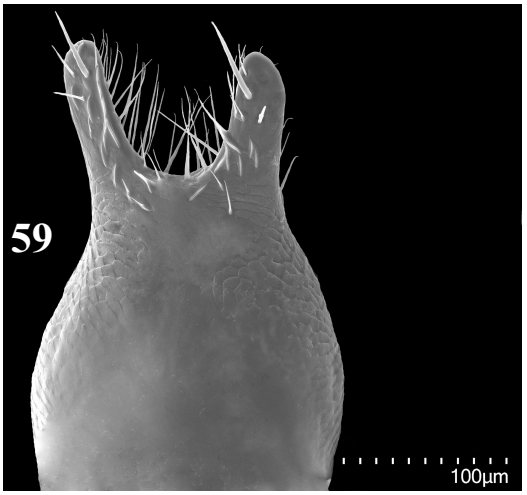
Body all black except mandibular apex ferruginous.

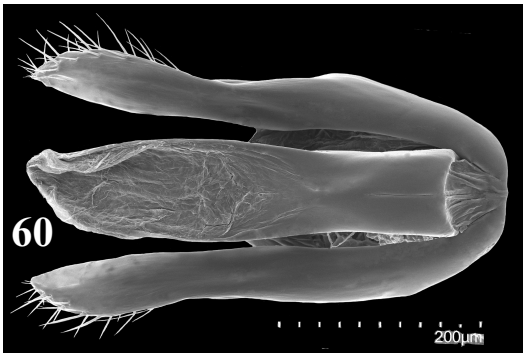
♀.– Upper interocular distance equal to 0.70–0.72 × lower interocular distance; ocellocular distance equal to 0.3 × hindocellar diameter, distance between hindocelli equal to 1.1–1.3 × hindocellar diameter (Fig. 55); eye height equal to 0.90–0.92 × distance between eye notches. Dorsal length of flagellomere I 1.4–1.8 × apical width. Length 4.8–6.0 mm; head width 1.4–1.6 mm.

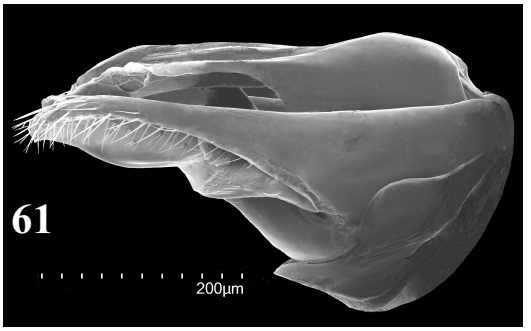
♂.– Upper interocular distance equal to 0.80 × lower interocular distance; ocellocular distance equal to 0.4 × hindocellar diameter, distance between hindocelli equal to 1.2 × hindocellar diameter; eye height equal to 0.92 × distance between eye notches. Dorsal length of flagellomere I 1.3 × apical width. Sternum VIII conspicuously emarginate apically (Fig. 59). Genitalia: Figs. 60 and 61. Length 4.2 mm; head width 1.3–1.4 mm.

Geographic Distribution (Fig. 62).— Northern part of Northern Territory, northern Queensland.

Records.— **Australia**: **Northern Territory**: Cattle Creek 54 km S Borroloola (Naumann, 1990b), Gregory National Park at 15°58.3′S 130°29.3′E (1 ♀, 1 ♂, ANIC), at 15°58′17″S 130°29′17″E (1 ♂, ANIC), at 16°03.7′S 130°27.1′E (1 ♂, USU), and 16°12′47″S 130°25′11″E







Figures 59–61. *Aulacophilinus weiri.* (59) Male sternum VIII (ventral surface); (60) Male genitalia dorsally; (61) Male genitalia laterally.

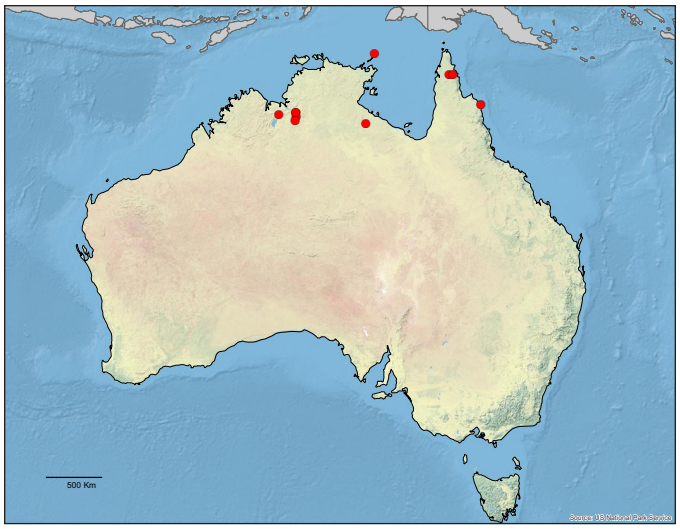


FIGURE 62. Collecting localities of *Aulacophilus weiri*.

(1 ♀, CAS; 1 ♂, USU), Gregory National Park near Timber Creek on Victoria River bank at 15°37.8′S 130°28.6′E (1 ♀, CAS), Island of Rimbija (1 ♀, 2 ♂, ANIC, holotype and paratypes of *weiri*), Keep River National Park at 15°45′30″S 129°06′28″E (1 ♂, CAS). **Queensland**: 4 km NE Batavia at 12°39′S 142°42′E (2 ♀, ANIC; 1 ♀, CAS), 4 km SW Casuarina Hill (Naumann, 1990b), 13 km SE Weipa at 12°40′S 143°00′E (2 ♀, ANIC).

ACKNOWLEDGMENTS

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Two New Records of Wing-reduced Tipulidae from North America

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We present two distribution records, COI sequence data, and photographs for the rare brachypterous species *Tipula* (*Vestiplex*) *aldrichiana* and *Tricyphona subaptera*, noting in particular a range expansion into Canada for *T.* (*V.*) *aldrichiana.*

Brachyptery (loss or reduction of flight wings) is associated with range size reduction and geographical isolation and is frequently associated with a high degree of local endemism in montane insect species (Kavanaugh 1985; McCulloch et al. 2016). Other flightless alpine insects are known to comprise cryptic species complexes even within mountain ranges (Schoville and Roderick 2010), largely reflecting the physical separation of alpine habitats, the strong topographic relief limiting dispersal, and the history of glacial events that subdivide contiguous mountain ranges, all leading to geographical isolation. Various hypotheses about the origin of flightless species in such environments, as well as about the role of dispersal after wing reduction versus *in situ* repeated evolution of brachyptery (Medeiros et al. 2015), can be tested once groups that display wing-reduction have been adequately sampled.

Here we report recent collections and a range expansion for two species of Tipulidae that display brachyptery, as well as the first published photographs and genetic data for either of these species. Although many wing-reduced species are known from several genera of Tipulidae (Byers 1969), many of them, especially those that inhabit remote areas where collection is difficult, have not been collected for decades. Therefore, these specimens might provide valuable taxonomic material for future studies on the biogeography of these groups and for the study of wing-reduction in general.

Methods

Specimens were collected by hand into vials containing 100% Ethanol, during surveys of rocky alpine habitats. Digital photographs of adults were taken with a Canon EOS-1D Mark II camera using a Microptics Digital Imaging System. DNA was extracted from the legs of specimens using the standard protocol described in Qiagen's (Valencia, CA, USA) DNeasy kits. The "barcoding" segment of the mitochondrial (mtDNA) protein coding gene COI was amplified using the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') and the following thermal profile: 2 min at 94°C; 34 cycles of 94°C for 1 min, 51°C for 1 min, and 72°C for 2 min; 12 min at 72°C. PCR product was purified using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) and then sequenced on an

Applied Biosystems (Grand Island, NY, USA) 3730 DNA Analyzer. Using mitochondrial COI sequences available in Genbank at time of publication, we used BLASTN (Altschul et al. 1990) to report the most genetically similar species with maximal coverage for this region of COI.

Results and Discussion

Taxonomy

I. *Tipula* (*Vestiplex*) *aldrichiana* Alexander 1929. Canada: British Colombia, Cassiar, N59.2486, W129.9095 (WGS84). 1 ♀, 8 Aug. 2014, 23:30–02:00 hrs., S.D. Schoville and M.J. Medeiros. Specimen code SDS14–562; Genbank accession code KY114055.

The collection of *T. aldrichiana* occurred at night, in a rocky habitat near a creek draining snowmelt (air temperature was just above freezing). The specimen (Fig. 1) was found walking slowly on a small snow-patch. Other insects foraging in the same habitat included *Grylloblatta campodeiformis nahanni* Kamp 1979, omaline rove beetles (Staphylinidae), and *Nebria* (*Boreonebria*) spp. (Carabidae). Specimen deposited in the California Academy of Sciences (CASENT 8125472).

Tipula (*Vestiplex*) *aldrichiana* has flightless and brachypterous females, although the males are fully winged. This species is previously known from Alaska and several areas of Russia, but has not been previously recorded in Canada. The last collection of this species occurred in 1958, in East Beringia, Russia (Starkevich and Paramonov 2016).

II. *Tricyphona subaptera* (Alexander 1917). USA: California: Ansel Adams Wilderness, Mono Co., East Donohue Pass, 37.7615°N, 119.2394°W (WGS84). 2 ♂, 17 July 2016, 13:00–14:00 hrs., S.D. Schoville and B.A. Pieper. Specimen code SDS16-335; Genbank accession code KY114056. Specimens deposited in the California Academy of Sciences (CASENT 8125473 and CASENT 81254754, respectively).

The collection of *T. subaptera* occurred at mid-day, in a grassy alpine meadow near a small creek (the air temperature was about 22–25°C). Talus habitat otherwise dominates the locality. The specimens, one of which is shown in Fig. 2, were found next to one another, walking in the grass, about two meters from the creek edge.

Tricyphona subaptera displays brachyptery in both sexes. Although this species has previously been collected from Yosemite National Park and nearby areas, the most recent of the earlier collections was made in 1957.

COI data

For *Tipula* (*Vestiplex*) *aldrichiana*, there is a 5% sequence divergence with the most similar sequence (KR756861) belonging to *Tipula* (*Vestiplex*) *balioptera*; there is 100% coverage between these two sequences. This fully winged species is known from Eastern Russia and is widespread in Canada and the northern United States (Alexander 1966). For *Tricyphona subaptera*, there is 10% sequence divergence as compared to *Tricyphona calcar*, but this sequence has only 96% coverage (KM571857) in common with our *Tricyphona subaptera* sequence. *Tricyphona calcar*, a fully winged species, is known from the eastern US and Canada (Alexander 1966). Due to very incomplete sampling of putative close relatives, attempting to present a hypothesis of phylogenetic relationships of these species to other Tipulidae would not be prudent at this time.

Concluding comments

Flightless insects can provide important information about species richness and endemism in a region, serving as useful surrogates for community-wide conservation priorities (Moritz et al.

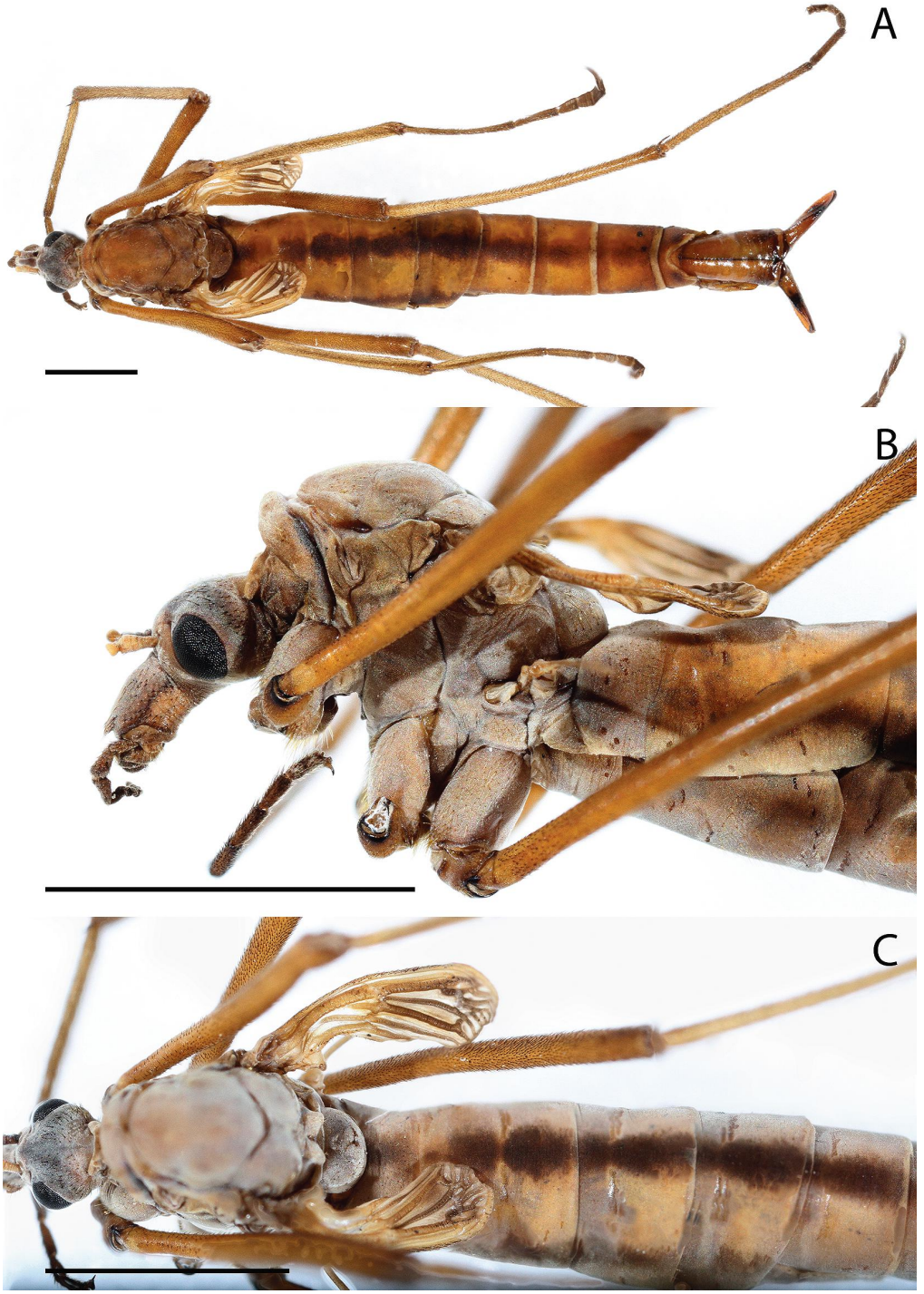

FIGURE 1. *Tipula* (*Vestiplex*) *aldrichiana* Alexander. A: Dorsal view. B: Left lateral view of head and thorax. C: Dorsal view showing wing morphology. Scale bars = 2 mm.

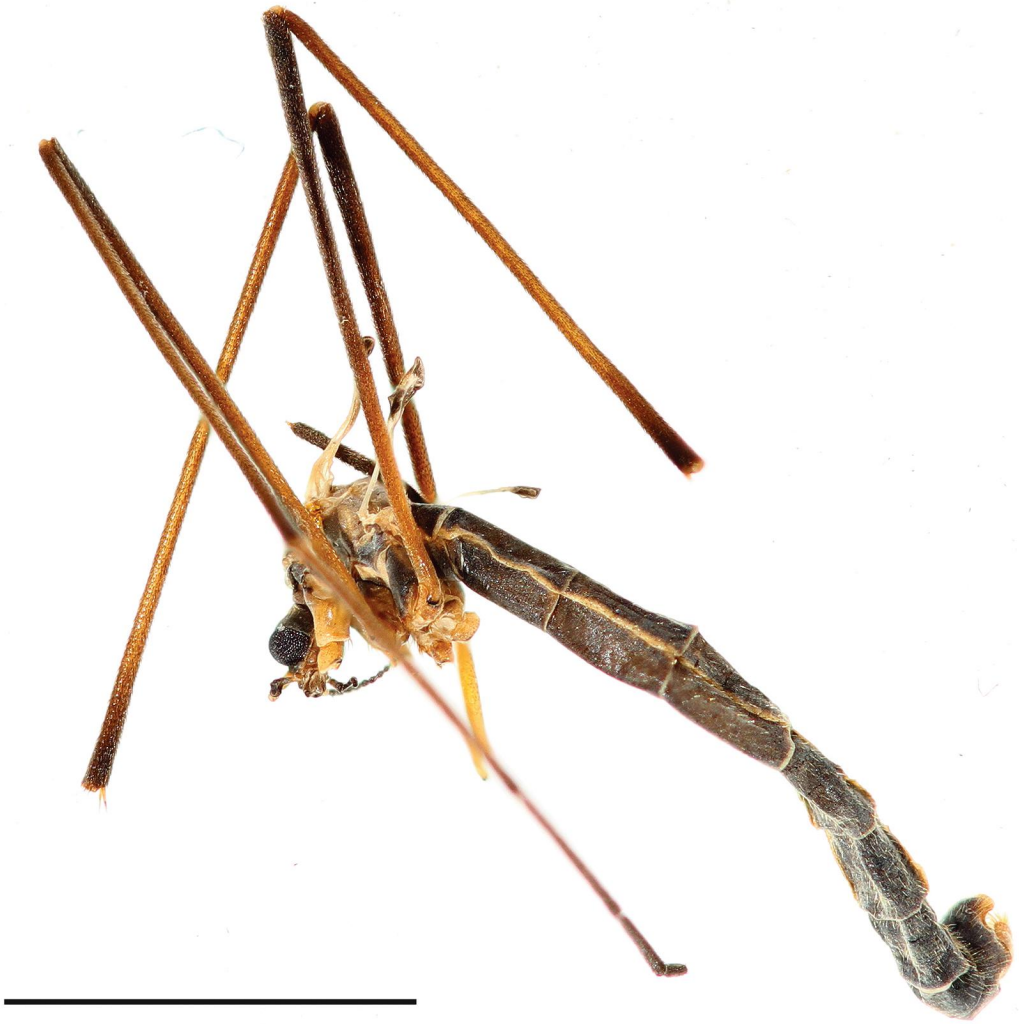

FIGURE 2. *Tricyphona subaptera* (Alexander). Left lateral view. Scale bar = 5 mm.

2001; Matenaar et al. 2015). Additionally, flightless insects offer the opportunity to test hypotheses regarding the ecological conditions and life-history traits most likely to lead to flight loss, but few groups with flightless species have been sampled adequately, a necessary first step in this process (Roff 1994). The lack of current knowledge of the distribution and diversity of flightless insects, including tipulids, is an unfortunate short-coming that needs to be addressed, and it is our hope that the records and information presented here are of use in future revisions of these large genera (*Tipula* subg. *Vestiplex* includes 214 known species; *Tricyphona* includes 130 species).

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Systematics of *Mendoncia* (Acanthaceae: Thunbergioideae) in the Paleotropics

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A taxonomic revision of the Paleotropical species of the amphi-Atlantic, acanthaceous genus *Mendoncia* recognizes 10 species in Africa and Madagascar. Herbarium specimens from throughout these regions were used to formulate descriptions of species, obtain distributional and ecological data, and acquire pollen for characterization and illustration of palynological features of species in the Old World. Aspects of floral biology of *M. cowanii* in Madagascar were studied in the field. Distribution maps, illustrations and photographs showing characteristic morphological features, and both comprehensive and geographic keys for identification of species accompany the revision. Lectotypes are designated for nine names pertaining to Paleotropical *Mendoncia*.

KEYWORDS: Taxonomy, distributions, floral biology, Madagascar, Africa, endemic species

Une révision taxonomique des espèces paléotropicales du genre amphi-atlantique et acanthacées *Mendoncia* reconnaît 10 espèces en Afrique et Madagascar. Des échantillons d'herbier provenant de toutes ces régions ont été utilisés pour formuler des descriptions d'espèces, obtenir des informations sur la distribution et d'écologie, et acquérir du pollen pour la caractérisation et l'illustration des caractéristiques palynologiques des espèces dans le Vieux Monde. Des aspects de la biologie floral de *M. cowanii* en Madagascar ont été étudiés dans la nature. Des cartes de distribution, des illustrations et des photographies montrant des caractéristiques morphologiques, et des clés complètes et géographiques pour l'identification des espèces accompagnent la révision. Les lectotypes sont désignés pour neuf noms appartenant à *Mendoncia* paléotropicale.

INTRODUCTION

Mendoncia Vell. ex Vand. consists of about 90 species occurring in tropical regions of both the Old World and the New World. The greatest concentration of species is in the Neotropics, where some 80 species occur in moist to wet forests from southeastern Mexico to Bolivia and Brazil. The richest region appears to be Colombia where about 35–40 species have been recorded. To date, there is no comprehensive taxonomic account for the entire genus; however, useful treatments have been provided for several regions of the New World, including: Colombia (Leonard 1951), Bolivia (Wasshausen and Wood 2004), Brazil (Profice 1989), Ecuador (Wasshausen 2013), Mexico (Daniel 1992), Panama (Durkee 1978), Costa Rica (Durkee 1986), and the Guianas (Wasshausen 2006). More recent checklists (e.g., Profice et al. (2010) for Brazil and Wood and Aymard (2015) for

Colombia) have augmented and revised some of these accounts, and added occurrence data from additional nations. Species in the Old World occur throughout tropical central Africa from Liberia east to Kenya and Tanzania, and on the Indian Ocean islands of Madagascar and Mayotte. Regional accounts include those for tropical western Africa (Hutchinson et al. 2013), tropical eastern Africa (Vollesen 2008), Gabon (Heine 1966), and Madagascar and the Comoros Archipelago (Benoist 1967). In this first systematic account of all Paleotropical *Mendoncia* 10 species are recognized, with four restricted to tropical Africa and six endemic to Madagascar and Mayotte.

Morphologically, the genus is unique among Acanthaceae by the combination of its twining habit, enlarged bracteoles subtending the flowers that form an epicalyx, highly reduced calyx, (4–) 5 (–6)-brevicolpate pollen, and drupaceous fruit that bears a single seed. This study is based on information obtained from more than 575 herbarium specimens, a literature review, field observations in Madagascar, and laboratory studies of pollen. A taxonomic revision of the Paleotropical species includes maps of geographic ranges and other ecogeographic data, illustrations and images of plants and pollen, and field observations on some aspects of floral biology for one of the Malagasy species, *M. cowanii*.

Taxonomic History

The genus *Mendoncia* was established by Vandelli (1788), who named it for Cardinal Mendonça, Patriarch of Lisbon. Subsequently, two species, *M. aspera* and *M. racemosa* (as "*Mendozia*," an orthographic variant), were described by Ruiz and Pavón (1798). These and several other species were treated by Nees (1847) in his comprehensive monograph of the family. In that account Nees also described the American genus *Engelia* Nees, which he distinguished from *Mendoncia* by having an anterior split in the limb of the corolla and a spur in the corolla tube. These characters were deemed insufficient to warrant separate generic status by Bentham (1876), who treated *Engelia* as a synonym of *Mendoncia.*

The Paleotropical species of *Mendoncia* were previously described under three generic names: *Monachochlamys* Baker, *Afromendoncia* Gilg ex Lindau, and *Lirayea* Pierre. *Monachochlamys* was described as a shrub by Baker (1883), placed in tribe Thunbergioideae, and considered to be distinct from both *Thunbergia* Retz. and *Mendoncia* by its habit and other unspecified characters. The illustration in the protologue clearly shows a twining plant. *Afromendoncia* was described as a new genus with two species from tropical western Africa (Lindau 1893) that differed from the American genus *Mendoncia* by its single ovary chamber. In his influential account of Acanthaceae, Lindau (1895) recognized *Mendoncia* from the Neotropics, *Monachochlamys* from Madagascar, and *Afromendoncia* from Africa. Subsequently, and with some trepidation, Pierre (1896) described *Lirayea* in this assemblage of genera, and distinguished it largely based on his observations of the ovules being "descending" (vs. purportedly "ascending" in the other genera). Burkill (1899) treated *Lirayea* as a synonym of *Afromendoncia*, and subsequently, Moore (1929) included *Afromendoncia* within *Monachochlamys*. Benoist (1925, 1944) included all of the species described in *Afromendoncia, Lirayea,* and *Monachochlamys* in *Mendoncia*, and indicated that characters used to distinguish the Paleotropical taxa from those of *Mendoncia* in the New World were insufficient.

Infrafamilial And Infrageneric Affinities

The convoluted taxonomic classification of *Mendoncia* was summarized by Turrill (1919), Profice (1988), Bremekamp 1953, Schönenberger and Endress (1998), and Borg et al. (2008), who noted treatment of the genus in the acanthaceous tribes Thunbergieae (Endlicher 1839; Bentham 1876) and Mendoncieae (Meisner 1840); in subfamilies Thunbergioideae (Scotland and Vollesen

2000) and Mendoncioideae (Lindau 1895) of Acanthaceae; and in families Thunbergiaceae (Van Tieghem 1908) and Mendonciaceae (Bremekamp 1953). Classifications based on both molecular and morphological data during the past 20 years have consistently treated the genus in Acanthaceae (Schönenberger and Endress 1998; McDade and Moody 1999; McDade et al. 2000; Scotland and Vollesen 2000; Borg et al. 2008). Within that family, *Mendoncia* is monophyletic and pertains to subfamily Thunbergioideae (Scotland and Vollesen 2000; Borg et al. 2008; McDade et al. 2008), where it is sister to *Thunbergia* and *Pseudocalyx* Radlk. (Borg et al. 2008), based on sampling to date (Fig. 1).

Thunbergioideae consist of five genera, *Anomacanthus* R.D. Good, *Mendoncia*, *Meyenia* Nees, *Pseudocalyx*, and *Thunbergia*, and can be distinguished by several probable morphological synapomorphies, including: climbing habit, enlarged and postgenitally united bracteoles forming an epicalyx, and reduced calyces (Brummitt 1989; Schönenberger and Endress 1998). In their study of floral development among three of these genera, Schönenberger and Endress (1998) showed that *Thunbergia, Mendoncia*, and *Pseudocalyx* share similar types of inflorescences and poricidal anther thecae with unicellular/lignified bristles and without an endothecial cell layer. Also, as previously suggested by earlier studies (e.g., Van Tieghem 1908; Benoist 1944), they demonstrated that *Mendoncia* initially has two ovary locules with four ovules, like many other members of the Acanthaceae, but later in development abortion results in a single locule with two fertile ovules, only one of which develops into a seed. It is noteworthy that among the five genera of Thunbergioideae, only *Mendoncia* occurs natively in the New World, where the vast majority of its species are found. Based on species of *Mendoncia* studied by Borg et al. (2008), the three Paleotropical species sampled form a grade from which the monophyletic Neotropical species are derived, two Malagasy species are sister to one another, and the sole African species sampled is sister to the Neotropical clade (Fig. 1). The five genera of Thunbergioideae can be distinguished by the following key.

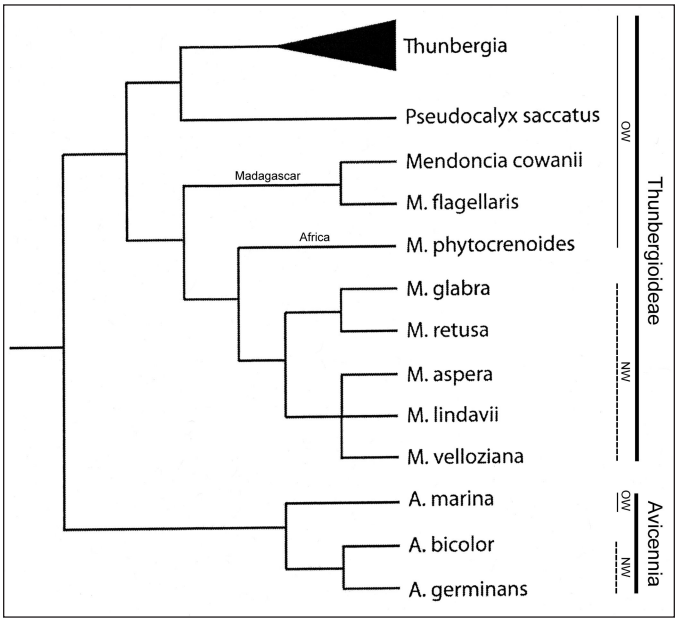

FIGURE 1. Phylogenetic relationships among genera of Acanthaceae subfamily Thunbergioideae and *Avicennia*. OW = Old World, NW = New World. Adapted from Borg et al. (2008).

Key to Genera of Thunbergioideae

1a. Fruit fleshy and indehiscent (drupe); ovules 2; seeds 1 or 2 2
1b. Fruit woody and dehiscent (capsule); ovules 4; seeds up to 4 3

2a. Mature ovary with 1 fertile locule (other locule rudimentary or aborted); drupe 1-seeded; pollen (4–) 5–6-colpate, colpi short (brevicolpate). . . . . *Mendoncia*
2b. Mature ovary with 2 fertile locules; drupe 2-seeded; pollen (fide Raj 1961) 3(–4)-colpate, colpi elongate. . . . . *Anomacanthus*

3a. Stigma ± equally 2-lobed, each lobe again divided into 2 unequal lobes; pollen 7–9-lobate and colpate. . . . . *Meyenia*
3b. Stigma funnelform to ± capitate or equally to unequally 2-lobed; pollen spiraperturate and unlobed 4

4a. Anthers opening by longitudinal slits . . . . . *Thunbergia*
4b. Anthers opening by apical slits or pores . . . . . *Pseudocalyx*

Morphology

Habit.— All Paleotropical species of *Mendoncia* are woody vines (lianas) that climb tens of meters into the canopy by twining. The young stems are subquadrate to quadrate-sulcate in cross-section. Mature stems can reach upwards of 30 mm in diameter, are prominently multi-sulcate, usually twisted, and generally have swollen nodes. Initially, the young stems are glabrous or more or less evenly pubescent with yellowish, straw-colored, or golden-brown, eglandular trichomes; trichomes of the internodes soon become sparse with maturity. Bark is usually smooth to corky and light in color. The wood is soft and corky and contains raphides in the phloem.

Leaves.— Leaves of *Mendoncia* are opposite-decussate and consist of a well-defined petiole and blade. Petioles are glabrous to pubescent and canaliculate. The blades are sometimes membranaceous, but more commonly subcoriaceous to coriaceous. They vary in shape from (lanceolate to) ovate to subdeltate to elliptic to subcircular to oblong to obovate to obcordate, but most often they are ovate to elliptic. The foliar margin is entire to sinuate, and can also be undulate and/or slightly revolute. The adaxial surface is darker green than the abaxial surface. Venation is brochidodromous (i.e., the secondary veins join together toward the margin in a series of prominent arches) with up to 5 orders of veins visible on dried material. The veins are flush with or slightly impressed into the adaxial laminar surface. The midvein and second order veins protrude prominently from the abaxial surface. The axils of the midvein with the secondary veins on the abaxial surface of some of the Malagasy species (especially *M. cowanii*) possess trichomes that form acarodomatia (for mites). Dense trichomes covering the surfaces of any plant may serve as refugia for mites, but there are four basic specialized forms of domatia: pouch, pit, pocket, and tuft types (O'Dowd and Willson 1989). In Malagasy species the domatia conform to the tuft type, and consist of dense tufts of intertwined trichomes in the vein axils (Figs. 2, 10B).

Vesture.—Plants of Paleotropical *Mendoncia* have, almost exclusively, eglandular trichomes on vegetative structures. These trichomes are unbranched (antrorsely appressed to erect to flexuous) and branched (dendritic to stellate) and are unicellular to multicellular. They can occur on most vegetative and reproductive structures. The density of trichomes is variable within species. Leaves vary from glabrous to having one or both surfaces sparsely to densely pubescent with the trichomes sometimes restricted to major veins. Vegetative and reproductive organs may also be "mealy-glandular." This designation refers to the presence of minute (mostly less than 0.5 mm in diameter), sessile glands or whitish pustules that sometimes appear somewhat papillose or mealy with age or on drying.

Inflorescences.— Unlike most Acanthaceae, the inflorescence of *Mendoncia* consists of solitary or clustered (usually up to 10), pedunculate dichasia in the axils of leaves or on older and woody stems, from leafless nodes. Often in *M. flagellaris* the dichasia are borne in the axils of subfoliose bracts on pedunculate, axillary or terminal racemes. Some of the axillary racemes could be interpreted as the terminal portion of an axillary branch with one or two pairs of leaves at the base, and with the subfoliose bracts becoming progressively smaller distally. The dichasia of *M. lindaviana* are somewhat unusual by being arranged in a racemose fashion on woody, peg-like short-

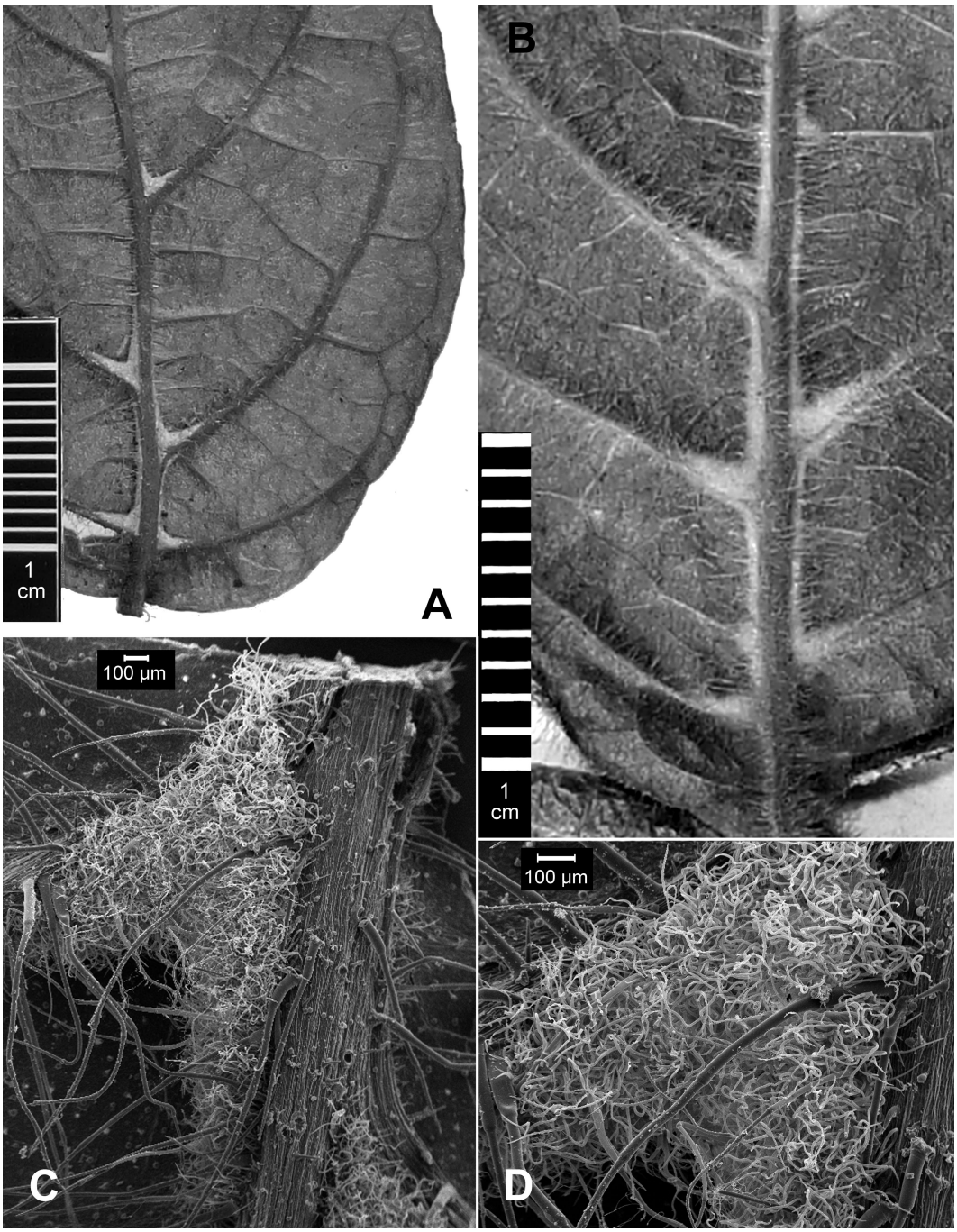

FIGURE 2. Domatia on abaxial surfaces of leaves of *Mendoncia cowanii* var. *cowanii*. A. *Daniels 98*. B. *Daniel et al. 9116*. C, D. Scanning electron micrographs of *Daniel et al. 9116* showing intertwined trichomes in axils of midvein with secondary vein.

shoots from the usually leafless nodes of woody older growth (Fig. 3F, 17D). The short-shoots are sometimes multi-branched with each branch bearing several dichasia per year; thus, over several seasons, 100 or more peduncular scars may be evident on the branched short-shoot in this species. Peduncles of the dichasia are sometimes conspicuously flared at the apex, especially in fruit. Each dichasium generally produces only a single flower (with apparently inactive supernumerary buds at the base of flowers reported by Harshberger (1929) for a Neotropical species). Flowers are sessile to subsessile (or borne on a pedicel to about two mm long, or sometimes longer in fruit) in the axil of two isomorphic, conspicuous, and partially fused bracteoles. The bracteoles are connate when the flower is in bud, become partially free from the apex as the corolla matures, can become entirely free with age, and are either deciduous as the fruit matures or persist (sometimes spreading outward) around the mature fruit. Because the calyx is reduced to a ring of tissue at the base of the corolla, the bracteoles effectively function as an epicalyx that initially encompasses the entire floral bud and eventually subtends the mature flower. The bracteoles in most (if not all) species are filled with a watery fluid before and during anthesis, and thus function much like a "water calyx" (cf. Carlson and Harms 2007). Harshberger (1929) hypothesized that this fluid is secreted by capitate trichomes on the adaxial surface of the bracteoles in a Neotropical species. We observed glandular trichomes on the adaxial surfaces of bracteoles in several species of Paleotropical *Mendoncia*. Water calyces have been reported in several plant families (Endress 1996), and are thought to protect the flower buds from desiccation and/or insect herbivory (Carlson and Harms 2007; Burtt and Woods 1975). Bracteoles are also variously pubescent and colored. Some plants of *M. flagellaris* exhibit a conspicuous pair of bulbous, white protuberances on the proximal portion of the abaxial surface of each bracteole (see discussion below; Figs. 11F and 13C, D). Bracteoles are mostly persistent on fruiting dichasia in some species and nearly always deciduous as the fruit matures in others. Characteristics of the bracteoles have been, and continue to be, of considerable importance in the characterization and identification of species because they are the most common (and often only) "fertile" element present on collections of the genus.

Flowers.— Flowers are sessile or very shortly pedicellate on (or in) the sometimes flaring apex of the peduncle (Fig. 19C). The calyx consists of a shallow, annular or cupular ring mostly one-half to two mm high with the margin entire, five-lobed with broadly triangular lobes, or shallowly and irregularly lobed (sometimes with a single prominent lobe). Although it is somewhat tubular during anthesis, the margin often flares outward and is sometimes conspicuously undulate with age. The abaxial surface varies from glabrous to pubescent. The calyx is often best observed in fruiting plants from which the bracteoles have dehisced. Internal to the calyx (evident after the corolla falls) is a somewhat fleshy or annular nectar disc (Fig. 10F) about two mm high that surrounds the base of the ovary. Corollas consist of a funnelform proximal tube that either gradually or more or less abruptly expands distally into a throat, which sometimes (e.g., *M. combretoides*) narrows toward mouth, and a bilabiate limb (Fig. 3C). The upper lip of the limb comprises two lobes and the lower lip consists of three lobes, the central of which is generally larger than the laterals. The lobes are convolute with left-contort aestivation in bud and are rounded to emarginate at their apices. Corolla color ranges from white to pink to purple, with some white corollas having purplish to pinkish markings on the internal surfaces of the lips and/or throat. Externally, flowers are glabrous. Glandular trichomes can be present on the internal surfaces of the lobes in several species. The androecium consists of four epipetalous stamens that are inserted near the middle of the corolla tube or near where the narrow distal portion of the tube is expanded into the throat. Stamens are didynamous with the pairs nearly equally inserted or with the ventral pair inserted distal to the dorsal pair. They are either included within the throat or partially exserted several millimeters beyond the mouth. Anthers consist of two subequally to unequally inserted, parallel, and lin-

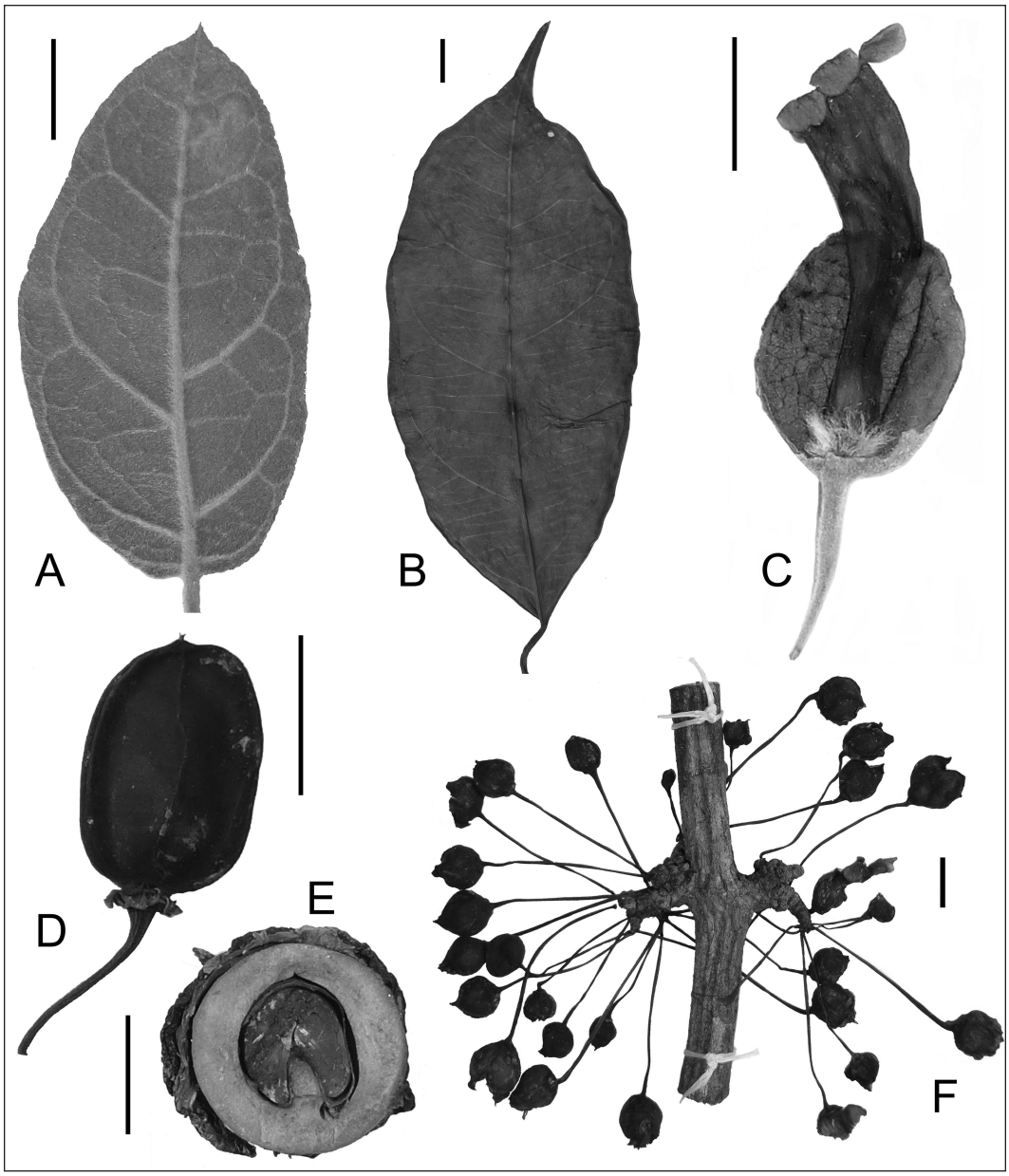

FIGURE 3. Morphological features of *Mendoncia* spp. A. Abaxial leaf surface of *M. cowanii* var. *coursii* (*Rakotonandrasana 485*). B. Abaxial leaf surface of *M. lindaviana* (*Vermoesen 191*). C. Dichasium of *M. cowanii* var. *coursii* (*Rakotonandrasana 485*) with one bracteole removed showing single flower with densely pubescent calyx. D. Oblong drupe of *M. lindaviana* (*Louis et al. 275*). E. Cross-section through dried drupe of *M. vinciflora* (*Lewis et al. 1353*) showing bony seed with embryo. F. Node of older shoot of *M. lindaviana* (*Breteler et al. 8106*) with dichasia borne on branched and woody short-shoots.

ear thecae that are either equal or unequal in size (Fig. 13F). Thecae open by short apical slits or pores and have a tuft of dense, short bristles either restricted to the base or becoming sparse and extending from there distally toward the apex or proximally along the filament. The filaments are short and intergrade with the connective. The connective usually extends up to several millimeters beyond the apex of the thecae. A staminode (rarely two staminodes), usually consisting of a sterile, finger-like projection, and sometimes also with small thecae, may develop between the dorsal (i.e., more proximally inserted) pair of stamens. The gynoecium consists of a bicarpellate, superior ovary, style, and capitate or equally to unequally bilobed stigma. The style and stigma are either included in the throat of the corolla or slightly exserted from the mouth. Anatomical studies on the development of the gynoecium (Schönenberger and Endress 1998) show it to be initially bicarpellate with each carpel containing 2 ovules. Only the abaxial carpel continues to develop, and only one of its ovules develops to maturity.

Fruit.—Fruits of *Mendoncia* are drupes. The only other genus of Acanthaceae to exhibit this fruit type is *Anomacanthus* (see key above). Based on limited observations and images of fresh drupes, they are generally broadly ellipsoid to spherical in shape. Shapes used herein are based exclusively on dried drupes, which vary from ovoid to ellipsoid to oblong to spherical to obovoid. Drupes of *M. gilgiana* have an asymmetrically truncated apex due to the shape of its seed. Six species of Paleotropical *Mendoncia* (*M. combretoides, M. delphina, M. flagellaris, M. gilgiana, M. lindaviana, M. vinciflora*) have glabrous drupes while the remaining four species (*M. kely, M. cowanii, M. decaryi, M. phytocrenoides*) have pubescent drupes. Color of the drupes changes from green to greenish yellow when young to dark purple-black when mature. The single seed is bony, glabrous, and covered with a reticulum of shallow ribs on the external surface (Figs. 3E, 10G, 13I). Being only slightly smaller than the drupe, seeds of *Mendoncia* are among the largest in the Acanthaceae.

Pollen

Examination of pollen from 12 herbarium specimens representing eight of the 10 Paleotropical species (Appendix 1) reveals it to have a polar diameter (P) of 23–38 μm and an equatorial diameter (E) of 23–41 μm. Grains can be described as subspheroidal to spherical (to euprolate) based on a P:E of 0.812–1.186, (4–) 5–6-brevicolpate, and subcircular to subtetragonal to subpentagonal in polar outline (Figs. 4, 5). The number of colpi is sometimes variable within a species (i.e., *M. cowanii*, *M. flagellaris*), but most species studied have some or all grains with five colpi. Four-colpate grains were more common among the four collections of *M. flagellaris* studied; indeed, grains with five apertures might be aberrant in that species (Fig. 5I). Six colpi were observed in two species (e.g., *M. cowanii* and *M. lindaviana*), and the exact number of colpi (either five or six) could not be determined for *M. kely* based on grains observed. Based on the limited samples studied, it is possible that further sampling might reveal additional variation in aperture number for other species. The relatively short colpi are linear (or becoming somewhat tapered at distal ends on swollen grains), 5.6–10.8 μm long (C), and have C:P = 0.17–0.36. The interapertural surfaces are finely rugulate with the rugulae smooth to microrverrucate to microgemmate to microbaculate (Fig. 6). Rugulae of pollen in some samples of *M. gilgiana* and *M. vinciflora* (Fig. 6E) appear smaller and/or less distinct than in other samples of these and other species. Damage to interapertural regions reveals the columellae underlying the tectum (Fig. 6F). In all of these sculptural attributes, pollen of species of *Mendoncia* from the Old World is similar to that of Neotropical species studied to date (e.g., Raj 1961; Daniel 1998 and unpublished observations). Daniel (1998) summarized other sources that have noted 3–6-colporate pollen for *Mendoncia*. Endoapertures, if present, were not visible in the unacetolyzed grains observed in our SEM preparations of Paleotropical species.

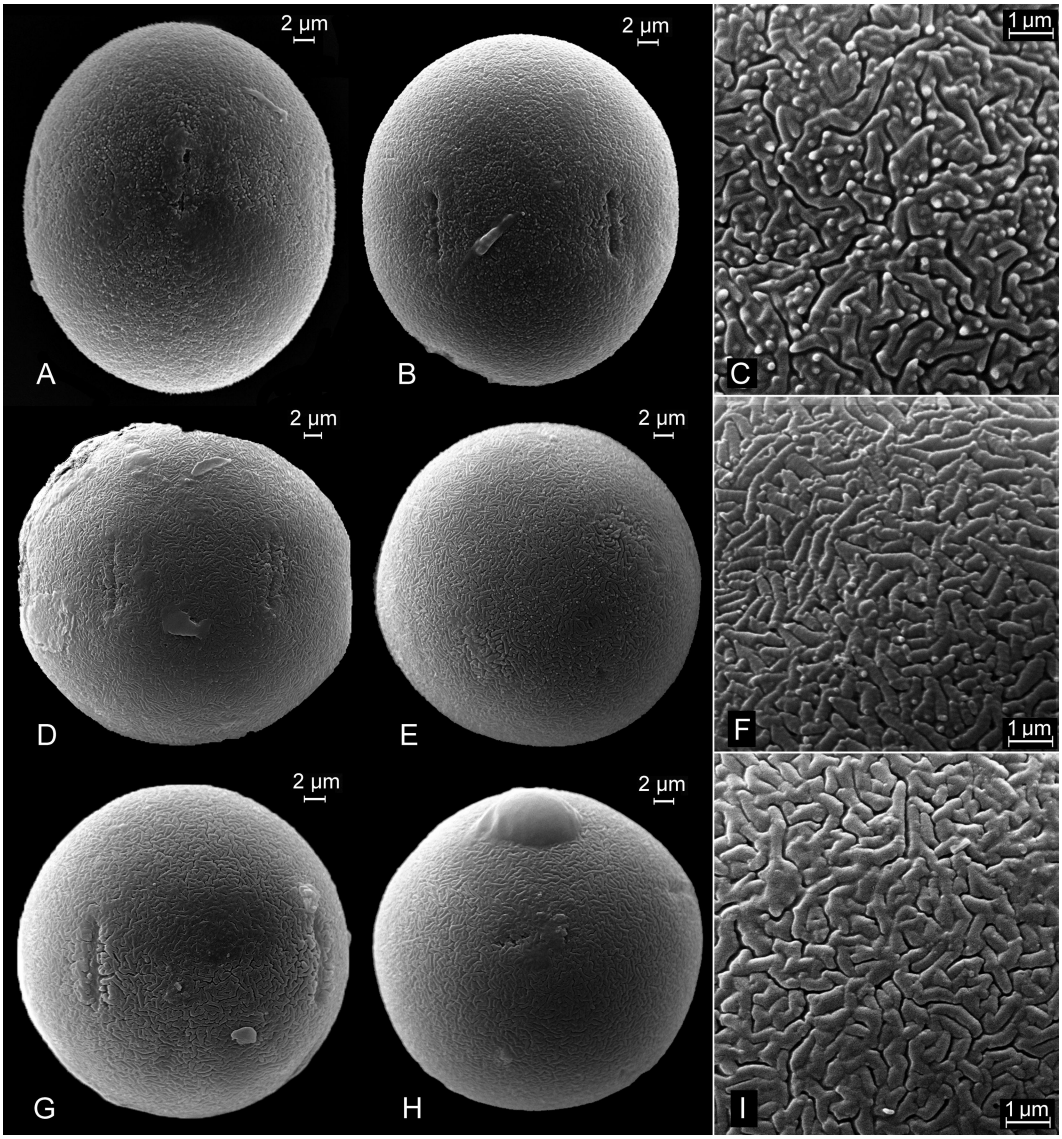

FIGURE 4. Pollen of *Mendoncia* spp. from Africa. A–C, *M. gilgiana* (*Breteler 1834*). A. Apertural view. B. Interapertural view. C. Rugulate (and densely microverrucate to microgemmate to microbaculate) exine. D–F, *M. lindaviana* (*Hladik s.n.*). D. Interapertural view. E. Oblique (or polar?) view. F. Rugulate (and sparsely microverrucate to microgemmate) exine. G–I, *M. phytocrenoides* (*Letouzey 4306*). G. Interapertural view. H. Polar view. I. Rugulate exine with smooth rugulae.

DISTRIBUTION AND HABITATS

Ten species of *Mendoncia* are found across tropical Africa and on the islands of Madagascar and Mayotte in the Indian Ocean. Occurrences of species by country are provided in Appendix 2. In mainland Africa four species (*M. combretoides, M. gilgiana, M. lindaviana, M. phytocrenoides*) range from Liberia and Guinea in the northwest to Kenya in the east and southward to southern Congo-Kinshasa (Figs. 7, 14, 18). Based on the phytochoria of White (1983), all African species and most occurrences of them are in the Guineo-Congolan region, with extensions into the Guinea-

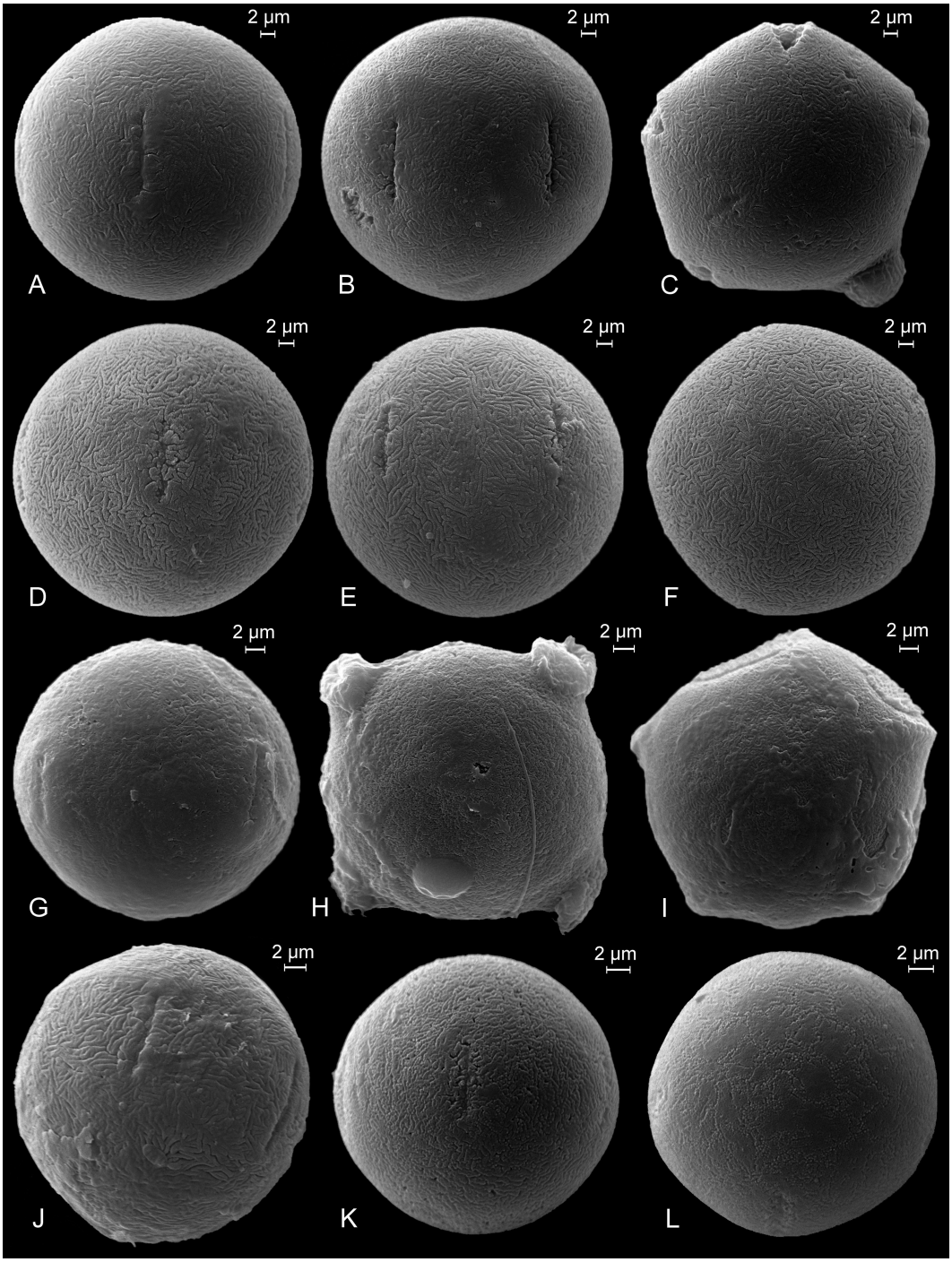

FIGURE 5. Pollen of *Mendoncia* spp. from Madagascar. A–C, *M. cowanii* (*Daniel et al. 11000*). D–F, *M. delphina* (*Malcomber et al. 1665*). G–I, *M. flagellaris*. G. Apertural view (*Daniel et al. 9276*). H. Polar view (4-aperturate grain; *Daniel et al. 9131*). I. Polar view (5-aperturate grain; *Daniel et al. 9239*). J, *M. kely* (*Andrianantoanina et al. 11*). Oblique view. K–L, *M. vinciflora* (*Humbert & Capuron 25734*). K. Apertural view. L. Polar view.

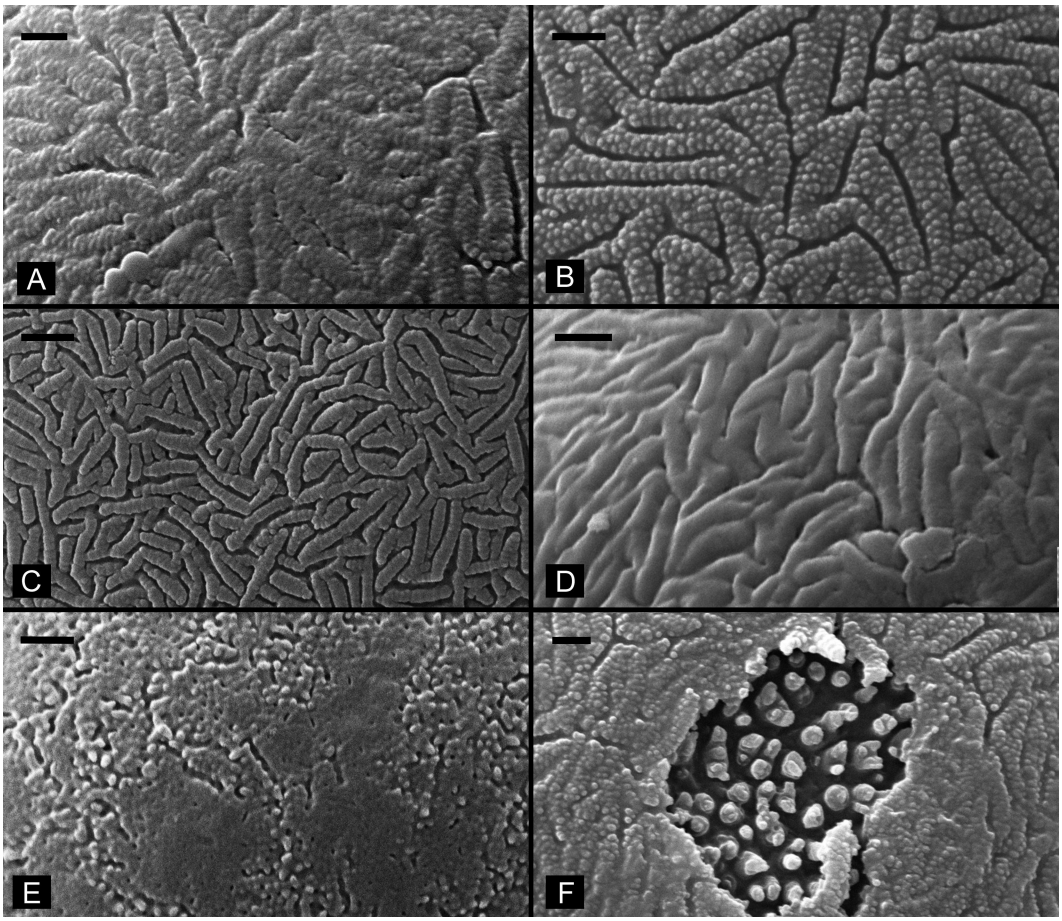

FIGURE 6. Interapertural surfaces of *Mendoncia* pollen from Madagascar. A. *M. cowanii* (*Daniel et al. 11000*), rugulae densely microverrucate to microgemmate. B. *M. delphina* (*Malcomber et al. 1665*), rugulae densely microverrucate to microgemmate. C. *M. flagellaris* (*Guillaumet 4110*), rugulae inconspicuously microverrucate to microgemmate. D. *M. kely* (*Andrianantoanina et al. 11*), rugulae smooth. E. *M. vinciflora* (*Humbert & Capuron 25734*), rugulae ± indistinct and densely microverrucate to microgemmate to microbaculate. F. *M. cowanii* (*Daniel et al. 11000*), tectum damaged and revealing underlying columellae. Scales = 1 μm.

Congolia/Zambezia, Guinea-Congolia/Sudania, and Lake Victoria regions. Habitats include primary and secondary, lowland to montane, moist to wet, semi-evergreen to evergreen forests; gallery and swamp forests; secondary bush; forest edges; roadside thickets; and grass fields. Plants occur at elevations from 60–1600 meters. *Mendoncia gilgiana* is the most widely distributed species of the genus in Africa, where it has an extent of occurrence (EOO; IUCN 2016) of 4,487,300 km^2 and occurs in 14 nations, whereas *M. combretoides* is the most geographically restricted, known from five nations of western Africa, and has an EOO of 565,420 km^2. We note intraspecific disjunctions of 800 km or more in the known occurrences of *M. combretoides*, *M. gilgiana*, and *M. phytocrenoides* in Africa. *Mendoncia gilgiana*, *M. lindaviana*, and/or *M. phytocrenoides* are sympatric in various parts of their ranges. *Mendoncia combretoides* occurs either sympatrically with, or within five to 10 kilometers of, *M. gilgiana*. The co-occurrences of continental African species is likely attributable to common habitat preferences.

All six species endemic to Madagascar occur primarily or exclusively in the lowland and mon-

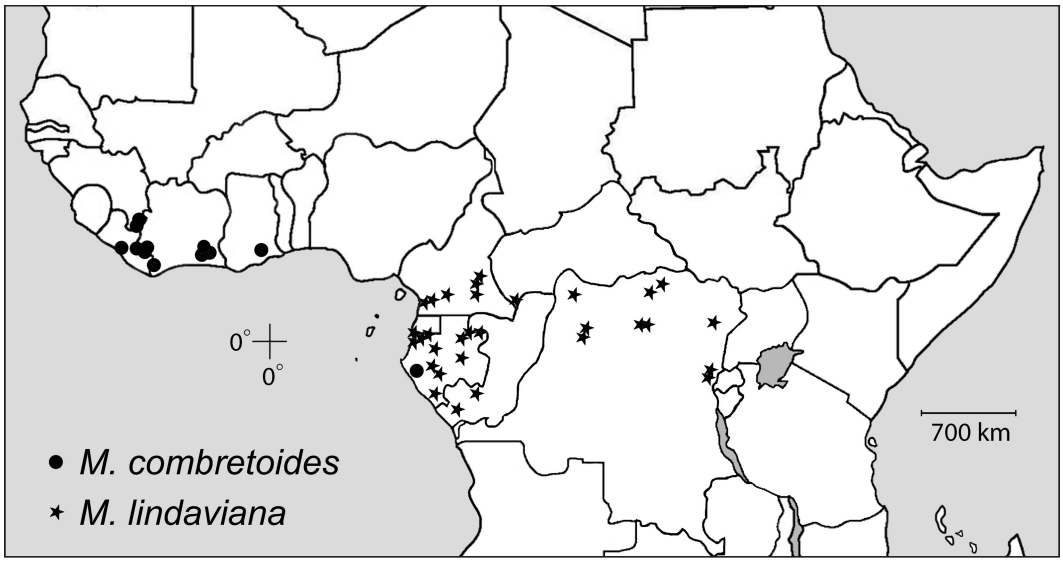

FIGURE 7. Map of central Africa showing distributions of *Mendoncia combretoides* and *M. lindaviana*.

tane regions in the eastern and northern portions of the island. They occur in primary and secondary (sometimes degraded), moist to wet evergreen forests (cf. perhumid, humid, and subhumid forests of Schatz and Rasolohery 2007); gallery forests; dry deciduous forests; coastal forests; and forest clearings and margins. Plants occur at elevations ranging from 5 to 2100 meters. *Mendoncia flagellaris* (EOO = 458,376 km^2) is the most widely distributed species in Madagascar; it also occurs about 350 km to the west-northwest of the nearest occurrences on Madagascar in wet montane forests on the island of Mayotte in the Comoros Archipelago. *Mendoncia delphina* has the most restricted distribution (EOO = 134 km^2) in Madagascar. Among Malagasy species of the genus, the only major intraspecific disjunction (more than 1000 km) is noted for *M. kely*. Like their African congeners, and probably due to similar habitat preferences, sympatry is not uncommon among Malagasy species. The ranges of *M. cowanii* and *M. flagellaris* overlap throughout wet forests in the provinces of Antsiranana, Antananarivo, Fianarantsoa, Mahajunga, Toamasina, and Toliara; and they often occur together. On the northern half of the island, these two species also occur with *M. vinciflora, M. kely*, and *M. decaryi*. In the south, they occur with *M. kely* and *M. delphina*. Because mainland Africa and Madagascar do not share any species, the six species endemic to Madagascar would appear to represent either paleoendemics that have since gone extinct on the continent or a radiation of taxa following one or more dispersal events to that island. It is noteworthy that all of the Malagasy taxa occur to the south of all African species.

REPRODUCTIVE BIOLOGY

Very little is known about the flowering periods, floral biology, or dispersal among species of *Mendoncia*. To better understand the ecological relationships of the Paleotropical species, we recorded flowering periods from herbarium specimens; made field observations, collected data and samples, and recorded information from herbarium specimens and literature on various aspects of the floral biology of *M. cowanii*; and reviewed literature for information on dispersal in the genus.

FLORAL PHENOLOGY.— In both Africa and Madagascar, species of *Mendoncia* occur in regions of tropical moist to wet forests that exhibit some degree of seasonality with respect to pre-

cipitation. The known months of flowering and fruiting for each taxon have been derived primarily from herbarium specimens, and the periods for both are summarized in the accounts below. Flowering periods are also shown in Table 1. Fruiting sometimes occurs simultaneously with flowering and continues after flowering has ended, or appears to occur only after flowering has ceased. Although wet vs. dry seasonality is somewhat complicated in tropical Africa due to a seasonal reversal on each side of the equator and local conditions, in general, to the north of the equator, the wet season occurs between March and November and a dry season occurs sometime between November and April. The three species that occur on both sides of the equator (*M. gilgiana*, *M. lindaviana*, and *M. phytocrenoides*) flower throughout the year. All studied collections of *Mendoncia combretoides* with flowers were collected north of the equator; they flower only during the wet season. The shorter (and more restricted) flowering period known for the latter species may be, at least partially, an artifact of fewer collections of it, and none in flower from south of the equator.

TABLE 1. Flowering periods of Paleotropical species of *Mendoncia*.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
M. combretoides			X	X	X	X	X	X				
M. cowanii		X	X	X	X	X	X	X	X			
M. decaryi		X	X	X								
M. delphina										X	X	
M. flagellaris	X	X	X							X	X	X
M. gilgiana	X	X	X	X	X	X	X	X	X	X	X	X
M. kely	X	X										
M. lindaviana	X	X	X	X	X	X		X	X	X	X	X
M. phytocrenoides		X	X	X	X	X	X	X	X			
M. vinciflora	X	X	X	X								X

In general for Madagascar, a rainy season occurs from December through March, and a dry season occurs from April through October. At least five of the Malagasy species of *Mendoncia* are known to flower during the rainy season, and four of them (*M. decaryi*, *M. flagellaris*, *M. kely*, and *M. vinciflora*) almost exclusively so. Although *M. cowanii* begins to flower in the latter half of the rainy season (with peak flowering near the end of the wet period), it continues to flower throughout the dry season. *Mendoncia delphina* is only known with flowers at the end of the dry season/beginning of the wet season. Perhaps only two Malagasy species, *M. cowanii* and *M. flagellaris*, are known from sufficient collections to accurately portray their flowering periods, which only partially overlap. These two species are sympatric throughout much of their respective ranges, and based on our field observations over several years in different seasons at sites of sympatry, only one of them is in flower at a time. It would be useful to study whether they rely on different seasonal pollinators/dispersers or whether the year-round production of flowers/fruits by the two species together helps to provide year-round sustenance for one or more common pollinators/dispersers.

FLORAL BIOLOGY.— Flowers of *Mendoncia* have funnelform corollas that are white to pink to purple to scarlet, sometimes with colored markings or nectar guides; anthers are included in the corolla tube or partially exserted from the mouth of the corolla; and the style/stigma is often exserted from the corolla tube, as well. This morphology and architecture suggests bee-, butterfly-, and/or

bird-pollination. Several authors report visitors to flowers of Brazilian species: hummingbirds to flowers of *M. velloziana* Mart. (e.g., Buzato 1990; Buzato et al. 2000; Braz et al. 2000; Abreu and Vieira 2004), and euglossine bees to flowers of *M. puberula* Mart. (Buzato 1990). We did not locate any published information on floral visitors and/or pollinators to Paleotropical species of *Mendoncia*. Here, we summarize and contribute data on various aspects of floral biology, primarily for the Malagasy endemic, *M. cowanii*.

We made observations and conducted studies of *M. cowanii* in Madagascar during 1–3 March, 2007 at Toamasina: Mantadia National Park (18°49′44.20″S, 048°25′58.70″E to 18°49′16.36″S, 048°26′8.05″E; *Daniel et al. 11000*, CAS, TAN), and on 6 March, 2007 at Fianarantsoa: Ranomafana National Park (21°15.73′S, 47°25.30′E; *Daniel et al. 11002*, CAS). Vegetation at both sites consists of moist to wet, evergreen forest at mid-elevations (ca. 975 meters at Mantadia and ca. 900 meters at Ranomafana). At the Mantadia site, a one kilometer transect was established along a road and flowers were tagged and observed over the three-day period at four sites along this transect. Ten large, unopened flower buds were tagged each day for two days. These flowers were monitored two to four times throughout daylight hours over the course of two to three rainless days, until all 20 flowers had withered or dehisced. Tagged flowers, which were accessible from the ground, were monitored and observed (with a hand-lens when needed) for time of corolla opening, presence of pollen on stigma, presence of pollen on corolla limb, visitation, changes in coloration, presence/absence of nectar and bracteolar fluid, and time of withering/dehiscence. Floral visitation was also observed for additional flowers in the forest canopy using binoculars. Additional flowers were tested for nectar volume and sucrose concentration. Nectar volume (standing crop) and percent sugar (sucrose equivalents) in the nectar were measured using 55 mm micropipettes and a calibrated pocket refractometer (Burlington + Stanley "Eclipse," model 45-03), respectively. Insects were collected using a net and stored in alcohol or pinned.

The dark pink flowers of *Mendoncia cowanii* at Mantadia are nocturnal and diurnal, open between sunset and sunrise (between 17:00 and 06:00), and persist up to between 25 and 30 hours prior to withering (or turning completely brown) or dehiscing. Floral rewards include nectar, pollen, and possibly bracteolar fluid. After visitation by insects, the limb of the corolla (with the lips/lobes at least partially reflexed; Fig. 11B) becomes discolored with whitish markings, which eventually turn brown, as does most of the limb when it eventually withers. This discoloration is not necessarily an indication of pollination, but often corollas with the whitish discoloration on the dark pink limb also had pollen present on the stigma and/or the limb. As the flowers are showy and open all day, multiple visits may occur to them, with or without simultaneous pollination.

Nineteen flowers (15 at Mantadia and four at Ranomafana) were sampled on the day the corollas opened between 06:00 and 15:30 for quantity and quality of nectar. Nectar varied in quantity from 0 to 32.3 µl (mean = 7.4, standard deviation = 9.61). Of the six samples lacking measurable nectar, one was from a shaded area, had slight discoloration of the corolla limb, and had pollen on the stigma; another one was from a sunny site, had no discoloration of the corolla limb, and had not been pollinated; and similar observations were not recorded for the other four. The percent sucrose concentration (corrected for ambient temperatures) of the 13 nectar samples taken at irregular intervals between 06:00 and 15:30 ranged from 20.70 to 31.11 (mean = 26.77, standard deviation = 2.58). There did not appear to be any noticeable correlation between either nectar quantity or quality with respect to temperature or time of collection, but the sampling was inadequate to state this with any confidence.

Bracteolar fluid is abundant when flowers are in large bud (ca. 8 mm long) and at least during the early stages of the fully open corolla, but absent when buds are smaller (ca. 2 mm long) and generally by the time the flower, whose base it engulfs, dehisces. Two samples of the watery fluid

from bracteoles bearing large (9.5 to 11 mm long) buds, revealed it to be tasteless, odorless, and colorless; vary in quantity from 2.2 to 2.8 ml (an additional sample from Ranomafana had 2.6 ml of bracteolar fluid); and contain no detectable sucrose. Further chemical analysis of this plant-secreted fluid should be undertaken to reveal any antimicrobial, antifungal, or electrolytic properties, at least the former of which has been reported for secreted fluid in pitchers of *Nepenthes* (Buch et al. 2013). As a potential floral reward, the fluid may be obtained by a floral visitor via probing between the partially fused bracteoles and the corolla. Secondarily, it may be an alternative source of water for birds and other animals, and in turn an attractant for potential pollinators.

The most common visitors we observed on the floral/bracteolar unit (i.e., the single-flowered dichasium) were at least two species of passerine birds, possibly *Neomixis* sp. (either Common Jery or Green Jery), or *Newtonia* sp. (either Common Newtonia or Dark Newtonia), and *Nectarinia souimanga* (Souimanga Sunbird). Ten sightings of visits from two to five seconds for each flower were recorded during daylight hours over two days. The sunbird was observed probing within the flowers and bracteoles possibly foraging for nectar and/or bracteolar fluid, respectively. The second most common floral visitors were Lepidoptera with six observations over the two days. Butterflies and/or moths were observed probing the corolla tube and alighting on the lower lip for periods of three to 20 seconds per flower. Other floral visitors consisted of a solitary bee (*Thrinchostoma* sp.), which perched on and probed in the corolla tube; a dipteran (hover fly), which alighted on the limb of the corolla; and two genera of ants (*Crematogaster* sp. and *Paratrechina* sp.), which were seen inside and outside the corolla tube and along nearby stems. Effective pollinators remain undocumented for flowers of *M. cowanii*, but likely include at least some of the floral visitors noted above.

Of 18 flowers (14 at Mantadia and four at Ranomafana) monitored for evidence of pollination (i.e., pollen on stigma), 11 (61%) were pollinated, 6 (33%) were not, and one (6%) was questionable as to whether pollen was present or absent. All 18 flowers had clean stigmas and no discoloration of the limb when first observed in the early morning after the corollas opened. For those pollinated, both pollination and limb discoloration (likely indicating visitation) took place within three to six hours. Interestingly, two flowers that were not pollinated and had no discoloration of the limb, had pollen on the limb within three hours after sunrise. Autogamy, if present, would not appear to be pervasive; examination of five flowers from which the corollas had recently fallen revealed that none had pollen on the stigma. In the flowering population at Mantadia, young (green) fruits were evident at various stages of development.

Flowers of *M. flagellaris*, which differ from those of *M. cowanii* by their smaller corollas that are mostly white with purplish markings on the limb, were noted to be visited by unidentified hymenoptera according to the label of *Birkinshaw 48*.

Dispersal.— Plant taxonomists and primatologists have noted herbivory and frugivory of species of *Mendoncia* by lemurs in Madagascar (e.g., *Birkinshaw 127,* specimen label; *Daniels 98,* specimen label; Dew and Wright 1998; Tan 1999). In their summary of the literature on food plants of lemurs, Birkinshaw and Colquhoun (2003) noted frugivory for *Mendoncia* by six species of lemurs. Lemurs are relatively abundant in the moist to wet forests of northern and eastern Madagascar where most species of *Mendoncia* occur. It remains unclear whether lemurs are effective seed dispersers, but because whole seeds of *Mendoncia* have been found in their dung (Dew and Wright 1998), effective dispersal by these primates would appear possible. Other potential dispersers of *Mendoncia* fruits/seeds include fruit bats and frugivorous birds in both Africa and Madagascar, and frugivorous primates in Africa.

Taxonomy

Taxonomy of Paleotropical *Mendoncia* has been (and remains to some extent) imperfectly resolved due to extensive variation in the characters traditionally used to distinguish species (e.g., pubescence, and size and shape of bracteoles and drupes) and the absence of sufficient flowering collections to fully characterize flowers in several taxa (e.g., *M. combretoides*, *M. cowanii* var. *coursii*, and *M. decaryi*). In the absence of comprehensive molecular phylogenetic studies of the genus, the following taxonomic account makes use of a morphological species concept, which uses suites of macro- and micro-morphological characters to delimit species.

Mendoncia Vell. ex Vand., *Fl. Lusit. Brasil*. 43. 1788. **Lectotype** (designated by Leonard 1951).— *M. aspera* Ruiz et Pav. (as "*Mendozia aspera*").

Engelia Nees in Alph. de Candolle, *Prodr*. 11:721. 1847. **Lectotype** (designated by Leonard 1951).— *E. tovarensis* Klotzsch. & H. Karst. ex Nees.

Monachochlamys Baker, *J. Linn. Soc., Bot*. 20:217. 1883 ("1884"). **Type**.— *M. flagellaris* Baker.

Afromendoncia Gilg ex Lindau, *Bot. Jahrb. Syst*. 17:111. 1893. **Type**.— *A. lindaviana* Gilg ex Lindau.

Lirayea Pierre, *Bull. Mus. Hist. Nat. (Paris)* 2:341. 1896. **Type**.— *L. floribunda* Pierre.

Lianas. Young stems subquadrate to quadrate-sulcate, glabrous or pubescent with eglandular, branched (stellate and dendritic) or unbranched trichomes. Leaves (membranaceous to) subcoriaceous to coriaceous, petiolate, petioles glabrous or pubescent, blades (lanceolate to) ovate to subdeltate to elliptic to subcircular to oblong to obovate to obcordate, surfaces somewhat discolorous (darker green adaxially than abaxially), glabrous or sparsely to densely pubescent with eglandular trichomes, especially along midvein, margin sometimes ± revolute. Inflorescences of 1–10 (–20), pedunculate, 1-flowered dichasia borne in axils of leaves on young, herbaceous shoots (most species) or at leafless nodes on older woody stems (i.e., *M. lindaviana* and *M. phytocrenoides*) or in axils of subfoliose bracts on axillary or terminal racemes (i.e., often in *M. flagellaris*); flowers sessile or short-pedicellate in axil of 2 isomorphic bracteoles. Bracteoles opposite, sessile, (lanceolate to) ovate to elliptic to subcircular to oblong to obovate, rounded to acute and often apiculate at apex, truncate to rounded to subcordate at base, sometimes with a pair of prominent, bulbous, white protuberances basally (i.e., *M. flagellaris*) on the abaxial surface, bracteolar pair at least partially connate and filled with watery fluid through most of anthesis in most (or all?) species. Calyx a rigid, entire or variously lobed (sometimes with a single prominent lobe, and/or irregularly and shallowly multi-lobed), often undulating, annular or cupular ring surrounding a ± fleshy nectar disc (evident after corolla dehisces). Corolla funnelform, white, white with purple spots, pink, or purple, glabrous (or inconspicuously mealy-glandular) on external surface, glabrous or with glandular trichomes on internal surface of throat, tube ampliate distally into a throat, which sometimes (e.g., *M. combretoides*) narrows toward mouth, limb bilabiate with upper lip 2-lobed, lower lip 3-lobed, lobes convolute (left-contort) in bud, entire to emarginate at apex. Stamens 4, didynamous, inserted near the middle of corolla tube, included or barely exserted from mouth of corolla, anthers bithecous, thecae linear, subequally to unequally inserted, parallel, densely pubescent at least at base with a tuft of pointed or papilla-like bristles, dehiscing by apical pore or slit, connective usually extending 0.2–3 mm beyond apex of thecae, 1 (–2) staminode(s) often present. Pollen (4–) 5 (–6)-brevicolpate, interapertural surfaces rugulate. Ovary situated on a prominent, ± fleshy or annular nectar disc, style included in or exserted from mouth of corolla, stigma equally to subequally 2-lobed or ± capitate. Drupes (when dry) ovoid to ellipsoid to oblong to spherical to obovoid, glabrous or pubescent, 1-seeded. Seed bony, generally shaped like and slightly smaller than drupe.

A genus of about 90 species occurring primarily in the Neotropics, but with 10 species in tropical Africa, Madagascar, and on the island of Mayotte in the Comoros Archipelago. The generic description is derived exclusively from the Paleotropical species.

Key to Paleotropical Taxa of *Mendoncia*

(see Appendix 3 for regional keys to taxa in Africa and Madagascar/Mayotte)

1a. Young stems, petioles, peduncles, and abaxial surface of bracteoles pubescent with at least some branched (stellate to dendritic) trichomes; Africa 2

1b. Young stems, petioles, peduncles, and abaxial surface of bracteoles glabrous or pubescent with unbranched trichomes only; Africa and Madagascar. 3

2a. Inflorescences borne in leaf axils on young, mostly herbaceous, leafy stems; corollas 17.5–22 mm long; style 16–18 mm long; drupes mealy-glandular (lacking elongate trichomes); leaves 44–133 mm long and 23–86 mm wide . . . . . *M. combretoides*

2b. Inflorescences mostly borne at naked nodes on older, woody, leafless stems; corollas 29.3–31.8 mm long; style 22.8–27 mm long; drupes pubescent with eglandular trichomes to 0.6 mm long; leaves 86–200 mm long and 57–114 mm wide . . . . . *M. phytocrenoides*

3a. Inflorescences mostly borne on peg-like, woody, sometimes branched short-shoots at naked nodes on older, woody, leafless stems; drupe oblong (symmetrical); Africa . . . *M. lindaviana*

3b. Inflorescences borne in leaf axils on young, mostly herbaceous, leafy stems; drupe variously shaped, but rarely oblong (asymmetrical or symmetrical); Africa and Madagascar. 4

4a. Ovary and drupe glabrous or mealy-glandular (i.e., with inconspicuous, sessile glands mostly < 0.05 mm in diameter), lacking elongate, eglandular trichomes; calyx glabrous or sparsely pubescent 5

4b. Ovary and drupe pubescent with elongate, eglandular trichomes; calyx usually densely pubescent 8

5a. Bracteoles mostly persistent in fruit, usually pubescent with trichomes up to 3 mm long; drupe 6.8–11.8 mm long, ± irregularly shaped (overall obovoid) and widest at or just below the truncate to shallowly acute (symmetrically or asymmetrically) apex; Africa . . . . . *M. gilgiana*

5b. Bracteoles mostly deciduous in fruit, if pubescent, then with trichomes up to 1.2 mm long; drupe 9.5–30 mm long, variously shaped and sometimes obovoid, but not as described above; Madagascar. 6

6a. Corollas pink or light to dark purple, 20–35 mm long, upper lip 10–17 mm long; bracteoles usually lacking dense pubescence at apex of adaxial surface; extension of connective beyond anther thecae pubescent with glandular and eglandular trichomes 0.1–0.3 mm long; drupe subspherical to spherical, 14.8–25 mm in diameter; northern Madagascar. . . . . *M. vinciflora*

6b. Corollas white and usually with purple markings near base of limb and/or throat (rarely purplish in *M. delphina*), 8–18.5 mm long, upper lip 2–12.5 mm long; bracteoles with dense pubescence at apex of adaxial surface; extension of connective beyond anther thecae (if present) glabrous to minutely glandular; drupe ovoid-ellipsoid to ellipsoid to spherical to obovoid, 6–15.7 mm in diameter; widespread 7

7a. Dichasia 1–2 in axils of leaves; apex of leaf blade acuminate to caudate, with tail-like apex to 12 mm long; bracteoles yellowish, lacking a pair of conspicuous, whitish, bulbous, gall-like basal protuberances; pollen 5-aperturate; southern Madagascar . . . . . *M. delphina*

7b. Dichasia 1–4 (–8) in axils of leaves or commonly in axils of bracts in an a raceme to 15 cm long; apex of leaf blade (acuminate) to acute to rounded to truncate to retuse, and sometimes with an apiculum to 1.6 mm long; bracteoles green, often with a pair of conspicuous, whitish, bulbous, gall-like basal protuberances; pollen mostly 4-aperturate; widespread. . *M. flagellaris*

8a. Corollas 13.2–19 mm long, tube 10–14 mm long; leaf blades mostly with length:width 1.4–1.7 . . . . . *M. kely*

8b. Corollas 26–49 mm long, tube 20–38; leaf blades mostly with length:width 1.7–2.8. 9

9a. Corollas white with purplish markings, limb 20.6–32.4 mm in diameter, upper lip 13.5 mm long with lobes 8–10 mm long and 11.2–13.2 mm wide, lower lip 16.5–19 mm long with lobes 9.4–13.5 mm long and 12.2–15.2 mm wide. . . . . *M. decaryi*

9b. Corollas light pink to dark pink (sometimes whitish externally), limb 6–21 mm in diameter, upper lip 1.8–10 mm long with lobes 1.8–7.4 mm long and 3.7–8.6 mm wide, lower lip 3–12.4 mm long with lobes 2.2–7.5 mm long and 3.4–9.1 mm wide. 10

10a. Young stems, petioles, abaxial surfaces of leaf blades and bracteoles, and peduncles subglabrous and/or pubescent with erect to flexuose to antrorse trichomes, underlying surfaces plainly visible; corolla with upper lip 4.4–10 mm long and lobes of lower lip 3.5–7.5 mm long and 3.5–9.1 mm wide . . . . . *M. cowanii* var. *cowanii*

10b. Young stems, petioles, abaxial surfaces of leaf blades and bracteoles, and peduncles densely pubescent with flexuose-interwoven trichomes such that underlying surfaces not visible (or only partially so on abaxial surface of leaf blades); corolla with upper lip 1.8–3.6 mm long and lobes of lower lip 2.2–3.3 mm long and 3.4–3.5 mm wide . . . . . *M. cowanii* var. *coursii*

1. *Mendoncia combretoides* (A. Chev.) Benoist, *Notul. Syst. (Paris)* 11:143. 1944. *Thunbergia combretoides* A. Chev., *Explor. Bot. Afrique Occ. Franç*. 1:490. 1920. **Type**.— IVORY COAST. **Bas Sassandra**: bassin du Cavally, pays des Tépos, village de Grabo, [ca. 04°55′02.14″N, 007°29′35.69″W], 4 Aug 1907, *Chevalier 19745* (lectotype, designated here: P-00435313-photo!; isolectotypes: P-00435314!, P-00435315-photo!).

Young stems evenly and densely pubescent with yellowish- to golden-brown, mostly branched (sometimes also with some unbranched and antrorse) trichomes 0.2–1 mm long, trichomes of internodes soon becoming sparse to nearly glabrous. Leaves subcoriaceous to coriaceous, petioles to 25.4 mm long, pubescent with cauline type trichomes, blades ovate to elliptic to obovate-elliptic, 44–133 mm long, 23–86 mm wide, rounded to truncate to subcordate at base, acuminate to acute-apiculate to rounded to slightly emarginate at apex, abaxial surface pubescent with scattered, branched trichomes 0.2–0.4 mm long, trichomes often restricted to major veins, adaxial surface glabrous to sparsely pubescent with branched trichomes 0.2–0.4 mm long and unbranched, antrorsely appressed trichomes to 1 mm long, trichomes usually restricted to midvein. Inflorescences borne in leaf axils on young, mostly herbaceous and leafy stems, solitary or opposite at nodes, dichasia 1–4 (–6) per axil, peduncles to 23 mm long, pubescent like young stems. Bracteoles yellowish brown to pale green, mostly persistent in fruit, elliptic to ovate-elliptic, 15–21 mm long, 7–13 mm wide, rounded at base, acute-apiculate at apex, abaxial surfaces densely pubescent with cauline type trichomes (sometimes becoming sparse to nearly absent on older bracteoles), adaxial surface glabrous or mealy-glandular. Calyx mealy-glandular and sometimes with sparse branched trichomes like those of young stems. Corolla white, 17.5–22 mm long, externally glabrous (or minutely mealy-glandular), tube 17–18 mm long, internally pubescent at base of stamens with glandular trichomes 0.2–0.5 mm long, limb 6.5 mm in diameter, lower lip ca. 4 mm long. Stamens not seen. Style 16–18 mm long, glabrous to minutely glandular, stigma subcapitate to subequally 2-lobed, lobes 0.1–0.4 mm long. Drupe ovoid to ± ellipsoid to obovoid, 16–19 mm long, 10–15 mm in diameter, surface glabrous to mealy-glandular.

Phenology.— Flowering: May–August; fruiting: February, August–November.

Distribution and habitats.— Tropical western Africa (Gabon, Ghana, Guinea, Ivory Coast,

Liberia; EOO = 565,420 km^2; Fig. 7). Plants occur in lowland and montane, moist to wet, evergreen forests; secondary forests; gallery forests; swamp forests; and grass fields. Elev. 100–850 m. Occurrence of plants is higher in forests where rainfall is between 1500–2500 mm/yr (Holmgren et al. 2004).

Illustration.— Fig. 8.

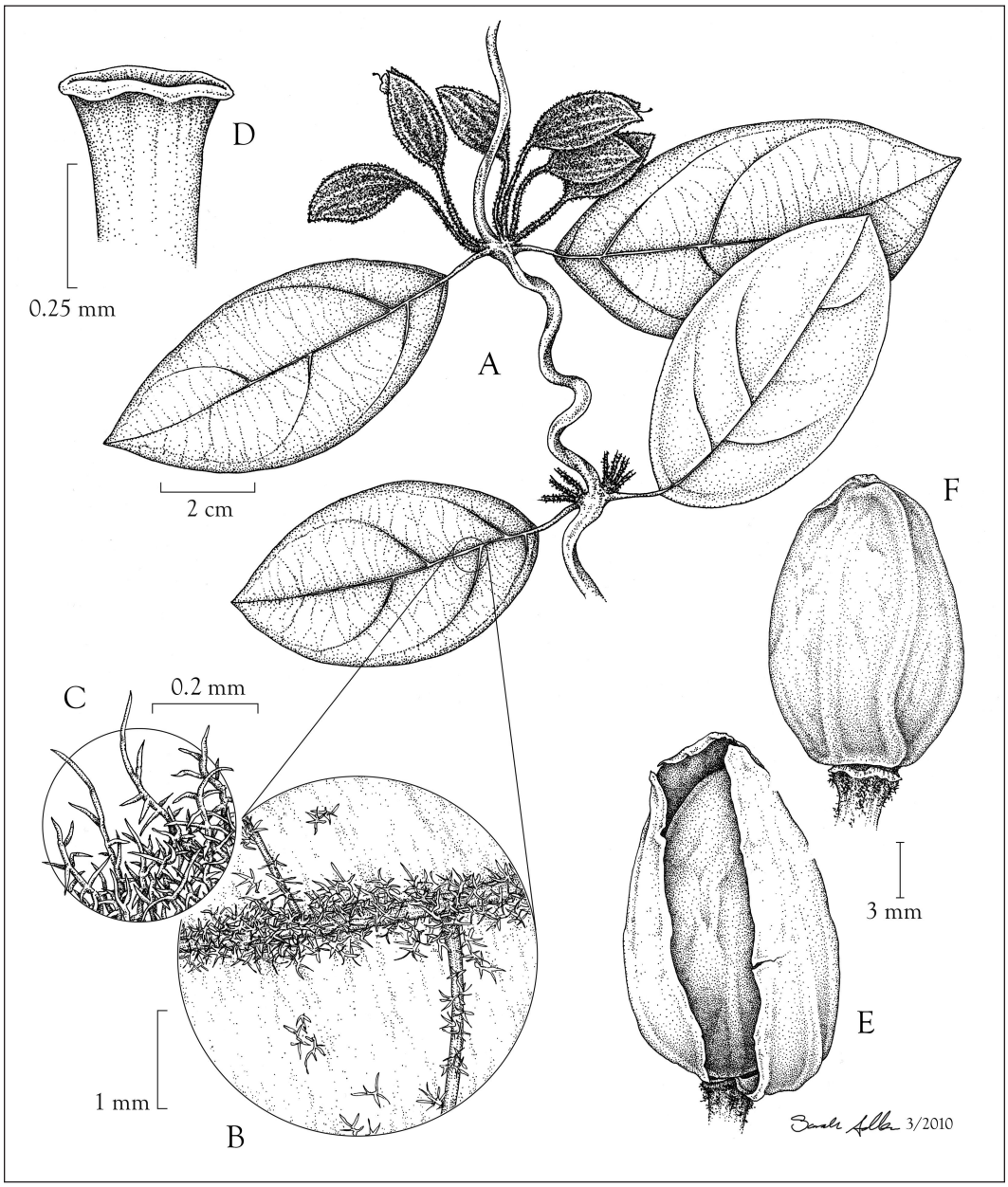

Figure 8. *Mendoncia combretoides*. A. Habit (*Chevalier 19600*, habit; *Jansen 2556*, inflorescence). B. Portion of midvein and secondary veins on abaxial surface of leaf (*Jansen 2556*). C. Enlargement of trichomes on midvein of abaxial surface of leaf (*Jansen 2556*). D. Apex of style and stigma (*Jansen 2556*). E. Drupe with persistent bracteoles (*Adam 24131*). F. Drupe with bracteoles removed (*Adam 24131*). Drawn by Sarah Adler.

Chevalier (1920) listed two of his collections, *19600* and *19745,* in the protologue. *Chevalier 19745* (P-00435313) is here designated as the lectotype based on the descriptive notes found on the specimen label.

Lock & Hall GC 44752 from Ghana differs from most other collections by the acute to subattenuate bases of the leaf blades. *McPherson 15543* from Gabon was identified as *M. gilgiana* by Vollesen. A duplicate of this collection at K was annotated by Breteler as an undescribed new species, "*M. rabiensis* Breteler." Using the keys to species herein, this collection conforms very nicely to *M. combretoides* (e.g., branched trichomes on young stems, petioles, peduncles, and abaxial surface of bracteoles; inflorescences borne at nodes of younger, leafy stems, etc.), but was collected beyond the currently known distributional range of that species. It differs from most collections of *M. combretoides* only in the relative sparseness of the branched trichomes and the somewhat narrower leaves. However, similarly narrow leaves are known among *M. combretoides* in western Africa (e.g., *Chatelain & Téhé 9366* from Ivory Coast), and *M. gilgiana* shows similar variation in leaf form. *McPherson 15543* is a fruiting collection that lacks flowers; thus, its ultimate identity should be reevaluated when flowers are available. However, based on the preponderance of characters available, it seem reasonable to treat this collection as *M. combretoides*, and a range extension of ca. 1470 kilometers to the southeast of its nearest known occurrence in Ghana.

Additional specimens examined.— GABON: **Ogooue-Maritime**: near Rabi, Shell Oil camp, 01°55′S, 009°55′E, *McPherson 15543* (K, MO). GUINEA. **Lola**: Nimba Mountains, Gouan Valley, 07°41.4′N, 008°22.9′W, *Jongkind et al. 8377* (FHO, MO). GHANA. **Eastern**: Atewa Range Extension F.R., [ca. 06°08′07.11″N, 000°37′12.27″W], *Lock & Hall GC 44752* (K). IVORY COAST. **Agnebi**: Forêt de Yapo, *Aké Assi s.n.* (MO); Agboville, Forêt de la Mamo, 05°44′N, 004°06′W, *Chatelain & Téré 712* (G); Réserve du Yapo [ca. 05°43′23.60″N, 004°05′41.47″W], *Cremers 556* (P); Agboville, S part of Yapo Forest, ca. 05°51′N, 004°08′W, *de Kruif 688* (CAS); KM 9 of Yakassé–Mé-Kodiousou road [05°49′N, 03°54′W], *Leewenberg 8042* (K, MO); Sous-prefecture, Azaguié, Forêt de Yapo, 05°44′N, 004°08′W, *Téré 1955* (G); Agboville, Forêt de Yapo, 05°45′N, 004°10′W, *Téré 2528* (G). **Bas Sassandra**: bassin du Cavally, pays des Tépos, entre Nékaougnié et Grabo, *Chevalier 19600* (K, P-00435310-photo only; P-00435311-photo only; P-00435312). **Lagunes**: 9 km W of Bécédi [ca. 05°37′53.49″N, 004°39′12.91″W], *Leeuwenberg 7908* (K, MO). LIBERIA. **Grand Bassa**: along the road from Tapita to Tchien, 13 mi NE of Tobli, [ca. 06°01′22.91″N, 009°52′57.98″W], *Jansen 873* (K, MO). **Grand Gedeh**: Webo District, Gletown, *Baldwin 6764* (K); along the road from Tchien to Zwedru Fijnhout exploitation, near Cavalla river, *Jansen 2556* (K, MO). **Nimba**: Yéképa, Granfield, Mt. Nimba, *Adam 24131* (MO); Yéképa, Nimba, Mont Alpha (mine) upper Jiti River, *Adam 27577* (CAS, MO, P); Gangra, *Adam 30077* (MO); Grassfield [07°29′10.44″N, 008°34′12.54″W], *Adam 31567* (MO); banks of Yiti River, 07°28.74′N, 008°34.22′W, *Jongkind & Bilivogui 9655* (K). **County unknown**: without locality, *Yallah 122* (K).

2a. *Mendoncia cowanii* (S. Moore) Benoist, *Bull. Mus. Hist. Nat*. (Paris). 31:387. 1925. *Afromendoncia cowanii* S. Moore, *J. Bot*. 44:150. 1906. *Monachochlamys cowanii* (S. Moore) S. Moore, *J. Bot*. 67:226, in clavi. 1929. **Type**.— MADAGASCAR. **Fianarantsoa**: Tanala, [ca. 21°51′30″S, 47°26′30″E], 1880, *Deans Cowan s.n.* (lectotype, designated here: BM-000930924-photo!). **var. *cowanii***

Afromendoncia madagascariensis S. Moore, *J. Bot*. 44:150. 1906. *Mendoncia madagascariensis* (S. Moore) Benoist, *Bull. Mus. Hist. Nat*. (*Paris*) 31:387. 1925, non Radlk. (1884). *Monachochlamys madagascariensis* (S. Moore) S. Moore, *J. Bot*. 67:227, in clavi. 1929. **Type**.—

Province unknown: Central Madagascar, *Baron 3810* (lectotype, designated here: BM-000930923-photo!; isolectotypes: K-000393676 photo!, P-00493668!).

Young stems subglabrous to pubescent with an understory of mostly erect, unbranched, eglandular trichomes < 0.05–0.2 mm long, and an overstory of yellowish, antrorse to flexuous, unbranched, eglandular trichomes 0.3–2 mm long, sometimes either overstory or understory trichomes soon breaking off or deciduous. Leaves membranaceous to coriaceous, petioles to 17 mm long, pubescent like young stems, blades ovate to elliptic (to obovate), 25–120 (–140) mm long, (11–) 16–63 (–77) mm wide, (acute to) rounded (to subcordate) at base, acute to acute-apiculate to acuminate at apex, abaxial surface pubescent with cauline type trichomes (sometimes denser on major veins), except with trichomes sometimes erect and overstory trichomes up to 3 mm long, domatia consisting of dense tufts of interwoven trichomes often conspicuous in axils of primary and secondary veins on abaxial surface as well, adaxial surface sparsely pubescent with erect to antrorse, unbranched, eglandular trichomes to 1 mm long, trichomes often denser on or mostly restricted to midvein and often with conspicuous pustullate bases. Inflorescences borne in leaf axils on young, mostly herbaceous and leafy stems, solitary or opposite at nodes, dichasia 1–3 per axil, peduncles to 47 mm long, pubescent like young stems. Bracteoles green (sometimes tinged with maroon) to dark purplish, mostly deciduous as fruit matures, ovate to elliptic to obovate, (11–) 16–31 mm long, 7–20 mm wide, rounded at base, rounded to rounded- to acute-apiculate at apex, apicule to 1 mm long, abaxial surface mealy-glandular and pubescent with erect to flexuose, unbranched, eglandular trichomes 0.2–2 mm long, adaxial surface mealy-glandular. Calyx glabrous to densely pubescent with erect to antrorsely appressed, unbranched, eglandular trichomes 0.05–2 mm long. Corolla light pink to dark pink (sometimes whitish externally), externally glabrous, internally glabrous, 26–45 mm long, tube 20–38 mm long, limb 6–21 mm diameter, upper lip 4.4–10 mm long with lobes emarginate, reflexed, 2–7.4 mm long and 3.7–8.6 mm wide, lower lip 5.7–12.4 mm long with lobes emarginate, reflexed, 3.5–7.5 mm long and 3.5–9.1 mm wide. Stamens 7–10 mm long, ventral pair inserted ca. 1 mm distal to dorsal pair, thecae 3.6–6.1 mm long, densely pubescent at base with a tuft of bristles 0.1–0.3 mm long, connective extending 0.2–0.4 mm beyond thecae, extension of connective attenuate, glabrous, staminode not seen. Pollen 5–6-colpate, E = 37–41 µm, P = 36–38 µm, P:E = 0.974–0.980, C = 10–10.8 µm, C:P = 0.263–0.297, rugulae microverrucate to microgemmate. Style 20–32.5 mm long, glabrous throughout or sometimes proximally pubescent with eglandular trichomes, stigma subequally 2-lobed with lobes 0.1–0.5 mm long. Drupe ovoid to ellipsoid to oblong, 11–21 mm long, 6.6–17 mm diameter, surface mealy-glandular and pubescent with yellowish, erect to flexuose to antrorse, unbranched, eglandular trichomes to 0.1–3 mm long.

Phenology.— Flowering: February–September with peak flowering February–March; fruiting: August–December.

Distribution and habitats.— Eastern Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Toamasina, Toliara; EOO = 298,998 km^2; Fig. 9). Plants occur in lowland to montane to cloud, primary and secondary, moist to wet, evergreen forests. Elev. 50–1200 m.

Illustrations.— Benoist (1967:5, Fig. 1); Figs. 10, 11A–D.

In the protologue of *Afromendoncia cowanii*, Moore (1906) cited an unnumbered collection of Deans Cowan at BM and *Baron 289* at K. The lectotype designated above is the more complete specimen (e.g., containing flowers, which are described in the protologue). The lectotype of *Afromendoncia madagascariensis* is chosen from the two collections of Baron from "central Madagascar" cited in the protologue. *Baron 3810* was noted by Moore (1906) to contain flowers and fruits, whereas *Baron 1448* was noted to be a fruiting collection. The protologue has descriptions

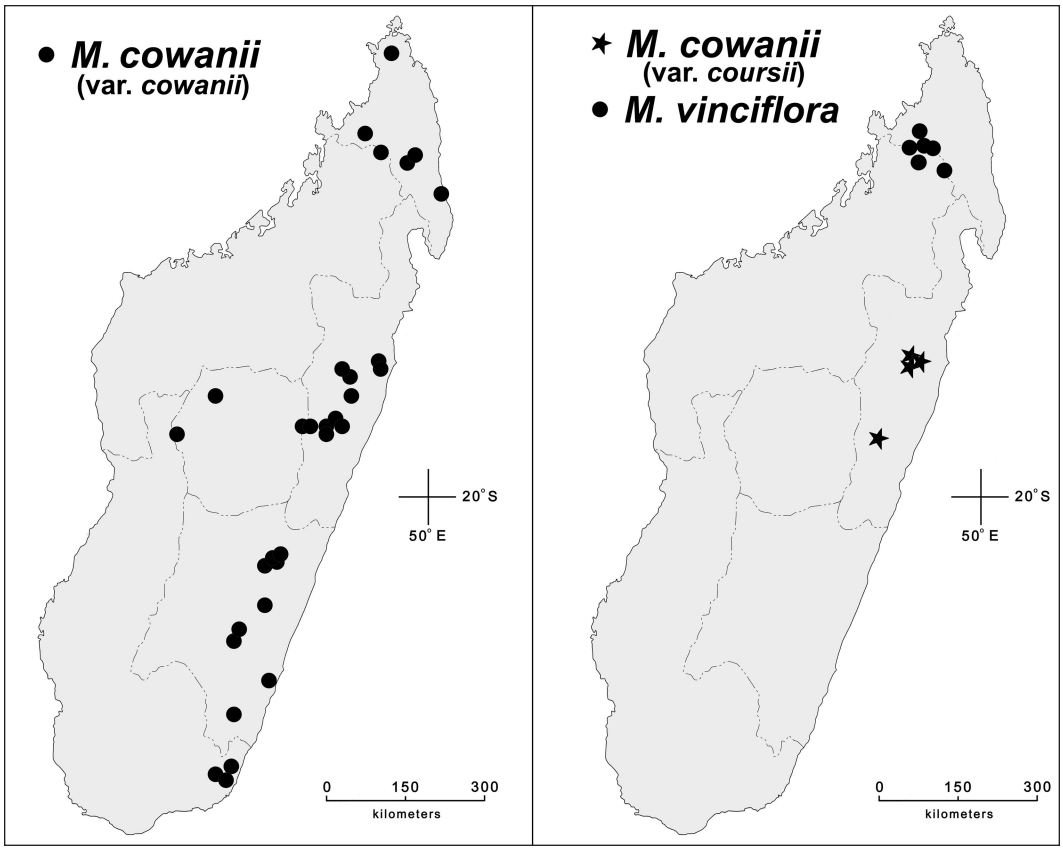

FIGURE 9. Maps of Madagascar showing distributions of *Mendoncia cowanii* var. *cowanii*, *M. cowanii* var. *coursii*, and *M. vinciflora*.

of both flowers and fruits. The lectotype at BM is particularly complete, and better reflects information in the protologue than the isolectotype at K, which contains the major set of Baron's collections from Madagascar. In describing these two species Moore (1906:151) perceptively noted that they were unlike their African congeners, but that they "bear a treacherous resemblance to each other, being as regards foliage virtually indistinguishable."

Leaves of *Mendoncia cowanii* var. *cowanii* vary from membranaceous (e.g., *Malcomber 2119*, *Randriamboavonjy et al. 838*) to conspicuously coriaceous (e.g., *Daniel et al. 10400*, *Razafindrabe et al. 157*). Irrespective of texture, leaves of this taxon frequently possess acarodomatia in axils of major veins on their abaxial surfaces. *Seigler 12818* is unusual in having fruiting pedicels up to 4 mm long and calyces to 7.7 mm long with one or more deep lobes (to 5.8 mm long).

Because flowers are most useful to adequately distinguish between *M. cowanii* and *M. decaryi*, specimens lacking them often cannot be identified with certainty (see under *M. decaryi* below for additional distinctions).

REPRESENTATIVE SPECIMENS EXAMINED.— MADAGASCAR. **Antananarivo**: Beanana (Fenoarivo), [ca. 18°23′S, 46°22′E], *Bosser 930* (P); Mandraka, P.K. 69, route d'Antananarivo à Toamasina, ca. 18°55′S, 47°56′E, *Dorr & Rakotozafy 2776* (MO); ca. 164 km W de Tsiroanomandidy, région de Bongolava, [18°52′19.77″S, 45°33′25.61″E], *Randriamboavonjy et al. 838* (CAS). **Antsiranana**: Réserve Naturelle Intégrale de Tsaratanana, Beangona, Fok. Ambinany Beangona, Fir. Marotolana, Fiv. Ambanja, 14°01′S, 048°47′E, *Antilahimena et al. 536* (BR, CAS, MO);

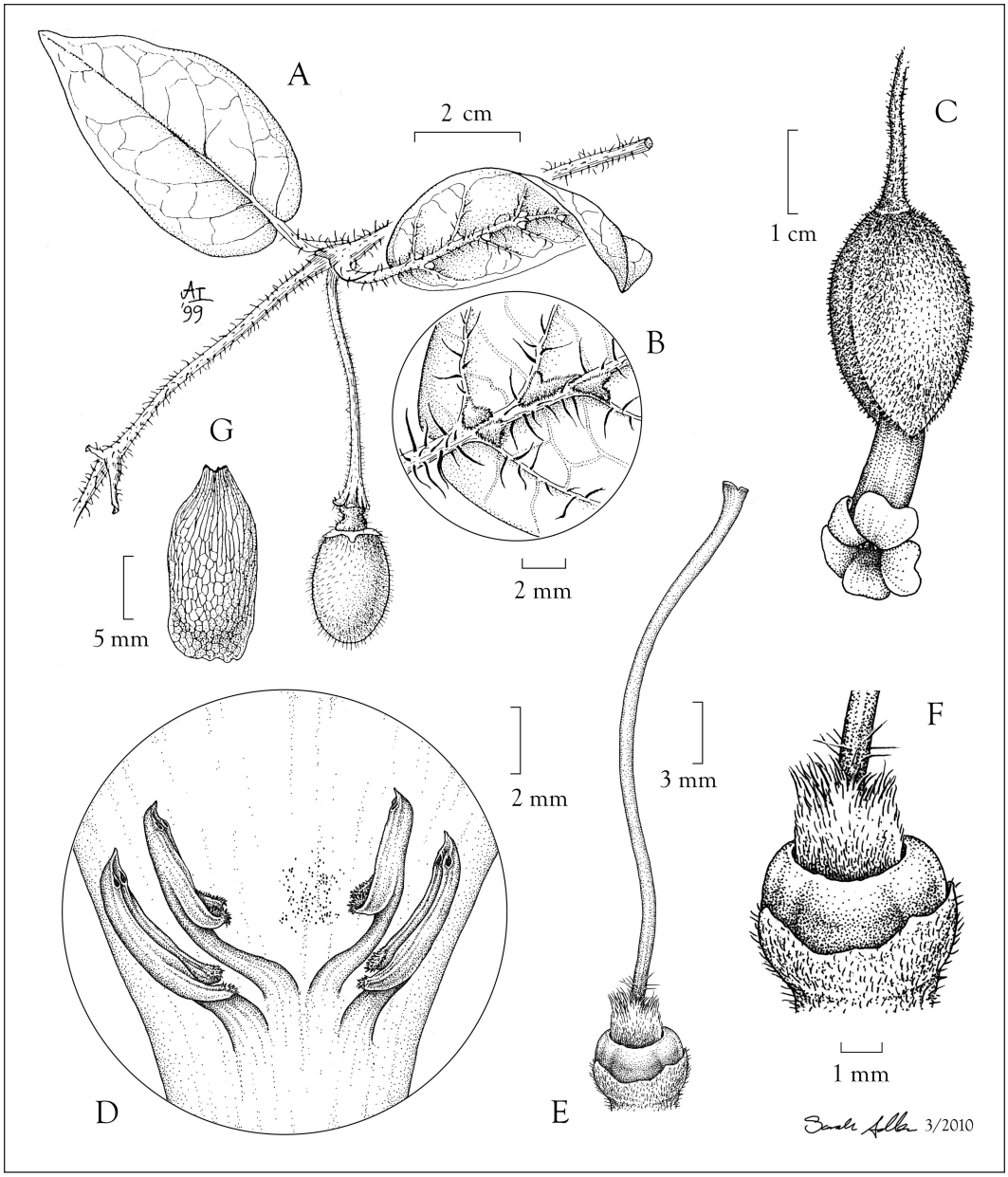

FIGURE 10. *Mendoncia cowanii* var. *cowanii* (A, B, G, *Daniel et al. 9116*; C–F, *Daniel et al. 11000*). A. Fertile node with a single dichasium in fruit. B. Portion of midvein and secondary veins, showing domatia, on abaxial surface of leaf. C. Flower partially encased by subtending bracteoles. D. Corolla tube split open to show androecium. E. Flower following dehiscence of corolla. F. Calyx, nectar disc, and pubescent ovary with style emerging. G. Seed. Drawn by Sarah Adler and Anya Illes.

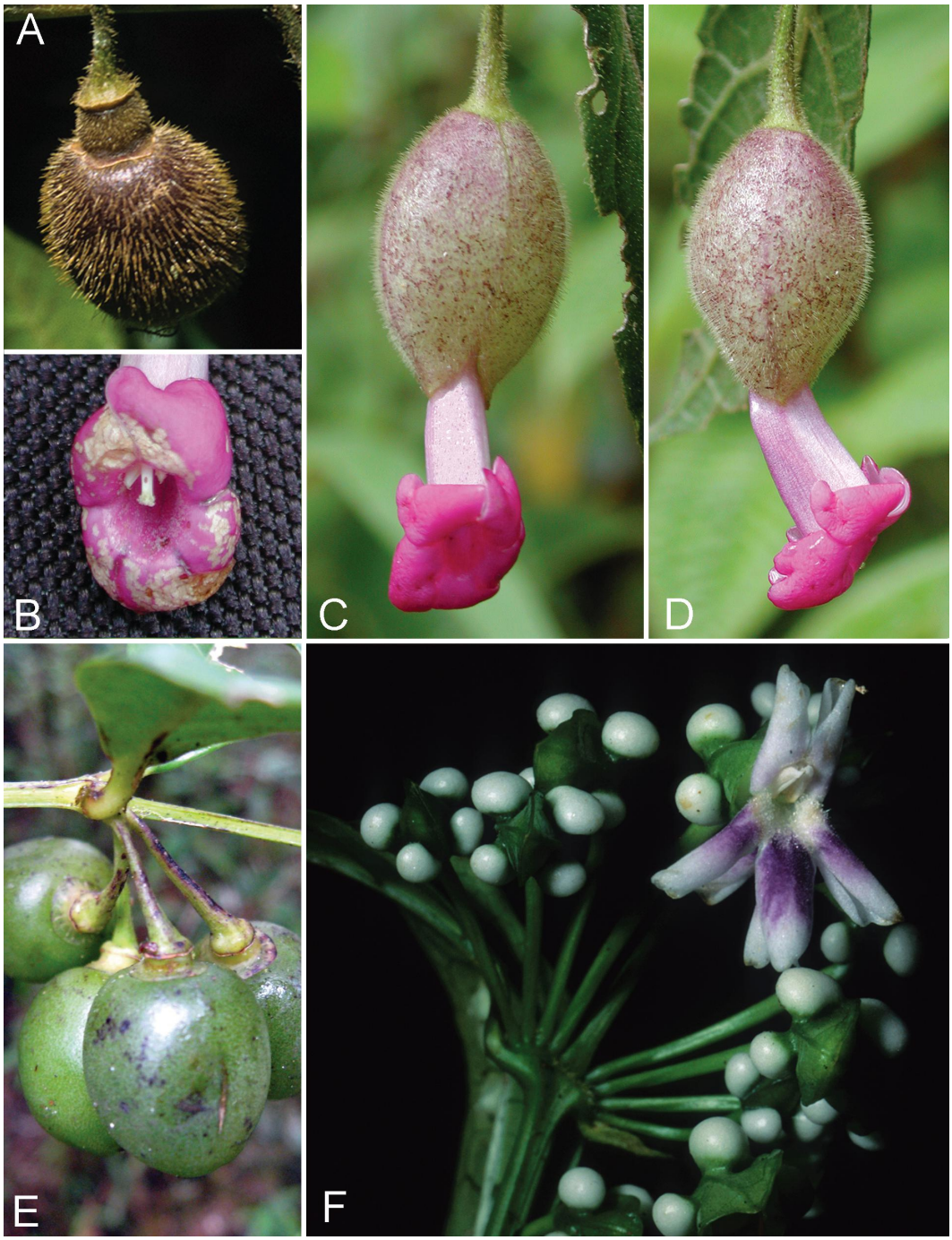

FIGURE 11. *Mendoncia cowanii* (A–D) and *M. flagellaris* (E, F). A. Mature drupe. B. Corolla limb showing discoloration due to insect visitation. C, D. Flowers with corolla tube encased by fluid-filled bracteoles. E. Immature drupes. F. Flower and bracteoles, each with a pair of prominent, white, and basal protuberances. (A–D, photos by T. Daniel of *Daniel et al. 11000*; E, photo [cropped] of *Razanatsima et al. 422*, copyright by Aina Razanatsima on Tropicos [www.tropicos.org/Image/100126998], CC by-NC-ND 3.0; F, photo by T. Daniel of *Daniel et al. 9239*).

Naturelle Marojejy, along trail to summit of Marojejy Est, NW of Mandena, 14°27′S, 049°47′E, *Miller 3372* (MO); Réserve Naturelle de Marojejy; western slopes of Mt. Beondroka, 14°27′S, 49°47′E, *Miller & Randrianasolo 4374* (MO); Réserve Naturelle de Marojejy; along the trail to the summit of Marojejy Est, N of Mandena, 14°26′S, 049°46′E, *Miller & Randrianasolo 4576* (MO); environs d'Antalaha, [ca. 14°54′S, 50°16′30″E], *Perrier de la Bathie 2169* (K, P); Montagne d'Ambre, partie sud, 12°41′03″S, 049°10′28″E, *Randimbiarison & Ramandimbimanana 188* (CAS); Marojejy RN1, Sambava, ca. 10 km à vol d'oiseau de Maroambihy à 310° au NW, ca. 6 km à vol d'oiseau de Mandena à 318° NW, soit 13 km suivant la piste entre Mandena et le sommet de Marojejy, 14°26′30″S, 049°46′20″E, *Rasoavimbahoaka 589* (MO); Marojejy RN1, Andapa, ca. 3.5 km a vol d'oiseau de Marovato (80°NE), et 2 km a vol d'oiseau de Sarahandrano (60° NE), soit 8 km environ a pied, 14°36′10″S, 49°39′50″E, *Rasoavimbahoaka 647* (MO). **Fianarantsoa**: Ranomafana Natl. Park, Talatakely Trail System, downslope from the BT trail toward the Namorona River surrounding a small natural pond, 21°15′S, 047°15′E, *Almeda et al. 8055* (CAS); Midongy du Sud, Beharena, 23°31′05″S, 047°05′34″E, *Andrianjafy 1234* (MO); Ranomafana Natl. Park, Talatakely trail system S of Namorona River, 21°16′S, 047°25′E, *Daniel et al. 9037* (CAS), *Daniel et al. 9116* (CAS), *9255* (CAS), *11002* (CAS); 7 km W of Ranomafana, just S of Namorona river, Duke Primate Center study site, 21°16′S, 047°25′E, *Daniels 98* (CAS, MO); Parc Natl. Ranomafana, Parcelle #3, Talatakely, piste vers Vohiparara, 21°15′S, 047°27′E, *Kotozafy 139* (MO); PN 45 Parc Natl. Ranomafana, between Fianarantsoa and Ifanadiona, around cabine de reserche S of Namorona River, *Malcomber 998* (MO); Ranomafana Natl. Park, Parcelle I, near village of Miaranony, Anosimasina, 21°09′S, 047°32′E, *Malcomber 1589* (MO); Fivondronana Ivohibe, Firaisana Ivohibe, limite N de la Réserve Speciale d'Ivohibe le long de la rivière Ifefitany, 7.5 km ENE d'Ivohibe, campement 1, 22°28′12″S, 046°57′36″E, *Rakotovao et al. 837* (MO); Haute Matsiatra, Ranomafana Natl. Park, Bevoahazo, 21°11′43″S, 047°28′55″E, *Ranarivelo et al. 971* (CAS); Ranomafana Natl. Park, piste touristique de Vohiparara E du village de Vohiparara, direction NE piste B, Ifanadiana, 21°14′S, 047°23′E, *Ravololonanahary 3* (MO); Ivohibe, Ivongo, Ambarongy, RN1 Andringitra, 22°13′S, 47°01′E, *Razafindrabe 157* (MO); Réserve Speciale #7, Manombo, 37 km S of Farafangana, parcel W of RN12, 23°02′S, 047°42′E, *Schatz 3188* (MO); near Ranomafana, near village of Ambodiamotana, *Seigler 12818* (K, MO, P). **Toamasina**: Andasibe-Mantadia Natl. Park, Parc a Orchidées, 18°56′00.5″S, 048°24′51.9″E, *Almeda et al. 9245* (CAS); route Moramanga à Anosibe, [ca. 18°54′6.29″S, 048°03′16.30″E], *Bosser & Millot 6470* (P); Analamazaotra, [ca. 18°56′S, 48°26′E], *Capuron 565-S.F.* (K, P); Forêt d'Analamazoatra, *Capuron s.n.* (P); Andasibe, Analamazoatra (Perinet), *Cheek & Dransfield B1383* (CAS); piste d'Ambatoharanana, massif du Rahobevava Bemainty, [ca. 18°00′S, 048°40′E], *Cours 4152* (P); de Didy à Brickaville, *Cours 4847* (P); 7 km N de Perinet vers Tamatave, *Cremers 1482* (MO, P); forest reserve in vicinity of Perinet, along Route #2 between Tananarive and Tamatave, *Croat 32280* (MO); Special Reserve Perinet-Analamozoatra in Andasibe (Perinet); *Daniel & Butterwick 6721* (CAS); Parc Natl. de Mantadia, ca. 10 km N of Andasibe, trail to piscine along Andranomanaponga River (Rinasoa Trail), 18°49′30″S, 048°25′48″E, *Daniel et al. 10400* (BR, CAS); Andasibe-Mantadia Natl. Park, Mantadia section, 14–19 km NE of RR station in Andasibe, 18°50′S, 048°26′E, *Daniel & Ranarivelo 10539* (CAS, TAN), *Daniel et al. 11000* (CAS, TAN); S de Moramanga, *Decary 7005* (P); forêt S de Moramanga, [ca. 18°59′14.42″S, 048°15′12.73″E], *Decary 7043* (P); Forêt de Sandrangato S de Moramanga, [ca. 19°06′30″S, 048°14′30″E], *Decary 17755* (K, P), *17785* (K, P); environs de Andasibe-Perinet, 18°56′S, 048°25′E, *Dorr & Barnett 3207* (MO); Analamazaotra, *Jardin Botanique Tana (TAN) 2160* (P); Forêt d'Analamazaotra, *Keraudren-Aymonin & Aymonin 25362* (P); Betampona Réserve Naturelle Integrale, 40 km NW of Toamasina, [ca. 17°54′46″S, 049°13′06.62″E], *Lewis & Razafimandimbison 667* (MO); Andasibe-Perinet,

N of road from Antananarivo to Tamatave, 1 km along trail SW of old C.T.F.T. sawmill at Analamazoatra, *Lowry & Schatz 4264* (CAS, MO); NE of Moramanga, at nickel mining exploration site, Ambatovy, plot 6 of Golder map, 18°51′34″S, 048°18′25″E, *McPherson 17517* (MO); Analamazaotra, *Perrier de la Bathie 10265* (P); Forêt d'Andasibe, sur l'Onive, *Perrier de la Bathie 17048* (P); Betampona, Ambodiziena, W de Tamatave, *Perrier de la Bathie 17408* (P); Moramanga Distr., Andasibe, Forêt d'Analamazaotra (Perinet), *Pettersson & Nilsson 253* (K); canton de Ambodiriana, district de Tamatave, *Rakotoniaina 5343-RN* (K, P); canton: Imerimandroso, district: Ambatondrazaka, *Rakotonao 10894RN* (P), *10895RN* (P); forestry station of Analamazaotra, SE of the old road between Moramanga and Andasibe, 18°56′S, 048°26′E, *Randrianansolo 427* (MO). **Toliara**: along road through mountain in Chaines Anosyennes from Fort Dauphin (Taolagnaro) to Ranomafana, *Croat 31844* (MO); haute vallée de la Manampanihy [ca. 24°33′30″S, 047°04′30″E], entre le col de Saindro et Eminiminy, *Humbert 14023* (P); NW of Taolagnaro, Réserve Naturelle Integrale #11 (Andohahela), parcelle I, NW of Eminiminy, beside River Itrotroky, 24°38′S, 46°46′E, *Malcomber 2119* (MO); Fort Dauphin (Taolagnaro), NW of town along road to Ranomafana, 24°46′S, 46°53′E, *McPherson & Rabevohitra 14970* (CAS, MO); Integrale Réserve #11, Andohahela, Parcelle 1, SW of Eminiminy, Manatavona River, 24°40′S, 46°48′E, *Randramampoinona 599* (BR, MO). **Province not determined**: Madag. Centre, *Baron 289* (P); central Madagascar, *Baron 1448* (K, P); Madagascar, *Baron 2586* (K, P); central Madagascar, *Baron 3810* (P); north Madagascar, *Baron 6143* (K); without locality, *Homolle s.n.* (P); Cameaka, *Jardin Botanique Tana (TAN*) *3689* (P); without locality, *Perrier de la Bathie 15968* (P).

2b. *Mendoncia cowanii* (S. Moore) Benoist **var. *coursii*** Benoist, *Notul. Syst.* (*Paris*) 11:141. 1944. **Type**.— MADAGASCAR. **Toamasina**: Ambatondrazaka, Sahalampy Onibé, [ca. 17°45′S, 048°51′E], Nov 1938, *Cours 1053* (holotype: P-00091099!; isotype: K-000393673!).

Young stems densely pubescent with yellowish to yellowish brown, interwoven, flexuose, unbranched, eglandular trichomes 0.2–2 mm long (velutinous), surface of stem not visible. Leaves subcoriaceous, petioles to 15 mm long, velutinous, blades ovate to elliptic to oblong-elliptic, 38–92.4 long, 18–47.3 mm wide, subcordate to rounded to acute at base, acute-apiculate to rounded to retuse at apex, abaxial surface pubescent like young stems but blade surface at least partially visible, adaxial surface pubescent with antrorse, eglandular trichomes 0.1–1 mm, trichomes on each surface usually denser on major veins. Inflorescences borne in leaf axils on young, mostly herbaceous and leafy stems, solitary or opposite at nodes, dichasia 1–2 per axil, peduncles to 50 mm long, velutinous. Bracteoles with color obscured by pubescence, persistent at least to immature stages of fruiting, ovate-elliptic to subcircular, 16.3–23.5 mm long, 10.2–21.4 mm wide, rounded to acute-apiculate at apex, rounded to truncate at base, abaxial surface velutinous, adaxial surface mealy-glandular. Calyx densely pubescent with mostly distally pointing, straight, eglandular trichomes to 3 mm long. Corolla purplish to pink, 30.5–38.7 mm long, externally glabrous, internally mealy-glandular, tube 28–33 mm long, limb 9–11.3 mm in diameter, upper lip 1.8–3.6 mm long with lobes rounded to emarginate, 1.8–3.2 mm long and 4–4.5 mm wide, lower lip 3–7.4 mm long with lobes rounded to emarginate 2.2–3.3 mm long and 3.4–3.5 mm wide. Stamens not seen. Style 27–29 mm long, glabrous, stigma subcapitate to subequally 2-lobed, lobes 0.1–0.3 mm long. Drupe (immature) ± ovoid, ca. 13 mm long, ca. 9 mm in diameter, densely pubescent with golden-brown, appressed eglandular trichomes 0.4–3 mm long.

Phenology.— Flowering May–September; fruiting October.

Distribution and habitats.— East-central Madagascar (Toamasina; EOO = 1,512 km^2; Fig. 9). Plants occur in lowland to montane, primary, moist to wet, evergreen forests. Elev. 500–1040 m.

Local Name.— "Vahiboloina" (*Andrianijafy et al. 186*).

A full description of this variety is provided above because it is possible that these plants represent a species distinct from *M. cowanii*. It differs from the nominate variety primarily by the young stems, petioles, abaxial surface of leaf blades (Fig. 3A), peduncles, and bracteoles being densely pubescent with yellowish, interwoven, flexuose, unbranched, eglandular trichomes such that the underlying surfaces are not visible (or only partially so on the abaxial leaf blades). The variety occurs in a limited region of Toamasina Province in east-central Madagascar. Domatia are not evident on the abaxial surfaces of leaves, or, if present, they are likely obscured by the dense trichomes that are ubiquitous on that surface. Also in this variety, the overall length of the upper lip of the corolla and the length and width of lobes of the lower lip are shorter and narrower than in *M. cowanii* var. *cowanii*, but this may be attributed to lack of flowering material for comparison. Measurements of other characters and flowering times overlap between the two varieties. Additional fertile collections of plants conforming to this taxon should clarify its status as a variety of *M. cowanii* (as treated here), a more densely pubescent form of that species, or a distinct species.

Additional specimens examined.— MADAGASCAR. **Toamasina**: Vavantenina, Commun de Miarinarivo, FKT Anamborano, Savaharina, PN Zahamena, à côté de la rivière Ihofika, limite de PN, 17°41′08″S, 048°59′43″E, *Rakotonandrasana 485* (MO); Réserve Naturelle Integrale Zahamena, forest of Amboditamenaka, 17°44′S, 049°00′E, *Malcomber 2584* (MO); Parc Natl. de Zahamena, Rivière de Sahemora, 17°38′27″S, 048°52′32″E, *Andrianjafy 186* (MO); PK 33, road Moramanga–Anosibe Anala, 19°10′56″S, 48°13′31″E, *de Block et al. 922* (BR, K).

3. *Mendoncia decaryi* (Benoist) Magnaghi, *Novon* 23:188. 2014. *Mendoncia cowanii* Benoist var. *decaryi* Benoist, *Notul. Syst. (Paris)* 11:141. 1944. **Type**.— MADAGASCAR. **Toamasina**: Zahamena (Réserve Naturelle Integrale 3), [ca. 17°38′30″S, 048°50′00″E], 23 Mar 1941, *Decary 16712* (lectotype, designated by Magnaghi and Daniel, 2014: P-00091101!).

Young stems sparsely to densely pubescent with yellowish to golden-brown, erect to flexuose, unbranched, eglandular trichomes 1–3 mm long, and sometimes also with an understory of mostly erect, eglandular trichomes <0.05–0.3 mm long. Leaves membranaceous to subcoriaceous, petioles to 15 mm long, pubescent like young stems, blades ovate-elliptic to elliptic, 28–123 long, 24–77 mm wide, rounded to cordate at base, acuminate to acuminate-subcaudate (sometimes abruptly so) at apex, abaxial surface (primarily major veins) bearing flexuous, eglandular trichomes like those of young stems except to 4.2 mm long and often intertwined, and sometimes also with understory trichomes like those of young stems, and rarely with tufts of woolly trichomes in axils of main veins forming domatia (see discussion below), adaxial surface pubescent (usually denser on major veins) with antrorse, eglandular trichomes 0.6–3 mm long. Inflorescences borne in leaf axils on young, mostly herbaceous and leafy stems, solitary or opposite at nodes, dichasia 1–3 per axil, peduncles to 20 mm long, pubescent like young stems. Bracteoles purplish, persistent as fruit matures, elliptic to ovate-elliptic to ovate, 11–29.8 mm long, 9–18.4 mm wide, rounded at base, acute-apiculate to acuminate-subcaudate at apex, apicule or slender, tail-like apex to 6 mm long, abaxial surface densely pubescent with cauline type trichomes (except overstory trichomes to 3.5 mm long), adaxial surface mealy-glandular. Calyx densely pubescent with unbranched, eglandular trichomes 1–3 mm long. Corolla white with purplish markings, 33.5–49 mm long, externally glabrous to mealy-glandular, tube 20–32.5 mm long, limb 20.6–32.4 mm diameter, upper lip 13.5 mm long with rounded or emarginate lobes 8–10 mm long and 11.2–13.2 mm wide, lower lip 16.5–19 mm long with rounded or emarginate lobes 9.4–13.5 mm long and 12.2–15.2 mm wide.

Stamens 6.3–11 mm long, ventral pair inserted 3.8 mm distal to the dorsal pair, thecae 4.4–6.4 mm long, densely pubescent at base with a tuft of bristles 0.1–0.3 mm long, sometimes thecae of ventral stamens with bristles along entire length, connective extending 0.3–0.7 mm beyond thecae, extension of connective attenuate, glabrous, staminode (if present) not seen. Pollen not seen. Style 15.3–28 mm long, pubescent near base with eglandular trichomes to 1 mm long, glabrous distally, stigma subequally to unequally 2-lobed with lobes 0.2–0.5 mm long. Drupe subellipsoid to obovoid, 12.5–20 mm long, 6.5–17 mm in diameter, pubescent with golden-brown, unbranched, eglandular trichomes 0.1–1.5 mm long.

Phenology.— Flowering: February–April; fruiting: March–September.

Distribution and habitats.—Northern and east-central Madagascar (Antananarivo, Antsiranana, Mahajanga, Toamasina; EOO = 105,283 km^2; Fig. 12). Plants occur in primary, montane, moist to wet, evergreen forests. Elev. 300–1400 m.

Illustration.— Magnaghi and Daniel (2014:189, Fig. 1).

Local names.— "Tsipolitrala" (*Ratovoson et al. 273*); "vahimpinaomby" (*Razafitsalama et al. 473*); "vahipisaka" (*Rakotondrafara et al. 238*).

Uses.— Infusion of the stems used to treat syphilis (*Razafitsalama et al. 473*). Williams et al. (2006; as "*M. cowanii*") reported the presence of two new bioactive molecules (cytotoxic naphthoquinones) in root and stem extracts of this species.

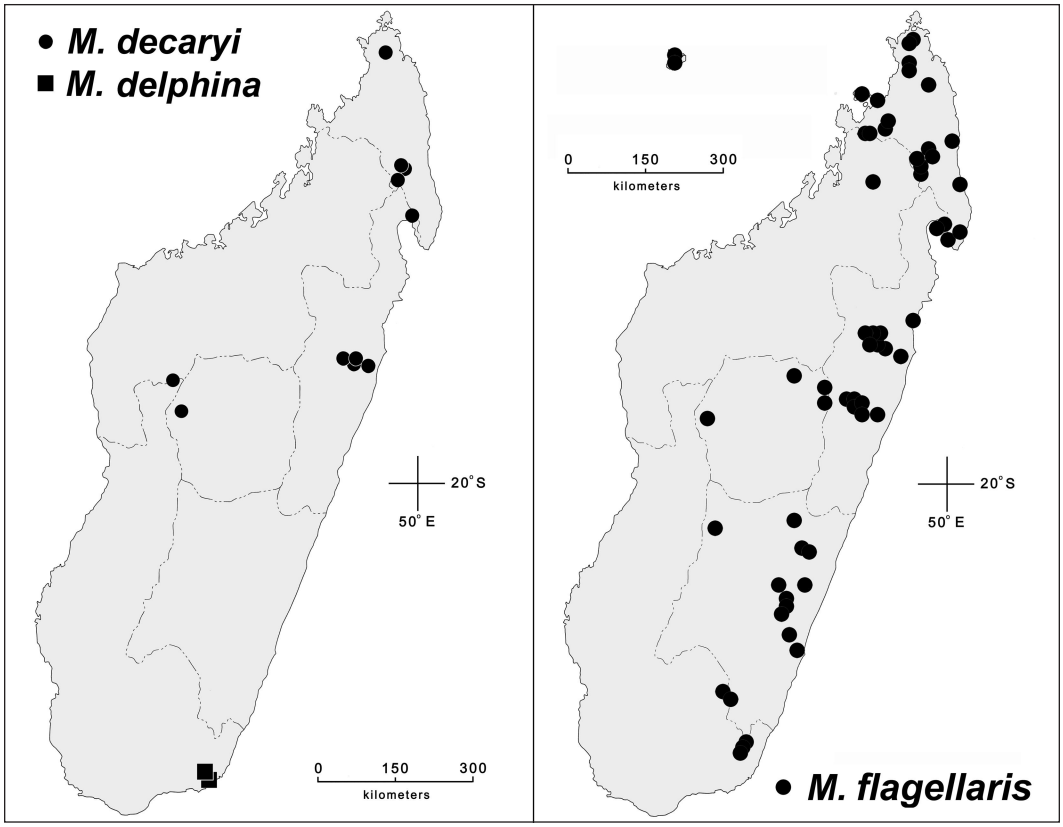

Figure 12. Map of Madagascar showing distributions of *Mendoncia decaryi* and *M. delphina*, and map of Madagascar and Mayotte showing distribution of *M. flagellaris*.

The major distinctions between *M. decaryi* and *M. cowanii* are color and sizes of components of the corolla, as indicated in the keys to species herein. Thus, identification of plants lacking corollas can be difficult. Some of the tendencies in characters that might help to distinguish these taxa include: leaves of *M. decaryi* are generally thinner, higher (4–5th) order veins more prominently protruding (or visible) on the abaxial leaf surfaces, prominent acarodomatia in axils of major veins on the abaxial leaf surface are entirely or usually absent (see below), and the apicule/narrowed, tail-like apex of the bracteoles is usually longer (up to 6 long mm vs. to 1 mm long in *M. cowanii*).

Two specimens, *Dorr 3538* and *Morat 4776*, lack adequate flowering material but possibly represent an undescribed taxon. They are included here because, like *M. decaryi*, they have stems, leaves, and bracteoles densely pubescent with golden-brown flexuose trichomes 1.3–3.5 mm long that sometimes overtop a shorter layer of dense trichomes (0.8–1 mm long) on the main veins of leaves and bracteoles. However, bracteoles on both of these specimens are smaller (10.3–10.8 mm long, 3.5 mm wide) than those of *M. decaryi*, and both have some domatia present on leaves (vs. absent in other collections of *M. decaryi*). *Dorr 3538* bears a single corolla with unmeasurable lobes. Label data indicate white petals with purple markings, as in *M. decaryi*. Both specimens were collected in west-central Madagascar (west of Tsiroanomandidy), well apart from other collections in wet forests of northern and eastern portions of the country. Study of additional material is needed to clarify the taxonomic status of these collections, which are here tentatively treated as *M. decaryi*.

Additional specimens examined.— MADAGASCAR. **Antananarivo**: Bongolava W de Tsiroanomandidy, [18°49′00.012″S, 045°40′00.012″E], *Morat 4776* (P). **Antsiranana**: E Madagascar, N of Maroantsetra, ca. 8 km E of Sahavary, off the River Andranofotsy, *Du Puy & Du Puy MB 163* (K); Sous-préfecture d'Andapa, Commune Rurale de Doany, Fokontany de Betsomanga, versant NW du Marojejy, 0.2 km au N du camp I, 14°25′S, 049°36′E, *Gautier et al. 3798* (K, MO); Réserve Naturelle de Marojejy, N slopes of Ambatosoratra, 14°32′S, 049°41′E, *Miller 4202* (CAS, MO, TAN); Andranotsarabe, Befingotra, Bealampona, Andapa, 14°42′20″S, 49°32′00″E, *Rasoavimbahoaka & Rastefanonirina 287* (BR, MO, TAN); SW d'Andapa, Réserve Speciale d'Anjanaharibe-Sud, Ambodisatrana, aux environs des sommets, 14°32′45″S, 049°35′15″E, *Ravelonarivo 145* (MO). **Toamasina**: Réserve Naturelle no.3 (Zahamena), *Decary 16741* (P-00091100, K-000393674-photo); Betampona-Réserve Naturelle no.1, [17°55′S, 049°13′E], *Decary 16924* (P, TAN-000438-photo); Ampitanonoka à Fotsialanana, near Lac Alaotra, *Herbier de la Station Agricole de L. Alaotra 2441* (MO); W of Vavatenina, Réserve Naturelle Integrale Zahamena, forest of Amboditamenaka, 17°44′S, 49°00′E, *Malcomber et al. 2516* (MO, TAN); Sous-préfecture Vavatenina, Commune Miarinarivo, Fokontany Anamborano, limite entre Vavatenina et Toamasina II, a 500 m d'Ifasina, 17°44′42″S, 048°58′26″E, *Rakotondrafara et al. 238* (MO); RNI Tamatave, *Rakotoniana 2875* (P); Parc Natl. de Zahamena, Andranofantsona, Manakambahiny I, Ambodimangavalo, 17°39′07″S, 048°58′14″E, *Ratovoson et al. 273* (MO); Fiv. Vavatenina, Com. Ambodimangavalo, secteur 2, aux environs (hors) du Parc Azhamena, forêt Ambinanin Antsahabesahona, vers 16 km SE d'Ambarifotsy, au bord du rivière Ihofika, 17°39′16″S, 048°, 58′50″E, *Razafitsalama 473* (MO). **Mahajanga**: 9.6 km NW of Ambohitsaratelo-Bebao (NW of Tsiroanomandidy), [ca. 18°18′8.54″S, 045°32′18.84″E], *Dorr 3538* (MO, TAN).

4. *Mendoncia delphina* Magnaghi, *Novon* 23:190. 2014. **Type.**— MADAGASCAR. **Toliara**: NW of Taolagnaro (Ft. Dauphin), Parc Natl. Andohahela, Réserve integral no. 11, parcel 1, E boundary, 24°45′S, 46°51′E, 250–500 m, 17–20 Oct 1992, *Malcomber et al. 1665* (holotype: MO-05003406!; isotypes: K, TAN).

Young stems glabrous to mealy-glandular or sometimes pubescent with sparse, whitish to yellowish, antrorsely appressed, unbranched, eglandular trichomes 0.05–0.5 mm long. Leaves subcoriaceous, petioles to 14 mm long, glabrous or pubescent like young stems, blades elliptic to ovate-elliptic, 44–83 mm long, 15–34 mm wide, acute to cuneate at base, caudate (with tail-like extension to 12 mm long) to acuminate at apex, surfaces glabrous to mealy-glandular. Inflorescence borne in leaf axils on young, mostly herbaceous, and leafy stems, solitary or opposite at nodes, dichasia 1–2 per axil, peduncles to 40 mm long, glabrous or pubescent like young stems. Bracteoles yellowish, deciduous by time of fruit maturation, ovate to elliptic, 6.9–14 mm long, 5.3–8.3 mm wide, rounded to truncate at base, acute at apex, abaxial surface glabrous or with a few short trichomes to 0.3 mm long, adaxial surface mealy glandular and very densely but minutely (trichomes < 0.05 mm long) pubescent at apical tip. Calyx glabrous or sparsely pubescent with unbranched eglandular trichomes 0.05 mm long (sometimes restricted to margin). Corolla (purplish) white with purple throat, 16.1–18.5 mm long, externally and internally mealy-glandular, tube 7.6–9.3 mm long, limb 14–18 mm in diameter, upper lip 7.2–9.1 mm long with rounded lobes 5.3–6.6 mm long and 4.5–5.8 mm wide, lower lip 8.5–9.5 mm long with rounded lobes 5–8.5 mm long and 3.5–5.7 mm wide. Stamens 8.5–8.8 mm long, ventral pair inserted 0.5 mm distal to the dorsal pair, filaments mealy-glandular proximally, thecae 4–4.3 mm long, densely pubescent at base with a tuft of bristles 0.1–0.2 mm long, these sometimes extending distally on thecae, connective extending 0.6–1 mm beyond thecae, extension of connective attenuate, glabrous, staminode 2 mm long. Pollen 5-colpate, E = 36–37 µm, P = 35–37 µm, P:E = 0.968–1.00, C = 8.7–10.6 µm, C:P = 0.248–0.302, rugulae microverrucate to microgemmate. Style 11–12.3 mm long, glabrous, stigma subequally to unequally 2-lobed, lobes 0.1–0.8 mm long. Drupe (immature ?) ovoid-ellipsoid, 13.5 mm long and 9 mm diameter, glabrous to mealy-glandular.

Phenology.— Flowering: October–November; fruiting: November.

Distribution and habitats.— Extreme southeastern Madagascar (Toliara; EOO = 134 km^2; Fig. 12). Plants occur in lowland, moist to wet, evergreen forests near Taolagnaro. Elev. 250–500 meters.

Illustration.— Magnaghi and Daniel (2014:192, Fig. 2).

Corollas of *Mendoncia delphina* resemble those of *M. flagellaris* in color (white with purple markings on the limb and throat), and its flowering period concurs with that species. The distribution of *M. delphina* overlaps those of both *M. cowanii* and *M. flagellaris*, but appears to be restricted to the southeastern-most Madagascar. The leaves of *M. delphina* are consistently elliptic with an acuminate apex and a unique venation pattern with the secondary veins branching from the midvein at angles of 35 to 45 degrees. A fruiting collection of *M. flagellaris* (*Ravelonarivo & Rabesonina 741*) from Antsiranana in northern Madagascar has leaves similar to those of *M. delphina* in both of these attributes. The identity of this collection, which lacks flowers, remains uncertain.

Additional specimens examined.— MADAGASCAR. **Toliara**: Préfecture de Fort Dauphin, Forêt Manantantely, [ca. 24°59′S, 046°55′E], *Dumetz 1395* (MO); NW of Taolagnaro (Fort Dauphin), RNI #11 (Andohahela), parcel 1, eastern boundary, [ca. 24°42′S, 46°44′E], *Malcomber et al. 1665* (MO).

5. *Mendoncia flagellaris* (Baker) Benoist, *Bull. Mus. Hist. Nat*. (Paris). 31:387. 1925. *Monachochlamys flagellaris* Baker, *J. Linn. Soc., Bot*. 20:217. 1883 ("1884"). **Type**.— MADAGASCAR. **Province unknown**: Central Madagascar, Oct 1882 (fide specimen at K), *Baron 1743* (syntypes: K-000393667-photo!, P-00091104!); *Baron 1789* (syntypes: K-000393668-photo!, P-00091103!).

Mendoncia madagascariensis Radlk., *Abh. Naturwiss. Vereins Bremen* 8:467. 1884. *Monachochlamys madagascariensis* (Radlk.) Baill., *Bull. Mens. Soc. Linn. Paris* 2:826. 1890 (as "*madagascarica"*). **Type**.— MADAGASCAR. **Antananarivo**: Ost-Imerina, Andrangolaoka [as "Andrangolóaka;" ca. 19°02′15.26″S, 047°54′57.70″E], Nov 1880, *Hildebrandt 3693* (syntypes: HBG-517341-photo!, JE-00003605-photo!, JE-00003606-photo!, JE-00003607-photo!, K-000393669-photo!, K-000393671-photo!, M-0186545-photo!, M-0186546-photo!, P-00493833!, WU-035583-photo!).

Monachochlamys boivinii Baill., *Bull. Mens. Soc. Linn. Paris* 2:826. 1890. **Type**.— MADAGASCAR. **Antsiranana**: Nossi-be, cratère d'Ampombilava [13°23′35.06″S, 048°14′48.74″E], 1850 (fide specimen), *Boivin s.n.* (holotype: P-00493802!)

Young stems glabrous (at least internodes) to mealy-glandular to sparsely (to densely) pubescent with antrorse to antrorsely appressed, straw-colored, unbranched, eglandular trichomes 0.1–0.5 mm long (or rarely densely pubescent with erect to flexuose to recurved trichomes to 1 mm long, i.e., pilose), nodes sparsely to densely pubescent with stiff, straw-colored, mostly appressed, eglandular, unbranched trichomes to 1 mm long (sometimes deciduous on older stems). Leaves membranaceous to coriaceous, petioles to 27 mm long, glabrous to pubescent with erect to flexuose trichomes like those at nodes (or pilose), blades ovate to narrowly elliptic to broadly elliptic to subcircular to oblong to obovate to obcordate, 14–137 mm long, 7–102 mm wide, truncate to rounded to cuneate at base, acuminate to acute to rounded to truncate to retuse and often apiculate (with apiculum to 1.6 mm long) at apex, abaxial surface glabrous to sparsely pubescent with antrorse to antrorsely appressed trichomes 0.1–0.5 mm long (or pilose), adaxial surface glabrous to mealy-glandular and occasionally with eglandular trichomes like those of abaxial surface (or pilose), foliar trichomes sometimes restricted to major veins. Inflorescences borne in leaf axils on young, mostly herbaceous, and leafy stems, solitary or opposite at nodes, consisting of axillary, pedunculate dichasia or of a pedunculate, bracteate raceme bearing pedunculate dichasia in axils of bracts, dichasia 1–4 (–8) per axil, peduncles to 40 (–55) mm long, glabrous to sparsely pubescent like young stems, racemes (when present) to 15 cm long, rachis pubescent like young stems, bracts of racemes subfoliose and reduced in size acropetally, 2–40 mm long, 0.8–14 mm wide. Bracteoles green to greenish white, mostly deciduous in fruit, ovate to elliptic to oblong to obovate, 4.3–11.2 mm long, 2.5–10 mm wide, rounded to cuneate to subtruncate at base, rounded to acute to acute-apiculate to subacuminate at apex, abaxial surface glabrous to mealy-glandular or sparsely to densely pubescent with straw-colored, unbranched, mostly antrorsely appressed, eglandular trichomes to 0.5 mm long (or pilose), basally often beset with a conspicuous pair of whitish, gall-like, bulbous protuberances up to 2.5 mm high and 1.5–3 mm in diameter, adaxial surface mealy-glandular or ± densely beset with larger, sessile glands, distal margin and apex of adaxial surface inconspicuously but densely pubescent with flexuose, eglandular trichomes to 0.3 mm long. Calyx glabrous to mealy-glandular (or sometimes with a fringe of trichomes 0.1–0.2 mm long, e.g., *Baron 3749*). Corolla white to white with purple markings near base of lower lip, 8–15 (–18) mm long, externally glabrous to mealy-glandular, internally glabrous to mealy-glandular (especially in throat near mouth), tube (3–) 5–12.7 mm long, limb 4.5–29.1 mm in diameter, upper lip 2–12.5 mm long with rounded to emarginate lobes 1.4–11.6 mm long and 1.3–11.1 mm wide, lower lip 2.3–16.7 mm long with rounded to emarginate lobes 1.7–14.5 mm long and 2.5–9 mm wide. Stamens 2.8–5.9 mm long, ventral pair inserted up to 1 mm distal to dorsal pair, thecae 1.1–4.4 mm long, pubescent at base with a tuft of bristles 0.1–0.2 mm long, these sometimes extending toward apex of thecae and thecae sometimes minutely glandular dorsally, connective not extending or extending up to 0.5 mm beyond thecae, extension of connective triangular to oblong, glabrous to minutely glandular, staminode (if present) 1.3–2 mm long, thecae (when present) up to 0.9 mm long. Pollen 4 (–5)-

colpate, E = 25–32 µm, P = 23–27 µm, P:E = 0.812–0.979, C = 5.8–9.1, C:P = 0.224–0.362 µm, rugulae microverrucate to microgemmate. Style 3–8.8 mm long, glabrous, stigma subcapitate with undulating margin/rim to unequally 2-lobed. Drupe ovoid-ellipsoid to ellipsoid to spherical to obovoid, 9.5–20 mm long, 6–15.7 mm diameter, glabrous to mealy-glandular. $n = 19$ (Daniel 2006).

Phenology.— Flowering: October–March; fruiting: year-round especially during July–March.

Distribution and habitats.— Throughout northern and eastern Madagascar (Antsiranana, Fianarantsoa, Toamasina, Toliara) and known from a few localities in central and west-central portions of the island (Antananarivo, Fianarantsoa, Mahajunga); also on Mayotte in the Comoros Archipelago (EOO = 458,376 km^2; Fig. 12). Plants occur in lowland and montane, primary and secondary, moist to wet, evergreen forests; degraded secondary forests; gallery forests; dry deciduous forests; and coastal forests. Elev. 5–2000 m.

Illustrations.— Baker (1883:t. 26); Benoist (1967:5, Fig. 1); Figs. 11E, F and 13.

Local names.— "Mbarahanjelinala" (*Razafitsalama et al. 136*); "vahimbarongy" (*Kotozafy et al. 372*); "vahivarongy" (*Kotozafy 125*).

Morphological variation within and among the many collections of *M. flagellaris* is apparent in size, shape, texture, and pubescence of leaf blades; bracteolar size, shape, and protuberance presence/absence; inflorescence development (dichasia in leaf axils vs. dichasia borne in axils of bracts on elongate racemes from leaf axils); and drupe size and shape. *Dorr et al. 3697* is atypical by having stems, leaves, peduncles, and abaxial surface of the bracteoles densely pubescent (pilose), as noted in the description above. Other collections (e.g., *van der Werff et al. 12665*) are somewhat intermediate between this collection and more typical ones by having more abundant trichomes, although shorter and antrorse to antrorsely appressed. The presence or absence of a pair of conspicuous, bulbous, and white protuberances on the basal portion of the abaxial surface of bracteoles is also variable. This feature, when present, is unique in the genus. Collections from throughout the geographic range of the species vary from having a pair of these on each immature and mature bracteole, having the protuberances when young but with the bracteoles becoming smooth at maturity, or having no protuberances on the immature or mature bracteoles. Some specimens show variation in this character on the same sheet. Several collections from northern Madagascar (e.g., *Andrianantoanina & Rocsceohclher 259, Andrianantoanina & Solotiana 74, Birkinshaw 127, Nicoll & Abraham 679, Rahajasoa et al. 202, Schatz et al. 1345*) have conspicuously spherical drupes (in dried state). In other characters (including presence/absence of bulbous basal protuberances on bracteoles) these plants show variation like that in non-spherical-fruited specimens.

Rakotomalala & Narison 227 (14°05′S, 048°24′E; MO), from the Réserve Spécial de Manongarivo in Antsiranana Province, appears similar to *M. flagellaris* in most characters, but differs in having dense, erect to flexuose trichomes to 2 mm long dispersed along the proximal third of the midvein on the abaxial leaf surface or forming domatia in the axils of the midvein and secondary veins. It is possible that all of these trichomes are associated with the domatia. This collection also has longer corollas (25 mm long) than otherwise observed in *M. flagellaris*, a pubescent calyx (with eglandular trichomes to 2 mm long), and a proximally pubescent style. The flower color (white with purplish markings) appears to conform to *M. flagellaris*. Although lacking flowers and the denser pubescence of *Rakatomalala & Narison 227*, *Gautier et al. 3512* (13°59′S 48°26′E; K, MO) from the same region, is otherwise similar and has what appear to be incipient domatia in the vein axils. The disposition of these collections requires additional study, and they are not treated as pertaining to *M. flagellaris* here. Other collections from the region of the Manongarivo Reserve

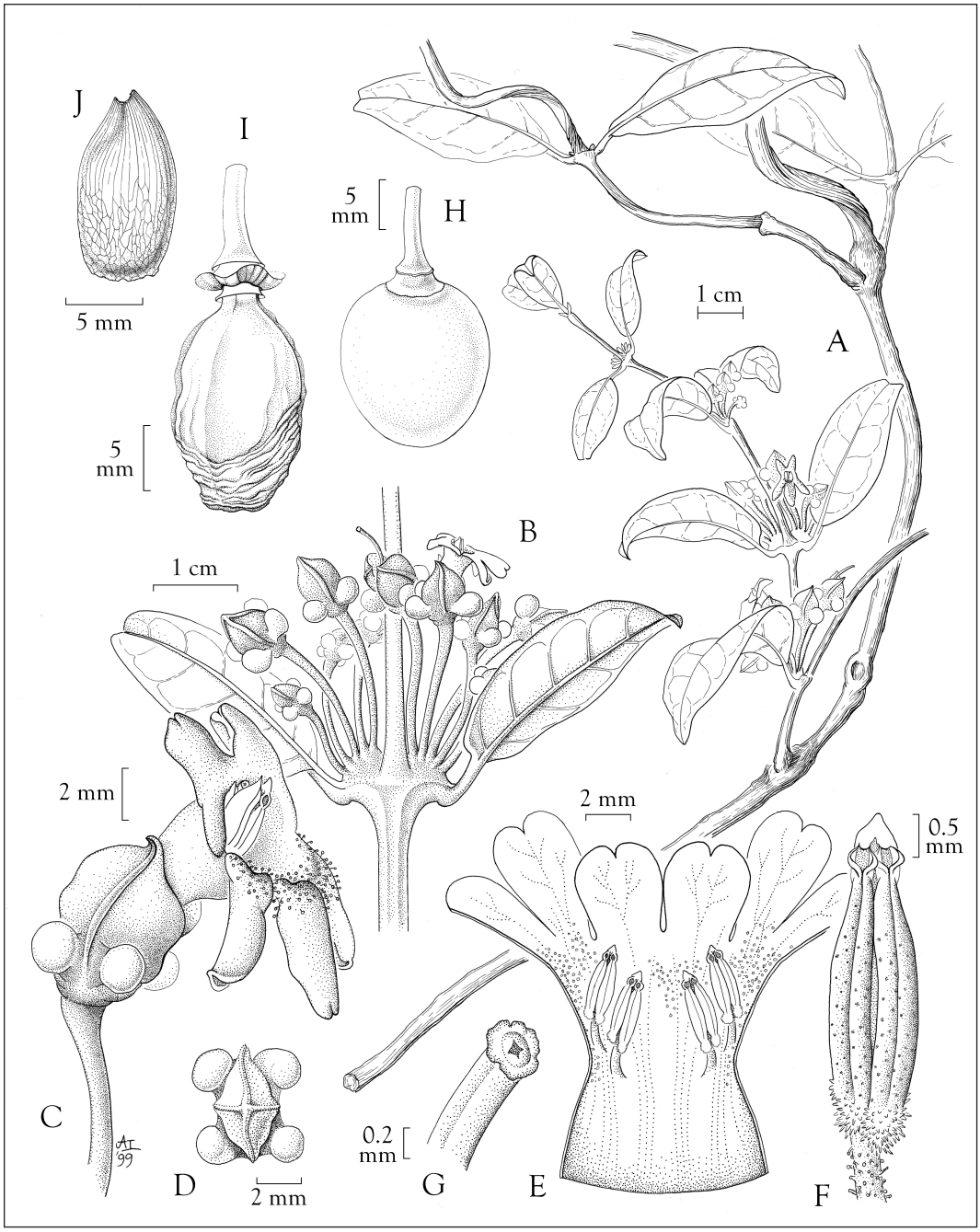

FIGURE 13. *Mendoncia flagellaris* (A–G, J, *Daniel et al. 9239*; H, I, *Razanatsima et al. 422*). A. Habit. B. Fertile node with multiple dichasia. C. Dichasium showing a flower and paired protuberances on bracteoles. D. Unopened bracteoles from above showing paired protuberances. E. Corolla split open to show androecium. F. Stamen showing two thecae bearing basal bristles, poricidal dehiscence, and extension of connective distal to pores. G. Apex of style and stigma. H. Fresh drupe (from photo) showing sequentially from top: distal portion of peduncle, calyx, and drupe. I. Dried drupe showing sequentially from top: distal portion of peduncle with flared apex, calyx with undulations, nectar disc, and drupe. J. Seed. Drawn by Jenny Speckels (A–G) and Becca Berezuk H–J.

(e.g., *McPherson & van der Werff 16410*, *Rakotomalala & Narison 103*) more closely conform to *M. flagellaris*, into which species they are placed here.

Two collections from Mt. Vato Vavy (21°24′S, 047°56′E) in eastern Fianarantsoa Province show similarities to *M. flagellaris* (e.g., white corollas with purplish markings), but appear to fall outside of the morphological variation of that species. Both collections represent fragments collected from the forest floor: *Daniel et al. 9291* (CAS) consists of dichasia from which the corollas have fallen, whereas *Daniel et al. 9295* (CAS), from a nearby site, consists of fallen corollas. Compared to *M. flagellaris*, the dichasia have mostly longer bracteoles (up to 16 mm long) and the corollas are larger in nearly all aspects (e.g., 24 to 34 mm long); thus both collections more closely resemble dichasia and corollas of *M. vinciflora*, which is currently known only from northern Madagascar. It remains unknown whether the corollas of the latter collection pertain to the dichasia of the former, and what characteristics the remainder of the plant(s) may have. Additional collections should resolve the identity or identities of these collections, which are not identified to species herein.

Additional specimens examined.— MADAGASCAR. **Antananarivo:** Mandraka, *D'Alleizette 1067* (P); La Mandraka, R.N. 2, at p.k. 69, 18°55′S, 047°56′E, *Dorr et al. 3697* (MO); PK 64 entre Tananarive à Perinet, *Keraudren-Aymonin & Aymonin 25314* (P); Bongolava, W de Tsiroanomandidy, [ca. 18°52′16.55′S, 45°42′08.53″E], *Morat 4645* (P); Manankazo, NE de l'Ankazobe, [ca. 18°09′S, 047°14′E], *Perrier de la Bathie 10247* (MO, P); Forêt d'Andranomay, 13 km SE d'Anjozorobe et 2 km E d'Andranomay, 18°28′48″S, 047°57′18″E, *Ranaivojaona 88bis* (MO); Ambohidratrimo, without collector, *435* (P), *s.n.* (P). **Antsiranana:** S d'Antsiranana, près de Joffre-Ville dans le PN de Montagne d'Ambre, campement de Ben Freed, 12°27′S, 049°13′E, *Andrianantoanina & Rocsceohclher 259* (BR, MO), *280*, (BR, MO); S d'Antsiranana, près de Joffre-Ville Parc Natl. de Montagne d'Ambre, campement de Chris, 12°35′S, 049°09′E, *Andrianantoanina & Rocsceohclher 309* (BR, MO); Montagne d'Ambre PN, 12°32′S, 049°07′E, *Andrianantoanina & Solotiana 74* (BR, CAS, MO); Montagne d'Ambre PN, 12°31′S, 049°09′E, *Andrianantoanina et al. 123* (CAS, MO); Nosy-Be, Réserve Intégrale de Lokobe, 13°24′35″S, 048°19′06″E, *Antilahimena 95* (MO); Réserve Naturelle Integrale de Tsaratanana, following Ramena River, Fok. Antsahabe, Fiv. Ambanja, 13°51′50″S, 048°50′53″E, *Antilahimena 433* (MO); Diana, Nosy Be, Lokobe Reserve Integral, 13°24′37″S, 048°18′33″E, *Antilahimena & Devigny 250* (CAS); Sahaenjika, Ampanavoana, Antalaha, Parc Masoala, 15°41′33″S, 050°13′30″E, *Bernard et al. 154* (CAS, MO); Nossi Be, Lokobe RNI, 5 km SE of Hellville, 13°25′S, 048°18′E, *Birkinshaw 48* (MO), *111* (MO) *127* (MO); Ambatosoratra, [ca. 14°32′S, 049°42′E], *Cours 3327* (P); Anjanaharibe, *Cours 3719* (P); Sous-préfecture d'Andapa, commune rurale de Doany, Fokontany de Betsomanga, versant NW du Marojejy, camp I, 14°25′S, 049°36′E, *Gautier & Andriamparany 3887* (K, MO); R.N. du Marojejy, *Guillaumet 4110* (P); Province de Diego-Suarez des Roussettes au grand lac de la Montagne d'Ambre, *Homolle s.n.* (P); Ankarana, forêt d'Analamalitso, S d'Arivorano-Nord, *Humbert 19070* (P); pentes E du Massif de Marojejy (NE), W de la Rivière Manantenina, affluent de la Lokoho, *Humbert 22550* (P); contreforts W du Massif de Marojejy (nord-est), près du col de Doanyanala (limite des bassins de la Lokoho et de l'Andraronga), [ca. 14°19′S, 049°37′20″E], *Humbert 23153* (P); partie W du Massif de Marojejy (NE) de la callée de l'Ambatoharanana au bassin supérieur de l'Antsahaberoka, *Humbert 31415* (P); Massif de l'Anjanaharibe (pentes et sommet N), W d'Andapa (haute Andramonta, bassin de la Lokoho, NE), [ca. 14°36′S, 049°27′E], *Humbert et al. 24655* (BR, K, MO, P) route Andapa–Doany, vallée de l'Andranotsara, *Jacquemin H565J* (P); N of Andapa, Anjanaharibe-Sud Réserve Speciale, 14°46′48″S, 049°28′42″E, *Malcomber et al. 2675* (MO); WNW of Andapa, NW of village of Ambodisatrana, 14°32′S, 049°26′E, *McPherson 17167* (MO); Manongarivo Massif, above millage of Ambodisakoana, E of Ankaramy,

14°05′S, 48°20′E, *McPherson & van der Werff 16410* (MO); Réserve Naturelle de Marojejy, N slopes of Ambatosoratra, 14°32′S, 049°41′E, *Miller 4206* (MO); RNI Ankarana, 12°51′S, 049°05′E, *Nicoll & Abraham 679* (CAS, MO); (Massif), M'Tsaratanana, [ca. 13°57′S, 048°52′E], *Perrier de la Bathie 2071* (P); M'Zaratanana (Massif Tsaratanana), *Perrier de la Bathie 15324* (P); Ambohitalana, Antalaha, [ca. 14°54′S, 050°16′30″E], *PN Madagascar 3382* (P); Sambava, *PN Madagascar (Sazy) 8837* (P); Réserve Speciale d'Ankarana, 12°55′S, 049°07′E, *Rahajasoa et al. 202* (MO); Réserve Speciale de Manongarivo, E d'Ankaramibe, Bekolosy, 14°03′05″S, 048°17′07″E, *Rakotomalala & Narison 103* (MO); Fiv. Andapa, Fir. Ambodiangezoka, Fok. Antanambe, Forêt Betaolana, 8.5 km NW d'Ambodiangezoka, le long de la rivière Ambolokopatrika, Campement 1, 14°32.3′S, 049°26.3′E, *Rakotomalaza & Ravelonarivo 1907* (MO); Andapa, Marojejy NP, near piscine naturelle, 14°26′26″S, 49°46′44″E, *Rakotonasolo et al. 1870* (CAS); Forêt de Besanatribe, Ambanja, *Rakotozafy 331* (P); Adnapa, Marojejy Natl. Park, 14°26′S, 49°43′E, *Ranarivelo & Ravelonarivo 783* (CAS); Andapa, Marojejy, ca. 15 km from Manantenina village, 14°26′50″S, 49°45′37″E, *Randriamboavonjy et al. 899* (CAS); Fiv. Ambanja, Forêt Classée d'Ambato, 40 km N d'Ambanja, près du village de Bevoay, piste vers Ankify, 13°27′S, 048°32′E, *Randrianaivo et al. 257* (MO); Sous-préfecture de Vohemar, commune rurale de Daraina, forêt d'Antsahabe, 13°12.88′S, 049°31.83′E, *Ranirison & Nusbaumer 1116* (MO); Réserve Naturelle integrale 12, Marojejy, N d'Andapa, aux environs du sommet de l'Est, 14°29′S, 049°38′E, *Rasoavimbahoaka 15* (MO); Réserve Speciale d'Anjanaharibe-Sud, Andapa, 14°36′S to 14°49′S, 049°23′E to 049°32′E, *Rasoavimbahoaka & Ravelonarivo 203* (MO); Préfecture d'Antalaha, Sous-préfecture d'Andapa, commune rurale de Bealampona, SW d'Andapa, Réserve Speciale d'Anjanaharibe-Sud, village d'Andranotsarabe, suivant la route Nationale d'Andapa–Bealanana de la piste à W, Ambatomainty, camp No. 2, 14°44′42″W, 049°27′42″E, *Ravelonarivo & Rabesonina 477* (CAS, MO); Fiv. d'Andapa, Fir. de Bealampona, Fok. de Befingotra, Réserve Speciale Anjanaribe-Sud, environs 37 km SW de l'ancien village de Mandritsarahely, piste vers Ranomafana, *Ravelonarivo & Rabesonina 741* (MO); Fiv. d'Andapa, Réserve Special d'Anjanaharibe Sud, aux environs du sommet, 14°46′15″S, 049°29′E, *Ravelonarivo et al. 17* (MO); Préfecture d'Andapa, commune rurale de Bealampona, village de Mandritsarahely, Réserve Speciale d'Anjanaharibe-Sud, suivant la piste vers Ranomafana, 5.5 km SW de Befingotra, campement no. 1, 14°45′03″S, 049°30′03″E, *Ravelonarivo et al. 420* (MO); Tsaratanana RN1, Fok. Beangona, 8 km de Beangona, Antsahamanara, 14°02′50″S, 048°47′09″E, *Razakamalala et al. 36* (CAS, MO). **Fianarantsoa:** col de Sakavalana, [ca. 20°44′48.41″S, 046°04′32.54″E], *Alluaud s.n.* (P); ca. 5 km NW of the main entrance to Ranomafana NP on the road to Vohiparara, 21°14′43″S, 047°23′48″E, *Almeda 8031* (CAS); Iakora, Begogo, Bekora, forêt de Sahalava S du village de Androizaha, 23°32′09″S, 046°32′21″E, *Andrianjafy et al. 740* (MO); environs d'Ivohibe, *Armand s.n.* (P); forêt basse au PK298 (sud Ambositra), *Cremers 3639* (P); Ranomafana Natl. Park, along road and Namorona River near cascade overlook ca. 5 km NW of main park entrance toward Vohiparara parcel, 21°15′S, 047°24′E, *Daniel et al. 9131* (CAS); Ranomafana Natl. Park, trail from Vatoharanana research camp to Valo research camp, 21°18′S, 047°25′E, *Daniel et al. 9157* (CAS); Ranomafana Natl. Park, Talatakely trail system S of Namorona River, 21°16′S, 047°26′E, *Daniel et al. 9239* (CAS); Ranomafana Natl. Park, Vohiparara trail system N of Namorona River (ca. 1.5 km N of cascade overlook along Hwy. 25), *Daniel 9271* (CAS); Ranomafana Natl. Park, Vohiparara trail system N of Namorona River (ca. 1.5 km N of cascade overlook along Hwy. 25), 21°14′S, 047°23′E, *Daniel et al. 9276* (CAS); Vondrozo, P. de Farafangana, [ca. 22°49′S, 047°19′30″E], *Decary 5311* (P); Massif di l'Kongo–P. de Farafangana, *Decary 5691* (MO, P); Fort Carnot, Prov. de Farafangana, [ca. 21°51′30″S, 047°26′30″E], *Decary 5804* (P); Ranomafana Natl. Park, trail to Vatoharanana from Talatakely, 21°17′S, 047°25′E, *de Nevers 11373* (CAS); Ranomafana Natl. Park, trail

between Vatoharanana and Takatakely parcels, 21°15′S 047°27′E, *Fritsch 1554* (CAS); Ranomafana Natl. Park, along trail between Vatoharanana and Takatakely parcels, just N of A1250 m trail marker, 21°15′S, 047°27′E, *Fritsch 1556* (CAS); Bassin de la Matitanana, Cascade d'Ankitso, Forêt de Tsianovoha, *Heim s.n.* (P); Réserve Speciale de Pic d'Ivohibe, forest of Marovitsika, [22°31′30″S, 046°59′E], *Hoffmann et al. 218* (K); Chaine du Vohibory (W d'Ivohibe), *Humbert 3126* (P); Pic d'Ivohibe (Bara), *Humbert 3309* (A, P, K, MO); haute valeé de la Rienana (bassin du Matitanana), *Humbert 3457* (K, P), *3564* (A, P); Akimba, near Ankerana, 30 km from Ambositra, E slope of watershed mountains, 20°37′S, 047°19′30″E, *Jongkind & Rapanarivo 908* (MO); 10 km S d'Ambalavao, *Keraudren-Aymonin & Aymonin 24621* (P); PN de Ranomafana, parcelle #3, Talatakely, piste AA, 21°15′S, 047°27′E, *Kotozafy 125* (BR, MO); PN de Ranomafana, parcelle #3, Vatoharanana, 21°15′S, 047°27′E, *Kotozafy & Randriamanantena 302* (MO); Parc Natl. de Ranomafana, aux environs de Vohiparara, 21°14′S, 047°23′E, *Kotozafy et al. 372* (BR, MO); Andringitra, Camp I, ca. 45 km S of Ambalavao, E bank of Iantara River, along Ambalamanenjana–Ambatomboay trail, edge of Andringitra Reserve, 22°13′20″S, 047°01′29″E, *Lewis et al. 759* (BR, MO); Andringitra, Camp III, ca. 40 km. S of Ambalavao, Andringitra Reserve, along tributary of Sahavatoy River, 22°13′22″S, 046°58′18″E, *Lewis et al. 944* (MO); between Fianarantsoa and Ifandiana, Route National 45, Parc Natl. Ranomafana, trail S from Cabine de Recherche to Vato camp, 21°15′S, 047°27′E, *Malcomber 1047* (MO); S of Farafangana, in Forêt Classée near Manombo Reserve, 23°03′16″S, 047°40′28″E, *McPherson & Rabenantoandro 18434* (CAS, MO); bord de l'Ihovika, bassin de Matitanana, *Perrier de la Bathie 10267* (P); Fiv. & Fir. Ivohibe, Réserve Speciale d'Ivohibe, 8 km E d'Ivohibe, 22°29′S, 046°58′06″E, *Rakotomalaza et al. 1447* (MO); Mahazony, Ambalavao, Ankotsobory, [ca. 22°13′30″S, 046°55′30″E], *Rakotonao 9178* (P); Sendrisoa, Ambalavao, [ca. 22°02′27″S, 047°00′34″E], *Rakotonao 9988* (P); Ivohibe, dans la RNI d'Andringitra, NO d'Ambarongy, SO du campement #3, 22°13′22″S, 046°58′18″E, *Rakotovao 270* (MO); Ivongo, Farafangana, Ankarenambe, *Rakotovao 613* (P); proche de Behazy-Sud Antomilahala, Farafangana, *Rakotovao 7485-RN* (P); Fiv. Ivohibe, Fir. Ivohibe, limite N de la Réserve Speciale d'Ivohibe le long de la rivière Ifefitany, 7.5 km ENE d'Ivohibe, Campement 1, 22°28′12″S, 046°57′36″E, *Rakotovao et al. 847* (MO); Ivohibe, Ivongo, Ambahatsy, RNI Andringitra, au 2e campement, forêt coupee par la riviere d'Iatara, 22°13′40″S, 047°00′13″E, *Razafindrabe et al. 98* (MO); Localité: R N V Canton: Antambohobe District: Ivohibe, *Razafindrakoko 3518-RN* (P); 7 km W of Ranomafana, on slopes above Namorona River, Duke Univ. Primate Center study site, 21°16′S, 047°25′E, *Schatz 2597* (MO); 7 km W of Ranomafana, just S of Namorona river, Duke Primate center study site, 21°16′S, 047°25′E, *Schatz & Miller 2444* (CAS, MO). **Mahajanga**: road from Antsohihy to Bealanana, 21–23 km E of Antsahabe, [ca. 14°44′7.95″S, 048°32′46.63″E], *Gentry 11738* (MO); Réserve Speciale d'Anjanaharibe-Sud, 11 km WSW Befingotra, 14°44′30″S, 049°26′30″E, *Lewis et al. 1309* (MO); Sous-préfecture de Befandriana-Nord, commune rurale de Matsoandakana, Quartier de Belalona, SW d'Andapa, Réserve Speciale Anjanaharibe-Sud, village d'Anjiamazava, suivant la route Nationale d'Andapa–Bealanana, piste vers le N approchant le sommet de Bevitsika, 14°42′S, 049°27′E, *Ravelonarivo & Rabesonina 558* (CAS, MO). **Toamasina**: Moramanga, Savoka, Ambodilongotra, village Coby André Daubercies, *Abraham 26779* (P); Phelps Dodge project site, ca. 15 air-km NE of Moramanga, ca. 11 km E of Antanambao, Ambatovy-South, 18°52′06″S, 048°18′23″E, *Andriatsiferana et al. 2162* (MO); PN de Masoala, sur la route d'Ambanizana à Analambolo (25 km N d'Ambanizana), ca. 6 km NE d'Ambanizana, Fiv. Maroantsetra, 15°34′07″S, 050°00′14″E, *Aridy et al. 44* (MO); 3 km ESE of Ankosy, on path from Ankosy to Antenina, 500 m from edge of RNI Zahamena, to 1000 m inside RNI, *Birkinshaw et al. 623* (MO); Ambohidavak'ely (D-43), District d'Ambatondrazaka, *Cours 515* (P); Moramanga, route d'Anjiro, *Cours 807* (P); District d'Ambatondrazaka, *Cours 953* (MO, P); Ambodimanga à

Antanambao, *Cours 2787* (P), *2792* (P); de Didy à Brickaville, *Cours 4832* (P), *Cours 4844* (P), *Cours 4874* (P); S de Moramanga, *Decary 6988* (P), *6994* (P); Fanovana, [18°55′30″S, 048°32′E], *Decary 17981* (K, MO, P); moyennevallée du Mangaro, *Decary 18475* (P); Lac Alaotra-D43, [ca. 17°29′16.28″S, 048°34′2.81″E], *Jardin Botanique de Tana 3901* (P); Soanierana–Antasibe, *Lam & Meeuse 825* (P); bords de torrents entre Sandrangato et Anosibe (S de Moramanga), *Leandri 1679* (K, MO, P); East Coast, Betampona Réserve Naturelle Integrale, 40 km NW of Toamasina, [ca. 17°54′S, 049°13′E], *Lewis & Razafimandimbison 688* (MO); Maroantsetra, trail E of village of Hiaraka, ESE of Maroantsetra, across bay, on NW coast of Masaola Peninsula, [15°29′S, 049°54′E], *Lowry et al. 4045A* (MO); Maroantsetra, Masoala Peninsula, Antalavia, ca. 22 km S of Ambanizana, along trail NE from "village" to Ampatra river, 15°46′S, 050°01′E, *Lowry 4330A* (CAS, MO); W of Vavatenina, Réserve Naturelle Integrale Zahamena, forest of Amboditamenaka, 17°44′S, 049°00′E, *Malcomber et al. 2518* (MO), *2575* (MO); NE of Moramanga, at nickel mining exploration site, Ambatovy, 18°51′25″S, 048°17′50″E, *McPherson 17475* (MO); near Andasibe, forest of Mantadia, beyond graphite mine, 18°55′S, 048°25′E, *McPherson & van der Werff 16472* (MO); near Andasibe, forest of Mantadia, beyond graphite mine, 18°55′S, 048°25′E, *McPherson & van der Werff 16539* (MO); Forêt d'Analamazoatra, *Perrier de la Bathie 10239* (P); Analamazoatra, *Perrier de la Bathie 10242* (P); Riv. Anove–Coli Est, *Perrier de la Bathie 10256* (P); Phelps Dodge project site, ca. 15 air-km NE of Moramanga, ca. 11 km E of Antanambao, Ambatovy, Antsahalava River east, 18°50′54″S, 048°17′56″E, *Rakotomalaza et al. 1102* (MO); fiv. Vivatenina, commune: Ambodimangavalo, 10 km W d'Antevibe-Sahandrazana, adjacente du Parc Natl. de Zahamena, 17°32′S, 48°48′E, *Rakotonandrasana et al. 714* (MO); Moramanga, commune: Ambohibary, fok.: Ampitambe, Ambatovy, NE de Moramanga, environ 22 km de Moramanga, 18°50′57″S, 048°17′18″E, *Rakotovao et al. 1321* (MO); district: Moramanga, commune: Ambohibary, fokontany: Ampitambe, Ambotovy, 22 km NE de Moramanga, 18°51′21″S, 048°18′22″E, *Rakotovao et al. 1407* (MO); Alaotra Mangoro, Moramanga, Andasibe, 18 km N from Andasibe, 18°48′49″S, 48°25′48″E, *Ranarivelo & Ranaivojaona* 322 (CAS); Maroanbehy, Tamatave, *Randriamahavita 9064-RN* (P); Parc Natl. de Zahamena, Antanandava, 2 km SW du village d'Ankosy, au sommet de la Forêt d'Ampangalambolosy, dans le parc, 17°29′38″S, 048°43′50″E, *Randrianasolo et al. 130* (MO); district: Fenerive-Est. Tampolo Forestry Station, along the "Grand Layon," ca. 1 km. from office, 17°17′S, 049°23′E, *Randrianasolo et al. 605* (BR, CAS, MO); sous-préfecture: Vavatenina, commune: Ambodimangavalo, fokontany: Manakambahiny, Parc Natl. de Zahamena, 17°29′30″S, 048°54′32″E, *Randrianjanaka et al. 652* (MO); Moramanga, Andasibe, Menalamba, entre Analamay et Ambatovy, 18°49′47″S, 048°18′41″E, *Razafindrabe et al. 127* (MO); fivondronana: Vivatenina, commune: Ambodimangavalo, fokontany: Manakambahiny I. Andranofantsona 10 km S de Manakambahiny I, au bord du rivière Ihofika, 17°39′17″S, 048°49′10″E, *Razafitsalama et al.136* (MO); Vatomandry, Ambalabe, Ambinanindrano II, NE du Tobin'I Foara, 19°09′26″S, 048°34′47″E, *Razanatsima & Ranaivojaona 36* (MO); Vatomandry, Ambalabe, Ambinaninandro II, E de Toby Foara, 19°09′46″S, 048°34′59″E, *Razanatsima et al. 66* (MO); Alaotra Mangoro, Moramanga, Beforona, Forêt Ankeniheny, 19°07′50″S, 048°32′10″E, *Razanatsima et al. 297* (MO); Alaotra Mangoro, Moramanga, Lakato, village Manasamena, forêt corridor Ankeniheny, *Razanatsima et al. 422* (MO); Alaotra Mangoro, Moramanga, Lakato, village Manasamena, forêt corridor Ankeniheny, 19°04′34″S, 048°30′40″E, *Razanatsima et al. 475* (MO); Nosy Mangabe, in the Bay of Antongil, 5 km S of Maroansetra, 15°30′S, 049°46′E, *Schatz & Carlson 2920* (MO); Nosy Mangabe, 5 km from Maroansetra in Bay of Antongil, 15°30′S, 049°46′E, *Schatz & Gentry 2177* (CAS, MO); Masoala Peninsula, just S of Ambanizana village, 15°36′S, 049°57′E, *Schatz et al. 1345* (MO); Nosy Mangabe, 5 km from Maroansetra in the Bay of Antongil, 15°30′S, 49°46′E, *Schatz et al. 2380* (MO); Perinet, Moramanga, *Service Forestier de Madagas-*

car 1214 (P); Analamazaotra, Perinet, *Service Forestier de Madagascar 1414* (P); Analamazaotra, *TAN 3746* (K, MO, P); Ranomafana, 19°06′S, 048°42′E, *van der Werff 12665* (MO); near Andasibe, forest of Mantadia, beyond graphite mine, 18°55′S, 048°25′E, *van der Werff et al. 13773* (MO); Masoala Peninsula, S of village of Ambanizana in Andranobe River watershed, 15°40′24″S, 049°57′51″E, *Vasey & Behasy 388* (MO); Province d'Andovoranto, District de Moramanga, Forêt d'Analamazaotra, près du col d'Amboasary, *Viguier & Humbert 984* (P). **Toliara**: Fort Dauphin, *Elliot 2532* (P); Massif de Beampingaratra (SE), du col de Bevava au sommet de Bekoho, [ca. 24°26′S, 046°53′30″E], *Humbert 6417* (P); bassin supérieur du Mandrare (sud-est), col et sommet de Marosoui, [24°32′S, 046°48′E], *Humbert 6599* (P); Massif du Kalambatitra (centre-sud), Mont Beanjavidy, [23°22′S, 046°27′E], *Humbert 12043* (P); Massif de l'Ivakoany (centre-sud), *Humbert 12217* (P); Fort Dauphin, Eminiminy, RN #11 Andohahela, Camp 3, 13.5 km NW d'Eminiminy, 24°35′S, 046°44′E, *Rakotomalaza 504* (MO). **Province undetermined**: Ankeramadinika, *Academie Malgache s.n.* (P); without locale, *Baron 1345* (P), *1743* (P), *1789* (P), *2828* (K, P), *2877* (P), *3214* (P), *3580* (K, P), *5149* (P), *Chapelier s.n.* (P), *Commerson s.n.* (P), without collector *345* (P); central Madagascar, *Baron 1463* (P), *2828* (K, P), *2920* (K, P), *3667* (K), *4196* (K, P); chiefly from NW Madagascar, *Baron 3749* (K); forêt N de la route de Nickelville sur les bords Ankotréano, *Cours 2079* (MO, P); S de Mangabe, *Cours 2505* (P); près Samalahaza, *Dequaire 27869* (P), *27963* (P); central Madagascar, Andrangaloaka, *Parker s.n*. (K); route Antsirabe à Fianarantsoa, Forêt d'Ambasofiterahana, *Keraudren 245* (P); Forêt de Fotsialanana, *Rakotozafy 672* (P); Sahamalaza, Forêt de l'Est aux confines du pays Sihanaka, *TAN 2827* (P). MAYOTTE (French island in Comoros Archipelago). **Grande Terre**: Combani, Bajoni, [ca. 12°47′39.06″S, 045°09′01.24″E], *Barthelat & Mchangama 1738* (CAS, K); Dzomougne, Réserve Forestière d'Hachiroungou, [ca. 12°43′01.85″S, 045°06′16.05″E], *Barthelat et al. 568* (CAS, MO, P); Accoua, Réserve Forestière d'Hachiroungou, [ca. 12°43′03.20″S, 045°03′54.22″E], *Barthelat et al. 597* (MO).

6. *Mendoncia gilgiana* (Lindau) Benoist, *Bull. Soc. Bot. France*. 85:679. 1939 ("1938"). *Afromendoncia gilgiana* Lindau, *Bot. Jahrb. Syst*. 20:1. 1894. *Monachochlamys gilgiana* (Lindau) S. Moore, *J. Bot*. 67:227, in clavi. 1929. **Type**.— CAMEROON. **Southwest**: Urwald zwischen Barombi-ba-Mbu und Kake [ca. 04°37′51.92″N, 009°23′46.03″E], 4 Sep 1890, *Preuss 481* (lectotype, designated here: K-000393683!; isolectotypes: BM. K-00393682!, P-00435324!).

Mendoncia gilgiana (Lindau) Benoist var. *tisserantii* Benoist, *Bull. Soc. Bot. France* 85:679. 1939 ("1938"). **Type**.— CENTRAL AFRICA REPUBLIC: **Ouaka**: région de la Oubangui, 20 km N de Bambari [ca. 05°56′0.74″N, 020°40′18.05″E], 10 Oct 1925, *Tisserant 2055* (lectotype, designated here: P-00435316!).

Young stems pubescent (sometimes sparsely so) with yellowish or golden-brown, antrorse to antrorsely appressed or retrorse to retrorsely appressed, unbranched, eglandular trichomes 0.1–1 mm long, sometimes also with minute (i.e., < 0.05 mm in diameter), sessile glands and/or an overstory of flexuose to antrorse to recurved, yellowish or golden-brown, unbranched, eglandular trichomes 1.6–2.3 mm long, trichomes of internodes soon becoming sparse. Leaves subcoriaceous, petioles to 57 mm long, pubescent like young stems, blades ovate-elliptic to elliptic, 20–116 mm long, 8–63 mm wide, rounded to truncate to subcordate at base, acute-apiculate to subacuminate- to acuminate-aristulate at apex, abaxial surface sparsely pubescent with scattered, erect to flexuose to antrorse to antrorsely appressed, golden-brown, unbranched, eglandular trichomes 0.2–1.5 mm long, trichomes sometimes concentrated on or restricted to major veins or only a few present on midrib near base of blade, adaxial surface glabrous or pubescent like abaxial surface. Inflorescences borne on young, leafy stems in axils of leaves, solitary or opposite at nodes, dichasia 1–5

per axil, peduncles to 25 mm long, sparsely pubescent like young stems. Bracteoles white to pale green (often tinged with pink or red) or purplish, mostly persistent in fruit, subcircular to elliptic to broadly ovate to lanceolate, 7.2–23 mm long, 3.6–16 mm wide, truncate to rounded to subcordate at base, acute to acuminate and sometimes apiculate at apex, apicule to 1 mm long, abaxial surface and margin mealy-glandular and usually pubescent (sometimes sparsely so) with an overstory of erect to flexuose trichomes similar those of overstory trichomes of young stems (except up to 3 mm long), adaxial surface glabrous to mealy-glandular. Calyx glabrous. Corolla white to purplish, 15.8–25.5 mm long, externally glabrous, internally with cluster of sessile, glandular trichomes in throat near stamen insertion, tube 9–20.4 mm long, limb 9–13.1 mm in diameter, upper lip 3.5–8.7 mm long with rounded lobes 2.8–5.3 mm long and 2.3–4.5 mm wide, lower lip 3.3–9.6 mm long with rounded lobes 2.3–7.4 mm long and 2.3–8.4 mm wide. Stamens 3.3–7 mm long, thecae 3.4–5 mm long, densely pubescent at base with a tuft of bristles 0.05–0.3 mm long and sometimes with sessile to subsessile grands dorsally, connective extending 0.4–1.1 mm beyond thecae, extension of connective attenuate, glabrous, staminode 0.8–1.5 mm long. Pollen 5-colpate, E = 24–34 µm, P = 27–35 µm, P:E = 1.049–1.186, C = 5.6–8.5 µm, C:P = 0.169–0.242, rugulae microverrucate to microgemmate to microbaculate. Style 6.5–20 mm long, glabrous or sometimes mealy-glandular near base, stigma subequally 2-lobed, lobes 0.1–0.4 mm long. Drupe ± irregularly shaped, overall obovoid and widest at or just below apex, 6.8–11.8 mm long, 4.8–9.0 mm in diameter (at widest diameter near apex), apically truncate to abruptly and either symmetrically or asymmetrically acute, glabrous to mealy-glandular.

Phenology.— Flowering: all year with peak flowering during July–November; fruiting: July–April.

Distribution and habitats.— Widespread throughout tropical Africa (Cameroon, Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea, Gabon, Ghana, Guinea, Ivory Coast, Kenya, Liberia, South Sudan, Tanzania, and Uganda; EOO = 4,487,300 km^2; Fig. 14). Plants occur in lowland and montane, primary and secondary, moist to wet, evergreen forests; secondary bush; gallery forests; swamp forests; forest edges; roadside thickets; and in clearings. Elev. 100–1600 m.

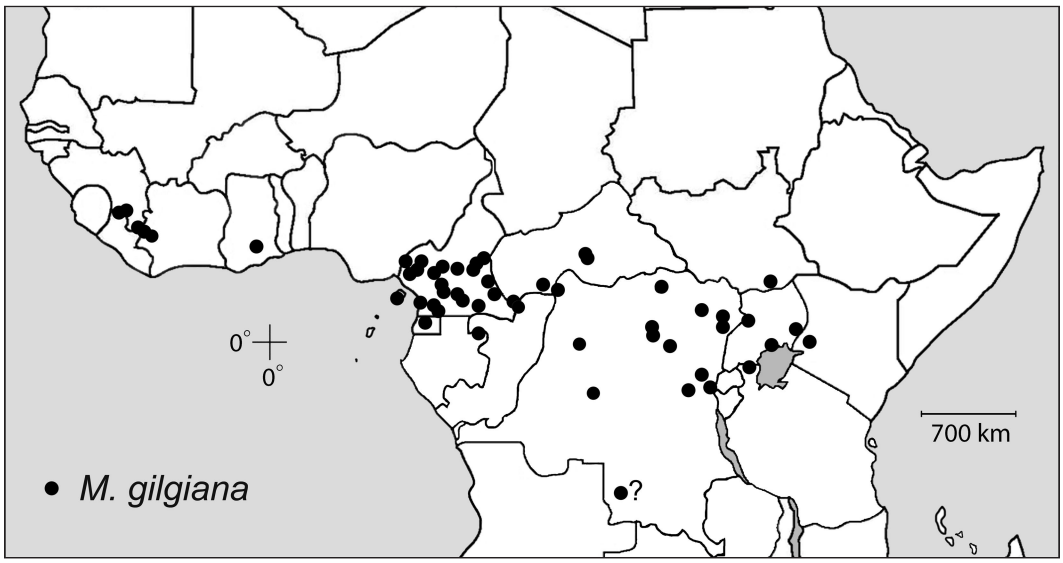

Figure 14. Map of central Africa showing distribution of *Mendoncia gilgiana* (see text for explanation of question mark).

Illustrations.— Lindau (1895:290, Fig. 115, D–M); Heine (1966:69, Pl. 14); Vollesen (2008:77, Fig. 12); Fig. 15.

In the progologue of *Mendoncia gilgiana* Lindau (1894) cited two collections (*Preuss 481* from Cameroon and *Stuhlmann 2690* from Congo-Kinshasa). The syntypes were presumably at B and are no longer extant. A lectotype is chosen from isosyntypes at K. Duplicates of *Stuhlmann 2690* were not located during our studies. The lectotype of *M. gilgiana* var. *tisserantii* is chosen from the three syntypes, all studied by us, cited in the protologue (Benoist 1939): *Tisserant 599*, *Tisserant 2055*, and *Lebrun 1613*.

Bracteolar shape among specimens of *Mendoncia gilgiana* varies widely from subcircular to ovate-elliptic to broadly ovate to lanceolate. Pubescence is also variable in this species. For example, some collections (e.g., *de Wilde 7888* and *Leeuwenberg 6236*, both from Cameroon) have both

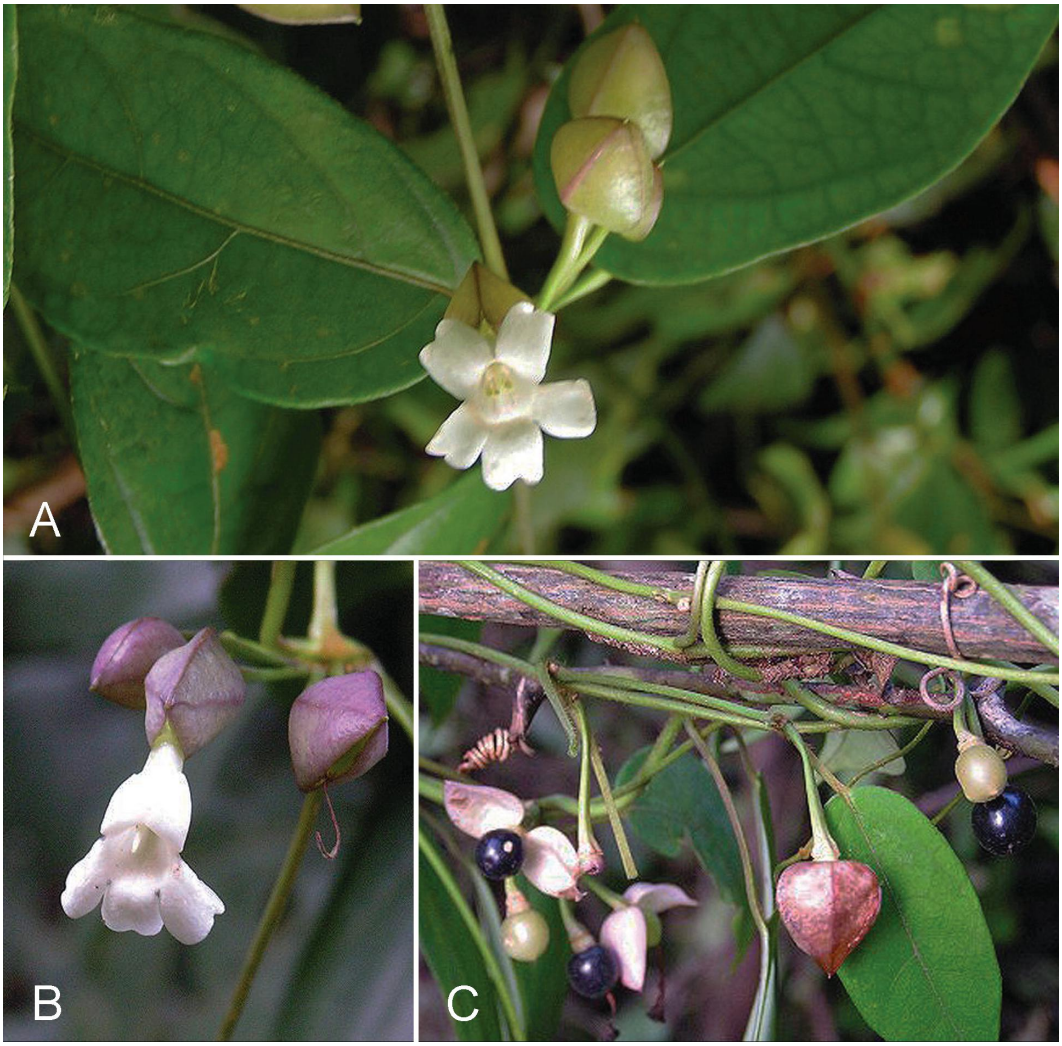

Figure 15. *Mendoncia gilgiana*. A. Node of young stem with open flower on one dichasium and greenish bracteoles. B. Flower and pinkish purple bracteoles. C. Mature drupes and spreading and deciduous bracteoles. (Photos by Jos Stevens from southeastern Congo-Kinshasa; African Plants-A Photo Guide: www.africanplants.senckenberg.de; non-commercial scientific and educational use; see text for additional information).

the overstory and understory trichomes on young stems, peduncles, and bracteoles, whereas others (e.g., *Adam 29700* and *29644*, both from Liberia) have only the sparse understory trichomes on young stems and peduncles and glabrous bracteoles. In *Aké Assi 5424* from Ivory Coast, the young stems, peduncles, and bracteoles all bear only the understory type trichomes. Benoist (1939) distinguished *M. gilgiana* var. *tisserantii* from the nominate variety by its stems, petioles, and bracteoles being sparsely pilose. A few years later, however, he only mentioned *M. gilgiana* (Benoist, 1944). After studying this species throughout its range, this variety was not accepted as distinct by Heine (1966). Pubescence varies widely throughout the range of the species, and we concur that recognition of var. *tisserantii* seems unwarranted.

Ndolo Ebika 906 from Congo-Brazzaville would appear to be the first record of *Mendoncia gilgiana* from that nation. Plants from southern Congo-Kinshasa (Katanga: vic. Ferme Randu, ca. 09°19′3.22″S, 022°55′55.18″E; Fig. 14), known to us only from photographs by Jos Stevens (Fig. 15), appear similar to *M. gilgiana*, but would seem to differ by the spherical ripe drupes. Because drupe shapes in the descriptions here are based on dried fruits, it is possible that the fresh fruits of *M. gilgiana* are or can be spherical. This occurrence, the southernmost known record of the genus in Africa, is tentatively treated as pertaining to *M. gilgiana*, included in the EOO, and is indicated on the map with a question mark. Collections of *Mendoncia* from this region are desirable to verify the identity of these plants.

Additional specimens examined.— CAMEROON. **Central**: toward Nom in Ndokwanen, 19 km S of Ndikiniméki, [ca. 04°37′14.27″N, 010°52′43.92″], *Asonganyi 341* (P), *373* (P); 35 km SE of Yaoundé, S of village Mfoe, [ca. 03°38′52.89″N, 011°43′9.31″E], *Breteler 1790* (P); 7 km NNW of Yaoundé, village Ngoya II, [ca. 3°55′34.94″N, 11°29′14.41″E], *Breteler 1953* (A, K, P, UC); Nanga-Eboko, [04°40′11.88″N, 012°22′36.05″E], *Jacques-Felix 4756* (P); Ngoro et Séréré (30 km NNE de Bafia), [ca. 04°51′40.17″N, 011°23′12.42″E], *Letouzey 7915* (K, P); près N'Dokononoro, à 15 km SW de N'Dikinimeki, [04°38′37.42″N, 010°48′37.72″E], *Letouzey 10888* (K). **East**: 14 km NE of Doumé, near road to Bertoua and Dimako, [ca. 04°20′49.89″N, 013°31′23.22″E], *Breteler 767* (A, K, P); 43 km NW of Bertoua, along road from Mbang to Ebaka, [ca. 04°56′47.05″N, 013°29′34.52″E], *Breteler 1383* (P); Yokadouma, near Catholic mission, [ca. 03°28′16.96″N, 015° 4′27.19″E], *Breteler 1496* (P); Bertoua, 15 km along road to Deng Deng, [ca. 04°42′5.11″N, 013°37′24.93″], *Breteler 1834* (K, P); Bétaré Oya [05°35′52.58″N, 014°04′58.78″E], *Jacques-Felix 4574* (P); Dengdeng, [05°11′46.87″N, 013°31′33.11″E], *Jacques-Felix 4666* (P), *4667* (P); 12 km N of Ndemba II = 32 km N of KM 29 of road Bertoua–Nanga Ebbko, [ca. 04°46′57.92″N, 013°22′9.68″E], *J. Leeuwenberg 5960* (K, MO); near Momjépom, KM 21 of road Yokadouma-Moloundou, [ca. 03°21′59.02″N, 014°59′22.70″E], *Leeuwenberg 6236* (K, MO, P); Bangue (KM 75 route Yokadouma–Moloundou), [02°55′44.46″N, 015°14′46.21″], *Letouzey 5112* (K, P); près Yabenot II, 30 km SSE de Ngoila (Axe Lomie-Souanke), [ca. 02°24′32.18″N, 014°04′59.27″E], *Letouzey 12006* (P). **Littoral**: Ebone, Nkongsamba–Douala, KM 114, 004°52′N, 009°54′E, *Bamps 1517* (K, P); Ebo Forest Research Station (proposed Natl. Park), New Masseng trail, *J. Osborne et al. 166* (K). **South**: around Zoetele, 52 km SE Mbalmayo, [ca. 03°14′40.49″N, 011°51′55.62″E], *Asonganyi 125* (P); Station du Cacaoyer de N'Koemvone, 02°49′N, 011°08′E, *de Wilde 7519* (MO); hill roughly between N'Kolandom and N'Koemvone, 02°49′N, 011°09′E, *de Wilde 7888* (K, MO, P); Dept. Dja et Lobo, Nkolembembe, 60 km SE of Akonolinga, 3°15′N, 012°31′E, *Dongmo & Nkongmeneck 553* (MO); près Aveubé (25 km ENE de D'joum), [ca. 02°40′49.80″N, 012°54′13.83″E], *Letouzey 8283* (K, P); Meyo–Nyaka (9 km SSE Ambam), [ca. 02°18′53.94″N, 011°17′59.97″E], *Raynal & Raynal 10106* (P). **Southwest**: vicinity of Nyasoso, *Cable et al. 2882* (K), *3246* (K); Kupe village, hunter's path from Kupe village to mountain top, running to S and parallel with Esense river, 04°47′N, 009°41′E, *Cheek 7092* (K); Nyasoso, Mount

Kupe, Walter's Trail, 04°50′N, 009°42′E, *Cheek 7487* (F, K, P); Mt. Kupe, Nyasoso, Max's trail to top of mountain, 04°49′N, 009°42′E, *Cheek & Ebwekoh 5660* (K); Division Kupe-Muanenguba, Muambong, 04°58′N, 009°46′E, *Cheek et al. 9366* (K); Mt. Kupe, Gazette-Nyasoso, Nyasoso–Bedume road, God-dat trail (opposite Ngusi road), 04°52′N, 009°41′E, *Etuge M. et al. 2515* (K, MO); Mount Kupe, *Schoenenberger 1* (K); Mount Kupe, SW slope, main trail to the top from Kupe village, 04°45′N, 009°41′E, *Schoenenberger 51* (F, K, P); Division Kupe-Muanenguba, above Nyasoso on Mann's trail up Mt. Kupe, *Sidwell et al. 384* (K); Korup Natl. Park between Ikenge and Esukutang, ca. 6 km W of Ikenge, ca. 05°17′N, 009°05′E, *Thomas et al. 7603* (MO); Bakossi Mts., W of Bangem, 05°05′N, 009°42′E, *Thomas & Mcleod 5280* (MO). **Province not determined**: Samnat (Dikel), et Messimni (confluent Mékié-Djérem), *Letouzey 3602* (P). CENTRAL AFRICAN REPUBLIC. **Lobaye**: bord de la Lobé, 5 km NW de Boubatiki, [ca. 03°59′54.21″N, 017°49′38.56″E], *Badré 55* (K, P); région de Mbaiki et Boukoko, [ca. 03°52′30.12″N, 017°57′30.75″E], *Tisserant 118* (P). **Ouaka**: région de Bambari, Riv. Gbatemoze, 15 km NW de Bambari, [ca. 05°58′22.61″N, 020°36′23.67″E], *Tisserant 599* (P); galerie Ruiss. aff. Yamwé, 20 km N Bambari, [ca. 05°59′55.98″N, 020°33′34.63″E], *Tisserant 2055* (P). **Sangha-Mbare**: 45 km S of Lidjombo, E side of Sangha River, Ndakan study area, 02°21′N, 016°09′E, *Harris 2576* (K, MO); Dzangha camp, 11 km NE of Bayanga, 02°57′ N, 016°21′ E, *Harris 3523* (E-photo); 2 km W of Kongana camp, 02°47′N, 016°25′E, *Harris 4070* (E-photo). CONGO-BRAZZAVILLE. **Sangha**: Bomassa, 02°12′38″N, 016°11′38″E, *Ndolo Ebika 906* (E-photo). CONGO-KINSHASA. **Equator**: Sud-Ubangi, Libenge-Ubangi, [ca. 03°36′57.63″N, 018°37′59.24″E], *Lebrun 1613* (F, P). **North-Kivu**: Manyema, Mutongo, Terr. Walikale, [01°21′00.61″S, 028°05′42.06″E], *Gutzwiller 3314* (K, MO). **Orientale**: Bambesa, [ca. 03°26′31.83″N, 025°41′8.31″E], *Blomme 143* (K); Yaliboto vers Yalibonga (Bengamisa), Yanonge, [ca. 00°34′08.45″N, 24°42′54.02″E], *Bolangi Bo'yanguma 64* (P); Ituri Distr., Mongbwalu, N of Msisi village, 01°59.56′N, 030°00.29′E, *Bytebier et al. 3293* (K); Bas-Uele, *Dewulf 135* (CAS); terr. Monkoto, Iwama, [ca. 02°08′38.46″S, 021°34′01.12″E], *Evrard 2830* (K); terr. Befale, Kikako, [ca. 00°16′20.68″N, 020°58′31.99″E], *Evrard 3055* (K); Bambesa, [03°27′33.85″N, 25°42′09.68″E], *Gerard 3286* (K)*, 4567* (MO); Irumu–Beni, KM 100, 01°27′N, 29°52′E], *Gille 261* (F, P); Wamba–Uele, [ca. 02°08′01.69″N, 28°00′43.19″E], *Lebrun 3281* (P); Haut-Zaire, 12 km E de Wanie-Rukula, [00°12′04.18″N, 25°35′40.19″E], *Lisowski 15616* (K), *16153* (K); Ituri**,** Mont Hoyo, bord de la route forestiere menant vers le Poste Hoyo, [ca. 01°13′05.37″N, 29°48′48.74″E], *Lisowski 41144* (K); Yangambi, KM 6 route de Ngazi, *Louis 517* (FHO); Yalibwa, en Yangambi, [ca. 00°54′20.78″N, 024°28′53.65″E], *Louis 1350* (CAS); Yangambi, reserve division cafeiers, *Louis 5700* (K, P); Yangambi, [ca. 00°48′40.29″N, 024°32′19.70″E], *Louis 7622* (K, MO-photo, P); Yambuya [ca. 01°15′45.47″N, 24°33′13.83″E], *Louis 7735* (K, P). **South-Kivu**: Panzi**,** galerie de la Makita, *Callens 3436* (K); Terr. Kalehe, près vill. Makwe, KM 105 route Kavumu–Walikale, [01°56′6.98″S, 028°27′57.96″E], *Christiaensen 1847* (MO); Muhaki Terr. Shabunda, [ca. 02°43′29.14″S, 027°20′54.96″E], *Leonard 3937* (CAS). **Province not determined**: Semlike, *Kassner 3102* (P). EQUATORIAL GUINEA. **Bioko Sur**: between Musola and Concepción, [ca. 03°24′48.92″N, 008°41′49.84″E], *Wrigley & Melville 549* (K). **Centro Sur**: KM 90–91, Bata–Niefang–Monte Alen, proximo a Niefang–Evinayong, [ca. 01°34′27.22″N, 010°22′25.58″E], *Carvalho 5376* (MO). GABON. **Ogooue-Ivindo**: Mekambo, [ca. 01°00′34.82″N, 013°57′07.65″E], *Hallé 2595* (P). GHANA. **Eastern**: Atewa Range F.R., [ca. 06°08′31.24″N, 00°36′26.58″W], *Hall & Enti 39461* (K). GUINEA. **Macenta**: Mts. Ziama, path from Sérédou to large antenna on Mt. Papo, [08°22′32.30″N, 009°19′34.63″W], *Burgt 1290* (K). IVORY COAST. **Dix-Huit Montagnes**: entre Danané et N'Zo, [07°07′30″N, 007°46′17″W], *Aké Assi 5424* (G); Nimpleu, près du Mont Momy [07°27′4.12″N, 008°04′43.59″W], *Aké Assi 7047* (P). **District not determined**: frontière Guinèe-

Côte d'Ivoire, *Nozerau s.n.* (P). KENYA. **Vihiga**: Yala River Forest, side opposite Nature Reserve, near Quarry Hill, [ca. 00° 00′11.40.67″N, 034°52′58.04″E], *Gilbert 6886* (K). LIBERIA. **Lofa**: Nekabozu District, Voinjama, [ca. 08°22′21.21″N, 009°44′14.46″W], *Baldwin 9971* (K). **Nimba**: Yéképa, forêt frontière Guinée, [ca. 07°34′08.39″N, 08°30′40.52″W], *Adam 29644* (MO); Yéképa, Gangra Road, *Adam 29700* (MO). SOUTH SUDAN. **Eastern Equatoria**: Talanga**,** Imatong Mountains, 04°01′N, 32°45′E, *Friis & Vollesen 494* (K). TANZANIA. **Kagera**: Bukoba Distr., Minziro Forest Reserve, 01°05′S, 031°32′E, *Bidgood et al. 4858* (CAS, K); Bukoba Rural Distr., Minziro Village, Nyakabanga, near Kagera River, 01°03′09″S, 031°35′59″E, *Festo et al. 266* (K, MO); Bukoba Rural Distr., Minziro Forest Reserve, SW of Minziri village toward Mtukula, 01°02′33″S, 031°29′47″E, *Festo et al. 1292* (K, MO); Bukoba Rural Distr., Minziro Forest Reserve, 01°01′06″S, 031°37′06″E, *Simon & Bayona 364* (K, MO). UGANDA. **Central**: Entebbe, [ca. 00°05′59.73″N, 032°28′07.20″E], *Brown 314* (K); Wakiso Distr., Kajansi Forest, mile 10 Entebbe Rd., [ca. 00°12′13.91″N, 032°33′02.57″E], *Chandler 1898* (K, P); Mengo Distr., ca. 5 mi SW of Mpigi, Mpanga Forest Reserve, [ca. 00°12′16.93″N, 032°18′30.07″E], *Drummond & Hemsley 4745* (K). **Eastern**: Bugisu Distr., Namatale L.F.R., [ca. 01°06′14.69″N, 034°25′07.00″E], *Philip 927* (K); **Western**: Busingiro, Budongo, *Harris 143* (K); Bulisa Distr.**,** Budongo Forest, [ca. 01°47′36.98″N, 031°35′38.77″E], *Loveridge 106* (A, K, MO-photo); Masindi Distr., Siba Forest, [ca. 01°41′49.74″N, 31°27′12.42″E], *Sangster 15* (K); Bunyoro Distr., Bujenje Co., Budongo Forest, [ca. 0147′46.52″N, 031°34′55.61″E], *Synnott 601* (K). **Region not determined**: Forest (Makia?), Mubango?, *Drummer 5586* (K); without locality, *Scott 7331* (K).

7. ***Mendoncia kely*** Magnaghi, *Novon* 23:191. 2014. **Type**.— MADAGASCAR. **Antsiranana**: contreforts occidentaux du massif de Marojejy (NE) près du col de Doanyanala (limite des bassins de la Lokoho et de l'Andraronga), N d'Andapa, [ca. 14°32′47″S, 049°40′6″E], 800–1200 m, 25 Jan–25 Feb 1949, *Humbert 23067* (holotype: P-00493688!; isotypes: K!, MO!).

Young stems evenly and densely pubescent with yellowish to golden-brown, retrorse to flexuous to erect, unbranched, eglandular trichomes 0.1–1 mm long. Leaves subcoriaceous, petioles to 18 mm long, pubescent like young stems, blades subdeltate to ovate to elliptic to subcircular, 26–75 mm long, 18–45 mm wide, truncate to rounded to subcordate at base, (retuse to) acute to acuminate to abruptly acuminate at apex, abaxial surface mealy-glandular and pubescent like young stems, except trichomes to 1.5 mm long and often denser on major veins, adaxial surface more sparsely (often denser on major veins) pubescent with mostly antrorse trichomes to 1 mm long, trichomes often with a prominently pustulate base. Inflorescences borne in leaf axils on young, mostly herbaceous, and leafy stems, solitary or opposite at nodes, dichasia 1–5 per axil, peduncles to 30 mm long, pubescent like young stems, except trichomes mostly erect to flexuose and up to 1.5 mm long. Bracteoles green to greenish-white, deciduous in fruit, (ovate-elliptic to) elliptic to subcircular, (4–) 6.2–15.6 mm long, 3–13 mm wide, rounded at base, rounded to rounded- (to truncate-) apiculate (to subacuminate) at apex, apicule 0.1–0.3 mm long, abaxial surface densely pubescent with yellowish to golden-brown, erect to flexuose, unbranched, eglandular trichomes to 1.7 mm long and mealy-glandular, adaxial surface mealy-glandular. Calyx densely pubescent with erect to flexuous, yellowish to golden-brown, unbranched, eglandular trichomes to 1 mm long. Corolla pink at base, white at apex, and otherwise white with purple markings or purple with white markings, 13.2–19 mm long, externally glabrous to mealy-glandular, internally glabrous to mealy-glandular (prominently so at and proximal to region of insertion of stamens) and with a patch of stipitate glandular trichomes to 0.5 mm long at base of lower lip and in throat, tube 10–14 mm long, limb 9.3–16.4 mm in diameter, upper lip 4.7–8 mm long with rounded lobes 3.6–6.5 mm long and

3–6 mm wide, lower lip 6.5–9 mm long with rounded lobes 3.5–7.2 mm long and 4.4–8 mm wide. Stamens 4–5 mm long, ventral pair inserted 0.8–1 mm distal to dorsal pair, filaments (and adjacent corolla tube) mealy-glandular, thecae 3.3–3.5 mm long, pubescent at base with a tuft of bristles 0.1–0.3 mm long, these extending towards apex of thecae, connective extending 0.2 mm beyond thecae, extension of connective triangular, glabrous, staminode not seen. Pollen 5- or 6-colpate [?], E = 27 µm, P = 28 µm, P:E = 1.03, C = 7.8–8.7 µm, C:P = 0.283–0.314, rugulae smooth. Style 9–9.8 mm long, glabrous, stigma asymmetrically subcapitate to subequally 2-lobed, lobes 0.2–0.4 mm long. Drupe ovoid-ellipsoid to ellipsoid to oblong to obovoid, 8.4–13.2 mm long, 7.1–10.5 mm in diameter, pubescent with erect to flexuose, eglandular, unbranched trichomes 0.3–1 mm long and mealy-glandular.

Phenology.— Flowering: January–February; fruiting: July–November.

Distribution and habitats.— Northeastern and southeastern Madagascar (Antsiranana, Toliara; EOO = 67,478 km^2; Fig 16). Plants occur in lowland and montane, wet, evergreen forests. Elev. 250–1200 m.

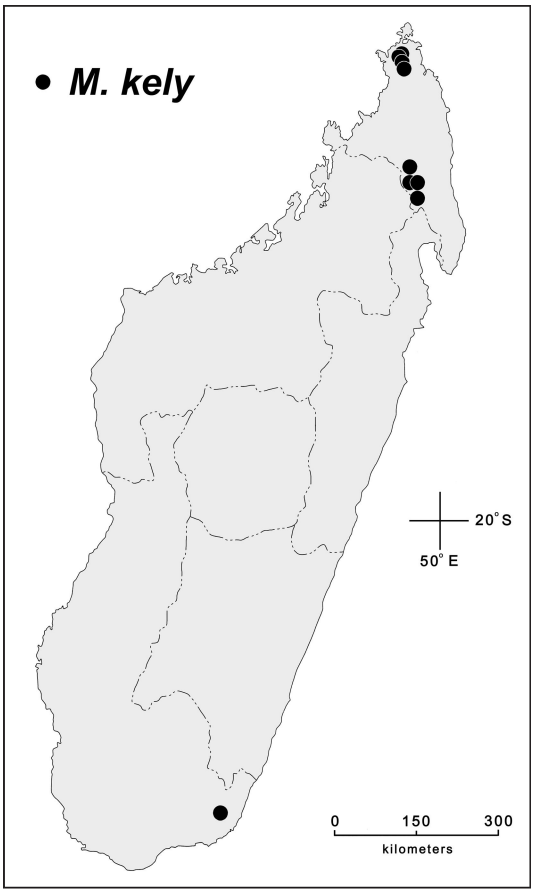

FIGURE 16. Map of Madagascar showing distribution of *Mendoncia kely*.

Most collections of *Mendoncia kely* have been determined previously as *M. cowanii*. It differs from that species by its shorter corollas with shorter tubes, leaf blades that lack domatia on the abaxial surface, shorter stamens and style, and smooth rugulae of pollen exine. Additionally, in most collections of *M. kely*, the leaf blades tend to be broadly ovate to elliptic (with length:width of 1.2–1.8 vs. length:width of 1.7–2.8 in *M. cowanii*) and short (up to ca. 6 cm long). In a few collections of this species (e.g., *Antilahimena et al. 4587*, *Rakotovao et al. 2740*) some or all blades are ovate (with length:width 2–2.3) and longer (up to 7.5 cm long).

Additional specimens examined.— MADAGASCAR. **Antsiranana**. Roussettes SF, 12°31′S, 049°08′E, *Andrianantoanina & Bezana 213* (BR, CAS, MO); Fivondronana Antsiranana II. Parc Natl. de Montagne d'Ambre, a environ 70 km SW d'Antsiranana par route, et 9 km W du village de Marovato Scama (Anivorano), campement Andasibe, 12°37′30″S, 049°11′43″E, *Andrianantoanina & Bezana 777* (BR, CAS, MO); S d'Ansiranana, près de Joffreville, à la station Roussette, 12°27′S, 49°13′E, *Andrianantoanina & Rocsceohclher 364* (BR, MO); près d'Antsalaka, Montagne d'Ambre PN, 12°27′S, 049°13′E, *Andrianantoanina et al. 221* (BR, MO); Andapa, Anjialavabe, Ankiakabe, Tsaralanto, 14°13′59″S, 049°23′17″E, *Antilahimena et al. 4587* (CAS); Montagne d'Ambre Natl. Park, SW of Ambohitra (Joffreville), ca. 12°30.5′S, 049°10′E, *Daniel & Butterwick 6742* (CAS), *Daniel 10591* et al. (CAS); WNW of Andapa, NW of village of Ambod-

isatrana, 14°32′S, 049°26′E, *McPherson 17159* (MO); Sava, Andapa, Ambodivohitra, à 12 km SW de la commune rurale d'Anjialavabe et N d'Anjialavahely, 14°14′12″S, 049°23′05″E, *Rakotovao et al. 2740* (MO); Préfecture d'Antalaha, sous-préfecture d'Andapa, commune rurale de Bealampona, village de Mandritsarahely. SW d'Andapa, Réserve Speciale d'Anjanaharibe-Sud, suivant la piste vers Ranomafana, 5.5 km SW de Befingotra, campement #1, 14°45′03″S, 049°30′03″E, *Ravelonarivo et al. 451* (MO). **Toliara**: Andohahela RNI, Parcelle #1, beside Itrotroky river, NW of Eminiminy, Fort-Dauphin, 24°38′S, 046°46′E, *Andrianantoanina et al. 11* (BR, MO).

8. *Mendoncia lindaviana* (Gilg ex Lindau) Benoist**,** *Mem. Soc. Linn. Normandie,* n.s.i. 2:44. 1928. *Afromendoncia lindaviana* Gilg ex Lindau *Bot. Jahrb. Syst*. 17:112. 1893. *Monachochlamys lindaviana* (Gilg ex Lindau) S. Moore *J. Bot*. 67:226, in clavi. 1929. **Type**.— GABON. **Estuaire**: Sibange-Farm on the Gaboon, Dec 1880, *Soyaux 156* (lectotype, designated here: K-000393685!).

Lirayea floribunda Pierre, *Bull. Mus. Hist. Nat. (Paris)* 2:342. 1896. *Afromendoncia floribunda* (Pierre) Burkill, *Fl. Trop. Afr.* 5:6. 1899. *Monachochlamys floribunda* (Pierre) S. Moore, *J. Bot*. 67:226, in clavi. 1929. *Mendoncia floribunda* (Pierre) Benoist, *Notul. Syst. (Paris)* 11:143. 1944. **Type**.— GABON. **Estuaire**: prope Libreville, [ca. 00°27′44.20″N, 009°28′34.84″E], 1891, *Jolly* 101 holotype: P-00435322!).

Afromendoncia klaineana Pierre ex Benoist, *Notul. Syst. (Paris)* 2:285. 1912, nomen nud.

Young stems glabrous to mealy-glandular, lacking elongate trichomes. Leaves coriaceous, petioles to 25 mm long, glabrous to mealy-glandular (rarely with antrorse, eglandular, unbranched trichomes to 2 mm long), blades ovate-elliptic to elliptic to lanceolate, 34–189 mm long, 11–80 mm wide, acute at base, (acute-apiculate to) subacuminate-aristate at apex, surfaces glabrous. Inflorescences (see discussion below) mostly borne on woody, peg-like short-shoots 2–10 mm long at leafless nodes of older, woody stems, short-shoots solitary or opposite at nodes, sometimes branched (branches appearing ± clustered or dendritic) in an axil and then to 20 mm long, dichasia 1–20 or more per axil at a time (but with peduncular scars on branched short-shoots revealing 100 or more dichasia present over time), peduncles purplish, to 42 mm long, glabrous. Bracteoles white to greenish white (often tinged with pink or purple) or pinkish or purplish, persistent as fruit matures and usually deciduous by maturity, ovate-elliptic to elliptic to subcircular to obovate, 6.6–16.7 mm long, 4.4–10 mm wide, acute- to acuminate-apiculate at apex, apicule 0.1–1.5 mm long, truncate to rounded at base, abaxial surface mealy-glandular (lacking elongate trichomes), adaxial surface mealy-glandular. Calyx mealy-glandular (sometimes mostly or exclusively so on or near marginal rim). Corolla white (sometimes pinkish at base), 13.5–24 mm long, externally ± mealy-glandular, internally mealy-glandular (especially on adaxial surface of lobes), tube 8.5–16.4 mm long, limb 7.2–18.3 mm in diameter, upper lip 2.8–8.4 mm long with rounded lobes 2.8–6.3 mm long and 2.2–6.5 mm wide, lower lip 5.7–11.2 mm long with lobes 2.9–7 mm long and 3.1–9 mm wide. Stamens 4.1–6.5 mm long, ventral pair inserted 1.2–1.6 mm distal to dorsal pair, thecae 2.2–4.6 mm long, pubescent at base with a tuft of bristles 0.1–0.2 mm long, these sometimes becoming sparse and extending toward apex, and also beset with mostly sessile glands on either dorsal or ventral surface, connective extending 0.2–0.5 mm beyond thecae, connective extension attenuate, sometimes with a cluster of sessile glands on dorsal surface at apex, staminode not seen. Pollen 6-colpate, E = 36 µm, P = 35 µm, P:E = 0.980, C = 7.8–8.2 µm; C:P = 0.223–0.236, rugulae sparsely microverrucate to microgemmate. Style 11.6–14 mm long, glabrous, stigma subequally to unequally 2-lobed, lobes 0.1–0.4 mm long. Drupe oblong, laterally compressed, 12.3–19.9 mm long, 6.5–14.5 mm in diameter, glabrous to ± mealy-glandular.

Phenology.— Flowering: August–June; fruiting: all year.

FIGURE 17. *Mendoncia lindaviana*. A. Older, woody shoot bearing dichasia with flowers and fruits at nodes. B. Flower. C. Dichasium with flower in background (showing relationship between style/stigma and anthers) and dichasium with corolla dehisced in foreground (showing 2-lobed stigma). D. Node of woody shoot showing dichasia borne on peg-like stubs and bearing young fruits. (A, C, photos by Xander van der Burgt of *M'Boungou et al. MR 421* from Congo-Brazzaville, used with permission; B, photo by Benedict John Pollard from Congo-Brazzaville, used with permission; D, photo and copyright by Ehoarn Bidault of *Bidault 900bis* from Gabon, on Tropicos [www.tropicos.org/Image/100228305], CC by-NC-ND 3.0).

DISTRIBUTION AND HABITATS.— Tropical central Africa (Cameroon, Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Gabon; EOO = 1,586,281 km^2; Fig. 7). Plants occur in lowland to montane, primary and secondary, wet, evergreen forests; semi-deciduous forests; swamp forests; gallery forests; and clearings. Elev. 60–1000 m. *Mendoncia lindaviana* also likely occurs in the continental portion of Equatorial Guinea, which lies between known occurrences in Cameroon and Gabon, but has no specimens have been seen from there.

ILLUSTRATIONS.— Thiselton-Dyer (1896:t. 2426); Heine (1966:67, Pl. 13); Fig. 17.

LOCAL NAME.— "Amokisemekiseme" (Kibila; *Madidi 332*).

Heine (1966) indicated that the holotype of *Afromendoncia lindaviana* was destroyed at B, and that there was an isotype at P. We were unable to locate the isotype at P, but there is another one at K, which we designate as the lectotype for this name.

A mature inflorescence bearing a branched short-shoot in *Mendoncia lindaviana*, as described above, is shown in Figures 3F, 17D. Rarely, dichasia are borne on younger shoots with leaves present at the nodes (e.g., *Breteler & Jongkind 10386*, *Madidi 332*). In these younger inflorescences, the short-shoots are present but only two to three mm long. Such plants are recognizable as pertaining to *M. lindaviana* by their lack of trichomes on stems, leaf blades, and peduncles; the usually aristate leaf apices (Fig. 3B); and the consistently oblong drupes (Fig. 3D).

Additional specimens examined.— CAMEROON. **Central**: Dja et Lobo, Koungoulou, 72 km SW of Akonolinga, *Nkongmeneck 1478* (K). **East**: Doumé, near Catholic mission, [ca. 04°14′34.60″N, 013°27′57.10″E], *Breteler 1858* (K, P); 27 km SW of Bertoua near Toungrélo village, *Breteler 2620* (K, P); Nkoue–Bertoua, *Letouzey 3051* (P); Ngondouma–Bertoua, *Letouzey 3102* (P); près des vallées du Dja et de l'Edjune–Abong-Mbang, [ca. 03°28′19.13″N, 013°22′41.29″E], *Letouzey 3806* (K, P); piste forestière Anpel-Mase–Abong-Mbang, *Letouzey 3994* (K, P); Matcheboum [04°06′39.58″N, 013°14′26.80″E] près Abong-Mbang, *Letouzey 4605* (K, P). **South**: colline Ongongo près Mbanga (km 81 route Kribi–Ebolowa, près Sous-préfecture Akom II), Nyabessan, *Letouzey 9484* (CAS, K, P); Bipinde [ca. 03°04′43.43″N, 010°24′58.48″E], *Zenker 194* (GH), *965* (K, P), *1801* (P), *s.n*. (P). CENTRAL AFRICAN REPUBLIC. **Sangha-Mbare**: Kongana, 25 km SE of Bayanga, 02°47′N, 016°25′E, *Harris 5029* (E-photo). CONGO-BRAZZAVILLE. **Kouilou**: Mayombe, near Niari River, 04°02′24.7″S, 012°09′52.4″E, *M'Boungou et al. MR 421* (MO); route Pounga–Dimonika, source "Paris Sangha," *Cusset 568* (P); environs de Dimonika, entre Tour Meteo et piste Kuilila–Makaba [ca. 04°08′3.44″S, 012°21′4.06″E], *Cusset 1193* (P); environs de Dimonika: versant E du Bamba, au-dessus de la Loubomo, *Cusset 1227* (P); Dimonika, *Moutsamboté 139* (P). **Lékoumou**: Mont Ndoumou, au niveau de village de Mandili, [ca. 03°22′9.19″S, 013°39′48.90″E], *Bouquet 1788* (P). **Department not determined**: Mayombe, *Hallé 1523* (P). CONGO-KINSHASA. **Equator**: Station Inéac Boketa, Riviere Wolo, [ca. 03°10′11.05″N, 19°48′01.59″E], *Evrard 1027* (BR); Bomputu (Boende), [ca. 00°18′51.74″S, 020°31′10.59″E], *Evrard 3977* (BR, K); Befale–Tolongote, [ca. 00°33′56.88″N, 020°45′18.57″E], *Evrard 4163* (BR). **Orientale**: Bambesa, [03°27′33.85″N, 25°42′09.68″E], *Gerard* 5537 (K); Terr. Isangi, Yabohondo, [ca. 00°44′22.47″N, 023°58′35.27″E], *Germain 8757* (K); Zone de Mambasa (Ituri), Epulu, 01°25′N, 028°35′E, *Hart 727* (BR, F), *925* (BR, F); Zone de Mambasa (Ituri Forest), Lenda [01°24′N, 028°34′E], *Kahimdo 87* (K, MO); Buta, [02°50′22.62″N, 024°44′9.04″E], *Lebrun 2539* (CAS); environs de Kisangani, le Kongole sur la Lindi, [ca. 00°34′11.07″N, 025° 07′57.16″E], *Lisowski 52254* (K); Jambao, a 25 km au NW de Jangambi, [ca. 0°54′40.16″N, 24°21′16.10″E], *Louis 8974* (MO, P); Lèlanda W de Janojambi, [ca, 00°47′58.47″N, 024°22′57.64″E], *Louis 10825* (K); Territoire Mambasa (Ituri Forest), Lenda, 01°24′N, 28°34′E, *Madidi 332* (K, MO). **North-Kivu**: Territory Kalehe, route Kavumu–Walikale, Trougi, [ca. 01°51′57.98″S, 028°29′54.26″E], *Troupin 2502* (K). **South-Kivu**: Tubalaka, Tsunyakini/Bunyakiri, Terr. Kalihe, [ca. 02°05′30.37″S, 028°34′36.47″E], *Gutzwiller 1398* (BR). GABON. **Estuaire**: Akoga, Mts. de Cristal, *Hallé 878* (P); Libreville, *Klaine 700* (CAS, P); 22 km Kougeleu–Asak, [ca. 00°26′5.99″N, 010°02′20.70″E], *Leeuwenberg & Persoon 13599* (K, MO, P); about 7 km E. of M'Voum, 24 km NE of Ntoum, 0°33′N, 009°52′E, *Louis et al. 275* (MO); River Muni, Corisco Bay, *Mann 1849* (K, P); Monts de Cristal: Tchimbélé Dam region, 00°37′N, 010°24′E, *McPherson 17918* (MO). **Moyen-Ogooué**: Missanga, 5-15 km NW of Ndjolé, 00°05′S, 101°45′E, *Breteler & Jongkind 10386* (CAS, G). **Ngounié**: between Mouila and Yeno, about 34 km on road from Mouila, 01°45′S, 011°20′E, *Breteler et al. 8106* (K, MO, P); old forest along Waka river, about 1–2 km SW of Forestry exploitation Camp Waka situated about 32 km SW of Sindara (by road 65km), 01°14′S, 010°53′E, *Louis et al. 1368* (MO); "Haute Ngounyé," *Le Tetsu 5497* (P); 60 km on road Mouila to Yeno, 01°41.91′S, 011°24.09′E, *Wieringa et al. 4552* (K). **Nyaga**: région du Nyanga; Manzembi,

[ca. -3.146086455, 10.91076607], *Le Tetsu 2104* (G, P). **Ogooué-Ivindo**: Belinga, Mines de Fer, [ca. 01°08′7.92″N, 13°12′07.74″E], *Aubreville et al. 20* (P); Belinga, about 2 km. along the lower track of Babiel Nord, *Breteler & de Wilde 723* (MO, P); Station I.R.E.T. (M'Passa Field Station), 10 km S de Makokou sur la rivière Ivindo [00°30′38.58″N, 012°48′15.73″E], *Dorr & Barnett 4241* (K, MO); Station d'Ipassa, 10 km S de Makokou, *Florence 812* (P); M'Passa Field Station, near Makokou on Riviere l'Ivindo, transect 17, *Gentry 33450* (MO); Makokou, [00°33′35.78″N, 12°53′17.72″E], *Hallé 1078* (P); 6 km NE de Mékambo, [ca. 01°01′12.92″N, 013°59′28.88″E], *Hallé 2599* (K, P); 15 km SW Makokou, CNRS Mission Biologique, [ca. 00°27′51.58″N, 012°45′33.04″E], *Hallé 2655* (K, P); Belinga, *Hallé 3005* (P), *3041* (P), *3240* (P), *3393* (P); Ipessa, 10 km S de Makokou, Layon J vers 620, *Hladik 2485* (P); Ipessa, Makokou, *Hladik s.n.* (P). **Ogooue-Lolo**: région de Lastoursville, [ca. 00°49′58.95″S, 012°40′21.68″], *Le Tetsu 7675* (P). **Woleu-Ntem**: about 22 km NE of Asok, [ca. 00°51′2.58″N, 010°27′48.27″E], *Breteler & de Wilde 234* (MO). **Province not determined**: région entre Ogooué et Cameroun, Bengò, *Le Tetsu 9117* (P); Ogoué (river), *Leroy s.n.* (P). COUNTRY UNDETERMINED. **Without locale**: *Hladik 1396* (P); "Nèuga," *Lana 191* (BR).

9. *Mendoncia phytocrenoides* (Gilg ex Lindau) Benoist, *Mem. Soc. Linn. Normandie*, n.s.i. 2:44. 1928. *Afromendoncia phytocrenoides* Gilg ex Lindau, *Bot. Jahrb. Syst*. 17:112. 1893. *Thunbergia phytocrenoides* T. Anderson ex Lindau, *Bot. Jahrb. Syst*. 17:113. 1893, pro syn. *Monachochlamys phytocrenoides* (Gilg ex Lindau) S. Moore, *J. Bot*. 67:227, in clavi. 1929. **Type**.—GABON. **Estuaire**: Muni River, Lat. 1°N, Sep 1862, *Mann 1839* (lectotype, designated here: K-000393679!; isolectotypes: P-00435325!, K-000393681!, K-000393680-photo!, W-0006693-photo!, S-SG128-photo!).

Afromendoncia iodioides S. Moore, *Cat. Pl. Oban* 74. 1913. *Monachochlamys iodioides* (S. Moore) S. Moore, *J. Bot*. 67:227, in clavi. 1929. *Mendoncia iodioides* (S. Moore) Heine, *Kew Bull.* 16:180. 1962. *Mendoncia phytocrenoides* var. *iodioides* (S. Moore) Heine (as "*ioides*"), *Fl. Gabon* 13:74. 1966. **Type.**—NIGERIA. **Cross River**: Oban [05°13′27.64″N, 008°33′18.53″E], 1911, *Talbot & Talbot 388* (holotype: BM-000930925-photo!; isotype: K-000393684-photo!).

Mendoncia letestui Benoist, *Notul. Syst. (Paris)* 11:143. 1944. **Type.**—GABON: **Ogooue-Lolo**: région de Lastourville, Moughounda [ca. 00°51′57.94″S, 012°46′57.20″E], 14 Aug 1930, *Le Testu 8250* (lectotype, designated here: P-00435326-photo!; isolectotypes: P-00435327!, BR-000000629448-photo!, BR-000000629442-photo!; K!; probable isolectotype: IFAN-16076-photo!).

Young stems evenly and densely pubescent with an overstory of flexuose to recurved, golden-brown or straw-colored, unbranched trichomes 1.4–5 mm long and a sparse to dense understory (sometimes ± inconspicuous) of branched (stellate to dendritic) trichomes 0.2–0.4 mm long, older stems sparsely pubescent to glabrate. Leaves subcoriaceous, petioles to 46 mm long, pubescent like young stems, blades broadly ovate to subcircular to elliptic to obovate-elliptic, 86–200 mm long, 57–114 mm wide, rounded to subcordate at base, subacute to acute at apex, abaxial surface pubescent with erect to flexuose, unbranched trichomes 1.3–2.7 mm long (especially on main veins), these sometimes overtopping an understory (sometimes very sparse) of branched trichomes 0.2–0.4 mm long (and sometimes very sparse and inconspicuous erect, glandular trichomes 0.1 mm long, as well), adaxial surface glabrous to ± mealy or pubescent along proximal portion of midvein with trichomes like those of abaxial surface. Inflorescences borne on older, woody, mostly leafless stems, solitary or opposite at nodes, dichasia 1–3 (–5) per axil, peduncles to 30 mm long, pubescent like young stems. Bracteoles red to purplish (or brown when dry), mostly persistent in fruit,

subcircular to ovate to elliptic to lanceolate, 12–37.8 mm long, 6.5–23.4 mm wide, rounded at base, acute-apiculate at apex, apiculum (usually obscured by pubescence) 1–2.8 mm long, abaxial surface and margin pubescent with flexuose to antrorse, mostly unbranched, golden-brown trichomes 1.5–5.5 mm long, these overtopping an understory of branched trichomes 0.1–1 mm long, adaxial surface ± mealy and sometimes with scattered trichomes to 1.5 mm long, major veins sometimes ± protruding abaxially resulting in a channeled appearance. Calyx pubescent with branched trichomes (fide Schönenberger and Endress 1998). Corolla white, 29.3–31.8 mm long, externally glabrous, tube 23.4–24.9 (–30) mm long, apically ampliate, limb 9.3–14.6 mm in diameter, upper lip 4.4–4.9 mm long with emarginate lobes 2.7–4.2 mm long and 4–5.2 mm wide, lower lip 6.5–7 mm long with emarginate lobes 4.4–5.3 mm long and 3.5–5.9 mm wide. Stamens 8.7–24.8 mm long, ventral pair inserted 1–2 mm distal to dorsal pair, thecae 2.4 mm long, pubescent at base with a tuft of bristles 0.1–0.2 mm long, these and glandular trichomes sometimes extending down the filament, connective extending 2–3 mm beyond thecae, connective extension attenuate, pubescent with glandular and eglandular trichomes 0.05–1 mm long, staminode 0.5–1.3 mm long. Pollen 5-colpate, E = 29–31 µm, P = 29 µm, P:E = 0.967–1.007, C = 6.8–8.6 µm, C:P = 0.234–0.295, rugulae smooth to very sparsely microverrucate to microgemmate. Style 22.8–27 mm long, stigma subequally 2-lobed, lobes 0.1–0.4 mm long. Drupe ovoid to subspherical, 17.6–24.8 mm long, 12.2–15.3 mm in diameter, pubescent with erect, mostly unbranched (and with a few scattered, apically branched) trichomes 0.1–0.6 mm long.

Phenology.— Flowering: February–September; fruiting: all year.

Distribution and habitats.— Tropical central Africa (Cameroon, Congo-Kinshasa, Gabon, Nigeria; EOO = 689,906 km^2; Fig. 18). Plants occur in wet, evergreen forests. Elev. 200–850 m. The species likely also occurs in the mainland African portion of Equatorial Guinea, which lies between occurrences in Cameroon and Gabon.

Illustrations.— Thiselton-Dyer (1896:t. 2427); Heine (1966:75, Pl. 15).

Although only a single collection (*Mann 1839*) of *Afromendoncia phytocrenoides* was cited in the protologue, several specimens of it exist. It is unknown whether Lindau had a specimen at B that is no longer extant, but it is clear that he saw and annotated materials at K, where three syn-

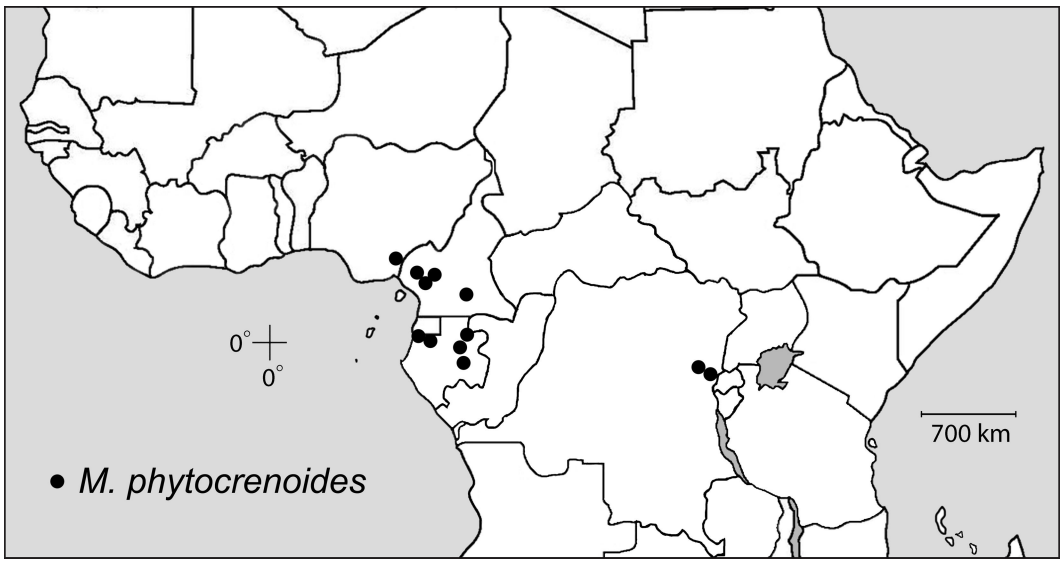

Figure 18. Map of central Africa showing distribution of *Mendoncia phytocrenoides*.

types are extant. One of these from Hooker's herbarium (K-00393679) was annotated as "holotype" by Breteler in 2013. Because this specimen bears the greatest amount of original label data as well as both Anderson's manuscript name and that of Gilg (both noted in the protologue), we designate this specimen as the lectotype for *A. phytocrenoides*. Similarly only a single collection of *Mendoncia letestui* was cited in the progologue, but multiple specimens of it exist, with at least two at P that bear the name in Benoist's handwriting. From these syntypes, P-00435326, with more complete locality information, is chosen as the lectotype.

We include *Mendoncia phytocrenoides* var. *iodioides* in the synonymy of *M. phytocrenoides*. The distinction between these varieties was primarily the presence or absence of a layer of dendritic to stellate trichomes on the leaves and bracteoles which underlies a layer of longer, simple, antrorse-appressed trichomes. Heine (1966) recognized var. *iodioides* and distinguished it from var. *phytocrenoides* on the basis of its pubescence consisting principally of stellate trichomes (vs. pubescence principally consisting of simple trichomes mixed with branched or substellate trichomes). This feature is not consistent, and sometimes trichomes on leaves, bracteoles, and drupes of mature specimens fall off. Also, the geographic ranges of the putative varieties overlap. With the limited availability of specimens (19) and thus limited flowering material, a comparison of the floral features of the two varieties was difficult. Until additional collections are studied, the stated differences between the putative varieties appear to be insufficient to warrant their recognition at this time.

Additional specimens examined.— CAMEROON. **Central**: près Ndokononoro, à 15 km SW de Ndikiniméki, [ca. 04°38′13.10″N, 010°46′00.59″E], *Letouzey 10888* (P). **East**: près Djouo, rive gauche du Dja (45 km SSE de Mesaména) [ca. 03°21′25.88″N, 012°56′17.08″E], *Letouzey 4306* (K, P). **Littoral**: Ebo Forest Research Station (proposed Natl. Park), north transect, *Osborne & Beheng 118* (K). **Southwest**: Gazette-Kupe Village, *Cable S. 3884* (MO); main trail from Kupe village toward Mt. Kupe, *Etuge M. 2769* (MO); Mount Kupe, SW slope, main trail to the top from Kupe village [ca. 04°46′44.72″N, 009°40′47″E], *Schönenberger 50* (F, K, P). CONGO-KINSHASA. **North-Kivu**: Kabunga Terr., Walikale [ca. 01°24′55.03″S, 028° 03′43.23″], *Leonard 1792* (BR). **South-Kivu**: Kalehe Terr., réserve IRSAC à Irangi, km 110, route Kavumu–Walikale, *Christiaensen 1796* (BR). GABON. **Estuaire**: Akoga, N des Monts de Cristal, *Hallé*, *892* (P). **Ogooue-Ivindo**: 15 km SW Makokou, [ca. 00°28′23.47″N, 012°44′59.25″E], *Hallé 2654* (P); Belinga [ca. 01°07′58.16″N, 013°11′50.27″E], *Hallé*, *3358* (K, P).

10. *Mendoncia vinciflora* Benoist, *Bull. Mus. Hist. Nat. (Paris)* 31:387. 1925. **Type**.— MADAGASCAR. **Mahajanga**: Ankaizinana [Ankaizina; 14°17′51.15″S, 048°39′56.55″E], Apr 1923, *Decary 1955* (lectotype, designated here: P-P00091112!).

Young stems glabrous to mealy-glandular or sparsely to densely pubescent with antrorsely appressed, golden-brown to yellowish, unbranched, eglandular trichomes 0.1–1.2 mm long. Leaves membranaceous to coriaceous, petioles to 40 mm long, glabrous or pubescent like young stems but with trichomes to 1.5 mm long, blades ovate to elliptic to obovate, 32–175 mm long, 19–86 mm wide, acute to rounded to subcordate at base, acute-apiculate to acuminate-caudate at apex, abaxial surface glabrous to mealy-glandular and veins (at least midvein) also pubescent with erect to flexuose, unbranched, eglandular trichomes 0.1–2 mm long, adaxial surface glabrous to sparsely or densely pubescent with eglandular trichomes to 0.5 mm long along major veins. Inflorescences borne in leaf axils on young, mostly herbaceous and leafy stems, solitary or opposite at nodes, dichasia 1–4 per axil, peduncles to 74 mm long, glabrous or pubescent like petioles. Bracteoles color unknown, deciduous by time of fruit maturity, elliptic to ovate-elliptic, 10–18.3 mm long, 5.6–13.7 mm wide, rounded at base, rounded to acute at apex, abaxial surface mealy-glandular and

pubescent with antrorse to antrorsely appressed, unbranched, eglandular trichomes 0.1–1.2 mm long, adaxial surface mealy-glandular and usually not densely pubescent at apex with dense and minute trichomes. Calyx glabrous to mealy-glandular or with a few eglandular trichomes to 0.5 mm long. Corolla pink or light to dark purple, 20–35 mm long, externally mealy-glandular, internally mealy-glandular to sparsely (to more densely in throat) pubescent with glandular trichomes 0.1–0.3 mm long, tube 9.4–15 mm long, limb 19–37 mm in diameter, upper lip 10–17 mm long with emarginate lobes 8–13 mm long and 6.6–14 mm wide, lower lip 9–21 mm long with emarginate lobes 5.7–18 mm long and 6–18 mm wide. Stamens 6.5–10 mm long, ventral pair inserted 1–2 mm distal to dorsal pair, thecae 4.2–7.5 mm long, pubescent at base with a tuft of bristles 0.1–0.2 mm long, these sometimes extending toward apex of thecae, connective extending 0.4–0.5 mm beyond thecae, extension of connective attenuate, pubescent with glandular and eglandular trichomes 0.1–0.3 mm long, staminode 0.5–0.6 mm long. Pollen 5-colpate, E = 23–25 µm, P = 23–24 µm, P:E = 0.973–0.974, C = 5.8 µm, C:P = 0.245–0.257, rugulae sometimes ± indistinct, sparsely to densely microverrucate to microgemmate to microbaculate. Style 11–15 mm long, glabrous to sparsely mealy-glandular or sparsely pubescent with eglandular trichomes 0.2–0.4 mm long, stigma subequally to unequally 2-lobed, lobes 0.2–0.8 mm long. Drupe subspherical to spherical, 16.4–30 mm long, 14.8–25 mm in diameter, glabrous to mealy-glandular.

Phenology.— Flowering: December–April; fruiting: November–April.

Distribution and habitats.— Northern Madagascar (Antsiranana, Mahajanga; EOO = 5,756 km^2; Fig. 9). Plants occur in montane, wet, evergreen forests. Elev. 1240–2100 m. *Mendoncia vinciflora* is restricted to upper elevations in the northern mountains near the border regions of Antsiranana and Mahajanga.

Illustrations.— Benoist (1967: Fig. 1); Fig. 19.

The lectotype of *Mendoncia vinciflora* is chosen from among the four collections cited in the protologue (Benoist 1925): *Decary 1955*, *Decary 1971*, *Perrier de la Bathie 15294*, and *Perrier de la Bathie 15324*, all of which are currently extant at P.

Sometimes two staminodes are evident in the flowers of this species. Among Paleotropical species, *Mendoncia vinciflora* has some of the largest corollas and the largest drupes, which unlike those of other species are usually spherical.

Additional specimens examined.— MADAGASCAR. **Antsiranana**: Massif de Marinorahona SW de Manambato (haute Mahavavy du nord, District Ambilobe), [ca. 13°45′24.19″S, 048°58′52.14″E], *Humbert & Capuron 25734* (P); Camp 3, summit vegetation of Anjanaharibe-Sud, 14°44′42″S, 049°25′58″E, *Lewis et al. 1353* (MO); E of Ankaramy, Réserve Speciale Manongarivo, Antsatrotro, SE of summit, river valley between Ansatrotro and massif, 14°05′S, 048°23′E, *Malcomber et al. 1489* (MO); Massif de Zaratanana, *Perrier de la Bathie 15294* (P), *15324* (P), *15546* (P); Andapa, Doany, forêt d'altitude d'Ambohimirahavavy, 22 km E du chef lieu de la commune Mangindrano, Bealanana, Montagne de Beampoko, 14°13′41″S, 049°08′14″E, *Randrianarivelo et al. 330* (MO). **Mahajanga**: Ankaizeriana (Ankaizinana), [ca. 14°30′S, 048°55′E], *Decary 1971* (P); montagnes N de Mangindrano (haute Maevarano), jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga: centre-nord), [ca. 14°16′S, 048°56′E], *Humbert & Capuron 25016* (K, MO, P), *Humbert & Capuron 25353* (BR, K, MO, P); Mangindrano, Bealanana, [ca. 14°32′30″S, 048°45′E], *Njila 7039* (P); Fiv. Bealanana, commune Mangindrano, Forêt Antetikalambazaha, aux environ de Rivière Befosa, dans le Massif de Tsaratanana, 9 km N de Mangindrano, 14°10′27″S, 048°56′42″E, *Razafitsalama et al. 308* (MO); Ankailatsaka, (nearest village), canton de Mangindrano, District Bealanana, RN IV, *Service Forestier Madagascar 47-RN* (P).

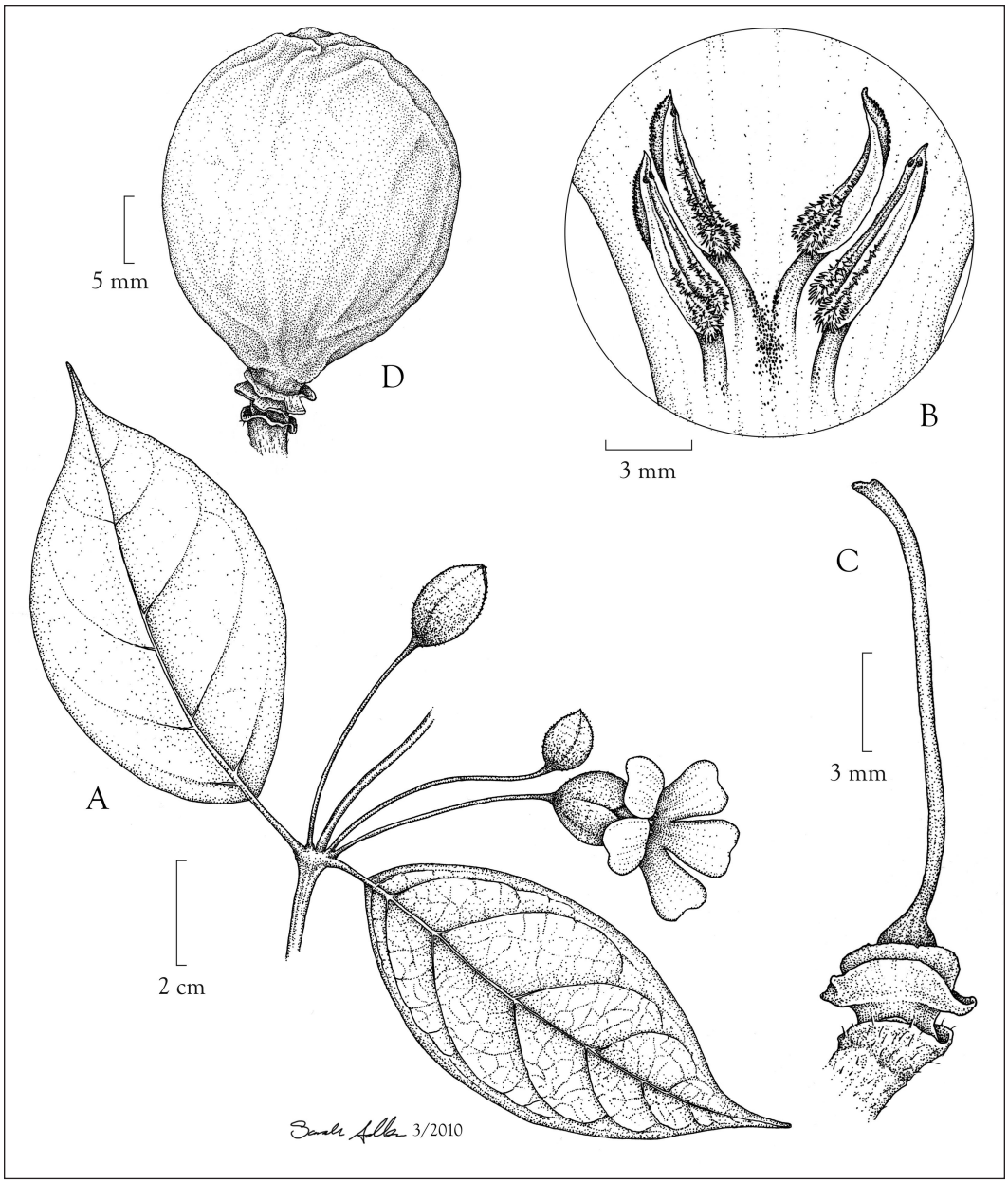

FIGURE 19. *Mendoncia vinciflora*. A. Fertile node with one dichasium bearing a flower (*Humbert 25016*). B. Corolla tube split open to show androecium (*Humbert 25016*). C. Apex of peduncle and flower following dehiscence of corolla, showing (from bottom) flared apex of peduncle, short pedicel, calyx, nectar disc, and gynoecium (*Humbert 7039*). D. Drupe (*Randrianarivelo et al. 330*). Drawn by Sarah Adler.

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Appendix 1.

Collections of Paleotropical *Mendoncia* used in pollen (SEM) studies

M. cowanii: *Daniel et al. 11000*
M. delphina: *Malcomber et al. 1665*
M. flagellaris: *Daniel et al. 9131*, *9239*, *9276*
M. gilgiana: *Breteler 1834*; *Jacques-Felix 4756*; *Tisserant 118*
M. kely: *Andrianantoanina et al. 11*
M. lindaviana: *Hladik s.n.*
M. phytocrenoides: *Letouzey 4306*
M. vinciflora: *Humbert & Capuron 25734*

Appendix 2.

Occurrences of Paleotropical species of *Mendoncia* by country and island

Cameroon: *M. gilgiana*, *M. lindaviana*, *M. phytocrenoides*
Central African Republic: *M. gilgiana*, *M. lindaviana*
Congo-Brazzaville: *M. gilgiana*, *M. lindaviana*
Congo-Kinshasa: *M. gilgiana*, *M. lindaviana*, *M. phytocrenoides*
Equatorial Guinea: *M. gilgiana*
Gabon: *M. combretoides*, *M. gilgiana*, *M. lindaviana*, *M. phytocrenoides*
Ghana: M. *combretoides*, *M. gilgiana*
Guinea: *M. combretoides*, *M. gilgiana*
Ivory Coast: *M. combretoides*, *M. gilgiana*
Kenya: *M. gilgiana*
Liberia: *M. combretoides*, *M. gilgiana*
Madagascar: *M. cowanii*, *M. decaryi*, *M. delphina*, *M. flagellaris*, *M. kely*, *M. vinciflora*
Mayotte: *M. flagellaris*
Nigeria: *M. phytocrenoides*
South Sudan: *M. gilgiana*
Tanzania: *M. gilgiana*
Uganda: *M. gilgiana*

APPENDIX 3

Geographically based keys to Paleotropical taxa of *Mendoncia*

Key to Species of *Mendoncia* in Continental Africa

1a. Young stems, petioles, peduncles, and abaxial surface of bracteoles pubescent with at least some branched (stellate to dendritic) trichomes 2
1b. Young stems, petioles, peduncles, and abaxial surface of bracteoles glabrous or pubescent with unbranched trichomes only 3

2a. Inflorescences borne in leaf axils on young, mostly herbaceous, leafy stems; corollas 17.5–22 mm long; style 16–18 mm long; drupes mealy-glandular (lacking elongate trichomes); leaves 44–133 mm long and 23–86 mm wide. . . . . *M. combretoides*
2b. Inflorescences mostly borne at naked nodes on older, woody, leafless stems; corollas 29.3–31.8 mm long; style 22.8–27 mm long; drupes pubescent with eglandular trichomes to 0.6 mm long; leaves 86–200 mm long and 57–114 mm wide. . . . . *M. phytocrenoides*

3a. Inflorescences mostly borne on peg-like, woody, sometimes branched short-shoots at naked nodes on older, woody, leafless stems; young stems, peduncles, and abaxial surface of leaves glabrous to mealy-glandular, lacking elongate trichomes; drupe oblong (symmetrical), 12.3–19.9 mm long . . . . . *M. lindaviana*
3b. Inflorescences borne in leaf axils on young, mostly herbaceous, leafy stems; young stems, peduncles, and abaxial surface of leaves pubescent (sometimes sparsely so) with eglandular trichomes to 2.3 mm long; drupe ± irregularly shaped, overall obovoid and widest at or just below apex, 6.8–11.8 mm long . . . . . *M. gilgiana*

Key to Taxa of *Mendoncia* in Madagascar and Mayotte

1a. Ovary and drupe glabrous or mealy-glandular (i.e., with inconspicuous, sessile glands mostly < 0.05 mm in diameter), lacking elongate, eglandular trichomes; bracteoles abaxially glabrous to sparsely pubescent (rarely densely pubescent); calyx glabrous or sparsely pubescent 2
1b. Ovary and drupe pubescent with elongate, eglandular trichomes; bracteoles abaxially densely pubescent; calyx usually densely pubescent 4

2a. Corollas pink or light to dark purple, 20–35 mm long, upper lip 10–17 mm long; bracteoles usually lacking dense pubescence at apex of adaxial surface; extension of connective beyond anther thecae pubescent with glandular and eglandular trichomes 0.1–0.3 mm long; drupe subspherical to spherical, 14.8–25 mm in diameter; northern Madagascar. . . . . *M. vinciflora*
2b. Corollas white and usually with purple markings near base of limb and/or throat (rarely purplish in *M. delphina*), 8–18.5 mm long, upper lip 2–12.5 mm long; bracteoles with dense pubescence at apex of adaxial surface; extension of connective beyond anther thecae (if present) glabrous to minutely glandular; drupe ovoid-ellipsoid to ellipsoid to spherical to obovoid, 6–15.7 mm in diameter; widespread 3

3a. Dichasia 1–2 in axils of leaves; apex of leaf blade acuminate to caudate, with tail-like apex to 12 mm long; bracteoles yellowish, lacking a pair of conspicuous, whitish, bulbous, gall-like basal protuberances; stigma subequally to unequally 2-lobed; pollen 5-aperturate; southern Madagascar . . . . . *M. delphina*
3b. Dichasia 1–4 (–8) in axils of leaves or commonly in axils of bracts in an a raceme to 15 cm long; apex of leaf blade (acuminate) to acute to rounded to truncate to retuse, and sometimes

with an apiculum to 1.6 mm long; bracteoles green, often with a pair of conspicuous, whitish, bulbous, gall-like basal protuberances; stigma capitate; pollen mostly 4-aperturate; widespread . . . . . *M. flagellaris*

4a. Corollas 13.2–19 mm long, tube 10–14 mm long; leaf blades mostly with length:width 1.4–1.8 . . . . . *M. kely*

4b. Corollas 26–49 mm long, tube 20–38; leaf blades mostly with length:width 1.7–2.8 5

5a. Corollas white with purplish markings, limb 20.6–32.4 mm in diameter, upper lip 13.5 mm long with lobes 8–10 mm long and 11.2–13.2 mm wide, lower lip 16.5–19 mm long with lobes 9.4–13.5 mm long and 12.2–15.2 mm wide . . . . . *M. decaryi*

5b. Corollas light pink to dark pink (sometimes whitish externally), limb 6–21 mm in diameter, upper lip 1.8–10 mm long with lobes 1.8–7.4 mm long and 3.7–8.6 mm wide, lower lip 3–12.4 mm long with lobes 2.2–7.5 mm long and 3.4–9.1 mm wide 6

6a. Young stems, petioles, abaxial surfaces of leaf blades and bracteoles, and peduncles subglabrous and/or pubescent with erect to flexuose to antrorse trichomes, underlying surfaces plainly visible; corolla with upper lip 4.4–10 mm long and lobes of lower lip 3.5–7.5 mm long and 3.5–9.1 mm wide . . . . . *Mendoncia cowanii* var. *cowanii*

6b. Young stems, petioles, abaxial surfaces of leaf blades and bracteoles, and peduncles densely pubescent with flexuose-interwoven trichomes such that underlying surfaces not visible (or only partially so on abaxial surface of leaf blades); corolla with upper lip 1.8–3.6 mm long and lobes of lower lip 2.2–3.3 mm long and 3.4–3.5 mm wide. . . . . *Mendoncia cowanii* var. *coursii*

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The Genus *Grasshoffia* with the Description of a New Deep-water Species from the Northern Philippines (Octocorallia: Pennatulacea: Virgulariidae)

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A new species of the recently described pennatulacean genus *Grasshoffia*, collected by beam trawl, is described from deep-water off southern Luzon in the Philippines. The new species is here allocated to the genus *Grasshoffia* based on the presence of numerous minute rod-like sclerites in the polyp walls and polyp leaves. The sclerites in the new species are distinctive in that they are more-or-less rectangular in shape with truncate apexes, unlike the type species of the genus, as well as other species of pennatulaceans. The two species of *Grasshoffia* are known only from widely disparate regions of the world – the Gulf of Guinea in eastern Atlantic and the Philippine Archipelago in the western Pacific.

KEYWORDS: Pennatulacea, virgulariid sea pen, *Grasshoffia*, northern Philippines, deep-sea, synopsis and key to species of the genus.

During the deep-water component of the 2011 Hearst Philippine Biodiversity Expedition of the California Academy of Sciences and various agencies in the Philippines (Williams & Gosliner, 2014), deep-water collecting was conducted in the Verde Island Passage from Batangas Bay to the northwest of the Lubang Islands, primarily utilizing either beam or otter trawling nets, and ranged in depth from 63–2350 m (Iwamoto and McCosker, 2014; Williams, 2014).

Materials and Methods

In the period between 28 May and 4 June 2011, thirty-one deep-water bottom trawl stations were explored on board the Philippine research ship *M/V DA-BFAR* in the Verde Island Passage of the Philippines — the region between southwestern Luzon, northern Mindoro, and the Lubang Islands. One such deep-water collecting station was in the eastern part of Balayan Bay (Figs. 1 and 2), which yielded (among other benthic fauna) two colonies of a new species of pennatulacean octocoral, which is here described. Scanning electron micrographs were made using a Hitachi SU3500 Scanning Electron Microscope and a Cressington 108 Auto Sputter Coater. An abbreviation used in the text is CASIZ (California Academy of Sciences, Invertebrate Zoology collection).

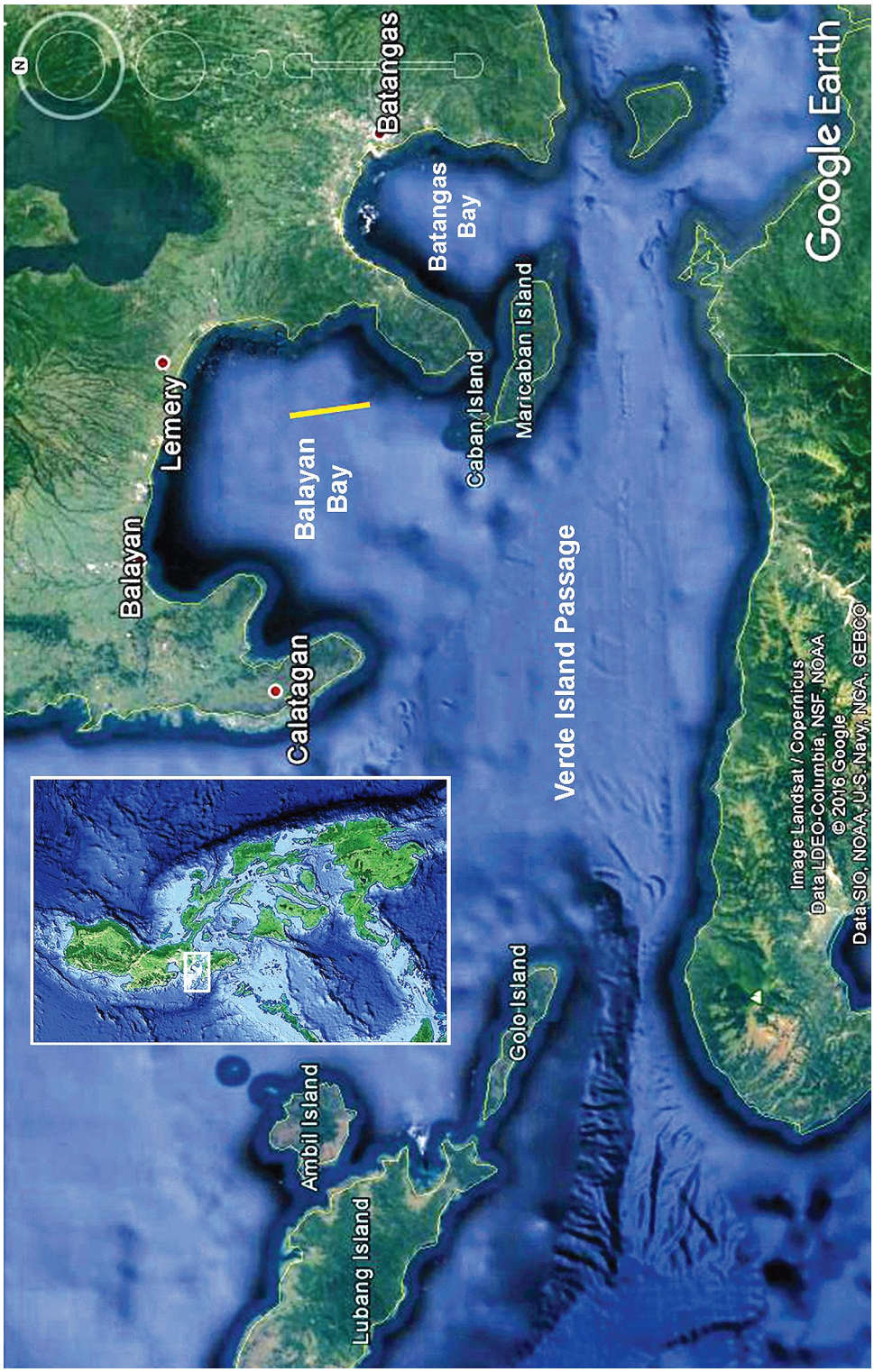

FIGURE 1. Map of the Philippine Archipelago (inset), boxed region of inset is enlarged below with the type locality of *Grasshoffia profundica* n. sp. shown in yellow as a trawling line.

FIGURE 2. Late afternoon view from the eastern shore of Balayan Bay, southern Luzon, Philippines – the eastern part of the bay shown here is the type locality of *Grasshoffia profundica* sp. nov.

SYSTEMATIC ACCOUNT

Subclass Pennatulacea Verrill, 1865
Family Virgulariidae Verrill, 1868
Grasshoffia Williams, 2015

Grasshoffia Williams, 2015:41.

GENERIC DIAGNOSIS (modified from Williams, 2015:41).— Virgulariid sea pens; polyp leaves funnel-shaped and rolled or ovate and flattened; 10–26 autozooids per polyp leaf; sclerites of polyp leaves slightly three-flanged rods with parallel lateral sides and ends triangular or truncate, 0.02–0.08 mm in length (modified from Williams, 2015:41).

TYPE SPECIES.— *Grasshoffia virgularioides* Williams, 2015.

***Grasshoffia profundica* Williams, sp. nov.**

Figures 3-7.

HOLOTYPE.— CASIZ 207514.

PARATYPE.— CASIZ 207515.

TYPE LOCALITY (Fig. 1).— Balayan Bay, southwestern Luzon, Philippines (13.77283°N, 120.8507°E to 13.764167°N, 120.85167°E); station number HEPD-010; 318–333 m depth; 30

May 2011; G.C. Williams on board the research ship of the Philippine Bureau of Fisheries and Aquatic Resources, *M/V DA-BFAR*, during the 2011 CAS Hearst Philippine Biodiversity Expedition; two partial specimens collected by beam trawl.

Habitat and Distribution.— Collected from muddy sea bottom in a north to south linear transect in the eastern part of Balayan Bay (Fig. 1), which represents the only known occurrence of the species.

Etymology.— The specific epithet is derived from the Latin *profundus* (deep or of the depths), and the suffix *–icus* (belonging to), referring to the deep-sea habitat of the holotype.

Description

External morphology (Fig. 3).— Both the holotype and the paratype are partial in the distal and proximal ends of each of the colonies are missing. In the holotype (which is 238 mm long), the portion of the peduncle that is remaining is 70 mm in length and up to 2 mm in width and the portion of the rachis that remains is 168 mm in length. The length of the partial paratype is 143 mm. The colonies are filiform – elongate and very thin. The coenenchyme of the rachis is extremely thin to indiscernible.

Axis (Figs. 3B, 4).— The cylindrical axis extends virtually throughout the entire length of the colony and is approximately 0.86 mm in diameter (Fig. 3B). In transverse section, the axis is conspicuously circular in shape (Fig. 4A). A typical pennatulacean morphology is evident in that it displays radiating wedges of calcareous material outward from the central core, and a central area that is composed of densely concentrated proteinaceous material (Figs. 4A–B). The external longitudinal surface of the axis is smooth, not lined or striated (Fig. 4C). However, under higher magnification, very fine longitudinal striations are evident along with small slit-like openings that vary in length from approximately 5-12 micrometers (Fig. 4D).

Polyp Leaves (Figs. 3C–F).— The polyp leaves are mostly flattened and oblong-ovate in shape, approximately 1.8-2.0 mm long by 1.0 mm wide (Fig. 3F). Each polyp leaf is attached to the rachis by a short and narrow proximal neck (Figs. 3C, F). Polyp leaf pairs are oppositely or suboppositely placed along the length of the rachis (Fig. 3A, C–D). They are sometimes disposed obliquely to the longitudinal plane of the axis such that the free, distal ends are higher up on the rachis than the opposite end adjacent to the proximal point of attachment (Figs. 3C–F). Approximately 1.5–3.0 mm of bare rachis separates many adjacent polyp pairs (Figs. 3C–D, F).

Polyps (Fig. 3F–G).— There are usually 10–12 autozooids per polyp leaf (Fig. 3F). The autozooids are cylindrical, approximately 1.0–1.2 mm in length. The tentacles were preserved mostly exserted in both the holotype and paratype and are approximately 0.3 mm in length. Both the polyp walls and the tentacles are densely-set with minute spicules. Siphonozooids were not detected by observation through a dissecting microscope in either the holotype or paratype.

Sclerites (Figs. 5–7).— The sclerites of the polyp leaves and polyp walls are numerous, minute, quadrilateral rods, more-or-less rectangular in shape with truncate ends, and vary in length from 0.040–0.085 mm. Sclerites were not observed and apparently are not present in the tissues of the peduncle.

Color (Fig. 3).— In the wet-preserved holotype and paratype, the axes are white, while the polyp leaves and polyps are tan to brownish is color, and all sclerites are colorless. The appearance and color of the colonies in life was not noted.

Discussion

Williams (2015:48) provided a definition of the family Virgulariidae, as well as a key to the six currently-recognized genera. See Williams (1995:122–125) for diagnoses of five of the six genera (*Acanthoptilum, Scytaliopsis, Scytalium, Stylatula,* and *Virgularia*). For a taxonomic diagnosis of the genus *Grasshoffia*, see Williams (2015:41).

Revised key to the genera of Virgulariidae Verrill. 1868

1A Sclerites are present in the polyp leaves 2
1B Sclerites are absent in the polyp leaves. 5

2A Sclerites in the polyp leaves are conspicuous spindles and/or needles, ≤ 1.50 mm in length. Sclerites are colorless. 3
2B Sclerites in the polyp leaves are small to minute ovals or somewhat three-flanged rods, ≤ 0.08 mm in length. 4

3A Robust spindles form a conspicuous fan-like armature at the bases of the polyp leaves. Sclerites are colorless. Eleven species of the east and west coasts of North and South America, Japan, New Zealand . . . . . *Stylatula*
3B Spindles and ovoid sclerites may form a weak cluster at the bases of the polyp leaves (but not in a fan-like arrangement), or they are scattered in the polyps leaves. Sclerites are colorless. Seven species of the west coast of North America, Gulf of Mexico, New Zealand . . . . . *Acanthoptilum*

4A Densely-set ovoid sclerites are present in the rachis and polyp leaves. Sclerites are noticeably red to red-violet. Two or three species of Indo-West Pacific distribution (Red Sea to Palau) . . . . . *Scytalium*
4B Indistinctly-three-flanged rod-like sclerites are numerous in the polyp leaves and polyp walls. Sclerites are colorless. Two species (West Africa and Philippines) . . . . . *Grasshoffia*

5A The polyps contained on a single polyp leaf are of equal size. Number of polyps per polyp leaf highly variable (few to 100 or more). Fifty-six described species, perhaps twenty of which are valid, worldwide in temperate and tropical latitudes . . . . . *Virgularia*
5B The polyps on the inner-most part of a single polyp leaf are smaller in size than those on the outer margin of the leaf. One species, *Scytaliopsis djiboutiensis* (East Africa). . . *Scytaliopsis*

Key to species of the genus *Grasshoffia* Williams, 2015

1A. Polyp leaves rolled, convoluted, or semicircular in shape. Polyp leaves appear densely congested along the rachis. Sclerites of polyp leaves and peduncle are rods with parallel sides and triangular ends, 0.02–0.06 mm long. Type locality Niger River Delta, Gulf of Guinea. . . . . *Grasshoffia virgularioides*
1B. Polyp leaves flattened and broadly ovate in shape. Polyp leaf pairs are separated by bare portions of the rachis. Sclerites of polyp leaves are rods, more-or-less rectangular in shape, 0.04–0.08 mm long. Sclerites of peduncle are apparently absent. Type locality northern Philippines . . . . . ***Grasshoffia profundica* sp. nov**.

Acknowledgments

I am grateful to the Margaret and William Hearst for their generous gift to the Research Division of the California Academy of Sciences that made possible the Hearst Biodiversity Expedition to the Philippines in 2011.

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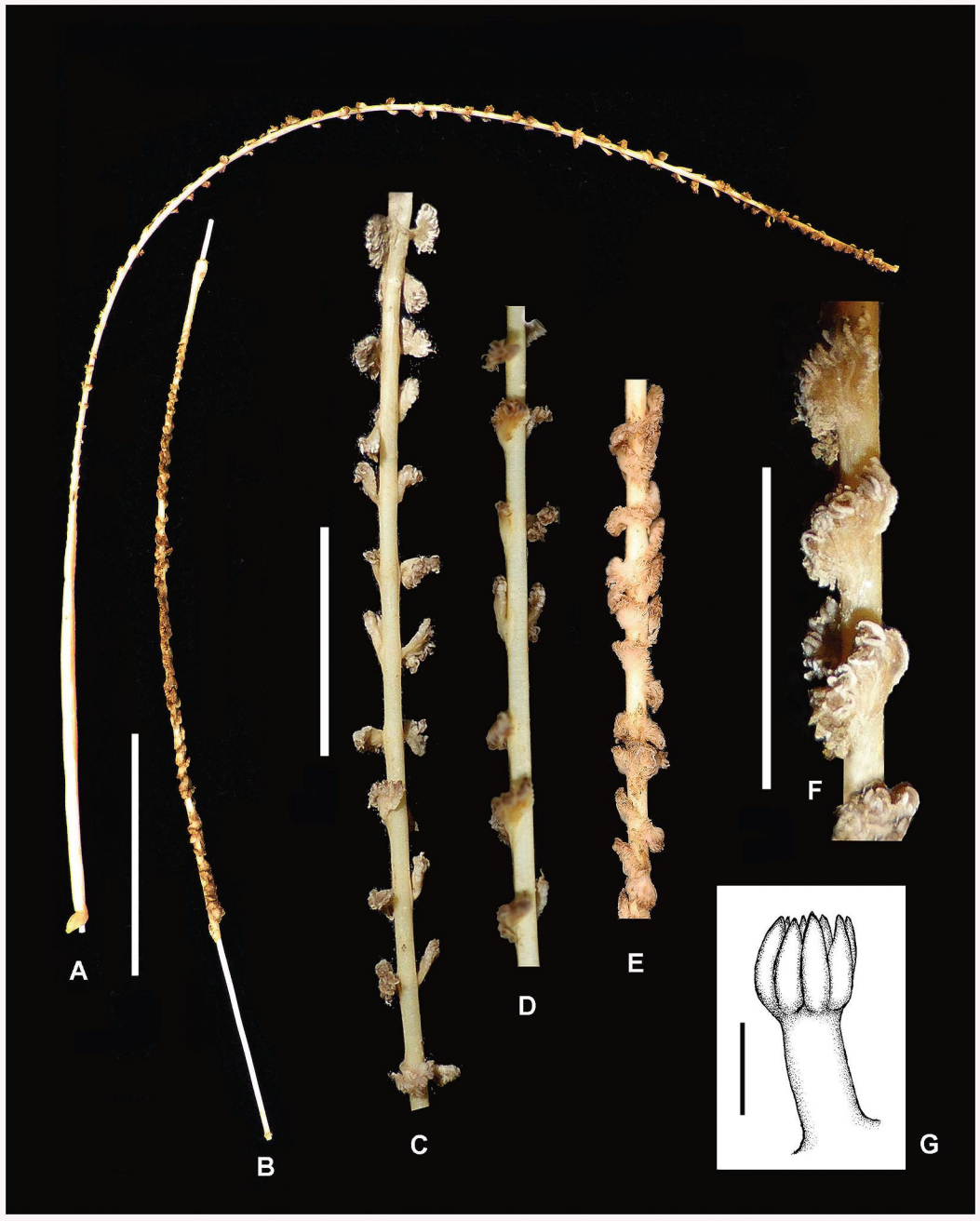

FIGURE 3. *Grasshoffia profundica* n. sp. External morphology. A. Holotype (CAS 207514). B. Paratype (CAS 207515); scale bar for A and B = 40 mm. C. Detail of holotype rachis. D. Detail of holotype rachis. E. Detail of paratype rachis; scale bar for C-E = 10 mm. F. Detail of rachis of paratype showing broadly ovate polyp leaves with narrow proximal region attached to the rachis; scale bar = 5.0 mm. G. Diagram of a single autozooid, pinnules not shown; scale bar = 0.5 mm.

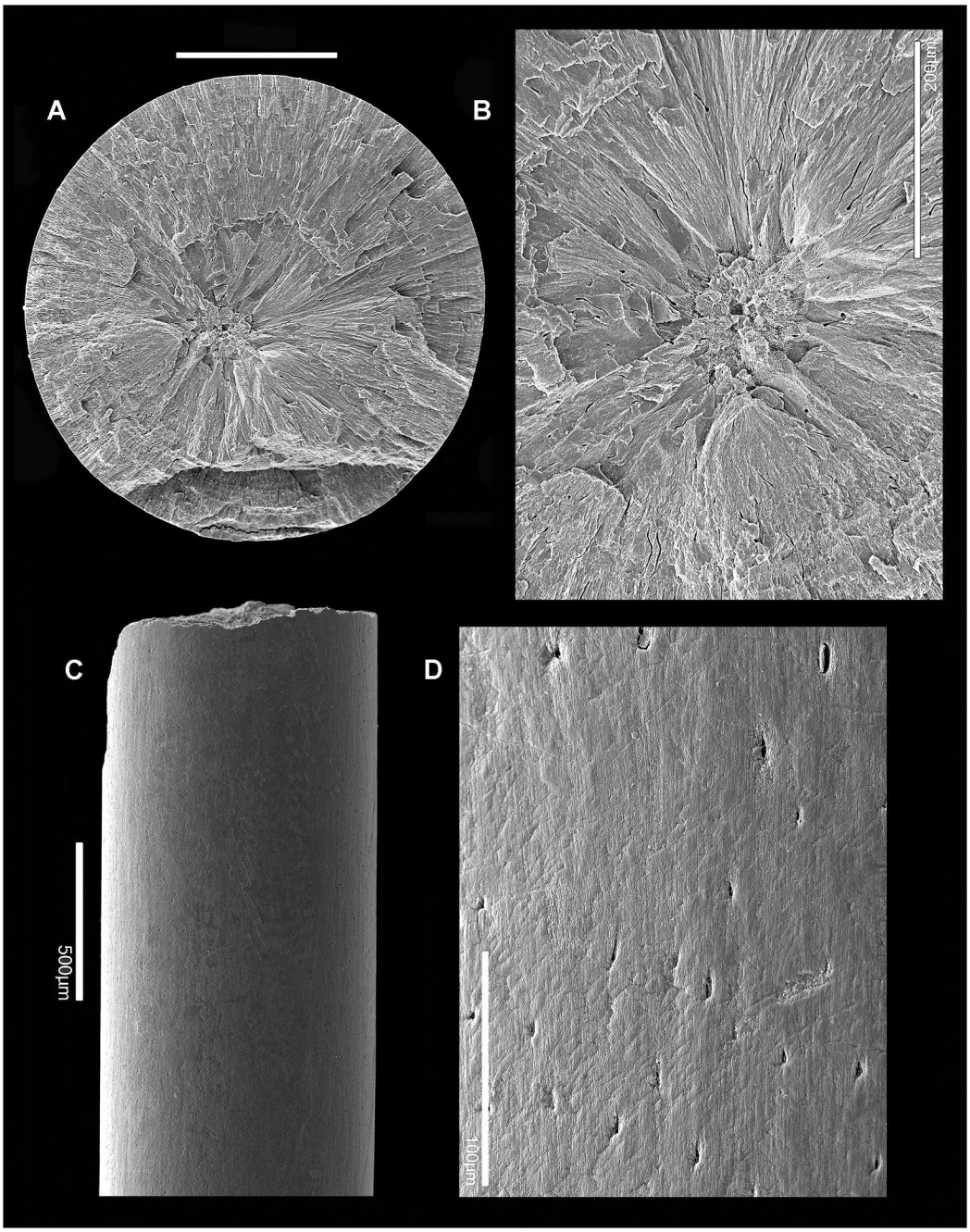

FIGURE 4. *Grasshoffia profundica* n. sp. Scanning electron micrographs of axial morphology. A. Transverse section of axis from the distal region of the rachis showing arrangement of wedge-shaped sections of calcareous material radiating outward from the central core; scale bar = 0.3 mm. B. Enlarged detail of the central region from Fig. 2A showing concentration of organic matter in the central core and several elongated, tadpole-shaped channels surrounding the core; scale bar = 0.2 mm. C. Longitudinal external view of portion of axis from the distal region of the rachis showing uniformly smooth surface; scale bar = 0.5 mm. D. Enlarged detail of axial surface (from Fig. 2C) showing short, slit-shaped orifices; scale bar = 0.1 mm.

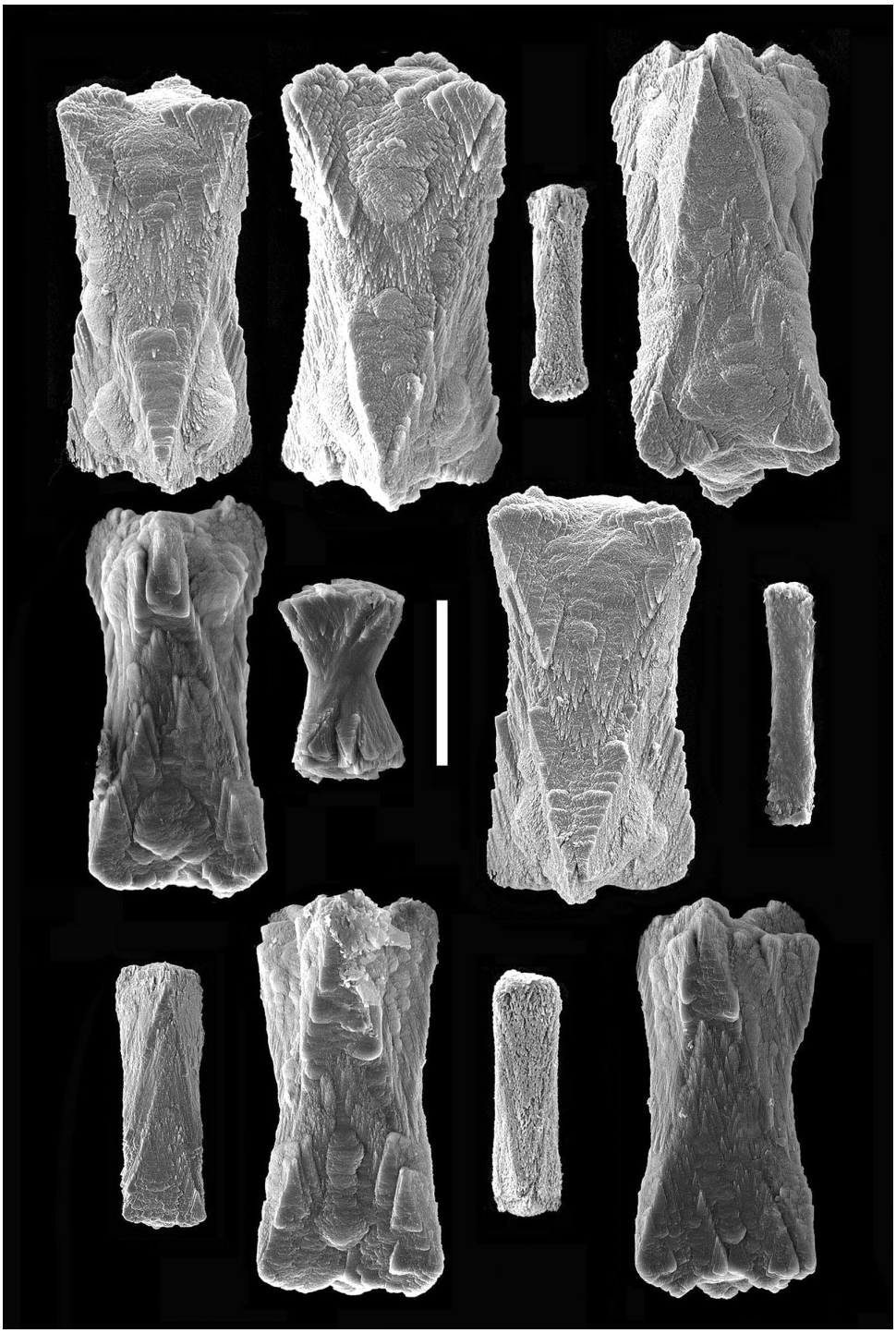

FIGURE 5. *Grasshoffia profundica* n. sp. Scanning electron micrographs of sclerites from polyps and polyp leaves. Scale bar = 0.03 mm.

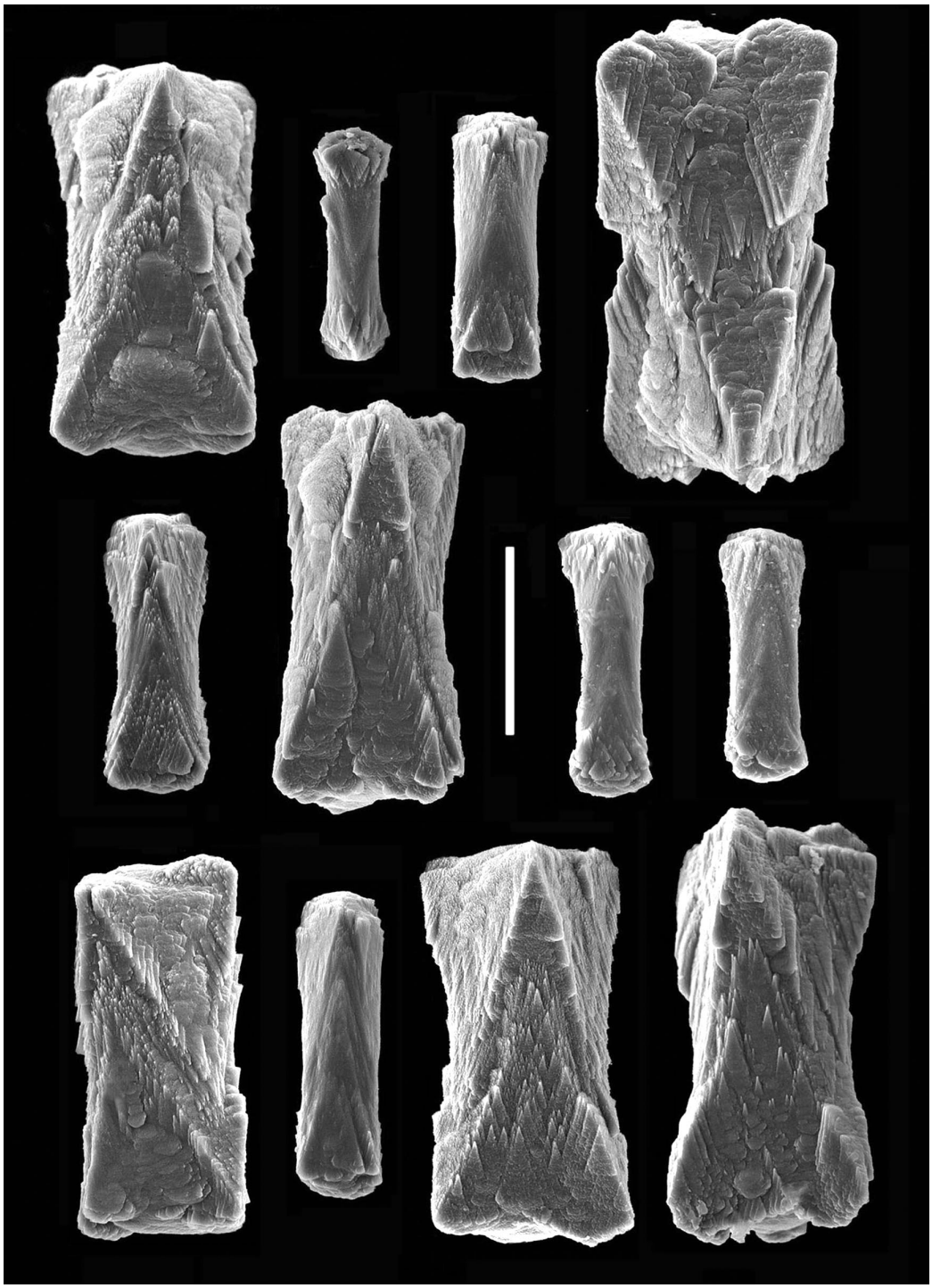

FIGURE 6. *Grasshoffia profundica* n. sp. Scanning electron micrographs of sclerites from polyps and polyp leaves. Scale bar = 0.03 mm.

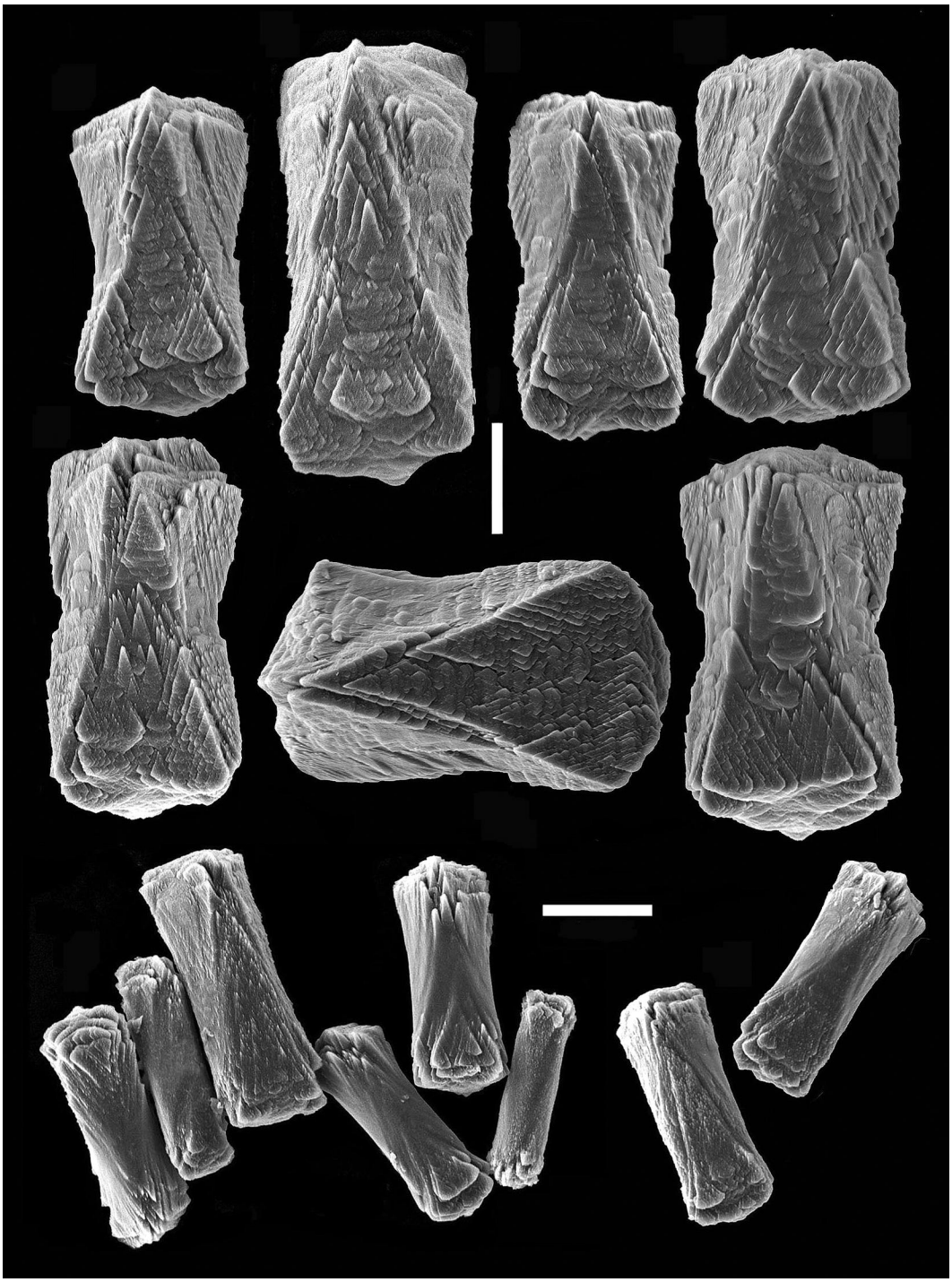

FIGURE 7. *Grasshoffia profundica* n. sp. Scanning electron micrographs of polyp sclerites from polyps and polyp leaves. Scale bars = 0.02 mm.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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First Records for *Cyclosomus inustus* Andrewes (Coleoptera: Carabidae: Cyclosomini) for Taiwan, with Notes on Habitat and Behavior

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Cyclosomus inustus **Andrewes is reported for the first time since 1924 and for the first time in Taiwan. The habitat distribution and feeding behavior of adults of this species are discussed and illustrated, and a checklist of carabid species inhabiting sandy sea beach habitats in northern Taiwan is provided and illustrated.**

KEYWORDS: Coleoptera, Carabidae, Cyclosomini, *Cyclosomus*, Taiwan, sandy sea beach fauna

The first two authors [LJW and JJC] conducted field investigations of the coastal carabid fauna of northern Taiwan during the period June 2005 to March 2017. In August, 2008, early in this study, they discovered and collected specimens of a species of *Cyclosomus* Latreille, a genus recorded from the Afrotropical and Oriental Regions but previously unknown from Taiwan. Based on his study of the genus for the Oriental Region (manuscript in preparation), the third author [DHK] was able to confirm their identification as members of *Cyclosomus inustus* Andrewes. Over the remainder of the study period, the lead authors continued their collections and observations of this species.

The purpose of this report is to document this first record of this species for Taiwan, describe its known geographical and habitat ranges on the island as well as observed activity and feeding behavior of adults of this species for the first time.

Material and Methods

Field observations were made on a monthly basis throughout the study period, June 2005 through March 2017. Temperature of sandy ground was measured using a non-contact infrared thermometer (model DIT 501A, TECPEL, Taipei, TAIWAN). Specimens collected were examined in the laboratory using a Leica MZ125 stereomicroscope and have been deposited in the following collections:

CAS	California Academy of Sciences, San Francisco, California, U.S.A.
CWT	L. J. Wang collection, Taipei, Taiwan.
NMNS	National Museum of Natural Science, Taichung, Taiwan
NMW	Naturhistorisches Museum Wien, Vienna, Austria
TFRI	Taiwan Forestry Research Institute, Taipei, Taiwan
ZSM	Zoologische Staatsammlung München, Munich, Germany

Cyclosomus inustus Andrewes in Taiwan

Cyclosomus inustus Andrewes, 1924:464-465. Type locality: Hong Kong.

Adults of this species are moderate in size (body length 7.0 to 8.7 mm), with a broadly ovoid and flattened body form. The base of the pronotum is only slightly narrower than the base of the elytra, giving these beetles a very stocky appearance, similar to that of many water beetles and especially to members of the carabid genus *Omophron* Latreille. However, they are so distinctive among beetles of the Taiwanese fauna that they cannot be confused with any other species recorded from the island. Two particularly distinctive features include: (1) markedly modified front legs, with the lateral portion of the apex of the tibia expanded laterally, and the first and second (and to a lesser extent the third) tarsomeres with distinct finger-like lateral projections; and (2) hind legs with the medial spur of the tibia markedly elongate, nearly equal in length to the first tarsomere. No other Taiwanese carabid shares this combination of features, both of which are consider modifications for life in or on dry sand.

Variation in color pattern.— In Taiwan, variation in color pattern seen among adults of this species is illustrated in Fig. 1. Color of the pronotal disc ranges from reddish brown (Figs. 1A–C) to dark brown or piceous (Fig. 1D). The color of the basal one-eighth of the elytra from the midline to elytral stria 5, together with the full length of elytral interval 1, ranges from reddish brown to black among individuals, and teneral specimens may have these areas entirely pale. The elytral "middle dark band" may be represented by a relatively thick, dark, jagged, roughly V-shaped band extended laterally onto interval 7 on each side (Fig. 1D), by a thinner, paler yet narrowly continuous band (Fig. 1C), or by reduced and disconnected vestiges of that band (Figs. 1A and 1B). The full range of this variation is seen within populations, so it appears to be simply individual variation and without an evident geographical component.

Material examined (a total of 160 specimens).— **TAIWAN:** *New Taipei City*, Shihmen, Lingshanbi, 30.VIII.2008, J. J. Cherng collector, 8 specimens (TFRI); same locality, 7. IX. 2008, L.J. Wang & J.J. Cherng collectors, 16 specimens (TFRI); same locality, 4.X.2008, J.J. Cherng collector, 2 specimens (TFRI); same locality, 23.V. 2009, J.J. Cherng collector, 5 specimens (TFRI); same locality, 10.VII. 2010, J.J. Cherng collector, 3 specimens (TFRI); same locality, 7.VIII.2011, J.J. Cherng collector, 2 specimens (TFRI); same locality, 23.V. 2009, J.J. Cherng collector, 2 specimens (TFRI); same locality, 17.IX. 2011, J.J. Cherng collector, 3 specimens (TFRI); same locality, 5.V. 2012, J.J. Cherng collector, 2 specimens (TFRI); same locality, 13.V. 2012, J.J. Cherng collector, 2 specimens (TFRI); same locality, 11.VII.2012, J.J. Cherng collector, 9 specimens (TFRI); same locality, 24.II.2013, J.J. Cherng collector, 1 specimen (TFRI); same locality, 27.VII.2013, J.J. Cherng collector, 3 specimens (TFRI); same locality, 3.X.2013, L.J. Wang collector, 18 specimens (CAS, CWT, TFRI); same locality, 19.X.2013, J.J. Cherng collector, 2 specimens (TFRI); same locality, 9.XI.2013, J.J. Cherng collector, 1 specimen (TFRI); same locality, 12.IV.2014, J.J. Cherng collector, 1 specimen (TFRI); same locality, 24.V.2014, J.J. Cherng collector, 2 specimens (TFRI); same locality, 24.VII.2016, J.J. Cherng collector, 1 specimen (TFRI); same locality, 25.XII.2016, J.J. Cherng collector, 5 specimens (TFRI); same locality, 7.I.2017, J.J. Cherng collector, 12 specimens (NMNS, NMW, TFRI , ZSM); same locality, 3.II.2017, J.J. Cherng collector, 6 specimens (TFRI); same locality, 4.II.2017, J.J. Cherng collector, 2 specimens (TFRI); same locality, 4.III.2017, J.J. Cherng collector, 9 specimens (TFRI). Kinshan, Chungjiao, 4.II.2017, J.J. Cherng collector, 10 specimens (CAS, CWT, TFRI); same locality, 12.III.2017, J.J. Cherng collector, 8 specimens (TFRI); Danshui, Shalun, 4.II.2017, J.J. Cherng collector, 16 specimens (TFRI); same locality, 12.III.2017, J. J. Cherng collector, 9 specimens (CAS, CWT, TFRI).

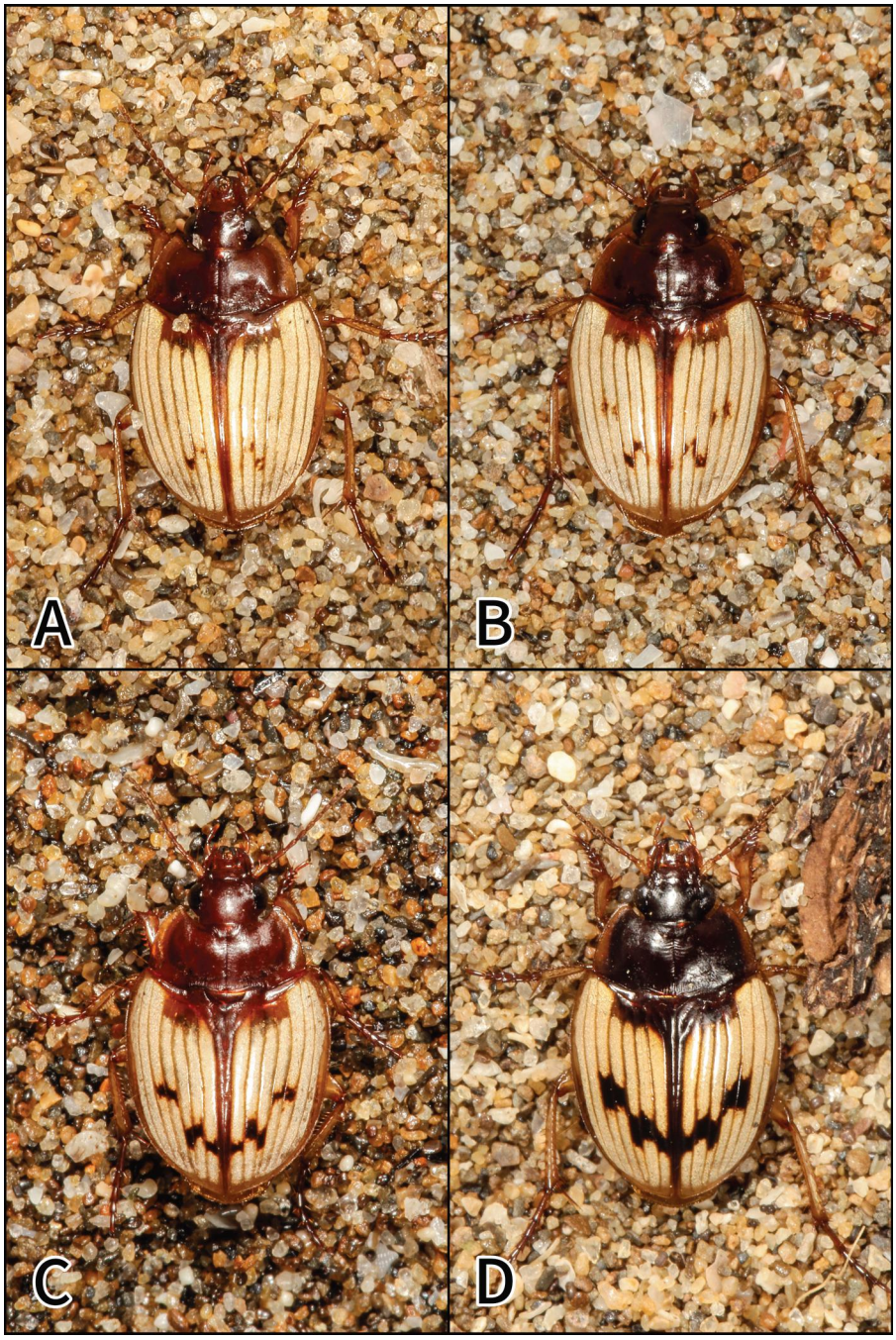

FIGURE 1. Range of variation in color pattern among adults of *Cyclosomus inustus* Andrewes in Taiwan.

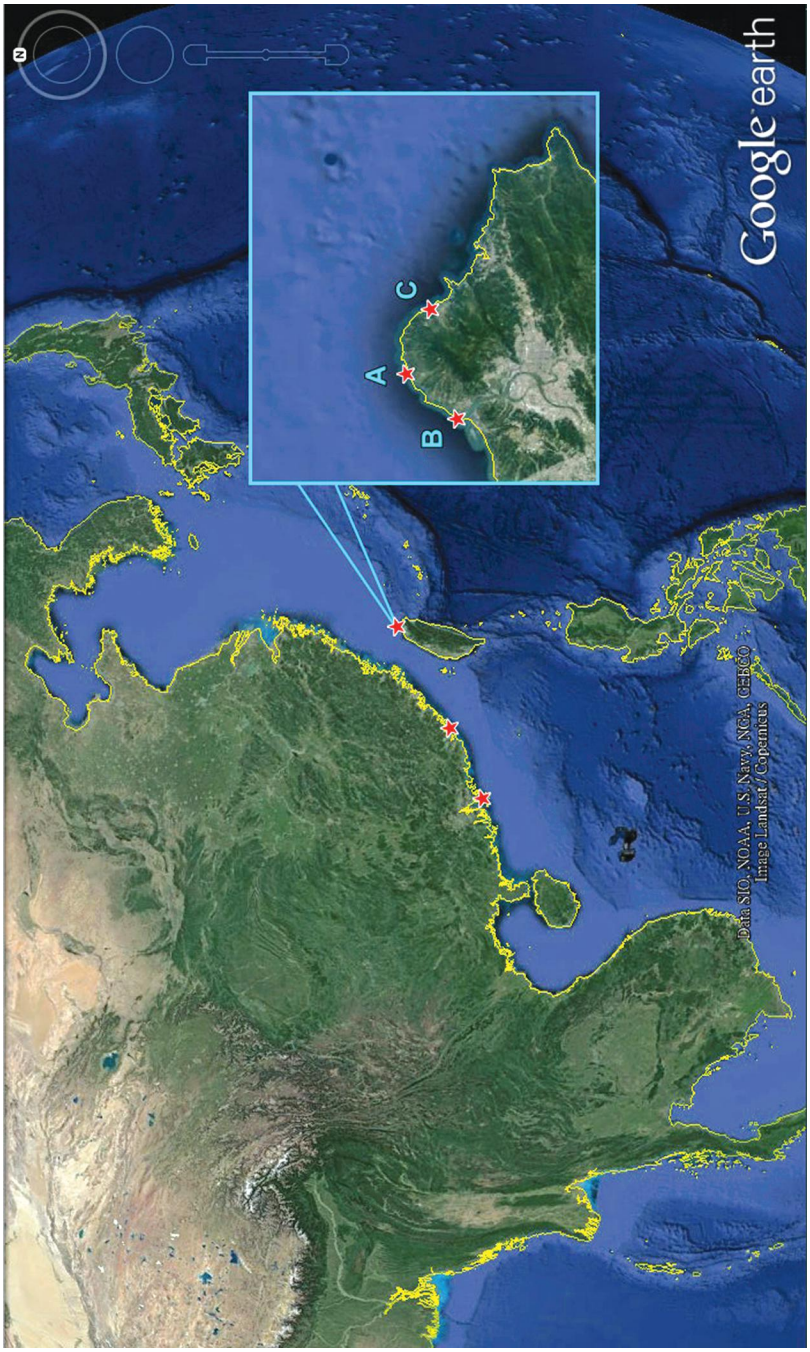

FIGURE 2. Geographical distribution of *Cyclosomus inustus* Andrewes in Taiwan and the adjacent mainland. A, Shihmen. B, Danshui. C, Kinshan.

Distribution (Fig. 2).— This species is now recorded from coastal mainland China (Hong Kong and Nanoa Island in Guongdong Province) and the three localities in northern Taiwan presented above.

Ecological observations.— *Cyclosomus inustus* inhabits the sandy sea coast of northern Taiwan (Fig. 3). It has not been found on sandy beaches without at least scattered plant cover present. Coast plants in the habitat of *C. inustus* include *Casuarina equisetifolia* L., *Hibiscus tiliaceus* L., *Pandanus odoratissimus* L., *Scaevola sericea* Forst. f. ex Vahl, *Crinum asiaticum* L., *Vitex rotundifolia* L. f., *Artemisia capillaris* Thunb., *Spinifex littoreus* (Burm. f.) Merr., *Carex pumila* Thunb., *Ipomoea pes-caprae* (L.) R. Brown subsp. *brasiliensis* (L.) Ooststt, *Vigna marina* (Burm.) Merr., *Tetragonia tetragonoides* (Pall.) Kuntze, *Oenothera laciniata* J. Hill, *Ixeris debilis* (Thunb.) A. Gray, and *Ixeris repens* (L.) A. Gray. This habitat is apparently quite different from that of all the other *Cyclosomus* species for which habitat information is available. All others apparently favor the exposed sandy banks of mid- to large-size rivers or sandy lake shores (Kavanaugh, 2015).

Adults of *C. inustus* have been observed in every month of the year. Like other congeneric species, they are active on the surface at night and hidden in the sand during the day. They are markedly and negatively phototaxis insects. At night, during their activity period, they are quick to burrow into the sand (Fig. 5A) if illuminated directly by the light of a flashlight. The earliest time at which adults have been observed active on the sand surface is 5:52 pm, just after sunset, in January, 2017. We observed that adults appear on the surface of the sand when the temperature on the beach is above 15°C (observations from three collecting sites during January through March). Although Nietner (1857) found adults of *Cyclosomus flexuosus* (Fabricius) hiding in the "driest, hottest and sandiest places that can be found" on the western coast of Sri Lanka, we have not yet determined the upper thermal tolerance of *C. inustus* in Taiwan or elsewhere.

In Taiwan, *C. inustus* adults have been observed in the field feeding on beetles, flies, and shield bugs (Figs. 5B–D). When maintained in the laboratory, they will not feed on live termites or caterpillars but will eat these same insects soon after they are dead. Consequently, we suggest that they are primarily scavengers, rather than predators.

Other carabid species found occupying the same habitat as *C. inustus* in northern Taiwan (i.e., are syntopic with this species) include *Bembidion fusiforme* Netolitzky (Fig. 6A), *Abroscelis anchoralis anchoralis* (Chevrolat) (Fig. 6C), *Calomera angulata* (Fabricius) (Fig. 6E, *Cicindela batesi* Fleutiaux (Fig. 6G) and *Cylindera kaleea angulimaculata* (Mandl) (Fig. 6H). Adults of all of these species are diurnally active and only those of *Bembidion fusiforme* are also active at night (at least in some parts of Taiwan). For completeness, we provide below a checklist of all the carabid species observed during our study in sandy sea beach habitats in northern Taiwan.

A checklist of carabid species found during 2005-2017 in sandy sea beach habitats of northern Taiwan

1. *Cyclosomus inustus* Andrewes (Fig. 1A-D)
2. *Bembidion fusiforme* Netolitzky (Fig. 6A)
3. *Mastax brittoni* Quentin (Fig. 6B)
4. *Abroscelis anchoralis anchoralis* (Chevrolat) (Fig. 6C)
5. *Abroscelis anchoralis punctatissima* (Schaum) (Fig. 6D)
6. *Calomera angulata* (Fabricius) (Fig. 6E)
7. *Cicindela batesi* Fleutiaux (Fig. 6G)
8. *Cylindera kaleea angulimaculata* (Mandl) (Fig. 6H)
9. *Lophyra cancellata subtilesculpta* (W. Horn) (Fig. 6F)
10. *Myriochile speculifera* (Chevrolat)

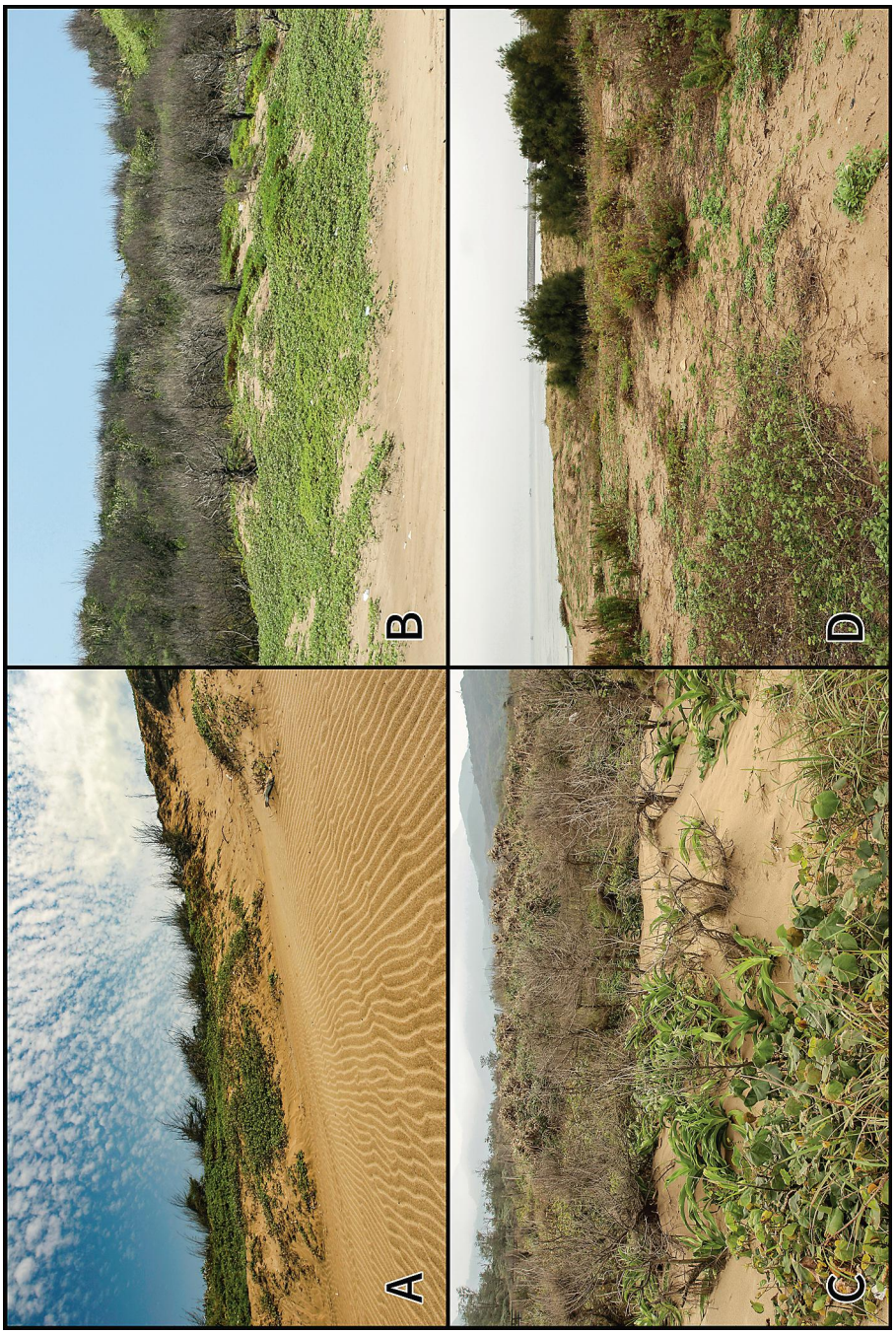

FIGURE 3. Habitats of *Cyclosomus imustus* Andrewes in Taiwan. A-B, Shihmen. C, Kinshan. D, Danshui.

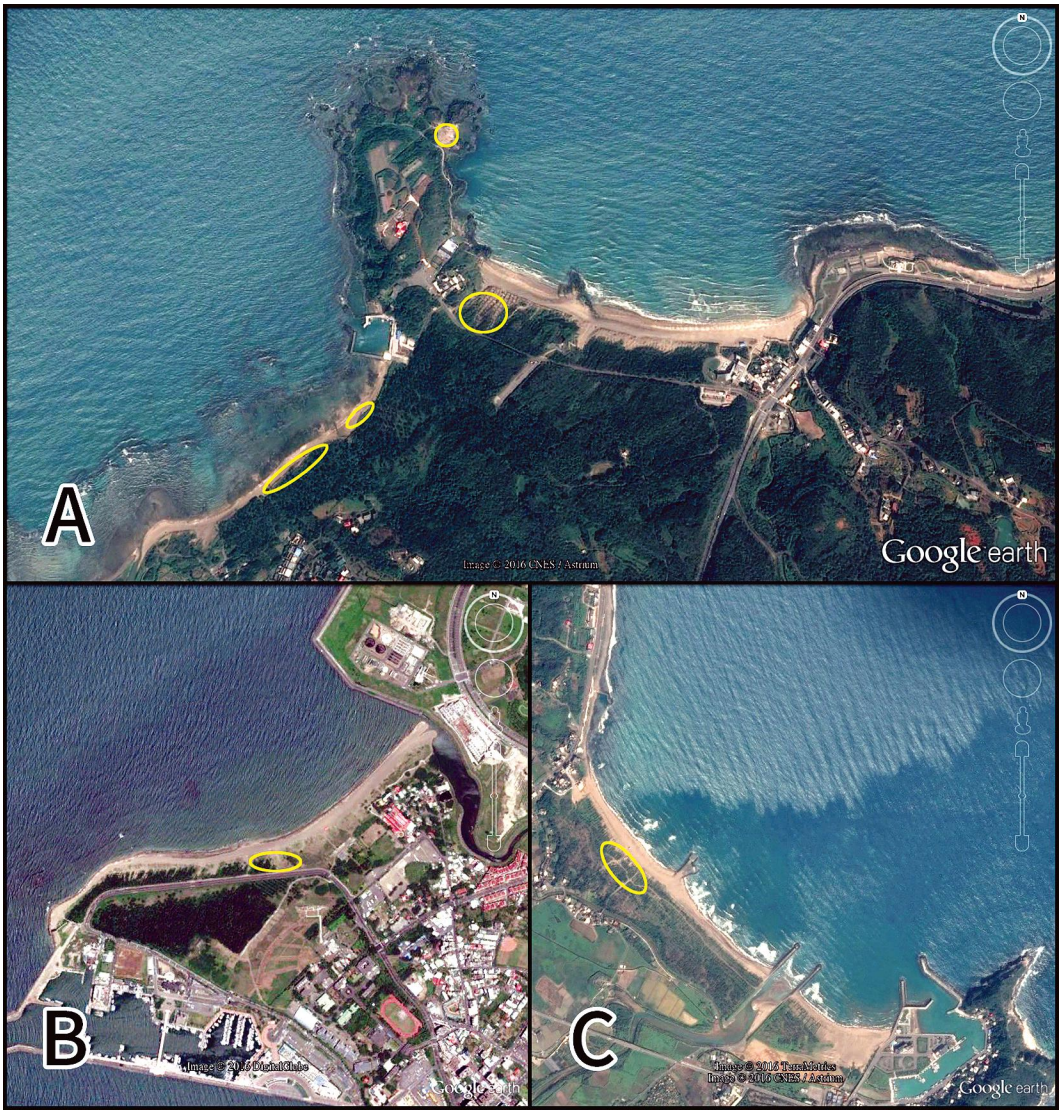

FIGURE 4. Distribution of habitats of *Cyclosomus inustus* Andrewes in Taiwan. A, Shihmen. B, Danshui. C, Kinshan. Areas outlined in yellow indicate the areas of the stabilized dunes where the beetles have been found (see also Fig. 3)..

FIGURE 5. *Cyclosomus inustus* Andrewes in Taiwan. A, Adult burrowing into sand, demonstrating negative phototaxis. B-D Adult feeding. B. On a small beetle (Tenebrionidae: *Nesocaedius* sp.). C. On a small fly. D. On a nymphal shield bug (Cydnidae).

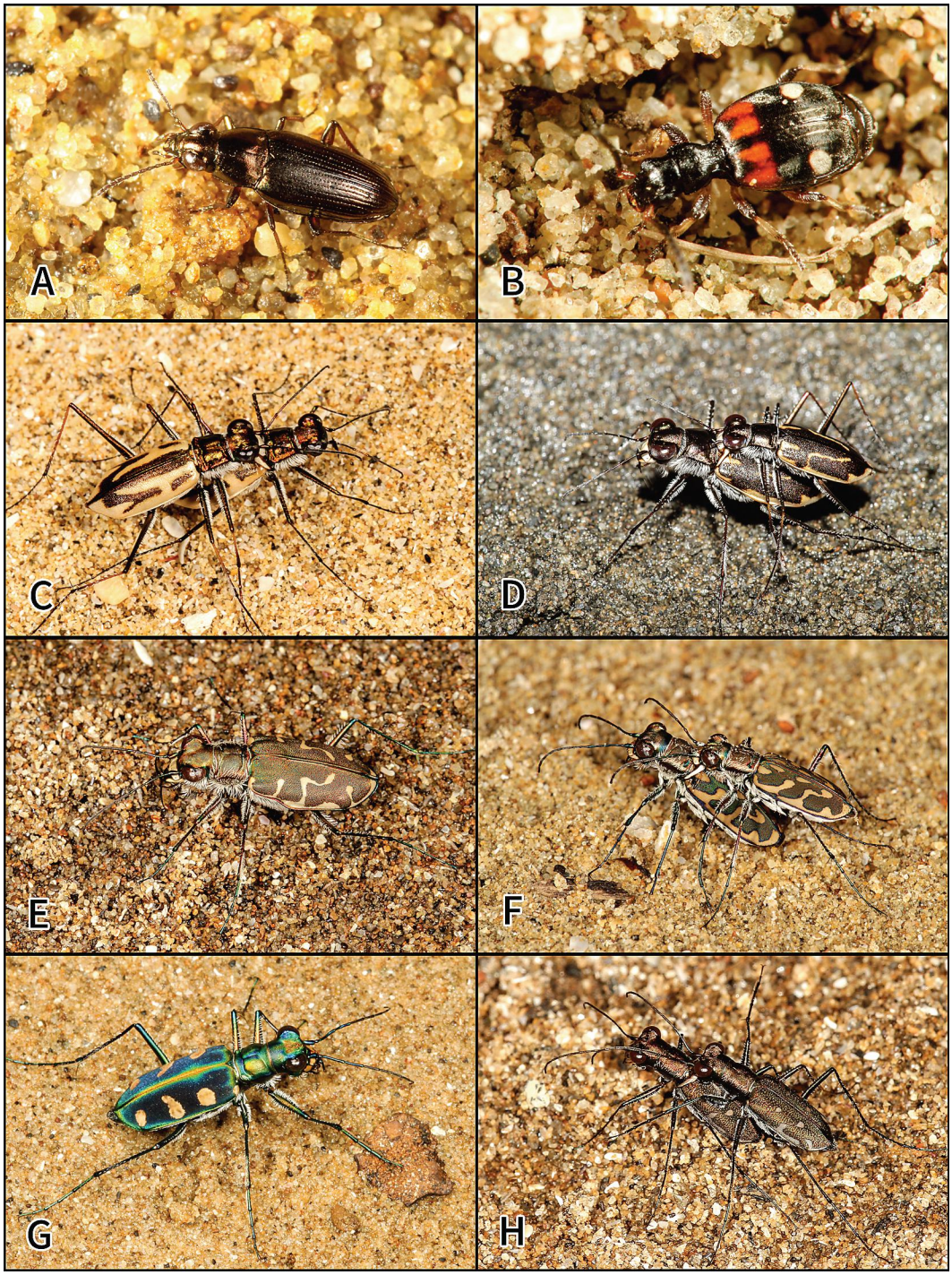

FIGURE 6. Other carabid species active on coastal sand in northern Taiwan. A. *Bembidion fusiforme* Netolitzky. B. *Mastax brittoni* Quentin. C. *Abroscelis anchoralis anchoralis* (Chevrolat). D. *Abroscelis anchoralis punctatissima* (Schaum). E. *Calomera angulata* (Fabricius), F. *Lophyra cancellata subtilesculpta* (W. Horn). G. *Cicindela batesi* Fleutiaux. H. *Cylindera kaleea angulimaculata* (Mandl).

Acknowledgements

We are grateful to Dr. Jing-Fu Tsai for his confirmation of the cydnid nymph in Fig. 5D.

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