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Front cover: *Tropidolaemus subannulatusi*, female, from Barangay Bariw, Municipality of Caramoan, Camarines Sur Province, Bicol Peninsula, Luzon Island, Philippines
(Photo by Rafe M. Brown [field no. RMB 26,176])

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Illustrated Key to the Snakes of the Philippines

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TABLE OF CONTENTS

| | |
|---|----|
| Introduction | 3 |
| Map of the Philippines | 4 |
| Methods | 3 |
| Taxonomic representation | 3 |
| Sources consulted for character data. | 5 |
| Types of characters included in dichotomous key | 7 |
| Illustrations | 7 |
| Key to the Families of Philippine snakes | 8 |
| Keys to the Family Subgroups | 12 |
| Acrochordidae: key to genera | 12 |
| Colubridae: key to subfamilies | 12 |
| Elapidae (marine): key to genera | 13 |
| Elapidae (terrestrial): key to genera. | 13 |
| Gerrhopilidae: key to genera | 14 |
| Homalopsidae: key to genera. | 14 |
| Lamprophiidae: key to genera | 14 |
| Pareidae: key to genera | 15 |
| Pythonidae: key to genera | 15 |
| Typhlopidae: key to genera | 15 |
| Viperidae: key to genera | 16 |
| Xenopeltidae: key to genera. | 17 |
| Keys to the Genera within Subfamily Groups of Colubridae. | 17 |
| Ahaetulliinae | 17 |
| Calamariinae. | 18 |
| Colubrinae | 18 |
| Natricinae | 19 |
| Sibynophiinae. | 19 |
| Keys to the Species within Genera | 19 |
| <i>Acrochordus</i> | 19 |
| <i>Acutotyphlops</i> | 19 |
| <i>Ahaetulla</i> | 19 |
| <i>Aipysurus</i> | 20 |
| <i>Aplopeltura</i> | 20 |
| <i>Boiga</i> | 20 |

| | |
|---|----|
| <i>Calamaria</i> | 20 |
| <i>Calliophis</i> | 21 |
| <i>Cerberus</i> | 21 |
| <i>Chrysopelea</i> | 22 |
| <i>Coelognathus</i> | 22 |
| <i>Cyclocorus</i> | 22 |
| <i>Dendrelaphis</i> | 23 |
| <i>Dryophiops</i> | 23 |
| <i>Emydocephalus</i> | 24 |
| <i>Gerarda</i> | 24 |
| <i>Gerrhopilus</i> | 24 |
| <i>Gonyosoma</i> | 24 |
| <i>Hemibungarus</i> | 24 |
| <i>Hologerrhum</i> | 24 |
| <i>Hydrophis</i> | 25 |
| <i>Indotyphlops</i> | 27 |
| <i>Laticauda</i> | 27 |
| <i>Liopeltis</i> | 28 |
| <i>Lycodon</i> | 28 |
| <i>Malayopython</i> | 29 |
| <i>Malayotyphlops</i> | 29 |
| <i>Myersophis</i> | 30 |
| <i>Naja</i> | 30 |
| <i>Oligodon</i> | 30 |
| <i>Ophiophagus</i> | 31 |
| <i>Opisthotropis</i> | 31 |
| <i>Oxyrhabdium</i> | 31 |
| <i>Psammodynastes</i> | 32 |
| <i>Pseudorabdion</i> | 32 |
| <i>Ptyas</i> | 33 |
| <i>Ramphotyphlops</i> | 33 |
| <i>Rhabdophis</i> | 33 |
| <i>Sibynophis</i> | 34 |
| <i>Stegonotus</i> | 34 |
| <i>Trimeresurus</i> | 34 |
| <i>Tropidolaemus</i> | 34 |
| <i>Tropidonophis</i> | 35 |
| Unnamed genus | 35 |
| <i>Xenopeltis</i> | 35 |
| Acknowledgements | 36 |
| Literature Cited | 36 |
| Appendix | 42 |
| Glossary | 42 |
| Table 1. Data for illustrated species and specimens | 45 |

INTRODUCTION

In this contribution we present an illustrated key to the snakes of the Philippine archipelago (Fig. 1). Following on our recent systematic review of all credible terrestrial and marine snake records for the country (Leviton et al. 2018), our goal here has been to distinguish comprehensively all species ascribed to the country, organize the taxa in accordance with the up-to-date classification, and assemble a dichotomous key, arranged hierarchically by superfamily, family, genus, and species. Here we also provide illustrations of the salient diagnostic characters, summarized so as to be accessible not only to academic herpetologists, but also biologists of other subdisciplines, Philippine government natural resource officers, local area wildlife managers, ecotourists, the general public, and most importantly, students.

The last systematic review and comprehensive key to the species of Philippine snakes was that of Taylor (1922a), who included the seven families, 41 genera, and 108 species known at the time. Various contributions since that time took the form of a field guide (Alcala 1986), selected reviews of portions of the fauna (i.e., Taylor 1963; Gaulke 2011), and a comprehensive series of papers constituting a systematic revision of the archipelago's fauna by Leviton (1957–1983) and colleagues (Inger and Marx 1965; Malnate and Underwood 1988; Brown et al. 1999, 2001; Wallach et al. 2007; Wynn et al. 2016). Following nearly a decade of focused terrestrial biodiversity inventory work (reviewed by Brown et al. 2013a) that resulted in the collection of many rare snake species from throughout the archipelago's major faunal regions (e.g., Phenix et al. 2011; Brown et al. 2012, 2013; Sanguila et al. 2016; Weinell et al. 2019) as well as amassing considerable genetic resources that are now to be found in biodiversity repositories (CMNH, TNHC, PNM, KU), genetic data from Philippine snake species has become accessible for inclusion in molecular phylogenetic studies. Consequently, our knowledge of the systematic affinities of many of the country's rare and diverse taxa has increased significantly (Vidal et al. 2007, 2010; Pyron et al. 2011; 2013; Pyron and Wallach 2014; Figueroa et al. 2016; Weinell and Brown 2017). Most recently, whole sections of the archipelago's snake fauna have been included in molecular phylogenetic analyses, thus allowing researchers to employ time-calibrated molecular phylogenetic analyses to investigate the time-frames for diversification, biogeographic inference, and species boundaries in the genera *Lycodon*, *Boiga*, *Calliophis*, *Malayopython*, *Cyclocorus*, *Hemibungarus*, *Oxyrhabdium*, *Myersophis*, and *Hologerrhum* (Castoe et al. 2007; Siler et al. 2013; Murray-Dickson et al. 2017; Weinell and Brown 2017; Weinell et al. *in review*; Brown et al. 2018) and others (Weinell et al. *unpublished data*). For those interested in the evolutionary biology, biogeography, and taxon-specific topics, we refer readers to the comprehensive synopsis of Leviton et al. (2018).

It is our hope that these biodiversity information products will serve as resources that may promote the scientific community's understanding and the lay public's appreciation of the diversity of Philippine snakes. Additionally, given that only a small portion of the country's terrestrial snake fauna, less than 15% of the species, are dangerously venomous, we hope that this key, taken with our earlier checklist with its numerous photo illustrations of the country's living snakes (Leviton et al. 2018), may result in reducing public fear of the archipelago's many harmless species, help prevent snake persecution in the country, promote public education, and advance conservation of the archipelago's diverse and fascinating snake fauna.

METHODS

Taxonomic representation.—The species and subspecies included in this key are those included in Leviton et al.'s (2018) checklist of Philippine snakes, with a few exceptions that account for recent taxonomic changes or personal observations. *Malayotyphlops manilae* (Taylor 1919) has been treated as a member of the genus *Gerrhopilus* (Leviton et al. 2018), but the only specimen

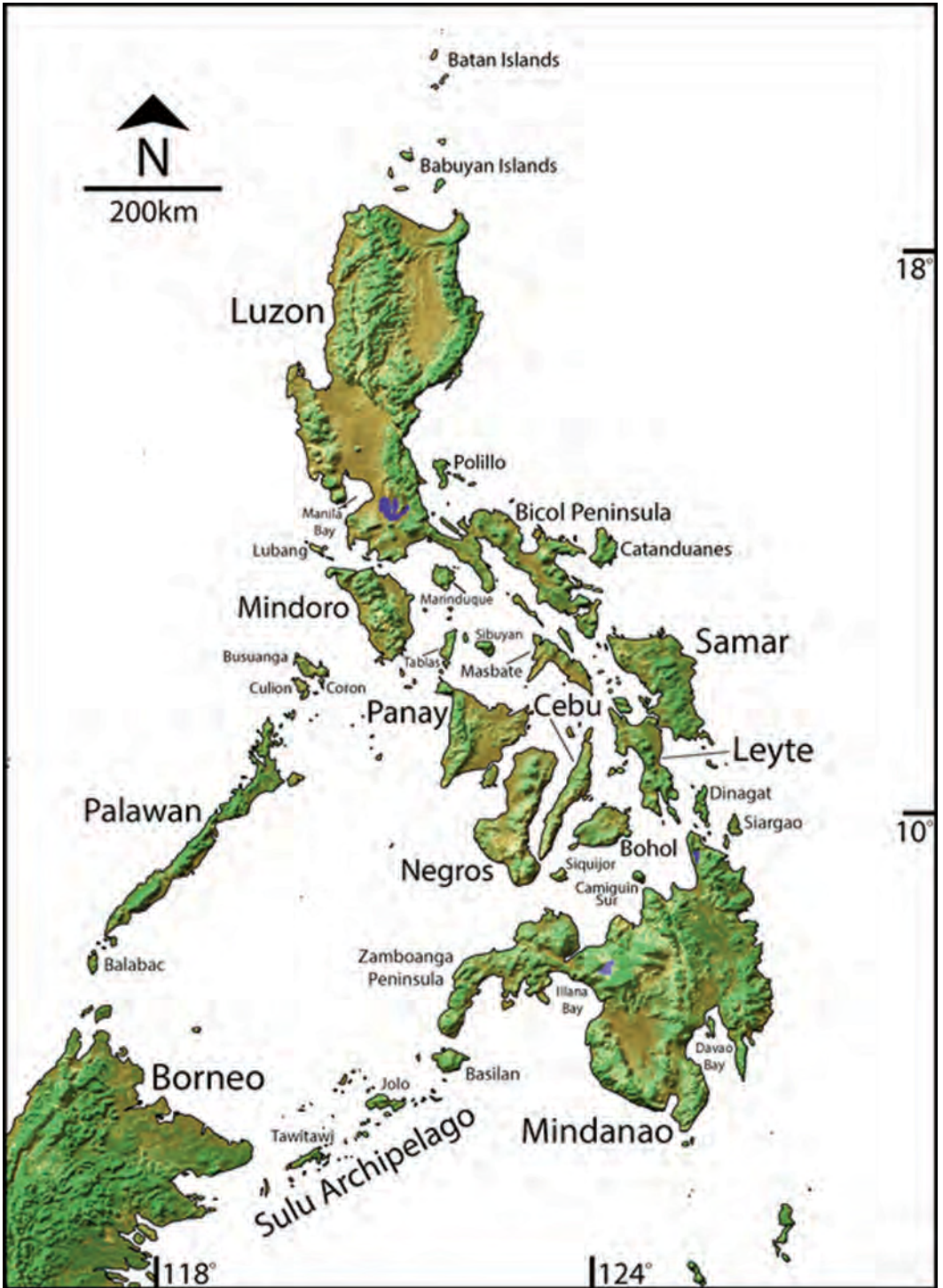


FIGURE 1. The Philippine Archipelago, with major landmasses labeled.

(the holotype, an unnumbered specimen in the Santo Tomas Museum, Philippines; collector and locality unknown) was never illustrated (Leviton et al. 2018; Wynn et al. 2016), and Taylor's (1919) description of the holotype is confusing to interpret. Nevertheless, we treat this species as a member of the genus *Malayotyphlops* rather than *Gerrhopilus*, because this species has a relatively small tail, rounded snout, and 28 longitudinal body scale rows, which are character states common for species of *Malayotyphlops* and are not known to occur in combination in other Philippine blind snake species (see Wynn et al. [2016] for a more detailed discussion of this species). Additionally, *Dryocalamus philippinus* (*sensu* Leviton et al. 2018) is here treated as *Lycodon philippinus*, because Figueroa et al. (2016) merged *Dryocalamus* into *Lycodon*.

We are including an "unnamed genus and species" (Cyclocorinae), which is currently being described as a new genus and species (Weinell et al. *in review*) and was formerly referred to as "unnamed Samar-Leyte lineage" by Weinell and Brown (2017). Additionally, we are also including *Pseudorabdion collaris*, which has not previously been reported from the Philippines, because we examined two specimens (KU 315197–98) from Pasonanca Park, Zamboanga City Province, Mindanao Island, which we tentatively assign to this species.

We have not included the four *Calamaria gervaisii* subspecies (*gervaisii*, *hollandi*, *iridescens*, and *polilloensis*) recognized by earlier authors (Taylor 1922a, 1923; Leviton et al. 2018) because the character state differences previously used to distinguish these subspecies are not geographically or genetically cohesive (i.e., do not correspond to geographically circumscribed or genetically-defined units; Weinell *pers. obs.*). Also, although the type locality of *Gerarda prevostiana* was reported as "Manille" [Luzon], this was almost certainly an error (Wallach et al., 2014; Leviton et al., 2018). Thus, we include this genus and species in the key based on the strength of a single record (voucher specimen UF 69099) from Brooke's Point, Palawan (Auth et al., 1990). In contrast, the presence of *Fordonia leucobalia* in the Philippines (Taylor 1922a) remains highly suspect (Leviton et al. 2018), and we do not include this genus or species in the key and believe it should be excluded from the Philippine faunal list in future works as well.

Sources consulted for character data.—This key builds upon many earlier works that treated subsets of the Philippine snake fauna, primarily in the form of dichotomous keys and taxonomic accounts. To construct the dichotomous key presented herein, we relied heavily upon the works of Taylor (1917, 1918, 1919, 1922a–c, 1923, 1925, 1963), Leviton (1957, 1963, 1964a–d, 1965a–c, 1967, 1968, 1970a–c, 1979, 1983), Inger and Marx (1965), Leviton et al. (2014), and Wynn et al. (2016). We also used character state data from additional publications for Philippine members of the following genera: *Acutotyphlops* (Wallach et al. 2007); *Ahaetulla* (Gaulke 1994); *Boiga* (Peters 1861, 1867; Gaulke 2004a); *Calliophis* and *Hemibungarus* (Brown et al. 2018); *Cerberus* (Murphy et al. 2012; Barrera Jr. et al. 2017); *Coelognathus* (Helfenberger 2001); *Dendrelaphis* (Gaulke 2004b; Rooijen and Vogel 2012; Vogel and van Rooijen 2008); *Gerrhopilus* (Savage 1950); *Gonyosoma* (Dowling 1958); *Hologerrhum* (Brown et al. 2001); *Hydrophis* (Kharin 1984; Rasmussen 1989 2011, 2014; Kharin and Hallerman 2009; Sherratt et al. 2018); *Laticauda* (Kharin 2005); *Lycodon* (Ota and Ross 1994; Lanza 1999; Gaulke 2002; Ota 2000); *Malayotyphlops* (Wynn and Leviton 1993; Hedges et al. 2014); *Naja* (Wüster and Thorpe 1996); *Oligodon* (Gaulke 1981; Green 2010); *Opisthotropis* (Brown and Leviton 1961; Yang et al. 2011); *Pseudorabdion* (Leviton and Brown 1959; Inger and Leviton 1966; Brown et al. 1999; Doria and Petri 2010); *Ptyas* (Ross et al. 1987; Malkmus et al. 2002); *Ramphotyphlops* (Gaulke 1995; Wallach 1993); *Sibynophis* (Gaulke 1993); *Stegonotus* (Boulenger 1893; Sanguila et al. 2016); *Trimeresurus* (Malhotra and Thorpe 2004; David et al. 2011); *Tropidonophis* (Malnate and Underwood 1988); and *Tropidolaemus* (Vogel et al. 2007). In addition to synthesizing data from earlier publications, we examined formalin/alcohol-preserved specimens at the University of Kansas Biodiversity Institute (KU).

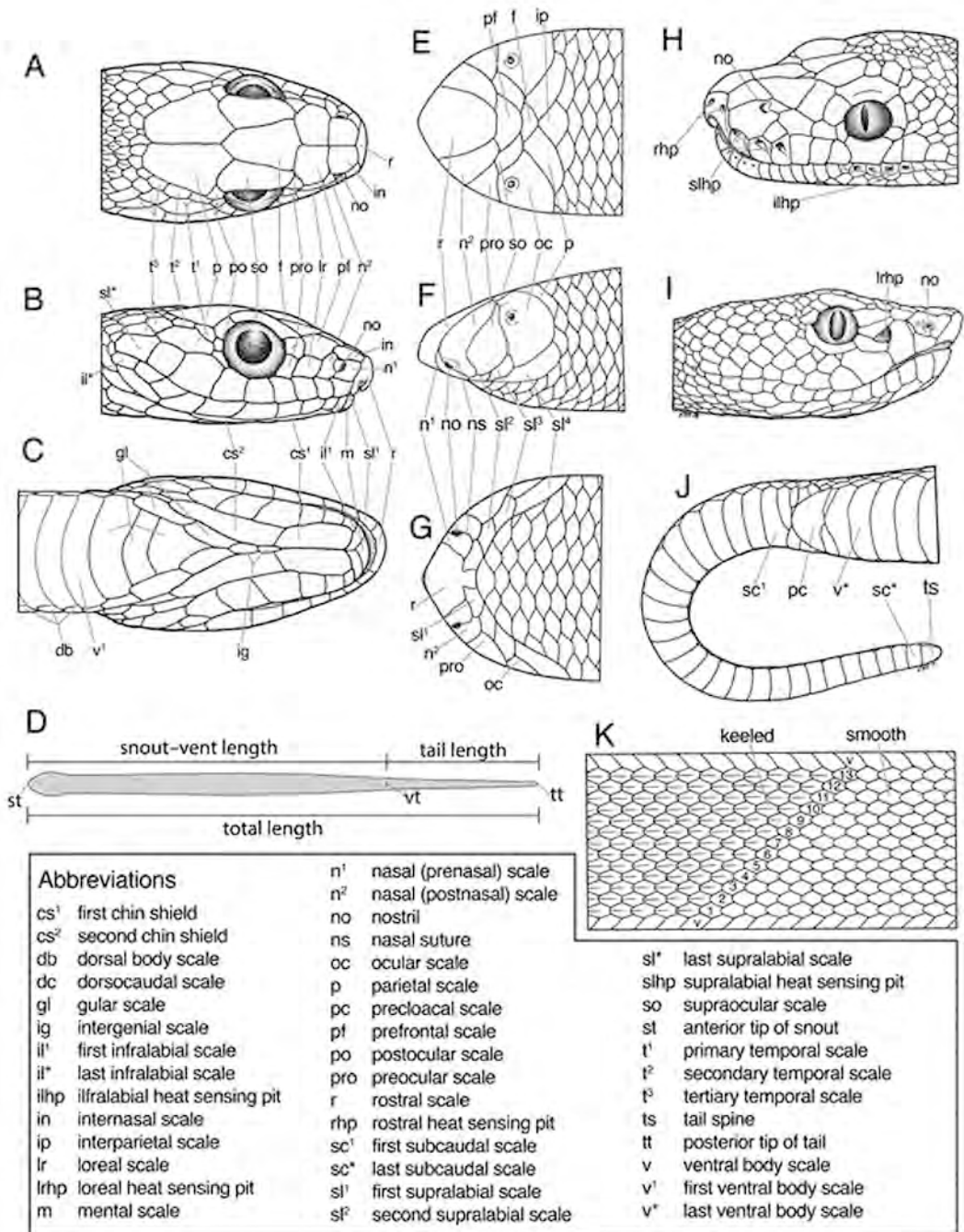


FIGURE 2. Typical characteristics of snakes. (A–C) scales of the head of most snakes (*Tropidonophis dendrophiops*, KU 310368); (D) body and tail length measurements of snakes; (E–G) scales of the head of most blindsnakes (*Ramphotyphlops suluensis*, PBS 2001, redrawn from Taylor 1918); heat sensing pits of (H) pythonids (*Malayopython reticulatus*, KU 330021), and (I) and viperids (*Trimeresurus flavomaculatus*; KU 329422); (J) scales of the ventral surface of the tail and posterior body of most snakes (*Cyclocorus lineatus alcalai*; KU 324539); (K) method for counting the number of dorsal body scale rows.

Types of characters included in dichotomous key.—We have tended to limit the types of characters included in the dichotomous key to those that can be easily observed (scored) by examining live or preserved specimens without dissection. For the most part, such characters include the number, shape, and arrangement of various types of scales, or the relative sizes of different parts of the head, body, and tail. In the absence of scalation and size differences, we do resort to consideration of color pattern differences, or less frequently, internal anatomy differences. Furthermore, when possible, we avoided using characters that can only be used to distinguish species of a particular sex (e.g., hemipenial characters) or age class, except when character states were known for all sex and age classes, or if additional characters were also provided. On the other hand, for some species, we do provide geographical information to supplement character information, if we considered species' range to be particularly useful for the purpose of identification. Occasionally, a species, or set thereof, could be distinguished only by geography, and in such cases it may be difficult or impossible to recognize additional range extensions or identify extralimital geographic records without additional information such as genetic data. Thus, we advocate the use of genetic data, in concert with geographical and phenotypic data whenever possible, but we recognize that, in many cases, morphological diagnostic characters may be the only source of information available to field biologists and students. As such, we have attempted to make use of phenotypic, scalation, and morphometric information wherever possible (the purpose of the present effort) and we expect that this key will be useful for identifying the vast majority of Philippine snakes. Characters and other specialized terminology used in this key are defined in the Glossary (see Appendix, pp. 42–44), and our definitions are consistent with those used by Dowling (1951), Powell et al. (2016), and Lillywhite (2008).

Illustrations.—We (EH) illustrated 69 of 154 species and subspecies and 43 of the 45 genera reported from the Philippines and included in this key (Figs. 3–47; Table 1). Illustrations were initially drawn using pencil on grid paper, and were then transferred to mylar film and redrawn with Rapidograph® pens and ink or felt-tip pens. Novel illustrations were drawn from either preserved specimens viewed under a dissecting microscope with camera lucida, from photographs of one or more specimens, or from one or more photographs of living animals. For species that occur both within and outside of the Philippines, we prioritized illustrations of Philippine specimens (Table 1). Some illustrations (especially the blind snakes) are adapted from earlier works (Brown et al. 2001; Leviton et al. 2014; Rasmussen et al. 2011; Savage 1950; Taylor 1918, 1919, 1922a; Wallach et al. 1993, 2007; Wynn et al. 1993, 2016; see also Acknowledgments section). Drawings were digitally scanned and arranged into figures using Adobe Photoshop CC v20.0.5 and Adobe Illustrator v23.0.04 (Adobe Inc.). See Table 1 for a full list of species and specimens illustrated, and for original sources of adapted illustrations.

The authors retain copyright for all original line drawings that are used in the figures herein.

KEY TO THE FAMILIES OF PHILIPPINE SNAKES

- 1a. Dorsal body scales spinose (Fig. 3A), and arranged in > 50 longitudinal rows at midbody Acrochordidae (p. 12)
- 1b. Dorsal body scales smooth or keeled (Fig. 3B–C), and arranged in < 50 longitudinal rows at midbody 2
- 2a. Tail laterally flattened, not conical or rounded (Fig. 4A) Elapidae (marine species) (p. 13)
- 2b. Tail conical or rounded, not laterally flattened (Fig. 4B) 3
- 3a. Ventral body scales about the same size as dorsal body scales (Fig. 5A); tail short, rounded. 4
- 3b. Ventral body scales much larger than dorsal body scales (> 1/3 width of body) (Fig. 5B); tail conical 5

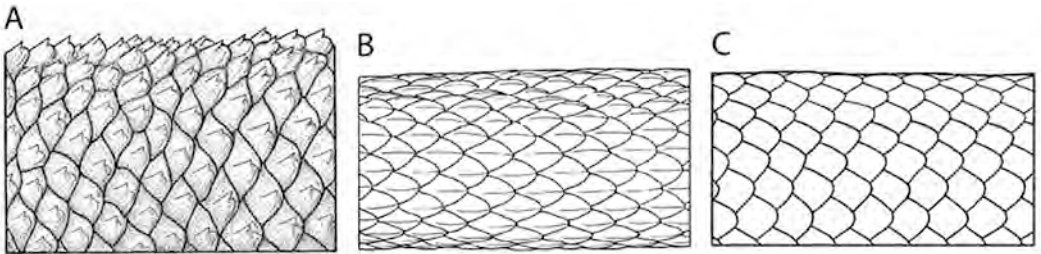


FIGURE 3. Dorsal body scales: (A) spinose (*Acrochordus granulatus*; KU 302951), (B) keeled (*Opisthotropis typica*; KU 327424), (C) smooth (*Oligodon maculatus*; KU 321699).

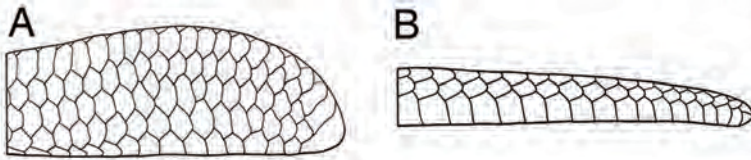


FIGURE 4. Tail shape of (A) *Laticauda colubrina* (KU 303033): laterally flattened, paddle-like, (B) *Ophiophagus hannah* (KU 321813): conical.

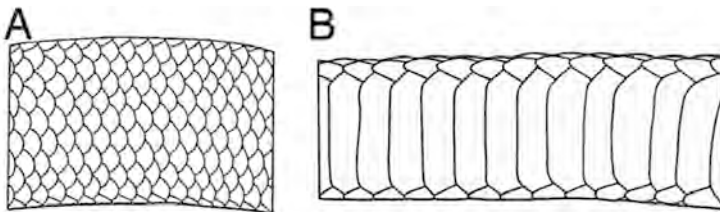


FIGURE 5. Ventral body scales of (A) *Ramphotyphlops cumingii* (KU 334468): ventral body scales about the same size as dorsal body scales; (B) *Calamaria gervaisii* (KU 307983): ventral body scales larger than dorsal body scales.

- 4a. Second supralabial scale overlaps preocular scale (Fig. 6A) Gerrhopilidae (p. 14)
- 4b. Preocular scale either overlaps second supralabial scale or does not contact it (Fig. 6B–C) Typhlopidae (p. 15)
- 5a. Heat sensing pits present on the head (Fig. 7) 6
- 5b. Heat sensing pits absent from head 7
- 6a. Single heat sensing pit present between eye and nostril (Fig. 7A) Viperidae (p. 16)
- 6b. Multiple heat sensing pits on each side of head, on labial scales and rostral scale (Fig. 7B) Pythonidae (p. 15)

- 7a. Head laterally compressed (Fig. 8A); number of loreal scales + preocular scales ≥ 4 ; supralabial scales do not border eye (Fig. 8B); second infralabial scales in contact medially. Pareidae (p. 15)
- 7b. Head not laterally compressed; number of loreal scales + preocular scales < 4 ; supralabial scales may or may not border eye; second infralabial scales not in contact medially. 8
- 8a. Nostrils positioned more dorsally than laterally; additionally, one of the following combinations of characters is true: (1) supralabial scales do not border eye; frontal scale fragmented into multiple smaller scales; internasal scales paired, positioned posterior to nasal scales; nasal scales paired and in contact with each other medially (Fig. 9A); or (2) one or more supralabial scales usually border eye; frontal scale not fragmented; internasal scale single, not paired, positioned medially between a pair of nasal scales; nasal scales not in contact with each other medially. Homalopsidae (p. 14)

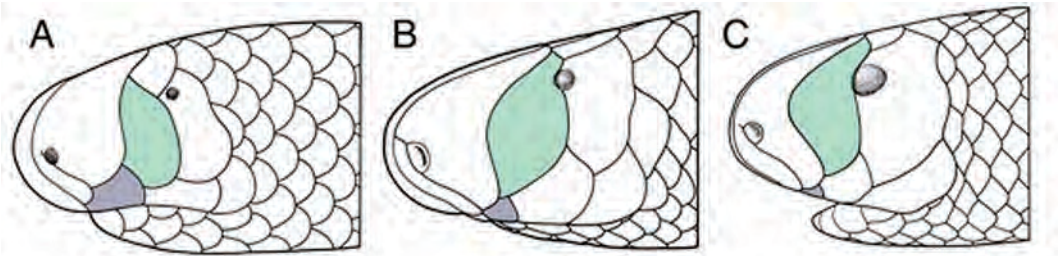


FIGURE 6. Lateral view of head of (A) *Gerrhopilus hedraeus* (CAS-SUR 12346; a redrafting by EH of original image in Savage 1950); (B) *Malayotyphlops luzonensis* (CM 2653; a redrafting by EH of original image in Wynn et al. 2016); (C) *Malayotyphlops denrorum* (PNM 9813; a redrafting by EH of original image in Wynn et al. 2016). Preocular scale (green), second supralabial scale (purplish-gray). Fig. A reproduced and modified with permission of J.M. Savage; Figs.B-C reproduced and modified with permission of A. Wynn and *Journal of Herpetology*.

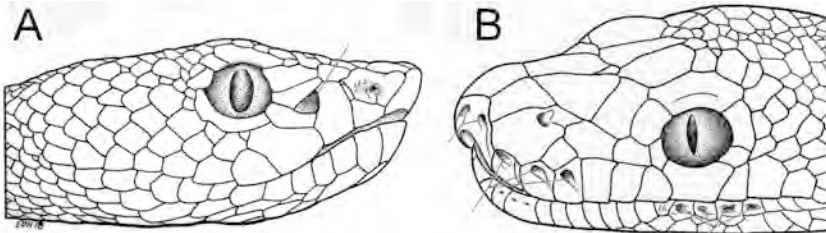


FIGURE 7. Location of heat sensing pits. (A) *Trimeresurus flavomaculatus* (KU 329422): loreal heat sensing pits, (B) *Malayopython reticulatus* (KU 330021): labial and rostral heat sensing pits.

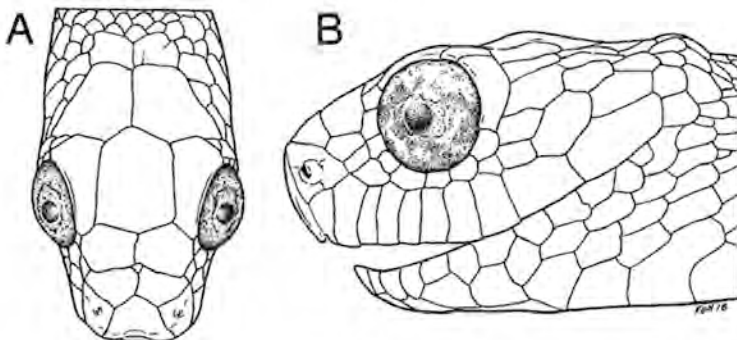


FIGURE 8. Head shape and scalation of *Aplopeltura boa*. (A) Dorsal view (KU 334473), (B) lateral view (KU 334474).

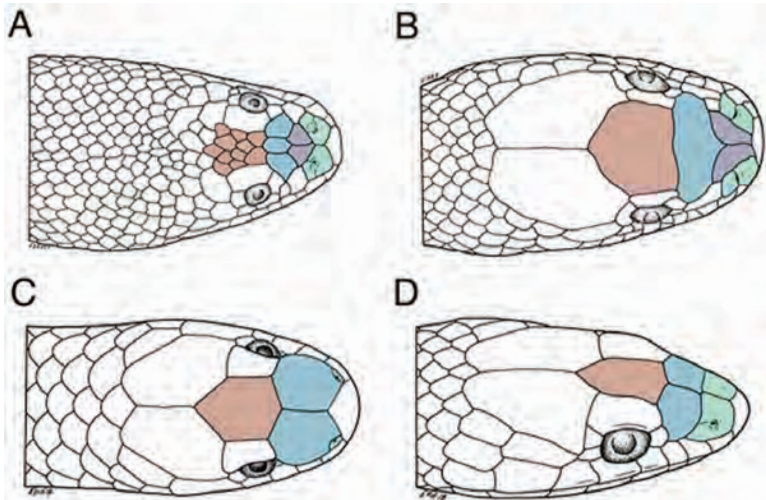


FIGURE 9. Dorsal view of head of (A) *Cerberus schneideri* (KU 305489), (B) *Opisthotropis typica* (KU 327424), (C) *Calamaria gervaisii* (KU 322329), (D) *Liopeltis philippinus* (KU 327731). Frontal scale (reddish brown), prefrontal scales (blue), internasal scales (purplish-gray), nasal scales (green).

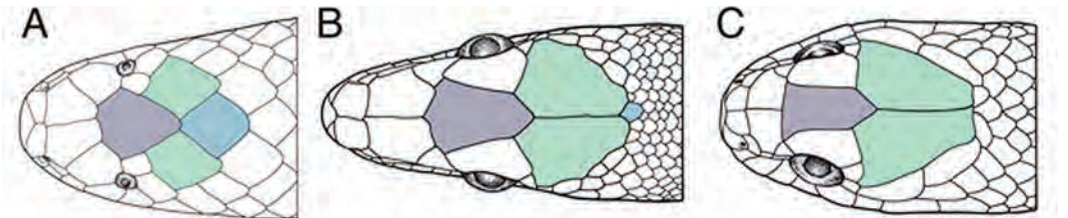


FIGURE 10. Dorsal view of head of (A) *Xenopeltis unicolor* (KU 79152), (B) *Gonyosoma oxycephalum* (KU 315168), (C) *Hologerrhum dermali* (CMNH 5075; drawn from photograph in Brown et al. 2001). Frontal scale (purplish-gray), interparietal scale (blue), and parietal scales (green).

- 8b. Nostrils positioned more laterally than dorsally; frontal scale not fragmented; supralabial scales may or may not border eye; internasal scales either (1) paired, positioned medially between nasal scales, or, (2) fused to either prefrontal scales or nasal scales (Fig. 9B–D) 9
- 9a. Frontal scale and interparietal scale similar in size; parietal scales not in contact with each other medially (Fig. 10A) *Xenopeltidae* (p. 17)
- 9b. Frontal scale much larger than interparietal scale (Fig. 10B), or interparietal scale is absent (Fig. 10C); parietal scales in contact with each other medially (Figs. 10B–C) 10
- 10a. Loreal scales absent; one or more preocular scales present and in contact with posterior nasal scale (Fig. 11A); one enlarged venom fang on each maxilla (although replacement fangs may also be present); venom fang short, permanently erect; maxillary bone elongate, usually with several small teeth behind front fang *Elapidae* (terrestrial) (p. 13)
- 10b. Loreal and preocular scales present or absent (Fig. 11B–C); if preocular scales present and loreal scales absent, preocular scales not in contact with nasal scales (Fig. 11B–C); enlarged fang(s) absent, numerous (> 5) maxillary teeth present 11
- 11a. Temporal scales present (Fig. 12B), dorsal body scales smooth, and at least one of the following characters or combinations of characters also true: (1) nasal scale divided (Fig. 13B) and subcaudal scales single, not paired (Fig. 14B); (2) nasal scale undivided (Fig. 13A), subcaudal scales paired (Fig. 14A), and dorsal body scales in 17 longitudinal rows at midbody;

(3) nasal scale divided (Fig. 13B), subcaudal scales paired (Fig. 14A), dorsal body scales in 15 longitudinal rows throughout length of body, and prefrontal scale ≥ 3 times size of supraocular scale. Lamprophiidae (p. 14)

11b. Subcaudal scales paired, and at least one of the following characters or combinations of characters also true: (1) temporal scales absent (Fig. 12A); (2) dorsal body scales keeled; (3) temporal scales present (Fig 12B), nasal scale undivided or incompletely divided (Fig. 13A), and dorsal body scales in 15 longitudinal rows at midbody; (4) temporal scales present, nasal scale divided, dorsal body scales smooth and in 15 longitudinal rows throughout length of body,

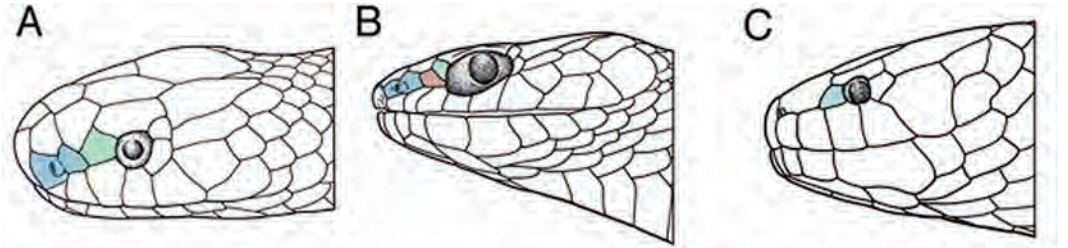


FIGURE 11. Lateral view of head of (A) *Hemibungarus mcclungi* (KU 313898), (B) *Sibynophis bivittatus* (KU 309608), (C) *Calamaria lumbricoidea* (KU 315159). Preocular scales (green), nasal scales (blue), loreal scale (reddish brown).

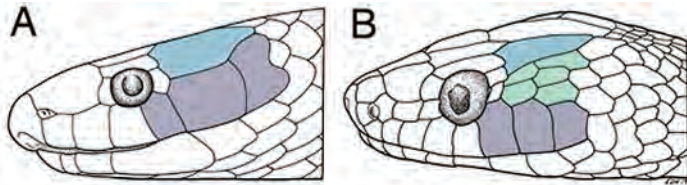


FIGURE 12. Lateral view of head of (A) *Calamaria gervaisii* (KU 322329), (B) *Lycodon muelleri* (KU 327575). Temporal scales (green), supralabial scales (purplish-gray), parietal scale (blue).

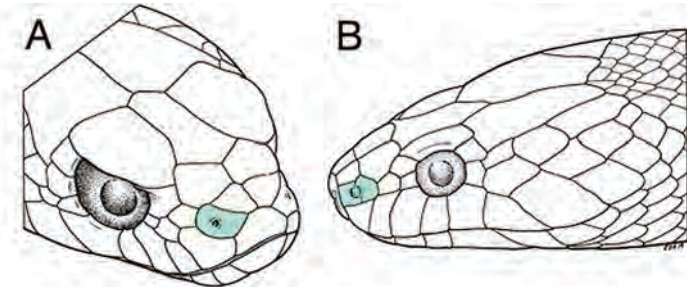


FIGURE 13. Lateral view of head of (A) *Psammodynastes pulverulentus* (KU 329688), (B) *Cyclocorus lineatus alcalai* (KU 324539). Nasal scale (green) undivided (A) or divided (B).

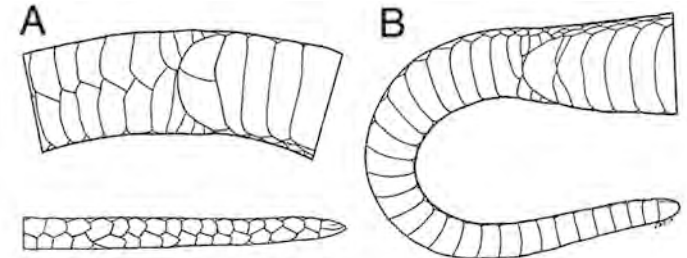


FIGURE 14. Arrangement of subcaudal scales, (A) *Opisthotropis typica* (KU 327424): subcaudal scales paired; (B) *Cyclocorus lineatus alcalai* (KU 324539): subcaudal scales single, not paired.

prefrontal scale less than twice size of supraocular scale; (5) temporal scales present, nasal scale divided, dorsal body scales not in 15 longitudinal rows throughout length of body
 Colubridae (p. 12)

KEYS TO FAMILY SUBGROUPS, ARRANGED ALPHABETICALLY BY FAMILY GROUPS

Acrochordidae

Represented by a single genus *Acrochordus* (p. 19)

Colubridae

Key to Philippine subfamilies.

- 1a. Temporal scales absent; parietal scales in contact with supralabial scales (Fig. 12A) Calamariinae (p. 18)
- 1b. Temporal scales present; parietal scales not in contact with supralabial scales (Fig. 12B) 2
- 2a. Supralabial scales either do not border eye, or supralabial scales 4–6 border eye; if supralabial scales 4–6 border eye, then dorsal body scales reduce from 19→17 or from 17→15 longitudinal rows posteriorly, and lateral body scales (except possibly first row) keeled (Fig. 3B) Natricinae (p. 19)
- 2b. One or more supralabial scales border eye; if supralabial scales 4–6 border eye and dorsal body scales reduce from 19→17 or 17→15 longitudinal rows posteriorly, then lateral body scales are smooth (Fig. 3C) 3
- 3a. Lateral body scales in oblique rows (Fig. 15A); dorsal body scales reduce from 17→13, 15→13, 15→11, or 13→11 longitudinal scale rows posteriorly; third supralabial scale does not border eye. Ahaetulliinae (p. 17)
- 3b. One of the following combinations of characters true: (1) lateral body scales in horizontal, not oblique rows (Fig. 13B), and dorsal body scales in 13 longitudinal rows at midbody; (2) lateral body scales in oblique rows (Fig. 15A) and dorsal body scales in 15–17 longitudinal rows at midbody, not reducing to fewer than 15 rows before vent; (3) lateral body scales in oblique or horizontal rows (compare Fig. 15A, B), and dorsal body scales in 19–23 longitudinal rows at midbody. 4

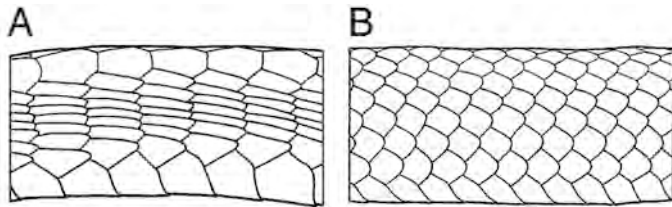


FIGURE 15. Lateral body scales of (A) *Dendrelaphis marenae* (KU 314131): oblique rows, (B) *Oligodon maculatus* (KU 321699): horizontal rows.

- 4a. Dorsal body scales in 17 smooth longitudinal rows throughout length of body; number of ventral body scales 144–185; subcaudal scales arranged in 89–145 pairs; numerous small teeth, 30–50, on each of maxillary and dentary bones Sibynophiinae (p. 19)
- 4b. Dorsal body scales in 15–23 smooth or keeled longitudinal rows at midbody; if dorsal body scales in 17 smooth longitudinal rows throughout length of body, then subcaudal scales arranged in < 80 or > 190 pairs; fewer than 30 teeth on each of maxillary and dentary bones Colubrinae (p. 18)

Elapidae (marine species)

Key to Philippine genera.

- 1a. Nasal scales separated by internasal scales; width of ventral body scales > 1/3 body width. *Laticauda* (p. 27)
- 1b. Internasal scales absent, nasal scales in contact with each other medially; width of ventral body scales variable 2
- 2a. Width of ventral body scales > 1/3 body width. *Aipysurus* (p. 20)
- 2b. Width of ventral body scales < 1/4 body width and often narrower than adjacent lateral body scales 3
- 3a. Three supralabial scales, second very elongate (Fig. 16). *Emydocephalus* (p. 24)
- 3b. More than three supralabial scales *Hydrophis* (p. 24)

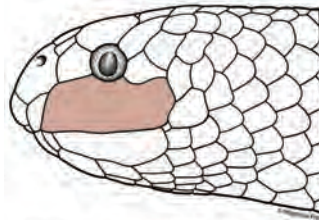


FIGURE 16. Lateral view of head of *Emydocephalus annulatus* (specimen number unknown; a redrafting by EH of original image in Rasmussen et al. 2011). Second supralabial scale (reddish brown). Fig. 16, modified original line drawing reproduced with permission of A. Rasmussen and *Zootaxa* and Magnolia Press.

Elapidae (terrestrial species)

Key to Philippine genera.

- 1a. Three postocular scales (Fig. 17A–B); lateral body scales in oblique or horizontal rows (Fig. 15). 2
- 1b. Two postocular scales (Fig. 17C–D); lateral body scales in horizontal rows (Fig. 15B); number of longitudinal rows of dorsal body scales not reducing posteriorly 3
- 2a. Dorsal body scales in 17–25 longitudinal rows at midbody; postnasal scale vertically elongate, separated from or only narrowly in contact with prefrontal scale (Fig. 17A) *Naja* (p. 30)
- 2b. Dorsal body scales in 15 longitudinal rows throughout length of body; postnasal scale triangular, about as long as tall, and broadly in contact with prefrontal scale (Fig. 17B). *Ophiophagus* (p. 31)

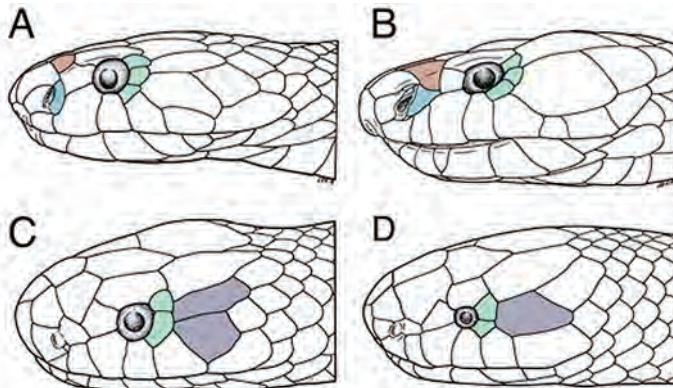


FIGURE 17. Lateral view of head of (A) *Naja samarensis* (KU 326653), (B) *Ophiophagus hannah* (KU 321813), (C) *Hemibungarus mcclungi* (KU 313898), (D) *Calliophis philippina* (KU 327218). Postocular scales (green), anterior temporal scales (purplish-gray), postnasal scales (blue), prefrontal scales (reddish brown).

- 3a. Two anterior temporal scales (Fig. 17C); dorsal body scales in 15 longitudinal rows throughout length of body *Hemibungarus* (p. 24)
- 3b. One anterior temporal scale (Fig. 17D); dorsal body scales in 13 longitudinal rows throughout length of body *Calliophis* (p. 21)

Gerrhopilidae

Represented by a single genus *Gerrhopilus* (p. 24)

Homalopsidae

Key to Philippine genera.

- 1a. Supralabial scales do not border eye; frontal scale fragmented into multiple smaller scales; internasal scales paired, positioned posterior to a pair of nasal scales; nasal scales in contact with each other medially (Fig. 9A). *Cerberus* (p. 21)
- 1b. One or more supralabial scales usually border eye; frontal scale not fragmented; internasal scale single, not paired, and is positioned medially between a pair of nasal scales; nasal scales not in contact with each other medially. *Gerarda* (p. 24)

Lamprophiidae

Key to Philippine genera.

- 1a. Nasal scale large, round and undivided (Fig. 13A) *Psammodynastes* (p. 31)
- 1b. Nasal scale divided (Fig. 13B) 2
- 2a. Snout broad (Fig. 18B); anterior chin shields smaller than or similar in size to posterior chin shields; subcaudal scales unpaired (Fig. 14B) 3
- 2b. Snout narrow (Fig. 18A); anterior chin shields much larger than posterior chin shields; subcaudal scales paired or unpaired (Fig. 14). 4

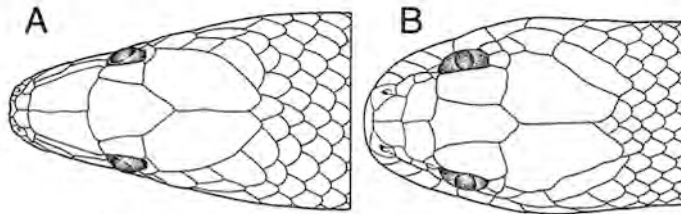


FIGURE 18. Dorsal head shape and scalation of (A) *Oxyrhabdium modestum* (KU 311301): narrow snout, (B) *Hologerrhum philippinum* (KU 330056): broad snout.

- 3a. Maxilla not strongly angled; no maxillary diastema, although anterior and posterior maxillary teeth are much larger than intervening teeth; posterior maxillary tooth grooved; five infralabial scales in contact with chin shields, and fourth infralabial scale broadly in contact with the anterior and posterior chin shields for about an equal length (Fig. 19A) *Hologerrhum* (p. 24)
- 3b. Maxilla strongly angled; large diastema between anterior and posterior maxillary teeth; posterior maxillary teeth not grooved; one of the following is also true: (1) five infralabial scales in contact with chin shields, and fourth infralabial scale either not in contact with or barely in contact with posterior chin shield (Fig. 19B), or (2) four infralabial scales in contact with chin shields, and third infralabial scale either not in contact with or barely in contact with posterior chin shield (Fig. 19C) *Cyclocorus* (p. 22)
- 4a. Five supralabial scales; subcaudal scales unpaired Unnamed genus (p. 35)
- 4b. Six or more supralabial scales; subcaudal scales paired 5

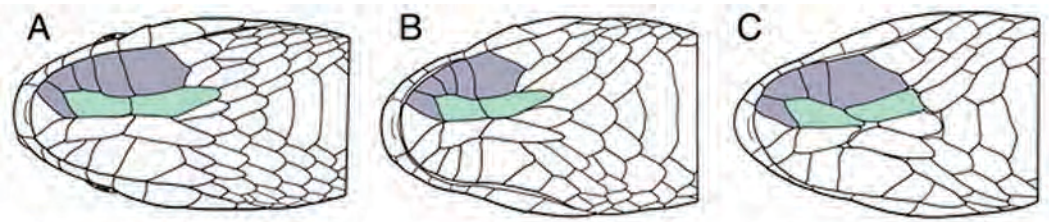


FIGURE 19. Ventral view of head of (A) *Hologerrhum philippinum* (KU 330065): five infralabial scales in contact with chin shields; anterior chin shields broadly contact infralabial scales 1–4; posterior chin shields broadly in contact with fourth and fifth infralabial scales; (B) *Cyclocorus lineatus lineatus* (KU 346571): five infralabial scales in contact with chin shields; anterior chin shields broadly in contact with infralabial scales 1–4; posterior chin shields broadly in contact with fifth infralabial scale; (C) *Cyclocorus nuchalis nuchalis* (KU 327765): four infralabial scales in contact with chin shields, anterior chin shields broadly in contact with infralabial scales 1–3; posterior chin shields broadly in contact with fourth infralabial scale.

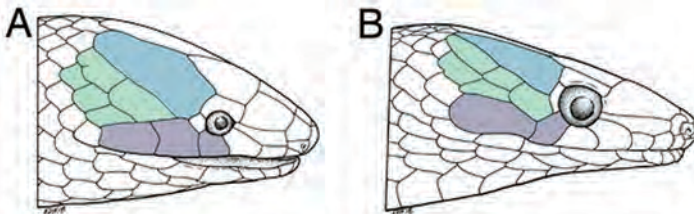


FIGURE 20. Lateral view of head of (A) *Myersophis alpestris* (KU 308684), (B) *Oxyrhabdium modestum* (KU 311301). Parietal scale (blue), temporal scales (green), posterior supralabial scales (purplish-gray).

- 5a. Parietal scales in contact with supralabial scales (Fig. 20A) *Myersophis* (p. 30)
- 5b. Parietal scales not in contact with supralabial scales (Fig. 20B) *Oxyrhabdium* (p. 31)

Pareidae

Represented by a single genus *Aplopeltura* (p. 20)

Pythonidae

Represented by a single genus *Malayopython* (p. 29)

Typhlopidae

Key to Philippine genera.

- 1a. Posterior origin of nasal suture is preocular scale (Fig. 21A) *Indotyphlops* (p. 27)
- 1b. Posterior origin of nasal suture is the second supralabial scale (Fig. 21B) 2

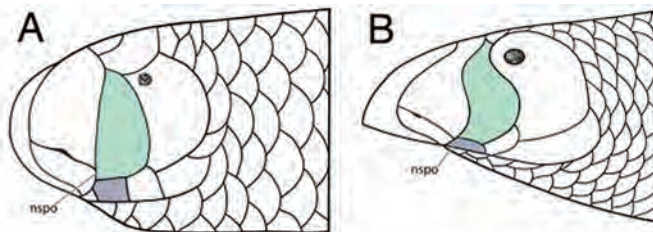


FIGURE 21. Lateral view of head of (A) *Indotyphlops braminus* (specimen number unknown; redrawn from Taylor 1922a), (B) *Ramphotyphlops cumingii* (EHT R-99; a redrafting by EH of original image in Taylor 1919). Second supralabial scale (purplish-gray); preocular scale (green); nsपो = nasal suture posterior origin scale.

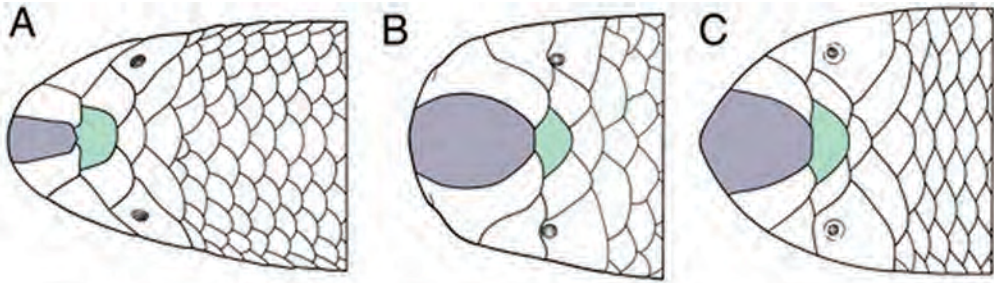


FIGURE 22. Dorsal view of head of (A) *Acutotyphlops banaorum* (FMNH 262249; a redrafting by EH of original image in Wallach et al. 2007), (B) *Malayotyphlops ruber* (SMF 16616; a redrafting by EH of original image in Wynn et al. 2016), (C) *Ramphotyphlops suluensis* (PBS 2001; a redrafting by EH of original image in Taylor 1918). Prefrontal scale (green), rostral scale (purplish-gray). Fig. A reproduced and modified with permission of V. Wallach and *Journal of Herpetology*. Fig. B reproduced and modified with permission of A. Wynn and *Journal of Herpetology*.

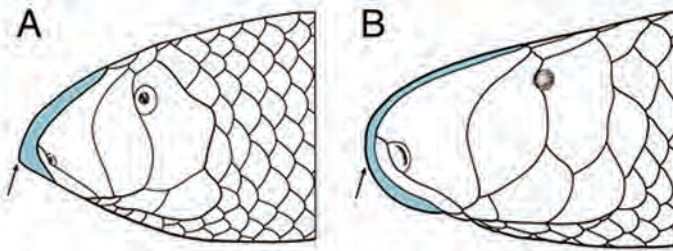


FIGURE 23. Lateral view of head of (A) *Ramphotyphlops marxi* (FMNH 96520; a redrafting by EH of original image in Wallach 1993), (B) *Malayotyphlops luzonensis* (CM 2653; a redrafting by EH of original image in Wynn et al. 2016). Rostral scale (blue); arrow indicates either (A) beaked shape of rostral scale, or (B) rounded shape of rostral scale. Fig. A reproduced and modified with permission of V. Wallach and *Journal of Herpetology*. Fig. B reproduced and modified with permission of A. Wynn and *Journal of Herpetology*.

- 2a. Prefrontal scale much wider than rostral scale (Fig. 22A) *Acutotyphlops* (p. 19)
- 2b. Prefrontal scale narrower than rostral scale (Fig. 22B–C) 3
- 3a. Rostral scale beaked (Fig. 23A) *Ramphotyphlops* (p. 33)
- 3b. Rostral scale rounded (Fig. 23B) *Malayotyphlops* (p. 29)

Viperidae

Key to Philippine genera.

- 1a. Some scales on head strongly keeled (Fig. 24a); second supralabial scale not in contact with scale forming anterior border of heat sensing pit *Tropidolaemus* (p. 34)
- 1b. Scales on head smooth (Fig. 24b); second supralabial scale in contact with scale forming anterior border of heat sensing pit *Trimeresurus* (p. 34)

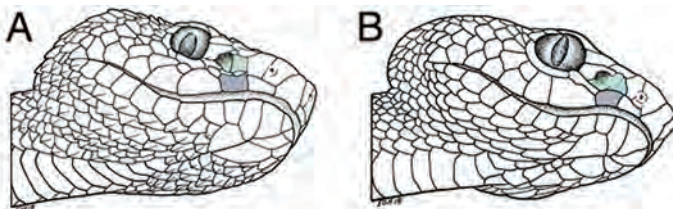


FIGURE 24. Ventral-lateral view of head of (A) *Tropidolaemus subannulatus* (KU 327425), (B) *Trimeresurus flavomaculatus* (KU 330050). Second supralabial scale (purplish-gray), scale anterior to heat sensing pit (green).

Xenopeltidae

Represented by a single genus *Xenopeltis* (p. 35)

KEYS TO THE GENERA WITHIN SUBFAMILY GROUPS OF THE FAMILY COLUBRIDAE

Ahaetulliinae

Key to Philippine genera.

- 1a. Pupil horizontally elongated and rectangular (Fig. 25A); ventral body scales laterally hinged, and their posterior edges unnotched (Fig. 26A) *Ahaetulla* (p. 19)
- 1b. Pupils may be circular or slightly horizontally elongate (Fig. 25B); ventral body scales laterally hinged, and their posterior edges notched (Fig. 26B) 2

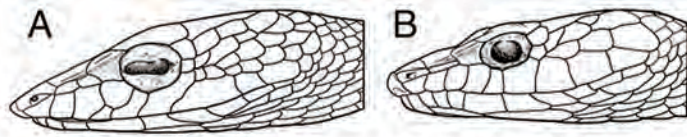


FIGURE 25. Lateral view of head of (A) *Ahaetulla prasina preocularis* (KU 347854), (B) *Dryophiops rubescens* (KU 328516). Note horizontally elongate pupil in *Ahaetulla* versus rounded pupil in *Dryophiops*.

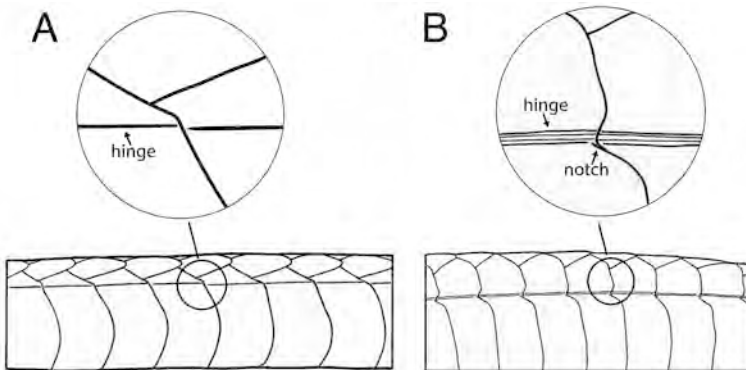


FIGURE 26. Ventral body scales of (A) *Ahaetulla prasina preocularis* (KU 349849): ventral body scales hinged, with posterior edge unnotched, (B) *Chrysopelea paradisi variabilis* (KU 337271): ventral body scales hinged, and posterior edge notched.

- 2a. Dorsal body scales in 17 longitudinal rows at midbody; last ventral body scale (i.e., the scale immediately before the precloacal scale) divided. *Chrysopelea* (p. 22)
- 2b. Dorsal body scales in 13–15 longitudinal rows at midbody; last ventral body scale undivided 3
- 3a. Dorsal body scales in 15 longitudinal rows at midbody; vertebral scales similar in size to other dorsal body scales; black postocular stripe absent. *Dryophiops* (p. 23)
- 3b. One of the following combinations of characters true: (1) dorsal body scales in 13 longitudinal rows at midbody, vertebral scales similar in size to other dorsal body scales; (2) dorsal body scales in 15 longitudinal rows at midbody, vertebral scales much larger than other dorsal body scales, and a black postocular stripe present *Dendrelaphis* (p. 23)

Calamariinae

Key to Philippine genera.

- 1a. Internasal scales absent (fused to prefrontal scales) (Fig. 27A); dorsal body scales in 13 longitudinal rows at midbody. *Calamaria* (p. 20)
- 1b. Internasal scales present (distinct from prefrontal scales) (Fig. 27B); dorsal body scales in 15 longitudinal rows at midbody. *Pseudorabdion* (p. 32)

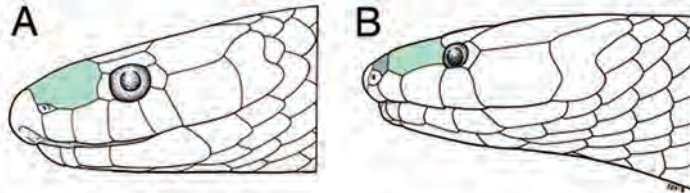


FIGURE 27. Lateral view of head of (A) *Calamaria gervaisii* (KU 322329), (B) *Pseudorabdion collaris* (KU 315197). Prefrontal scales (green), internasal scales (purplish-gray).

Colubrinae

Key to Philippine genera.

- 1a. Dorsal body scales in 19–27 longitudinal rows at midbody. 2
- 1b. Dorsal body scales in 14–18 longitudinal rows at midbody. 4
- 2a. Pupil strongly vertically elliptical (Fig. 28A) *Boiga* (p. 20)
- 2b. Pupil circular or slightly vertically elliptical (Fig. 28B). 3

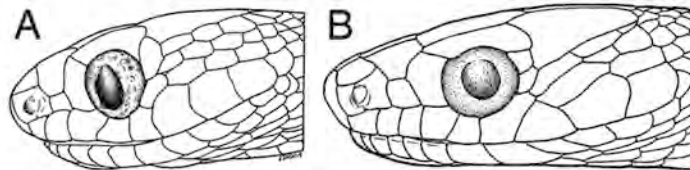


FIGURE 28. Lateral view of head of (A) *Boiga angulata* (KU 343853), (B) *Coelognathus erythrurus manillensis* (KU 335195). Note vertically elliptical (A) versus rounded pupil (B).

- 3a. Dorsal body scales in 23–27 longitudinal rows at midbody; body emerald green in life, blue after preservation in alcohol. *Gonyosoma* (p. 24)
- 3b. Dorsal body scales in 21 longitudinal rows at midbody; body not emerald green in life, not blue after preservation in alcohol *Coelognathus* (p. 22)
- 4a. Dorsal body scales in 15–17 longitudinal rows that do not reduce posteriorly; subcaudal scales 27–54 pairs *Oligodon* (p. 30)
- 4b. Dorsal body scales may or may not reduce posteriorly; if dorsal body scales do not reduce posteriorly, then subcaudal scales in > 100 pairs 5
- 5a. Lateral edge of supraocular scale robust, protruding over eye rather than curving around eye (Fig. 29A); dorsal body scales usually in 14, 16, or 18 longitudinal rows at midbody. *Ptyas* (p. 33)
- 5b. Lateral edge of supraocular scale not robust, and curves with contour of eye (Fig. 29B); dorsal body scales usually in 15 or 17 longitudinal rows at midbody 6
- 6a. Loreal scale absent; dorsal body scales in 15 longitudinal rows at midbody . . *Liopeltis* (p. 27)
- 6b. Loreal scale present; dorsal body scales in 15–17 longitudinal scale rows at midbody 7

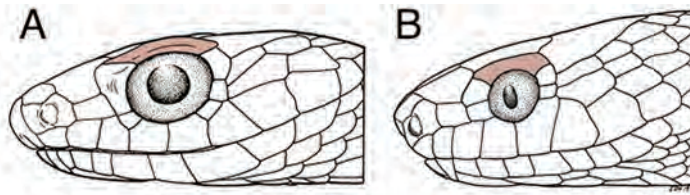


FIGURE 29. Lateral view of head of (A) *Ptyas luzonensis* (KU 306605), (B) *Stegonotus muelleri* (KU 344097). Supraocular scale (reddish brown) of *Ptyas robusta*, protruding over eye.

- 7a. One or more of the following combinations of characters true: (1) dorsal body scales in 17 longitudinal rows at midbody, and 184–216 smooth ventral body scales; (2) dorsal body scales in 15 longitudinal rows at midbody and ventral body scales keeled *Lycodon* (p. 28)
- 7b. Dorsal body scales in 17 longitudinal rows at midbody, 220–232 smooth ventral body scales *Stegonotus* (p. 34)

Natricinae

Key to Philippine genera.

- 1a. Fewer than 10 supralabial scales 2
- 1b. More than 10 supralabial scales. *Opisthotropis* (p. 31)
- 2a. One of the following combinations of characters true: (1) dorsal body scales in 15–17 longitudinal rows at midbody and background color of ventral body scales black; (2) dorsal body scales in 19 longitudinal rows at midbody and background color of ventral body scales pale (but not pinkish) in life *Rhabdophis* (p. 33)
- 2b. One of the following combinations of characters true: (1) dorsal body scales in 17 longitudinal rows at midbody and background color of ventral body scales pale; (2) dorsal body scales in 19 longitudinal rows at midbody and background color of ventral body scales pinkish in life *Tropidonophis* (p. 35)

Sibynophiinae

Represented in the Philippines by a single genus *Sibynophis* (p. 34)

KEYS TO THE SPECIES OF PHILIPPINE SNAKES,
ARRANGED ALPHABETICALLY BY GENUS

Acrochordus

Represented in the Philippines by a single species *Acrochordus granulatus*

Acutotyphlops

Represented in the Philippines by a single species. *Acutotyphlops banaorum*

Ahaetulla

Key to Philippine species and subspecies.

- 1a. Preocular scale not divided; ≥ 2 preocular scales *Ahaetulla prasina preocularis*
- 1b. Preocular scale divided; one preocular scale 2
- 2a. Usually two loreal scales; endemic to Sulu Archipelago *Ahaetulla prasina suluensis*
- 2b. Usually one loreal scale; endemic to Palawan *Ahaetulla prasina prasina*

Aipysurus

Represented in the Philippines by a single species *Aipysurus eydouxi*

Aplopeltura

Represented in the Philippines by a single species *Aplopeltura boa*

Boiga

Key to Philippine species and subspecies.

- 1a. Dorsal body scales in 19 or 23 longitudinal rows at midbody 2
- 1b. Dorsal body scales in 21 longitudinal rows at midbody 5
- 2a. Dorsal body scales in 23 longitudinal rows at midbody; three anterior temporal scales; eighth infralabial scale anterior to center of eye (Fig. 30A) *Boiga cynodon*
- 2b. Dorsal body scales in 19 longitudinal rows at midbody; two anterior temporal scales; eighth infralabial scale posterior to center of eye (Fig. 30B) 3

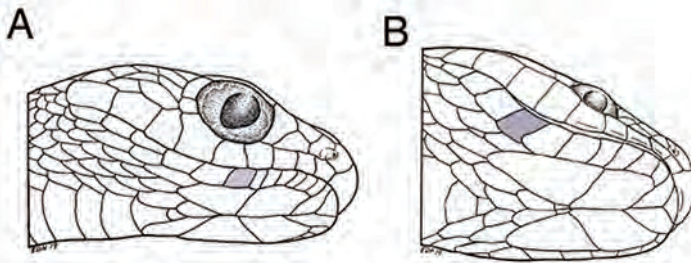


FIGURE 30. Ventral-lateral view of head of (A) *Boiga cynodon* (KU 328496), (B) *Boiga philippina* (KU 304855). Eighth infralabial scale (purplish-gray).

- 3a. Number of preocular scales two; number of ventral body scales < 250 *Boiga philippina*
- 3b. Number of preocular scales one; number of ventral body scales > 250 4
- 4a. Number of dark dorsal body crossbands ~40, each widening laterally *Boiga angulata*
- 4b. Number of dark dorsal body crossbands ~70, not widening laterally *Boiga schultzei*
- 5a. Dorsal color black, with most scales possessing a yellow or white speckle; yellow or white not arranged into distinct crossbands *Boiga dendrophila levitoni*
- 5b. Dorsal color black, with yellow or white crossbands on body and tail 6
- 6a. Yellow or white crossbands ≥ 2 scale rows wide, becoming wider laterally
. *Boiga dendrophila latifasciata*
- 6b. Yellow or white crossbands < 2 scale rows wide that do not widen laterally 7
- 7a. Interspaces between narrow light crossbands black *Boiga dendrophila multicincta*
- 7b. Interspaces between narrow light crossbands, which are edged with black, bluish gray to bluish brown *Boiga dendrophila divergens*

Calamaria

Key to Philippine species.

- 1a. Mental scale not in contact with anterior chin shields (Fig. 31A) 2
- 1b. Mental scale in contact with anterior chin shields (Fig. 31B) 4
- 2a. Number of pair of subcaudal scales < 30 (males), < 25 (females) 3

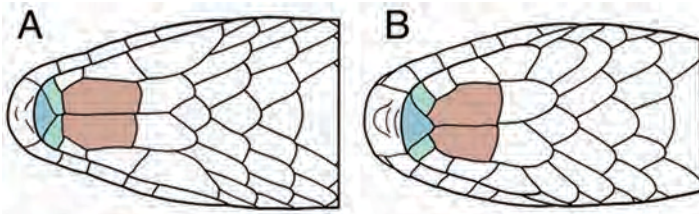


FIGURE 31. Ventral view of head of (A) *Calamaria palavanensis* (KU 309445), (B) *Calamaria gervaisii* (KU 307983). Mental scale (blue), anterior chin shields (reddish brown), first infralabial scales (green).

- 2b. Number of pair of subcaudal scales >40 (males), > 30 (females) *Calamaria* sp. Mindoro (Weinell et al., in review)
- 3a. Number of pairs of subcaudal scales ≤ 21 (males), ≤ 14 (females) *Calamaria virgulata*
- 3b. Number of pairs of subcaudal scales 23–25 (males), 16–20 (females) *Calamaria palavanensis*
- 4a. Ventral surface of body with dark bands *Calamaria lumbricoidea*
- 4b. Ventral surface of body without dark bands 5
- 5a. Dorsal surface behind head has 2–6 dark, black-edged crossbands *Calamaria bitorques*
- 5b. Dorsal surface behind head lacks dark, black-edged crossbands 6
- 6a. Diameter of eye less than eye-mouth distance *Calamaria joloensis*
- 6b. Diameter of eye equal to or greater than eye-mouth distance 7
- 7a. Each dorsal body scale with a light network; a continuous light stripe on first row of dorsal body scales present. *Calamaria suluensis*
- 7b. Each dorsal body scale above first row yellowish with a dark network; a dark-edged, interrupted, light stripe on first row of dorsal body scales usually present. *Calamaria gervaisii*

Calliophis

Key to Philippine species.

- 1a. Dorsal body surface with black and white crossbands, rather than longitudinal stripes; head black dorsally; tail red dorsally *Calliophis salitan*
- 1b. Dorsal body surface with pale longitudinal stripes, rather than crossbands. 2
- 2a. Black bands on ventral body surface not in contact with black of lateral body surface; distinct white longitudinal stripe present on lateral body surface, occupying entire first, or parts of first and second, dorsal body scale rows *Calliophis bilineata*
- 2b. Black bands on ventral body surface in contact with black of lateral body surface; distinct white stripe absent from first or second dorsal body scale rows 3
- 3a. Cream-colored bands on ventral body surface do not extend onto side of body above first dorsal body scale row. *Calliophis suluensis*
- 3b. Cream-colored bands on ventral body surface extend onto side of body, often to fourth dorsal body scale row. *Calliophis philippina*

Cerberus

Key to Philippine species.

- 1a. Dorsal body scales in 27–31 longitudinal rows at midbody; supralabial scales and other scales of head have a strongly papillate texture *Cerberus microlepis*
- 1b. Dorsal body scales in < 28 longitudinal rows at midbody; supralabial scales and other scales on head smooth *Cerberus schneideri*

Chrysopelea

Key to Philippine subspecies.

- 1a. Lateral body scales speckled (black with a bright central fleck); distinct transverse bands only in young animals; in the Philippines, only known from Sibutu Island (Sulu Archipelago).
 *Chrysopelea paradisi paradisi*
- 1b. Lateral body scales mostly light; color pattern of dorsal body surface variable, but transverse bands almost always present; occurs throughout the Philippines, but not known from Sabtang Island (Batanes Island group, off northern Luzon) *Chrysopelea paradisi variabilis*

Coelognathus

Key to Philippine species and subspecies.

- 1a. Number of subcaudal scales 87–107; number of ventral body scales + subcaudal scales < 330; adults lack distinctive black-edged white bars on side of body; juveniles usually with whitish crossbands present. 2
- 1b. Number of subcaudal scales 102–114; number of ventral body scales + subcaudal scales > 325; adults and juveniles with a series of short black-edged white bars on side of body
 *Coelognathus philippinus*
- 2a. Adults with tail much lighter than posterior portion of body
 *Coelognathus erythrurus erythrurus*
- 2b. Adults without a distinct change in dorsal color between posterior portion of body and tail; posterior portion of body may or may not be darker than anterior portion of body 3
- 3a. Adults uniform light brown to reddish brown throughout the length of body and tail; no darkening posteriorly *Coelognathus erythrurus manillensis*
- 3b. Adults become darker posteriorly along length of body and tail
 *Coelognathus erythrurus psephenourus*

Cyclocorus

Key to Philippine species and subspecies.

- 1a. Ventral body scales > 137; hemipenes narrow, elongate with minute spines ornamenting walls; usually eight supralabial scales, three bordering eye; usually two anterior temporal scales (Fig. 32A); prominent white spots present along lateral edge of ventral body scales; many dark, usually triangularly-shaped, blotches on ventral body scales 2
- 1b. Ventral body scales < 136; hemipenes robust, inner walls uniformly spinose, spines of moderate size; supralabial scales 7–8, two or three bordering eye; anterior temporal scale usually one (Fig. 32B); white spots along lateral edge of ventral body scales, if present, obscure; few or no dark triangular blotches on ventral body scales 3

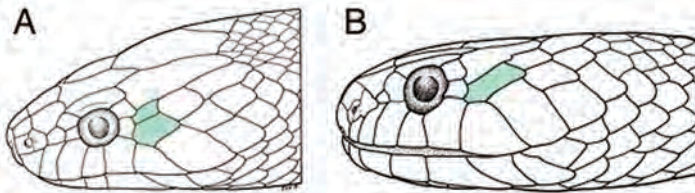


FIGURE 32. Lateral view of head of (A) *Cyclocorus lineatus alcalai* (KU 324539), (B) *Cyclocorus nuchalis taylori* (KU 344152). Anterior temporal scales (green).

- 2a. Tail length/total length 0.295–0.371 (males), 0.196–0.262 (females); subcaudals 52–59 (males), 42–48 (females); white spots along lateral edge of ventral body scales prominent.
 *Cyclocorus lineatus lineatus*
- 2b. Tail length/total length 0.235–0.296 (males), 0.152–0.223 (females); subcaudal scales 42–53 (males), 33–44 (females); white spots along lateral edge of ventral body scales very small . . .
 *Cyclocorus lineatus alcalai*
- 3a. Usually seven supralabial scales, two bordering eye. *Cyclocorus nuchalis nuchalis*
- 3b. Usually eight supralabial scales, three bordering eye *Cyclocorus nuchalis taylori*

Dendrelaphis

Key to Philippine species.

- 1a. Dorsal body scales in 15 longitudinal rows at midbody; vertebral scales enlarged relative to other dorsal body scales *Dendrelaphis marenae*
- 1b. Dorsal body scales in 13 longitudinal rows at midbody; vertebral scales not enlarged relative to other dorsal body scales 2
- 2a. Pale ventrolateral body stripe absent; black longitudinal dorsal body stripes absent. 3
- 2b. Pale ventrolateral body stripe present; 2–8 black longitudinal dorsal stripes present (minimally) on posterior part of body 4
- 3a. Yellow stripe present on neck (in life); endemic to Sulu Archipelago
 *Dendrelaphis flavescens*
- 3b. Yellow stripe absent from neck (in life); not known from Sulu Archipelago.
 *Dendrelaphis fuliginosus*
- 4a. Number of black longitudinal stripes at midbody eight; known from Palawan, Balabac, and Busuanga Islands *Dendrelaphis levitoni*
- 4b. Fewer than eight black longitudinal stripes at midbody; not from Palawan, Balabac, and Busuanga Islands. 5
- 5a. Thin black stripe usually present along border of ventral scales and first row of dorsal body scales; second narrow black stripe may or may not be present on anterior one-fifth of body along border of second and third dorsal body scale rows; additional dark body stripes absent
 *Dendrelaphis philippinensis*
- 5b. Distinct black stripe present along border of ventral scales and first longitudinal row of dorsal body scales, and along border of second and third dorsal body scale rows; additional distinct dark stripes present on posterior third of body, along border of fourth and fifth, and fifth and sixth dorsal body scale rows *Dendrelaphis luzonensis*

Dryophiops

Key to Philippine species.

- 1a. Loreal scale absent (Fig. 33A); number of ventral body scales 177–188
 *Dryophiops philippina*
- 1b. Loreal scale present (Fig. 33B); number of ventral body scales 188–199
 *Dryophiops rubescens*

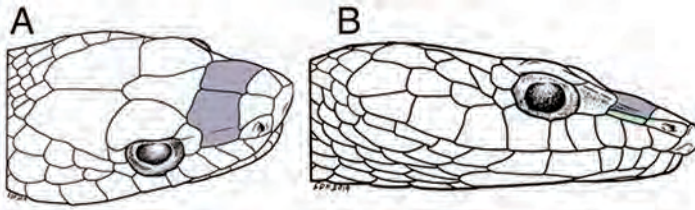


FIGURE 33. Lateral view of head of (A) *Dryophiops philippina* (UPLB MNH-Z-NS 4907), (B) *Dryophiops rubescens* (KU 328516). Loreal scale (green), prefrontal scales (purplish-gray).

Emydocephalus

Represented in the Philippines by a single species *Emydocephalus annulatus*

Gerarda

Represented in the Philippines by a single species *Gerarda prevostiana*

Gerrhopilus

Represented in the Philippines by a single species *Gerrhopilus hedraeus*

Gonyosoma

Represented in the Philippines by a single species *Gonyosoma oxycephalum*

Hemibungarus

Key to Philippine species.

- 1a. Temporal region of head heavily pigmented with melanin; number of white dorsal body bands usually < 60 2
- 1b. Temporal region of head not heavily pigmented with melanin; number of white dorsal body bands usually > 60 *Hemibungarus gemianulis*
- 2a. Number of ventral body scales 223–233 (males), 252–259 (females); black ventral body bands not divided by thin white bands *Hemibungarus calligaster*
- 2b. Number of ventral body scales < 223 (males; unknown for females); black ventral body bands divided by thin white band *Hemibungarus mcclungi*

Hologerrhum

Key to Philippine species.

- 1a. Posterior border of parietal scales unnotched (Fig. 34A); dark midventral stripe present; dark midlabial stripe present *Hologerrhum dermali*
- 1b. Posterior border of parietal scales notched (Fig. 34B); dark midventral stripe absent; dark midlabial stripe absent. *Hologerrhum philippinum*

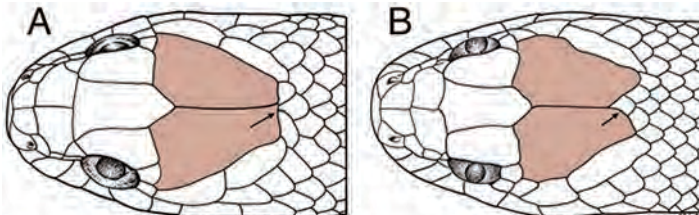


FIGURE 34. Dorsal view of head of (A) *Hologerrhum dermali* (CMNH 5075), (B) *Hologerrhum philippinum* (KU 330056). Parietal scales (reddish brown); black arrows point to posterior margin of parietal scale, showing unnotched parietal pattern (A), or notched parietal pattern (B).

Hydrophis

Key to species reported from or likely to occur in marine waters in the Philippines.

- 1a. Longitudinal scale rows around thickest part of body > 72 *Hydrophis annandalei*
- 1b. Longitudinal scale rows around thickest part of body 25–70 2
- 2a. Rostral scale fragmented into four or five smaller scales (Fig. 35); dorsal head scales with thickened edges *Hydrophis anomalus*
- 2b. Rostral scale not fragmented into four or five smaller scales 3

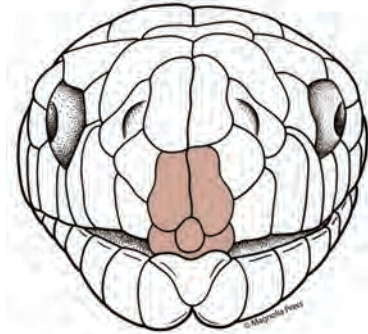


FIGURE 35. Rostral scale fragmented into four or five scales in *Hydrophis anomalus* (specimen number unknown; a redrafting by EH of original image in Rasmussen et al. 2011). Rostral scale (reddish brown). Fig. 35, modified original line drawing reproduced with permission of A. Rasmussen and *Zootaxa* and Magnolia Press.

- 3a. Ventral body scales large (> 1/4 body width) on anterior part of body and small on posterior part of body *Hydrophis viperinus*
- 3b. Ventral body scales small on both anterior and posterior parts of body 4
- 4a. Ventral surface of body uniform yellow or white; dorsal part of body uniform dark brown or black *Hydrophis platurus*
- 4b. Ventral surface of body not uniform yellow or white; dorsal part of body not uniform dark brown or black 5
- 5a. Mental scale elongate, not triangular (Fig. 36A) *Hydrophis schistosus*
- 5b. Mental scale triangular, not elongate (Fig. 36B) 6
- 6a. Enlarged chin shields absent 7
- 6b. Enlarged chin shields present, one or two pairs 8
- 7a. Midbody scales in > 45 longitudinal rows around body *Hydrophis stokesii*

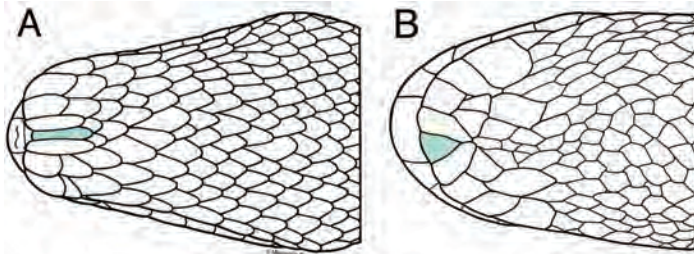


FIGURE 36. Ventral view of head of (A) *Hydrophis schistosus* (specimen number unknown; a redrafting by EH of original image in Rasmussen et al. 2011), (B) *Hydrophis curtus* (KU 40063). Mental scale (green), and either elongate (A) or triangular (B). Fig. 36A modified original line drawing reproduced with permission of A. Rasmussen and *Zootaxa* and Magnolia Press.

- 7b. Midbody scales in < 45 longitudinal rows around body *Hydrophis curtus*
- 8a. Longitudinal scale rows around thickest part of body ≤ 2 *Hydrophis jerdoni*
- 8b. Longitudinal scale rows around thickest part of body ≥ 25 9
- 9a. Frontal scale and parietal scales more or less fragmented (Fig. 37A). *Hydrophis peronii*
- 9b. Frontal scale and parietal scales unfragmented (Fig. 37B). 10

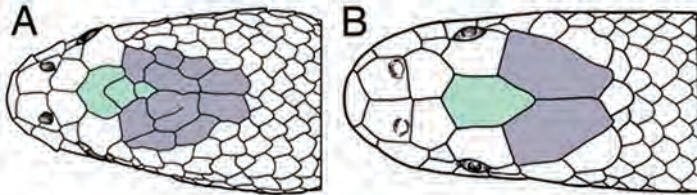


FIGURE 37. Dorsal view of head of (A) *Hydrophis peronii* (CAS 136104; a redrafting by EH of original image in Leviton et al. 2014), (B) *Hydrophis melanocephalus* (KU 94556). Frontal scales (green), parietal scales (purplish-gray). Fig. A reproduced and modified with permission of A. Leviton and the California Academy of Sciences.

- 10a. Maxillary teeth behind fangs ≥ 9 11
- 10b. Maxillary teeth behind fangs ≤ 8 13
- 11a. Neck width divided by width at widest part of body 0.45–0.56; maxillary teeth behind fangs 14–18. *Hydrophis caerulescens*
- 11b. Neck width divided by width at widest part of body ≥ 0.57 ; maxillary teeth behind fangs 9–13 12
- 12a. Interspaces between black transverse dorsal bands thin, less than two scale rows wide *Hydrophis ornatus* or *H. inornatus*
- 12b. Interspaces between black transverse dorsal bands broad, more than two scale rows wide *Hydrophis lamberti*
- 13a. Width of neck > 1/2 width of widest part of body; anterior temporal scale one 14
- 13b. One or both of the following true: (1) width of neck < 1/2 width of widest part of body; (2) anterior temporal scales two 15
- 14a. Longitudinal scale rows around midbody 8–18 more than around neck . . *Hydrophis belcheri*
- 14b. Longitudinal scale rows around midbody 4–8 more than around neck . . *Hydrophis spiralis*
- 15a. Head very small, width of neck $\leq 1/3$ width of widest part of body; longitudinal scale rows around neck 17–23; ventral body scales of anterior part of body wider than adjacent scale rows; ventral body scales of posterior part of body are divided by a long longitudinal furrow *Hydrophis gracilis*
- 15b. One or more of the following combinations of characters true: (1) head small or moderate in size, width of neck > 1/3 width of widest part of body; (2) longitudinal scale rows around neck ≥ 23 ; (3) ventral body scales of posterior part of body not divided by a long longitudinal furrow 16
- 16a. Longitudinal scale rows around midbody 29–35; ventral body scales 278–325; dorsal surface of head uniformly dark brown to black *Hydrophis coggeri*
- 16b. One or more of the following combinations of characters true: (1) longitudinal scale rows around midbody > 35; (2) ventral body scales > 325; (3) dorsal surface of head has yellow spot behind nostrils and yellow streak behind eye. 17

- 17a. Anterior temporal scales one 18
- 17b. Anterior temporal scales two 20
- 18a. Ventral body scales < 360; maxillary teeth behind fangs 6–8. *Hydrophis melanocephalus*
- 18b. One or both of the following true: (1) ventral body scales ≥ 360; (2) maxillary teeth behind fangs < 6 19
- 19a. Longitudinal scale rows around midbody 37–45; dorsal body scales on thickest part of body hexagonal or quadrangular. *Hydrophis brookii*
- 19b. Longitudinal scale rows around midbody 31–39; dorsal body scales on thickest part of body with rounded or bluntly pointed tips *Hydrophis klossi*
- 20a. Width of neck ≤ 1/2 width of widest part of body; longitudinal scale rows around midbody 12–20 more than around neck; anterior surface of body dark with pale oval spots laterally that sometimes connect as crossbands. *Hydrophis atriceps*
- 20b. One or both of the following true: (1) width of neck > 1/2 width of widest part of body; (2) longitudinal scale rows around midbody < 12 more than around neck; (3) anterior and posterior surface of body dark with distinct white annuli 21
- 21a. Head yellowish or olive (adults) or black (juveniles); ventral body scales with a black longitudinal stripe that may fade with age; ventral body scales 290–390 *Hydrophis cyanocinctus*
- 21b. Head black; ventral body scales usually black; ventral body scales 314–356; [non-marine] endemic to Lake Taal (Luzon) *Hydrophis semperi*

Indotyphlops

Represented in the Philippines by a single species *Indotyphlops braminus*

Laticauda

Key to the Philippine species.

- 1a. Scales in 19 longitudinal rows at midbody; two prefrontal scales (Fig. 38A) *Laticauda laticaudata*
- 1b. Scales in 21–25 longitudinal rows at midbody; three prefrontal scales (Fig. 38B) 2
- 2a. Rostral scale not divided horizontally; upper lip yellow; ventral body scales 213–245 *Laticauda colubrina*
- 2b. Rostral scale divided horizontally; upper lip brown; ventral body scales 195–205 *Laticauda semifasciata*

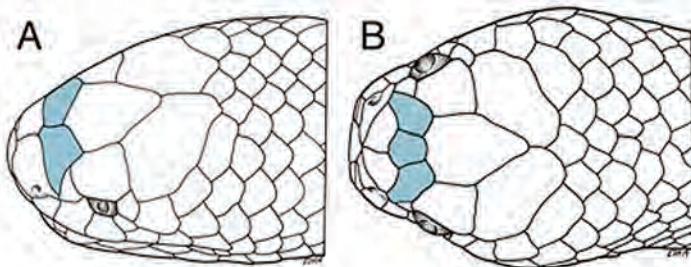


FIGURE 38. Dorsal view of head of the (A) *Laticauda laticaudata* (KU 94559), and (B) *Laticauda colubrina* (KU 303031). Prefrontal scales (blue).

Liopeltis

Key to Philippine species.

- 1a. Nasal scales fused to internasal scales anterior to rostral (Fig. 39); dorsal surface of body with four brown longitudinal stripes *Liopeltis philippinus*
- 1b. Nasal scales not fused to internasal scales; dorsal surface of body uniformly colored above, without longitudinal stripes *Liopeltis tricolor*

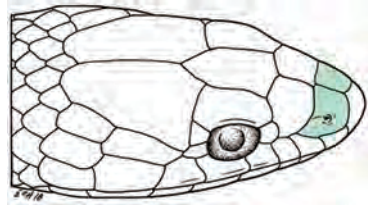


FIGURE 39. Dorsolateral view of head of *Liopeltis philippinus* (KU 327731). Nasal scales (green).

Lycodon

Key to Philippine species.

- 1a. Ventral body scales and subcaudal scales strongly keeled; dorsal body scales in 15 longitudinal rows at midbody *Lycodon philippinus*
- 1b. Ventral body scales and subcaudal scales smooth; dorsal body scales in 17 longitudinal rows at midbody 2
- 2a. Subcaudal scales in > 130 pairs *Lycodon fausti*
- 2b. Subcaudal scales in < 130 pairs 3
- 3a. Some dorsal body scale rows keeled along the entire length of the body (keels may be faint or absent from scales that have lost their outermost layer). *Lycodon sealei*
- 3b. Dorsal body scales either all smooth, or, keeled on posterior part of body 4
- 4a. Subcaudal scales in > 100 pairs 5
- 4b. Subcaudal scales in < 100 pairs *Lycodon capucinus*
- 5a. Dorsal part of body without light crossbands; ventral surface of body does not have dark markings, except for a large spot in lateral corner of each ventral body scale. 6
- 5b. Dorsal surface of body with light crossbands (at least the anterior part of body); ventral surface of body or tail has dark dots, spots, and/or transverse bands 7
- 6a. Ventral body scales > 200; vertebral scales > 205. *Lycodon alcalai*
- 6b. Ventral body scales < 200; vertebral scales < 205. *Lycodon chrysopteros*
- 7a. Crossbands absent from tail and posterior part of body; ventral bands absent; number of infralabial scales in contact with anterior and posterior chin shields five. *Lycodon solivagus*
- 7b. Dorsal crossbands present throughout length of body and tail; additionally, at least one of the following combinations of characters true: (1) number of infralabial scales in contact with anterior and posterior chin shields six; (2) ventral bands present. 8
- 8a. Dorsal light crossbands > 50 on body, > 27 on tail; tail length 36–45% (usually > 38%) of snout-vent length *Lycodon muelleri*
- 8b. Dorsal light crossbands < 30 on body, < 25 on tail; tail length 33–39% (usually < 38%) of snout-vent length 9

- 9a. Dorsal light crossbands > 20 on body, > 15 on tail *Lycodon bibonius*
- 9b. Dorsal light crossbands < 20 on body, < 15 on tail 10
- 10a. Body and tail with dark rings completely encircling the body; number of supralabial scales usually ten (fourth through sixth border eye); dorsal body scales reducing to 15 longitudinal rows at approximately ventral 119 *Lycodon ferroni*
- 10b. Dorsal part of body and tail with dark crossbands often extending onto lateral edges of ventral body scales, but not completely encircling the body; number of supralabial scales 8–9 (fourth and fifth border eye); dorsal body scales reduce to 15 longitudinal rows between ventral body scales 131–145 *Lycodon dumerili*

Malayopython

Represented in the Philippines by a single species *Malayopython reticulatus*

Malayotyphlops

Key to Philippine species.

- 1a. Small subocular scale present, in contact with second and third supralabial scales, preocular scale, and ocular scale *Malayotyphlops manilae*
- 1b. Small subocular scale absent 2
- 2a. Dorsal body scales in < 29 longitudinal rows at midbody 3
- 2b. Dorsal body scales in ≥ 29 (usually 30) longitudinal rows at midbody; a dark dorsal stripe present with sharply defined lateral edges 9
- 3a. Third supralabial scale does not extend dorsally to levels of nostrils (Fig. 40A) *Malayotyphlops denrorum*
- 3b. Third supralabial scale extends dorsally to levels of nostrils (Fig. 40B) 4
- 4a. Preocular scale overlaps second supralabial scale, and postnasal scale does not overlap third supralabial scale (Fig. 40B) 5
- 4b. Preocular scale does not overlap second supralabial scale and postnasal scale overlaps third supralabial scale (Fig. 40C) 6
- 5a. Dorsal body scales in 26 longitudinal rows behind head; dorsal stripe ≥ 17 scale rows wide on anterior of body *Malayotyphlops hypogius*
- 5b. Dorsal body scales in 28 longitudinal rows behind head; dorsal stripe 15 scale rows wide on anterior of body, narrowing posteriorly *Malayotyphlops luzonensis*

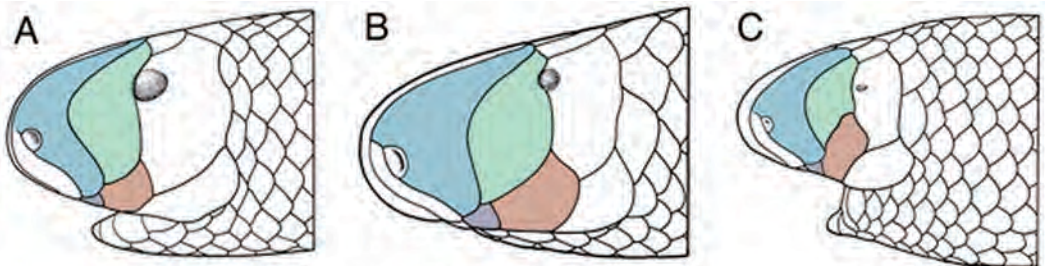


FIGURE 40. Lateral view of head of (A) *Malayotyphlops denrorum* (PNM 9813; a redrafting by EH of original image in Wynn et al. 2016), (B) *Malayotyphlops luzonensis* (CM 2653; a redrafting by EH of original image in Wynn et al. 2016), (C) *Malayotyphlops castanotus* (CAS SUR-27940; a redrafting by EH of original image in Wynn et al. 1993). Postnasal scale (blue; or posterior part of nasal scale, if nasal scale incompletely sdivided), preocular scale (green), second supralabial scale (purplish-gray), third supralabial scale (reddish brown). Figs. A–C reproduced and modified with permission of A. Wynn and *Journal of Herpetology*.

- 6a. Well-delineated, dark dorsal stripe 9–11 scale rows wide, not narrowing posteriorly *Malayotyphlops castanotus*
 6b. Lateral scale rows of dorsal stripe lighter than (or not as completely pigmented as) medial rows; dorsal stripe narrows posteriorly 7
- 7a. Pale (unpigmented) collar present behind head; dorsal body scales in > 400 transverse rows between head and tail *Malayotyphlops collaris*
 7b. No pale collar behind head; dorsal body scales in < 400 transverse rows between head and tail 8
- 8a. Dark dorsal body stripe 15 scale rows wide on anterior of body *Malayotyphlops ruber*
 8b. Dark dorsal body stripe 13 scale rows wide on anterior of body *Malayotyphlops andyi*
- 9a. Dorsal body scales in > 350 transverse rows between head and tail *Malayotyphlops canlaonensis*
 9b. Dorsal body scales in < 350 transverse rows between head and tail *Malayotyphlops ruficaudus*

Myersophis

Represented by a single species *Myersophis alpestris*

Naja

Key to Philippine species.

- 1a. Dorsal body scales in 21–23 longitudinal rows at midbody; dorsal color uniformly light brown or olive *Naja philippinensis*
 1b. Dorsal body scales in 17–19 longitudinal rows at midbody; dorsal color black or dark brown 2
- 2a. A few anterior ventral body scales light yellow, followed by band of black that gradually fades posteriorly; 162–178 ventral body scales *Naja samarensis*
 2b. Ventral body surface dark or light but without a distinctive black band on anterior portion; 178–189 ventral body scales *Naja sumatrana*

Oligodon

Key to Philippine species.

- 1a. Dorsal body scales in 15 longitudinal rows at midbody 2
 1b. Dorsal body scales in 17 longitudinal rows at midbody 3
- 2a. Light vertebral stripe present; no prominent dorsal body blotches; quadrangular black spots present on ventral body scales *Oligodon modestus*
 2b. Light vertebral stripe absent; light dorsal body spots or blotches usually present; distinctive markings absent from ventral body scales *Oligodon notospilus*
- 3a. Number of supralabial scales usually six; number of anterior temporal scales two; no transverse markings on dorsal surface of body *Oligodon meyerinki*
 3b. Number of supralabial scales usually seven; number of anterior temporal scales one or two; transverse markings present on dorsal surface of body 4
- 4a. Dorsal body blotches > 30, irregularly shaped, forming poorly defined dark crossbands; number of ventral body scales > 180; number of ventral body scales + subcaudal scales > 230 (females; unknown for males) *Oligodon perkinsi*

- 4b. Dorsal body blotches well-defined, numbering < 30; number of ventral body scales < 180; number of ventral body scales + subcaudal scales < 220 5
- 5a. Dark dorsal body blotches extend laterally to ventral body scales; two preocular scales (Fig. 41A); number of ventral body scales + subcaudal scales 211–216 *Oligodon maculatus*
- 5b. Dark dorsal body blotches saddle-shaped, not extending to ventral body scales; usually one preocular scale (Fig. 41B); number of ventral body scales + subcaudal scales 183–207
 *Oligodon ancorus*

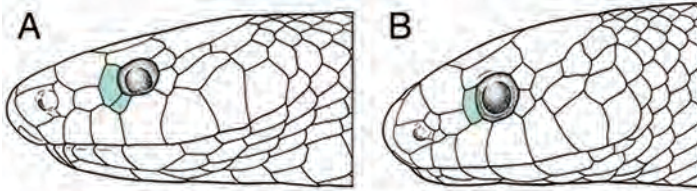


FIGURE 41. Lateral view of head of (A) *Oligodon maculatus* (KU 321699), (B) *Oligodon ancorus* (KU 346379). Preocular scales (green).

Ophiophagus

Represented by a single species *Ophiophagus hannah*

Opisthotropis

Key to Philippine species.

- 1a. Dorsal body scales in 19 longitudinal rows at 25th ventral body scale . . . *Opisthotropis typica*
- 1b. Dorsal body scales in 21 longitudinal rows at 25th ventral body scale. . . *Opisthotropis alcalai*

Oxyrhabdium

Key to Philippine species.

- 1a. Loreal scale separated from or in contact with second supralabial scale; if loreal scale in contact with second supralabial scale, their length of contact is less than half the length of the contact between loreal and postnasal scales (Fig. 42A); usually eight supralabial scales (rarely seven), with fifth and six (rarely fourth and fifth) supralabial scales bordering eye (Fig. 42A); dorsal surfaces of head, body, and tail brown or reddish-brown in color; juveniles have distinct white nuchal collar, but lack light crossbands on other parts of the body
 *Oxyrhabdium modestum*
- 1b. Length of contact between loreal scale and second supralabial scale similar to length of contact between loreal scale and postnasal scale (Fig. 42B); seven supralabial scales, with fourth and fifth supralabial scales bordering eye (Fig. 42B); dorsal surfaces of head, body, and tail dark gray or olive in color; juveniles have distinct white nuchal collar plus light crossbands on other parts of body and tail; pale crossbands may be faintly visible in adults. 2

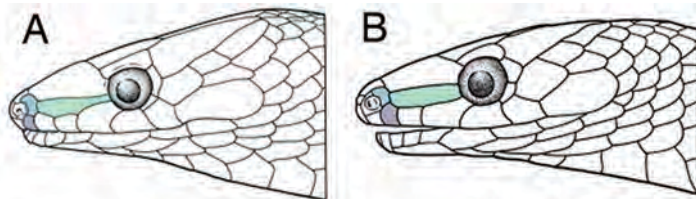


FIGURE 42. Lateral view of head of (A) *Oxyrhabdium modestum* (KU 311301), (B) *Oxyrhabdium leporinum leporinum* (KU 322335). Loreal scale (green), postnasal scale (blue), second supralabial scale (purplish-gray).

- 2a. Adult dorsal color pattern uniform (lacking pale crossbands); number of ventral body scales + subcaudal scales 192–230 *Oxyrhabdium leporinum leporinum*
- 2b. Adults and juveniles with narrow white dorsal body crossbands and white nuchal collar; number of ventral body scales + subcaudal scales 221–235 *Oxyrhabdium leporinum visayanum*

Psammodynastes

Represented in the Philippines by a single species. *Psammodynastes pulverulentus*

Pseudorabdion

Key to Philippine species.

- 1a. Loreal scale absent, prefrontal scale in contact with supralabial scales (Fig. 43B–D). 2
- 1b. Loreal scale present, prefrontal scale not in contact with supralabial scales (Fig. 43A) 4
- 2b. Frontal scale does not border eye; supraocular and postocular scales present, fused to each other (Fig. 43C–D) 3
- 2a. Frontal scale borders eye; supraocular scale absent (Fig. 43B) 6
- 3a. Parietal scale in contact with fourth and fifth supralabial scales (Fig. 43C); each scale of first dorsal body scale row has dark center and light edges; each ventral body scale dark brown, lighter along posterior edge; supraocular and postocular scales usually fused to eye; ventral body scales 132–144 (males), 144–157 (females); subcaudal scales 22–24 (males), 16–17 (females) *Pseudorabdion oxycephalum*
- 3b. Parietal scale in contact with fifth, but not fourth, supralabial scale (Fig. 43D); each scale of first dorsal body scale row has light center and dark edges; each ventral body scale whitish, with dark brown pigment confined to a broad transverse band; supraocular and postocular scales not fused to eye; ventral body scales 146–148 (males), 154–161 (females); subcaudal scales 28 (males), 21–24 (females) *Pseudorabdion montanum*
- 4a. Light nuchal collar usually present; subcaudal scales 26–29 (males), 17–23 (females) *Pseudorabdion mcnamarae*
- 4b. Light nuchal collar absent; subcaudal scales > 30 (males and females). 5

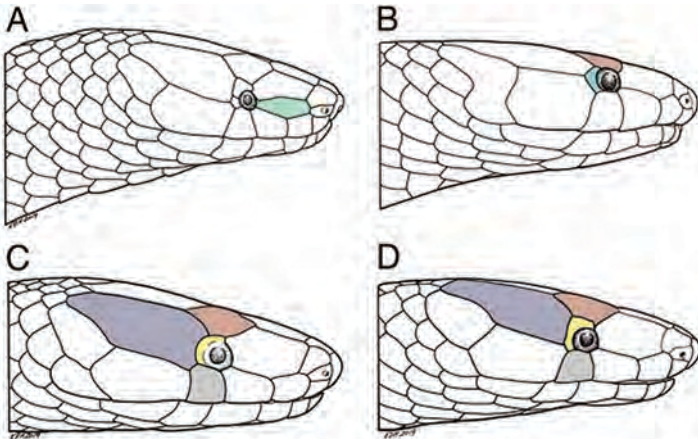


FIGURE 43. Lateral view of head of (A) *Pseudorabdion mcnamarae* (KU 327199), (B) *Pseudorabdion* cf. *collaris* (KU 315197), (C) *Pseudorabdion oxycephalum* (KU 324641), (D) *Pseudorabdion montanum* (KU 305063). Loreal scale (green; A), parietal scale (purplish-gray; C–D), fourth supralabial scale (light gray; C–D), postocular scale (blue; B), frontal scale (reddish brown; B–D), scale formed from fusion of supraocular and postocular scales (yellow; C–D).

- 5a. Dorsal body scales uniform pale brown, each thinly edged with pigmentless border; distal portion of hemipenes calyculate, subcaudal scales 33–35 (females), 40 (males) *Pseudorabdion taylori*
- 5b. Dorsal body scales pale, centers and posterior tips nearly without pigment; anterior edge of each dorsal body scale with brown mottling; large areas of lateral portion of ventral body scales without pigment; distal portion of hemipenes minutely spinose; subcaudal scales 36–39 (males; unknown for females) *Pseudorabdion talonuran*
- 6a. Postocular scale absent (fused to ocular scale); maxillary teeth 10–12 . . . *Pseudorabdion ater*
- 6b. Postocular scale present, not fused to ocular scale (Fig. 43B); maxillary teeth 22–25 *Pseudorabdion cf. collaris*

Ptyas

Key to Philippine species.

- 1a. Dorsal body scales in 16 or 18 longitudinal rows on anterior third of body; mid-dorsal body scales keeled. *Ptyas carinata*
- 1b. Dorsal body scales in 14 longitudinal rows on anterior third of body; mid-dorsal body scales smooth. *Ptyas luzonensis*

Ramphotyphlops

Key to Philippine species.

- 1a. Ocular scale overlaps third supralabial scale (Fig. 44A) *Ramphotyphlops marxi*
- 1b. Third supralabial scale overlaps ocular scale (Fig. 44B)

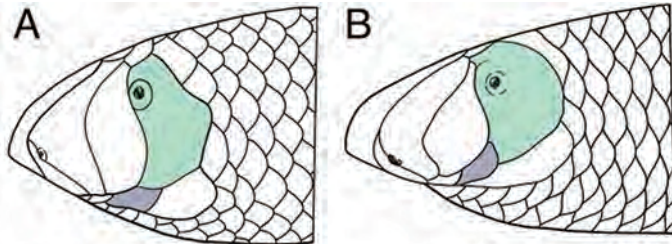


FIGURE 44. Lateral view of head of (A) *Ramphotyphlops marxi* (FMNH 96520; a redrafting by EH of original image in Wallach et al. 1993), (B) *Ramphotyphlops suluensis* (PBS 2001; a redrafting by EH of original image in Taylor 1918). Ocular scale (green), third supralabial scale (purplish-gray). Fig. A reproduced and modified with permission of V. Wallach and *Journal of Herpetology*.

- 2a. Longitudinal scale rows around midbody 24–28 *Ramphotyphlops cumingii*
- 2b. Longitudinal scale rows around midbody 20–22 3
- 3a. Width of preocular scale about equal to width of ocular scale; width of rostral scale ~0.75 head width; nasal scale nearly, but not completely, divided. *Ramphotyphlops olivaceus*
- 3b. Preocular scale much narrower than ocular scale; width of rostral scale about half the width of head; nasal scale completely divided *Ramphotyphlops suluensis*

Rhabdophis

Key to Philippine species.

- 1a. Dorsal body scales in 15–17 longitudinal rows at midbody; background color of ventral body scales black 2
- 1b. Dorsal body scales in 17–19 longitudinal rows at midbody; background color of ventral body scales pale 3

- 2a. Light lateral body stripe not continuous across angle of jaw, separated from white patch behind eye *Rhabdophis auriculatus auriculatus*
- 2b. Light lateral body stripe continuous across angle of jaw to postocular region
 *Rhabdophis auriculatus myersi*
- 3a. Dorsal body scales in 17 longitudinal rows at midbody 4
- 3b. Dorsal body scales in 19 longitudinal rows at midbody 5
- 4a. Pale dorsolateral body stripes present; pale nuchal spot present (except for hypermelanistic individuals from Lubang Island) *Rhabdophis spilogaster*
- 4b. Pale dorsolateral body stripes absent; pale nuchal spot absent *Rhabdophis barbouri*
- 5a. Distinct white stripe extends across supralabial scales; one anterior temporal scale, in contact with the sixth supralabial scale; usually two preocular scales (Fig. 45A) . . *Rhabdophis lineatus*
- 5b. No distinct white stripe on supralabial scales; two anterior temporal scales, neither in contact with the sixth supralabial scale; one preocular scale (Fig. 45B) *Rhabdophis chrysargos*

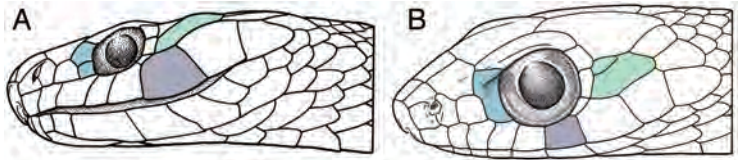


FIGURE 45. Lateral view of head of (A) *Rhabdophis lineatus* (KU 326696), (B) *Rhabdophis chrysargos* (composite drawing from photographs of multiple individuals). Anterior temporal scales (green), sixth supralabial scale (purplish-gray), preocular scales (blue).

Sibynophis

Key to Philippine species and subspecies.

- 1a. Pale interocular bar present; usually eight (rarely nine) supralabial scales
 *Sibynophis bivittatus*
- 1b. Pale interocular bar absent; usually nine (rarely eight) supralabial scales
 *Sibynophis geminatus geminatus*

Stegonotus

Represented in the Philippines by a single species *Stegonotus muelleri*

Trimeresurus

Key to Philippine species.

- 1a. Tail color distinctly different from body color (in life: tail color red, body color green); hemipenes spinose *Trimeresurus schultzei*
- 1b. Tail color not distinctly different from body color (in life: tail and body may be green, red, orange, yellow, gray, or white); hemipenes lack spines 2
- 2a. Body and tail color green (adults and some juveniles in life) or red (some juveniles in life) *Trimeresurus flavomaculatus*
- 2b. Body and tail color yellow, gray, or white (in life) *Trimeresurus mcgregori*

Tropidolaemus

Key to Philippine species.

- 1a. Longitudinal rows of dorsal body scales at midbody 21–23 (males), 21–29 (females); dorsal scales on head 9–16 along a line passing between the supraocular scales (Fig. 46A); third supra-

labial scale usually separated from subocular scale by one or two scales; color variable, shades of green, blue or green, and blue in females, and green in males, but blue in some Negros Island populations; crossbands on body blue and white, red and white, or blue, red and white; color of postocular stripe variable (females), white or red (males), or red (juveniles).

..... *Tropidolaemus subannulatus*

1b. Longitudinal rows of dorsal body scales at midbody 18–19 (males and females); dorsal scales on head 6–8 along a line between the supraocular scales (Fig. 46B); third supralabial scale usually in contact with subocular scale (rarely separated by one scale); in life: background body color turquoise-green (males) or green (females); postocular stripe usually black (rarely white)

..... *Tropidolaemus philippensis*

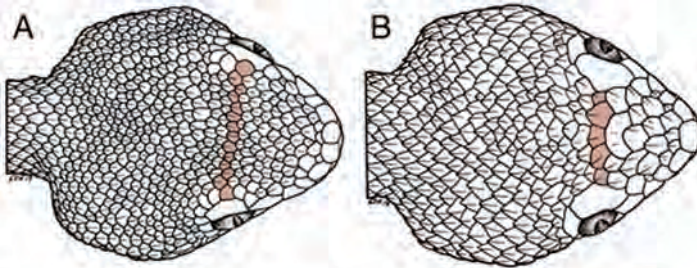


FIGURE 46. Dorsal view of head of (A) *Tropidolaemus subannulatus* (KU 324585), (B) *Tropidolaemus philippensis* (KU 334672). Dorsal scales of head along line between supraocular scales (reddish brown).

Tropidonophis

Key to Philippine species.

1a. Dorsal body scales in 17 longitudinal rows at ventral 25 *Tropidonophis dendrophiops*

1b. Dorsal body scales in 19 longitudinal rows at ventral 25 *Tropidonophis negrosensis*

Unnamed genus

Represented by a single species. unnamed genus and species (Fig. 47)

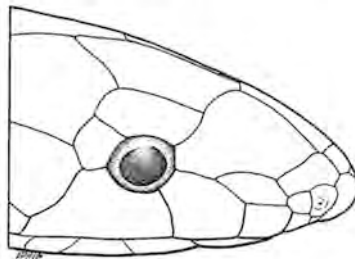


FIGURE 47. Lateral view of anterior part of head of a recently discovered (Weinell and Brown 2018) unnamed lineage (KU 337269).

Xenopeltis

Represented in the Philippines by a single species *Xenopeltis unicolor*

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APPENDIX

Glossary

- Annulus.** (*pl. -i*) Transverse ring of color encircling the body.
- Anterior.** At or near the front (head) end of the body. *Anterior to* means relatively nearer to the anterior end of the body compared to another structure.
- Band.** A broad, transverse area of contrasting color that may or may not completely encircle the body.
- Blotch.** An area of color differing from the ground color, usually somewhat round or square in shape, and may have a contrasting border.
- Calyculate.** Covered by cup-shaped structures.
- Chin shield.** Any of paired, elongated scales on the lower jaw of snakes and situated behind one or more pairs of infralabial scales that are in contact medially.
- Cloaca.** The common chamber where the urinary, digestive, and reproductive ducts release their contents; opens to the exterior through the vent.
- Collar.** A transverse band of color on the dorsal surface of the neck.
- Crossband.** A transverse area of color that extends towards (but usually not onto) the ventral body surface; a band that does not encircle the body and is usually restricted to the dorsal surfaces of the body.
- Dorsal.** At or near the upper (back) surfaces of the head, body, or tail; *dorsal to* means relatively nearer to the upper surfaces of the head, body, or tail compared to another structure of interest.
- Dorsal body scale.** Any of the scales on the upper surface of the body.
- Dorsocaudal scale.** Any of the scales on the upper surface of the tail.
- Eye–mouth distance.** The vertical distance from the ventral margin of the eye to the edge of the mouth.
- Frontal scale(s).** The scale(s) on mid-top of the head between the supraocular scales; if supraocular scales are absent, the frontal scale is between the ocular scales.
- Ground color.** The background or base color on which more prominent aspects of color pattern (e.g., stripes, blotches, crossbands) may appear. If no specific types of markings are present, the coloration may be called uniform.
- Gular scale.** A scale on the lower jaw of snakes, situated between the infralabial scales, chin shields, and ventral body scales; sometimes lateral gular scales and medial gular scales are distinguished.
- Hemipenis.** (*pl. -es*) Either of paired copulatory organs (of males) lying in a cavity at the base of the tail in squamate reptiles.
- Heat sensing pit.** Specialized infrared receptors located either within the rostral scale and labial scales, or as single structures between the eye and nostril on either side of the head.
- Hypermelanistic.** Having excessive pigmentation or blackening of the skin or other tissues.
- Infralabial scale.** Any of the scales along the lower lip of the mouth behind the mental scale.
- Intergential scale.** Any scale situated between a pair of chin shields.
- Internasal scale.** Any of enlarged scales on the dorsal surface of the head, situated between the nasal scales, behind the rostral scale, and before the prefrontal scales.
- Interocular bar.** A transverse band of color located on the dorsal surface of the head between the eyes.
- Interparietal scale.** A scale on the dorsal midline of the head, situated behind the parietal scales.
- Keel.** Longitudinal ridge on a scale.

- Labial scale.** Any of the scales on the side of the head bordering the mouth opening; supralabial scale refers to a labial scale along the upper lip of the mouth; infralabial scale refers to a labial scale along the lower lip of the mouth.
- Lateral.** At or near the left or right side surfaces of the head, body, or tail; the opposite of medial. *Lateral to* means relatively nearer to the side surfaces of the head, body, or tail compared to some other structure.
- Lateral gular scale.** Any of the relatively elongate gular scales positioned laterally, rather than medially, on the throat, and arranged in an oblique row.
- Lateral body scale.** Any of the dorsal body scales not located on the middorsal line of the body.
- Longitudinal.** Running along, or parallel to, the long axis of the body.
- Loreal scale.** Either a scale between a nasal scale and a preocular scale (more common condition), or an elongate scale situated between a nasal scale and the eye (less common condition). The latter condition is mostly found in the genera *Oxyrhabdium*, *Myersophis*, and some *Pseudorabdion* species, and the scale is sometimes called a lori-ocular scale (Leviton et al. 2018).
- Medial.** Situated toward or at the midline of a body or structure.
- Medial gular scale.** A gular scale along the ventral midline of the throat.
- Mental scale.** Single median scale situated on the front of the lower jaw, bordered on both sides by the first infralabial scales.
- Nasal scale.** A scale that borders or contains a nostril. This scale may be entire or partially or completely divided by a suture. If divided, the scale anterior to the suture is called the prenasal scale and the scale posterior to the suture is called the postnasal scale.
- Nasal suture.** A deep furrow or cleft running from the posterior-ventral end of the nasal scale through the nostril to the prefrontal scale, dividing or nearly dividing the nasal scale into prenasal and postnasal scales.
- Nostril.** The nasal opening.
- Nuchal.** Pertaining to neck; the dorsal surface immediately behind the head.
- Ocular scale.** Either: (1) a scale bordering the eye, including preocular scales, postocular scales, supraocular scales, and subocular scales, or (2) a scale covering a rudimentary eye of blind snakes.
- Papillate.** Having or bearing papillae, or nipple-shaped protuberances.
- Parietal scale.** Either of a pair of large scales on the head, immediately behind the frontal scale and forming the last pair of scales usually distinguishable from the dorsal body scales.
- Posterior.** At or near the tail end of the body. *Posterior to* means relatively nearer to the posterior (tail) end of the body compared to another structure.
- Postocular region.** Of or pertaining to the region immediately behind the eye.
- Postocular scale.** A scale bordering the posterior margin of the eye.
- Precloacal scale.** A scale on the ventral surface of the body that covers the vent, and is situated behind the ventral body scales and before the subcaudal scales; may be single or divided.
- Prefrontal scale.** Any of the scales on the dorsal surface of the head situated immediately anterior to the frontal scale.
- Preocular scale.** A scale bordering the anterior margin of the eye.
- Rostral scale.** A scale at the tip of the snout, bordering the mouth and separating the two rows of supralabial scales.
- Snout.** The anterior part of the head, which includes the nostrils.
- Snout–vent length (SVL).** A measure of body length representing the distance from the tip of the snout to the vent along the midline of the body.

Subcaudal scale. Any scale on the ventral surface of the tail, either in a single or divided (two) longitudinal series.

Subocular scale. Any scales situated between the lower margin of the eye and one or more supralabial scales.

Supralabial scale. Any of the scales along the upper lip of the mouth behind the rostral scale.

Supraocular scale. A scale on the dorsal surface of the head, bordering the upper margin of the eye.

Tail spine. The terminal scale on the tail tip of snakes.

Temporal scale. Any scale behind the postocular scales, below the parietal scale, and above the supralabial scales. Anterior temporal scales are those belonging to the first vertical row immediately behind the postocular scales.

Transverse. Placed or running at right angles to the long axis of the body; across.

Vent. The external opening of the cloaca.

Ventral. At or near the lower surfaces of the head, body, or tail. *Ventral to* means relatively nearer to the lower surfaces of the head, body, or tail compared to some other structure.

Ventral body scale. Following the definition used by Dowling (1951): any of the scales on the ventral surface of the body anterior to the precloacal scale and in contact with both of the first longitudinal rows of dorsal body scales.

Vertebral body scale. Any of the dorsal body scales located on the middorsal line of the body.

Vertebral stripe. A longitudinal stripe of color located on the middorsal line of the body.

Table 1: Data for illustrated species and specimens.

TABLE 1. Illustrated specimens. California Academy of Sciences (CAS); Carnegie Museum (CM); Edward H. Taylor collection (EHT); Field Museum of Natural History (FMNH); University of Kansas Natural History Museum and Biodiversity Institute (KU); Philippine Bureau of Science (PBS); National Museum of the Philippines (PNM); Senckenberg Forschungsinstitut und Naturmuseum (SMF); Camila G. Meneses field tag (UPLB-MNS). (*) Illustration was reflected along a vertical axis; (**) one side of illustration is a mirror of the other; (***) composite illustration, drawn from multiple source specimens, illustrations, or photos.

| Species | Catalog # | Locality | Figures | Sources |
|--|-------------|---|--|---|
| <i>Acutotyphlops banaorum</i> | FMNH 262249 | Barangay Balbalasang, Municipality of Balbalan, Kalinga Province, Luzon Island, Philippines | 22A [dorsal head] | Redrawn from Wallach et al. 2007 Fig. 2 |
| <i>Acrochordus granulatus</i> | KU 302951 | Barangay Old Poblacion, Municipality of Buena Vista, Guimaras Island, Guimaras Province, Philippines | 3A [lateral body] | original |
| <i>Ahaetulla prasina preocularis</i> | KU 347854 | Barangay Cawayan, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines | 25A* [head lateral] | original |
| | KU 349849 | Barangay Lidong, Municipality of Presentacion, Camarines Sur Province, Luzon Island, Philippines | 26A* [ventral scales] | original |
| <i>Aplopeltura boa</i> | KU 334473 | Eye Falls (crossing of Dayhopan and Agay rivers, Mt. Hilong-Hilong), Municipality of Remedios T. Romualdez, Agusan del Norte Province, Mindanao Island, Philippines | 8A | original |
| | KU 334474 | May Impit, Mt. Hilong-Hilong, Agusan del Norte Province, Mindanao Island, Philippines | 8B | original |
| <i>Boiga angulata</i> | KU 343853 | Barangay Dinaayan, Municipality of Burauen, Leyte Province, Leyte Island, Philippines | 28A [head lateral] | original |
| <i>Boiga cynodon</i> | KU 328496 | Khao Luang National Park, Karome, Nakhon Si Thammarat Province, Thailand | 30A [head ventral] | original |
| <i>Boiga philippina</i> | KU 304855 | Barangay Babuyan Claro, Babuyan Island, Municipality of Calayan, Cagayan Province, Philippines | 30B [head ventral] | original |
| <i>Calamaria gervaisii</i> | KU 322329 | Barangay Villa Aurora, Aurora Memorial National Park, Municipality of Maria Aurora, Aurora Province, Luzon Island, Philippines | 9C [head dorsal] | original |
| | | | 12A*/27A* [head lateral] | original |
| | KU 307983 | Camiguin Norte Island, Municipality of Calayan, Cagayan Province, Philippines | 5B [body ventral]; 31B [head ventral] | original original |
| <i>Calamaria lumbricoidea</i> | KU 315159 | Barangay Baluno, Pasonanca Natural Park, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 11C* [head lateral] | original |
| <i>Calamaria palawanensis</i> | KU 309445 | Barangay Irawan, Municipality of Puerto Princesa, Palawan Island, Palawan Province, Philippines | 31A [head ventral] | original |
| <i>Calliophis philippina</i> | KU 327218 | Barangay Pandan, Municipality of Mambajao, Camiguin Province, Camiguin Sur Island, Philippines | 17D* [head lateral] | original |
| <i>Cerberus schneideri</i> | KU 305489 | Barangay Dalipay, Municipality of Sorsogon, Sorsogon Province, Luzon Island, Philippines | 9A | original |
| <i>Chrysopelea paradisi variabilis</i> | KU 337271 | San Rafael Barangay, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines | 26B [ventral scales] | original |

| Species | Catalog # | Locality | Figures | Sources |
|--|------------------------------|---|--|---|
| <i>Coelognathus erythrurus manillensis</i> | KU 335195 | Angat Watershed, Municipality of Norzagaray, Bulacan Province, Luzon Island, Philippines | 28B* [head lateral] | original |
| <i>Cyclocorus lineatus alcalai</i> | KU 324539 | Barangay Patag, Municipality of Silay, Negros Occidental Province, Negros Island, Philippines | 13B/32A [head lateral] | original |
| | | | 2J/14B [tail ventral] | original |
| <i>Cyclocorus lineatus lineatus</i> | KU 346571 | Barangay Cogon, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines | 19B* [head ventral] | original |
| <i>Cyclocorus nuchalis nuchalis</i> | KU 327765 | Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province, Mindanao Island, Philippines | 19C* [head ventral] | original |
| <i>Cyclocorus nuchalis taylori</i> | KU 344162 | Barangay Guinmaayohan, Municipality of Balangiga, Eastern Samar Province, Samar Island, Philippines | 32B [head lateral] | original |
| <i>Dendrelaphis marenae</i> | KU 314131 | Barangay San Marcos, Municipality of Bunawan, Agusan del Sur Province, Mindanao Island, Philippines | 15A [body lateral] | original |
| <i>Dryophiops philippina</i> | UPLB MNH-Z-NS 4907 | Barangay Tampayan, Sibuyan Island, Municipality of Magdiwang, Philippines | 33A [head lateral] | original |
| <i>Dryophiops rubescens</i> | KU 328516 | Khao Luang National Park, Nakhon Si Thammarat Province, Thailand | 25B*/33B [head lateral] | original |
| <i>Emydocephalus annulatus</i> | specimen number not reported | — | 16 [head lateral] | Redrawn from Rasmussen et al. 2011 Fig. 3 |
| <i>Gerrhopilus hedraeus</i> | CAS-SUR 12346 | fide Savage (1950): "1500 ft. above Luzuriaga, ca. 6 miles southwest of Dumaguete, Oriental Negros, Philippines." | 6A [head lateral] | Redrawn from Savage, 1950 Fig. 1 |
| <i>Gonyosoma oxycephalum</i> | KU 315168 | Pasonanca Natural Park, Barangay Pasonanca, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 10B** [head dorsal] | original |
| <i>Hemibungarus mcclungi</i> | KU 313898 | Barangay Tulay Na Lupa, Mt. Labo, Municipality of Labo, Camarines Norte Province, Luzon Island, Philippines | 11A*/17C* [head lateral] | original |
| <i>Hologerrhum dermali</i> | CMNH 5075 | Mt. Madja-as, Barangay Alojipan, Municipality of Culasi, Antique Province, Panay Island, Philippines | 10C/34A [head dorsal] | Brown et al. 2001 Fig. 4A |
| <i>Hologerrhum philippinum</i> | KU 330056 | Barangay Magrafil, Mt. Cagua, Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines | 18B/34B [head dorsal] | original |
| | | | 19A* [head ventral]; some artistic license reflecting scales on left side of head] | original |
| <i>Hydrophis anomalus</i> | specimen number not reported | — | 35 [rostral view] | Redrawn from Rasmussen et al. 2011 Fig. 2 |
| <i>Hydrophis curtus</i> | KU 40063 | Phet Buri Province, Thailand | 36B [head ventral] | original |
| <i>Hydrophis melanocephalus</i> | KU 94556 | Chiling Harbor, Taiwan | 37B [head dorsal] | original |
| <i>Hydrophis peronii</i> | CAS 136104 | Ashmore Reef, West Island, Timor Sea, Australia | 37A [head dorsal] | Redrawn from Leviton et al. 2014 Fig. 42. |

| Species | Catalog # | Locality | Figures | Sources |
|----------------------------------|------------------------------|--|--|---|
| <i>Hydrophis schistosus</i> | specimen number not reported | — | 36A [head ventral] | Redrawn from Rasmussen et al. 2011 Fig. 5 |
| <i>Indotyphlops braminus</i> | specimen number not reported | "East Indies" | 21A* [head lateral] | Redrawn from Taylor 1922a Fig. 2b. |
| <i>Laticauda colubrina</i> | KU 303031 | Barangay San Vicente, Municipality of Concepcion, Maestro de Campo Island, Romblon Province, Philippines | 38B [head dorsal] | original |
| | KU 303033 | Barangay San Vicente, Municipality of Concepcion, Maestro de Campo Island, Romblon Province, Philippines | 4A* [tail lateral] | original |
| <i>Laticauda laticaudata</i> | KU 94559 | Buckner Bay, Okinawa Prefecture, Japan | 38A [head dorsal] | original |
| <i>Liopeltis philippinus</i> | KU 327731 | Barangay Samarina, Municipality of Brooke's Point, Palawan Island, Palawan Province, Philippines | 9D/39 [head dorsal-lateral] | original |
| <i>Lycodon muelleri</i> | KU 327575 | Barangay Biak na Bato, Biak na Bato National Park, Municipality of San Miguel, Bulacan Province, Luzon Island, Philippines | 12B [head lateral] | original |
| <i>Malayopython reticulatus</i> | KU 330021 | Barangay Magrafil, Mt. Cagua, Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines | 2H/7B [head lateral] | original |
| <i>Malayotyphlops castanotus</i> | CAS SUR-27940 | Inampulugan Island, Municipality of Sibunag, Guimaras Province, Philippines | 40C [head lateral] | Redrawn from Wynn et al. 1993 Fig. 1 |
| <i>Malayotyphlops denrorum</i> | PNM 9813 | Barangay Dibuluan, Municipality of San Mariano, Isabela Province, Luzon Island, Philippines | 6C/40A [head lateral] | Redrawn from Wynn et al. 2016 Fig. 4 |
| <i>Malayotyphlops luzonensis</i> | CM 2653 | Mt. Makiling, Laguna Province, Luzon Island, Philippines | 6B/23B/ 40B [head lateral] | Redrawn from Wynn et al. 2016 Fig. 3 |
| <i>Malayotyphlops ruber</i> | SMF 16616 | Samar Island, Philippines | 22B [head dorsal] | Redrawn from Wynn et al. 2016 Fig. 2 |
| <i>Myersophis alpestris</i> | KU 308684 | Barangay Maddiangat, Mt. Palali, Municipality of Quezon, Nueva Vizcaya Province, Luzon Island, Philippines | 20A [head lateral] | original |
| <i>Naja samarensis</i> | KU 326653 | Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province, Mindanao Island, Philippines | 17A [head lateral] | original |
| <i>Oligodon ancorus</i> | KU 346379 | Barangay Salvacion, Municipality of Bulusan, Sorsogon Province, Luzon Island, Philippines | 41B* [head lateral] | original |
| <i>Oligodon maculatus</i> | KU 321699 | Pasonanca Natural Park, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 3C*/15B* [body lateral] | original |
| | | | 41A* [head lateral] | original |
| <i>Ophiophagus hannah</i> | KU 321813 | Pasonanca Natural Park, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 4B [tail lateral] | original |
| | | | 17B [head lateral] | original |
| <i>Opisthotropis typica</i> | KU 327424 | Barangay Mainit, Municipality of Brooke's Point, Palawan Island, Palawan Province, Philippines | 3B [body lateral] | original |
| | | | 9B [head dorsal-lateral] | original |
| | | | 14A [tail ventral] Note:artistic licence taken to omit protruding hemipenes | original |

| Species | Catalog # | Locality | Figures | Sources |
|--|------------|---|--|--|
| <i>Oxyrhabdium modestum</i> | KU 311301 | Barangay Kilim, Municipality of Baybay, Leyte Province, Leyte Island, Philippines | 18A [head dorsal] | original |
| | | | 20B/42A* [head lateral] | original |
| <i>Oxyrhabdium leporinum leporinum</i> | KU 322335 | Barangay Villa Aurora, Aurora Memorial National Park, Municipality of Maria Aurora, Aurora Province, Luzon Island, Philippines | 42B* [head lateral] | original |
| <i>Psammodynastes pulverulentus</i> | KU 329688 | Barangay Adams, Mt. Pao, Municipality of Adams, Ilocos Norte Province, Luzon Island, Philippines | 13A [head dorsal-lateral] | original |
| <i>Pseudorabdion collaris</i> | KU 315197 | Barangay Baluno, Pasonanca Natural Park, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 27B/43B* [head lateral] | original |
| <i>Pseudorabdion mcnamarae</i> | KU 327199 | Municipality of San Mariano, Isabela Province, Luzon Island, Philippines | 43A [head lateral] | original |
| <i>Pseudorabdion montanum</i> | KU 305063 | Mt. Lihidan, Barangay Duyong, Municipality of Pandan, Antique Province, Panay Island, Philippines | 43D [head lateral] | original |
| <i>Pseudorabdion oxycephalum</i> | KU 324641 | Municipality of Masbate City, Masbate Province, Masbate Island, Philippines | 43C [head lateral] | original |
| <i>Ptyas luzonensis</i> | KU 306605 | Barangay Valencia, Municipality of Dumaguete, Negros Oriental Province, Negros Island, Philippines | 29A* [head lateral] | original |
| <i>Ramphotyphlops cumingii</i> | EHT R-99 | Municipality of Bunawan, Agusan del Sur Province, Mindanao Island, Philippines | 21B [head lateral] | Redrawn from Taylor 1919 Fig. 1a. |
| | KU 334468 | Municipality of Remedios T. Romualdez, Agusan del Norte Province, Mindanao Island, Philippines | 5A [body ventral] | original |
| <i>Ramphotyphlops marxi</i> | FMNH 96520 | Barangay Tarabucan, Municipality of Matuguinao, Western Samar Province, Samar Island, Philippines | 23A/44A [lateral head] | Redrawn from Wallach et al. 1993 Fig. 1a. |
| <i>Ramphotyphlops soluensis</i> | PBS 2001 | Bubuan Island, Basilan Province, Philippines | 2E/22C [head dorsal]; | Redrawn from Taylor 1918 Fig. 11a. |
| | | | 2F; 44B [head lateral] | Redrawn from Taylor 1918 Fig. 11b. |
| | | | 2G [head ventral] | Redrawn from Taylor 1918 Fig. 11c. |
| <i>Rhabdophis chrysargos</i> | — | — | 45B* [head lateral] | original; composite illustration from photos |
| <i>Rhabdophis lineatus</i> | KU 326696 | Visayas State University Campus, Municipality of Baybay, Leyte Province, Leyte Island, Philippines | 45A [head lateral] | original |
| <i>Sibynophis bivattatus</i> | KU 309608 | Boundary of Barangay Samarina and Barangay Saulog, Municipality of Brooke's Point, Palawan Island, Palawa Province, Philippines | 11B [head lateral]; Note: mouth closed digitally for aesthetics | original |
| <i>Stegonotus muelleri</i> | KU 344097 | Barangay Dinaayan, Municipality of Burauen, Leyte Province, Leyte Island, Philippines | 29B [head lateral] | original |

| Species | Catalog # | Locality | Figures | Sources |
|------------------------------------|-----------|---|----------------------------|----------|
| <i>Trimeresurus flavomaculatus</i> | KU 329422 | Barangay Kabayunan, Municipality of Dona Remedios Trinidad, Bulacan Province, Luzon Island, Philippines | 2I/7A [head lateral] | original |
| | KU 330050 | Barangay Magrafil, Mt. Cagua, Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines | 24B [head ventral-lateral] | original |
| <i>Tropidolaemus philippensis</i> | KU 334672 | Pasonanca Natural Park, Municipality of Pasonanca, Zamboanga del Sur Province, Mindanao Island, Philippines | 46B** [head dorsal] | original |
| <i>Tropidolaemus subannulatus</i> | KU 327425 | Barangay Samarinana, Municipality of Brooke's Point, Palawan Island, Palawan Province, Philippines | 24A [head ventral-lateral] | original |
| | KU 324585 | Barangay Patag, Municipality of Silay, Negros Occidental Province, Negros Island, Philippines | 46A [head dorsal] | original |
| <i>Tropidonophis dendrophiops</i> | KU 310368 | Barangay Pandan, Municipality of Mambajao, Camiguin Province, Camiguin Sur Island, Philippines. | 2A [head: dorsal] | original |
| | | | 2B [head lateral] | original |
| | | | 2C [head ventral] | original |
| Unnamed genus and species | KU 337269 | San Rafael Barangay, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines | 47 [head anterior-lateral] | original |
| <i>Xenopeltis unicolor</i> | KU 79152 | Municipality of Puerto Princesa, Palawan Island, Palawan Province, Philippines | 10A [head dorsal] | original |

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**Incorporation of *Danguya* into *Anisotes*
(Acanthaceae: Justiceae), a New Combination,
and Lectotypification of *D. pulchella***

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Macromorphological and palynological characters are used to show that the unispecific Malagasy genus *Danguya* is not distinct from *Anisotes*. A new combination for *D. pulchella* in *Anisotes* is proposed, and a lectotype for that species is designated. *Anisotes pulchella* is described, illustrated by a line drawing and photographs, and mapped. A preliminary conservation assessment of endangered (EN) is suggested for the species.

KEYWORDS: Madagascar, macromorphology, pollen, conservation

Caractères macromorphologiques et palynologiques sont utilisés pour montrer que le genre unispécifique malgache *Danguya* n'est pas distinct de *Anisotes*. Une nouvelle combinaison pour *D. pulchella* dans *Anisotes* est proposée et un lectotype pour cette espèce est désigné. *Anisotes pulchella* est décrite, illustrée par un dessin et des photographies, et cartographiée. Une évaluation préliminaire de la conservation de en danger (EN) est suggérée pour l'espèce.

Generic circumscription among Acanthaceae in Madagascar has been problematic and remains unresolved for several putatively endemic taxa (cf. Onjalalaina and Darbyshire 2016). Among endemic genera of Malagasy Acanthaceae, unispecific *Danguya* Benoist has received little attention. Benoist (1930) indicated that it was similar to both *Macrorungia* C.B. Clarke (cf. *Metarungia* Baden; Baden 1984) and *Anisotes* Nees, but that it differed in characters of the calyx and pollen. Although he did not specify how the calyx differed, it appears to be distinctive by having heteromorphic lobes with two pairs fused for much of their length but becoming free distally into two apical segments and the fifth (posterior?) lobe greatly reduced in size or absent. He indicated that pollen of *Danguya* could be distinguished from these other genera by lacking the rows of tubercles (i.e., insulae of Raj 1961; Daniel 1998; and others) that accompany the colpi. To the extent that genera of Acanthaceae were known in the first half of the twentieth century, these were indeed characteristics seemingly worthy of generic status.

Recent studies of the strictly Paleotropical genus *Anisotes* (e.g., Baden 1981b; Daniel et al. 2007, Daniel et al. 2013; Vollesen 2010; Daniel 2014) have discussed its generic status, palynological diversity, and infrageneric classification. Currently known generic synonyms (e.g., Vollesen 2010), are *Calasias* Raf. (nom. rej.), *Chlamyodostachya* Mildbr., *Himantochilus* T. Anderson ex Benth & Hook.f., *Macrorungia* C.B. Clarke, *Metarungia* Baden, and *Symplectochilus* Lindau; however, based on molecular phylogenetic data, Kiel et al. (2017) revealed that this circumscription results in a polyphyletic taxon. Inflorescences, corollas, and anthers of *Danguya* appear similar to those of *Anisotes*, and a reassessment of the putative distinctions of the former genus was



FIGURE 1. *Anisotes pulchella* (Rakotonasolo et al. 2254). Remnant forest habitat on the Vohombohitra massif (top). Branch with leaves and inflorescences (middle left). Inflorescence showing bracts and flowers (bottom left). Flowers (front view). Photos by L. Rokiman.

undertaken to better understand this poorly collected genus. Our effort was greatly facilitated by a recent collection of the sole species, *D. pulchella* Benoist, along with photographs of the plants (Fig. 1).

MATERIALS AND METHODS

Herbarium specimens were studied at CAS, K, MO, P, US, and TAN. Pollen was observed and photographed with both light and scanning electron microscopy (Hitachi model SU3500 SEM).

RESULTS

Studies of both macro- and micromorphological characters of *Danguya pulchella* strongly suggest a close relationship with *Anisotes*, into which genus we include the sole species with the new combination proposed below. Descriptions and discussion of the putative distinguishing characters are provided in the following taxonomic account. *Anisotes* and *Metarungia* were revised by Baden (1981a as *Macrorungia*, 1981b), some renovations of African taxa were made by Vollesen (2010), and additional species from Madagascar and the Comoros Archipelago were proposed by Daniel (2014, 2015) and Daniel et al. (2007, 2013). As circumscribed by Vollesen (2010, 2015) and Daniel (2014), the genus consists of 33 species occurring in Africa, the Arabian Peninsula, Socotra, Madagascar, and the Comoros Archipelago.

TAXONOMY

Anisotes pulchellus (Benoist) T.F. Daniel, Letsara & Rakotonas, comb. nov.

Danguya pulchella Benoist, Bull. Soc. Bot. France 76: 1038. 1930 ("1929"). **TYPE.**—MADAGASCAR. **Mahajanga:** Tampoketsa au dessus de Mahatsinjo, [ca. 17°45'00"S, 047°01'00"E], 1600 m, près du bois, IV-1925 (flr), *H. Perrier de la Bâthie 17238* (lectotype, designated here: P!-barcode P00089775; isolectotype: P!-barcode P00089776).

Shrubs to 2 m tall. Young stems subquadrate, evenly and usually densely pubescent with straight and erect to downward pointing or flexuose or retrorsely curved eglandular trichomes 0.05–0.4 mm long. Leaves petiolate, petioles 5–33 mm long, blades ovate to elliptic, 18–86 mm long, 12–42 mm wide, 1.3–2.2 (–3.3) times longer than wide, rounded to subacute (to acuminate) at apex, cordate to rounded at base, adaxial surface pubescent with mostly antrorse to antrorsely appressed eglandular trichomes (these sometimes sparse and restricted to major veins), abaxial surface more densely pubescent (especially along major veins) with antrorse to antrorsely appressed eglandular trichomes, margin entire and ciliate. Inflorescence of pedunculate spikes from leaf axils, peduncles 4–24 mm long, pubescent like young stems, spikes 1 (–2) per axil, alternate or opposite at nodes, (13–) 20–43 mm long (excluding peduncle and flowers), 11–23 mm in diameter near midspike (measured flat and excluding flowers), rachis not visible, pubescent with antrorse eglandular trichomes to 0.3 mm long and with an inconspicuous understory of erect sessile to stipitate glandular trichomes to 0.05 mm long. Bracts red-maroon (at least along margin and distally), spirally arranged on rachis, ± spatulate (i.e., proximally stalked and abruptly ovate to broadly elliptic to subcircular distally), 10–19 mm long and 3.5–12 mm wide (sometimes with smaller and often green sterile bracts at base of spike), apiculate at apex with apiculum to 1.9 mm long, abaxially venose, pubescent like rachis, prominently 5–7-veined from base, basal stalk infolding and partially enveloping basal portion of bracteoles and calyx. Bracteoles lanceolate to lance-linear to lance-elliptic, 4–5 mm long, 0.5–0.8 mm wide, abaxially pubescent like rachis. Calyx 8–11 mm long, abaxially pubescent like rachis, 4- or 5-lobed, lobes with 2 pairs fused

for much of their length forming 2 apically 2-lobed segments and the fifth (posterior?) lobe greatly reduced in size or absent, fused segments 5–9.5 mm long with apical lobes 0.6–6 mm long, reduced 5th lobe (when present) triangular-lanceolate to lanceolate, 2–3 mm long, 0.4–0.5 mm wide. Corolla red-maroon, 30–37 mm long, conspicuously arched, externally pubescent with erect to flexuose eglandular trichomes to 0.8 mm long and with a \pm conspicuous understory of stipitate glandular trichomes less than 0.1 mm long, tube 14–16 mm long, upper lip 13–21 mm long, internally rugulate, apically entire, lower lip recoiled, 13–21 mm long, apically 3-lobed, lobes 2.5 mm long, 0.5–1.5 mm wide. Stamens 15–21 mm long, filaments glabrous distally and sparsely pubescent with eglandular trichomes proximally, thecae greenish white, subparallel to subsagittate, unequally inserted but overlapping, 2.5–3.3 mm long, subequal in size, glabrous, upper theca with a basal appendage 0.1–0.2 mm long, lower theca with a basal appendage 0.3–0.4 mm long. Pollen (see discussion) globose-elliptic (i.e., longer E:shorter E > 1 but < 1.5), 2-colporate, 4-pseudocolpate, colpi extending to near poles, pseudocolpi equaling (or slightly shorter than) colpi, colpi and pseudocolpi microverrucate to microgemmate, interapertural exine \pm bireticulate, P = 37–45 μ m, E (apertural views) = 22–25 μ m, E (interapertural view) = 19 μ m, P:E (apertural view) = 1.68–1.8, P:E (interapertural view) = 2.05, E (apertural view):E (interapertural view) = 1.16–1.32. Style 27–32 mm long, sparsely pubescent with eglandular trichomes (except near apex), stigma 0.1 mm long, inconspicuously and unequally 2-lobed. Capsule 9.5–11 mm long, glabrous, retinacula and placentae not elastically rising; seeds (immature) 1.2–1.5 mm diam., surface pubescent with papilla-like trichomes.

PHENOLOGY.— Flowering: March–November; fruiting: November.

DISTRIBUTION AND HABITAT.— Central Madagascar (northern Antananarivo and southeastern to east-central Mahajanga; Fig. 2); plants occur in remnant or gallery forests at elevations of 1200–1600 meters.

ILLUSTRATIONS.— Figures 1, 3.

CONSERVATION.— A preliminary conservation assessment based on IUCN (2017) criteria using GeoCat (2019) calculations was performed for *Anisotes pulchellus* using the locality and collection information provided herein. An EOO of 6,042 km² and an AOO (based on 2 km² grid) of 28 km² were calculated for the species. No protected lands are currently within the EOO; however, the Réserve Spéciale d'Ambohitantly lies adjacent to (but outside of) its southeastern boundary. Two collections of the species are from the Vohombohitra massif, a region known for the richness of precious stones found there, and where the local population partakes in the mining of these stones, gathering of wood for heating and construction purposes, and agricultural activities (Ralainaorina 2016). Indeed, Ralainaorina (2016) specifically notes that the

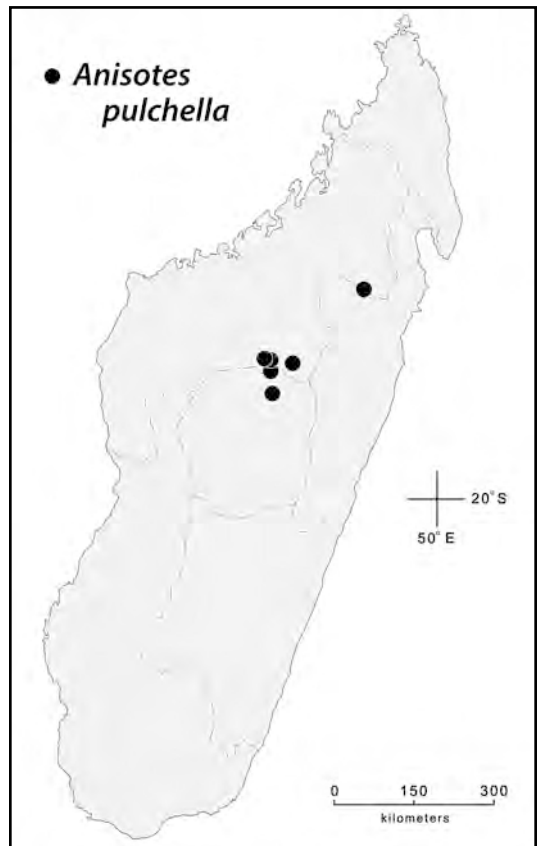


FIGURE 2. Map of Madagascar showing provincial boundaries and the distribution of *Anisotes pulchella*.

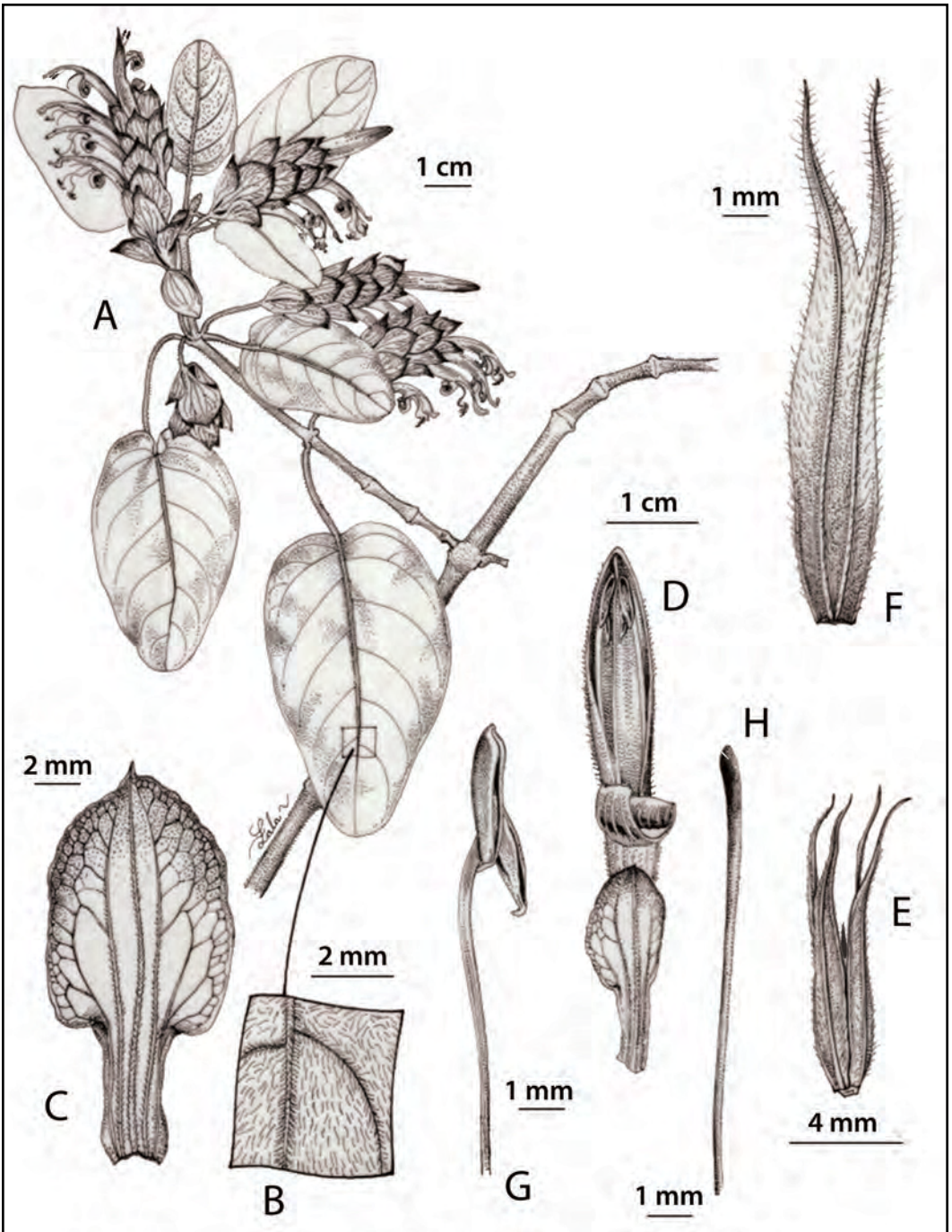


FIGURE 3. *Anisotes pulchella* (Rakotonasolo et al. 2254). A. Flowering branch. B. Close-up of abaxial surface of leaf showing pubescence. C. Bract. D. Flower subtended by bract. E. Calyx. F. Pair of partially fused calyx lobes. G. Portion of stamen with anther. H. Portion of style with stigma. Drawn by Roger Lala Andriamiarisoa.

vegetation of Vohombohitra continues to lose its floristic richness due to these and other anthropogenic pressures (e.g., brush fires). Collection sites to the west of Vohombohitra, including the type locale, occur in small forest fragments that have been and continue to be impacted by burning (to clear forest for grazing land) and timber cutting (Ratsirarson et al. 2003). These sites are treated as a second location based on the threat of forest clearing. *Humbert 17981* occurs at the north-eastern-most extent of the species' distribution, and it appears to occur in the western edge of the humid eastern escarpment forest in northern Madagascar. No threat is currently known for that site. Given these threats and an inferred continuing decline in the numbers of plants and their habitats based on the continuation of the threats, we propose a preliminary assessment of endangered (EN) for this species (B2(a, biii)).

TYPIIFICATION.— In the protologue, Benoist (1930) listed two collections (numbers 17238 and 17643) of Perrier de la Bâthie from the vicinity of Mahatsinjo. For at least part of their careers both Benoist and Perrier de la Bâthie worked at or for P (Dorr 1997), where the latter's Madagascar herbarium and a previously deposited set of his collections reside. Two specimens of each collection cited in the protologue are extant at P, all of which were putatively verified by Benoist and all of which conform to elements of the protologue. From among these, the specimen of *Perrier de la Bâthie 17238* with Benoist's name in his handwriting and with a dissected flower, is designated above as the lectotype.

DISCUSSION.— The two distinguishing characters of *Danguya* noted by Benoist in the protologue are worth analyzing. The calyx, consisting of two large segments (each distally 2-lobed) and a minute (presumably posterior) lobe between them sometimes present (Fig. 3E), is unusual among Acanthaceae and possibly unique in *Anisotes*. Similar fusion among calyx lobes was described and illustrated by Ezcurra (1993) for the 3-segmented, 5-lobed calyx of *Ruellia erythropus* (Nees) Lindau; however, in this species, the posterior lobe is not conspicuously reduced in size. Most species of *Anisotes* have 5-lobed calyces with the lobes homomorphic (Baden 1981a, 1981b; Daniel et al. 2007; Vollesen 2010). However, three recently described species show greater diversity in the number and relative lengths of calyx lobes for the genus. In both *A. venosus* T.F. Daniel, Letsara & Martín-Bravo and *A. comorensis* (Lindau) T.F. Daniel, the posterior lobe is distinctly shorter than the other four lobes. In *A. mayottensis* T.F. Daniel calyces with both five heteromorphic lobes (the posterior lobe shorter than the other four lobes) and with only four homomorphic lobes (the posterior lobe lacking) are present. Thus, the calyx of *A. pulchella* is distinctive in the genus only by the fusion of the four homomorphic lobes into two apically lobed pairs. The presence of such fusion for a subset of species in genera with otherwise homomorphic lobes is evident elsewhere in the family (e.g., *Ruellia*), as noted above.

The description of pollen provided above is based solely on *Rakotonasolo et al. 2254* (Fig. 4). Utilizing a different collection of this species (*Humbert 17981*), Muller et al. (1989) described and illustrated pollen of this species as 2 (–3)-porate and 4 (–6)-pseudocolpate, which differs from the description above primarily by the lack of compound apertures (i.e., colpi). It therefore appears that apertures of pollen in *Anisotes pulchella* can vary from two to rarely three in number and from porate to colpate in type. Such palynological variation is not common within species of Acanthaceae. Baden (1981a, 1981b) and Daniel et al. (2013) noted the following types of pollen among species of the genus: 2-, 3-, and 4-colporate grains with 4, 6, and 8 pseudocolpi, respectively and 2- and 3-aperturate grains with apertures (pores or colpi) in a trema region studded with one or two rows of insulae on each side of the aperture. It is noteworthy that Baden (1981a; 1981b) indicated that the apertures of 2- and 3-porate grains sometimes showed faint indications of colpi at the pores and that at least one taxon (*A. sessiflorus* subsp. *iringensis* C. Baden) showed variation in aperture number from two to three. Indeed, colpi evident on *Rakotonasolo et al. 2254* are some-

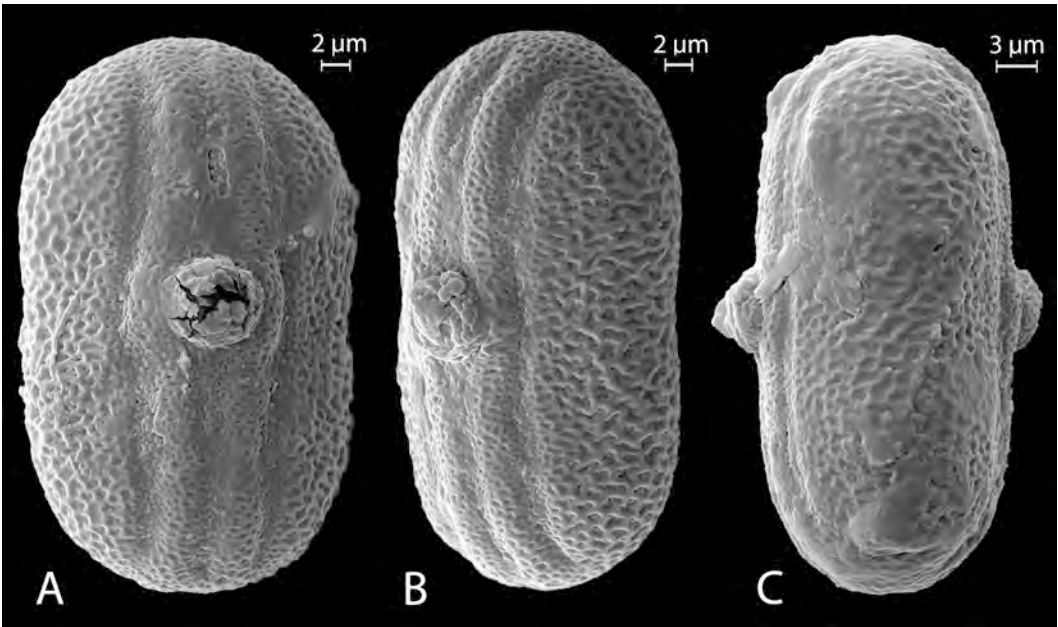


FIGURE 4. Pollen of *Anisotes pulchella* (Rakotonasolo et al. 2254). A. Apertural view. B. Oblique view. C. Interapertural view.

what faint, or at least not as distinct as in species described and illustrated by Baden (1981b) as being colporate.

Thus, the putative morphological characters used by Benoist (1930) only partially, and not very effectively, distinguish *Danguya* from *Anisotes* in the current circumscription of the latter genus. Only in instances where pollen of *A. pulchella* is 2-porate, 4-pseudocolpate, and lacking insulae (e.g., usually in *Humbert 17981*; Muller et al. 1989, Plate 182/XXX, figs. 1–8) does it differ from that of other species in the genus. The only unique character of *A. pulchella* within the genus appears to be the fusion of four of the calyx lobes into two pairs. Indeed, this fusion, is likely synapomorphic for the species and readily serves to distinguish it from its congeners.

The few known specimens of *A. pulchella* are rather homogeneous in most characters. However, two collections (*Bosser 18484* and *Humbert 17981*) are noteworthy by their young stems, which have much sparser and shorter trichomes with the longer (to 0.2 mm long) ones concentrated in two lines; leaves, which are narrower (up to 3.3 times longer than wide), acute at the base, acuminate at the apex, and mostly pubescent only along the major veins; and the very inconspicuous trichomes on abaxial surface of bracts, which appear almost glabrous. In other characters, they agree with the typical form of the species. They possibly represent either a seasonal (both of these collections were collected later in the year [August and November] than most of the other collections studied here) or an ecological form of the species.

Anisotes pulchella shows numerous similarities to plants from the transitional forest remnants between Sakaraha and Isalo National Park in southwestern Madagascar (e.g., *Bosser 17314*, *Du Puy et al. MB644*, and *Rogers et al. 441*). These yet to be identified plants, which occur at elevations between 720 and 770 m, differ by having pink bracts and white corollas with pink to red markings on the lower lip.

Preliminary molecular phylogenetic studies that included some Old World Justiceae (McDade et al. 2000) suggested that *Anisotes*, as currently delimited, is not monophyletic. Indeed, Kiel et al.

(2017) confirmed this; revealed that *A. perplexus* T.F. Daniel, Letsara & Martín-Bravo from Madagascar, which shows morphological affinities to *Anisotes* but has pollen like that found in Whitfieldieae and Isoglossinae, pertains to the latter subtribe; and that a potentially monophyletic *Metarungia* pertains to a clade sister to that containing most species of *Anisotes*. Comprehensive molecular and morphological studies of *Anisotes* are much to be desired in order to better unravel relationships among taxa of Justiceae in the Old World.

ADDITIONAL SPECIMENS EXAMINED.— MADAGASCAR. **Antananarivo:** Tompoketsa d'Ankazobe, P.K. 135 [ca. 17°55'S, 47°06'E], *J. Bosser 18484* (MO); Ambohimalaza près d'Ankazobe [18°19'S, 047°06'E], *R. Decary 7719* (K, P). **Mahajanga:** KM 180 de la route Tananarive–Majunga, sur le Tompoketsa [17°45'S, 047°01"E], *P. Boiteau 3012* (K, P); Massif du Vohimbohitra près de Manakana, district de Tsaratanana, au sommet du massif, [ca. 17°49'52.61"S, 047°26'08.91"E], *G. Cours 1522* (P, K); entre Mandritsara et Andilamena, [ca. 16°38'48.81"S, 048°39'9.36"E], *H. Humbert 17981* (K, P, US); près de Mahatsinjo sur le Tompoketsa entre l'Ikopa et le Betsiboka, [ca. 17°44'26.49"S, 047°04'15.34"E], *H. Perrier de la Bâthie 17643* (K, P); Distr. Tsaratanana, Region Betsiboka, Ambohimanga, Commune Manakana, Vohimbohitra, 17°47'44.8"S, 047°26'06.2"E, *F. Rakotonasolo et al. 2254* (CAS, K, TAN).

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New and Reconsidered Mexican Acanthaceae XIII. *Justicia*

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Five new species of Mexican *Justicia* are described, illustrated, and mapped: *J. alanae*, *J. matudae*, *J. mexiae*, *J. olmeca*, and *J. totonaca*. Descriptions, phenological data, habitats, and provisional conservation assessments are provided for each of them. A new name in *Justicia*, *J. amplifolia*, is proposed for the species previously known as *Sericographis macrophylla* Oerst. and *Jacobinia macrophylla* (Oerst.) Benth. & Hook.f. ex Hemsl. A lectotypification, detailed taxonomic account, and illustrations are provided for this species. New state distribution records are documented for *J. phlebodes* Leonard & Gentry (Nayarit), *J. pilosella* (Nees) Hilsenb. (Veracruz), and *J. spicigera* Schldtl. (Tabasco).

KEYWORDS: New species, new name, distribution records, pollen, endemism, conservation

Se describen, ilustran y mapean cinco especies nuevas de *Justicia* mexicanas: *J. alanae*, *J. matudae*, *J. mexiae*, *J. olmeca* y *J. totonaca*. Se proporcionan descripciones, datos fenológicos, hábitats y evaluaciones provisionales de conservación para cada una de ellas. Se propone un nombre nuevo en *Justicia*, *J. amplifolia*, para la especie conocida anteriormente como *Sericographis macrophylla* Oerst. y *Jacobinia macrophylla* (Oerst.) Benth. & Hook.f. ex Hemsl. También se proporciona una lectotipificación, cuenta taxonómica detallada e ilustraciones para esta especie. Se documentan nuevos registros de distribución por estado para *J. phlebodes* Leonard & Gentry (Nayarit), *J. pilosella* (Nees) Hilsenb. (Veracruz), y *J. spicigera* Schldtl. (Tabasco).

As currently circumscribed, *Justicia* L. is the largest genus of Acanthaceae and occurs throughout the worldwide distributional range of the family. Of the more than 700 species, about 105 of them are known to occur in Mexico (Daniel, unpublished). Additional undescribed species continue to be discovered there, especially in the seasonally moist to wet forests in southern portions of the country. Many are local or regional endemics. Five new species of *Justicia* from southern Mexico are described below; a new name in *Justicia* for the species originally described as *Sericographis macrophylla* Oerst. is proposed; and the distributions of *J. phlebodes* Leonard & Gentry, *J. pilosella* (Nees) Hilsenb., and *J. spicigera* Schldtl. are documented from states from which they have not been reported previously.

No attempt is made here to provide sectional affiliations for the taxa treated because recent phylogenetic studies on the infrageneric classification of *Justicia* and its relatives in the Justiceae (e.g., Kiel et al. 2017, 2018) reveal that most of the currently recognized sections and subsections of *Justicia* in the New World are not monophyletic, and that the phylogenetic affinities of many species remain unresolved. However, similarities, distinctions, and identification keys are noted/provided for previously described species that appear to be morphologically similar.

MATERIALS AND METHODS

Selected herbarium specimens were studied from the following herbaria: ARIZ, C, CAS/DS,

F, GH, K, LL, MEXU, MO, NY, P, US, W, and XAL. Specimens indicated as “image only” were only studied via digital images, primarily from herbarium websites/portals or JSTOR Global Plants (2019). Pollen was studied as described by Daniel (1998) and imaged in the Scanning Electron Microscopy Laboratory at the California Academy of Sciences. Provisional conservation assessments are offered based on IUCN (2017) guidelines using herbarium specimen data and historical imagery in Google Earth Pro (2019); extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCat (2019).

NEW SPECIES

Justicia alanae T.F. Daniel, sp. nov.

TYPE.— MEXICO. **Puebla:** Mpio. Xicotepéc de Juárez, 5 km NE de Xicotepéc, carr. a La Ceiba, 20°19'N, 097°48'W, 1200 m, bosque mesófilo perturbado, 24-II-1987 (flr, frt), *G. Toriz A., A. Campos V., O. Vega T., & P. Tenorio L. 298* (holotype: MEXU-image only; isotype: CAS!). Figures 1–3.

Perennial herbs to 1.5 m tall. Young stems subquadrate-sulcate, becoming subquadrate to quadrate proximally, distally densely 2-fariously pubescent with retrorse to retrorsely appressed eglandular trichomes 0.2–0.4 mm long and often also with sparse and flexuose eglandular trichomes to 0.4 mm long between the 2 lines of denser trichomes, trichomes usually with conspicuous maroon septae, stems soon becoming more sparsely pubescent or glabrate. Leaves petiolate, petioles 20–95 mm long, at least medial ones nearly as long as or longer than blade, blades ovate, 45–140 mm long, 16–65 mm wide, 2.0–2.8 times longer than wide, acuminate to falcate at apex, subcordate to rounded to truncate at base, adaxial surface glabrous, abaxial surface pubescent along main veins with antrorse to antrorsely appressed eglandular trichomes 0.1–0.2 mm long, margin entire to subsinuate, sparsely ciliate. Inflorescence of axillary and/or terminal pedunculate dichasiate spikes or more commonly panicles of dichasiate spikes to 90 mm long (including peduncles but excluding flowers), 6–10 mm wide near midspike (measured flat), (alternate or) opposite at nodes, sometimes clustered in leaf axils, peduncles of spikes to 40 mm long, pubescent like young stems or becoming ± evenly pubescent distally with variously oriented eglandular trichomes 0.05–0.2 mm long, rachis pubescent like peduncle; dichasia opposite or alternate at spike nodes, 1 per axil, 1-flowered, sessile. Bracts at a node homomorphic (when each subtending a dichasium, i.e., dichasia opposite and both bracts fertile) or heteromorphic when only 1 dichasium present at a node (i.e., dichasia alternate and 1 bract sterile); fertile bracts oblanceolate to elliptic to obovate to broadly spatulate, 3.2–8 mm long, 1–4.5 mm wide, rounded to acute at apex, abaxially and marginally pubescent with flexuose eglandular trichomes to 1 mm long and also with mostly erect glandular trichomes 0.05–0.2 mm long, glandular trichomes often sparse and rarely absent on some bracts; sterile bracts conspicuously reduced, narrowly linear to oblanceolate, 0.7–4 mm long, 0.2–0.8 mm wide. Bracteoles (linear to) oblanceolate to narrowly obovate-spatulate, 2.5–7.5 mm long, 0.5–1.6 mm wide, pubescent like bracts. Flowers sessile. Calyx 5-lobed, 3–4 (–4.5 in fruit) mm long, lobes homomorphic, lance-linear to lance-subulate, 2.6–3.5 (–4 in fruit) mm long, 0.3–0.5 mm wide, abaxially nearly glabrous to sparsely pubescent with flexuose to antrorse eglandular trichomes and sometimes also with very sparse and inconspicuous glandular trichomes < 0.05 mm long. Corolla white with maroon markings on lower lip, 7.5–13 mm long, externally pubescent with erect to flexuose eglandular trichomes 0.05–0.3 mm long, tube 5–8 mm long, narrow proximal portion of tube 2.5–4 mm long, longer than or equal to throat in length, throat 2–4 mm long, 1.8–3 mm in diameter at mouth (measured flat), upper lip 3–5 mm long, 2-fid, lower lip 3–5.5 mm long with three lobes 1–2 mm long and 1.5–2.5 mm wide, central lobe largest. Stamens 5–5.5 mm long, filaments glabrous, thecae of a pair superposed (contiguous, overlapping by

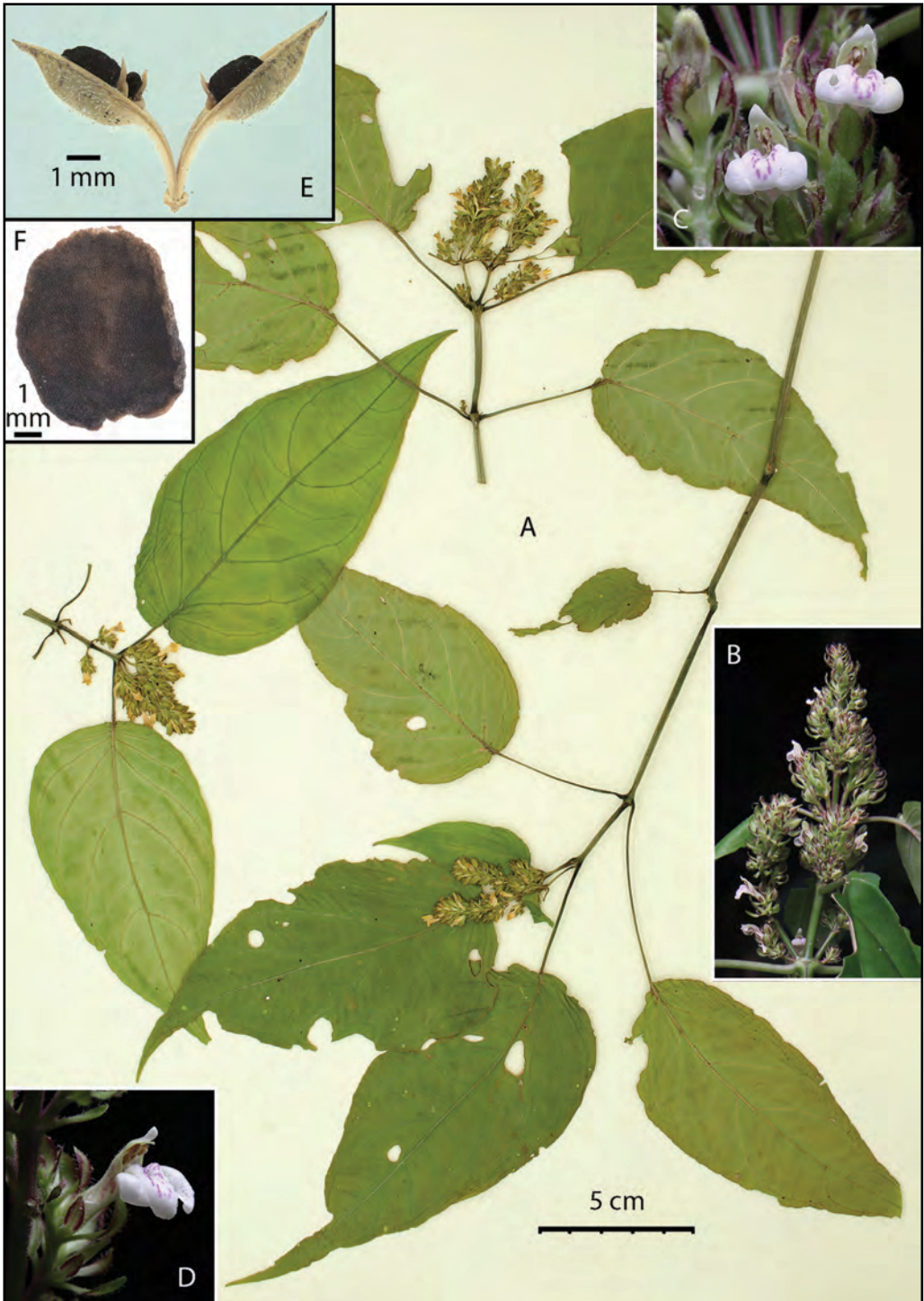


FIGURE 1. *Justicia alanae* (Jiménez C. & Gorostiza S. 31242). –A. Habit. B. Inflorescence. C. Flowers, front view. D. Flower, profile view. E. Capsule. F. Seed. Field photos B–D by J. Amith, used with permission.

0.1–0.2 mm, or separated by a gap to 0.05 mm long), \pm parallel or somewhat offset, subequal in size, upper theca 0.8–1.1 mm long, lacking a basal appendage, lower theca 1–1.4 mm long, with a prominent basal appendage 0.5–0.6 mm long, appendage oriented 90° to fertile portion of theca, thecae dorsally pubescent with flexuose eglandular trichomes to 0.7 mm long (lower theca often with shorter and less prominent trichomes); 2 densely pubescent staminode-like invaginations of the corolla present near midpoint of corolla tube. Pollen 3-colporate, 6-pseudocolpate, exine between colpi and pseudocolpi sometimes partially separating into insulae. Style 6–11 mm long, proximally pubescent with eglandular trichomes, stigma subcapitate, 0.05–0.1 mm long. Capsule 5–7 mm long, pubescent with erect to flexuose eglandular trichomes 0.1–0.3 mm long, stipe 1–2.5 mm long, head 4–4.5 mm long. Seeds flattened, \pm ovate to broadly oblong, 1.6–2.2 mm long, 1.3–1.7 mm wide, surface minutely papillose, margin entire.

PHENOLOGY.— Flowering: February–April; fruiting: February–April.

DISTRIBUTION AND HABITATS.— Mexico (Puebla; Fig. 2), endemic to the Sierra Nororiental in northern Puebla; plants occur in tropical subperennial forest and mesophytic montane forest (these sometimes secondary forests or plants occurring at disturbed sites therein) at elevations of 276–1200 meters.

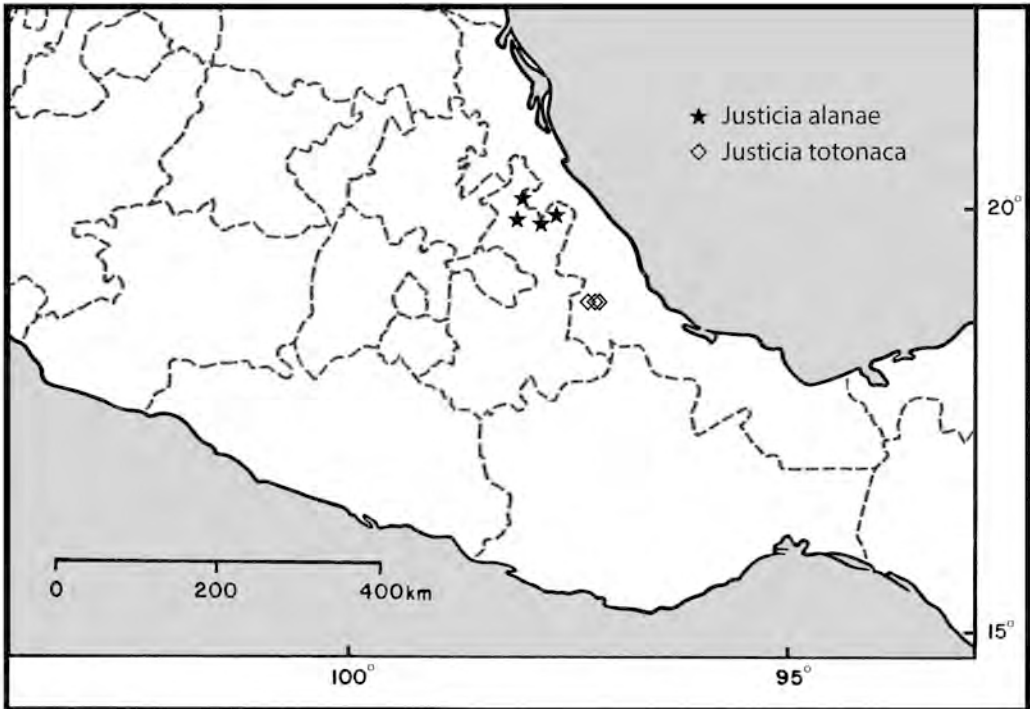


FIGURE 2. Map of part of southern Mexico showing distributions of *Justicia alanae* and *J. totonaca*.

CONSERVATION.— Based on the four known collection sites for this species, the EOO = 804 km², the AOO = 16 km², and the greatest linear extent of its distributional range (NW–SE) = 51 km. No collections are known to occur in protected areas. In addition to the type, at least three other collections have been made at different times at the type locality. No threats have been identified for this species, and thus it is provisionally assessed as Least Concern (LC).

ETYMOLOGY.— The epithet honors Jonathan Amith, a proponent of this species who also took useful photographs of it in Puebla, and his sometime young field assistant and daughter Alana.

PARATYPES.— MEXICO. **Puebla:** Mpio. Xicotepec de Juárez, 5 km NE de Xicotepec, carr. a La Ceiba, 20°19'N, 097°48'W, *A. Campos V. & G. Toriz A. 206* (CAS, MEXU-image only), *P. Tenorio L., G. Toriz A., A. Campos V. & O. Vega T. 12613* (CAS, MEXU-image only), *G. Toriz A. & A. Campos V. 374* (CAS, MEXU-image only); Mpio. Ayotoxco de Guerrero, Cuauhtémoc, en la loma de Santa Cecilia, cerca del Río Atekakalach, 20.03894°, -97.40643°, *M. Jiménez C. & M. Gorostiza S. 31242* (CAS); Mpio. Atlequizayán, Atlequizayán, camino a Lhimakgathlakgna', en localidad de Tatitsapsni', 20.00266°, -97.62263°, *C. Ledesma C., O. López F. & M. Gorostiza S. 22328* (CAS); Mpio. Ahuacatlan, Agua Dulce, 4 km SE de Ahuacatlan, brecha a Zapotitlan, 20°01'N, 097°50'W, *P. Tenorio L., G. Toriz A., A. Campos V. & O. Vega T. 12722* (CAS; MEXU-image only), *G. Toriz A., A. Campos V., P. Tenorio L. & O. Vega T. 320* (CAS, MEXU-image only).

DISCUSSION.— In spite of slight variation in type and disposition of cauline pubescence and variation in degree of glandularity among individuals, plants of *J. alanae* are morphologically homogeneous. Distinctive features of this species include the variation in bracts with either two fertile and homomorphic bracts at a node or one sterile and one fertile bract at a node with those bracts differing in size and usually also in shape. Heteromorphic bracts appear to be more frequent on spikes from leaf axils and/or on those forming the lateral branches of a panicle. Homomorphically bracteate spikes tend to be the ones terminating shoots. Bracts and bracteoles of *J. alanae* are green and are often tinged with maroon at the margins and apex (Fig. 1). Relatively long and naked petioles are prominent in this species, as are the pouch-like invaginations of the corolla near the midpoint of the corolla tube (cf. Daniel 2002). These staminode-like structures appear to be associated with the basal portion of the rugula and veins in the corolla tube leading thereto.

Justicia alanae undoubtedly pertains to a group of species known from various regions of the Neotropics that were discussed by Wasshausen and Daniel (1995) and Daniel (2002, 2007). A suite of morphological characters shared among four of these species (*J. chol* T.F. Daniel, *J. karsticola* T.F. Daniel, *J. alanae*, and *J. wendtii* T.F. Daniel) include: maroon septa of the cauline trichomes; some or all of the bracts heteromorphic (by size, shape, and whether fertile or sterile) and with their abaxial surface nearly always including glandular trichomes; relatively small corollas with maroon markings and with a pair of invaginations forming pouch-like and pubescent appendages internally in the corolla tube; anther thecae of a pair parallel to subparallel, unequally inserted to superposed, both dorsally pubescent with the lower one usually less densely so, and with the lower theca bearing a conspicuous basal appendage (commonly oriented at a 90° angle to the fertile portion of the theca); and 3-colporate, 6-pseudocolpate pollen (Fig. 3). These four similar species can be distinguished by the key below. Other similar Mexican species with either heteromorphic bracts and/or staminode-like invaginations of the corolla, but which differ conspicuously by their pollen, include *J. nevlingii* Wassh. & T.F. Daniel (pollen 4-colporate, 8-pseudocolpate) and *J. chimalapensis* T.F. Daniel (pollen 2-colporate with apertures flanked on each side by 1 row of insulae).

- 1a. Bracts inconspicuously ciliate with trichomes (0.05–0.2 mm long) and sometimes also with scattered flexuose eglandular trichomes to 0.3 mm long; corolla externally pubescent with eglandular and glandular trichomes; seeds sparsely pubescent with branched eglandular trichomes; southern Veracruz. *J. wendtii*
- 1b. Bracts conspicuously ciliate with trichomes up to 2 mm long (some, usually most, longer than 0.3 mm); corolla externally pubescent with eglandular trichomes only; seeds lacking branched trichomes 2
- 2a. Cauline trichomes mostly retrorse to retrorsely appressed; petioles elongate, at least medial ones nearly as long as or longer than blade, blades rounded to truncate to subcordate at base; floral bracts opposite or alternate; corolla white and with maroon markings; stamens 5–5.5 mm long; Puebla. *J. alanae*
- 2b. Cauline trichomes flexuose to antrorse; petioles not elongate as described above, blades acute to attenuate at base; floral bracts opposite; corolla pale yellow to yellow-green and with maroon markings; stamens 3.5–4.5 mm long 3

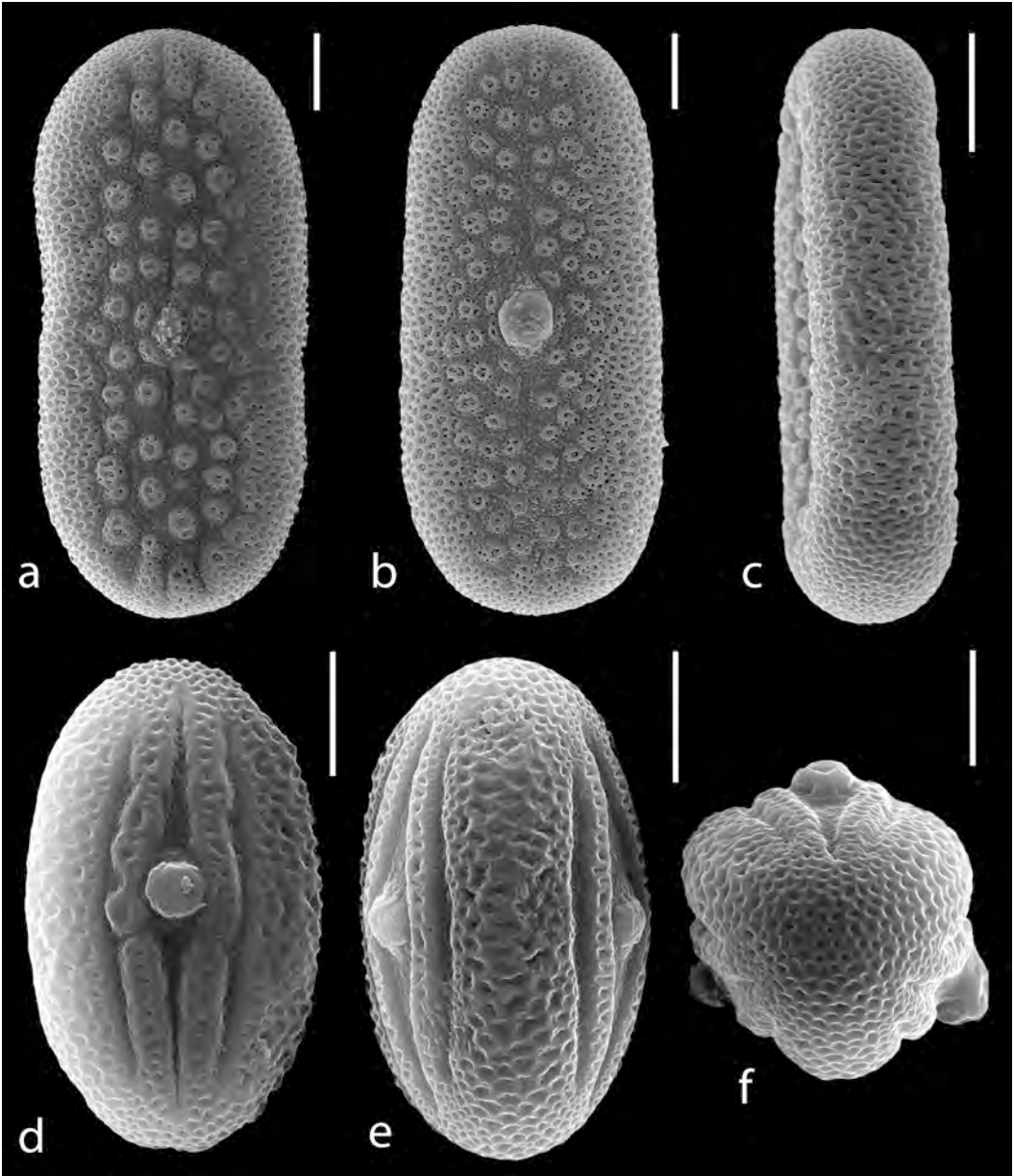


FIGURE 3. Scanning electron micrographs of *Justicia* pollen I. A–C. *Justicia amplifolia*. A. Apertural view (Amith & Mendoza 1419). B. Apertural view (Luther s.n.). C. Interapertural view (Luther s.n.). D–F. *Justicia alanae* (Toriz A. et al. 320). D. Apertural view. E. Interapertural view. F. Polar view. Scales = 10 μ m.

- 3a. Fertile bracts rounded- to truncate-apiculate at apex; inflorescence of axillary pedunculate dichasiate spikes to 6.5 cm long (including peduncles but excluding flowers), dichasia alternate, 1-flowered; Chiapas and Tabasco *J. chol*
- 3b. Fertile bracts rounded-subacute to acute at apex (lacking a conspicuous apiculum); inflorescence of (axillary and) terminal pedunculate panicles (7–15 cm long) of spicate axes, spicate axes (= modified dichasia?) opposite, mostly 3–5-flowered; southern Veracruz *J. karsticola*

***Justicia matudae* T.F. Daniel, sp. nov.**

TYPE.— MEXICO. **México:** Distr. V. de Bravo, Oztoloapan, [ca. 19°07'08"N, 100°17'18"W], ladera húmeda, matorral bajo, 1300 m, 5-IX-1954 (flr), *E. Matuda et al.* 31440 (holotype: MEXU!; isotypes: ARIZ!, CAS!, CODAGEM-images only). Figures 4–6.

Shrubs to 1.5 m tall. Young stems ± evenly and ± densely pubescent with mostly antrorse or retrorse (also including erect to flexuose) eglandular trichomes 0.1–1.3 mm long, or with 2 ± conspicuous bands of denser trichomes and with additional trichomes between the bands. Leaves subsessile to short-petiolate, petioles 2–7 mm long, blades broadly ovate to ovate (to elliptic), 26–95 mm long, 11–58 mm wide, 1.4–3.2 × longer than wide, sometimes reduced in size distally, acute to acuminate at apex, subcordate to rounded to acute at base, adaxial surface pubescent throughout (denser on younger growth) with antrorse to antrorsely appressed eglandular trichomes 0.05–0.8 mm long, abaxial surface densely pubescent throughout with antrorse (to flexuose) eglandular trichomes to 1 mm long, dense clusters of trichomes at junctions of midvein and secondary lateral veins not evident (if possibly present, then inconspicuous), margin ± entire, ciliate from base to apex. Inflorescence of axillary and terminal dense headlike dichasiate clusters (± appearing like verticels, especially at apex of shoot; see discussion); clusters opposite at nodes, 1 (–2) per axil, multi-flowered, sessile. Bracts, green (sometimes dark colored when dry), ovate to elliptic to oblong to obovate (proximally) and becoming oblanceolate distally, 7–16 mm long, 2–9.5 mm wide, acute at apex, abaxially and marginally pubescent with mostly antrorse eglandular trichomes to 0.4 mm long, distal portion of bracts often recurved. Bracteoles obovate to oblanceolate to narrowly elliptic, 4–14 mm long, 0.6–3.2 mm wide, becoming progressively narrower from primary to tertiary pairs, abaxially and marginally pubescent like bracts, distal portion of bracteoles often recurved. Flowers sessile. Calyx 5-lobed, 6–8 mm long, lobes homomorphic, ovate to lance-ovate, 2–4 mm long, 1.1–1.7 mm wide, apically attenuate, abaxially sparsely pubescent with antrorse eglandular trichomes to 0.2 mm long, marginally ciliate with erect to flexuose eglandular trichomes to 0.8 mm long. Corolla red, 25–37 mm long, externally pubescent with flexuose to retrorse eglandular trichomes 0.1–0.6 mm long, tube gradually expanded distally, 16–20 mm long, 2.5–5 mm in diam. (measured flat) at mouth, upper lip 9–17 mm long, entire to 2-fid at apex, lower lip 9–19 mm long, 3-lobed, lobes 2–7 mm long, 1.8–4 mm wide. Stamens 8.5–15 mm long, filaments distally glabrous, proximally pubescent with eglandular trichomes, thecae of a pair subparallel to subsagittate, subequally to unequally inserted (overlapping by 1.5–2 mm), 1.9–2.5 mm long, equal to subequal in length, glabrous, lacking basal appendages. Pollen 2-aperturate, apertures consisting of a narrow colpus and a prominent central os, flanked on each side by 3–4 rows of insulae (farthest rows from aperture sometimes entirely or partially consisting of peninsulae). Style 22–27 mm long, glabrous throughout; stigma subellipsoid, 0.2 mm long. Capsules and seeds not seen.

PHENOLOGY.— Flowering: August–September; fruiting: unknown.

DISTRIBUTION AND HABITATS.— Mexico (central Michoacán and western México; Fig. 5); plants occur in thornscrub and tropical deciduous forest at elevations of 650–1300 m.

CONSERVATION.— Based on the five known collections of this species, the EOO = 7,530 km², the AOO = 20 km², and the greatest linear extent of its distributional range (W–E) = 250 km. *Stein-*

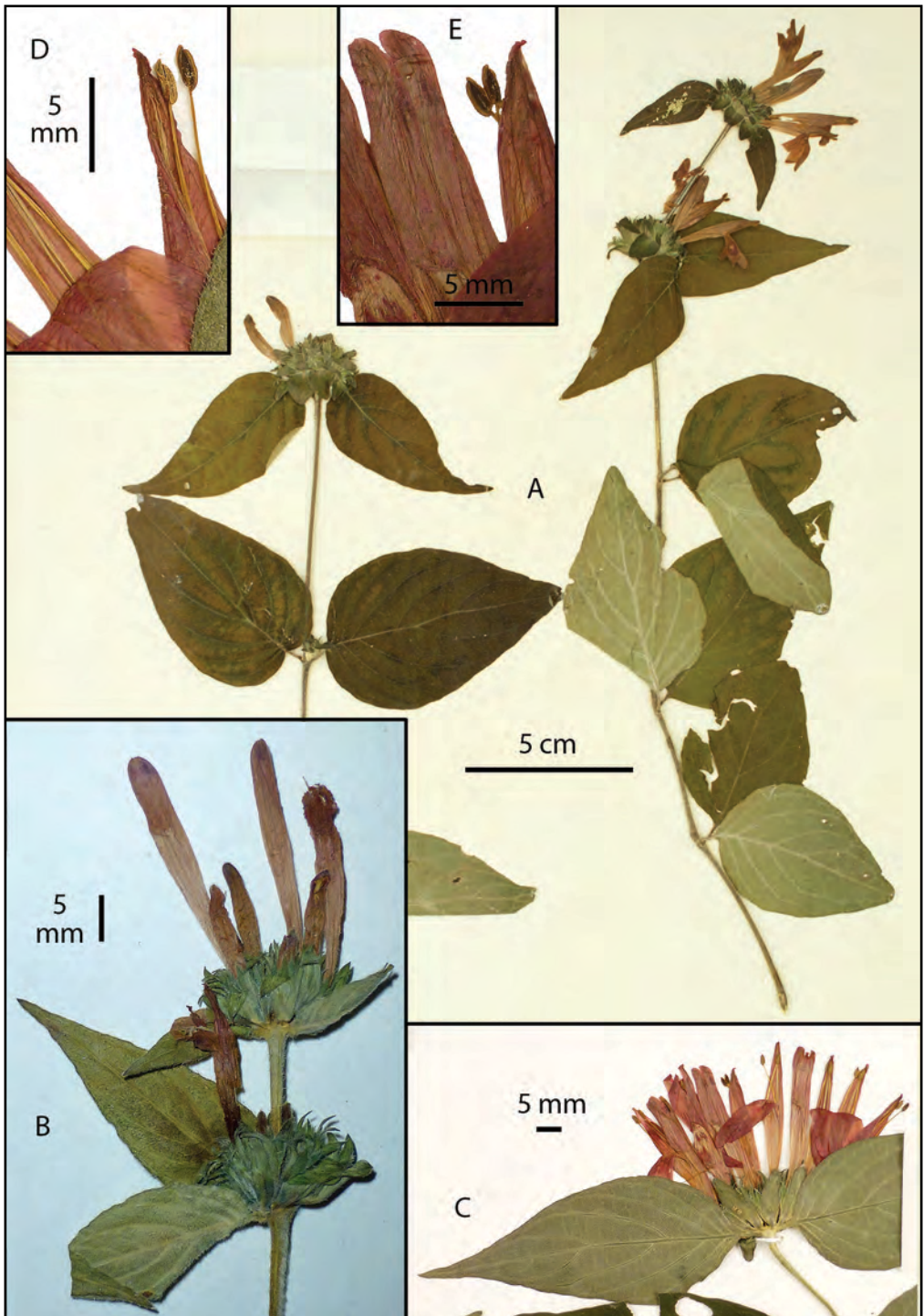


FIGURE 4. *Justicia matudae*. A. Habit (Hinton et al. 15189, NY). B. Branch with inflorescences (Hinton et al. 15189, US). C. Inflorescence (Ibarra M. 6764). D. Views inside upper lip of corolla with stamens and rugula (Ibarra M. 6764). E. View of upper lip (from side) and lower lip of corolla (Ibarra M. 6764).

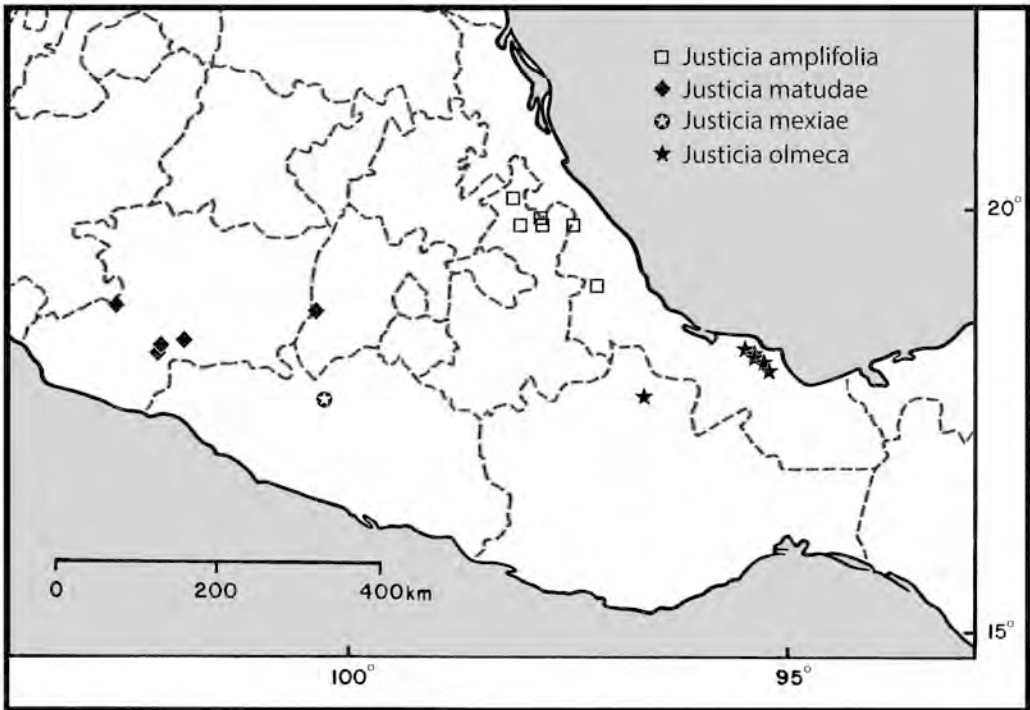


FIGURE 5. Map of part of southern Mexico showing distributions of *Justicia amplifolia*, *J. matudae*, *J. mexiae*, and *J. olmeoca*.

mann 4528 indicates that plants were uncommon at that collection site. Plants are not known from any protected areas, but at least one small protected area occurs within the EOO. At least one of the three subpopulations (the westernmost occurrence in Michoacán) is within an area threatened by active volcanoes, but threats remain unknown for the majority of the population. Based on IUCN (2017) criteria and current knowledge of the species and its threats, *J. matudae* is probably best assessed as Least Concern (LC).

PARATYPES.— MEXICO. **Michoacán:** Distr. Apatzingan, Rancho Viejo, [Mpio. Buenavista, ca. 19°12'N, 102°40'W], *G. Hinton et al.* 15189 (GH, NY, US); Mpio. Churumuco, El Limón, Ejido Llano de Ojo de Agua, 18°43'52"N, 101°40'28"W, *G. Ibarra M.* 6764 (MEXU); Mpio. La Huacana, ca. 2 km (air) ENE of Los Ranchos, along ridge top of Cerro El Barril, 18°42'35"N, 102°00'00"W, *V. Steinmann* 3455 (CAS); Mpio. La Huacana, Sierra Las Cruces, 6.5 km (air) SW of Los Ranchos, Cañada Las Cruces, 18°39'59"N, 102°03'46"W, *V. Steinmann* 4528 (CAS).

DISCUSSION.— Leaves of *Hinton et al.* 15189 are beset with either prominent punctate gland-like protrusions or a parasitic infestation; because these structures are not evident on other collections of the species, they are assumed to represent the latter. The dichasiate clusters appear to be reduced dichasiate spikes (i.e., lacking an elongate rachis; thus bearing both bracts and bracteoles), but it is possible that they are compound dichasia, in which case all of the bracteal units represent bracteoles.

Justicia matudae (Fig. 4) appears closely allied morphologically to *J. mexiae* (see below) with which it shares numerous morphological traits, including: densely clustered axillary inflorescences that appear as verticels at vegetative nodes; red corollas of similar size, shape, and pubescence; anther thecae of similar orientation and size that are glabrous and that lack basal appendages; and

2-aperturate (colporate with apertures flanked by 2 or more rows of insulae) pollen (Fig. 6). Distinctions between them are noted under *J. mexiae* below. *Justicia candicans* (Nees) L.D. Benson, a widespread and variable species of the southwestern United States and western Mexico, shares some of these characteristics (e.g., corollas, anther thecae, and pollen). It differs by its less dense and rarely verticillate axillary inflorescences that sometimes form multi-flowered, short dichasiate spikes (terminating shoots or in leaf axils) or consist of solitary 1-flowered dichasia in leaf axils; narrower bracts; and corollas that usually have white markings on the lower lip.

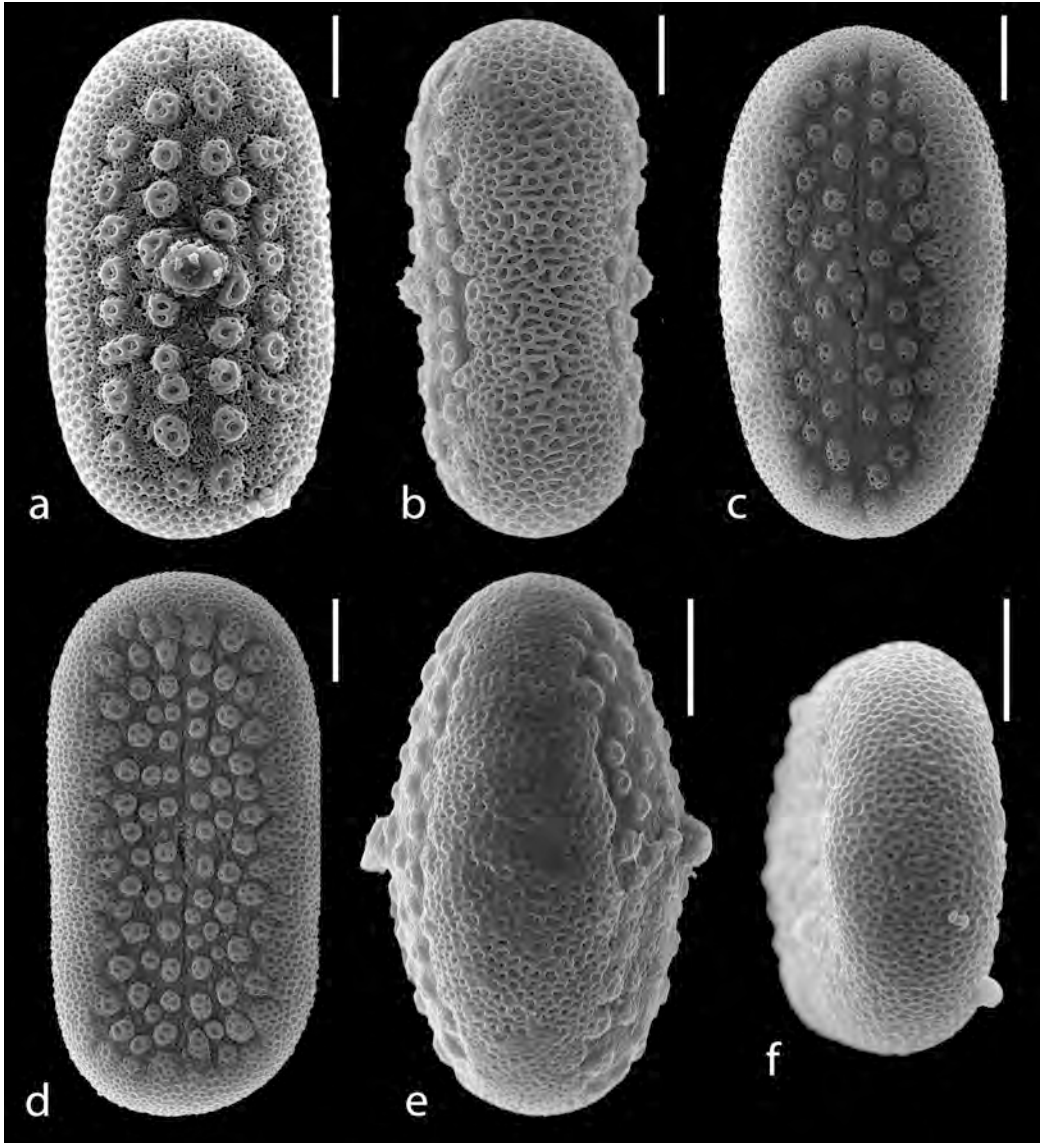


FIGURE 6. Scanning electron micrographs of *Justicia* pollen II. A–B. *Justicia totonaca* (Ventura 15945). A. Apertural view. B. Interapertural view. C. *Justicia mexiae*, apertural view (Mexia 8732). D–F. *Justicia matudae*. D. Apertural view (Steinmann 4528). E. Interapertural view (Matuda et al. 31440). F. Polar view (Matuda et al. 31440). Scales = 10 μm .

Justicia mexiae T.F. Daniel, sp. nov.

TYPE.— MEXICO. **Guerrero:** Distr. Aldama, Sierra Madre del Sur, N of Río Balsas, Temisco, Barranca El Salto, [ca. 18° 8'17.20"N, 100°13'34.94"W], 350 m, 3-XI-1937 (flr), *Y. Mexia* 8732 (holotype: MO!; isotypes: CAS!, F!, GH!, LL!, NY!, US!). Figures 5-7.

Shrubs of unknown height. Young stems 2-fariously pubescent with mostly antrorse to antrorsely appressed eglandular trichomes 0.2–0.7 mm long, trichomes mostly restricted to the 2 bands but soon becoming sparse and/or intermixed with retrorse to retrorsely appressed eglandular trichomes. Leaves petiolate, petioles 5–18 mm long, blades ovate-elliptic to elliptic, 60–121 mm long, 20–52 mm wide, (1.8–) 2.2–3.3 × longer than wide, not or only slightly reduced in size distally, acuminate at apex, (acute to) subattenuate to attenuate at base, adaxial surface sparsely pubescent with flexuose to antrorse eglandular trichomes to 1 mm long, abaxial surface sparsely pubescent along veins with similar trichomes, junctions of midvein with second-order lateral veins ± densely pubescent with a cluster of trichomes (i.e., with domatia), margin ± entire, sparsely ciliate only proximally or ± throughout. Inflorescence of axillary and terminal (i.e., in axils of distalmost pair of leaves) dense headlike dichasiate clusters (± appearing as verticels, especially at apex of shoot); clusters opposite at nodes, apparently 1 per axil, multi-flowered, sessile. Bracts dark colored (when dry), obovate to subcircular to oblate, 7–11 mm long, 3.9–9 mm wide, rounded to acute at apex, abaxially and marginally pubescent with mostly antrorse to antrorsely appressed eglandular trichomes 0.05–0.4 mm long, distal portion of bracts erect. Bracteoles oblong to obovate to obovate-spatulate to narrowly oblanceolate, 7–10 mm long, 0.6–8 mm wide, becoming progressively narrower from primary to tertiary pairs, abaxially and marginally pubescent like bracts, distal portion of bracteoles erect. Flowers sessile. Calyx 5-lobed, 5.5–6.5 mm long, lobes homomorphic, ovate to lance-linear to linear, 4.5–5.5 mm long, 1–2 mm wide, apically attenuate to aristate (arista to 0.5 mm long), abaxially pubescent like bracts, margin distally ciliate with flexuose to crinkly eglandular trichomes to 0.4 mm long. Corolla red, 26–30 mm long, externally pubescent with erect to flexuose eglandular trichomes to 0.7 mm long, tube gradually expanded distally, 16–20 mm long, 3.8–4 mm in diameter (measured flat) at mouth, upper lip 9–13 mm long, entire at apex, lower lip 9–12 mm long, 3-lobed, lobes 0.5–3 mm long, 1–2.5 mm wide, central lobe largest. Stamens 11–15 mm long, filaments distally glabrous, proximally pubescent with eglandular trichomes, thecae of a pair subparallel to subsagittate, unequally inserted (overlapping by 1.5–1.7 mm), 1.8–2.3 mm long, subequal in length, glabrous, lacking basal appendages. Pollen 2-aperturate, apertures consisting of a narrow colpus with a prominent central os, flanked on each side by 2–3 rows of insulae (farthest rows from aperture sometimes partially or entirely consisting of peninsulae). Style 25–28 mm long, distally glabrous, proximally pubescent with eglandular trichomes; stigma asymmetrically subcapitate, 0.2 mm long. Capsule and seeds not seen.

PHENOLOGY.— Flowering: November; fruiting: unknown.

DISTRIBUTION AND HABITAT.— Mexico (north-central Guerrero; Fig. 5); plants were noted to be common in undergrowth on a wooded slope at an elevation of 350 m.

LOCAL NAME.— “Chilillo” (*Mexia* 8732).

CONSERVATION.—This species is known only from the type collection made in 1937. Without additional information or known threats, following IUCN (2017) guidelines, it is provisionally assessed as data deficient (DD).

DISCUSSION.— It is not without hesitation that *Justicia mexiae* (Fig. 7) is described as distinct from *J. matudae* (see above); additional collections may reveal them to be a geographic variants of a single species or entirely conspecific. However, at this time, the distinctions noted in the key below appear to warrant their recognition at specific rank. Although the pollen of both species is very similar, among grains studied to date, those of *J. mexiae* (Fig. 6) often have fewer rows of

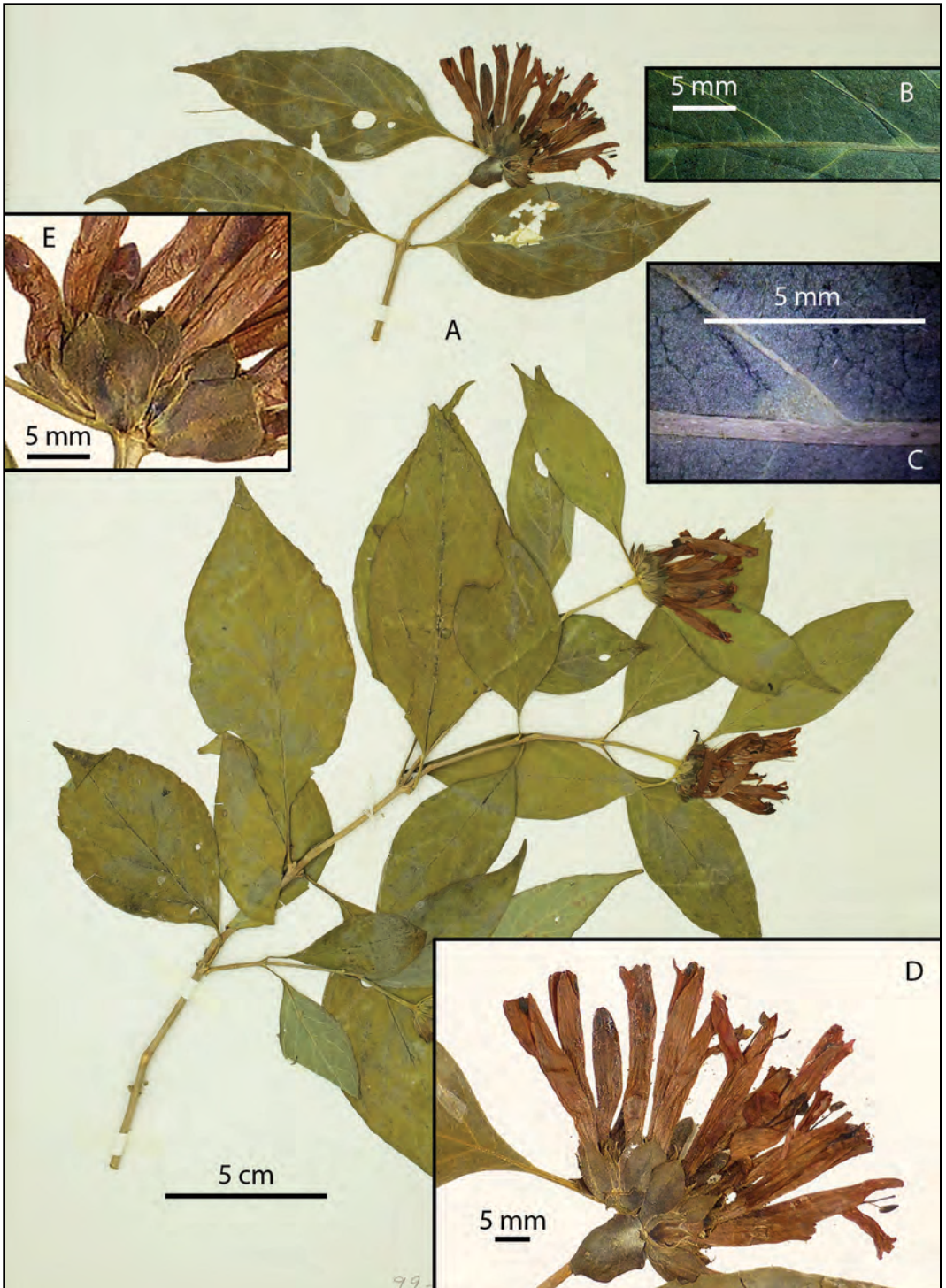


FIGURE 7. *Justicia mexiae* (*Mexia* 8732). A. Habit (MO). B. Domatia on abaxial surface of leaf (US). C. Close-up of domatia in axil of midvein and secondary vein (US). D. Inflorescence (MO). E. Close-up of bracts, bracteoles, and base of flowers (CAS)

insulae flanking the aperture than those of *J. matudae*. As in *J. matudae* it is not entirely clear whether the dense axillary clusters are expanded dichasia lacking peduncles/pedicels (therefore with only bracteoles of several orders present) or, as treated here, a reduced dichasiate spike (lacking a rachis) with bracts and bracteoles present. The bracts and bracteoles of *J. mexiae* are apparently tinged reddish, and are usually darker than the leaves on drying.

- 1a. Leaves subsessile or with petioles 2–7 mm long, blades subcordate to rounded to acute at base, abaxial surface pubescent throughout and lacking dense clusters of trichomes (domatia) at junctions of midvein and secondary lateral veins (if possibly present, then inconspicuous); bracts and bracteoles often distally recurved; calyx 6–8 mm long with lobes 2–4 mm long; style glabrous throughout; México and Michoacán *J. matudae*
- 1b. Leaves petiolate with petioles 5–18 mm long, blades (acute to) subattenuate to attenuate at base, abaxial surface sparsely pubescent with trichomes restricted to veins, and with dense clusters of trichomes at junctions of midvein with second-order lateral veins (domatia); bracts and bracteoles erect; calyx 5.5–6.5 mm long with lobes 4.5–5.5 mm long; style distally glabrous and proximally pubescent; Guerrero *J. mexiae*

***Justicia olmeca* T.F. Daniel, sp. nov.**

TYPE.— MEXICO. **Oaxaca:** Mpio. San Felipe Usila, Cerro Verde, camino al “Vainilla” de J. Roldán, 5 km NNE de Usila, 17°56'N, 096°30'W, selva alta perennifolia sobre suelos kársticos, 550 m, 1-X-1992 (flr), G. Ibarra M., J. Meave del Castillo & M. Vargas 3742 (holotype: MEXU!; isotype: MO!). Figures 5, 8, 9.

Perennial herbs to 1 m tall. Young stems densely and ± evenly to ± 2-fariously pubescent with flexuose and conspicuously multi-septate eglandular trichomes 0.5–2.5 mm long. Leaves long-petiolate, petioles 17–58 mm long, (those near midstem ca. 0.5–1 × as long as blades), pubescent like young stems, blades (ovate-elliptic to) ovate to broadly ovate to deltate, 70–113 mm long, 45–72 mm wide, 1.2–1.9 × longer than wide, truncate to rounded to subacute at base, shortly acuminate at apex, adaxial surface sparsely pubescent with cauline type trichomes, abaxial surface similarly pubescent but with trichomes denser (especially along major veins), margin entire, ciliate throughout with cauline type trichomes. Inflorescence of terminal (and also sometimes in axils of distalmost pair of leaves) subsessile to pedunculate dense dichasiate spikes to 57 mm long (including peduncle and excluding flowers), 13–20 mm wide (measured flat) near midspike, peduncles of spikes 3–33 mm long, pubescent like young stems, rachis not visible, pubescent like young stems; dichasia opposite, 1 per axil, 1-flowered, sessile. Bracts sessile to short-petiolate, ovate to elliptic to broadly obovate, 10–16 mm long, 5–8.5 mm wide, apically rounded to acute, abaxially and marginally pubescent with cauline type trichomes. Bracteoles lanceolate to linear-elliptic to linear-oblancheolate to oblanceolate, 7–11.5 mm long, 0.8–1.5 mm wide, pubescent like bracts. Flowers sessile. Calyx 5-lobed, 5–9 mm long, lobes equal to subequal in length, linear-lanceolate to lanceolate, 4.5–6.6 mm long, 0.7–1.3 mm wide, abaxially and marginally glabrous or with very few cauline type trichomes, margin ± hyaline. Corolla red, 29–35 mm long, externally pubescent with cauline type trichomes and flexuose glandular trichomes 0.1–0.9 mm long, internally with stipitate glands on the lower lip, tube 20–26 mm long, gradually expanded distally, 3–5 mm in diameter (measured flat) at mouth, upper lip 7–9.5 mm long, 2-fid at apex, lower lip 7–11 mm long, 3-lobed, lobes 1.2–3 mm long, 1.5–2.5 mm wide, central lobe usually largest. Stamens 8–10 mm long, thecae of a pair subparallel to subsagittate, unequally inserted (overlapping by 1.6 mm), 2–2.5 mm long, ± equal in size (or distal theca slightly longer), glabrous, not or inconspicuously appendaged at base (i.e., upper theca sometimes with a basal appendage up to 0.05 mm long and lower theca sometimes with a basal appendage to 0.15 mm long). Pollen 5-colporate, 10-pseudocolpate, pseudocolpi variously fused (see discussion). Style 30–35 mm long, distally

glabrous, stigma \pm capitate, 0.2 mm long, 0.3–0.5 mm wide. Capsule 9 mm long, pubescent with cauline type trichomes, stipe 3 mm long, head 6 mm long. Seeds not seen.

PHENOLOGY.— Flowering: October–January; fruiting: January.

DISTRIBUTION AND HABITATS.— Mexico (northern Oaxaca and southern Veracruz; Fig. 5); plants occur (sometimes on karstic substrates) in moist to wet forests (e.g., selva alta perennifolia, selva mediana subperennifolia, and bosque mesófilo de montaña), scrub, forests in canyons, and cafetales at elevations of 200–1350 m.

LOCAL NAME.— “Monchyvay” (Popoluca; *Leonti et al. 488*).

USE.— Boiled leaves used to wash snake-bites (*Leonti et al. 488*).

CONSERVATION.— Based on the nine known collections, the EOO = 3,410 km², the AOO = 32 km², and the greatest linear extent of its distributional range (SW–NE) = 176 km. Six of the nine collections (i.e., all of those from Veracruz) were made in the Reserva de la Biosfera Los Tuxtlas. Both collections of Ventura from Veracruz indicate that plants were scarce at those locales, whereas Calzada’s collection from the same general region noted that plants were abundant at that collection site. Plants in Veracruz would all appear to be threatened by the continuing deforestation documented by aerial imagery in the reserve between 1967 and 2000, a threat that has since diminished only to some extent (Los Tuxtlas Biosphere Reserve 2019). Threats are not known for the plants occurring in Oaxaca. Thus, at least two possible locations exist for the species. Based on IUCN (2017) criteria, this species is provisionally assessed as Endangered (EN: B1ab(iii) + 2ab(iii)).

ETYMOLOGY.— The specific epithet refers to the indigenous Olmec people whose culture and influence once dominated much of the region in which this species occurs.

PARATYPES.— MEXICO. **Oaxaca:** Mpio. San Felipe Usila, Cerro Verde, *A. Hanan & R. de Santiago s.n.* (CAS); Mpio. San Felipe Usila, Cerro Verde, camino al “Vainilla” de J. Roldán, 5 km NNE de Usila, 17°56’N, 096°30’W, *G. Ibarra M., J. Meave del Castillo & M. Vargas 3741* (MEXU, MO). **Veracruz:** Mpio. Soteapan, Sierra de Santa Marta, 5 km W de Santa Marta, 18°26’N, 094°57’W, *J. Calzada 5187* (F); Mpio. Soteapan, 2.5 km N de Santa Marta, ladera E del Volcán Santa Marta, 18°21’06.51”N, 094°53’49.56”W, *A. Campos V. & C. Granados M. 6609* (MEXU); Mpio. Soteapan, Sierra Santa Marta, 3 km NW de San Fernando, [18°17’4.49”N, 094°54’24.14”W], *M. Leonti et al. 488* (MEXU); Mpio. Catemaco, Cerro Buenavista, 3 km N de Catemaco, carr. a Sontecomapan, 18°29’N, 095°06’W, *A. Torres R. 427* (MEXU); Mpio. San Pedro Soteapan, Ejido Santa Martha, 18°25’N, 094°56’W, *F. Vázquez B. & D. Hernández L. 44* (F, XAL); Mpio. Catemaco, Pipiapan, [ca. 18°26’14.7”N, 095°03’8.9”W], *F. Ventura 12178* (CAS); Mpio. Santiago Tuxtla, Loma Quemada, [ca. 18°32’5.40”N, 095°16’51.42”W], *F. Ventura 14895* (CAS).

DISCUSSION.— Plants of *J. olmeca* (Fig. 8) are morphologically homogenous; however, the leaves are rarely (i.e., one leaf of *Hanan & de Santiago s.n.* at a distal node) elliptic and abruptly acute at the base. Morphological allies of this species remain undetermined. It is distinctive by combination of the following characteristics: elongate petioles (especially those near midstem), stipitate glands on the internal surface of the lower lip of the corolla, subcapitate stigmas that appear to consist of a disk-like platform subtending two rounded mounds, and the 5-aperturate pollen.

Five-aperturate pollen apparently is not otherwise known among Mexican species of *Justicia* (e.g., Daniel 1998). It is common among Mexican species of *Poikilacanthus* Lindau, a genus that is not monophyletic, and whose relationship to *Justicia* is currently being investigated (Kiel et al. 2017, 2018). However pollen of *Poikilacanthus* (e.g., Daniel 1991, 1998, 2017) consists of two related types bearing circular apertures (simple or compound?) with the interapertural surface covered with subcircular to rectangular to polygonal insulae (gemmate regions enclosed by thick

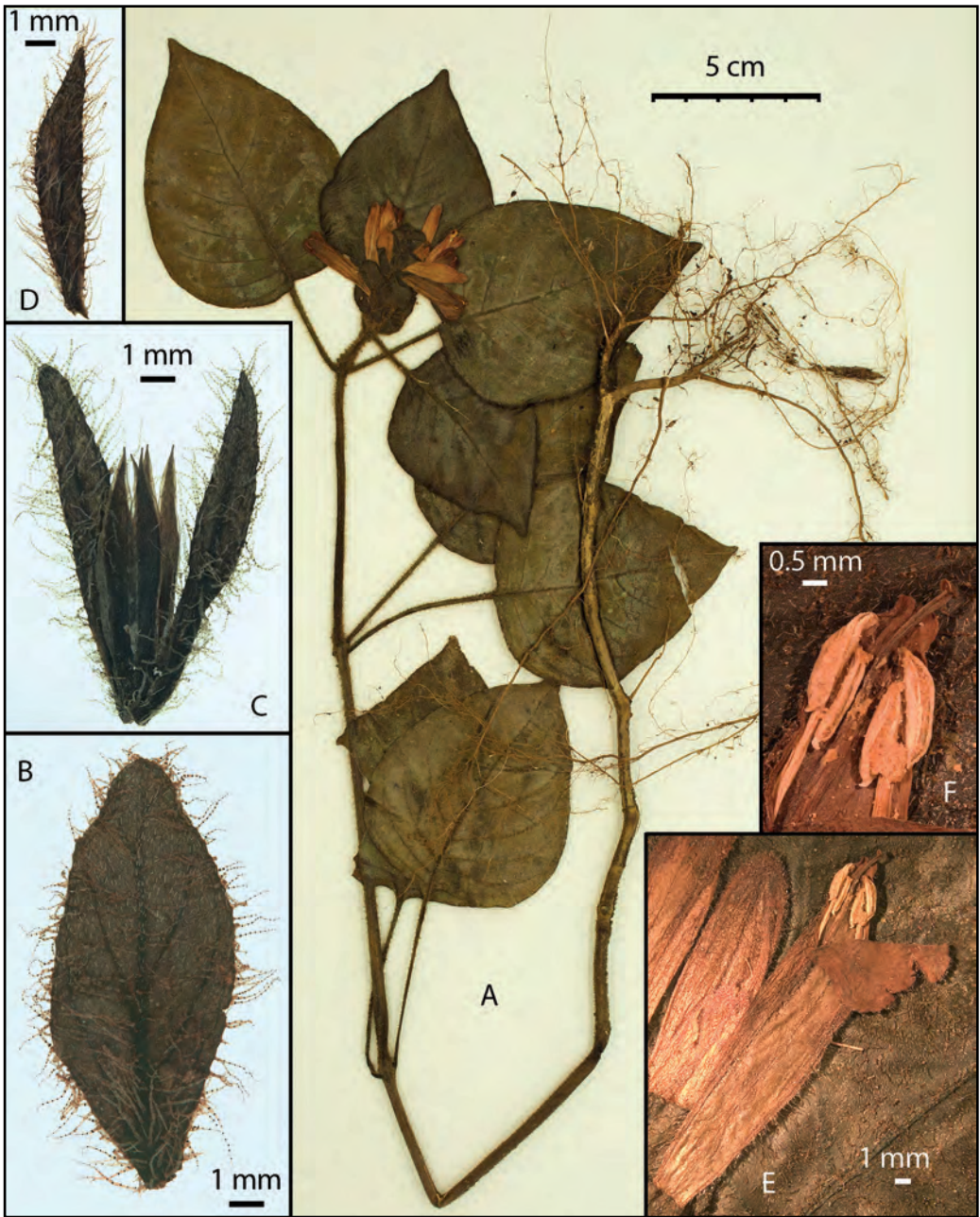


FIGURE 8. *Justicia olmea*. A. Habit (Ventura 14895). B. Bract (Hanan & de Santiago s.n.). C. Bracteoles and calyx (Hanan & de Santiago s.n.). D. Bracteole (Hanan & de Santiago s.n.). E. Flower and buds (Ventura 12178). F. Upper lip of corolla with anthers and upper portion of style with stigma (Ventura 12178).

muri) that are either 1) discrete and more or less evenly distributed over the surface or 2) share common endwalls and are arranged in loops and bands (loops enclosing a band). Pollen of *J. olmeca* shows some slight similarities to *Poikilacanthus* pollen of this second type. Pollen of both *Hanan & de Santiago s.n.* and *Ventura 14895* (Fig. 9) show sculptural variation in curving and fusion of pseudocolpi with 1) the pair in each mesocolpium distinct (Fig. 9b), 2) the pair in each mesocolpium fused toward one pole (i.e., forming pseudocolpal arches in the mesocolpia; Fig. 9a), 3) the pair in each mesocolpium fused toward both poles (i.e., forming pseudocolpal ellipses in the mesocolpia; Fig. 9d), or 4) the pair of pseudocolpi flanking a colporus (i.e., those in adjacent mesocolpia) fused (or nearly fused) toward poles and forming a pseudocolpal ellipse surrounding the colporus + a ring of interapertural exine (Fig. 9c). Molecular phylogenetic analyses that include this species could be potentially informative regarding relationships among clades of *Justicia* and its relatives among *Justicieae* in the New World.

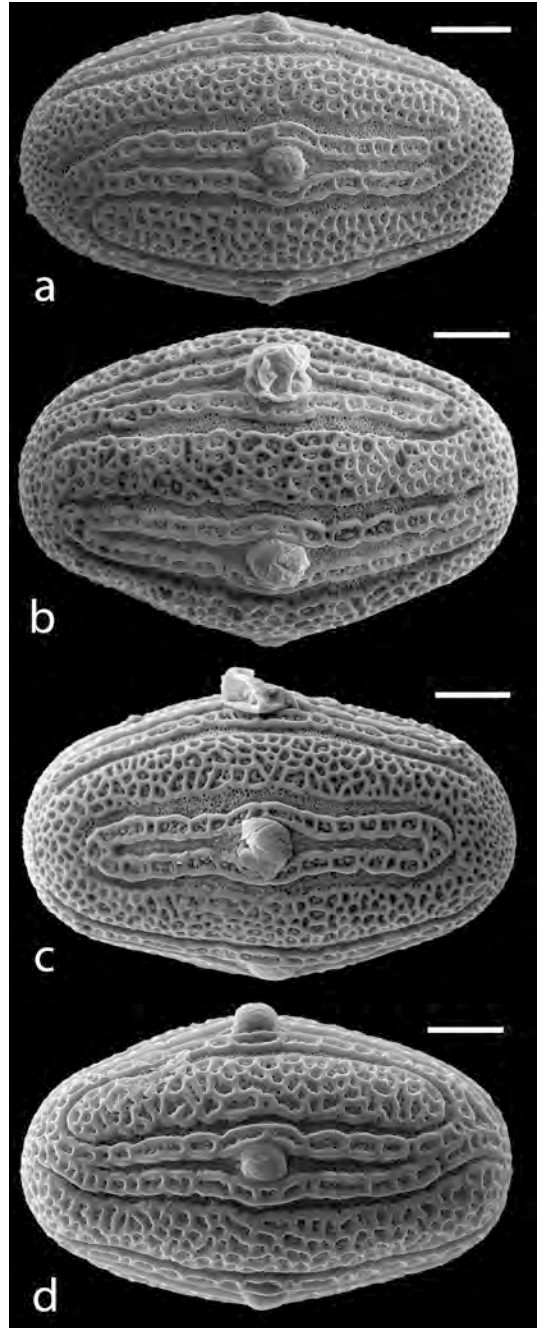


FIGURE 9. Scanning electron micrographs of *Justicia* pollen III. A–C. *Justicia olmeca* (Hanan & de Santiago *s.n.*). A. Apertural view with pseudocolpal arches in mesocolpia. B. Interapertural view with free pseudocolpi. C. Apertural view with pseudocolpi \pm encircling apertural region. D. *Justicia olmeca* (Ventura 14895), apertural view with pseudocolpal ellipses in mesocolpia. Scales = 10 μm .

Justicia totonaca T.F. Daniel, sp. nov.

TYPE.— MEXICO. **Veracruz:** Mpio. Atoyac, Cerro La Perla, 3 km SE de Miraflores, 18°57'N, 096°48'W, selva mediana subperennifolia, suelo kárstico, 900 m, 17-V-1985 (frt), *R. Acevedo R. & R. Acosta P. 109* (holotype: MEXU!; isotypes: IEB-not seen, XAL-not seen). Figures 2, 6, 10.

Shrubs to 2 m tall. Young stems subquadrate, evenly and densely pubescent (i.e., stem surface not clearly visible) with erect to flexuose to retrorse to antrorse eglandular trichomes 0.2–0.8 mm long. Leaves petiolate, petioles 7–41 mm long, blades (ovate-elliptic to) elliptic, 151–265 mm long, 57–130 mm wide, 1.6–2.9 × longer than wide, acuminate at apex, subattenuate to attenuate at base, adaxial surface pubescent with mostly erect to antrorse eglandular trichomes 0.2–1 mm long, abaxial surface and margin similarly pubescent, margin entire, ciliate throughout. Inflorescence of axillary (in axils of distalmost 1–2 pairs of sometimes smaller leaves) and terminal pedunculate dichasiate spikes, these forming a terminal panicle of spikes to 60 mm long (including peduncle but excluding flowers), peduncles of spikes to 20 mm long, pubescent like young stems, rachis pubescent with trichomes like those of young stems but these conspicuously sparser; dichasia opposite (or with some alternate) at nodes, 1 per axil, 1-flowered, sessile. Bracts triangular to ovate to oblong, 1.5–5 mm long, 1–1.3 mm wide (often subfoliose and larger at base of spike, i.e., petiolate, obovate to subcircular, and up to 21 × 12 mm in size), apically acute to subacute, abaxially pubescent like rachis. Bracteoles triangular to subulate, 1.5–2.2 mm long, 0.5–1 mm wide, abaxially pubescent like rachis. Flowers sessile. Calyx 5-lobed, 5–7.5 mm long, lobes homomorphic, lanceolate, 3.5–5.5 mm long, 1–1.5 mm wide, abaxially and marginally pubescent like rachis. Corolla orange, 40–49 mm long, externally pubescent with erect to flexuose eglandular trichomes 0.1–0.4 mm long, tube gradually expanded distally, 31 mm long, 6 mm in diameter (measured flat) at mouth, upper lip 15–17 mm long, 2-fid at apex, lower lip 13 mm long, recoiled, 3-lobed, lobes 1.5–2 mm long, 1–1.6 mm wide, central lobe widest. Stamens ca. 20 mm long, filaments pubescent with eglandular trichomes except glabrous in distal ca. one-fifth), thecae of a pair parallel to subsagittate, subequally inserted, 3.3–3.8 mm long, subequal in length, glabrous, each with a rounded basal appendage 0.1–0.2 mm long. Pollen 2-aperturate with a central pore-like aperture flanked on each side by 2 rows of insulae (and sometimes with peninsulae as well). Style 44 mm long, glabrous throughout; stigma globose to subellipsoid, 0.2–0.3 mm long, Capsule 33–43 mm long, glabrous, stipe 17–21 mm long, head 15–22 mm long. Seeds 7 mm long, 3.5–5 mm wide, surfaces pustulate-roughened, lacking elongate trichomes.

PHENOLOGY.— Flowering: March; fruiting: May–June.

DISTRIBUTION AND HABITATS.— Mexico (west-central Veracruz; Fig. 2); plants occur on montane slopes (sometimes noted as karsted) in “selva mediana subperennifolia” and oak forests at elevations of 600–900 m.

CONSERVATION.— Based on the three known collection sites for this species, the calculated EOO = 2.2 km² (altered to 12 km² because it is less than the AOO), the AOO = 12 km², and the greatest linear extent of its distributional range (E–W) = 19 km. The species does not occur in a protected area. *Ventura 15945* indicated that species was rare at the collection site, whereas *Acevedo R. & Castillo C. 216* indicated that plants were abundant at their site. In spite of the small EOO and AOO, no threats have been identified for this species. Its montane habitats do not appear to have been severely impacted based on Google Earth historical imagery between 2001 and 2019 (Google Earth Pro 2019). A provisional assessment of Least Concern (LC) is proposed for this species based on current knowledge.

ETYMOLOGY.— The specific epithet derives from the name of the indigenous Totonac people of central Veracruz.

PARATYPES.— MEXICO. **Veracruz:** Mpio. Atoyac, La Joya, ca. 1.5 km NW del Rancho de

Santa Rosa, 18°57'N, 096°46'W, *R. Acevedo R. & G. Castillo C. 216* (IEB-not seen, MEXU, MO, XAL-not seen); Mpio. Córdoba, Lagunilla, [18.961389, -96.942222], *F. Ventura 15945* (IEB-not seen, MEXU, XAL-not seen).

DISCUSSION.— Prominent characteristics of *J. totonaca* (Fig. 10) include: dense cauline trichomes, large leaf blades, orange corollas externally pubescent with eglandular trichomes only and with the lower lip recoiled, elongate capsules, and large seeds. This species shares several morphological characteristics with a trio of similar species (each of them sometimes cultivated) that also occur in this general region of Mexico: *J. amplifolia* T.F. Daniel, *J. leonardii* Wassh., and *J. spicigera* Schtdl. All have orange corollas of similar shape and size, with the lower lip recoiled. *Justicia spicigera* is the only species in this group that produces a bluish dye when herbage is placed in water. Pollen of *J. totonaca* (Fig. 6), unlike that of other members of this assemblage, lacks distinct colpi. These species can be distinguished using the following key.

- 1a. Young stems evenly pubescent with trichomes dense (stem surface not clearly visible); calyx 5–7.5 mm long; corolla externally pubescent throughout with eglandular trichomes 0.1–0.4 mm long; anther thecae 3.3–3.8 mm long, both with basal appendages 0.1–0.2 mm long; capsule 33–43 mm long; seeds 7 × 3.5–5 mm; pollen 2-aperturate, but lacking colpi *J. totonaca*
- 1b. Young stems nearly glabrous or evenly to 2-fariously pubescent with trichomes sparse to ± dense (stem surface clearly visible); calyx 2.5–5 mm long; corolla externally glabrous or appearing glabrous but with sparse and inconspicuous glandular (and sometimes eglandular) trichomes up to 0.1 mm long located proximally and/or distally; anther thecae 1.5–3 mm long, lacking basal appendages; capsule 15–21 mm long (unknown in *J. amplifolia*); seeds 2.7–4 × 2.5–3.5 mm (unknown in *J. amplifolia*); pollen 2-colporate 2
- 2a. Leaves sessile or subsessile with petioles up to 2 mm long, blades large (100–340 × 55–146 mm), glabrous (although with inconspicuous punctate glands), broadly attenuate or rounded and ± abruptly constricted at base where sometimes ± auriculate-clasping; external surface of corolla appearing glabrous but sparsely and inconspicuously pubescent with stipitate glands located mostly on the distal portion of the tube and/or limb; pollen 2–brevicolporate *J. amplifolia*
- 2b. Leaves petiolate, petioles 3–24 mm long (if less than 3 mm long as in some *J. leonardii*, then blades shorter than 100 mm and narrower than 55 mm and narrowly attenuate at base), blades usually pubescent with elongate trichomes (at least along major veins), acute to attenuate at base; external surface of corolla glabrous or appearing so but with sparse and inconspicuous stipitate glands usually restricted to proximal portion of tube; pollen 2–colporate (elongate colpi at least evident if not prominent) 3
- 3a. Stems and leaves yielding a bluish dye when placed in water; leaves glabrous or pubescent with trichomes mostly restricted to major veins; bracteoles abaxially glabrous or glandular–punctate; capsules (rarely present) glabrous *J. spicigera*
- 3b. Stems and leaves not yielding a dye when placed in water; leaves (at least abaxially) ± evenly pubescent or the intercostal regions conspicuously pubescent; bracteoles pubescent with eglandular trichomes 0.05–0.5 mm long; capsules pubescent with inconspicuous sessile to subsessile glands < 0.05 mm long
. *J. leonardii*

NEW NAME

Justicia amplifolia T.F. Daniel, nom nov.

Sericographis macrophylla Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 149. 1855, non *Justicia macrophylla* Spreng. (1824, as “1825”). *Jacobinia macrophylla* (Oerst.) Benth. & Hook.f. ex Hemsl., Biol. Cent.-Amer., Bot. 2: 521. 1882. **TYPE.**—MEXICO. **Veracruz:** Sta. María Tlapacoyo, [Tlapacoyan, ca. 19°57'37.67"N, 097°11'24.84"W], V-1841 (flr), *F. Liebmann (Liebm. Pl. Mex. Nr.) 10666* (lectotype, designated here: C!; isolectotypes: CAS!, K!, K ex hb. Hook.!, P!). Figures 3, 5, 11, 12.

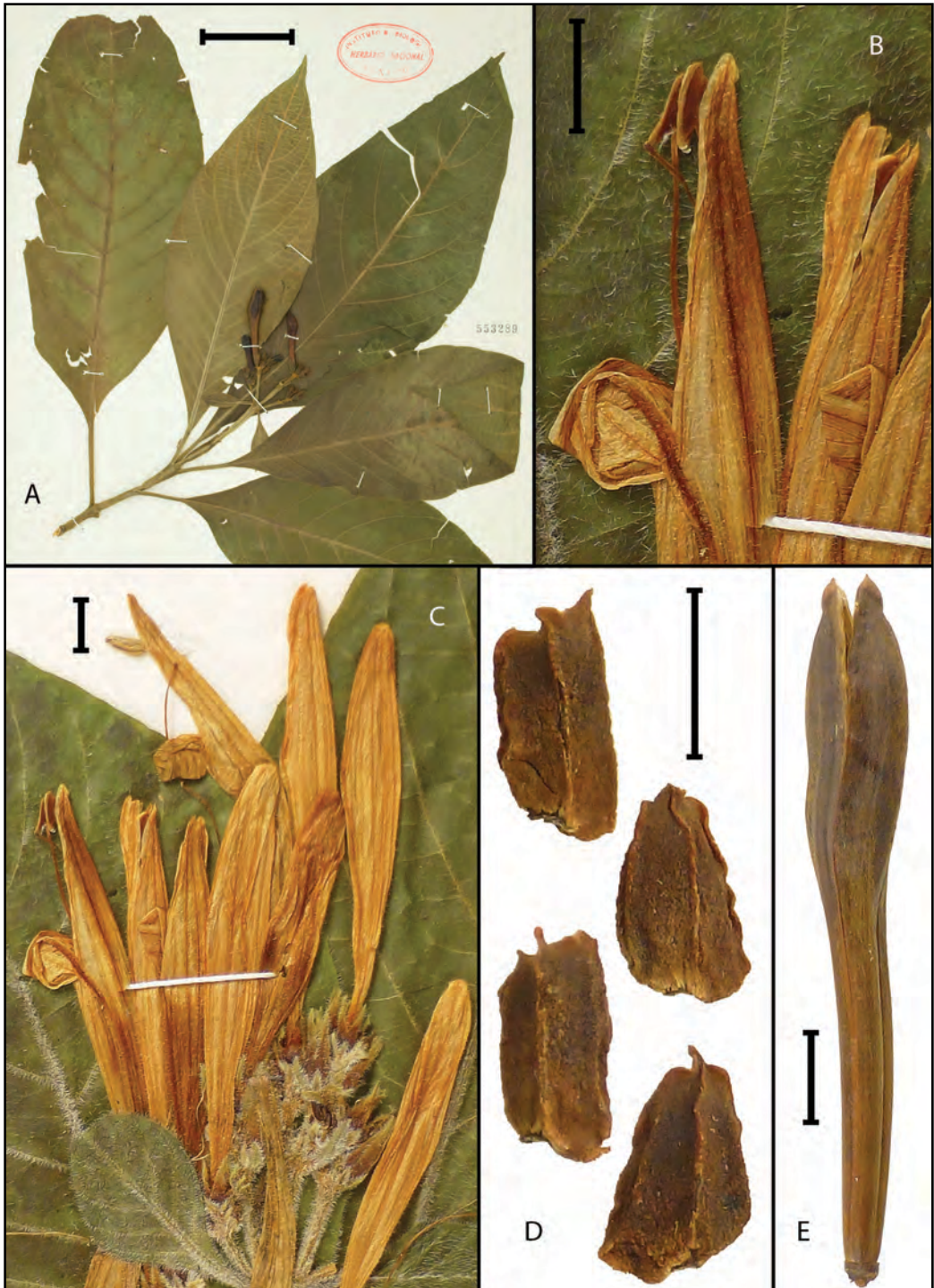


FIGURE 10. *Justicia totonaca*. A. Fruiting branch (holotype). B. Close-up of distal portion of flowers (Ventura 15945). C. Inflorescence (Ventura 15945). D. Seeds (Acevedo R. & Castillo C. 216, MEXU). E. Capsule (Acevedo R. & Castillo C. 216, MO). Scale for A = 5 cm, for B–E = 5 mm.

Erect perennial herbs to shrubs to 2 m tall. Young stems distally quadrate and 2-sulcate, nearly glabrous or 2-fariously pubescent (trichomes sometimes only along a portion of internodes) with flexuose to antrorse eglandular trichomes to 1.8 mm long, proximally quadrate and sometimes glabrate. Leaves sessile to subsessile, naked petiole (if present) to 2 mm long, blades ovate-elliptic to elliptic to broadly elliptic to obovate-elliptic, 100–340 mm long, 55–146 mm wide, 1.4–2.8 × longer than wide, rounded and abruptly acute to apiculate at apex, broadly attenuate or rounded and ± abruptly constricted at base and sometimes ± auriculate-clasping there, adaxial surface glabrous, abaxial surface glabrous, both surfaces minutely and inconspicuously punctate glandular, punctations < 0.05 mm diam. and sometimes drying dark reddish or black, margin entire, proximally ciliate with eglandular trichomes to 1.8 mm long. Inflorescence of axillary (in distal 1–2 pairs of leaves or reduced leaves, 1–2 per axil, opposite at nodes) and/or terminal pedunculate panicles of unilateral dichasiate spikes, these sometimes collectively forming a dense and broad cluster of flowers, peduncles of panicles to 50 mm long, ± glabrous or pubescent like young stems, rachis glabrous; dichasia mostly 1 per node (alternate), 1 per axil, 1-flowered, sessile to subsessile (i.e., with peduncles < 1 mm long). Bracts subtending dichasia opposite to subopposite, homomorphic, broadly triangular, 1–2 mm long, 1–1.2 mm wide, abaxially glabrous. Bracteoles narrowly triangular to broadly triangular, 1–2 mm long, 0.4–0.8 mm wide, abaxially glabrous. Flowers sessile to subsessile (i.e., with pedicels to 0.5 mm long). Calyx 5-lobed, 3–5 mm long, lobes homomorphic, lance-subulate, 2–3 mm long, 0.8–1 mm wide, abaxially and marginally glabrous. Corolla orange, 25–42 mm long, externally glabrous except for very sparse and inconspicuous stipitate glandular trichomes < 0.05 mm long, these located mostly or entirely on the distal portion of the corolla tube and/or limb, tube 14–31 mm long, gradually expanded distally (i.e., no clear distinction between narrow proximal portion and throat), 3.5–4.5 mm diam. (measured flat) at mouth, upper lip 9–18 mm long, apically entire to very shallowly 2-fid, lower lip recoiled, 9–20, lobes 1–1.5 mm long, 1.5–2 mm wide. Stamens 9–19 mm long, filaments glabrous, thecae 2.5–3 mm long, those of a pair sagittate, subequally to unequally inserted (overlapping by up to 2.6 mm), equal to subequal in length, glabrous, lacking basal appendages. Pollen 2-aperturate, apertures consisting of a relatively short colpus (brevicolpate) and a prominent os, flanked on each side by 2–3 rows of insulae (farthest rows from aperture sometimes consisting partially or entirely of peninsulae). Style 20–45 mm long, glabrous; stigma oblong, 0.2–0.4 mm long, unequal and inconspicuously 2-lobed. Capsule not seen (ovary glabrous).

PHENOLOGY.— Flowering: March–June; fruiting: unknown.

DISTRIBUTION AND HABITATS.— Mexico (Puebla and Veracruz; Fig. 5); plants occur in gallery forests and in disturbed areas (e.g., roadsides, cultivated lands) at elevations of 690–977 meters. The species is known in cultivation, and some collections noted below might pertain to remnants or escapes therefrom.

USE.— Planted for living fence (*Amith et al. s.n.*).

CONSERVATION.— Based on the six collections that are potentially from native habitats, the EOO = 3,343 km², the AOO = 20 km², and the greatest linear extent of the distributional range of the species (NW–SE) is 158 km. The lectotype is likely from an area that is now protected, the Parque Estatal Río Filobobos y su Entorno. Threats have not been identified for this species, although some likely exist. Thus, the number of locations is unclear. Given these data, and the likelihood that some of the collections cited represent cultivated or naturalized plants, this species is provisionally assessed as Data Deficient (DD).

ADDITIONAL SPECIMENS EXAMINED.— MEXICO. **Puebla:** Mpio. Cuetzalan, between San Miguel Tzinacapan and Ayotzinapan, en el pueblo de Tecoloapa, 20°02'54.63"N, 097°32'20.72"W, *J. Amith & P. Mendoza 1419* (CAS; MEXU-image only); Mpio. Cuetzalan, San Miguel,

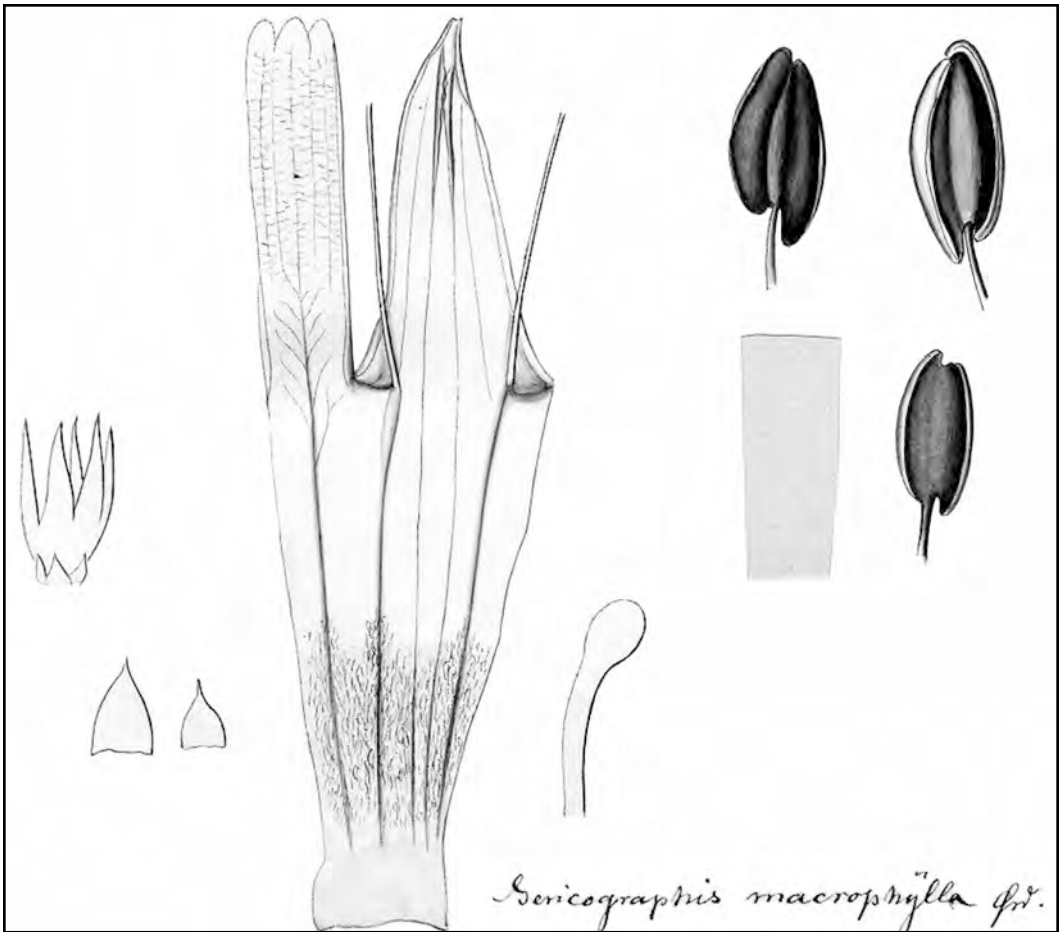


FIGURE 11. *Justicia amplifolia*. Drawing of *Sericographis macrophylla* (presumably by Oersted) at C showing (from left): calyx subtended by a bract and two bracteoles, bract, bracteole, a corolla cut open showing insertion of filaments, apex of style with stigma, and several views of the bithecous anthers. Used with permission of, and copyright reserved to, the herbarium (C) at the Natural History Museum of Denmark.

[ca. 20°01'52.83"N, 097°32'33.91"W], *J. Amith et al. s.n.* in 2015 (CAS); Mpio. Zongozotla, carr. Zongozotla–Cuautempan, en la cascada Tuxpinicin, 19.98164, -97.75716, *C. Ledesma C., O. López F. & A. Sotero H. 21907* (CAS); Mpio. Zihuateutla, Zihuateutla, 40 m de la clínica de Zihuateutla, en la casa de Regina Villegas, 20.25152, -97.88684, *C. Ledesma C. et al. 86044* (CAS). **Veracruz:** Mirador [ca. 19°12'N, 096°52'W], *F. Liebmann (Liebm. Pl. Mex. Nr.) 10667* (syntype: C!). **Cultivation:** Selby Botanical Gardens (ex Gardino Nursery, Delray Beach, Florida), *H. Luther s.n.* in 2006 (CAS), in 2009 (CAS).

DISCUSSION.— A lectotype is designated above from the original material at C, where the first set of Liebmann's collections from Mexico and Central America is deposited, and where Oersted studied them. Oersted (1855) cited two collections of Liebmann from Veracruz, a syntype from Mirador (*Liebmann 10667*) and the lectotype noted above. From the original material, Liebmann's flowering collection with the larger leaves, represented by several duplicate specimens, is chosen as the lectotype. An unpublished illustration at C, bearing Oersted's name for the species in his handwriting, is also likely original material (Fig. 11).



FIGURE 12. *Justicia amplifolia*. Habit (top left), shoot with inflorescence showing large leaves (top right), inflorescence (bottom left), flower from below (bottom right). Photos of cultivated plants taken at Fairchild Tropical Botanical Garden by the author, except photo of flower by J. Amith (used with permission) taken in Puebla.

In 1977 Wasshausen annotated, as *Jacobinia macrophylla*, two Mexican specimens from Veracruz at P that were collected by Hahn in 1866 at Chiquihuite (Cerro del Chiquihuite, ca. 18°56'14"N, 96°46'22"W) and at "Veracruz." Both superficially resemble *J. amplifolia* by their large leaves. However leaves on both collections differ from those of *J. amplifolia* by having petioles much longer than 2 mm and blades pubescent and narrowly attenuate at the base. Additional-

ly, collector's notes on the specimen from Chiquihuite indicate that the corollas were brilliant red. The identity or identities of these two plants will require additional study.

Daniel (1995) included this species in, and annotated specimens of it as, *Justicia spicigera*. Subsequent studies of recent collections and living plants (e.g., at Fairchild Tropical Botanic Garden, Fig. 12) reveal it to be at least as distinct from that species as *J. leonardii*. *Justicia spicigera*, which has human uses (medicine, dye, ornament) and does not often produce fruits, might have been derived from *J. leonardii* by early human cultivation/selection. If so, it is possible that *J. amplifolia*, which has at least ornamental uses, might also be a human-influenced derivative of either *J. spicigera* or *J. leonardii*. All three species are cultivated and share several characteristics, including orangish corollas with the lower lip recoiled. Pollen of *J. amplifolia* is similar to but appears to differ slightly from that of *J. spicigera* and *J. leonardii* by its shorter colpi. Additional distinctions among them are noted in the key above under *J. totonaca*.

NEW DISTRIBUTION RECORDS

Justicia phlebodes Leonard & Gentry

MEXICO. **Nayarit:** along route 28 between Tepic and Jalcacatlan [Nay rte. 66 or Mex. rte. 76 and Jalcocotán on recent maps], between KM 14 and KM 15, [ca. 21°31'47.25"N, 105° 02'0.74"W], ca. 1000 m, 7-I-1979 (flr, frt), *T. Croat 45204* (MO); Tepic, 5-I-6-II 1892 (flr), *E. Palmer 2007* (US).

These two collections from west-central Nayarit are the first records of *J. phlebodes* from the state, extend the distribution of the species ca. 225 km south of its nearest known locale in southern Sinaloa, and closely resemble conspecifics from other regions of northwestern Mexico. Indeed, the 2-aperturate pollen with 2–2.5 rows of insulae (to peninsulae) of *Croat 45204* matches pollen previously noted for the species (Daniel 2004). These collections from Nayarit differ from/augment information in Daniel's (2004) description of plants occurring to the north only in the following minor (and mostly continuous) characteristics: bracteoles up to 7 mm long and down to 0.3 mm wide; corolla ± infundibuliform with the tube slightly expanding ca. 4 mm distal to the base and thence slightly expanded toward the mouth, the upper lip up to 11 mm long, and the lower lip up to 11.5 mm long with lobes up to 5 mm long; and the gap between the two anther thecae down to 0.2 mm long, and the lower theca with a basal appendage down to 0.1 mm long. The species has been reported previously from Chihuahua, Durango, Sonora, and Sinaloa (Daniel 2004).

Justicia pilosella (Nees) Hilsenb.

MEXICO. **Veracruz:** Mpio. Tempoal, 5 km del entronque al Higo dirección alrededores del Ejido San Andrés, 21°49'N, 098°24'W, 20 m, selva baja espinosa, 10-VI-1986 (flr), *C. Gutierrez B. & E. Montoya 1834* (MEXU, XAL).

In addition to its occurrences in the United States (New Mexico, Texas), Daniel (2011) recorded this species from the the following Mexican states: Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas, and Zacatecas. The collection noted above extends the distribution of *J. pilosella* into northwestern Veracruz, ca. 75 km southwest of its known occurrence near Tampico in southern Tamaulipas, and ca. 135 km east of an occurrence in eastern San Luis Potosí.

Justicia spicigera Schltldl.

MEXICO. **Tabasco:** Edo. Puyacatengo, Centro Régional de Chapingo, orilla del río, 60 m, 27-V-1979 (flr), *K. Hormia 174* (US, W).

Justicia spicigera is otherwise known from cultivated collections from Tabasco, but this collection would appear to possibly represent either a native or naturalized occurrence of the species in that state. It is somewhat unusual among conspecifics by the corollas bearing inconspicuous glands not only proximally on the corolla tube, but also distally on the tube and on the lips. The species is widely cultivated in Mexico, where it is presumed to be native. Daniel (1995, 2003) noted likely native occurrences in Chiapas, Oaxaca, and Veracruz.

ACKNOWLEDGMENTS

I thank Jonathan Amith for photographs, specimens, and supporting my fieldwork in Puebla in 2015; Nina Rønsted and Ib Friss at C for allowing access to and permitting use of Oersted's illustration of *Sericographis macrophylla*; Victor Steinman for providing collections; and the herbaria noted above for loans or permitting visits to their collections.

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Atherigonini (Diptera: Muscidae) from Madagascar

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This paper deals with additional material to that of Couri, Pont and Penny (2006) on Madagascan Muscidae and should be used with and regarded as being a supplement to that paper.

KEYWORDS: *Atherigona*, Muscidae, shoot flies, Madagascar, new distribution records, new species.

Deeming (1987) produced a key to the Malgasian species of *Atherigona* Rondani (example of a typical *Atherigona* species, Photo 1), which included the Madagascan species *Atherigona* (*sensu stricto*) *bifurcata* Deeming, *A. bimaculata* Stein, *A. contrastiloba* Deeming, *A. laevigata* (Loew), *A. madagascarensis* Deeming, *A. matilei* Deeming, *A. trapezia* van Emden, *A. ferruginea* van Emden and *A. humeralis* (Wiedemann). Since then the types of the last two species listed here have been



PHOTO 1. Example of a typical *Atherigona* species: *Atherigona basitarsalis* Deeming, 1987. NMW; Male; Det. J. C. Deeming; 'Seychelles: Silhouette, Grande Barbe'; Coll.: J. Gerlac; Date: vi.2001.

examined, resulting in a change of names. To avoid confusion the two species and their synonyms prove to be: (1) *A. bedfordi* van Emden, 1940. Synonym *A. humeralis* (Wiedemann) *sensu* Hennig 1964 *et auctt.*, non Skidmore 1965 *nec* Pont 1986 (see also Pont 1997). (2) *A. humeralis* (Wiedemann) *sensu* Pont 1986 *et* Skidmore 1985, non Hennig 1964 *nec auctt.*, Syn. *ferruginea* van Emden 1940. Since then Dike 1989 has described *A. alaotrana* from Madagascar and Couri, Pont and Penny 2006 have described *A. (s.s.) nigradorsalis*, *A. quadriseta* and *A. variata* as new species and recorded *A. addita* Malloch and *A. (Acritochaeta) orientalis* Schiner, all from Madagascar. In the present paper three new species are described, being *A. clavata*, *A. dikei* and *A. lamina*, and *A. aster* van Emden, *A. basitarsalis* Deeming, *A. erectisetula* Muller, *A. lineata* (Adams), *A. marginifolia* van Emden, *A. naqvii* Steyskal and *A. (Acritochaeta) yorki* Deeming are recorded for the first time from Madagascar. In all cases the identifications are based upon males, but the undescribed females of *A. quadriseta* Couri, Pont and Penny and *A. nigradorsalis* have their diagnostic eighth tergites figured. All other females are returned to the California Academy of Sciences air dried and unmounted and it is hoped that at some time a molecular biologist can use this material to identify the females of the new species *A. dikei* and *A. lamina*.

Species of *Atherigona* (*sensu stricto*) are all phytophagous and develop in the shoots of cereals and grasses, including bamboo. Most notorious of these is the “sorghum shoot fly”, *Atherigona soccata* Rondani. Those of the subgenus *Acritochaeta*, however, prey upon the larvae of other Diptera and Lepidoptera in shoots and stems as well as being found in fruits (e.g., tomatoes) that are infested with fruit fly larvae.

Other species known from the Malgasian Region, but not yet found in Madagascar, are *Atherigona* (*sensu stricto*) *fuscisquama* Deeming, 1978 (Comores); *A. grisea* Malloch, 1923 (Rodriguez); *A. minor* Malloch, 1923 (Rodriguez); *A. soccata* Rondani, 1871 (Mauritius, Réunion) and *A. (Acritochaeta) maculipennis* Stein, 1910 (Seychelles).

**Key to males of Madagascan *Atherigona* spp.
(modified from Couri, Pont and Penny, 2006 to include additional species)**

1. Cercal plate simple. Hypopygial prominence absent — Subgenus *Acritochaeta* Grimshaw 2
— Cercal plate developed into a trident-shaped organ, consisting of three apical lobes on a long stem (in some African species yet more complicated in structure). Hypopygial prominence usually present, but rarely absent. Male palpus always short, clublike, with its oblique apical surface covered in short pale setulae — Subgenus *Atherigona* Rondani 3
2. Palpus elongate, flattened. Fore femur in male only with a dorsoapical excision, which is covered in short forwardly-curved setulae *A. orientalis* Schiner
— Palpus short, club-like, apically obliquely truncate. Fore femur lacking a dorsoapical excision.
. *A. yorki* Deeming
3. Palpus black 4
— Palpus yellow, though it may be black on extreme base 5
4. Fronto-orbital plate shiny black, without trace of dust; wing with brown clouds on humeral crossvein and on wing margin between subcostal and vein R1. Hypopygial prominence knoblike. Tergite 4 with a pair of lateral black bars in addition to the spots and tergite 5 with a strong downwardly-directed seta on each of the dark spots *A. bimaculata* Stein
— Fronto-orbital plate weakly yellowish-grey dusted. Wing hyaline with a trace of brown clouding apically and on posterior crossvein. Hypopygial prominence knob-shaped, wider at apex than at base. Dorsum of abdomen extensively black *A. madagascarensis* Deeming
— Fronto-orbital plate densely dusted. Wing lacking dark markings. Hypopygial prominence bifurcate
. *A. quadriseta* Couri, Pont and Penny
5. Interfrontalia yellow or partially yellow, even if very narrowly so anteriorly 6
— Interfrontalia entirely black 11
6. Trifoliate process of very distinctive form, knob-shaped, the apical surface quadrate, slightly higher than wide, with a central rounded protrusion and four lesser elevations connecting it to the corners. Trifoliate process with hyaline lateral lobe with a brown seam *A. aster* van Emden
— Not so 7
7. Pleura extensively yellow in ground colour 8
— Pleura black, with any yellow ground colour limited to postpronotal lobe and propleuron 10
8. Interfrontalia with upper part suffusedly infusate, without abrupt change of colour. Trifoliate process with median lobe black, in profile broad spindle-shaped and bearing a pair of lanceolate black apical setae, the lateral lobe and area connecting lobes largely yellow *A. marginifolia* van Emden
— Interfrontalia with an abrupt change of colour 9
9. Interfrontalia with the anterior yellow part restricted to a narrow band (in mainland African specimens this is longer). Hypopygial prominence knob-shaped. *A. laevigata* (Loew)
— Interfrontalia yellow on anterior third. Hypopygial prominence bifurcate. Trifoliate process with lateral lobe bearing a blunt inner projection. *A. addita* Malloch
— Interfrontalia yellow throughout. Apex of scutellum a yellow ground colour . *A. humeralis* (Wiedemann)

10. Wing tip narrowly and faintly infuscated; fore tarsus with long erect fine sinuous dorsal hairs, tarsomere 4 anteriorly concave on basal half and convex and with a brush of fine sinuate hairs on apical half. Legs entirely yellow *A. bedfordi* van Emden
 — Wing hyaline throughout. No such specialized tarsal chaetotaxy. Interfrontalia often becoming infuscate in the upper corners lateral to the frontal triangle. Trifoliate process largely hyaline, the median lobe with a pair of long setae. Fore femur black on apical two fifths of length *A. naqvii* Steyskal
11. Hypopygial prominence absent. Trifoliate process clavate in lateral aspect, with base of median lobe very broad *A. clavata* sp. nov.
 — Hypopygial prominence present 12
12. Fronto-orbital plate shiny, undusted. Hypopygial prominence knob-like. Trifoliate process black
 *A. nigridorsalis* Couri, Pont and Penny
 — Fronto-orbital plate dusted 13
13. Fore femur and fore tibia both entirely yellow 14
 — At least fore tibia partially black 15
14. Hypopygial prominence weakly bifurcate, the branches apically rounded. Trifoliate process entirely black, the lateral lobe with a distinct inner projection *A. bifurcata* Deeming
 — Hypopygial prominence knob-shaped, longer below than above, so that its apical surface is inclined at an angle of c. 45°. Lateral lobes of trifoliate process very much inwardly inclined apically, where they are almost touching *A. alaoatrana* Dike
15. Fore femur entirely yellow. Hypopygial prominence bilobed. Trifoliate process with all lobes black, the median lobe at apex medially deeply emarginated, almost as wide as one half of its length, the lateral lobe with a conspicuous inner projection *A. matilei* Deeming
 — Fore femur partially black 16
16. Trifoliate process with lobes black, the lateral lobe having a peculiar oblong hyaline area at mid-length occupying about one quarter of its length. Hypopygial prominence knob-shaped with a narrower stem *A. erectisetula* Muller
 — No such peculiar development 17
17. Trifoliate process with median lobe laterally flattened, bladelike, concave on apical two thirds of its length. Hypopygial prominence knob-shaped, two and a half times as wide preapically as the stem, its apical surface roundedly trapezoid, much wider above than below *A. lamina* sp. nov.
 — Trifoliate process with lateral lobe not compressed and bladelike 18
18. Median lobe of trifoliate process partially or completely white in contrast to the black lateral lobes . . 19
 — Trifoliate process with all lobes black throughout 20
19. Fore femur with apical half black. Entire median lobe of trifoliate process white. Hypopygial prominence bifurcate with apical surfaces of branches truncate, rimmed and slightly upwardly directed
 *A. contrastiloba* Deeming
 — Fore femur with apical two thirds black. Median lobe of trifoliate process only white on its apical half, which is membranous. Hypopygial prominence bifurcate with branches rather pointed
 *A. variata* Couri, Pont and Penny
20. Palpus infuscate. Hypopygial prominence bifurcate *A. lineata* (Adams)
 — Palpus clear yellow 21
21. Fore femur with a weak darker dorsal streak. Median lobe of trifoliate process slightly broadened in lateral view. Tergites extensively infuscate *A. trapezia* van Emden
 — Fore femur with a broad black band on apical half. Trifoliate process with the membrane connecting the lobes large and triangular, hyaline, only its lateral margins black, the point of connection of the median lobe to the stem well basad of the base of this triangle. Hypopygial prominence knoblike, apically emarginate, the apical points being somewhat downwardly directed *A. dikei* sp. nov.

MATERIAL EXAMINED: KNOWN SPECIES

Atherigona (sensu stricto) aster van Emden: Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 2°54.22'S 43°28.53'E, 21-23.viii.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, MA-02-18A-66, CASLOT 020404. 3 Males, HG-18A-74, CASLOT 020401. 1 male. Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 2°54.22'S 43°28.53'E, 21-23.viii.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, MA-02-18A-66, CASLOT 020404. 1 Male.

Described from Zaire and widespread from West to East Africa, this species is new to Madagascar.

A. basitarsalis Deeming: Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 28.iii-8.iv.2003, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, 28.iii-8.iv.2003, MA-02-20-20, CASLOT 020389. 1 Male.

Described from the Seychelles and new to Madagascar.

A. bimaculata Stein: Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 28.i-12.ii.2004, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-53, CASLOT 020385. 5 Males. Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 28.ix-5.x.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise trap in deciduous forest, MA-25-17, CASLOT 020408. 7 Males. 9-20.xi.2003, MA-25-23, CASLOT 020391. 1 Male. Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken bridge, alt. 1110m, 25.v-4.vi.2002, 21°13.57'S 47°22.19'E, R. Harin'Hala, Malaise trap in high altitude rainforest, MA-02-09A-30, CASLOT 020400. 1 Male. 15-22.xii.2001, MA-02-09A-25. CASLOT 020394. 1 Male.

Described from the Seychelles and recorded widely in Africa from South Africa north to Arabia and east to Madagascar and Mauritius.

A. contrastiloba Deeming: Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 2°54.22'S 43°28.53'E, 21-23.viii.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, MA-02-18A-66, CASLOT 020404. 5 Males. Same data but 12-23.xi.2003, HG-18A-74, CASLOT 020401. 11 Males. Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 9-12.xii.2002, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-08, CASLOT 020410. 2 Males. 30.x-9.xi.2003, MA-02-20-44, CASLOT 020406. 3 Males. 15-28.I.2004, MA-02-20-52, CASLOT 020397. 2 Males. 17-24.viii.2003, MA-20-36, CASLOT 020405. 1 Male. 8-18.iii.2003, MA-02-20-18 CASLOT 020407. 5 Males. 28.iii-8.iv.2003, MA-02-20-20, CASLOT 020389. 2 Males. 28.i-12.ii.2004, MA-02-20-53, CASLOT 020385. 2 Males. Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 28.ix-5.x.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise trap in deciduous forest, MA-25-17, CASLOT 020408. 2 Males. MA-25-17, CASLOT 020390. 1 Male. 9-20.xi.2003, MA-2523, CASLOT 020399. 12 males. Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, alt. 1130m, 21°15.05'S 47°24.43'E, 15-21.xii.2001, R. Harin'Hala, Malaise trap in mixed tropical forest. MA-02-09B-07, CASLOT 020398. 1 Male. 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 1 Male.

Described from Madagascar.

A. erectisetula Muller: Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken bridge, alt. 1110m, 25.v-4.vi.2002, 21°13.57'S 47°22.19'E, R. Harin'Hala, Malaise trap in high altitude rainforest, MA-02-09A-30, CASLOT 020400. 1 Male.

Described from South Africa and new to Madagascar.

A. laevigata (Loew): Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, alt. 1130m, 21°15.05'S 47°24.43'E, 15-21.xii.2001, R. Harin'Hala, Malaise trap in mixed tropical forest. MA-02-09B-07, CASLOT 020383. 3 Males. Province Fianarantsoa, Ranomafana, JIRAMA waterworks, 21°14.91'S 47°27.13'E 15-21.xii.2001, alt. 690m, Malaise trap near river, R. Harin'Hala, MA-02-09D-07, CASLOT 020373. 1 Male. Unlike other specimens from Africa all this material has the yellow marking on the front of the frons reduced to a narrow line.

Described from Mozambique and widespread in Africa north to Yemen, Israel and Egypt, this species is recorded also from the Comores and Seychelles Islands and Madagascar.

A. lineata (Adams) nominate ssp.: Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 22°54.22'S 43°28.53'E, 21-23.viii.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, MA-02-18A-66, CASLOT 020404. 1 Male. Tulear Province, Andohahela National Park, Tsimelaha, Parcelle II, 22°44.22'S 43°28.53'E, 21-23.viii.2003, Malaise trap in deciduous dry forest, alt. 30m, M. Irwin, F. Parker, R. Harin'Hala. MA-18A-66, CASLOT 020404. 1 Male. Majunga Ampijotoa National Park, 160km N. of Maeyatanana on RN 04, 16°19.16'S 46°08'E, 26.ix-5.x.2003, Malaise trap in deciduous forest, alt. 43m, R. Harin'Hala, MA-25-17, CASLOT 020408. 1 Male.

Described from "Rhodesia" (which included Zambia and Zimbabwe) and widespread in the Afrotropical Region, extending northwards to the United Arab Emirates and Oman, this species is new to Madagascar.

A. matilei Deeming: Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, alt. 1130m, 21°15.05'S 47°24.43'E, 26-31.iii.2002, R. Harin'Hala, Malaise trap in mixed tropical forest. MA-02-09B-22, CASLOT 020409. 3 Males. These are of a dark form having the yellow markings on the antennae very much reduced.

Described from Kenya, Uganda, Cameroon and Nigeria and further recorded from Angola, Madagascar, and South Africa, further specimens in NMWC are from Botswana and Mauritius. In Kenya it has been reared by Dr. Delobel from shoots of *Panicum maximum*.

A. marginifolia van Emden: Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 29.vi-10.vii.2003, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-31, CASLOT 020372. 1 Male. 6-18.iii.2004, MA-02-20-56, CASLOT 020393. 3 Males.

Described from Uganda and further recorded from Ghana, R.P. Benin, Kenya, Mali, Nigeria, Senegal, South Africa and Tanzania and new to Madagascar.

A. naqvii Steyskal: Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 22°54.22'S 43°28.53'E, 12-23.xi.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, HG-18A-74, CASLOT 020401. Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 9-12.xii.2002, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-08, CASLOT 020410. 2 Males. 17-24.viii.2003, MA-20-36, CASLOT 020405. 7 Males. 28.iii-8.iv.2003, MA-02-20-20, CASLOT 020389. 1 Male. 28.i-12.ii.2004, MA-02-20-53, CASLOT 020385. 1 Male. Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 9-20.xi.-xi.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise trap in deciduous forest. MA-25-23, CASLOT 020399. 1 Male.

Described from Pakistan attacking wheat and barley. First recorded in the Afrotropical Region in 1971 where it was found attacking cultivated millet, this species has become one of the most prolific in Africa since then. It is further recorded from India, Sri Lanka, the Philippines, Australia, the Canary Islands, Ethiopia, United Arab Emirates, Saudi Arabia and South Africa. It was the then undescribed species of which Ramachandra Rao (1924) discovered for the first time

the trifoliate process and described it with a photograph. He referred to it as the “Sind wheat-stem-fly”, with descriptive notes on p. 334 and Plate 33 on p.332. Species new to Madagascar.

A. nigradorsalis Couri, Pont and Penny: Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, 21°15.05'S 474.43'E, 15-21.xii.2001, R. Harin'Hala, Malaise trap in mixed tropical forest, alt. 1130m, MA-02-09B-07, CASLOT 020379. 9 Males, 1 Female. 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 1 Male. Ranomafana National Park, Vohiparara, at broken bridge, 21°18.57'S 4722.19'E, 16.x-8.xi.2001, alt. 1110m, Malaise trap in high altitude rainforest, R. Harin'Hala. MA-02-09A-01, CASLOT 020396. 1 Male. 15-25.vii.2002, MA-02-09A-35, CASLOT 020384. 1 Male. Female: Eighth tergite (Fig. 2) almost identical to that of its sister species *A. trapezia* van Emden (see Deeming 1971:169, fig. 110).

Described from Madagascar.

A. quadriseta Couri, Pont and Penny: Tulear Prov., Mikea Forest, NW of Manombo, alt. 30m., 22°54.22'S 43°28.53'E, 21-23.viii.2003, collector R. Harin'Hala, Malaise trap in deciduous dry forest, MA-02-18A-66, CASLOT 020404. 1 Male. Tulear Prov. Andohahela Nat'l. Park, Tsime-lahy, Parcelle II, 24°56.21'S 46°37.60'E, 9-12.xii.2002, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, 19-26.xi.2002, MA-02-20-05, CASLOT 020388. 1 Male. 15-28.I.2004, MA-02-20-52, CASLOT 020397. 1 Male. Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 28.ix-5.x.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise trap in deciduous forest, MA-25-17, CASLOT 020399. 5 Males. Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, alt.1130m, 21°15.05'S 4724.43'E, 15-21.xii.2001, R. Harin'Hala, Malaise trap in mixed tropical forest. MA-02-09B-07, CASLOT 020383. 25 Males from paratype locality. 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 3 Males. Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken bridge, alt. 1110m, 25.v-4.vi.2002, 21°13.57'S 4722.19'E, R.Harin'Hala, Malaise trap in high altitude rainforest, MA-02-09A-30, CASLOT 020400. 1 Female, here described and figured (Fig. 1). Province Fianarantsoa, Ranomafana, JIRAMA waterworks, 21°14.91'S 4727.13'E 21°14, 15-21.xii.2001, alt. 690m, Malaise trap near river, R. Harin'Hala, MA-02-09D-07, CASLOT 020373. 2 Males.

Described from Madagascar. Female: Resembling male except in abdominal and secondary sexual characters. Fore leg black on all but coxa, trochanter, extreme base of femur and narrowly on knee, the mid and hind tarsi obscurely infuscate. Eighth tergite (fig.1) with the pair of basal separated sclerites hardly sclerotized or visible, the median lobe broad with anterior margin slightly concave.

A. trapezia van Emden: Fianarantsoa Prov., Parc National Ranomafana, Vohipararara, at broken bridge, 21°13.57'S 4722.19'E, Malaise trap in high altitude rainforest, alt. 1110m, 25.v-4.vi.2002, R. Harin'Hala, MA-02-09A-30, CASLOT 020400. 2 Males. Vohiparara, 19-26.ii.2002, MA-02-09A-17, CASLOT 020374. Ranomafana, JIRAMA waterworks, 21°14.91'S 4727.13'E, 15-21.xii.2001, Malaise trap near river, alt. 690m, R. Harin'Hala, MA-02-09D-07, CASLOT 020373. 1 Male. Parc National Ranomafana, radio tower at forest edge, 21°15.05'S 474.43'E, 15-21.xii.2001, Malaise trap in mixed tropical forest, alt. 1130m, R. Harin'Hala, MA-02-09B-07, CASLOT 020379. 14 Males. Parc National Ranomafana, radio tower in mixed tropical forest, 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 2 Males, 1 Female.

Described from Uganda, Kenya and Ethiopia, this species is further recorded from Burundi, Cameroun, Democratic Republic of the Congo, Madagascar, Nigeria, Rwanda, South Africa, Sudan, Tanzania and Zimbabwe.

A. variata Couri, Pont and Penny: Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 28.ix-5.x.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise

trap in deciduous forest, MA-25-23, CASLOT 020399. 2 Males.

Described from Madagascar.

A. (Acritochaeta) orientalis Schiner: Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 19-26.xi.2002, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-05, CASLOT 020388. 1 Male. Parcelle II, 28.i-12.ii.2003, MA-02-20-53, CASLOT 020385. 1 Male. Tulear Province, Mikea Forest, NW of Manombo., 22° 54.22'S 43°28.53'E, Malaise trap in dry deciduous forest, alt. 30m, 27.xi.2001-6.i.2002. R. Harin'Hala. MA-02-18A-08. CASLOT 020402. 1 Male. Majunga Ampijotoa National Park, 160 km N. of Maevatanana on RN 04. alt. 43m. 28.ix-5.x.2003, 16°19.16'S 46°48.80'E, Rin'ha Harin'Hala, Malaise trap in deciduous forest, MA-25-23, CASLOT 020399. 1 Female.

Described from Nicobar Island, this species is found throughout the tropics of the World.

A. yorki Deeming: Tulear Prov. Andohahela Nat'l. Park, Tsimelaha, Parcelle II, 24°56.21'S 46°37.60'E, 9-12.xii.2002, M. Irwin, F. Parker, R. Harin'Hala, alt. 180m. Malaise trap in transitional forest, MA-02-20-08, CASLOT 020410. 1 Male.

Described from Nigeria, Kenya, Senegal, Sierra Leone and Sudan. New to Madagascar.

NEW SPECIES

Atherigona (sensu stricto) clavata sp. nov.

Figures 3–4.

MATERIAL.— **Holotype** Male (dry-mounted with abdomen in a van Doesburg tube of glycerine pinned under specimen; dorsum of thorax rubbed and denuded; hind legs missing), labelled MADAGASCAR: Fianarantsoa Prov., Ranomafana, JIRAMA waterworks, 21°14.31'S 47°27.13'E, alt. 690m, 15-21.xii.2001, Malaise trap near river, R. Harin'Hala, Code MA-02-09D-07, CASLOT 020373, Deposited in the California Academy of Sciences.

DESCRIPTION.— **Colouration:** All setae and setulae black; dusting on dark parts grey; head and antenna black, yellow on face, parafacialia, gena, lower occiput and palpus; thorax black, yellow on postpronotal lobe, proepisternum and extreme fore margin of anepisternum, hind margin of meron, greater ampulla, tegula, basicosta and haltere; wing veins brown, becoming paler towards base; legs yellow but fore leg infuscate on apical three fifths of fore femur except for extreme apex, on apical three fifths of fore tibia and on entire fore tarsus; abdomen yellow in ground colour with a pair of large oval black markings occupying 0.8 times length of tergite 3 and a smaller more rounded pair occupying one third of length of tergite 4; surstylus infuscate on the narrowed apical part and lobes of trifoliate process black, the stem brownish yellow.

Head: Ocellar triangle, fronto-orbits and occiput lightly dusted throughout; ocellar setae long, longer than orbitals and postocellars.

Thorax: Bases of the three katepisternal setae forming an isosceles triangle; two strong proepisternal setae, the more posteriorly-situated the longer; one weaker proepimeral.

Legs: Fore tarsus lacking specialized structure or chaetotaxy.

Wing: Hyaline throughout.

Abdomen: Hypopygial prominence absent; trifoliate process (Fig. 3) clavate in lateral aspect, with base of median lobe very broad, the stem one quarter of the length of the abdomen when macerated; surstylus (Fig. 4) much deeper than is usual.

Length: c.2.4mm, of wing 2.5mm.

Female: unknown.

AFFINITIES.— This species shares with the afrotropical species *Atherigona tetrastigma* Pateron, *A. alticola* Deeming, *A. haplopyga* van Emden, *A. maliensis* Dike and *A. mambillaensis*

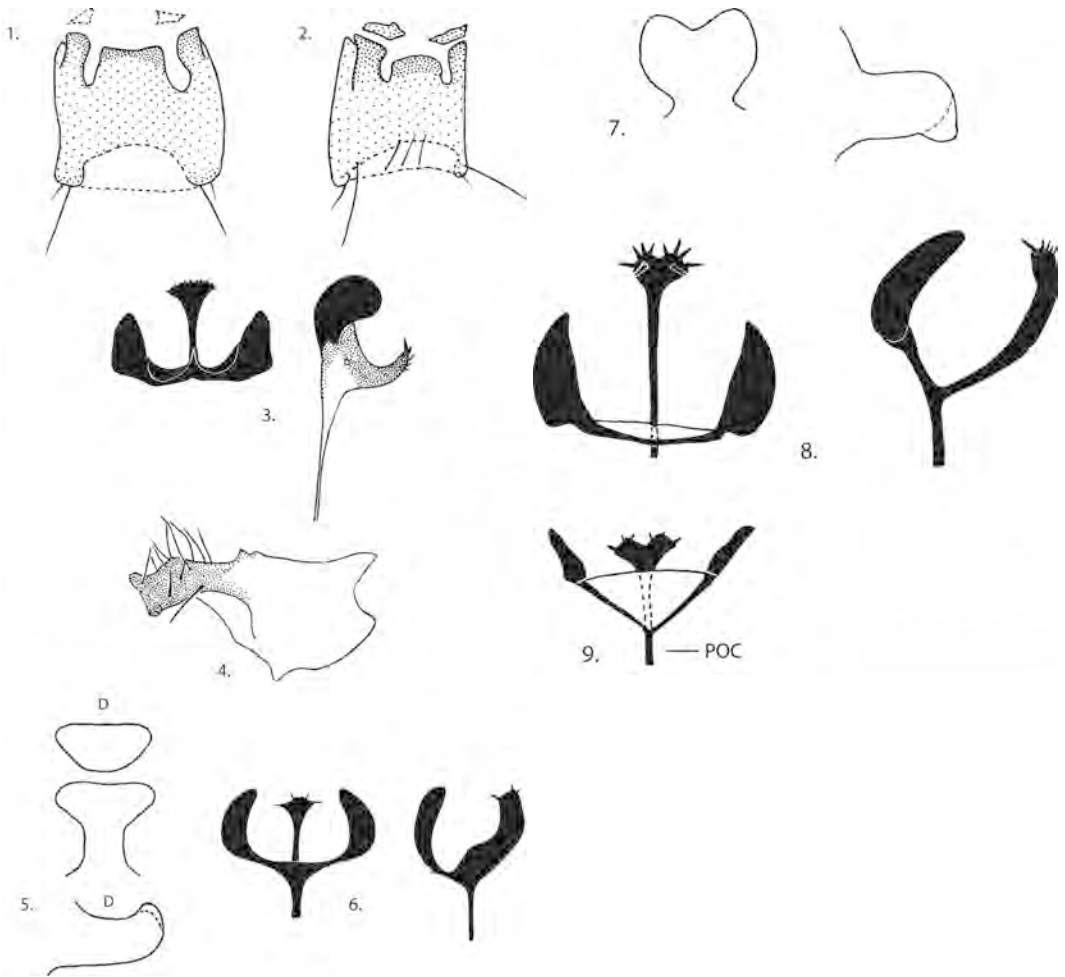


FIGURE 1. *Atherigona quadriseta* Couri, Pont and Penny female 8th tergite.

FIGURE 2. *Atherigona nigradorsalis* Couri, Pont and Penny female 8th tergite.

FIGURE 3. *Atherigona clavata* sp. nov. male trifoliate process from above and in profile.

FIGURE 4. *Atherigona clavata* sp. nov. male surstylus in profile.

FIGURE 5. *Atherigona lamina* sp. nov. male hypopygial prominence apical surface, from above and in profile (D denotes dorsal).

FIGURE 6. *Atherigona lamina* sp. nov. male trifoliate process from above and in profile.

FIGURE 7. *Atherigona dikei* sp. nov. male hypopygial prominence from above and in profile.

FIGURE 8. *Atherigona dikei* sp. nov. male trifoliate process from above and in profile.

FIGURE 9. *Atherigona dikei* sp. nov. male trifoliate process to show point of connection (POC) of median lobe to stem (semi-diagrammatic)

Deeming the lack of a hypopygial prominence, but differs from all of them in the peculiar structure of the trifoliate process, which is similar in structure to that of *A. latibasilaris* Muller, 2015 from South Africa (KwaZulu-Natal), but that species has a bifurcate hypopygial prominence and yellow interfrontalia.

ETYMOLOGY.— The Latin specific name describes the trifoliate process, which in profile resembles a club.

Atherigona (s.s.) dikei sp. nov.

Figures 7–9.

MATERIAL.— HOLOTYPE: Male (dry-mounted and in good condition) labelled MADAGASCAR: Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge. 21°15.05'S 47°04.43'E, alt. 1130m, Malaise trap in mixed tropical forest, 15-21.xii.2001, R. Harin'Hala, Code MA-02-09B-07, CASLOT 020383. Deposited in the California Academy of Sciences. PARATYPES: Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge, alt. 1130m, 21°15.05'S 47°04.43'E, 15-21.xii.2001, R. Harin'Hala, Malaise trap in mixed tropical forest. MA-02-09B-07, CASLOT 020383. 42 Males. 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 10 Males. Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken bridge, alt. 1110m, 25.v.-4.vi.2002, 21°13.57'S 47°22.19'E, R. Harin'Hala, Malaise trap in high altitude rainforest, MA-02-09A-30, CASLOT 020400. 3 Males. 15-25.vii.2002, 21°13.57'S 47°22.19'E, MA-02-09A-35 CASLOT 020385. 2 Males. Province Fianarantsoa, Parc Nat. Ranomafana, Belle Vue at Talatakeley, 1020m, 21°15.99'S 47°25.21'E, 26.ii-4.iii.2002, R. Harin'Hala, Malaise trap in secondary tropical forest MA-02-09C18, CASLOT 020376. 1 Male.

Fifteen paratypes in National Museum of Wales.

DESCRIPTION.— **Colouration:** All setae and setulae black; dusting on dark parts grey; head and antenna black, yellow on face, parafacialia, gena and palpus; thorax black, yellow on postpronotal lobe and proepisternum; scutum with three barely perceptible darker longitudinal lines, these being medially and on dorsocentral lines; legs yellow, fore femur infuscate on a preapical band occupying one third of its length, the knee narrowly yellow, the tibia and tarsus infuscate throughout; wing hyaline with brown veins becoming yellow at base and with squamae pale yellow; haltere yellow.

Head: Fronto-facial angle more acute than a right angle, parafacialia at point of insertion of antenna four times as wide as at narrowest point.

Thorax: Two proepisternal setae, of which the lower is only two thirds of the length of the upper and much weaker, the two prostigmatics much shorter and weaker than these. The lower-situated of the three katapisternal setae very much the weaker and situated much closer to the more posterior of the two upper setae.

Legs: Fore tarsus lacking specialized structure or chaetotaxy.

Wing: Not unusual in any way.

Abdomen: Not unusual in any way. Hypopygial prominence (Fig. 7) weakly bifurcate in dorsal aspect, in profile the two lobes somewhat pointing downwards. Trifoliate process (Figs. 8–9) black with the membrane separating the lateral lobes pale grey, large and triangular, so that the base of the median lobe is situated very much below the bases of the lateral lobes, the lateral lobes on their inner surfaces bearing a lattice-shaped paler pattern and sparse fine pruinosity, on their outer surfaces bearing a stronger, but not longer, compact pruinosity.

Length: c.3.0mm, of wing 3.0mm.

Female: unknown.

AFFINITIES.— In Dike's 1989 key this species would trace to *A. angustiloba* van Emden, but differs from it in that the hypopygial prominence is weakly bifurcate, rather than roundedly truncate, and the trifoliate process has the peculiar interval of space between the insertion of the medial and lateral lobes, which *A. angustiloba* has not.

ETYMOLOGY.— This species is dedicated to the memory of my late friend and colleague Prof. Michael C. Dike of the Institute for Agricultural Research, Samaru of the Ahmadu Bello University, Nigeria. A fellow shootfly enthusiast who described a number of species of *Atherigona*, he was tragically killed in a traffic accident in 2015.

Atherigona (s.s.) lamina sp. nov.

Figures 5–6; Photo 2.

MATERIAL.— **HOLOTYPE:** Male (dry-mounted and in good condition) labelled MADAGASCAR: Fianarantsoa, Parc National Ranomafana, Vohipara, at broken bridge, 21°13.57'S 4722.19'E, alt. 1110m, 25.v.-4.vi.2002, Malaise trap in high altitude rainforest, R. Harin'Hala, Code MA-02-09A-30, CASLOT 020400. Deposited in the California Academy of Sciences. **PARATYPES:** Fianarantsoa Prov., Parc National Ranomafana, radio tower at forest edge 21°15.05'S 474.43'E, alt. 1130m, 15-21.xii.2001, Malaise trap in mixed tropical forest, R. Harin'Hala, MA-02-09B-07, CASLOT 020383. 48 males. 26-31.iii.2002, MA-02-09B-22, CASLOT 020409. 6 Males. Fianarantsoa Prov., Parc National Ranomafana, Vohipara, at broken bridge, 21° 13.57'S 4722.19'E, alt. 1110m, 25.v.-4.vi.2002, Malaise trap in high altitude rainforest, R. Harin'Hala, MA-02-09A-30, CASLOT 020400.1 Male. 16.x-8.xi.2001, MA-02-09A-01, CASLOT 020396. 2 Males. 19-26.ii.2002, MA-02-09A-17, CASLOT 020374. 1 Male. Parc National Ranomafana. Belle Vue at Talatakely, 21° 15.99'S 4725.21'E, alt. 1020m, 26.ii-4.iii.2002, Malaise trap in secondary tropical forest, R. Harin'Hala. MA-02-09C-18, CASLOT 020376. 3 males. Tulear Prov., Andohahela Nat'l. Park, Tsimelahy, Parcelle II, 24°6.21'S 4637.60'E, alt. 180m, 28.i-12.ii.2004, Malaise trap in transitional forest, M. Irwin, F. Parker and R. Harin'Hala, MA-02-09C-18, CASLOT 020376. 3 Males. 15-28.i.2004, MA-02-20-52, CASLOT 020397. 2 Males. In California Academy of Sciences with some paratypes in National Museum of Wales.

DESCRIPTION.— **Colouration:** All setae and setulae black. Head, inclusive of antenna, black, yellow on inferior orbits, face, parafacialia, gena, palpus and suffusedly on lower occiput, the black parts greyish dusted, appearing deeper black on median third of occiput, the yellow parts yellow dusted. Thorax black, yellow on postpronotal lobe, prosternum, and anterior one third of anepisternum, the scutum and scutellum grey dusted, the former with faintly visible darker medial and dorsocentral vittae; pleura yellow on prosternum and anterior one third of anepisternum and with darker parts yellowish grey dusted. Legs, including coxae yellow, the fore leg infuscate on apical two thirds of length of tibia and on tarsus. Wing hyaline with yellowish brown veins, the base up to basicosta clear yellow; squamae pale with yellow margins; haltere white with a yellow stem. Abdomen yellow, tergite 3 with a pair of long rectangular black markings occupying all but its apex; tergite 4 with a pairs of oval; black spots occupying one half of its length; trifoliate process black throughout.



PHOTO 2. *Atherigona lamina* sp. nov. NMW: Paratype; Male; Desig. J C. Deeming; 'Madagascar: Fianarantsoa Prov., Ranomafana Nat. park, Belle Vue at Talatakely'; 1020m; Coll.: R. Harin 'Hala; Date: 26.ii-4.iii. 2002; Malaise trap

Head: Fronto-facial angle slightly more than a right angle; parafacialia at narrowest part linear, no wider than the vibrissa.

Thorax: Proepisternum with two strong setae, one twice the length of the other; two very short and weak proepimeral setulae; katepisternum with the three large setae forming an isosceles triangle, the lower seta situated equidistant to the two upper setae.

Legs: Fore tarsus lacking specialized structure or chaetotaxy.

Wing: Not unusual in any way.

Abdomen: Hypopygial prominence (Fig. 5) consisting of a broad truncate apex that is roundly trapezoid in shape, which in dorsal aspect is nearly three times as broad as the stem and which in profile extending dorsally above the stem. Trifoliate process (Fig. 6) with lateral lobes somewhat incurved apically, in profile the medial lobe seen as broad, especially so at base, and bearing a few short apical setae.

Length: c.2.3mm, of wing 2.2mm.

Female: Unknown.

ETYMOLOGY.— The name is derived from the Latin *lamina*, a sword blade.

AFFINITIES.— This species would trace to *A. longifolia* van Emden in Dike's 1989 key, differing from it in the structure of the hypopygial prominence and trifoliate process. In *A. longifolia* the hypopygial prominence is truncate knob-shaped and is scarcely wider at apex than it is at base. Also the lobes of the trifoliate process are all long and slender, the median lobe being boomerang-shaped when viewed in profile. The trifoliate process of *A. lamina* has a similar appearance to that of another Madagascan species, *A. alaotrana* Dike, the lateral lobes converging towards their apices, but that species has the median lobe in profile almost straight, the hypopygial prominence is a simple knob, extending longer ventrally than dorsally, so that the apical surface is of an inclination of about 45° (see Dike 1989:547, figs. 1 and 2) and its fore leg black only on tarsus.

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Record of the Long-horned Beetle, *Derobrachus hovorei* Santos-Silva, 2007: (Coleoptera: Cerambycidae), being Accidentally Transported to Ohio, USA

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Hovore's long-horned beetle, *Derobrachus hovorei* (Coleoptera: Cerambycidae), is a large species native to the southwestern United States and northern México. On 30 June 2017, one adult male *D. hovorei* was collected inside an office building in Dayton, Ohio, having been transported in baggage on a commercial aircraft from Scottsdale (Phoenix), Arizona to Ohio on the previous day (29 June). This is the first report of this species outside of its native range in the United States and México and demonstrates how insects can be transported accidentally over great distances via modern transportation.

El longicornio de Hovore, *Derobrachus hovorei* (Coleoptera: Cerambycidae), es una gran especie nativa del suroeste de los Estados Unidos y el norte México. En el 30 de junio 2017, un adulto masculino de *D. hovorei* fue recogido dentro de un edificio de oficinas en la ciudad de Dayton en el estado de Ohio. El longicornio fue transportado en el equipaje en un avión comercial de la ciudad Scottsdale (Phoenix) en el estado de Arizona al estado de Ohio en el día anterior (el 29 de junio). Este es el primero informe de esta especie de la región más allá de la extensión nativa en los Estados Unidos y México y también demuestra cómo los insectos pueden transportarse accidentalmente a distancias largas por los transportes modernos.

KEYWORDS: long-horned beetle, geographic distribution, accidental transport.

Many terrestrial and aquatic invertebrates and vertebrates have been transported, both accidentally and purposefully, to areas outside of their natural distribution. Species of beetles, spiders, crustaceans, reptiles, and amphibians, among others, have been moved great distances for hundreds of years primarily on ships capable of crossing seas and oceans. More recently, because of increased and more rapid international trade of goods, human travel, and the pet trade, importations of nonnative species has increased dramatically (Allen 1928; Kauffeld 1932; Lanteri and Marvaldi 1995; McLaughlin et al. 2005; Lingafelter and Nearn 2006; Liebhold et al. 2006; McCullough et al. 2006; Beatty et al. 2008; Krysko et al. 2011; Rochford et al. 2015). The United States has approximately 50,000 introduced species of plants and animals (Pimentel et al. 2000; Pimentel et al. 2005), many of which require control measures to reduce their negative ecological and economic impacts. Nonnative species of plants and animals cause numerous problems, and the cost of damages and control measures was estimated to be about 120 billion dollars or more per year in the United States alone, which is likely an underestimate (Pimentel et al. 2000; Pimentel et al. 2005). Insects in particular can become serious pests of agricultural or ornamental plants and forest trees (Young et al. 1950; Herms and McCullough 2014; Haack et al. 2015). The white-

fringed beetle, *Naupactus leucoloma* Boheman, 1840 (Curculionidae), has both sexual and parthenogenetic populations and has been introduced to several continents, including North America, outside of its native range in South America (Lanteri and Marvaldi 1995; Voss and Poly 2002; Guzmán et al. 2012). The emerald ash borer, *Agrilus paniplennis* Fairmaire, 1888 (Buprestidae) is a far-eastern Asian beetle species introduced into North America; its infestations of ash trees have decimated populations of several ash tree species (Haack et al. 2002; Haack 2006; Herms and McCullough 2014; Haack et al. 2015; WJP, pers. obs.). Some introductions are interstate movements (the case herein), whereas others are intercontinental (Lanteri and Marvaldi 1995; Lingafelter and Nearn 2006; Guzmán et al. 2012). Nonnative species introduced into a new area sometimes exist in low numbers for years, then rapidly expand, whereas others experience rapid population expansion. In some cases however, established populations of nonnative species decline and even become extirpated (Simberloff and Gibbons 2004).

The taxonomy of the cerambycid genus *Derobrachus* has been revised and updated during the past decade, resulting in the recognition of 21 valid species in the genus (Santos-Silva 2007; Heffern and Santos-Silva 2016; Santos-Silva et al. 2018). Herein, the accidental transport of a large cerambycid beetle, *Derobrachus hovorei* Santos-Silva, 2007 from Arizona to Ohio is documented.

MATERIALS AND METHODS

The beetle was collected alive inside an office building in Dayton, Ohio, Montgomery Co., Ohio (Lat./Long.: 39.759756°N / -84.180624°W) on 30 June 2017 by William J. Poly; it was photographed, kept alive for several days in captivity, then was frozen until 29 July 2018 when it was preserved in 95% EtOH. The beetle was identified using Santos-Silva (2007) and subsequent descriptions of new species of *Derobrachus* (Heffern and Santos-Silva, 2016; Santos-Silva et al., 2018). The specimen was deposited in the Entomology collection of the California Academy of Sciences, San Francisco, CA (CAS ENT 8277806 (n = 1 male, 52.4 mm TL)).

RESULTS AND DISCUSSION

After returning on a roundtrip flight from Dayton, Ohio (origin) to Scottsdale (Phoenix), Arizona (26–29 June 2017), the traveler was startled to find a large insect inside her shoulderbag on the following day (30 June) and notified the author of its presence. Presumably it had entered the bag at the hotel or at some point in transit in Scottsdale, Arizona. The beetle was collected and identified on 30 June 2017 as a long-horned beetle, *Derobrachus* sp. Later it was identified further as a male *Derobrachus hovorei* based on possession of the following characters listed in the key of Santos-Silva (2007) (see Fig. 1): 1) scutellum glabrous, 2) internal lateral face of protibiae with longitudinal furrow, 3) antennomere III distinctly thickened and expanded apically; urosternite V equal to IV, apex broad and semicircularly emarginated; urosternite VI exposed, 4) antennomere III robust, thickened apically, apical width equal to or greater than one-third of segment length ($W 2.2 / L 6.2 = 0.35$), and 5) pronotal disc not rugose, glabrous, antennae not attaining elytral apex, and 6) antennomere III distinctly coarsely granulate on lateral and/or ventral face (in this specimen on about basal 2/3, not apically); pilosity of metasternum relatively long and very abundant; lobes of metatarsomere III with an apical spine (spine sometimes lacking, but the lobes are uniformly acuminate from apical third or fourth). Sutural apex of each elytra with a small, distinct spine (also possessed by other species of *Derobrachus*).

Until the recent revision of *Derobrachus*, *D. hovorei* had been included within *D. geminatus* LeConte, 1853, and *D. geminatus* and *D. leechi* Chemsak and Linsley, 1977 have overlapping distributions with *D. hovorei* (LeConte, 1853; Chemsak and Linsley 1977; Santos-Silva 2007).

The distribution of *D. hovorei* includes five states in the United States (Nevada, California, Arizona, New Mexico, Texas) and five states in México (Sonora, Chihuahua, Coahuila de Zaragoza, Durango, Nuevo Leon) (Santos-Silva 2007). Now there is one verified record of this species being transported to Ohio accidentally on a commercial aircraft. The closest record of a species of *Derobrachus* to Ohio is that in Klingeman et al. (2017), which included a single record of *D. brevicollis* Audinet-Serville, 1832 from Coffee Co., south-central Tennessee. There weren't any other collection data associated with that record; however, *D. brevicollis* is known from North Carolina, South Carolina, Alabama, Georgia, and Florida (Santos-Silva 2007) and Tennessee (Klingeman et al. 2017).

Haack (2002) reported interceptions of insects by the United States Department of Agriculture, Animal and Plant Health Inspection Service (APHIS) on shipments entering the United States from 1985 to 2000; there were 1,649 interceptions of cerambycid beetles, including 81 genera. During the period 1985 to 2000, there were 422 interceptions of wood-associated insects in Ohio (Haack 2006). Eyre and Haack (2017) summarized information on the various pathways by which cerambycid beetles get transported to new locations.

The numerous interception records for cerambycids associated with wood products or packaging brought into the United States from 1984 through 2008 ($n = 3,483$) and identified to species ($n = 677$) included one occurrence for *D. geminatus* originating from México (Eyre and Haack 2017). It is suggested here that the species identity *D. geminatus* might require confirmation considering recent updates to the taxonomy of *Derobrachus* spp. (Santos-Silva 2007; Heffern and Santos-Silva 2016; Santos-Silva et al. 2018). Another known case of a large cerambycid beetle having been transported a great distance was the collection of a then-new species, *Phoenicus sanguinipennis* Lacordaire, 1869, taken from a shipment of dyewood carried from the Caribbean to Poland on a ship (Lingafelter and Nearns 2006). The accidental transport of pest insects via passenger baggage and cargo has been treated in detail by other authors recently (Liebhold et al. 2006; McCullough et al. 2006; Meurisse et al. 2019) and typically involves live plants or fruits harboring the pest insects. There have been relatively high numbers of detections made by APHIS, but as only about 2% of cargo gets checked (Haack 2002; McCullough et al. 2006), the number of known detections must be much lower than actual occurrences (Haack, 2006), and cases such as the one documented herein must occur more frequently and go unnoticed or undocumented, with insects either being detected by the traveler and being killed or discarded, evading detection and escaping at its destination, or dying naturally (desiccation, starvation).



FIGURE 1. Dorsal view of *Derobrachus hovorei* Santos-Silva, 2007 (male, 52.4 mm TL) (CAS ENT 8277806).

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The Pennatulacean Genus *Protoptilum*, with the Description of a New Deep-Sea Species from the Continental Slope of Central California (Octocorallia, Pennatulacea, Protoptilidae)

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The Farallones Oceanic Research Expedition (FORE) was carried out by the Moss Landing Marine Laboratories in the early 1990's under the direction of Dr. James W. Nybakken. The Expedition yielded a wealth of benthic invertebrate material, which was collected by beam trawl on board the R/V *Point Sur* within the U.S. Navy Chemical Munitions Dumping Area. The California Academy of Sciences was the repository for many of the collected invertebrates. The material was subsequently curated and incorporated into the collections of the Department of Invertebrate Zoology and Geology. At present, at least six species of *Protoptilum* are recognized as valid and are distributed in the Indo-West Pacific and North Atlantic Oceans. The new species described herein, *Protoptilum nybakkeni*, sp. nov., is distinguished by possessing 2–4 short calyx teeth and the calyxes are strongly appressed to the sides of the rachis; it also documents the extension of the range of the genus to the Eastern Pacific and increases to seven the number of species in the genus currently recognized as valid.

KEYWORDS: *Protoptilum*, deep-sea pennatulaceans, sea pens, new species, Eastern Pacific, west coast of North America, key to species of the genus.

Protoptilum Kölliker, 1872, is a deep-sea pennatulacean genus of at least six described species currently known from the Atlantic and Indo-Pacific (Table 1; Cordeiro et al. 2019), with a known depth distribution of 250–4000 m (Williams 1995:114; m 2011: 6). Pennatulaceans have been characterized as a morphologically distinct and specialized group octocoral cnidarians (Williams 1990:34, 1995: 3, 2011:2). As a group, pennatulaceans produce a calcitic central axis that has been associated with deep-water habitats as far back in geological time as the Late Cretaceous (Voigt 1958; Murray Roberts et al. 2009). Morphologically, the pennatulacean axis shows a remarkable similarity in structural characteristics with the axis of ellisellid gorgonians (Bayer 1956:224). In addition, a close affinity between ellisellids and pennatulaceans based on molecular evidence was subsequently established as well (McFadden et al. 2006:517–521). The genus *Protoptilum* has previously been reported from the Oregon Province (Vancouver Island, British Columbia to Point Conception, California; 150–3306 m in depth) as *Protoptilum* sp., based on three institutional database records (California Academy of Sciences, NOAA National Database of Deep-Sea Corals and Sponges, and Monterey Bay Aquarium Research Institute) (Whitmire et al. 2017), but further details have not been published up until now.

Since 2012, exploration by remotely operated vehicles of the mesophotic and deep-sea region to the west of the San Francisco Bay Area and in or around three local National Marine Sanctuaries – Cordell Bank, Greater Farallones, and Monterey Bay – has resulted in new biodiversity discoveries. This endeavor has resulted in the acquisition of collected material for the description of new species, as well as the establishment of a new genus name for a previously described binomen that was incorrectly allocated to a different genus (Williams and Breedy 2016, 2019; Williams, 2013).

HISTORICAL ASSESSMENT OF THE TYPE LOCALITY

Chemical Munitions and Radioactive Waste Dumpsites.— In July of 1991, the Farallones Oceanic Research Expedition (FORE) – under the auspices of Moss Landing Marine Laboratories – took place to document benthic invertebrate diversity in an impacted region east of the Farallon Islands. This is an area of overlap between the former Chemical Munitions Dumpsite (Naval Ocean Dump Site) and the Farallon Islands Radioactive Waste Dump (FIRWD). In 1946, the FIRWD was designated by the Atomic Energy Commission as a disposal site for the dumping of numerous canisters containing low-level radioactive wastes (Chin and Ota 2001). The overlap area is the type locality for the new species of *Protoptilum* that was collected by trawling operations during FORE, and is also in close proximity to the southern boundaries of both Cordell Bank NMS and Greater Farallones NMS (Fig. 1).

The National Marine Sanctuary system and the National Marine Sanctuaries of central California.— There has been a history of substantial anthropogenic impacts in the benthic region to the west of the San Francisco Bay Area and the Farallon Islands. Included here are the dumping of dredged sediment from SF Bay due to Gold Rush era hydraulic mining in the foothills of the Sierra Nevada, dumping of chemical and radioactive waste material by the US government, the sinking of the aircraft carrier USS Independence in 1951 after it was severely damaged during atomic testing at Bikini Atoll, destructive trawling practices, overfishing, industrial pollution and agricultural runoff from nearby urban areas of the Bay Area, etc.

The San Francisco Bay Area and the area around the Farallon Islands have a long history of maritime industry and military history. Maritime trade in the region includes rapidly expanded maritime activity since the beginning of the California Gold Rush in 1849, the subsequent emergence as the center of Pacific Rim trade, commercial fishing in San Francisco Bay for rich resources of fish and shellfish, and the world's largest canning operations from 1899 to 1937, as well as significant military activity. Although fishing activity contributed to the economy and national security, it also has had historic impacts to the ocean environment in the form of shipwrecks, scuttled vessels, munitions and radioactive waste dumps, and fishing gear impacts to the seafloor. Regarding military activity, the Presidio, at the mouth of San Francisco Bay, functioned as a military reservation from 1776–1994, serving colonial Spain, Mexico, and the United States, including the Spanish-American War, and World Wars I and II.

The environmental movement in the United States in the 1960s and 1970s led to the passage of a several federal environmental protection laws. In 1972, the United States Congress passed legislation that led to the establishment of the National Marine Sanctuary Program (later renamed the Office of National Marine Sanctuaries, ONMS). The National Marine Sanctuary Program was established under the National Oceanic and Atmospheric Administration (NOAA) to protect areas of the marine environment with special national significance due to their conservation, recreational, ecological, historical, scientific, cultural, archeological, educational or esthetic qualities as national marine sanctuaries. In the 1970's, NOAA began a process to study and designate areas as

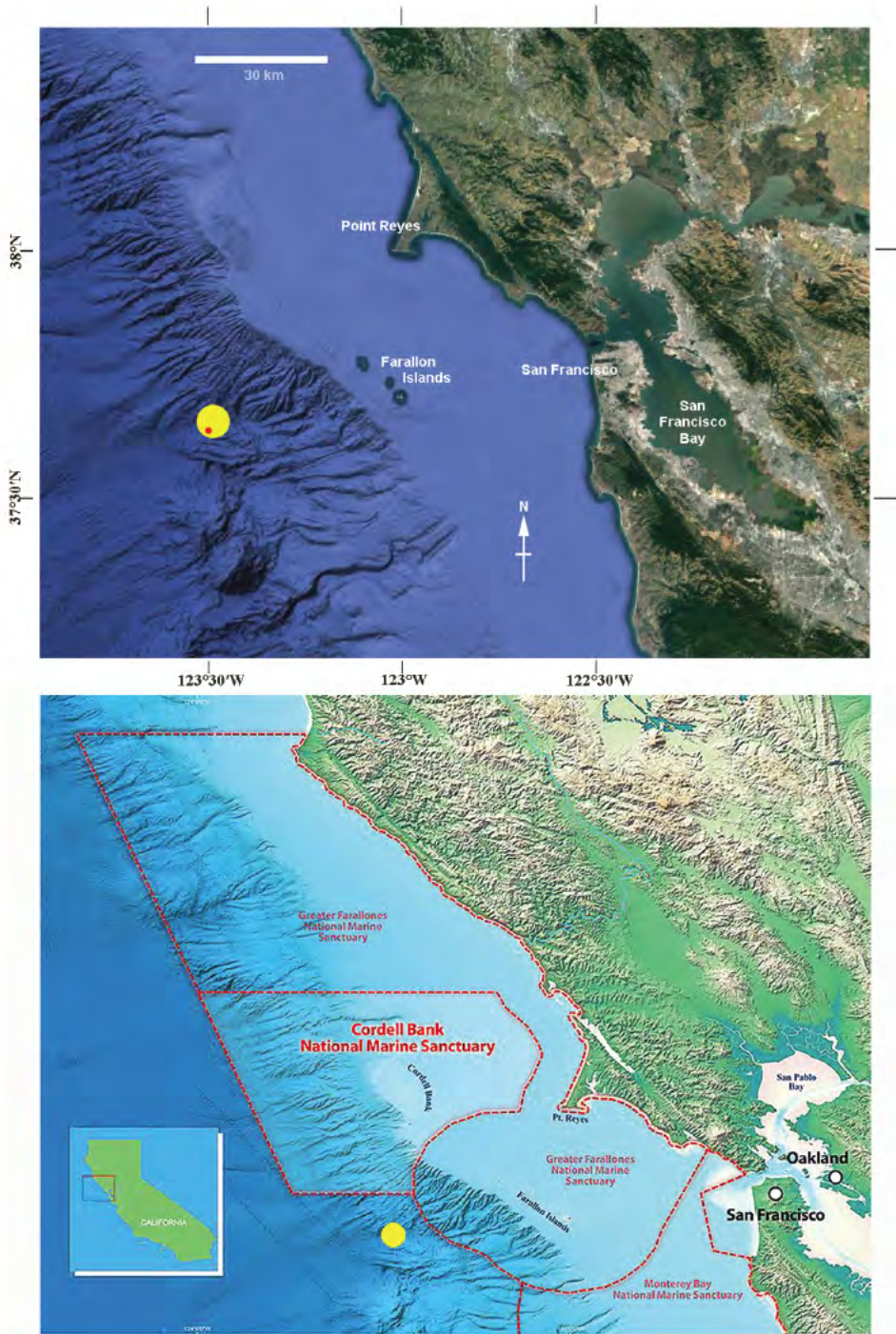


FIGURE 1. Map of the central California region showing a portion of the U.S. Navy Chemical Munitions Dumping Area (yellow circle), in which all material examined in this paper was collected, including the type locality of *Protoptilum nybakkeni* sp. nov. (red dot in yellow circle).

national marine sanctuaries. The first national marine sanctuary was designated in 1975 to protect the Civil War shipwreck the USS Monitor off the coast of North Carolina and by 2019 there were 13 national marine sanctuaries and 2 national marine monuments managed by ONMS. In central California, Point Reyes-Farallon Islands National Marine Sanctuary was established in 1981 and renamed the Gulf of the Farallones National Marine Sanctuary in 1997. Cordell Bank National Marine Sanctuary was established in 1989, followed by Monterey Bay National Marine Sanctuary in 1992. In 2015, NOAA expanded Gulf of the Farallones National Marine Sanctuary from 1,282 to 3,295 square miles, extending from Bodega Bay in Sonoma County north to Manchester Beach in Mendocino County (Fig. 1), and renamed it Greater Farallones National Marine Sanctuary. In addition, Cordell Bank National Marine Sanctuary was expanded from 529 to 1,286 square miles, and was extended to the west to include a region of continental slope, as well as slightly to the north (Fig. 1). The three contiguous national marine sanctuaries in central California extend over 450 km (280 mi) of coastline from San Simeon, CA north to Point Arena, CA. Although there is some variation in the regulations at each sanctuary, in general these three sanctuaries protect against disturbance of the seafloor, discharge of material or matter, and oil and gas development. The waste dump that is described in this paper lies outside of sanctuary boundaries, at the edge of both CBNMS and GFNMS. In addition to regulatory protections, national marine sanctuaries are charged with research and monitoring, and education and outreach that may include education of the general public, teachers, students, national marine sanctuary users, and ocean and coastal resource managers. This mandate has resulted in investments in mapping, exploring, characterizing, and monitoring the seafloor. Projects have used various technologies such as submersibles, camera sleds, and remotely operated vehicles to collect imagery of seafloor and biological and geological specimens. California Academy of Sciences is the repository for all biological specimens collected within GFNMS and CBNMS, and CAS and sanctuaries have collaborated since 2012 on targeted surveys and collections. This collaboration has facilitated a distinct focus on the benthic invertebrate taxonomy of the region. Recently, targeted missions to unexplored parts of the sanctuaries have greatly enhanced our understanding of these protected areas and has resulted in several publications on the benthic coral diversity of the region (Williams 2013; Williams & Breedy, 2016, 2019). However, mining the historic archives of CAS has yielded even further discoveries about this region, as evidenced by the recent discovery described in this paper. This collaboration between ONMS and CAS has led to a greater understanding of the habitat, species, and communities in the deep sea and a better appreciation of the value of these “out of sight, out of mind” places. Information about the species and communities in these areas can inform decisions about protecting areas, or allowing commercial and industrial activities to take place.

MATERIALS AND METHODS

Numerous colonies of the new taxon were collected in July of 1991 by beam trawl in the region of overlap between the US Navy Chemical Weapons Dumping Area and the Farallon Islands Radioactive Waste Dump, adjacent to current boundaries of Cordell Bank National Marine Sanctuary and Greater Farallones National Marine Sanctuary, approximately 70 miles west of San Francisco, California. The protocol for the isolation of sclerites from colonial tissues follows that of Williams & Mattison (2018). Scanning electron micrographs were made using a Hitachi SU3500 scanning electron microscope. Abbreviations used in the text are CASIZ – California Academy of Sciences Invertebrate Zoology and MLML – Moss Landing Marine Laboratories.

SYSTEMATIC ACCOUNT

Class Anthozoa Ehrenberg, 1831
Subclass Octocorallia Haeckel, 1866
Order Pennatulacea Verrill, 1865
Family Protoptilidae K lliker, 1880

***Protoptilum* K lliker, 1872**

Protoptilum K lliker, 1872:192. K lliker, 1880: 28. Jungersen, 1904:51. Balss, 1910:34. K kenthal & Broch, 1911:256. K kenthal, 1915:37. Hickson, 1916:97. Williams, 1995:113.

GENERIC DIAGNOSIS.— Colonies whip-like, elongate, slender. Polyp leaves absent. Rachis bilaterally symmetrical. Polyps often arranged in oblique rows along opposite sides of the rachis, usually two to four polyps per row, sometimes not in rows and arranged singly. Anthocodiae retractile into calyces. Calyces with varying number of terminal teeth, usually 3-8, or teeth absent altogether. Calyces often flattened and closely appressed to sides of rachis. Siphonozooids sparse to numerous between rows and along margins of bare rachis. Sclerites present in most parts of colonies, three-flanged spindles, needles, rods or ovals (K kenthal 1915:37; Williams 1995:114).

TYPE SPECIES.— *Protoptilum carpenteri* K lliker, 1872.

***Protoptilum nybakkeni* Williams and Lipski, sp. nov.**

Figures 2-5.

HOLOTYPE.— **CASIZ 106702**; CALIFORNIA, within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°37.5'N, 123°30'W – 37°37.8'N, 123°29'W; 2900 m; 30 July 1991; coll. Moss Landing Marine Laboratories aboard R/V *Point Sur*, Farallones Oceanic Research Expedition; one entire colony wet-preserved in 75% ethanol, original fixative 10% formalin.

PARATYPES.— **CASIZ 207521**; CALIFORNIA, within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°37.5'N, 123°30'W – 37°37.8'N, 123°29'W; 2900 m; 30 July 1991; coll. Moss Landing Marine Laboratories aboard R/V *Point Sur*, Farallones Oceanic Research Expedition; one entire colony wet-preserved in 75% ethanol, original fixative 10% formalin. **CASIZ 207522**; CALIFORNIA, within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°37.5'N, 123°30'W; 37°37.8'N, 123°29'W; 2900 m; 30 July 1991; coll. Moss Landing Marine Laboratories aboard R/V *Point Sur*, Farallones Oceanic Research Expedition; one partial colony wet-preserved in 75% ethanol, original fixative 10% formalin – proximal tip of peduncle missing.

OTHER MATERIAL.— **CASIZ 180555**; CALIFORNIA: within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°35'N, 123°30.1'W – 37°35'N, 123°28.8'W; 3015-2690 m; 30 July 1991; coll. Moss Landing Marine Laboratories, Farallones Oceanic Research Expedition; one partial colony sorted from CASSIZ 106718 – distal tip of rachis missing; one wet-preserved specimen in 75% ethanol, original fixative 10% formalin. **CASIZ 106703**; CALIFORNIA: within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°37.5'N, 123°30'W – 37°37.8'N, 123°29'W; 2900 m; 30 July 1991; coll. Moss Landing Marine Laboratories aboard R/V *Point Sur*, Farallones Oceanic Research Expedition; one whole colony wet-preserved in 75% ethanol, original fixative 10% formalin. **CASIZ 106722**; CALIFORNIA: within U.S. Navy Chemical Munitions Dumping Area, west of the Farallon Islands; 37°38.4'N, 123°28.6'W – 37°39.1'N, 123°27.5'W; 2910–2850 m; 27 July 1991; coll. Moss Landing Marine

Laboratories aboard R/V *Point Sur*, Farallones Oceanic Research Expedition; two whole colonies wet-preserved in 75% ethanol, original fixative 10% formalin.

DISTRIBUTION AND HABITAT.— Central California, approximately 90 km west of San Francisco; 2300–3975 m in depth. Habitat not recorded.

ETYMOLOGY.— The new species is named in honor of Dr. James W. Nybakken, late Professor of Biological Sciences at Moss Landing Marine Laboratories, Moss Landing, California, and Chief Scientist of the Farallones Oceanic Research Expedition.

DESCRIPTION OF THE HOLOTYPE

EXTERNAL MORPHOLOGY.— The holotype is an entire colony, extremely slender and delicate, 98 mm in total length. The rachis is 58 mm long and approximately 1.5–1.8 mm in width throughout. The peduncle is 40 mm in length and < 1.5 mm in width. The internal calcareous axis extends throughout the length of the colony. The axis in transverse section shows the radiating pattern of columns of calcareous material (Fig. 2A), that is characteristic of the pennatulaceans as a group as well as the ellisellid gorgonians (Bayer 1956:224).

POLYPS.— The anthocodiae are completely retractile within densely spiculated calyces (Fig. 3B–C). The calyces are densely set along the length of the rachis, approximately fifteen rows of autozooids throughout the length of the rachis. In some colonies, the calyces appear to be present in oblique rows of two to three polyps per row. In other colonies with very thin rachis the polyps may be arranged singly and do not appear in oblique rows. The calyces are more-or-less flattened to gently rounded, elliptical or somewhat fan-shaped, with axial sides closely appressed to the sides of the rachis (Figs. 2E–G; 3B–C). An individual calyx has 2–4 discernible teeth (Fig. 3B–C), sometimes exhibiting rounded distal tips (Fig. 2G), or distinguishable teeth are absent altogether. The siphonozooids are minute and inconspicuous. They appear in a sinuous single longitudinal column alongside the calyces. The siphonozooid calyces are similar in shape and appearance to the autozooid calyces, only in miniature (lower left portion of Fig. 2F).

SCLERITES.— Sclerites of the calyces and rachis are smooth, conspicuously three-flanged needles and spindles, 0.2–0.8 mm in length (Fig. 4). Conspicuous sclerites of the peduncle are not apparent. The surface coenenchyme and interior of the peduncle do contain extremely minute, elliptical to ovoid bodies that often appear in clumps or dense aggregations, and are too small to isolate and successfully prepare for examination under the scanning electron microscope. The individual calcareous bodies differ little in length or diameter, usually 0.003–0.006 mm. A single clump of these minute sclerites may vary from 0.010 mm to 0.040 mm (Fig. 5).

COLOR.— Overall color of the holotype as well as the paratype colonies is white to pale grey or cream white (Fig. 2).

VARIABILITY.— Taking into account the type specimens as well as other material not allocated as types, the total length of the colonies observed varies from approximately 65–235 mm. Rarely, a particular colony can appear a light pinkish red due to the color of the sclerites that comprise the calyces.

DISCUSSION AND CONCLUSION

Key to the species of *Protoptilum* Kölliker, 1872

- 1a. Distinct calyx teeth absent or indistinguishable. Siphonozooids few and inconspicuous. Colony color red and yellowish white *Protoptilum carpenteri*
- 1b. Distinct calyx teeth present, which can be very short to elongate or needlelike 2

- 2a. Peduncle equal in length or longer than rachis; colony color white to yellow 3
 2b. Peduncle length shorter than rachis 4
 3a. Two to four short calyx teeth; greyish white overall colony color *Protoptilum nybakkeni*
 3b. Three to eight calyx teeth 5
 4a. Two distinct calyx teeth; colony color dark red *Protoptilum celebense*
 4b. Three to eight calyx teeth; colony color red or blue-grey 6
 5a. Three to five short calyx teeth; yellowish colony color *Protoptilum smitti*
 5b. Six to eight long calyx teeth; whitish colony color *Protoptilum denticulatum*
 6a. Three small calyx teeth; colony color red *Protoptilum thomsoni*
 6b. Six to eight long calyx teeth; colony color blue-grey *Protoptilum cyaneum*

SPECIES COMPARISONS (Table 1).— The two major works that have discussed all ten described species of the genus *Protoptilum* are those of Kükenthal, 1915 and Hickson, 1916. These two authors have reviewed suggestions of synonymies by other authors as well as the assessment of dubious taxa (some of which may belong to other genera), and with the addition of *Protoptilum nybakkeni* sp. nov., is here consolidated to seven species, four of which are distributed in the Atlantic Ocean (Deichmann 1936:263–264). The various species are differentiated mainly by comparative characteristics of the calyx teeth.

Table 1. Principal characters and distribution of *Protoptilum*, deep-sea pennatulacean genus of at least six described species currently known from the Atlantic and Indo-Pacific.

| Species | Peduncle Length | Calyx teeth | Color | Geographic Distribution | Source |
|------------------------------|-------------------------------|--|-----------|-------------------------|----------------|
| <i>P. carpenteri</i> | Shorter than rachis | Distinct teeth absent | Red | North Atlantic Ocean | Kükenthal 1915 |
| <i>P. celebense</i> | Shorter than rachis | 2 distinct teeth | Dark red | Western Pacific Ocean | Hickson 1916 |
| <i>P. cyaneum</i> | Shorter than rachis | 6-8 long teeth | Blue Grey | East Africa | Kükenthal 1915 |
| <i>P. denticulatum</i> | As long or longer than rachis | 6-8 long teeth | Colorless | Northern Atlantic Ocean | Kükenthal 1915 |
| <i>P. nybakkeni</i> sp. nov. | Roughly as long as rachis | 2-4 short teeth or distinct teeth absent | Colorless | California | This work |
| <i>P. smitti</i> | As long or longer than rachis | 3-5 short teeth | Yellow | North Atlantic Ocean | Kükenthal 1915 |
| <i>P. thomsoni</i> | Shorter than rachis | 3 small teeth | Red | North Atlantic Ocean | Kükenthal 1915 |

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Our thanks go to curatorial staff of the California Academy of Sciences, Department of Invertebrate Zoology – especially Christina Piotrowski and Johanna Loacker for curation of material used in this study. We thank Stephen Cairns, Allen Collins, William Moser, and William Keel for their support and for making visits possible to the Museum Support Center, Department of Invertebrate Zoology, National Museum of Natural History of the Smithsonian Institution, to study the extensive pennatulacean holdings in the museum collections.

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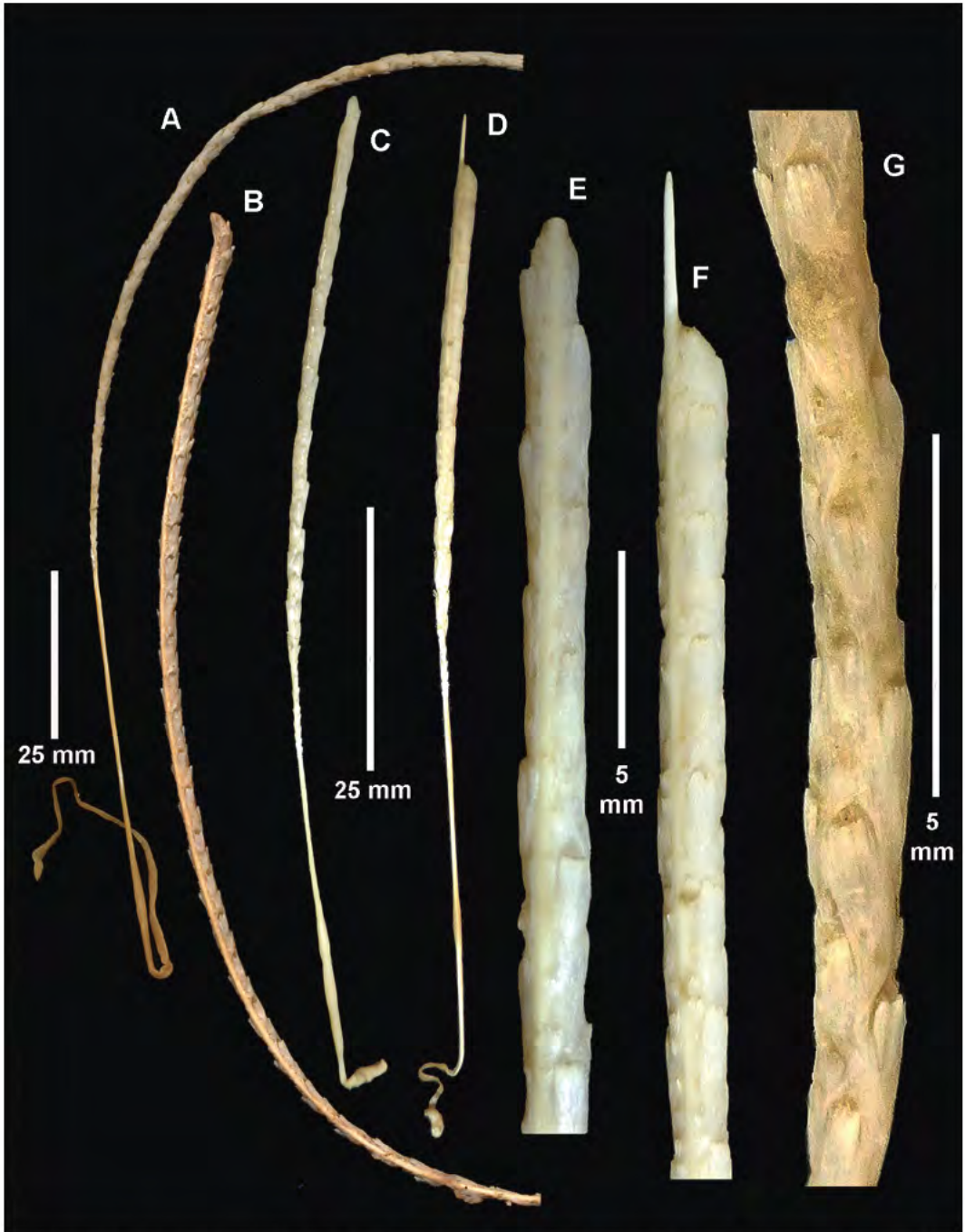


FIGURE 2. *Protoptilum nybakkeni* sp. nov. External morphology. A. Partial colony with distal tip missing (CASIZ 180555); far left scale bar = 25 mm. B. Partial colony with proximal portion missing (CASIZ 106722); center left scale bar = 25 mm. C. Holotype, entire colony (106702); center left scale bar = 25 mm. D. Paratype, entire colony (207521); center left scale bar = 25 mm. E. Detail of partial holotype colony, distal portion (106702); center right scale bar = 5 mm. F. Paratype, detail of distal portion of colony (207521); center right scale bar = 5 mm. G. Detail of colony and calyces (CASIZ 180555); far right scale bar = 5 mm.

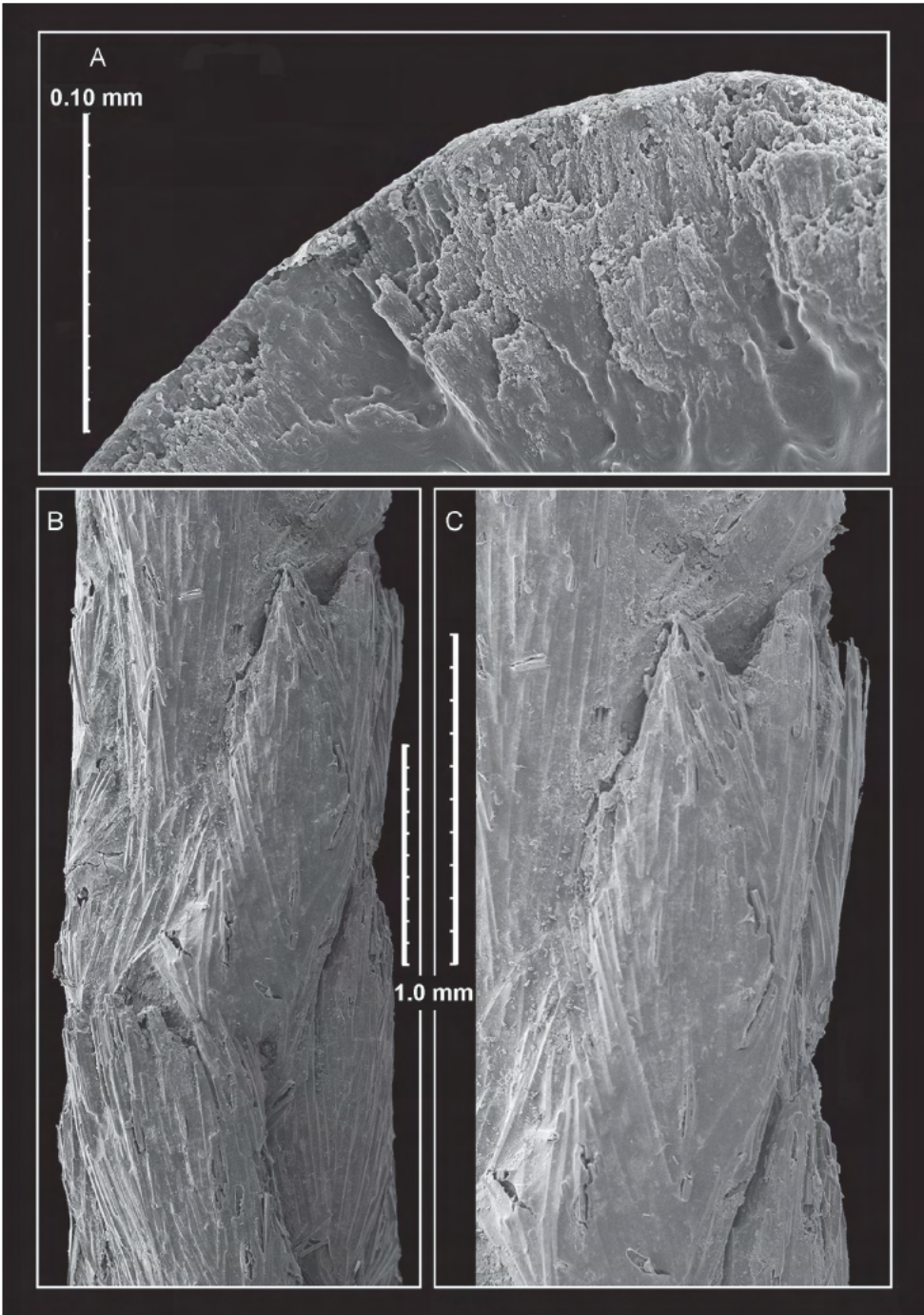


FIGURE 3. *Protoptilum nybakkeni* sp. nov. (CASIZG 180555). Scanning electron micrographs of morphological details. A. Outer edge of a portion of the axis in cross section, showing the radiating pattern of calcareous material; scale bar = 0.10 mm. B. Detail of the rachis showing three polyps closely appressed to the rachis, as well as a varying number of terminal teeth per polyp. Outlines of the longitudinally placed needle-like sclerites are seen under the epidermis; scale bar = 1.0 mm. C. Detail of a single polyp from B; scale bar = 1.0 mm.

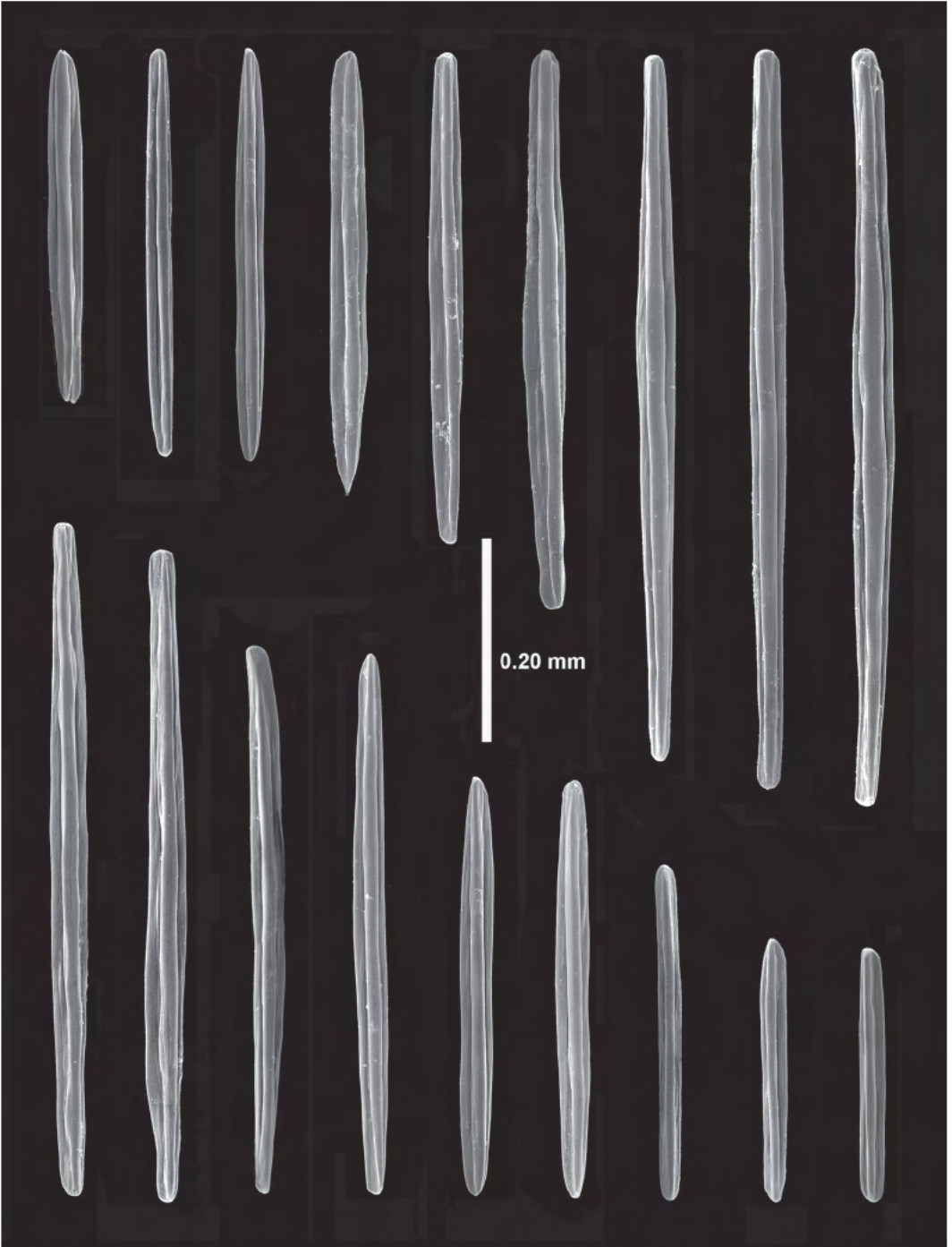


FIGURE 4. *Protoptilum nybakkeni* sp. nov. (CASIZG 106702). Scanning electron micrographs of sclerites from the calyx and rachis; scale bar = 0.20 mm.

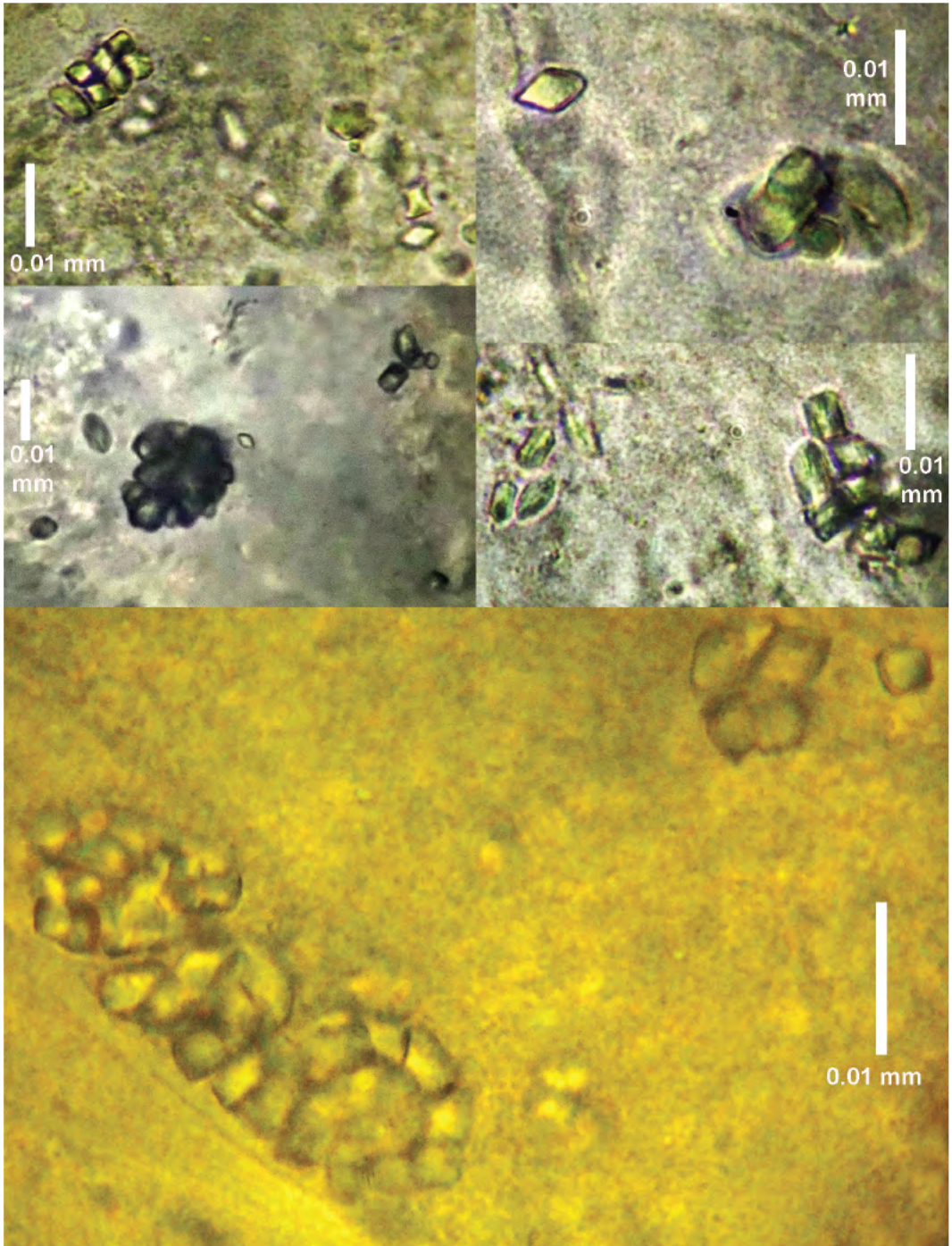


FIGURE 5. *Protoptilum nybakkeni* sp. nov. (CASIZG 106703). Light Microscope photographs of minute sclerites from the peduncle; scale bars = 0.01 mm.

A Review of the Wasp Genus *Tachytes* Panzer, 1806 of Madagascar (Hymenoptera: Crabronidae)

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Two new species from Madagascar, *Tachytes galeatus* and *Tachytes melanogaster*, are described. An original key to all eight species of Madagascan *Tachytes* is provided, including several previously unobserved characters. The identity of *Tachytes oviventris* de Saussure, 1891 is discussed and its generic position remains uncertain.

The first person to study *Tachytes* of Madagascar was de Saussure who described *T. argyropis* in 1887 and *T. oviventris* in 1891 (the identity of the latter remains a mystery). Subsequently Arnold (1945) included *Tachytes* in his revision of the Malagasy sphecoid wasps. He treated all Madagascan species of this genus known to him (including five new ones), and provided a key for their determination. The key allows recognition of the vast majority of specimens except for some females of *T. rufomarginatus*. Arnold, who saw only two, thought that all specimens of that species can be recognized by a partly ferruginous gaster, although the gaster is all black in some females.

The Malagasy *Tachytes* were studied by Dana A. Jensen during her stay at the California Academy of Sciences as a student of the Summer Systematic Institute program in 2009. She correctly recognized the two new species, discovered some new characters, and developed a preliminary key for species discrimination. The present paper completes the study, including a number of previously unobserved recognition characters.

MORPHOLOGICAL TERMINOLOGY.— I follow Bohart and Menke (1976) in their morphological terminology, except I use gonocoxite for their gonostyle. Tergum and sternum refer to gastral tergum and sternum.

ORIGIN OF MATERIAL.— I collected a number of specimens during a 1994 expedition to Madagascar. Since 1998 California Academy of Sciences has been conducting an intense insect collecting program there, providing a total of 472 Madagascan *Tachytes* to our collection, representing all the species treated by Arnold (1945) and two new ones (as compared with 95 specimens seen by Arnold). Some specimens were also borrowed from the Muséum National d'Histoire Naturelle, Paris, France, and Musée d'Histoire Naturelle, Genève, Switzerland.

INSTITUTIONAL ABBREVIATIONS.— The following are the abbreviations by which institutions housing the Madagascan *Tachytes* are designated below (the name of the contact person is given in parentheses):

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

MHNG: Musée d'Histoire Naturelle, Genève, Switzerland (Bernard Landry).

MNHN: Muséum National d'Histoire Naturelle, Paris, France (Claire Villemant).

Key to species

1. Galea longer than scape, not separated from stipes by sulcus (Figs. 1, 2); first article of labial palpus approximately as long as scape (Fig. 3) 2
— Galea shorter than scape, separated from stipes by transverse sulcus; first article of labial palpus less than half as long as scape 3
2. Maxillary palpus with five articles, labial palpus with three articles (Fig. 3). Female: tergum IV with silvery, apical fascia, as on preceding terga (fascia visible at least from certain angles). Male: midbasitarsus with ventral projection at about two thirds of length, looking emarginate in profile (Fig. 4); setae of hindfemoral venter shorter than half of maximum hindfemoral width (Fig. 5) *argyropis* de Saussure, p. 00
— Maxillary palpus with six articles, labial palpus with four articles. Female: tergum IV without silvery, apical fascia, contrasting with preceding terga. Male: midbasitarsus without ventral projection, not emarginate in profile; setae of hindfemoral venter longer than half of maximum hindfemoral width (Fig. 19). *galeatus* sp. nov., p. 00
3. Tergal setae all dark (Fig. 27), those of terga II-IV all oriented posteriorly. *melanogaster* sp. nov., p. 00
— Terga with silvery apical fasciae (visible at least from certain angles), setae of terga II-IV divergent posteriorly from midline on apical depressions 4
4. Females 5
— Males. 9
5. Sternum II finely punctate throughout, apical depressions of sterna III-V finely punctate; postocellar punctures large, without micropunctures (Fig. 30); galea slightly longer than wide *picticornis* Arnold, p. 00
— Apical depression of sternum II impunctate mesally (only next to posterior margin in some *T. rufomarginatus*), apical depressions of sterna III-V impunctate; postocellar punctures either partially or uniformly minute; galea varying 6
6. Postocellar punctures uniformly fine (Fig. 21); antenna all black; mid- and hindfemora all ferruginous *indifferens* Arnold, p. 00
— Postocellar punctures of two distinct sizes; antenna partly ferruginous (only scape in many *T. rufomarginatus*); femora all or largely black 7
7. Scutum anterolaterally with ill-defined (almost absent) patch of silvery appressed pilosity (Fig. 33); gaster in most specimens partly reddish (especially apical segments) *rufomarginatus* Arnold, p. 00
— Scutum anterolaterally with well-defined patch of silvery appressed pilosity, best seen in dorsal view (Fig. 14); gaster black 8
8. Clypeal lamella not emarginate mesally (Fig. 12); galea slightly longer than wide (Fig. 13); admedian scutal line not concealed by vestiture; scutal punctures not excessively fine (Fig. 15) *flavocinereus* Arnold, p. 00
— Clypeal lamella in most specimens emarginate mesally, inconspicuously so in some; galea shorter than wide; admedian scutal line concealed by vestiture; scutal punctures excessively fine (Fig. 7). *copiosus* Arnold, p. 00
9. Flagellum all black 10
— Flagellum partly brown or reddish brown ventrally (at least slightly so). 11

10. Postocellar punctures of two distinct sizes; scutal punctures larger (Fig. 8); sterna without fringes of preapical setae, only with a few stiff preapical setae *copiosus* Arnold, p. 00
 — Postocellar punctures uniformly fine (Fig. 21); scutal punctures minute (Fig. 22); sterna III-VI with preapical fringes of loose setae (Fig. 23). *indifferens* Arnold, p. 00
11. Scape all or predominantly brown ferruginous (black dorsally in some specimens); gaster partly ferruginous (especially apical segments); galea shorter than wide
 *rufomarginatus* Arnold, p. 00
 — Scape all black or (*T. flavocinereus*) translucent ferruginous apicoventrally; gaster black; galea slightly longer than wide. 12
12. Scape all black; apical two or three flagellomeres all black at least ventrally, contrasting with more basal ones, which are ferruginous; volsella shorter than penis valve and than gonocoxite (Fig. 31) *picticornis* Arnold, p. 00
 — Scape translucent ferruginous apicoventrally; apical three flagellomeres same color as more basal ones; volsella about as long as penis valve and as gonocoxite (Fig. 16)
 *flavocinereus* Arnold, p. 00

REVIEW OF SPECIES

All the Malagasy *Tachytes* recognized here share the following: propodeal side microscopically areolate and with fine, sparse punctures, not ridged; scape, vertex, and tergum I (at least posterolaterally) with erect setae; apical hindfemoral lobe narrow, parallel-sided or nearly so; female clypeus with bevel not differentiated, two or three inconspicuous teeth on each side of the clypeal lamella, and apical depression of tergum V all punctate and setose (very narrowly impunctate and asetose adjacent to posterior margin in some species).

All species of *Tachytes* occurring in Madagascar are endemics of that island.

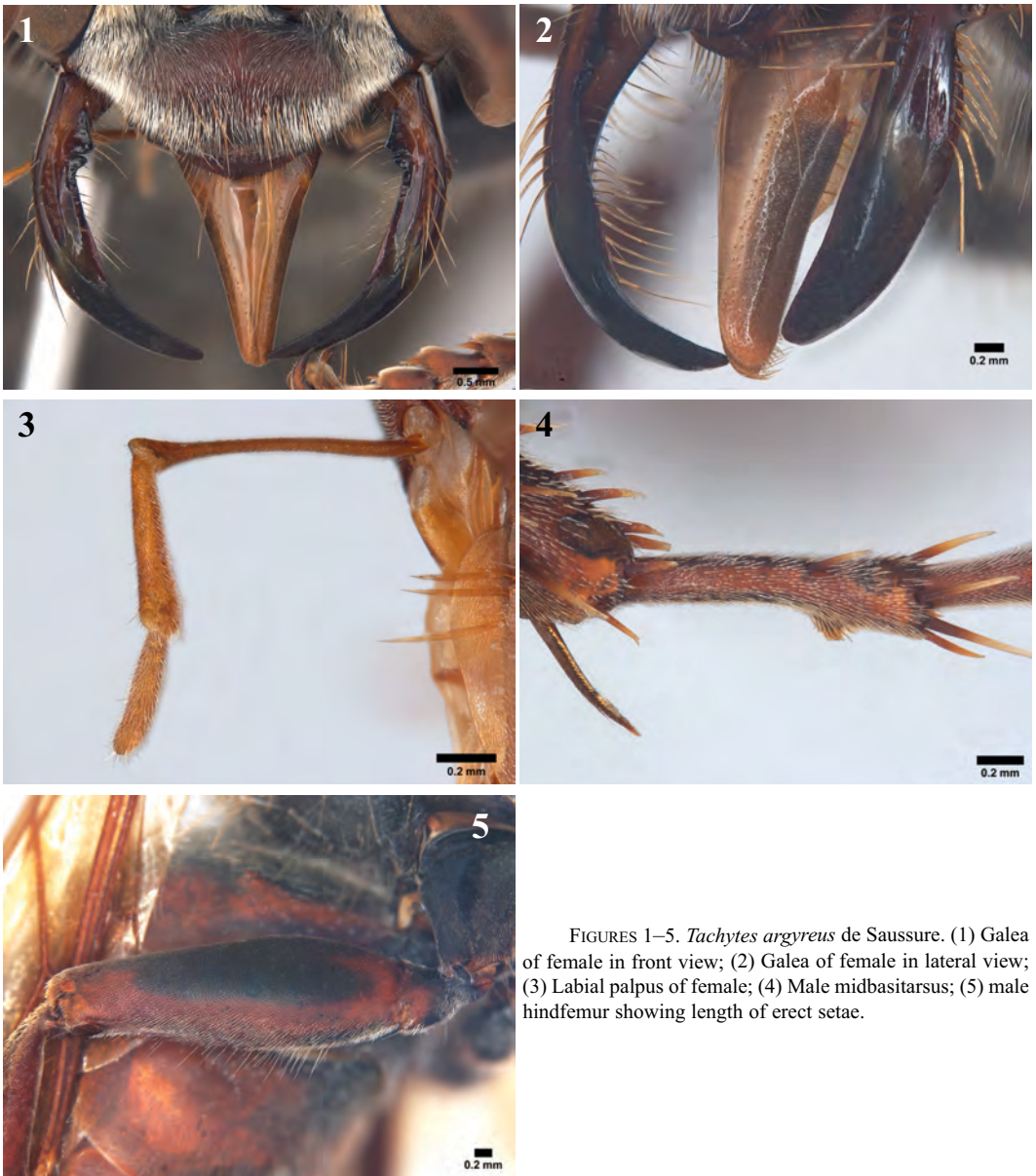
Tachytes argyropis de Saussure

Figures 1–6.

Tachytes argyropis de Saussure, 1887:18, ♀. Lectotype: ♀, Madagascar: no specific locality (MHNG), **present designation**, examined. — de Saussure, 1890:pl. 10, fig. 8a and pl. 11, figs. 8 and 8m), 1892:476 (Madagascar, redescription); Dalla Torre, 1897:687 (in catalog of world Hymenoptera); Kohl, 1909:372 (Madagascar: Imerina, Toamasina, Toliara); von Schulthess in Friederichs, 1918a:47 (Madagascar: Antananarivo); Arnold, 1945:108 (in revision of *Tachytes* of Madagascar); Leclercq, 1960:99 (Madagascar: locality records), 1961:111 (Madagascar: locality records); R. Bohart and Menke, 1976:263 (in checklist of world Sphecidae); Leclercq, 1990:118 (Madagascar: locality records); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:986 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

LECTOTYPE SELECTION.— Owing to the kindness of Monsieur Bernard Landry, I was able to examine two female and two male syntypes of this species, bearing the original name labels by de Saussure, and preserved in the MHNG. The labels read “Madagascar, Sikora”, with no specific locality (Franz Sikora was a renowned collector). I have selected a female as the lectotype of this species. It agrees perfectly well with the current interpretation of this species.

COMPARISON WITH SIMILAR SPECIES.— *Tachytes argyropis* shares the reduced number of palpomeres (palpal formula 5 + 3), and closely resembles, three species from continental Africa: *T. admirabilis* Turner, 1916, *T. danae* Arnold, 1923, and *T. marshalli* Turner, 1912 (that were placed by Turner, 1917 in his subgenus *Calotachytes*). All three species have an elongate galea (Figs. 1, 2), longer than the scape, markedly elongate basal segment of the labial palpus (Fig. 3), and the



FIGURES 1–5. *Tachytes argyreus* de Saussure. (1) Galea of female in front view; (2) Galea of female in lateral view; (3) Labial palpus of female; (4) Male midbasitarsus; (5) male hindfemur showing length of erect setae.

male midbasitarsus, looking emarginate in profile (Fig. 4). *Tachytes argyropis* differs from *T. admirabilis* and *T. danae* in having well-defined silvery fasciae on the preapical depressions of terga I–IV (the setae on the remaining parts of terga appear dark from most angles, but silvery from some angles). In the other two species the gastral setae are uniformly golden; also, in *T. admirabilis* the forewing is markedly infumate (yellowish in *T. argyropis*). *T. argyropis* differs from *T. marshalli* by a number of characters: the wing membrane is yellowish, darkened along the apical margin, in the female the postocellar area is longer than wide and the setae of tergum V are the same color as on the preceding terga, and in the male the basal emargination on the venter of midbasitarsus is about twice as long as the nonemarginate apical part, which is less prominent, and

the venter of flagellomeres II and III has no erect setae (in *T. marshalli* the wing membrane is conspicuously infumate, in the female the postocellar area is about as wide as long and the setae of tergum V are black, clearly contrasting with the setae on the preceding terga; in the male the basal emargination on the venter of midbasitarsus is about as long as the nonemarginate apical part, which is more prominent, and the venter of flagellomeres II and III has silvery, erect setae whose length is up to about 0.5 of midocellar diameter).

The elongate galea (longer than the scape) and the markedly elongate basal segment of the labial palpus are also found in *T. galeatus* and in the Saharan species *T. basilicus* Guérin Méneville and its Afrotropical relatives. The palpal formula of these species, however, is 6 + 4.

RECORDS.— (Fig. 6; M: from Madl, 2014).—

Antananarivo Province: Ambatoloana (M), Ampefy at Lac Kavitaha (M), Analavory (M), Antananarivo (1 ♀, 2 ♂, CAS), Imerina (Kohl, 1909). **Antsirana** (= Diego Suarez) **Province:** Montagne des Français at 12°19'22"S 49°20'17"E (1 ♀, CAS), Parc National Montagne d'Ambre at 22°30'52"S 49°10'53"E (1 ♀, CAS). **Fianarantsoa Province:** Ambalavao (M), Ambositra (M), Ampitavananima Forest 50 km S Farafangana at 23°7.79'S 47°43.02'E (15 ♀, 9 ♂, CAS), Fianarantsoa (Leclercq, 1990), Ifaty: coastal dunes at 23°10.78'S 43°37.01'E (1 ♂, CAS), Ihosy (M), 40 road km W Ihosy at 22°28'S 45°49'E (13 ♀, CAS), 22 km SW Ilakaka at 22°46.75'S 45°1.50'E (16 ♀, 12 ♂, CAS), Isalo National Park at 22°36'S 45°10'E (1 ♀, 2 ♂, CAS), near Isalo National Park at 22°37.60'S 45°21.49'E (3 ♀, 13 ♂, CAS), Italaviana 35 km SSE Antsirabe at 20°10.40'S 47°05.16'E (1 ♀, 5 ♂, CAS), Mananjary (M), Ranohira (M), Ranomafana National Park at 21°15'05"S 47°24'43"E (6 ♀, 3 ♂, CAS), 21°15.99'S 47°25.21'E (1 ♀, CAS), and 21.25537°S 47.45515°E (1 ♀, CAS), 7 km W Sendrisoa at 21°57.96'S 46°55.95'E (3 ♀, 1 ♂, CAS). **Toamasina Province:** Andasibe National Park (1 ♀, CAS), Fampanambo (M), Toamasina (Kohl, 1909), 20 road km SW Toamasina at 18°15'S 49°16'E (1 ♀, 1 ♂, CAS). **Toliara Province:** Ambohimahavelona village 33 km NE Toliara at 23°26.45'S 43°53.98'E (1 ♀, 1 ♂, CAS), Ambovombe (M), Andohahela National Park at 24°56.21'S 46°37.60'E (2 ♀, CAS), Antanimora (Arnold, 1945), Behara (Arnold, 1945), Bekily (Arnold, 1945), Betroka (M), Beza Mahafaly Réserve at 23°41.19'S 44°35.46'E (1 ♀, CAS), Cap Sainte Marie Special Reserve at 25°35.26'S 45°09.78'E (1 ♀, CAS), Lake Ranobe at 23°02.468'S 43°36.607'E (1 ♀, CAS), Réserve Privée Berenty at 25°00.40'S 46°18.20'E (2 ♀, 3 ♂, CAS), Sakaraha (M), Taolagnaro (Leclercq, 1960, as Fort Dauphin), Toliara (Kohl, 1909), Tsiamanampetsotsa National Park at 23°59'32"S 43°52'50"E (2 ♂, CAS). **Locality unknown** ([F.] Sikora collector): 2 ♀, 1 ♂, CAS, determined by F. Kohl; 2 ♀, 2 ♂, Muséum d'Histoire Naturelle, Genève, Switzerland, determined by H. de Saussure, including female lectotype of *T. argyropis*.

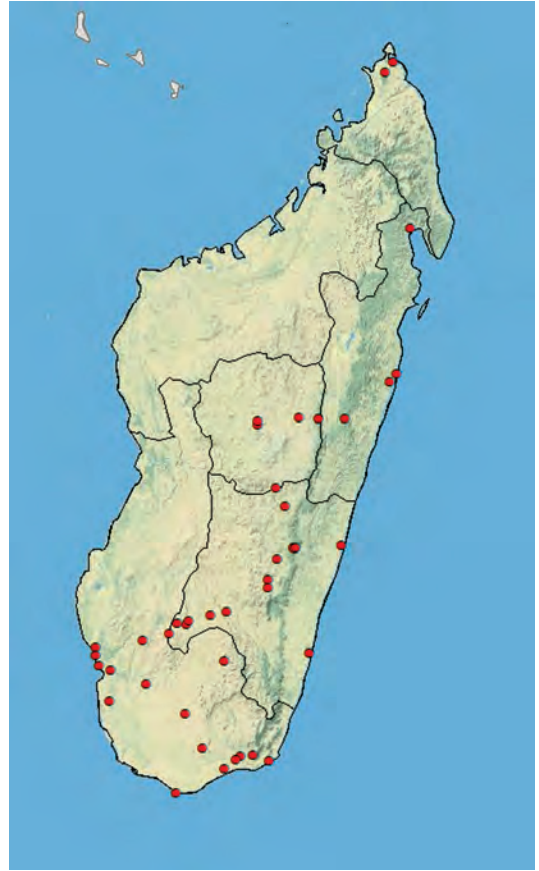


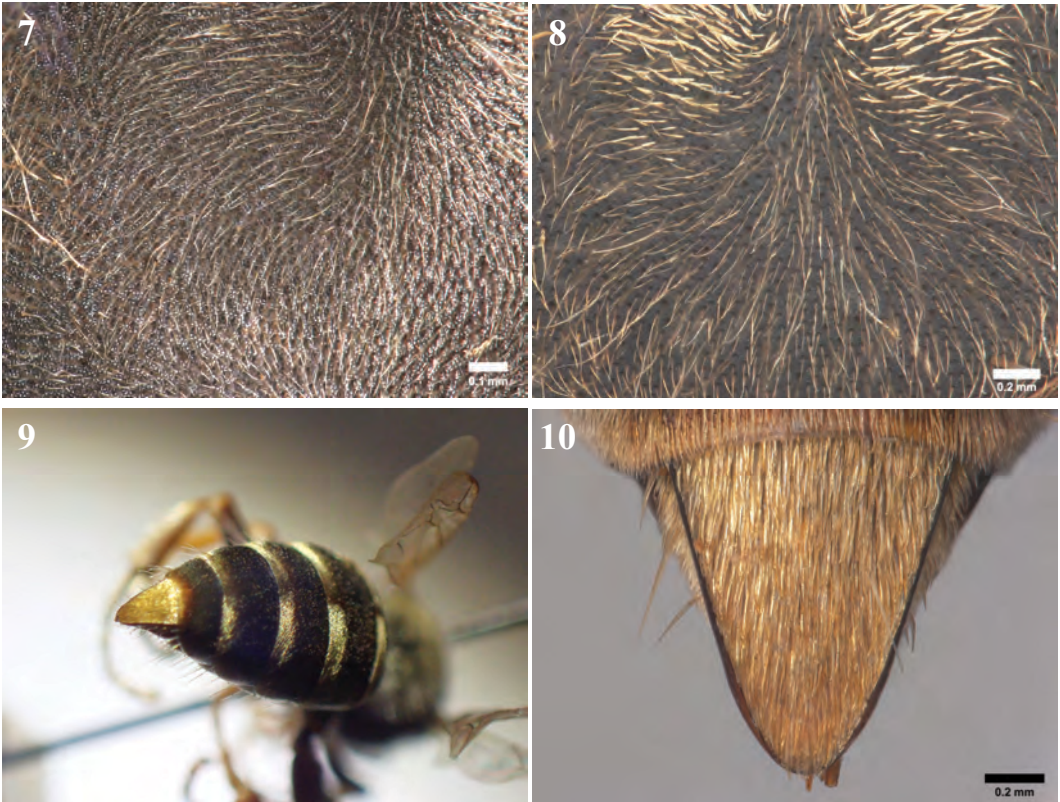
FIGURE 6. Collecting localities of *Tachytes argyreus* de Saussure.

***Tachytes copiosus* Arnold**

Figures 7–11.

Tachytes copiosus Arnold, 1945:111, ♀, ♂ (as *copiosa*, incorrect original termination). Syntypes: Madagascar: Behara (MNHN). – R. Bohart and Menke, 1976:264 (in checklist of world Sphecidae); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:986 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

RECOGNITION.— The female of *Tachytes copiosus* lacks unique diagnostic features, therefore it can be recognized only by a long suite of characters that eliminate the other species. So, its galea is shorter than wide and the gaster is all black, with silvery, apical fasciae of setae on the terga.



FIGURES 7–10. *Tachytes copiosus* Arnold. (7). Scutal punctures of female; (8) Scutal punctures of male; (9) Gaster of syntype female showing color of pygidial plate, image generated by Madame Claire Villemant (Muséum National d’Histoire Naturelle, Paris, France); (10) Pygidial plate of female with silvery setae.

Unlike *T. picticornis*, the apical depressions of its sterna II–V are impunctate (rather than punctate). Unlike *T. indifferens* the postocellar punctures are of two distinct sizes (the dense minute punctures are interspersed with larger, sparser punctures) rather than being uniformly small, the flagellum is partly ferruginous (rather than all black), and the femora are largely black (whereas the mid- and hindfemora are ferruginous in *T. indifferens*). It differs from *T. rufomarginatus* in having a well-defined patch of appressed setae anterolaterally on the scutum (rather than the patch ill defined, almost absent), and in having the setae on the hindfemoral venter sparser and less dense. Finally, unlike *T. flavocinereus*, the clypeal lamella is emarginate mesally, although only inconspicuously so in some specimens (rather than non-emarginate), the admedian scutal line is concealed by the

vestiture (rather than not concealed), and the scutal punctures are excessively fine (rather than not excessively fine).

The male shares an all black flagellum with *T. indifferens*, from which it differs in having the postocellar punctures of two distinct sizes, the scutal punctures larger (Fig. 8), and the sterna without fringes of preapical setae. In *T. indifferens*, the postocellar punctures are uniformly small, the scutal punctures are minute (Fig. 22), and sterna III-VI have preapical fringes of loose setae (Fig. 23).

COLOR VARIATION.—Arnold described the setae of the female pygidial plate as being bright golden, which I confirmed from an image of one of the syntypes kindly sent by Madame Claire Villemant (Fig. 9). The specimens in the California Academy of Sciences collection, however, have the setae of the pygidial plate either pure silver or silver with a golden tinge (Fig. 10). As all other characters agree perfectly well with the original description, I conclude that the color of these setae vary among individuals.

RECORDS (Fig. 11).—**Antsiranana** (= Diego Suarez) **Province**: Parc National Montagne d’Ambre at 12°30’52’’S 49°10’53’’E (1 ♂, CAS), 1 km W Sakalava Beach at 12°15’59’’S 49°23’42’’E (1 ♂, CAS), 3 km W Sakalava Beach at 12°17.17’S 49°22.00’E (2 ♂, CAS). **Fianarantsoa Province**: near Isalo National Park at 22°37.60’S 45°21.49’E (1 ♀, CAS). **Majunga Province**: Ambovomamy Belambo at 15°27.07’S 47°36.80’E (2 ♀, 1 ♂, CAS). **Toliara Province**: Behara (Arnold, 1945), Bereboka village at 19°58.65’S 44°39.92’E (1 ♀, CAS), Beza Mahafaly Reserve at 23°41.19’S 44°35.46’E (1 ♀, CAS), Forêt de Kirindy at 20°02’42’’S 44°39’44’’E (1 ♀, CAS), Parc National Zombitsy at 22°53’10’’S 44°41’30’’E (1 ♀, CAS).



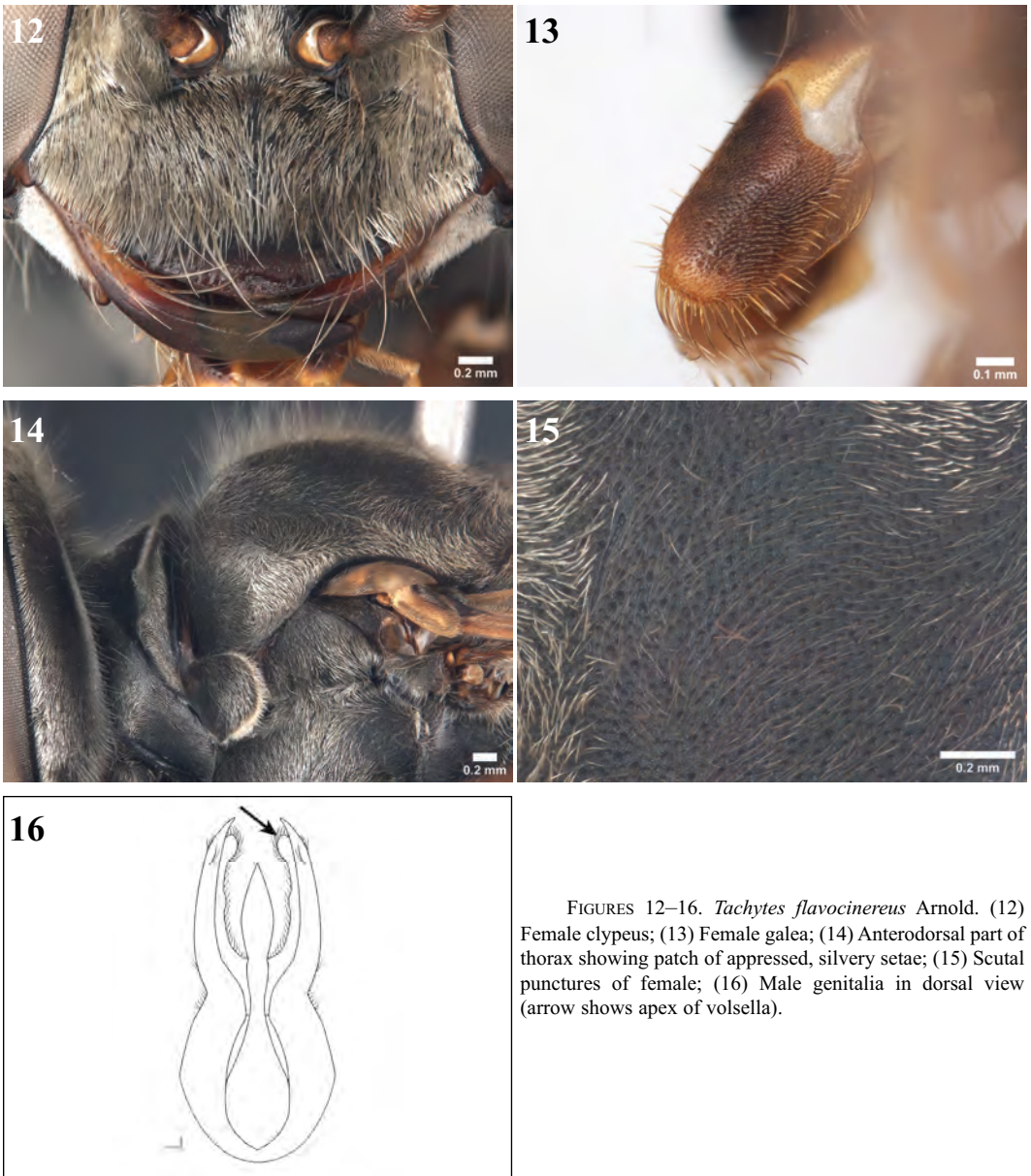
FIGURE 11. Collecting localities of *Tachytes copiosus* Arnold.

Tachytes flavocinereus Arnold

Figures 12–17.

Tachytes flavocinereus Arnold, 1945:112, ♀, ♂ (as *flavocinerea*, incorrect original termination). Lectotype: ♂, Madagascar, Bekily (MNHN), **present designation**. – Leclercq, 1961:112 (Madagascar: locality records). – As *Tachytes flavocinereus*: R. Bohart and Menke, 1976:265 (in checklist of world Sphecidae); Leclercq, 1990:118 (Madagascar: locality records); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:986 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

LECTOTYPE SELECTION.—Madame Claire Villemant of the MNHN kindly sent me, in 2009,



FIGURES 12–16. *Tachytes flavocinereus* Arnold. (12) Female clypeus; (13) Female galea; (14) Anterodorsal part of thorax showing patch of appressed, silvery setae; (15) Scutal punctures of female; (16) Male genitalia in dorsal view (arrow shows apex of volsella).

a pair of Arnold's syntypes of *Tachytes flavocinereus*, both collected at Bekily, Madagascar. I have selected the male as the lectotype, and the female as a paralectotype.

RECOGNITION.— Among the species with the galea shorter than the scape, the female of *T. flavocinereus* can be recognized by the non-emarginate clypeal lamella (Fig. 12). Subsidiary recognition features are: apical depressions of terga I–IV with silvery setal fasciae; galea slightly longer than wide (Fig. 13); admedian scutal line not concealed by vestiture; scutal punctures not excessively fine (Fig. 15); setae of the pygidial plate cupreous. In the other such species, the clypeal lamella is emarginate mesally, although the emargination is inconspicuous in some

T. copiosus and some *T. melanogaster*. The latter differs in having the gastral setae all black, the former in having the galea slightly shorter than wide, admedian scutal line concealed by vestiture, scutal punctures excessively fine, and in some specimens the setae of the pygidial plate silvery.

In the male, the flagellum is partly brown or reddish brown ventrally, although only slightly so in some specimens. *Tachytes picticornis* and *T. rufomarginatus* are similar, but *T. flavocinereus* can be recognized by the following combination: scape translucent ferruginous apicoventrally, galea slightly longer than wide, apical three flagellomeres same color as more basal ones, gaster all black, and volsella about as long as penis valve and as gonocoxite (Fig. 16). In *T. picticornis*, the scape is all black, and the two or three apical flagellomeres are all black (at least ventrally), contrasting with the more basal flagellomeres which are ferruginous, and the volsella is shorter than the penis valve and the gonocoxite (Fig. 31). In *T. rufomarginatus*, the scape is all or predominantly brown ferruginous, the galea is shorter than wide, and the gaster is partly ferruginous, especially on the apical segments.

RECORDS (Fig. 17; M: from Madl, 2014)..—

Antsiranana (= Diego Suarez) Province: Forêt d'Ampondrabe at 12°58'12"S 49°42'00"E (1 ♀, CAS), Montagne des Français at 12°19'22"S 49°20'17"E (1 ♂, CAS), Parc National de Marojejy at 14°26'12"S 49°46'30"E (1 ♀, CAS), Parc National Montagne d'Ambre at 12°31'13"S 49°10'45"E (1 ♀, CAS). **Fianarantsoa Province:** Ihosy (M), Ranomafana National Park at 21°15.99'S 47°25.21'E (1 ♂, CAS). **Majunga Province:** Ambovomamy Belambo at 15°27.07'S 47°36.80'E (2 ♂, CAS), Forêt d'Analamanitra at 16°8'S 45°42'E (1 ♀, 2 ♂, CAS), Forêt de Tsimembo at 19°01'17"S 44°26'26"E (1 ♀, CAS), Namoroka at 16°28.4'S 45°23.48'E (2 ♀, CAS), Parc National d'Ankarafantsika at 16°13'41"S 46°08'37"E (1 ♂, CAS). **Toamasina Province:** Fampanambo (Leclercq, 1990), Ivondro (Arnold, 1945, M), Mahavelona (M), Soanierana-Ivongo (M). **Toliara Province:** Antanimora (Arnold, 1945), Bekily (1 ♀, 1 ♂ lectotype of *Tachytes flavocinereus*, MNHN), Bereboka at 19°58.65'S 44°39.92'E (1 ♀, CAS), Beza Mahafaly Reserve at 23°41.19'S 44°35.46'E (1 ♀, 1 ♂, CAS), Parc National d'Andohahela at 24°56.21'S 46°37.60'E (1 ♀, 1 ♂, CAS).

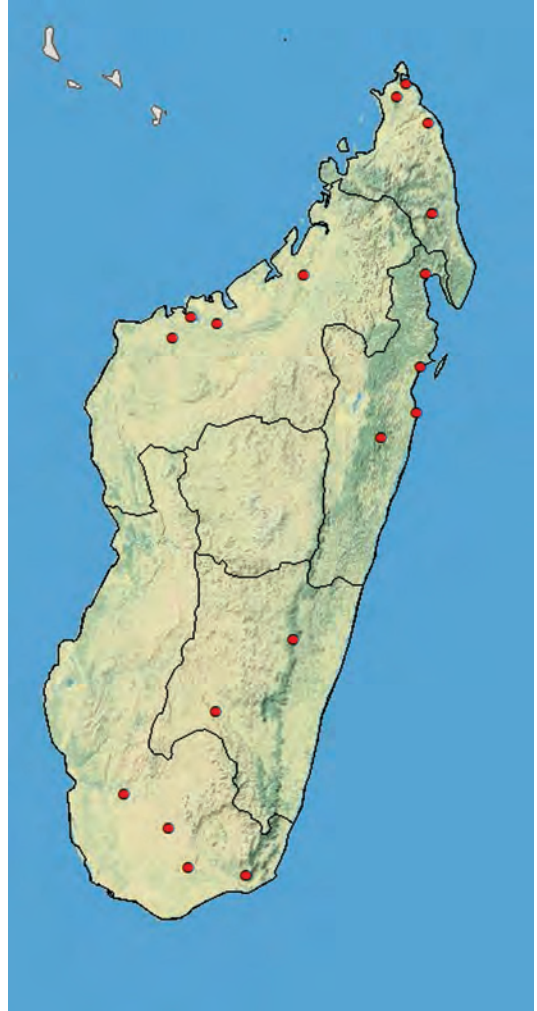


FIGURE 17. Collecting localities of *Tachytes flavocinereus* Arnold.

***Tachytes galeatus* Pulawski, species nova**

Figures 18–20.

NAME DERIVATION.— *Galeatus* is an adjective derived from *galea*, which is unusually long in this species.

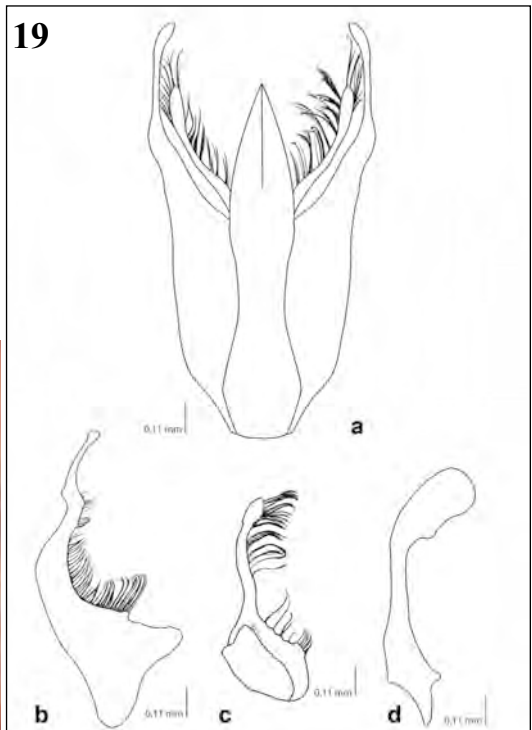
RECOGNITION.— Like *T. argyropis* and unlike all other Madagascan *Tachytes*, the galea of this species is longer than the scape, as in Figs. 1 and 2 (rather than shorter) and the first article of the labial palpus is about as long as the scape, as in Fig. 3 (rather than markedly shorter). Unlike *T. argyropis*, the palpal formula of *T. galeatus* is 6+4 (rather than 5+3); see the key for other differences.

Tachytes galeatus resembles several continental African species in having an elongate galea and the first article of the labial palpus and in lacking the golden setae arranged in a checkered pattern on the gastral terga (these setae are present in *T. basilicus* Guérin-Ménéville and its relatives). It differs from all these species in having the gaster dark reddish or at least with dark reddish zones rather than all black.

DESCRIPTION.— Head round in frontal view. Gena in dorsal view slightly narrower than in *T. panzeri* (Dufour). Galea 1.5 × as long as scape. First article of labial palpus about as long as scape.

Appressed silvery pilosity concealing integument on pronotal collar, sparse and not concealing integument on remaining thorax and propodeum (scutum anterolaterally without conspicuous appressed pilosity). Setae of postocellar area as long as 0.5–0.6 × scape, those on scutum 0.4 × scape in female, 0.5 × in male; sternum II without erect setae in female, in male with erect setae posteromedially (setal length about 2.0 × midocellar diameter).

Head, thorax and propodeum black; male mandible yellowish reddish in basal half or only mesally; scape dark ferruginous except black dorsally. Gaster dark reddish except tergum I black basally, terga I–IV in some males only with dark reddish preapical zones. Female femora all black or forefemur largely brown; male femora partly to largely brown; female foretibia brown, midtibia brown or black, hindtibia black; male tibiae ferruginous to brown (hindtibia the darkest); tarsi dark to



FIGURES 18–19. *Tachytes galeatus* sp. nov. (18) Male hindfemur showing length of erect setae; (19) Male genitalia: a – genitalia in dorsal view, b – right gonocoxite in lateral view; c – volsella, d – penis valve.

partly ferruginous in female, ferruginous in male. Pilosity of frons and clypeus silvery.

♀.— Minimum interocular distance equal to $0.30\text{--}0.32 \times$ clypeal width and to $1.2\text{--}1.4 \times$ of dorsal length of flagellomere I; the latter $1.9\text{--}2.1 \times$ apical width. Postocellar punctures of two distinct sizes: relatively large (averaging more than one diameter apart) and minute (averaging about one diameter apart). Sternum II minutely, closely punctate except apical depression impunctate. Forebasitarsus with six rake spines.

♂.— Minimum interocular distance equal to $0.30 \times$ clypeal width and to $1.3 \times$ of dorsal length of flagellomere I; the latter $1.8\text{--}2.2 \times$ apical width. Postocellar punctures of uneven size, approximately one diameter apart. Genitalia: Fig. 19.

RECORDS (Fig. 20).— Holotype: ♀, Majunga Province: Ambovomamy Belambo at $15^{\circ}27.07'S$ $47^{\circ}36.80'E$, 22–27 Jan 2007, R. Harin 'Hala, M. Irwin, and F.D. Parker (CAS).

Paratypes: **Antsiranana** (= Diego Suarez)

Province: Forêt d' Orangéa at $15^{\circ}15'32''S$ $49^{\circ}22'29''E$, 22–28 Feb 2001, B. Fisher, Ch. Griswold et al. (1 ♂, CAS). **Fianarantsoa Province:** Isalo National Park at $22^{\circ}36'S$ $45^{\circ}10'E$, 18–19 Mar 1994, W.J. Pulawski (1 ♂, CAS). **Majunga Province:** same locality and collectors as holotype: 4–14 Jan 2007 (1 ♂, CAS), 22–27 Jan 2007 (1 ♀, CAS), 11–20 Dec 2007 (1 ♀, CAS). **Toliara:** Zombitsy National Park at $22^{\circ}50.43'S$ $44^{\circ}43.87'E$, 13–20 Mar 2002, R. Harin 'Hala (1 ♀, CAS).

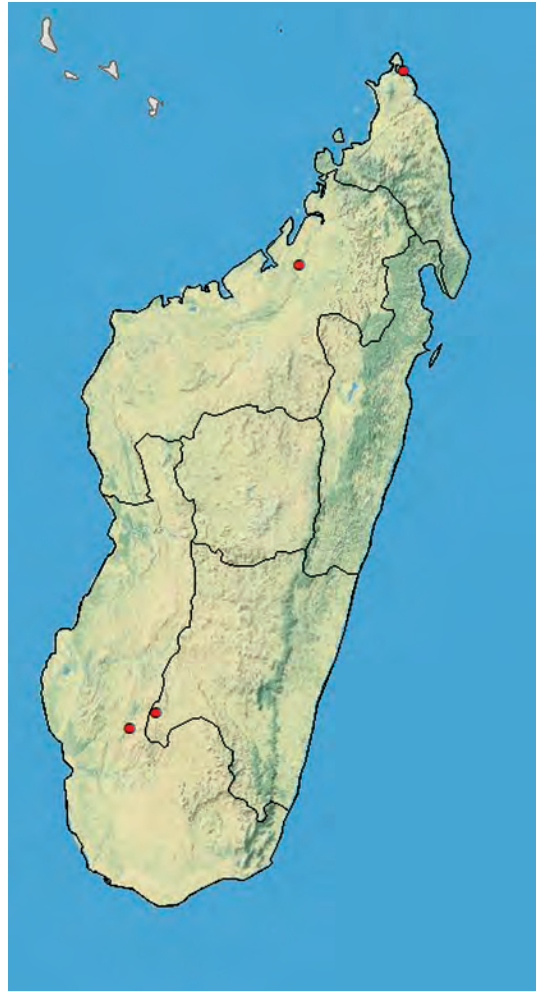


FIGURE 20. Collecting localities of *Tachytes galeatus* sp. nov.

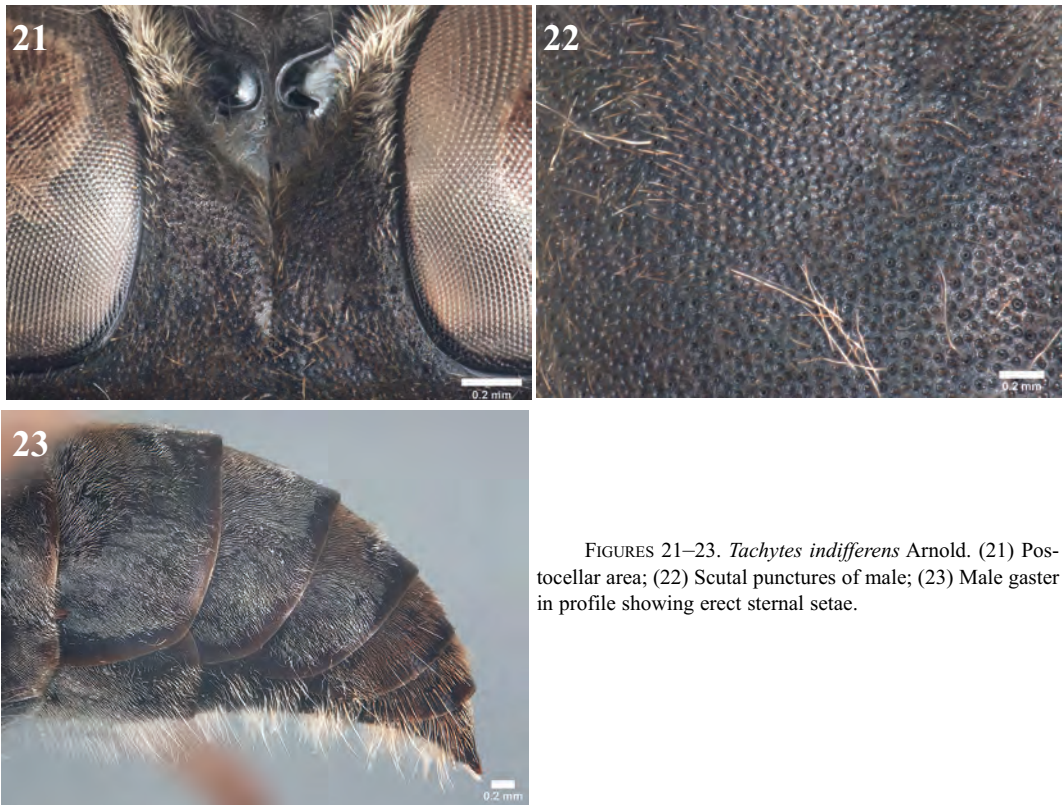
Tachytes indifferens Arnold

Figures 21–24.

Tachytes indifferens Arnold, 1945:110, ♀, ♂. Syntypes: Madagascar: Behara, Bekily (MNHN). – Leclercq, 1960:99 (Madagascar: locality records), 1961:111 (Madagascar: locality records); R. Bohart and Menke, 1976:265 (in checklist of world Sphecidae); Leclercq, 1990:118 (Madagascar: locality records); Madl, 1997:820 (Madagascar: Nosy Boraha Island), 821 (in checklist of Nosy Boraha Sphecidae); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:986 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

RECOGNITION.— The female of *T. indifferens* is characterized by the uniform, minute punctures of the postocellar area, all black antenna, and ferruginous mid- and hind femora and all tibiae. In all other species the postocellar punctures are of two distinct sizes (the small punctures are absent in *T. picticornis*), and the femora (except some *T. argyropis*) are all or largely black.

The male is unique among its Madagascan congeners in having preapical fringes of loose setae on sterna III–VI (Fig. 23); it can also be recognized by the all black antenna combined with the uni-



FIGURES 21–23. *Tachytes indifferens* Arnold. (21) Postocellar area; (22) Scutal punctures of male; (23) Male gaster in profile showing erect sternal setae.

form, minute postocellar punctures. It differs from *T. copiosus* by much smaller scutal punctures (Fig. 22).

RECORDS (Fig. 24).—**Antsiranana** (= Diego Suarez) **Province**: Forêt d'Orangéa at 12°15'32"S 49°22'29"E (1 ♂, CAS), 7 km N Joffreville at 12°20'S 49°15'E (1 ♀, CAS), Parc National Montagne d'Ambre at 12°30'52"S 49°10'53"E (4 ♀, 5 ♂, CAS), 12°31'13"S 49°10'45"E (1 ♀, 1 ♂, CAS), and 12°31'S 49°11'E (1 ♀, CAS), 1 km W Sakalava Beach at 12°15'59"S 49°23'42"E (2 ♀, 2 ♂, CAS), 3 km W Sakalava Beach at 12°17'10"S 49°22'00"E (2 ♀, 1 ♂, CAS). **Fianarantsoa Province**: Ambinany 7 km W Manombo (1 ♀, CAS), Forêt d'Ampitavananima at 23°7.79'S 47°43.02'E (4 ♀, CAS), Ihosy (Leclercq, 1990), Isalo National Park at 22°36'S 45°10'E (4 ♀, 14 ♂, CAS), near Isalo National Park at 22°37.60'S 45°21.49'E (3 ♂, CAS), 2 km SW Manakara at 22.168°S 48.00°E (1 ♀, 1 ♂, CAS). **Majunga Province**: Ambato-Boena (Madl, 2014), Amborovy 8 km NE Majunga at 15°40'S 46°20'E (3 ♂, CAS), Ambovomamy Belambo at 15°27.07'S 47°36.80'E (16 ♀, 6 ♂, CAS), 10 km E Majunga at 15°43'S 46°25'E (1 ♀, 5 ♂, CAS). **Toamasina Province**: Island of Nosy Boraha (Madl, 2014), Mahavelona (Madl, 2014), near entrance to Parc National d'Andasibe at 18°55'58"S 48°24'47"E (1 ♀, CAS), Toamasina at 18°07'S 49°24'E (1 ♂, CAS). **Toliara Province**: 22 km E Ampanihy at 24°41'S 44°46'E (1 ♂, CAS), Behara (Arnold, 1945), Bekily (Arnold, 1945), 2 km N Betioky at 23°21'S 44°20'E (2 ♂, CAS), Beza Mahfaly Reserve at 23°41.19'S 44°35.46'E (1 ♀, 1 ♂, CAS), Parc National d'Andohahela at 24°56.21'S 46°37.60'E (2 ♀, CAS), Réserve Privée Berenty at 24°57'25"S 46°16'17"E (1 ♀, CAS), 25°00'S 46°18'E (12 ♂, CAS), 25°00'40"S 46°18'20"E (5 ♀, CAS), 38 km E Sakaraha at 22°46'S 44°51'E (3 ♂, CAS), Taolagnaro (Leclercq, 1960, 1990, as Fort Dauphin), Toliara (Leclercq, 1990, as Tuléar), 10 km NE Toliara at 23°18'S 43°45'E (13 ♂, CAS), and 12 km SE Toliara at 23°25'S 43°45'E (2 ♀, 21 ♂, CAS).

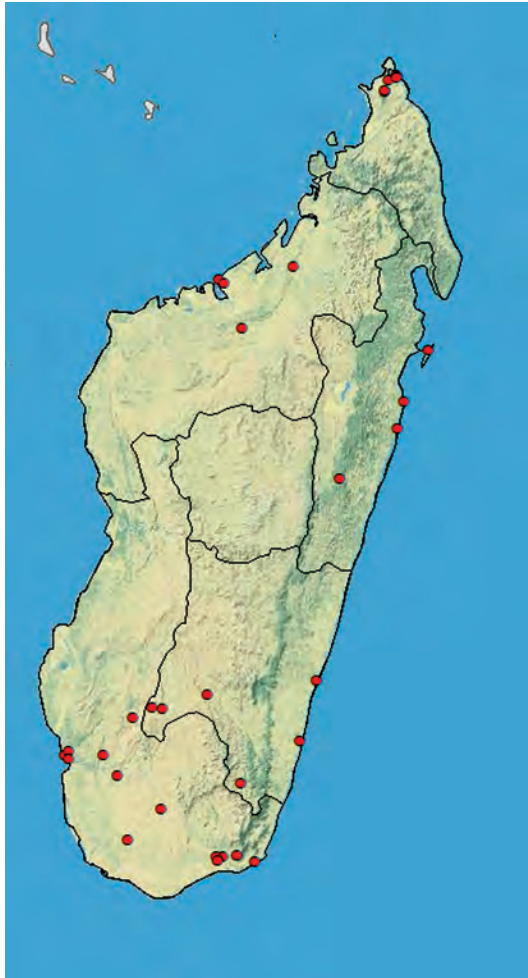


FIGURE 24. Collecting localities of *Tachytes indifferens* Arnold.

***Tachytes melanogaster* Pulawski, species nova**

Figures 26–29.

NAME DERIVATION.— *Melanogaster* is derived from two Greek words: *μελανός* (black, dark) and *γαστήρ* (gaster); with reference to the presence of black setae only on this species terga I–V.

RECOGNITION.— Only the female of this species is known. Unlike all other Madagascan species, and like *T. nigropilosellus* (Cameron) and *T. nudiventris* Turner from the continental Africa, *T. melanogaster* has the setae of terga I–V all black (Fig. 27) and directed posteriorly (rather than all golden or silvery on apical depression and diverging posteriorly on the apical depressions of at least terga IV and V). Unlike these two species, the female of *T. melanogaster* has five rather than six rake spines on the forebasitarsus and the setae of the pygidial plate (Fig. 28) cupreous (rather than black). The postocellar punctures in *T. melanogaster* are mainly large and sparse, intermixed with smaller and denser punctures (Fig. 26), whereas in *T. nudiventris* the fine punctures are absent and only the larger, sparse punctures are present (Fig. 25); also, the wing veins are light

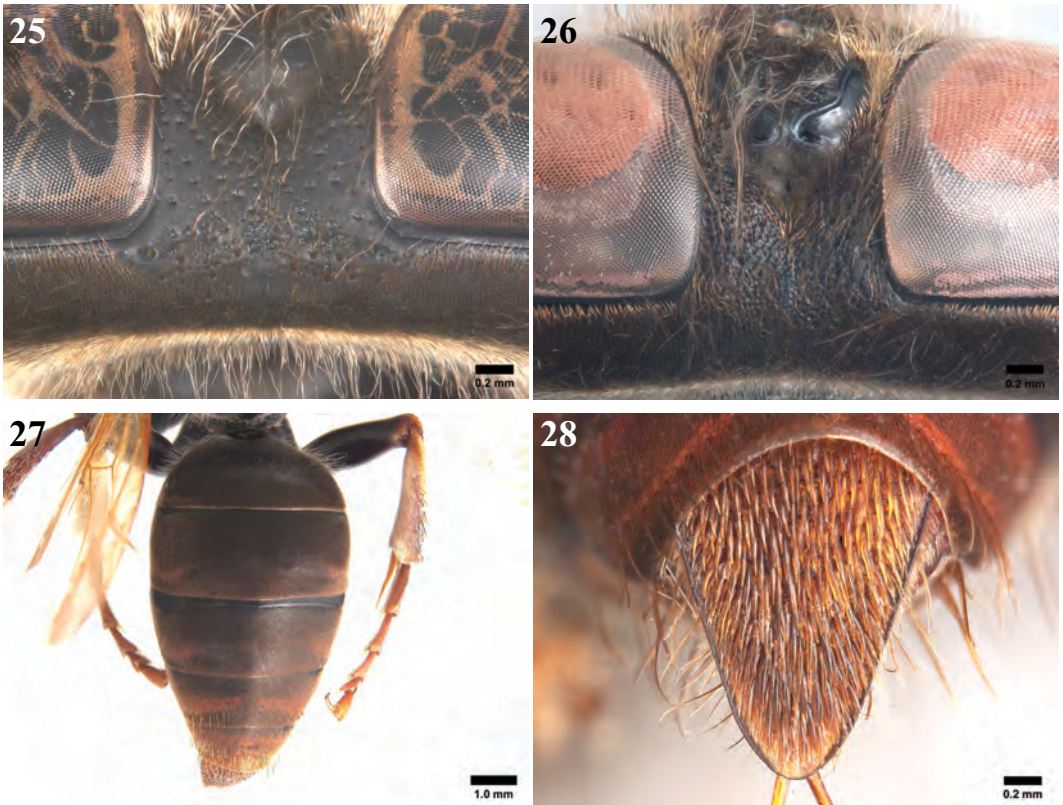


FIGURE 25. *Tachytes nudiventris* Turner. Postocellar area of female.

FIGURES 26-28. *Tachytes melanogaster* sp. nov. (26) Postocellar area of female; (27) Female gaster in dorsal view; (28) Pygidial plate of female showing color of setae.

brown in *T. melanogaster*, but the costal and subcostal veins are black in *T. nudiventris*. *T. nigropilosellus* differs conspicuously in having the erect setae of the head, thorax, and propodeum black (rather than silvery), the wings deep black with violet shimmer (rather than nearly hyaline, with yellow tinge), and by its much larger size (the female length is 23-30 mm, while 14.5-15.0 mm in *T. melanogaster*).

DESCRIPTION.—♀. Head nearly round in front view; minimum interocular distance equal to 0.32-0.34 of the clypeal width and to 1.4 × of dorsal length of flagellomere I; the latter 2.3-2.4 × apical width. Postocellar punctures mainly large, sparse, intermixed with smaller and denser punctures (Fig. 26). Gena narrow in dorsal view, narrower than in *T. panzeri*. Sternum II minutely, closely punctate throughout except narrowly impunctate apicomesally in one specimen. Forebasitarsus with five rake spines.

Pronotal collar posteriorly with appressed silvery setae, remaining thorax and propodeum without such setae. Setae of postocellar area about as long as 0.5 × scape; scutum anterolaterally without conspicuous appressed pilosity; scutal setae about as long as 0.4 × scape; sternum II anterolaterally with sparse, inconspicuous erect setae whose length is up to about 2 × midocellar width; longest setae of hindfemoral venter equal to about 0.4 × hindfemur greatest width. Setae of terga I-V all black and directed posteriorly; setae of pygidial plate cupreous (Fig. 28).

Head, thorax, and gaster all black; scape ferruginous (except partly or all black dorsally), fla-

gellum black. Femora all black or forefemur ferruginous in apicoventral half; foretibia brown or ferruginous, midtibia brown ferruginous, hindtibia brown; tarsi varying from brown to ferruginous.

♂.— Unknown.

GEOGRAPHIC DISTRIBUTION.— Known only from higher elevations (1020–1130 m above sea level) of Ranomafana National Park, Madagascar.

RECORDS (Fig. 29).— All specimens were collected in Ranomafana National Park, Fianarantsoa Province.

Holotype: ♀, Belle Vue at Talatakely at 21°15.99'S 47°25.21'E, alt. 1020 m, 14–21 Jan 2002, M. Irwin and R. Harin 'Hala (CAS).

Paratypes: Radio tower at forest edge at 21°15.05'S 47°24.43'E, alt. 1130 m, 23 Aug–7 Sept 2006 and 1–11 Nov 2006, M. Irwin and R. Harin 'Hala (2 ♀, CAS); same data as holotype except 22–28 Nov 2001 and R. Harin 'Hala alone (1 ♀, CAS); Vohiparara at 21°13.57'S 47°22.19'E, alt. 1110 m, 22–28 Nov 2001, R. Harin 'Hala (1 ♀, CAS).

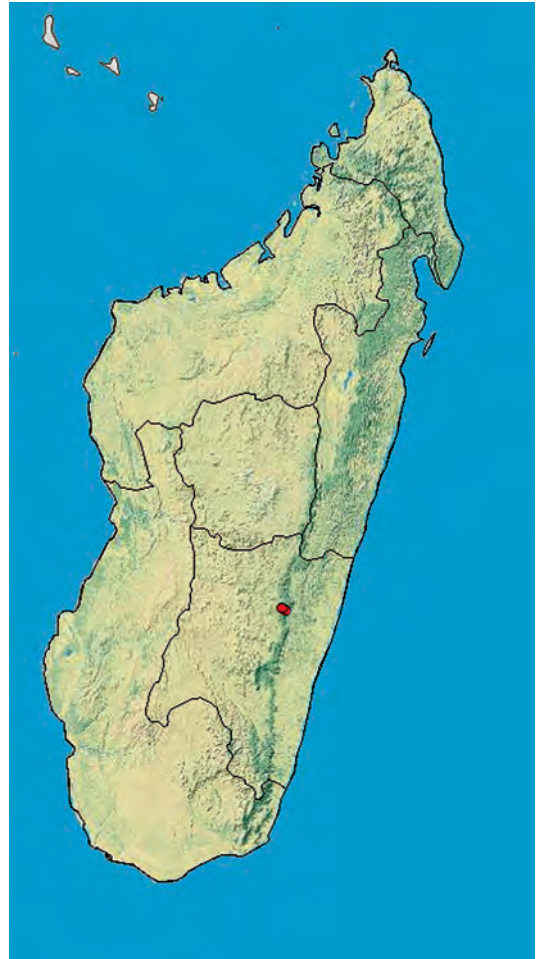


FIGURE 29. Collecting localities of *Tachytes melanogaster* sp. nov.

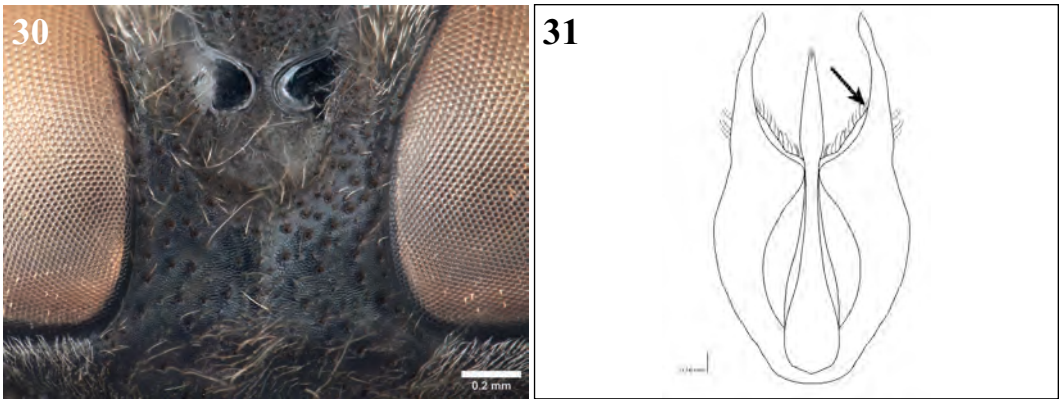
Tachytes picticornis Arnold

Figures 30–32.

Tachytes picticornis Arnold, 1945:111, ♀, ♂. Lectotype: ♂, Madagascar: Bekily (MNHN), **present designation.** — R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae); Leclercq, 1990:118 (Madagascar: locality records); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:987 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

LECTOTYPE SELECTION.— Through the kindness of Madame Claire Villemant of the MNHN, I received for examination in 2009 a pair of Arnold's syntypes of *Tachytes picticornis*, both collected at Bekily, Madagascar. I have selected the male as the lectotype, and the female as a paralectotype.

RECOGNITION.— Like most *Tachytes melanogaster*, the female of *T. picticornis* has the apical depressions of sterna II–V finely punctate. Also, it has the postocellar punctures large, without micropunctures there (Fig. 30). In the other species the depression of sternum II is impunctate mesally (only next to posterior margin in some *T. rufomarginatus*), the depressions of sterna III–V



FIGURES 30-31. *Tachytes picticornis* Arnold. (30) Postocellar area of female; (31) Male genitalia in dorsal view (arrow shows apex of volsella).

are impunctate, and the postocellar punctures are either of two distinct sizes or uniformly minute. The male can be recognized by the following color combination: scape black, apical two or three flagellomeres black at least ventrally and contrasting with the middle flagellomeres which are ferruginous. In addition, the volsella is shorter than the penis valve or the gonocoxite (Fig. 31).

RECORDS (Fig. 32).— **Antsiranana** (= Diego Suarez) **Province**: Parc National Montagne d'Ambré at 12°30'52''S 49°10'53''E (3 ♂, CAS) and 12°31'13''S 49°10'45''E (2 ♂, CAS), Réserve Spéciale d'Ankarana at 12°55'S 49°3'E (4 ♀, CAS), Sakalava Beach at 12°15'46''S 49°23'42''E (1 ♂, CAS), 1 km W Sakalava Beach at 12°15'59''S 49°23'42''E (1 ♂, CAS). **Fianarantsoa Province**: Forêt d'Ampitavananima at 23°7.79'S 47°43.02'E (3 ♀, CAS), 22 km SW Ilakaka at 22°46.75'S 45°1.50'E (14 ♀, 11 ♂, CAS), Isalo National Park at 22°36'S 45°10'E (1 ♂, CAS), near Isalo National Park at 22°37.60'S 45°21.49'E (3 ♀, 1 ♂, CAS), 7 km W Sendrisoa at 21°57.96'S 46°55.95'E (2 ♀, 1 ♂, CAS). **Majunga Province**: Ambovomamy Belambo at 15°27.07'S 47°36.80'E (3 ♀, 4 ♂, CAS), Forêt d'Analamanitra at 16°8'S 45°42'E (3 ♂, CAS). **Toliara Province**: Antanimora (Arnold, 1945), Bekily (1 ♀, 1 ♂ lectotype of *Tachytes picticornis*, MNHN), Bereboka village at 19°58.65'S 44°39.92'E (1 ♂, CAS), Beza Mahafaly Reserve at 23°41.19'S 44°35.46'E (4 ♂, CAS), Forêt de Mite at 23°31'27''S 44°7'17''E (1 ♀, CAS), Parc National d'Andohahela at 24°56.21'S 46°37.60'E (2 ♀, 2 ♂, CAS), Réserve Privée Berenty at 25°00'40''S 46°18'20''E (1 ♀, 3 ♂, CAS).

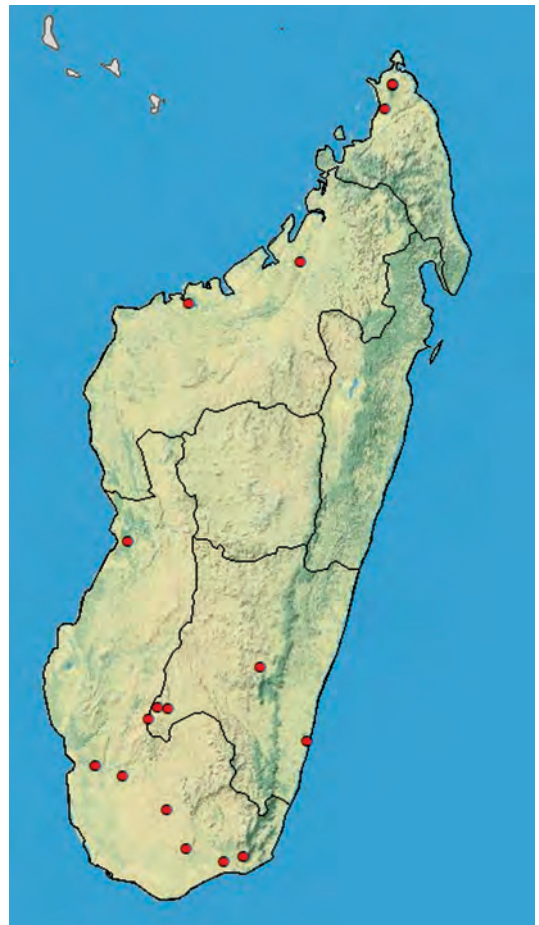


FIGURE 32. Collecting localities of *Tachytes picticornis* Arnold.

***Tachytes rufomarginatus* Arnold**

Figures 33–34.

Tachytes rufomarginatus Arnold, 1945:109, ♀, ♂ (as *rufomarginata*, incorrect original termination). Syntypes: Madagascar: Bekily (MNHN). – As *Tachytes rufomarginatus*: R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae); Nilsson, Jonsson, Rason, and Randrianjohany, 1986:412 (Madagascar: Toamasina: 4 km S Mahavelona, as Foulpointe, as *rufomarginata*); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:987 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

RECOGNITION.— The galea of *T. rufomarginatus* is slightly shorter than wide and terga I-III (I-IV in some specimens) are silvery fasciate apically. The female differs from similar species (*T. copiosus*, *T. flavocinereus*, *T. indifferens*, and *T. picticornis*) in having an ill-defined (almost absent) patch of silvery, appressed setae anterolaterally on the scutum (Fig. 33); the patch is well defined in the other species (e.g., Fig. 14). The males and most females differ from them by a partly reddish gaster, especially the apical segments. In the four other species, the gaster is all black. Subsidiary recognition features of *T. rufomarginatus* are: the scape all or predominantly ferruginous, and in the male a partly reddish brown flagellum.

RECORDS (Fig. 34).— **Antsiranana (= Diego Suarez) Province:** Montagne des Français at 12°18'8"S 49°38'51"E (1 ♀, CAS), Sakalava Beach at 12°15'46"S 49°23'51"E (1 ♀, CAS), 3 km W Sakalava Beach at 12°17.17'S 49°22.00'E (1 ♂, CAS). **Fianarantsoa Province:** Forêt d'Ampitananima at 23°7.79'S 47°43.02'E (1 ♀, CAS), near Isalo National Park at 22°37.60'S 45°21.49'E (3 ♀, 13 ♂, CAS), Réserve Spéciale Manombo at 23°01.31'S 47°43.20'E (2 ♀, 1 ♂, CAS). **Majunga Province:** Ambovomamy Belambo at 15°27.07'S 47°36.80'E (1 ♀, CAS), Forêt d'Analamanitra at 16°8'S 45°42'E (2 ♀, CAS). **Toamasina Province:** Forêt d'Analava Mandrisy at 16°29'08"S



Figure 33. *Tachytes rufomarginatus* Arnold. Anterodorsal part of thorax showing ill-defined patch of appressed, silvery setae.



FIGURE 34. Collecting localities of *Tachytes rufmarginatus* Arnold.

49°50'49"E (1 ♀, CAS), 4 km S Mahavelona (Nilsson, Jonsson, Rason, and Randrianjohany, 1986, as Foulpointe). **Toliara Province:** Bekily (Arnold, 1945), Parc National d'Andohahela at 24°56.21'S 46.37.60'E (3 ♀, 2 ♂, CAS).

Unrecognizable Species

Tachytes oviventris de Saussure

Tachytes oviventris de Saussure, 1891:260, ♀. Holotype or syntypes: ♀, Madagascar: no specific locality (originally A. von Schulthess collection, now destroyed). – de Saussure, 1892:478 (Madagascar, redescription); Dalla Torre, 1897:693 (in catalog of world Hymenoptera); Arnold, 1945:109 (unrecognizable species); R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae); Pulawski, 2003:798 (in checklist of Malagasy Sphecidae); Madl, 2014:987 (in catalog of Ampulicidae, Crabronidae, and Sphecidae of Madagascar, with synonymy and locality records).

Tachytes oviventris de Saussure, 1892:478, ♀. Objective synonym of *Tachytes oviventris* de Saussure, 1891.

DISCUSSION OF SPECIES IDENTITY.—The species was described rather concisely in 1891, in Latin only. In 1882, de Saussure repeated the Latin diagnosis almost verbatim, but provided a much more detailed description in French. Arnold (1945) commented about its unusual gaster coloration (he was not able to recognize the species). Indeed, the 1892 description mentions three characters unusual for a *Tachytes*: the gaster with bluish reflexes (*abdomine coerulescente* in Latin, *abdomen ... brillant de reflets bleuâtres et pourprés* in the French text), the postscutellum somewhat reddish mesally (*postécusson un peu roux au milieu*), and the recurrent veins attaining the 2nd submarginal cell very close to each other (*très près l'une de l'autre*). Evidently, none of the Madagascan *Tachytes* show this unusual character combination, and it is unclear, what other genus might be involved. Unfortunately, the holotype seems to be lost. De Saussure (1892) said that the specimen belonged to A. von Schulthess, whose collection is now housed in the Eidgenössische Technische Hochschule in Zurich, Switzerland. Ms. Franziska Schmid of that institution wrote the following on 23 June 2009:

“Unfortunately I only found two types of *Tachytes argyropis* from Madagascar in the Schulthess collection. Because the Schulthess collection had passed a serious pest damage about 50 years ago, the individuals of *Tachytes oviventris* might have been lost”.

As Monsieur Bernard Landry kindly informed me (his e-mail of 13 September 2018), no specimen of *T. oviventris* can be found in de Saussure's collection in the Muséum d'Histoire Naturelle de Genève, Switzerland, either. In conclusion, the species identity remains a mystery.

ACKNOWLEDGMENTS

I am greatly indebted to Monsieur Bernard Landry (Musée d'Histoire Naturelle, Genève, Switzerland) and Madame Claire Villemant (Muséum National d'Histoire Naturelle, Paris, France) for sending specimens under their care, Madame Villemant also for sending images of a syntype of *Tachytes copiosus*. I sincerely thank Robert L. Zuparko (California Academy of Sciences) for having critically reviewed the manuscript. Erin Prado (San Leandro, California) generated color illustrations using the Automontage software package by Syncrosopy, and Corinne Fuchs (Goleta, California) drew the male genitalia. Jere Schweikert (San Rafael, California) generated a database of all the localities mentioned here with their latitudes and longitudes, and Erika Garcia (Denver, Colorado) used it to produce the distribution maps.

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Table of Contents

| | |
|--|---------|
| JEFFREY L. WEINELL, ERROL HOOPER, ALAN E. LEVITON, AND RAFE M. BROWN: Illustrated Key to the Snakes of the Philippines | 1–49 |
| THOMAS F. DANIEL, LETSARA ROKIMAN, AND RAKOTONASOLO FRANCK: Incorporation of <i>Danguya</i> into <i>Anisotes</i> (Acanthaceae: Justiceae), a New Combination, and Lectotypification of <i>D. pulchella</i> | 51–59 |
| THOMAS F. DANIEL: New and Reconsidered Mexican Acanthaceae XIII: <i>Justicia</i> | 61–85 |
| JOHN C. DEEMING: Atherigonini (Diptera: Muscidae) from Madagascar | 87–98 |
| WILLIAM J. POLY: Record of the Long-horned Beetle, <i>Derobrachus hovorei</i> Santos-Silva, 2007 (Coleoptera: Cerambycidae), being Accidentally Transported to Ohio, USA | 99–103 |
| GARY C. WILLIAMS AND DANIELLE LIPSKI: The Pennatulacean Genus <i>Protoptilum</i> , with the Description of a New Deep-Sea Species from the Continental Slope of Central California (Octocorallia, Pennatulacea, Protoptilidae) | 105–116 |
| Wojciech J. Pulawski: A Review of the Wasp Genus <i>Trachytes</i> Panzer, 1806 of Madagascar (Hymenoptera: Crabronidae) | 117–135 |