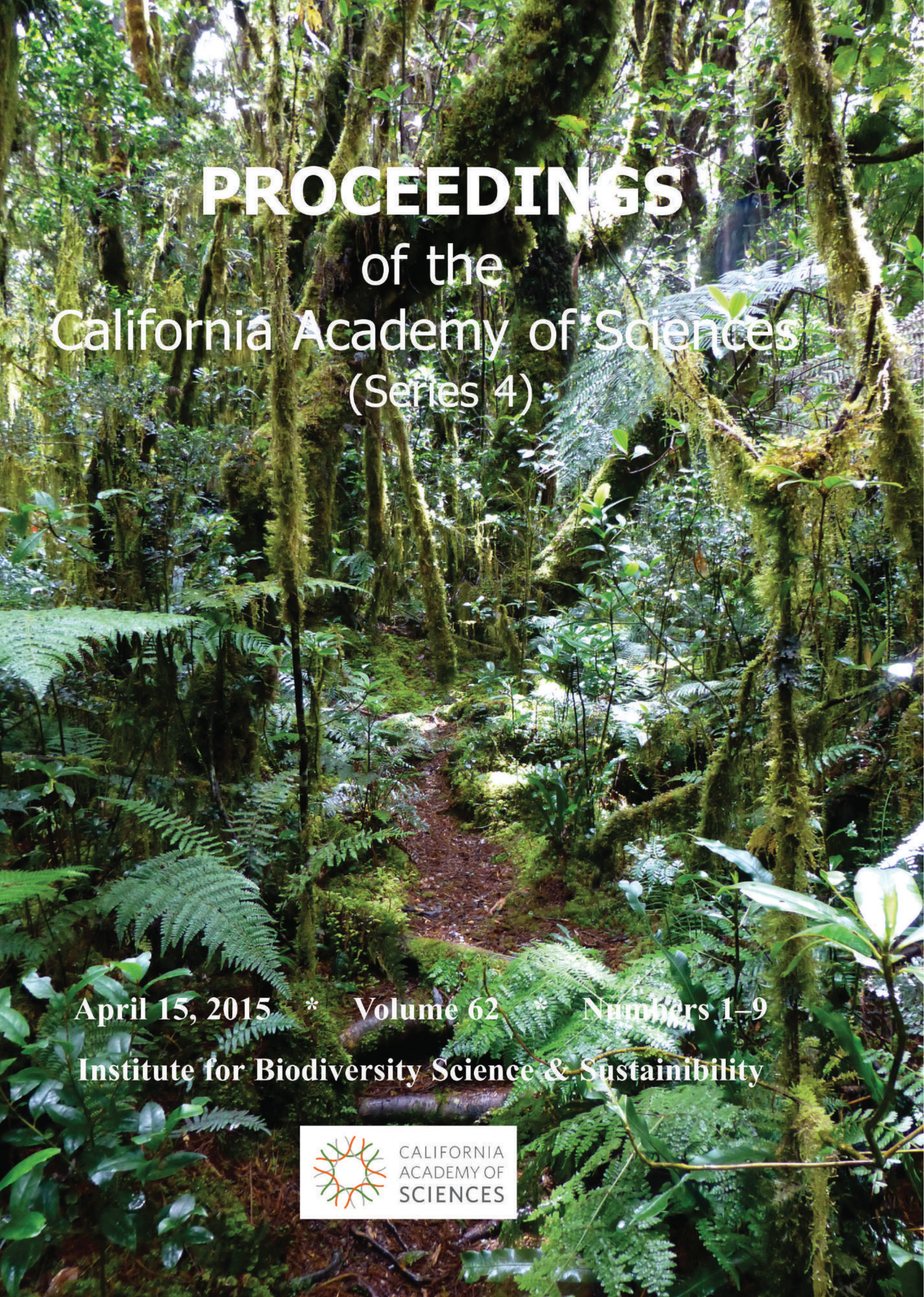

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Institute for Biodiversity Science & Sustainibility

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**COVER IMAGE**
**“Moss forest, Mindanao Island, Republic of the Philippines”**
(See Azuelo et al., Mosses New for Mindanao Island, p. 133, fig. 2)
Photo by James Shevock

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# Synopsis of *Trichanthera* (Acanthaceae: Ruellieae: Trichantherinae)

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***Trichanthera*** **consists of two Neotropical species of shrubs and trees.** ***Trichanthera gigantea*** **is widespread in northern South America and Panama, whereas** ***T. corymbosa*** **is restricted to northeastern Colombia and northwestern Venezuela. The unusual pollen of both species is characterized and conforms to that of most other genera of Trichantherinae. Pollination of** ***T. gigantea*** **by bats has been documented, and other floral visitors to that species include hummingbirds, bees, and ants. A key to genera of Trichantherinae is followed by a generic description, key to species, species descriptions, and discussions. Local common names and uses are listed for both species.** ***Trichanthera gigantea*** **demonstrates potential as an important tropical forage crop, and its use in northern South America contributes to local sustainability. Preliminary conservation assessments for each species are proposed. Maps of geographic ranges and illustrations of each species are provided.**

***Trichanthera*** **consta de dos especies neotropicales de arbustos y árboles, uno de los cuales,** ***T. gigantea*****, se encuentra en el norte de América del Sur y Panamá. La otra especie,** ***T. corymbosa*****, se limita al noreste de Colombia y noroeste de Venezuela. El polen inusual de ambas especies se caracteriza y ajusta al de la mayoría de los otros géneros de Trichantherinae. La polinización de** ***T. gigantea*** **por murciélagos ha sido documentada, y otros visitantes florales para esta especie incluyen colibríes, abejas y hormigas. Una clave para los géneros de Trichantherinae es seguida por una descripción genérica, clave para las especies, descripciones de cada especie, y discusiones. Nombres comunes locales y usos se incluyen para ambas especies.** ***Trichanthera gigantea*** **demuestra potencial como un importante cultivo de forraje tropical, y su uso en el norte de América del Sur contribuye a la sostenibilidad local. Se proponen evaluaciones preliminares de conservación para cada especie. Se incluyen mapas de distribución geográfica e ilustraciones de cada especie.**

*Trichanthera* Kunth consists of two Neotropical species that occur in southern Central America and northern South America. Leonard (1930) provided a taxonomic synopsis of the genus in which both species and a variety of *T. gigantea* were recognized. The present account summarizes and augments morphological, geographical, ecological, and phylogenetic knowledge gained about *Trichanthera* during the past 85 years. The increasing use of *T. gigantea* as a forage crop in various parts of the world highlights the need for accurate information about these aspects of the genus.

*Trichanthera* has traditionally been treated in tribe Trichanthereae of subfamily Ruellioideae along with four other Neotropical genera (*Bravaisia* DC., *Sanchezia* Ruiz & Pav., *Suessenguthia* Merxm., and *Trichosanchezia* Mildbr.), all of which share the morphological synapomorphy of "loxodicolporate" pollen (Daniel 1998). Recent molecular phylogenetic studies reveal this assemblage (i.e., "core Trichantherinae") to be monophyletic and sister to the Neotropical (primarily

Mexican) genus *Louteridium* S. Watson (Tripp et al. 2013). All six genera were treated as subtribe Trichantherinae by Tripp et al. (2013). *Louteridium* differs from other Trichantherinae by numerous morphological distinctions (see key below), and was previously treated in its own tribe. The tree habit, which is rare among Acanthaceae, is probably best expressed in this subtribe. It occurs in both species of *Trichanthera,* as well as among species of *Louteridium*, *Suessenguthia*, and *Bravaisia*. Among core Trichantherinae, *Trichanthera* and *Bravaisia* are sister to the remaining three genera, which form a strongly supported "staurogynoid clade." Tripp et al. (2013) treated all six genera as Trichantherinae, one of seven subtribes of tribe Ruellieae. Taxonomic revisions have been provided for *Bravaisia* (Daniel 1988), *Louteridium* (Richardson 1972; Daniel and Tripp in prep.), *Sanchezia* (Leonard and Smith 1964), *Suessenguthia* (Wasshausen 1970; Schmidt-Lebuhn 2003), and *Trichanthera* (Leonard 1930). These genera, and unispecific *Trichosanchezia* (Mildbraed 1926), can be characterized and identified by the morphological attributes in the following key:

## Key to Genera of Trichantherinae

1a. Calyx 3-lobed; corolla throat conspicuously gibbous-saccate ventrally; seeds 12–24 per capsule; pollen pantoforate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Louteridium*
1b. Calyx 5-lobed; corolla throat sometimes ampliate but not conspicuously gibbous-saccate ventrally; seeds up to10 per capsule; pollen loxodicolporate . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Corolla subcylindric (or at least with the tube subcylindric and elongate; or if with a ± ampliate throat as sometimes in *Suessenguthia multisetosa*, then with flowers borne in headlike involucres subtended by several pairs of bracts); fertile stamens 2 or 4. . . . . . . . . . . . . . . . . 3
2b. Corolla ± campanulate (i.e., throat ampliate; flowers not borne in headlike involucres as described above); fertile stamens 4 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

3a. Fertile stamens 2 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Sanchezia*
3b. Fertile stamens 4 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4a. Thecae awned at base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Suessenguthia*
4b. Thecae awnless . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Trichosanchezia*

5a. Thecae awnless, rounded at base; capsule pubescent at maturity; flowers borne on pedicels 2–11 mm long; stigma 1.5–4.5 mm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Trichanthera*
5b. Thecae awned with a single, subulate projection 0.3–1 mm long at base; capsule glabrous at maturity; flowers sessile or borne on pedicels to 2 mm long; stigma to 1 mm long. *Bravaisia*

Both species of *Trichanthera* exhibit the loxodicolporate pollen characteristic of the core Trichantherinae (Fig. 1). Grains can be characterized (with shapes, measurements, and ratios in parentheses based on data from Raj 1961) as globose-elliptic to globose-oblong, longer equatorial axis:shorter equatorial axis = 1.03–1.75, 2-colporate, polypseudocolpate, polar axis = 67–79 (–101) μm, equatorial axis of apertural face = 55–70 (–96) μm, equatorial axis of interapertural face = 40–62 (–83) μm, apertural face subcircular to broadly elliptic in outline, interapertural face broadly elliptic to oblong in outline, colpi and pseudocolpi microgemmate to gemmate, exine between colpi divided into bands by pseudocolpi, bands psilate and perforate to foveolate with a single and central row of round to elongate lumina 0.3–3.3 μm in diameter or long, portion of the 2 bands flanking ora protruding and liplike, sculptural features of one apertural face usually oriented ± 90° to those of opposing face. Roubik and Moreno P. (1991) described pollen of *T. gigantea* from Barro Colorado Island in Panama as "spheroidal" and 63–127 μm.

Although fossil pollen showing similarities to that of core Trichantherinae has been described

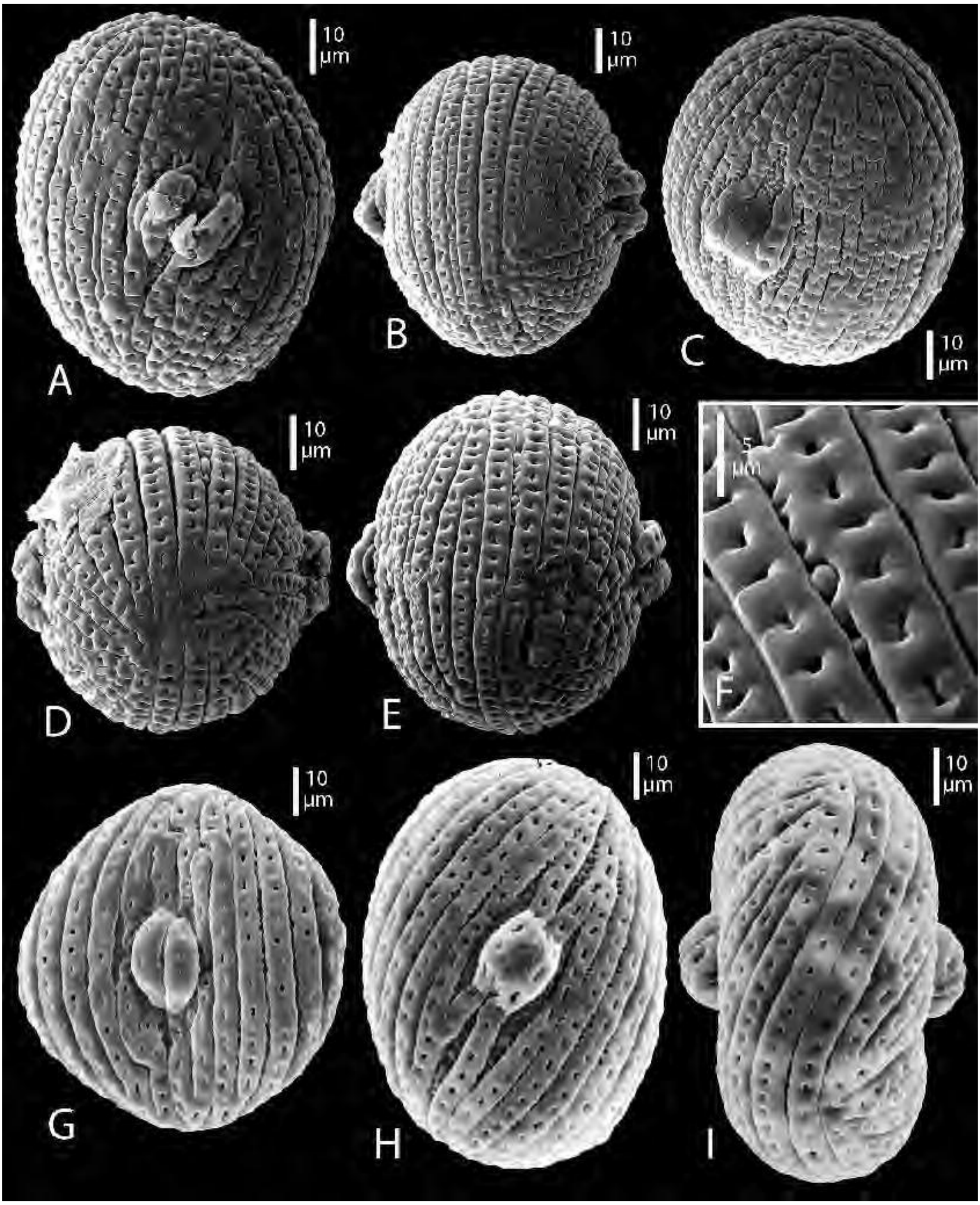

FIGURE 1. Pollen of *Trichanthera*. A–F. *T. corymbosa* (*Romero-Castañeda 10753*). A. Apertural view. B. Interapertural view with apertural faces oriented at ± right angles to each other. c. Subapertural view. D. Interapertural view of subradially symmetric grain. E. Interapertural view with apertural faces offset but oriented less than 90° relative to each other. F. Close-up of pseudocolpi and exine bands. G–I. *T. gigantea* (*Daniel et al. 5474*). G. Apertural view. H. Apertural view showing sculpturing of colpi and pseudocolpi. I. Interapertural view with apertural faces oriented at right angles to each other.

from both the Triassic (Pocock and Vasanthy 1988; North America, ca. 227–231 Ma) and Jurassic (Cornet and Habib 1992; Europe, ca. 157–163 Ma) periods of the Mesozoic era, the likelihood of highly derived angiospermous pollen from times as early as these would appear to be anomalous. Similar pollen from the Miocene has been used in dating analyses (Tripp and McDade 2014; q.v. for a ranking of the utility of various reports).

Elsewhere among Ruellieae, the normally 3-colporate and polypseudocolpate pollen of *Strobilanthes neilgherrensis* Bedd. (as *Nilgirianthus neilgherrensis* (Bedd.) Bremek.) in Strobilanthinae was observed to have several rare variants in aperture number and torsion of exinal features that included a single 2-aperturate grain with opposing faces ± 90° out of phase with one another (Vasanthy and Pocock 1986). These authors also noted the occurrence of rare transitional (i.e., with partially rotated hemispheres) grains, and very rare radially symmetric grains, among the otherwise loxodicolporate grains of *Bravaisia integerrima* (Spreng.) Standl. and *Sanchezia lampra* Leonard & L.B. Sm. Pollen of *Trichanthera corymbosa* examined here also varies from nearly radial to the rotated symmetry (up to 90°) common among Trichantherinae. Thus, variation in pollen of these species from two subtribes of Ruellieae likely provides insights into the origin of pollen characteristic of core Trichantherinae. Whereas the rare occurrence of loxodicolporate pollen in *S. neilgherrensis* appears to be anomalous, this type of pollen has become generally “fixed” among core Trichantherinae.

***Trichanthera*** Kunth in Humboldt, Bonpland and Kunth, Nova Gen. Sp. 2:243. 1818 (“1817”) (non Ehrenberg 1829). **TYPE.**— *Trichanthera gigantea* (Bonpl.) Nees ( ≡ *Ruellia gigantea* Bonpl.)

*Trixanthera* Raf., Sylva Tell. 146. 1838. **TYPE.**— *Trixanthera angularis* Raf., nom. illeg. ( ≡ *Ruellia gigantea* Bonpl.)

Shrubs or medium-sized trees with cystoliths, sometimes with multiple trunks and prop roots. Young stems quadrate-sulcate, often with warty or blisterlike tubercles on surface. Leaves opposite, petiolate, the pair at a node equal or usually unequal in size, blades subcoriaceous. Inflorescence of terminal thyrses (i.e., bearing pedunculate dichasia with pedicellate flowers) or, when branched, a terminal panicle of thyrses; each dichasium + peduncle subtended by a bract, each flower + pedicel subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic or heteromorphic (4+1), imbricate during anthesis, sometimes elongating in fruit. Corolla ± campanulate, internally ± waxy or glossy, externally densely pubescent (except for proximal portion), tube funnelform with narrow proximal portion subcylindric and throat ampliate, limb 2-labiate or appearing ± actinomorphic, upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud. Stamens 4, in two pairs, each pair consisting of a longer and a shorter stamen that are fused proximally, inserted at or near base of throat, exserted from mouth of corolla, extending beyond lips of corolla, longer stamen of each pair posterior and central in display of stamens, anthers 2-thecous, thecae of a pair equally inserted, parallel to subsagittate, rounded at base, lacking appendages, dehiscing toward lower lip (i.e., flower nototribic), pollen loxodicolporate. Style exserted from mouth of corolla, extending beyond lips, stigma asymmetric, usually exserted beyond anthers, 1 lobe ± vestigial. Capsule ellipsoid, estipitate, bearing retinacula. Seeds up to 10 per capsule, lenticular, surfaces smooth, shiny, and lacking trichomes.

The genus consists of two species and is native to southern Central America (Panama) and northern South America (Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela). Both species occur in moist to wet forests.

The generic name *Trichanthera* is nearly universally cited as having been published by Kunth in Humboldt, Bonpland, and Kunth’s *Nova Genera et Species Plantarum* vol. 2, on page 243 (the quarto edition was published earlier, in February, than the folio edition, which was published in June, of 1818; the publication date listed on the printed copies was “1817;” Stafleu and Cowan 1979). In this publication, Kunth indicated that *Ruellia gigantea*, “certe distincti generis ob stamina exserta, antheras pilosas et capsulae loculos dispermos. Fortasse Trichanthera nominandum.” Thus, he was indicating that the species was deserving of generic status and proposed “Trichanthera” as a possible name, but did not accept it in this publication. In 1829, Ehrenberg published *Trichanthera* Ehrenb. for an Old World genus of Zygophyllaceae (subsequently treated in Malvaceae and Sterculiaceae). This name has been treated as illegitimate due to the prior existence of Kunth’s name. *Eurynema* Endl. was proposed by Endlicher (1842) as a new name for Ehrenberg’s “illegitimate” name, but no combination was made for the sole species, *T. modesta* Ehrenb., which is now known as *Hermannia modesta* (Ehrenb.) Mast. (the combination for this name was effected by Masters in 1868, where the combination was attributed to Planchon, who instead made the combination *Mahernia modesta* (Ehrenb.) Planch. in 1855; *Mahernia* L. is sometimes treated as a synonym of *Hermannia*). However, if Kunth’s name was not validly published, *Trichanthera* Ehrenb. becomes legitimate; it is currently treated as a heterotypic synonym of *Hermannia* L. The next generic name proposed for the acanthaceous species treated by Kunth was *Trixanthera* Raf., proposed by Rafinesque (1838) specifically for *Ruellia gigantea*, to which species he gave the name *T. angularis* Raf. If Kunth’s generic name had been validly published, *Trixanthera* would be a synonym of it and *Trixanthera angularis* would be an illegitimate name and synonym of *Trichanthera gigantea*. Apparently, the first publication of the acanthaceous genus *Trichanthera* was that of Meisner (1840), who attributed the generic name to Kunth, but provided his own description. In 1847, Nees made the combination for the type, *T. gigantea* (Bonpl.) Nees

From the preceding summary, it is clear that *Trichanthera* Kunth is not validly published and that *Trichanthera* Ehrenb. has priority over *Trichanthera* Meisn. Without proactive nomenclatural actions (e.g., conservation), the oldest legitimate name for the genus containing *Ruellia gigantea* is *Trixanthera* Raf., and new combinations for *R. gigantea* and *T. corymbosa* in that genus would be necessary. It might be argued that Rafinesque’s name should be considered an orthographic error (“trich” refers to hairs, “trix” refers to three-fold) for Kunth’s name, and that he was, in effect, validating Kunth’s proposed name. Were it not for Ehrenberg’s publication of *Trichanthera* for the sterculiaceous genus nine years before Rafinesque’s publication, this might have been a fortuitous argument to preserve the original spelling of Kunth’s name.

A proposal for conservation of the acanthaceous name *Trichanthera* is currently being prepared for submission to the Nomenclature Committee for Vascular Plants of the International Association for Plant Taxonomy. Although incorrect, the traditional author citation for the genus is used herein in accordance with Recommendation 14A.1 of McNeill et al. (2012).

## Key to the Species of *Trichanthera*

1a. Thyrse usually corymbose; calyx 14–24 mm long during anthesis, lobes heteromorphic with 1 lobe conspicuously longer and wider (ca. 1.5 × or more wider) than others, the four similar lobes linear to linear-elliptic to linear-lanceolate, 2–4 mm wide, acute at apex; bracteoles and secondary bracteoles oblanceolate to linear, 4–12 (–25) mm long . . . . . . . . . 1. *T. corymbosa*

1b. Thyrse elongate; calyx 6–13 mm long during anthesis, lobes homomorphic and ± equal in size, ovate-elliptic to elliptic, 3.5–7.3 mm wide, rounded at apex; bracteoles and secondary bracteoles triangular, 2–4 mm long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2. *T. gigantea*

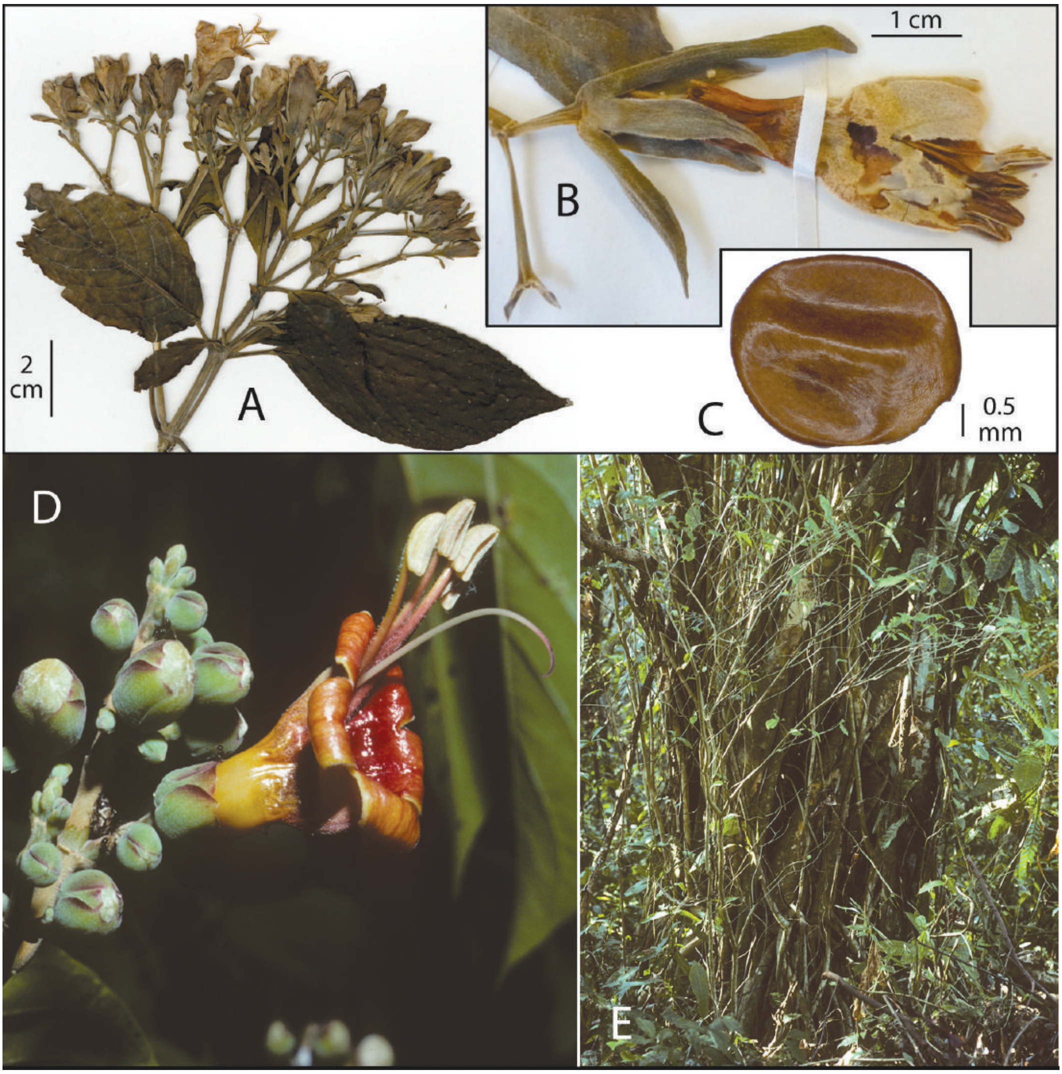

FIGURE 2. *Trichanthera corymbosa* (A–C) and *T. gigantea* (D, E). A. Corymbose inflorescence (*Romero C. 10753*, MO). B. Flower showing calyx with heteromorphic lobes (*Pittier 12828*, NY). C. Seed (*Trujillo & Fernández 16379*, US). D. Inflorescence and flower (*Daniel et al. 5474*). E. Base of tree with suckering (*Daniel et al. 5474*).

**1. *Trichanthera corymbosa*** Leonard, J. Wash. Acad. Sci. 20:487. 1930. **TYPE.**— COLOMBIA. **Norte de Santander**: Culagá Valley, near Tapatá (N of Toledo), 1500–2100 m, 3–8 March 1927, *E. Killip & A. Smith 20140* (holotype: US!; isotypes: BM!, GH-image!, NY!). Figure 2.

Trees to 20 m tall; young stems covered with sessile and lenticular glands to 0.05 mm in diameter (often inconspicuous; punctate-glandular) and puberulent with antrorse eglandular trichomes to 0.1 mm long, nodes sometimes with longer flexuose eglandular trichomes as well. Leaves petiolate, petioles to 45 mm long, blades ovate to elliptic to broadly elliptic, 33–265 mm long, 16–140 mm wide, 1.3–2.4 × longer than wide, rounded to cuneate at base, acute to acuminate at apex, surfaces punctate-glandular and sometimes with eglandular trichomes along major veins on abaxial surface, margin sinuate to sinuate-crenate. Inflorescence a terminal corymbose thyrse (or if basally branched, then a panicle of thyrses) 48–149 mm long, rachis punctate-glandular and pubescent with antrorse eglandular trichomes 0.05–0.2 mm long, dichasia expanded to a greater or lesser degree, pedunculate, peduncles to 55 mm long, pubescent like rachis, secondary peduncles similar to peduncles. Bracts often caducous, subfoliose and reduced in size distally, ovate to elliptic to oblanceolate to linear, 7–72 (–170) mm long, 2–34 (–80) mm wide, pubescent like leaves (proximal bracts) or rachis (distal bracts). Bracteoles and secondary bracteoles (subfoliose to) oblanceolate to linear, 4–12 (–25) mm long, 1–3.2 (–5) mm wide. Flowers pedicellate, pedicels 4–11 mm long. Calyx green with purplish tinge, 14–24 mm long during anthesis, tube 2–4 mm long, lobes heteromorphic (4 + 1), four similar lobes linear to linear-lanceolate to linear-elliptic, 8–19 mm long, 2–4 mm wide, acute at apex, fifth (posterior) lobe lanceolate to elliptic to oblong to obovate-elliptic, 12–27 mm long 4.5–8.5 mm wide, longer than and ca. 1.5 or more × wider than other lobes, rounded to acute to attenuate at apex, lobes with abaxial surface punctate-glandular and with eglandular trichomes like those of rachis, margin ciliate with similar eglandular trichomes. Corolla whitish to maroon or purplish (see discussion), (18–) 23–43 mm long, externally punctate-glandular and densely pubescent with retrorsely appressed eglandular trichomes to 0.5 mm long (except for proximal portion of tube which lacks eglandular trichomes), narrow proximal portion of tube 7–15 mm long, throat 8–18 mm long, 9–13 mm in diameter near midpoint, limb 18–34 mm in diameter, lobes oblong to broadly ovate to triangular, 6–12 mm long. Stamens ca. 20–27 mm long, filaments pubescent proximally with flexuose eglandular trichomes to 3 mm long and sometimes with glandular trichomes as well, sometimes glabrous or nearly so distally, thecae 4–6.5 mm long, (glabrous or) pubescent with flexuose eglandular trichomes to 1.5 mm long and on dorsal surface and connective also pubescent with sessile glands (≤ 0.05 mm diam.), pollen (*Romero-Castañeda 10753*) 72–74 µm (polar axis) × 55–60 µm (equatorial axis, apertural face) × 56–62 µm (equatorial axis interapertural face). Style 28–38 mm long, pubescent proximally, glabrous distally, stigma with 1 lobe straight, 1.5–4 mm long, other lobe vestigial, 0.05–0.2 mm long. Capsule 16–21 mm long, densely pubescent with straight to flexuose eglandular trichomes to 1 mm long. Seeds 3.6–4 mm long, 2.9–3.6 mm wide.

**PHENOLOGY**.— Flowering: October–March. Fruiting: October–March.

**DISTRIBUTION AND HABITATS**.— Northern South America (northeastern Colombia and northwestern Venezuela; Fig. 3). Plants occur along streams in moist to wet lowland to montane primary and secondary forests (including cloud forests) at elevations from 900 to 1800 m (possibly up to 2300 m fide Bono 1996). The distribution of this species occurs exclusively within that of the more widespread *T. gigantea*. Indeed, the two species of *Trichanthera* would appear to be sympatric or at least to grow in the near vicinity of one another; the type of *T. corymbosa* and a collection of *T. gigantea* were both collected at the same locality by Killip and Smith in the department of Norte de Santander, Colombia.

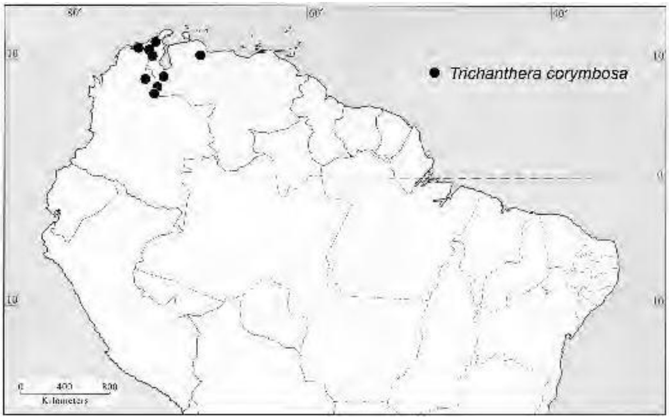

FIGURE 3. Distribution of *Trichanthera corymbosa*.

**Local name**.— Yátago (Venezuela; Bono 1996).

**Uses**.— Planted as living fences along roads and streams in Venezuela (Bono 1996).

**Conservation**.— *Trichanthera corymbosa* is known from fewer than 20 collections in a limited geographic region (extent of occurrence = ca. 114,900 km$^2$; area of occupancy with grid cell area of 4 sq. km = 44 km$^2$; north-south linear distance = ca. 390 km; east-west linear distance = ca. 560 km). Based on the AOO, the species could be considered as endangered (EN) if two subcriteria under criterion B are met. Three geographically isolated subpopulations could be recognized, all of which are potentially threatened by deforestation; thus, a single location for this species is currently proposed. Based on satellite imagery (e.g., Google Inc. 2013), local deforestation is evident for at least five of the 11 mapped collection sites for this species. Thus two of the three subcriteria needed to make an assessment in a threatened category for this species are fulfilled, and a status of EN (B2, a, b) is provisionally proposed for this species.

**Morphological variation**.— Corollas of *T. corymbosa* are sometimes described as white, whitish, yellow, or flesh-colored. Some of these descriptions possibly refer to the dense covering of whitish trichomes on the external surface. The internal surface is described as white (e.g., *Bunting et al. 12260*), maroon (e.g., *Ruiz T. & López F. 1385*), or purple (e.g., *Pittier 12828*). Thus, as in *T. gigantea* (see below), there appears to be variation in the color of corollas of this species.

As is evident from the description above there is also variation in the pubescence of the androecium in this species. The thecae of *Romero C. 7504* are glabrous whereas they are pubescent (where seen) among other collections. In *Romero C. 10753* the portion of the filaments that is exserted from the corolla tube is glabrous; in *Trujillo & Fernández 16379*, that portion is pubescent with both eglandular and glandular trichomes proximally and glabrous distally. Additional observations on entire androecia in flowers of this species are desirable; based on these observations, however, variation in androecial pubescence of *T. corymbosa* appears similar to that in *T. gigantea*.

Inflorescences of *T. corymbosa* are almost always corymbose; however, in *Trujillo & Fernández 16379* from Venezuela they are elongate (up to 230 mm), like those of *T. gigantea*. Calyx lobes and bracteoles of this collection are like those typical of *T. corymbosa*, in which species this collection is treated here. Overall length of the inflorescence (measured from the first lateral branch bearing dichasia or, if such is absent, then from first dichasium to the apex of the inflorescence, excluding corollas), although often shorter in *T. corymbosa* than in *T. gigantea*, overlaps to an extent that it does not appear to be distinctive for either species. *Bunting et al. 12260* is somewhat unusual by its exceptionally large foliose bracts (to 170 × 80 mm) at the base of the inflorescence and its large bracteoles (to 25 × 5 mm) on the proximal dichasia.

A Colombian collection (*Cañas 810*) shows intermediacy between *T. gigantea* and *T. corymbosa* in calyx length (to 15 mm) and form (lobes slightly heteromorphic with the smaller lobes rounded to acute apically). Bracteoles of this collection are like those of *T. gigantea*, however, in which species this collection is treated. Another collection from Colombia (Norte de Santander: Ocaña, 6000 ft., *Kalbreyer 1264* at K) shows intermediacy between the two species in most of the characters noted in the key. Given the apparent sympatry of these species as noted above, similarity of their flowers, and relative ease of artificial interspecific hybridization demonstrated in several genera of Acanthaceae (e.g., Long 1975 and Daniel 2007 for *Ruellia* L.; Daniel 1983 for *Carlowrightia* A. Gray; Daniel 1984 for *Anisacanthus* Nees; Daniel 1986 for *Tetramerium* Nees), hybridization between the two species of *Trichanthera* might account for the rare instances of intermediacy observed.

**Additional specimens examined**.— **Colombia: Cesar**: Sierra de Perijá, eastern Manaure, hoya del Río Manaure, San Antonio, *J. Cuatrecasas & R. Romero-Castañeda 25341* (F, US);

Cordillera Oriental, Corregimiento Manaure, Finca Los Venados, *R. Romero-Castañeda 7504* (MO, US). **Magdalena**: de San Pedro a Cebolleta, *R. Romero-Castañeda 10753* (F, MO, NY). **Norte de Santander**: environs de Ocaña, *L. Schlim 135* (BM, K, P).— **Venezuela: Mérida**: vicinity of Tovar, along Río Mocoties, *H. Pittier 12828* (G, NY, US). **Táchira**: Distr. Junín, Las Lajas, entre Delicias y Villa Páez, *L. Ruiz T. & M. López F. 1385* (US). **Yaracuy**: Distr. Bruzual, Mpio. Campoelías, vertiente sur, próxima a carretera Campoelías–La Laguna–Tupe, *B. Trujillo 16021* (MO); Distr. Bruzual, Mpio. Campoelías, La Puente, riachuelo permanente en carretera Campoelías–Tierrita Blanca, km 10, *B. Trujillo & A. Fernández 16379* (MO, US). **Zulia**: Distr. Mara, alrededores de Puesto "El Bosque" de la Guardia Nacional, 10°47′N, 072°40′W, *G. Bunting et al. 12260* (NY, US); Ayapa [Ayapaina], Sierra Perijá, W of Machiques, *Bro. Ginés 147* (US); Sierra de Perijá, a lo largo de la quebrada del Río Omira–Kuná (Tumuriasa), cerca de la frontera Colombo-Venezolana, SW de Pishikakao e Iría, *J. Steyermark et al. 105547* (G, MO, US).

**2. *Trichanthera gigantea*** (Bonpl.) Nees in A. de Candolle, Prodr. 11:218. 1847. *Ruellia gigantea* Bonpl. in Humboldt and Bonpland, Pl. Aequinoct. 2:75, t. 102. 1810–1811 ("1809"). *Trichanthera gigantea* Bonpl. ex Steud, Nomencl. ed. 1, p. 708. 1821, nom. illegit. (in syn.). *Trixanthera angularis* Raf., Sylva Tellur. 146. 1838, nom. illegit. **Type**.— Colombia. "Habitat frequentissime in sylvis fluvii Magdalenae, prope Badillas et juxta Ybague," (fide protologue), without locality or date (specimen), *A. Humboldt & A. Bonpland s.n.* (lectotype, designated here; see discussion below: P-00719181!). Figure 4.

*Clerodendrum verrucosum* Splitg. ex de Vriese, Ned. Kruidk. Arch. 1:351. 1848 (as "*Clerodendron verrucosum*"). *Besleria verrucosa* (Splitg. ex de Vriese) Pulle, Recueil Trav. Bot. Néerl. 9:163. 1912. **Type**.— Suriname. "Crescit ad margines fluminum Parae cet. satis frequens," January 1838, *F. Splitgerber 523* (fide Wasshausen, 2006: holotype: L; isotype: P).

*Besleria surinamensis* Miq., Linnaea 22:471. 1849. **Type**.— Suriname: without locality, *F. Hostmann 764* (lectotype, designated by Wasshausen in 2006: U-image!; possible isolectotypes, see discussion below: MO!, P!, S!).

*Trichanthera gigantea* var. *guianensis* Gleason, Bull. Torrey Bot. Club 54:617. 1927. **Type**.— Guyana. **East Berbice-Corentyne**: Greale, Corentyne River, Oct 1879, *G. Jenman 371* (lectotype, designated here; see discussion below: K-image!).

Shrubs to trees to 15 (–25) m tall and to 30 (–140) cm in diameter (DBH), often suckering from and/or with prop roots at base, sometimes with multiple trunks, branches sometimes long and pendant; young stems densely pubescent with flexuose to antrorse eglandular trichomes 0.05–0.3 mm long, trichomes sometimes deciduous in patches, mature stems glabrate. Leaves petiolate, petioles to 75 mm long, blades ovate to elliptic 60–310 mm long, 34–150 mm wide, 1.4–2.6 × longer than wide, rounded to acute to subattenuate at base, acute-apiculate to acuminate at apex, surfaces covered with sessile and lenticular glands to 0.05 mm in diameter (sometimes inconspicuous; punctate-glandular), otherwise nearly glabrous and with any trichomes mostly restricted to major veins, margin entire to sinuate. Inflorescence an elongate terminal thyrse or panicle of thyrses, 50–200 mm long, rachis hidden by dense trichomes like those of young stems, dichasia expanded to a greater or lesser degree, pedunculate, peduncles 6–17 mm long, pubescent like rachis, secondary peduncles similar to peduncles. Bracts caducous or persistent, ovate to triangular, 2–5 mm long, 2–3 mm wide, proximal pair(s) sometimes somewhat leaflike and larger, pubescent like rachis. Bracteoles and secondary bracteoles triangular, 2–4 mm long, 1.5–2.4 mm wide. Flowers pedicellate, pedicels 2–8 mm long. Calyx green or purplish (at least distally), 6–13 mm long during anthesis, tube 1–3 mm long, lobes homomorphic, imbricate, ovate-elliptic to elliptic to oblong

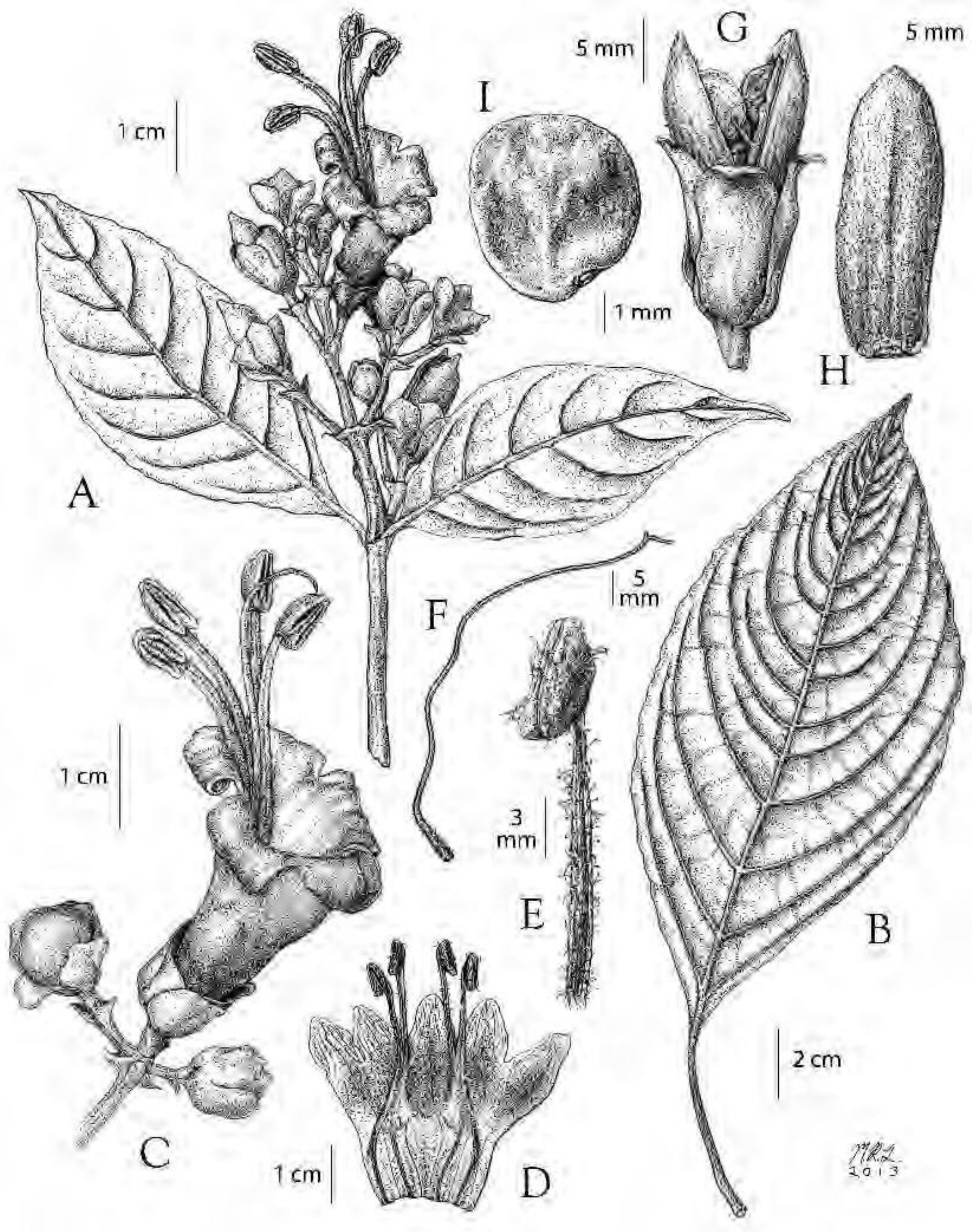

FIGURE 4. *Trichanthera gigantea*. A. Distal portion of branch with inflorescence (*Luteyn & Pipoly 9378*, CAS). B. Leaf from proximal portion of shoot (*McPherson 7081*, CAS). C. Dichasium (*Daniel et al. 5474*, CAS). D. Corolla opened to show stamens (*Daniel et al. 5474*, CAS). E. Stamen (*Daniel et al. 5474*, CAS). F. Style and stigma (*Daniel et al. 5474*, CAS). G. Calyx and capsule (*Daniel & Herrera 5490*, CAS). H. Capsule (*Luteyn & Pipoly 9378*, CAS). I. Seed (*Daniel et al. 5474*, CAS). Drawn by M. Logies.

to obovate-elliptic, 5–11 mm long, 3.5–7.3 mm wide, rounded at apex, abaxial surface punctate-glandular and pubescent with antrorse eglandular trichomes, margin ciliate with erect to flexuose eglandular trichomes to 0.7 mm long. Corolla appearing ± glossy where not covered with trichomes, salmon-colored to dark reddish to brownish red to maroon in throat with lobes similarly colored or often tinged with yellow (along margins or distally) or entirely yellowish internally, 27–45 mm long, externally punctate-glandular and distally densely pubescent with appressed eglandular trichomes (such that the obscured surface appears pale) while lacking eglandular trichomes proximally, narrow proximal portion of tube 7–20 mm long, throat (6.5–) 9–20 mm long, 8–16 mm in diameter near midpoint, limb (15–) 20–30 mm in diameter, lobes often reflexed to recoiled, ovate, 6–11 mm long. Stamens 25–35 mm long, filaments salmon-colored to reddish or maroon proximally and often yellowish distally, pubescent (the longer stamen of each pair more densely so) with glandular (sometimes sparse or inconspicuous) and eglandular trichomes, thecae yellowish, 4.5–7 mm long, pubescent with flexuose eglandular trichomes to 3 mm long and dorsally puberulent with subsessile glands to 0.1 mm long (also on connective), pollen (*Daniel et al. 5474*) 67–79 µm (polar axis) × 63–70 µm (equatorial axis, apertural face) × 40 µm (equatorial axis, interapertural face). Style reddish, 25–47 mm long, pubescent near base, glabrous distally, stigma with 1 lobe 2–4.5 mm long, straight to coiled, other lobe vestigial, 0.3–0.5 mm long. Capsule 16–20 mm long, densely pubescent with antrorsely appressed eglandular trichomes. Seeds 4.5–4.7 mm long, 4–4.3 mm wide.

**PHENOLOGY.**— Flowering throughout the year; fruiting: January–August (and probably other months as well).

**DISTRIBUTION AND HABITATS.**— Southern Central America (Panama), northeastern South America (Brazil, French Guiana, Guyana, Suriname, and Venezuela), and northwestern South America (Colombia, Ecuador, and Peru)—occurring from the Province of Veraguas in central-western Panama (ca. 08°7′49.33″N, 080°56′52.89″W) southward to the Amazonian lowlands near Belém in northeastern Brazil (ca. 01°26′55.04″S, 048°22′45.41″W) in the east and to the eastern slope of the Andes in the region of San Martín in north-central Peru (ca. 06°34′7.19″S, 076°18′28.88″W) in the west (Fig. 5); plants occur in swampy ground and agricultural lands (pastures, cafetales), and especially along streams, fencerows, and roadsides in regions of tropical (dry to) moist to wet, lowland to montane, primary and secondary forests at elevations from sea level to 2250 m (to 3500 m *fide* Wasshausen 2013). Because *Trichanthera gigantea* is often cultivated (e.g., as a living fence, or for forage), the anthropogenic distribution of this species is undoubtedly more extensive than that suggested by the localities noted in the specimens cited; collections explicitly indicating that plants were cultivated are not included in that list. The species is especially common (or at least commonly collected) in Colombia. In Venezuela, plants are restricted to two regions on opposite sides of the country—both branches of the Cordillera Oriental in the west and lowlands of the Orinoco delta in the northeast.

The species has been noted to occur as far north as lowlands in Costa Rica (Leonard 1938; McDade 1983; Durkee 1986). The only two specimens from Costa Rica attributed to this species (Leonard 1930), both from Guanacaste in the northwestern part of the country (Tilarán, *P. Standley & Valerio 46569* at US; Nicoya, *Tonduz s.n.* in 1900 at US), are sterile, although *Standley & Valerio 46569* has immature inflorescences. Both appear superficially similar to *Trichanthera gigantea*. However, comparison of these plants to those of *T. gigantea* reveals that they lack the very conspicuous foliar cystoliths, triangular bracts, and feltlike pubescence of the young stems of the latter species. Thus, I remain unconvinced that either of these specimens represents *T. gigantea*, and Costa Rica is excluded from the known geographic range of this species.

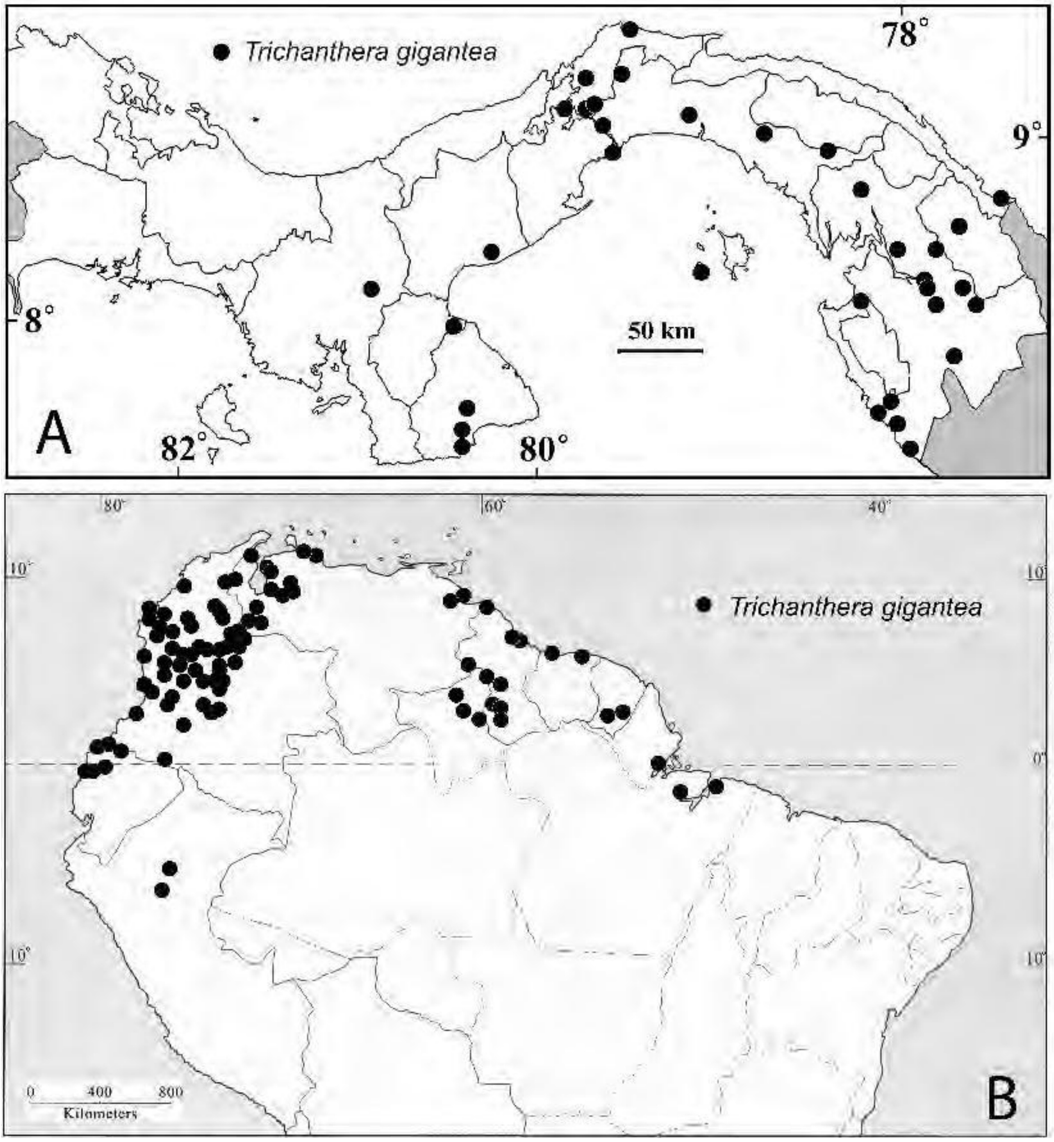

FIGURE 5. Distribution of *Trichanthera gigantea*. A. Distribution in Central America (Panama). B. Distribution in South America.

**LOCAL NAMES.**— Wasshausen (1992), Record and Hess (1943), and Cook et al. (2005) listed the following local names for the species (including those from countries where it is only cultivated): aro blanco, cajeto, cenicero, fune, madre de agua, nacedero, quiebrabarriga/quiebrabarrigo, suiban (Colombia); tuno (Guatemala); naranjillo (Venezuela); palo de agua (Colombia and Panama); and beque, canella de Garca, pau santo (Brazil). "Nacedero" appears to have the widest usage in both Colombia, where the plant is abundant, and in agricultural literature concerning *Trichanthera gigantea*. Indeed, this name and "cajeto" were listed by Bonpland (1810–1811). Additional local names and their sources from Colombia include: rompebarriga (*Archer 523*); arbol de agua, aro, cafetero, cafeto, chumbaguás, cuchiyuyo/cuchuyuyo, güibán, naceró, paloesal, sanantigua, sietenudos, tumbaguás, yátago, and zanca de araña (Bernal et al. 2013); zanco (*Forero & Jaramillo 461*); and cajón de fraile (*von Sneidern 5698*). Other names encountered on herbarium specimens include: canela de velho (Brazil, *Rabelo et al. 2009*), curuta (Venezuela, *L. Ruiz Terán 458*), janau (Brazil, *Pires 51848*), montonero (Ecuador; *Pennington & de la Cruz 10516*), naiang (Venezuela, *M. Lizarralde 306*), sapote yacu (Peru; *Williams 4894*), and watra-oedoe (Suriname; *Werkhoven & v. Troon UVS 16450*).

**Uses**.— Leaves and green stems of *Trichanthera gigantea* have been shown to be a useful forage crop in its native geographic range and elsewhere. Numerous studies have documented its ecological parameters for cultivation, nutritive value as fodder, relative usefulness for various domesticated mammals, and harvest times and yields (e.g., Rosales 1997; Cook et al. 2005). Due to the broad ecological tolerance of this species (e.g., see above for ranges in elevation and biotic communities) and ease of propagation from cuttings, it can be grown in diverse habitats (Rosales 1997). Outside of its native range, the species has been grown for its agricultural use in other parts of tropical America, southeastern Asia, and Malesia.

Other uses attributed to this species include: windbreak (Leonard 1930), living fence (e.g., *D'Arcy & Sytsma 14473*; Wasshausen 1992), and cultivated ornamental (Wasshausen 2013). Rosales (1997) indicated that "sprouts" of the species are used in maize porridge for human consumption. The wood is considered to be of relatively low quality (i.e., only suitable for unfinished wood products), but it is used for fuel and to make charcoal (Fern 2014). Wood anatomy of *Trichanthera gigantea* was studied and described by Williams (1928; based on *Pittier 12,056*), Carlquist and Zona (1988; based on Forest Products Laboratory, Madison, Wisconsin sample 1117; likely from *Williams 4894* ), and Mennega (2006; Utrecht Wood coll. 175a and 2001). Corothie (1961; without citation of voucher) described wood anatomy of "*Trichanthera* sp." Wasshausen (1992) noted that woodcutters usually leave plants of *T. gigantea* standing to protect springs and streams.

Numerous medicinal uses for *Trichanthera gigantea* have been recorded for humans and domesticated animals. The following uses have been ascribed to humans: infusions of leaves used to treat flu and plants used for treatment of white vaginal discharges (de la Torre et al. 2008; Ecuador); a decoction of leaves used by women in labor to speed delivery (*Lescure 2236*; Ecuador); "en infusión como colagogo y diurético y en cocimiento como antiflogístico" (*Puentes s.n.*; Colombia); used as a remedy for fevers (Wasshausen 1992; Colombia); plants used as a blood tonic, to treat nephritis, and as a lactogenic drink for nursing mothers (Cook et al. 2005); and green stems used to cure nephritis and roots used as a blood tonic (Rosales 1997; Colombia). Medicinal uses for domesticated animals include: leaves used to treat hernias (de la Torre et al. 2008; Ecuador); hot poultices of leaves used to cure abdominal hernias of horses (Wasshausen 1992; Colombia); and plants used to treat colic and hernia in horses, retained placenta in cows, and intestinal obstructions in domestic animals (Rosales 1997; Colombia).

**Conservation**.— *Trichanthera gigantea* is known from more than 200 collections from a broad geographic area (extent of occurrence = ca. 4,591,000 km$^2$; north-south linear distance = ca. 1,980 km; east-west linear distance = ca. 3,625 km). Even if the EOO is reduced by one-half to two-thirds to account for open water (marine and terrestrial) and large regions from which the species has not been recorded, the geographic distribution of *T. gigantea* remains quite large, and there would appear to be significant amounts of suitable habitat for this species in much of the region (i.e., the northern and central portions of the Amazon basin) in which it could potentially occur. Based on its wide distribution (both natural and anthropogenic), local abundance (plants are sometimes noted to be common where found, e.g., *Piedad R. et al. 40)*, occurrence in several protected areas in portions of its geographic distribution, and broad ecological amplitude, *T. gigantea* appears to be a taxon of least concern (LC) based on IUCN criteria (IUCN 2014).

Flowers of *Trichanthera gigantea* are reputed to be the major food (nectar) source for the endangered (IUCN category EN) chestnut-bellied hummingbird, *Amazilia castaneiventris*, the abundance of which appears to be affected by the availability of these trees and which exhibits territorial behavior where flowers are common (Cavanzo 2011; BirdLife International 2012). Cavanzo (2011) also noted that reproduction of *A. castaneiventris* was observed in periods of increased floral abundance of *T. gigantea*.

**Nomenclature.**— According to the protologue of *Ruellia gigantea*, the type locality is in the basin of the Río Magdalena in Colombia. Plants were either collected or noted to occur near Badillas (sometimes cited as "Badillo" or "Badilla," ca. 07°58′20.00″N, 073°51′11.60″W) and in the valley of the Río Combeima near Ibagué at 1300 m (04°27′14.65″N, 075°15′20.15″W). Both Pérez A. (1956) and Wasshausen (1992) noted that Mutis had previously described and illustrated this plant, and that Bonpland had likely made use of these materials. At least five specimens of *Trichanthera gigantea* resulted from Humboldt and Bonpland's trip up the Río Magdalena, and it is likely that there were at least two collections (based on numbers noted in handwritten descriptions of the specimens at P). The known extant specimens are discussed below.

Leonard (1930) indicated that the type locality of *Trichanthera gigantea* was "in sylvis fluvii magdalenae prope Badillas." He subsequently noted that type material of *T. gigantea* was at B and K-Hooker (Leonard 1951), from where specimens had been seen and noted by Nees (1847). The holotype is sometimes cited as having been a specimen destroyed at B (Wasshausen 1992; Wasshausen 2006). Field Museum photo 5887 from the Berlin Negatives database (emuweb.fieldmuseum.org/botany/berDisplay.php?irn=240003&QueryPage=%2Fbotany%2Fsearch_berlin.php) of the destroyed specimen at B reveals that this specimen lacked collection data (at least on the face of the specimen bearing the plant). This specimen was undoubtedly part of the set of collections given to Kunth by Humboldt prior to his return to Berlin in 1829 (Hiepko 2006), and included in the general collection at B. It would have been a duplicate of one of the collections at P, and thus an isosyntype. There are no specimens of *T. gigantea* (under that name or *R. gigantea*) in the Willdenow herbarium at B (Hiepko 1972). Among the major sets of collections of Humboldt and Bonpland (Hiepko 2006), there are three specimens of *T. gigantea* at P (where Bonpland began working up the primary set of their collections prior to Willdenow and subsequently Kunth taking on that task). From the specimens and extensive notes of Bonpland (on at least two of three sheets of paper attached to one of the specimens; these two bear extensive descriptions, which generally correspond to information in the protologue, and are apparently based on collections numbered *1545* and *1828*), it seems reasonable to assume that the original material for this species is at P. At least one of the specimens at P likely was in Bonpland's set that was incorporated into the general herbarium at P in 1832 (Hiepko 2006). Because there are at least two discernible localities in the protologue and undoubtedly at least two different collections, there appear to be syntypes. The specimen from the general herbarium to which all of the descriptive materials are attached, and which is the most complete of those at P, is designated as the lectotype. The other specimens at P, at least one of which could be an isolectoype, are P- Bonpl.-00670081 and P-00719182. A duplicate of one of the Humboldt and Bonpland collections (an isosyntype or an isolectotype) is extant at K.

Neither specimens nor images of types of *Clerodendrum verrucosum* have been seen. The herbaria of deposit noted above is derived from Wasshausen (2006).

From among the syntypes of *Besleria surinamensis* (i.e., *Kappler 1639* and *Hostmann 764*), Wasshasuen (2006) designated *Hostmann 764* at U as the lectotype. The presumed isolectotypes at MO, P, and S indicate Hostmann's number as "764a." Neither the protologue nor the presumed isolectotypes provide place or date of collection. Locality data for the other syntype, *Kappler 1639*, which was collected in 1844, is noted in the specimens cited below. The lectotype is mounted on the same sheet as a specimen of *Kappler 1639* at U.

Gleason (1927) did not designate a type for *Trichanthera gigantea* var. *guianensis*. Among the five collections of *T. gigantea* he cited in the protologue, at least two of them appear to pertain to his new taxon. Leonard (1930) did not indicate a type for var. *guianensis*. Although Wasshausen (2006) cited *Jenman 371* at K as the lectotype of this variety, he did not indicate that it was being designated as such by him and it is not listed among the new lectotypifications made in his treatment (Wasshausen 2006:163); thus, his indication does not constitute a lectotypification (McNeill et al. 2012). Although I searched the literature on Acanthaceae in the region in which this taxon was collected, I did not find a lectotypification for this species conforming to the rules of nomenclature. Thus, I have designated *Jenman 371* at K as the lectotype of *T. gigantea* var. *guianensis*.

**Morphological variation.**— Gleason (1927:617) noted that *Trichanthera gigantea* var. *guianensis* consisted of lowland plants that differed by their “larger flowers, more hirsute filaments, smaller and more loosely branched inflorescences, and somewhat glaucous leaves, with the veins not elevated on the upper side.” Leonard (1930) provided more precise distinctions (inflorescences 3–8 vs. 5–15 cm long and 2–3 vs. 4–5 cm wide, and filaments pilose throughout vs. filaments pilose proximally and glabrous distally), but noted corollas of the same size as those of the nominate variety. He indicated that var. *guianensis* occurs in Brazil, Guyana, and Suriname whereas var. *gigantea* occurs in Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela. Bremekamp (1938a, 1938b) did not make reference to this variety in his detailed account of the genus for the *Flora of Suriname*, and his description noted that filaments of plants from Suriname are densely pubescent proximally but glabrescent distally. Most recently, Wasshausen (2006) recognized var. *guianensis* for the plants occurring in Guyana, Suriname, and French Guiana. Based on my studies, similar variation in corolla length, filament pubescence, and inflorescence length is evident among plants in the eastern portion of the species’ range (Brazil, Guyana, Suriname), its western range in South America (Venezuela, Colombia, Ecuador), and in Panama. There appears to be some geographic tendencies in pubescence of the filaments. For example, 1) all plants from Ecuador have few or no eglandular trichomes distally on the filaments (but this condition is also evident in other parts of the species’ geographic range), and 2) plants from Guyana, Suriname, and Brazil generally have trichomes on the filaments, but these are more abundant in some plants than others (and this variation is also seen elsewhere in the geographic range of the species). Thus, no infraspecific taxa are recognized in this account.

Plants that are somewhat morphologically intermediate with *T. corymbosa*, at least in some characters, are discussed under that species.

**Floral biology and pollination.**— The following information pertaining to the floral ecology of *Trichanthera gigantea* is based on personal observations, information noted on herbarium specimens, and published studies. The relatively large, somewhat fleshy corollas (Fig. 2) open in the afternoon (Perez A. 1956; pers. obs., *Schmalzel 372*, *Judziewicz 4493*) when nectar is present (Perez A. 1956; *Schmalzel 372*) and detectable odors absent (pers. obs., *Judziewicz 4493*, *Pennington & de la Cruz 10516*, *Piedad R. et al. 40*). Floral rewards include pollen and nectar. Corollas dehisce and fall from the inflorescence before morning of the next day. The style remains attached to the ovary for at least several days following anthesis; ovaries that do not set fruit fall from the plant within three days (McDade 1983). Working at a site in Panama, McDade (1983) demonstrated that flowers are neither autogamous nor apomictic (at least not showing autonomous agamospermy), that at least eight pollen grains are necessary for fruit and seed set, and that mean seed set per fruit was very low at this site, probably because of pollen limitation (low vigor of pollen, low numbers of grains deposited on stigmas, or both).

Pollination of *Trichanthera gigantea* by bats (*Glossophaga soricina*) was documented by Steiner (1981) and photographed by Merlin Tuttle (Anonymous 1984; image can be viewed at: <*http://www.scientificamerican.com/slideshow/bats-in-history-and-world/*> and <*http://www.wbur.org/npr/181634051/this-bat-knows-how-to-drink?ft=3&f=181634051*>). These bats hover in front of flowers, gather nectar with their highly specialized tongues (Harper et al. 2013), and contact stigmas and/or pollen with the top of their heads. Visitation to flowers by bats was also noted on labels of several herbarium specimens (e.g., *Monslave B. 807* from Colombia). Elsewhere among Acanthaceae, bat pollination has been noted for *Harpochilus neesianus* Mart. ex Nees (Acanthoideae: Justicieae) by Vogel et al. (2004). Flowers that share the characteristic syndrome of floral adaptations associated with bat pollination have been noted for several other Neotropical species of *Louteridium* (e.g., Vogel et al. 2004) and *Ruellia* (e.g., Vogel et al. 2004; Ramamoorthy 1991; Tripp 2010).

Other floral visitors to *Trichanthera gigantea* include red wooly opossum (*Caluromys derbianus*; Steiner 1981), hummingbirds (Pérez A. 1956; McDade 1983; Cavanzo 2011, which shows a photograph of *Amazilia castaneiventris* visiting and possibly pollinating a flower of *T. gigantea*; Henry Stockwell in Panama, pers. comm.; *Nee 10446*; *Tripp & Lujan 520*, which indicates hummingbirds as pollinators), large bees (Perez A. 1956; McDade 1983), and ants (Perez A. 1956; Rosales 1997). Some of these floral visitors likely effect pollination as well. Collectors have been particularly attentive to the presence of aggressive ants on inflorescences or flowers of plants (e.g., *Almeda & McPherson 6022, Daniel et al. 5475, Haught 4549, Judziewicz 4493, Luteyn & Pipoly 9378, Phillippe et al. 21186*). The ants have been described as "swarming," "stinging," and "guarding flowers." Some collections note that the ants make "mudlike" nests in the inflorescences.

**Additional specimens examined** (only images were seen for specimens cited from CDMB and COL).— **Brazil: Amapa**: Macapá, Rio Vila Nova, *B. Rabelo et al. 2009* (NY, US). **Pará**: Belém, igapó do I.A.N., *G. Black 826* (NY, US); IPEAN grounds, Belém, *A. Gentry & A. Pinheiro 13102* (MO, US); Amazon estuary, Breves, *E. Killip & A. Smith 30230* (F, NY, US); Crauateua, Rio Guamá, *R. de Lemos Fróes 20392* (NY, US); beira do Guamá, *J. Pires 3454* (CAS, US); vic. of Belem, *J. Pires 51848* (NY, US); Belém, R. Guamá, *N. Silva 57808* (NY, US). **Roraima**: Mun. Alto Alegre, Reserva Ecológica de Maracá, N tip of island at Três Igaripés, Corredeira de Rapariga, ca. 1 km upriver from jct. Furo de Santa Rosa with Rio Trairão, *P. Edwards 2649* (C, MO, NY, UPS); Canto Galo, Rio Mucajaí between Pratinha and Rio Apaiú, *G. Prance et al. 3980* (CAS, NY, S, US); 10 km SE of Serra de Lua, 02°25–29′N, 060°11–14′W, *G. Prance et al. 9336* (NY, S, US).— **Colombia: Antioquia**: 0–5 km S of Q. La Tirana along the river, vic. Planta Providencia, 28 km S of Zaragoza, *W. Alverson et al. 328* (MO, NY, WIS); 4 km N of Fredonia, *W. Archer 523* (NY); Mpio. Frontino, San Andrés, vía Dabeiba–Fuemia, 18–33 kms., 06°40′N, 076°23′W, *R. Callejas et al. 5850* (MO, NY, US); Mpio. Chigorodó, 2 km E of Chigorodó, Had. Pasatiempo, 07°40′N, 076°42′W, *R. Callejas et al. 9721* (NY); Mpio. Cocorná, La Piñuela, carretera a San Francisco, 06°02′N, 075°08′W, *D. Cañas 810* (MO); Mpio. San Luis, camino de la vereda Las "Confusas" a la autopista Medellín–Bogotá, 06°00′N, 074°45′W, *D. Cárdenas L. & J. Ramírez 2570* (COL, MO); Parque Nacional Natural "Las Orquideas," Sector Venados, margen derecha del Río Venados, 06°33′N, 076°19′W, *A. Cogollo et al. 3010* (COL); near Río León, ca. 20–30 km upstream and S of river mouth and ca. 15 km W of Chigorodó (ca. 07°45′N, 076°50′W), *C. Feddema 1917* (MICH, NY, US); Pavarandó Grande, Río Pavarando, *R. Fonnegra et al. 1716* (MEXU, MO, NY, US); Mpio. Río Negro, 7 km from Turbo on road to Necocli, 08°9′0″N, 076°41′48″W, *A. Gentry 9223* (COL, MO, NY, US); Turbo, 10 km E of Turbo, *O. Haught 4549* (P, US); cerca de Villa Arteaga, *F. López & M. Sánchez M. 61* (NY); de Puerto Bélgica por la carretera hasta el Río Man, *R. Romero-Castañeda 2333* (COL); Andes, carretera Andes–Jardín, 05°40′N, 075°55′W, *D.*

*Sánchez et al. 1155* (MO); vic. of Medellín, *R. Toro 78* (NY); Mpio. Carepa, 2 km N of Carepa, 07°52′N, 076°42′W, *J. Zarucchi et al. 5005* (MO, NY); Mpio Andes, km 13 of road Jardín–Andes (3 km before Andes), 05°39′N, 075°52′W, *J. Zarucchi et al. 7023* (COL, MO, US). **Bolívar**: 1 km de Arenal, *E. Forero & R. Jaramillo 461* (NY); Sahagun, *F. Pennell 4101* (NY); Mpio. Barranco de Loba, corr. El Pueblito, sector Las Payayas, 08°40′N, 074°10′W, *F. Roldán et al. 1837* (NY); Cordillera Occidental, Guimarí, *K. von Sneidern 5698* (PH). **Boyacá**: Mpio. Puerto Boyacá, Inspección de Puerto Boyacá, Quebrada La Cristalina, 05°50′60″N, 074°19′60″W, *R. Bernal et al. 2247* (COL); Mpio. Santa María, Arrayanes, Puerto de Agua Caliente, en la ruta a San Luis de Gaceno, cercanias del Río Lengupá, 04°50′57.8″N, 073°13′45.3″W, *J. Betancur et al. 11530* (COL); Mpio. Zataquirá, Hormigas, *A. Cadena G. 237* (COL); Valle de Soatá, *J. Cuatrecasas & H. García B. 1085* (COL). **Caquetá**: Mpio. San Vicente del Caguán, Trazado de la carretera entre Neiva y San Vicente, Las Perlas, bajo Río Pato, Finca Galicia, *J. Betancur et al. 2276* (COL, MO, US). **Casanare**: Mpio. El Yopal, *J. Campo K. & L. Pinzón P. 208* (COL). **Cauca**: Mpio. Guapi, Parque Nal. Natural Isla de Gorgona, camino a Playa Blanca, *G. Lozano et al. 5641* (COL). **Cesar**: Poponte, Magdalena Valley, *C. Allen 876* (MO). **Chocó**: Mpio. Acandí, Corregimiento San Francisco, Golfo de Urabá, 08°23′N, 077°07′W, *J. Betancur et al. 1216* (MO); Mpio. Acandí, corr. Triganá, Reserva Zazardí, 08°20′N, 077°10′W, *F. Cardona N. et al. 1641* (NY); Mpio. Quibdó, Corregimiento Bebará, sector La Calle en el Río Bebará, *W. Córdoba 411* (MO); Río Chintado, above La Nueva, *J. Duke 9850* (MO); Río Yuto between Lloró and La Vuelta, *A. Gentry & E. Rentería A. 24340* (MO); Río Mecana, 06°16′N, 077°21′W, *A. Juncosa 1745* (MO); Mpio. Quibdó, barrio Bahia Solano, *R. Moreno et al. 5* (MO); Río Tolo, región de Guayabal, al SE de Acandí, *L. Quiñones et al. 4* (COL, MO, US); Parque Nacional Natural Los Katíos, sector Bijao, *S. Zuluaga R. 785* (COL). **Córdoba**: Mpio. San Antero, Cerro de Buenos Aires, 09º17’48.6″N, 075°50’02.9″W, *J. Aguirre S. et al. 181* (COL); Mpio. Lorica, Corregimiento Nariño, Quebrada Cardozo, *O. Rivera D. et al. 1729* (COL); Mpio. Chima, Corregimiento Sitio Viejo, El Cerro, Cerro Tofeme, 09°04′58″N, 075°35′13″W, *O. Rivera D. et al. 2534* (COL). **Cundinamarca**: Caqueza in descendu And. bogotens. orienteus versus, *E. André 1875* (P); Sierra de Subia, 10 km N of Cumaca on road to Viotá, *A. Barclay et al. 3527* (COL, US); Mpio. La Mesa, carretera de La Mesa a Anapoima, El Placer, *A. Fernández & L. Mora 1373* (COL, NY); Mpio. Arbeláez, 7 km antes de Pandi, *J. Fernández A. et al. 7007* (COL, NY); Mpio. Viotá, La Victoria, Finca El Retazo, *J. Jácome 437* (COL); Mpio. Sasaima, Río Agua Dulce, Quebrada Doroga, *G. Lozano C. 654* (COL); Mpio. Viotá, Las Palmas, Finca Pensilvania, *A. Rodríguez A. 3* (COL); La Mesa, vía La Mesa–San Javier, *A. Salama et al. 251* (COL); Mpio. El Colegio, Inspección El Triunfo, La Soledad, desvío por El Quiosco, *A. Sanabria G. et al. 388* (COL); Mpio. Nilo, Inspección de Pueblo Nuevo, camino al Cerro del Cualamaná, *J. Torres R. et al. 774* (COL); entre La Mesa et le Magdalena, *J. Triana s.n.* (NY, P); Santandercito, a orillas del Río Bogotá, *L. Uribe U. 334* (COL); Pradilla near San Antonio de Tena, *J. Wood 4137* (COL, MEXU, US). **Huila**: along river, E of San Antonio Fortalecillas, *E. Little 7930* (UC); Mpio. La Argentina, El Progresso, 02°12′40.1″N, 075°56′40.1″W, *G. Silva et al. GAS0358A* (COL). **Meta**: floodplain of Río Metica just E of Puerto López, 3°55’43″N, 73°2′44″W, *G. Davidse & F. Llanos 5470* (COL, MO, US); caños cercanos a Villavicencio, *J. Fernández A. et al. 5573* (MO); P.N.N. Tinigua, Serranía Chamusa, Centro de Investigaciones Primatológicas La Macarena, *P. Stevenson 922* (MO). **Norte de Santander**: región de Sarare, hoya del Río Chitagá, en La Cabuya, *J. Cuatrecasas 13437* (COL, US); Culagá Valley, near Tapatá (N of Toledo), *E. Killip & A. Smith 20504* (NY, US); W side of Culagá Valley, N of Labateca, *E. Killip & A. Smith 20534* (NY, US); between Chinácota and La Esmeralda, *E. Killip & A. Smith 20891* (US); km 20 carretera via Pamplona, *D. Villamizar V. 72* (MO). **Putumayo**: Río Putumayo, Puerto Porvenir, arriba de Puerto Ospina, hacia La Loma, *J. Cuatrecasas 10733* (COL). **Quindío**: Mpio.

Calarcá, La Bella, km 4 vía Calarcá–Barcelona, 04°30′03″N, 075°41′02″W, *M. González 141* (COL); Mpio. Filandia, El Placer vía a Filandia, *L. Piedad R. et al. 23* (COL); Mpio. Génova, Finca El Janeiro, *L. Piedad R. et al. 40* (COL). **Santander**: 10 km N de Bacaramanga, *J. Araque M. & F. Barkley 18S.212* (NY, US); Mpio. Suaita, Corregimiento San José de Suaita, zona cercana a la quebrada La Vega, *J. Fernández-Alonso et al. 20862* (COL); Mpio. Floridablanca, predios del campus del la Universidad Pontificia Bolivariana, *E. García & J. Benavides 3835* (CDMB); Oiba, *F. González 3591* (NY); Bucaramana and vicinity, *E. Killip & A. Smith 15452* (NY, US); Río Suratá valley , between El Jaboncillo and Suratá, *E. Killip & A. Smith 16426* (US); La Corcova (Tona), *E. Rentería et al. 692* (NY); alrededores de Oiba, *R. Puentes s.n.* (COL); Río Servita, vic. Málaga, *J. Wood 4338* (COL). **Tolima**: El Fresno, *J. Cuatrecasas 9374* (COL); Ibagué, *I. Holton s.n.* in 1853 (NY); Mpio. Ibagué, Tres Esquinas, 04°29′6″N, 075°15′51″W, *A. López 4* (COL). **Valle de Cauca**: Río San Juan, *E. Core 1501* (US); Cordillera Occidental, vertiente occidental, hoya de Albán, entre Quebradita del Retiro y el Río Albán, *J. Cuatrecasas 22631* (F); El Frejito, *E. Dryander 47* (US); Cali, *H. Garcia B. 4314* (US); Mpio. Ginebra, Inspección de Policia, Costa Rica, Mina la Emilia, *L. Jiménez et al. 06* (COL); Bajo Calima, Concesión Pulpapel/Buenaventura, 03°55′N, 077°W, *M. Monslave B. 807* (MO, US); “La Manuelita,” Palmira, *F. Pennell & E. Killip 6193* (NY); cerca de Cali, *E. Pérez A. & J. Cuatrecasas 6332* (COL, US); Timba, *K. von Sneidern 1240* (NY).— **ECUADOR: Carchi**: between Chical and Peña Blancas, valley of Río San Juan on Colombian border, *A. Gentry & G. Shupp 26496* (MO); environs of Chical, 12 km below Maldonado on Río San Juan, 01°04′N, 078°17′W, *M. Madison et al. 4474* (F, MO); below Maldonado, ca. 80 km W of Tulcan, *T. Pennington & R. de la Cruz 10516* (US); Maldonado, *L. Werling & S. Leth-Nissen 420* (NY). **Esmeraldas**: Limones–Borbón, 5 km before Borbón, 01°07′N, 079°00′W, *L. Holm-Nielsen et al. 26040* (MO, NY); Macedonia, Esmeraldas–Atacames, *C. Játiva & C. Epling 466* (NY, UC, US); Atacames, 25 km SW de Esmeraldas, *E. Little & R. Dixon 21002* (NY, US); San Lorenzo Cantón, Reserva Etnica Awá, Centro Ricaurte, 01°10′N, 078°32′W, *G. Tipaz et al. 2223* (MEXU). **Los Ríos**: Río Palenque Biological Station, km 56 Quevedo–Santo Domingo, *C. Dodson 5846* (MO, US). **Manabí**: El Recreo, *H. Eggers 14823* (MA, US); 5 km E de Chone, carretera hacia Santo Domingo de los Colorados, 00°40’S, 080°05′W, *D. Neill & M. Asanza 7979* (MO). **Santo Domingo de los Tsáchilas:** near Santo Domingo, *C. Jativa & C. Epling 530* (NY, UC, US); carretera Quito–Chiriboga–Empalme, entre kms. 75 and 85, 00°15′S, 078°50′W, *V. Zak & J. Jaramillo 2326* (RSA, MEXU, MO, NY, US). **Without locality**: *A. Gilmartin 221* (MO).— **FRENCH GUIANA: Cayenne**: Rivière Camopi, en amont du Saut Yaniwé [ca. 03°5′20″N, 052°45′11.69″W], *J. de Granville 2071* (U). **St. Laurent du Maroni**: Saut Pierkourou sur le Tampok [ca. 02°49’59.88″N, 053°33′0.03″W], *Moretti 1268* (P).— **GUYANA: Barima-Waini**: Anabisi River, *J. de la Cruz 1348* (NY, US); Hossororo, near Port Kumaka via Aruka River, 08°10′07″N, 059°48′17″W, *T. Hollowell et al. 453* (MO); Barima River, *G. Jenman 7037* (K-image, NY). **Cuyuni-Mazaruni**: Mazaruni Station, *Forest Dept. of British Guiana F624 (3360)*(NY); Roraima, *Schomburgk 998* (P). **Demerana-Mahaica**: E bank of Demerara River at Atkinson Field, *H. Irwin 167* (US); Canaan, Demerara River, *Jenman 5356* (K, NY). **Essequibo Islands-West Demerara**: Naamryck Canal, ca. 3.5 km SW of Parika, 06°50′N, 058°27′W, *L. Gillespie & D. Gopaul 1042* (US); Naamrye Canal just W of Lookout, 06°50′N, 058°25′W, *J. Pipoly & G. Samuels 11752* (NY, P, US). **Potaro-Siparuni**: ca. 0.5 km from Paramakatoi, trail to Youwang and Monkey Mt., 04°41′N, 059°42′W, *H. Clarke & S. Grose 1261* (NY, US). **Upper Takutu-Upper Essequibo**: Rupununi area, Surama, 04°05′N, 059°04′W, *P. Acevedo et al. 3389* (MO, NY, US); Essequibo, South Rupununi savanna, SE of Aishalton, 02°25′N, 059°10′W, *T. Henkel & R. James 3723* (MO, NY, US); NW Kanuku Mts., 2–4 km N of Nappi Mt., 03°19′N, 059°33′W, *B. Hoffman & R. Foster 3597b* (MO); S Pakaraima Mts., 3 km E of Tipuru village, 04°12′N, 059°32′W, *B. Hoffman &*

*R. Jacobs 1147* (NY, US); Rupununi Distr., Kanuku Mts., Crabwood Cr., Camp 23, 03°07′N, 059°06′W, *M. Jansen-Jacobs et al. 3300* (MO, NY, P, US); NW slopes of Kanuku Mts., drainage of Moku-Moku Creek (Takutu tributary), *A. Smith 3405* (MO, NY, P, US).— **Panama:** “**Canal Zone**:” without locality, *P. Allen 1725* (MO, NY); without locality, *M. Correa A. et al. 1719* (MO); Madden Forest Road 2, *T. Croat 8957* (MICH, MO). **Coclé**: lower portion of valley along R. Antón, El Valle de Antón, *A. Hunter & P. Allen 385* (MO). **Colón**: Juan Mina Plantation, Río Chagres, region above Gamboa, *P. Allen 4106* (MO); Boyd-Roosevelt Hwy., 5 mi W of Sabanitas, *T. Croat 14073* (MO, NY, RSA, UC, US); vic. of Río Indio on road from Portobelo to Nombre de Dios, *T. Croat 33620* (MO, NY); along Pipeline Road, 1–5 km NW of Gamboa, 09°08′N, 079°42′W, *E. Judziewicz 4493* (MO, WIS); Chagres River, ca. 3 mi above Gamboa Bridge, *H. Kennedy et al. 2302* (MO, RSA); Parque Nacional Soberania (Pipeline Road), 3–7 km NW of Gamboa, *L. McDade 542* (CAS); along Pipeline Road, 3.5 km NW of Gamboa, *M. Nee 10446* (MO, RSA, US). **Darién**: Serranía de Pirre, near Cana mining camp in region of Alturas de Nique on road to Boca de Cupe, *F. Almeda & G. McPherson 6022* (CAS, NY); vicinity of Canglon, 110 mi from Bayano Dam Bridge, *T. Antonio 4578* (MO); trail from Punta Guayabo Grande to Río Jaque, *T. Antonio & W. Hahn 4432* (MO); without locality, *N. Bristan 124* (MO, UC); Rancho Frio Station, Río Perrecénega, ca. 10 mi E of El Real, *W. D’Arcy & G. McPherson 16165* (MO); 10 km NE of Jaque, Río Tabuelitas above Birogueirá, village on Río Jaque below mouth of Río Pavarandó, *W. D’Arcy & K. Sytsma 14473* (MEXU, MO); 1–5 mi downstream from El Real, *J. Duke 4924* (MO, UC, US); Cerro Piriaque, *J. Duke 8110* (MO); 18 km SE of Jaqué, Ensenada del Guayabo, *N. Garwood et al. 93* (MEXU, MO); Ensenada del Guayabo, 16–19 km SE of Jaqué, *N. Garwood 1201* (MO); Río Tuira between Río Paya and Río Cube, *A. Gentry 4354* (MO); El Real, trail to Río Pirre, *H. Kennedy 2828* (F, MO, NY); trail from Canglón–Yaviza road to Río Chucanaque, 7.7 mi E of Canglón, 08°20′N, 077°50′W, *S. Knapp & J. Mallet 3965* (CAS, MEXU, MO); S of El Real along trail at base of Cerro Pirre, ca. 08°00′N, 077°45′W, *G. McPherson 7081* (CAS, MO); Sambú River above tide limit, *H. Pittier 5541* (NY); El Real airport, *O. Sexton 260* (MO), *261* (MO); Cerro Piriaque, *E. Tyson et al. 3814* (MO); Rio Cocalito, *C. Whitefoord & A. Eddy 118* (MEXU, MO). **Emberá**: Marraganti and vicinity, *R. Williams 1007* (NY). **Herrera**: El Barrero de Pesé, *M. Rodríguez 53* (MO, NY). **Los Santos**: vicinity of Tonosí along Quebrada Ocho Paso tributary of Río Tonosí, *W. Stern et al. 1834* (MICH, MO, US); 10 mi N of Tonosí, *E. Tyson et al. 2948* (MO); road from Tonosí to Guánico, *E. Tyson et al. 3118* (MO). **Panamá**: drowned forest of upper Río Pequeni between Salamanca Hydrographic Station and Río Boquerón, *P. Allen 17275* (MICH, MO, P); Río Villalobos–Pedregal, *D. Botello 26* (MO); Barro Colorado Island, *T. Croat 4632* (NY), *8528* (MO, NY, RSA, US); Río Maje, ca. 30 minutes by speedboat from confluence with Río Bayano, *T. Croat 34378* (MO); along Pipeline Road between entrance to Parque Nac. Soberania and fourth bridge, *T. Daniel & H. Herrera 5490* (CAS, MO); along road to Farfan Beach just W of Bridge of the Americas, *T. Daniel et al. 5474* (CAS, MICH); Barro Colorado Island, *R. Dressler 3427* (MO); between Río Pacora and Chepo, *J. Dwyer et al. 5124* (CAS, MO, US); Barro Colorado Island, *R. Foster 1680* (F, MO); Pipeline Road, 09°15′N, 079°45′W, *C. Hamilton et al. 3253* (MEXU, MO); San José Island, Camp Valley, *I. Johnston 679* (MO, P, US); along Gaillard Hwy., 1.5 km NW of Summit Garden, *M. Nee 9392* (MO, NY); Barro Colorado Island, *R. Schmalzel 372* (MEXU, MO); ca. 15 km SW of Cañaza near Río Torti, base of Serranía de Cañazas, 08°52′N, 078°22′W, *B. Stein 1365* (MEXU, MO); Barro Colorado Island, *W. Stoutamire 2092* (MICH). **Guna (San Blas)**: W side of Loma Armila, *W. D’Arcy & G. McPherson 16133* (MO). **Veraguas**: Santiago, Loma de Regina, *I. Gordon & F. Camarena 43* (MO); Santiago, *L. Urriola 30* (MO).— **Peru: Loreto**: lower Río Huallaga, Santa Rosa [155–200 m], *L. Williams 4894* (US). **San Martín**: prope Tarapoto, Peruviae orientalis, *R. Spruce 3951* (K, NY, P, US).— **Suriname: Commewijne:**

Plant. Liberté, *J. Florschütz & P. Florschütz 1007* (NY). **Nickerie**: Wageningen I, km 172, *M. Werkhoven & F. v. Troon USV no. 16450* (US). **Paramaribo**: ad margines sylvarum pr. u. Paramaribo, *A. Kappler 1639* (MO, P, S). **Wanica**: Domburg, fluv. Suriname inferior, old plantation, *K. Kramer & W. Hekking 2349* (NY); bank of Para River, 2–4 km S of Houttuinen, *K. Kramer & W. Hekking 2748* (DAV, NY).— **VENEZUELA: Barinas**: las afueras de Puntax de Piedras, *Bernardi 1099* (NY); ca. 34 km NE of Altamira and 5 km NE of Caldas, ca. 08°55′N, 070°20′W, *J. Luteyn & J. Pipoly 9378* (CAS, MO, NY, US). **Delta-Amacuro**: medio Río Grande, 60 km NE de El Palmar, ca. 08°25′N, 061°45′W, *G. Aymard C. 5378* (MO); Dept. Tucupita, 13–14 km SE of Piacoa, along trail to Río San José, 8°32′N, 62°3′W, *G. Davidse & A. González 16453* (MEXU, MO); Dpto. Antonio Díaz, Cano Merejina, 08°46′N, 061°10′W, *A. Fernández 3990* (MO, NY). **Falcón**: Mpio. Jacura, Distr. Acosta, base del Cerro de La Mina, *L. Ruiz T. 458* (MO); Distr. Colina, Río Ricoa, S de Las Dos Bocas, 11°19′N, 069°24–25′W, *J. Steyermark & A. Gonzáles 113647* (MO). **Lara**: road from Guarico to Chabasaquén, 09°35′8.5″N, 069°50′54.3″W, *E. Tripp & M. Lujan 520* (CAS, RSA). **Mérida**: Zea, *Bernardi 1051* (MEXU, NY); San Cristoval, *N. Funck & L. Schlim 1506* (P); Río Caparo, ca. 1 km upstream from dam site, ca. 07°41′N, 071°28′W, *R. Liesner & A. González 9393* (MEXU, MO, US); 0.5–2 km above dam site on Río Guaimaral, ca. 07°45′N, 071°29′W, *R. Liesner & A. González 10578* (MEXU, MO, NY, US); carretera Santa Cruz de Mora–El Portón, *L. Valverde et al. 1119* (MO). **Portuguesa**: Distr. Guanare, terrenos de la UNELLEZ, 09°04′N, 069°49′W, *G. Aymard 1030* (MO); 30 km (air) W of Guanare, along Río Tucupido, 09°2′N, 070°01′W, *R. Liesner et al. 12460* (MEXU, MO, NY, US); NW of Guanare on Río Guanare, 09°2.55′N, 069°48.38′W, *L. Phillippe et al. 21186* (MO); Paso del Guanare, *H. Pittier 12056* (NY); Mpio. Mesa de Cavacas, Distr. Guanare, el lecho del Río Guanare, tramo ca. 1 km desde el Puente de la carretera Guano–Barinas, *B. Stergios et al. 7898* (MO, NY); Río María, Boca del Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en el sitio Las Marías, N de Guanare, 09°18′N, 069°43′W, *J. Steyermark et al. 127152* (MO, US). **Táchira**: near Palo Grande, *A. Alston 7097* (NY). **Trujillo**: entre Campo Elías y Batatal, *C. Benítez de Rojas 976* (F). **Zulia**: límite Distr. Bolívar-Baralt, Río Misoa, 10 km SE del empalme de las carreteras Maracaibo– Carora–Valera, *G. Bunting & L. Aristeguieta 5175* (NY); Distr. Bolívar, Cuenca de la Represa Burro Negro (Pueblo Viejo), 12 km de la vía Campo Lara–Piedras Blancas–Río Chiquito, *G. Bunting et al. 7204* (NY); Sierra de Perijá, 3.8 km 50° of Saimadodyi, 09°36′N, 072°55′W, *M. Lizarralde 306* (MO, NY); near Riocito [10°34′59.72″N, 072°22′0.06″W], *C. Mell s.n.* in 1923 (NY).

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## LITERATURE CITED

Anonymous. 1984. *The Most Famous Bat in the World*. Bacardi Imports, Miami, USA.

Bernal, R., G. Galeano, A. Rodríguez, H. Sarmiento, and M. Gutiérrez. 2013. Nombres Comunes de las Plantas de Colombia. Universidad Nacional de Colombia, Sede Bogotá, Facultad de Ciencias-Instituto de Ciencias Naturales. [<*http://www.biovirtual.unal.edu.co/nombrescomunes/*>]. Accessed on 21 June 2013.

BirdLife International. 2012. *Amazilia castaneiventris*. The IUCN Red LIST of Threatened Species. Version 2014.2. [< *http://www.iucnredlist.org*>]. Accessed on 30 October 2014.

Bono, G. 1996. Flora y Vegetación del Estado Táchira, Venezuela. *Monografie di Museo Regionale di Scienze Naturali, Torino* 20:1–951.

Bonpland, A. 1810–1811. *Ruellia gigantea*. Pages 75-77 *in* A. Humboldt and A. Bonpland, *Plantae Aequinoctiales*, vol. 2. Lutetiae Parisiorum, Paris, France.

Bremekamp, C. E. B. 1938a. Acanthaceae. Pages 166–252 *in* A. A. Pulle, ed., *Flora of Suriname*. J.H. deBussy, Amsterdam, Netherlands.

Bremekamp, C. E. B. 1938b. Notes on the Acanthaceae of Surinam. *Recueil des Travaux Botaniques Néerlandais* 35:130–171.

Carlquist, S., and S. Zona. 1988. Wood anatomy of Acanthaceae: A survey. *Aliso* 12:201–227.

Cavanzo, L. 2011. Especies de Colombia en Peligro de Extinción, el Colibrí Ventricastaña (*Amazilia castaneiventris*). [<*http://especiesdecolombiaenpeligrodeextincio.blogspot.com/2011/11/amazilia-ventricastana-amazilia.html*>]. Accessed on 30 October 2014.

Cook, B. G., B. C. Pengelly, S. D. Brown, J. L. Donnelly, D. A. Eagles, M. A. Franco, J. Hanson, B. F. Mullen, I. J. Partridge, M. Peters, and R. Schultze-Kraft. 2005. Tropical Forages: An Interactive Selection Tool. *Trichanthera gigantea*. [<*http://www.tropicalforages.info/key/Forages/Media/Html/Trichanthera_gigantea.htm*>]. Accessed on 15 March 2013.

Cornet, B., and D. Habib. 1992. Angiosperm-like pollen from the ammonite-dated Oxfordian (Upper Jurassic) of France. *Review of Palaeobotany and Palynology* 71:269–294.

Corothie, H. 1961. Anatomía de la madera de dos géneros de las Acanthaceaes. *Revista Forestal Venezolana* 4:7–15.

Daniel, T. F. 1983. *Carlowrightia* (Acanthaceae). *Flora Neotropica* 34:1–116.

Daniel, T. F. 1984. Artificial interspecific hybridization of three species of *Anisacanthus* (Acanthaceae). *Journal of the Arizona-Nevada Academy of Science.* 19:85–88.

Daniel, T. F. 1986. Systematics of *Tetramerium* (Acanthaceae). *Systematic Botany Monographs* 12:1–134.

Daniel, T. F. 1988. A systematic study of *Bravaisia* DC. (Acanthaceae). *Proceedings of the California Academy of Sciences,* ser. 4, 45:111–132.

Daniel, T. F. 1998. Pollen morphology of Mexican Acanthaceae: Diversity and systematic significance. *Proceedings of the California Academy of Sciences*, ser. 4, 50: 217–256.

Daniel, T. F. 2007. Artificial interspecific hybridization of two Mexican species of *Ruellia* (Acanthaceae). *Contributions from the University of Michigan Herbarium* 25:191–197.

Durkee, L. H. 1986. Acanthaceae. Pages 1–92 *in* W. Burger , ed., Flora Costaricensis. *Fieldiana: Botany* 18. Field Museum of Natural History, Chicago, Illinois, USA.

Ehrenberg, C. G. 1829. Plantarum cotyledonearum nova genera. *Linnaea* 4:396–404.

Endlicher, S. 1842. *Mantissa Botanica sistens Genera Plantarum, Supplementum Secundum*. Friedrich Beck, Wien, Austria.

Fern, K. 2014. Useful Tropical Plants. [<*http://tropical.theferns.info/viewtropical.php?id=Trichanthera+gigantea*>]. Accessed on 24 October 2014.

Gleason, H. A. 1927. Studies on the flora of northern South America-X. *Bulletin of the Torrey Botanical Club* 54:603–618.

Google Inc. 2013. Google Earth 7.1.2.2041. [< *https://www.google.com/earth/*>]. Accessed on 13 November 2014.

Harper, C. J., S. M. Swartz, and E. L. Brainerd. 2013. Specialized bat tongue is a hemodynamic nectar mop. *Proceedings of the National Academy of Sciences* 110:8852–8857.

Hiepko, P., ed. 1972. *Herbarium Willdenow Alphabetical Index*. Inter Documentation Company, Zug, Switzerland.

Hiepko, P. 2006. Humboldt, his botanical mentor Willdenow, and the fate of the collections of Humboldt & Bonpland. *Botanische Jahrbücher für Systematik, Plfanzengeschichte und Pflanzengeographie* 126: 509–516.

Humboldt, A., A. Bonpland, and C. S. Kunth. 1818 ("1817"). *Nova Genera et Species Plantarum,* vol. 2. Librairie Grecque-Latine-Allemande, Paris, France.

IUCN. 2014. Guidelines for using the IUCN red list categories and criteria. Version 11. [<*http://www.iucnredlist.org/documents/RedListGuidelines.pdf*>]. Accessed on 30 October 2014.

Leonard, E. C. 1930. The genus *Trichanthera*. *Journal of the Washington Academy of Sciences* 20:484–488.

Leonard, E. C. 1938. Acanthaceae. Pages 1188–1263 *in* P. C. Standley, ed., *Flora of Costa Rica*. *Field Museum of Natural History, Botanical Series* 18(3).

Leonard, E. C. 1951. The Acanthaceae of Colombia, I. *Contributions from the United States National Herbarium* 31:1–117.

Leonard, E. C. and L. B. Smith. 1964. *Sanchezia* and related American Acanthaceae. *Rhodora* 66:313–343.

Long, R. W. 1975. Artificial interspecific hybridization in temperate and tropical species of *Ruellia* (Acanthaceae). *Brittonia* 27:289–296.

Masters, M. T. 1868. Sterculiaceae. Pages 214–239 *in* D. Oliver, ed., *Flora of Tropical Africa*, vol. 1. L. Reeve & Co., London, England, UK.

McDade, L. A. 1983. Pollination intensity and seed set in *Trichanthera gigantea* (Acanthaceae). *Biotropica* 15:122–124.

McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, J. Prado, W. F. Prud'homme van Reine, G. F. Smith, J. H. Wiersema, and N. J. Turland. 2012. *International Code of Nomenclature for Algae, Fungi, and Plants* (*Melbourne Code*). Koeltz Scientific Books, Königstein, Germany.

Meisner, C. F. 1840. *Plantarum Vascularium Genera*, pars prior. Libraria Weidmannia, Leipzig, Germany.

Mennega, A. M. W. 2006. Wood and timber. Pages 152–161 *in* M. J. Jansen-Jacobs, ed., *Flora of the Guianas, ser. A: Phanerogams*, fasc. 23. Royal Botanic Gardens, Kew, England.

Mildbraed, J. 1926. Plantae Tessmannianae Peruvianae III. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9 (89):964–997.

Nees von Esenbeck, C. G. 1847. Acanthaceae. Pages 46–519 *in* Alph. de Candolle, ed., *Prodromus Systematis Natrualis Regni Vegetabilis,* vol. 11. Victor Masson, Paris, France.

Pérez A. 1956. *Plantas Útiles de Colombia*. Sucesores de Rivadeneyra, Madrid, Spain.

Planchon, J. E. 1855. Affinités et synonymie de quelques genres nouveaux ou peu connus. *Annales des Sciences Naturelles; Botanique,* sér. 4, 3:292–296.

Pocock, S. A. J., and G. Vasanthy. 1988. *Cornetipollis reticulata*, a new pollen with angiospermid features from Upper Triassic (Carnian) sediments of Arizona (U.S.A.), with notes on *Equisetosporites*. *Review of Palaeobotany and Palynology* 55:337–356.

Rafinesque, C. S. 1838. *Sylva Telluriana Mantissa Synoptica*. Printed for the author and publisher. Philadelphia, Pennsylvania, USA.

Raj, B. 1961. Pollen morphological studies in the Acanthaceae. *Grana Palynologica* 3:3–108.

Ramamoorthy, T. P. 1991. *Ruellia* section *Chiropterophila* (Acanthaceae): a novelty from Mexico. *Botanical Journal of the Linnean Society* 107:79–88.

Record, S. J., and R. W. Hess. 1943. *Timbers of the New World*. Yale University Press, New Haven, USA.

Richardson, A. 1972. Revision of *Louteridium* (Acanthaceae). *Tulane Studies in Zoology and Botany* 17:63–76.

Rosales, M. 1997. *Trichanthera gigantea* (Humboldt and Bonpland) Nees: a review. *Livestock Research for Rural Development* 9:1–9.

Roubik, D. W., and J. E. Moreno P. 1991. Pollen and spores of Barro Colorado Island. *Monographs in Systematic Botany from the Missouri Botanical Garden* 36:1–270.

Schmidt-Lebuhn, A. N. 2003. A taxonomic revision of the genus *Suessenguthia* Merxm. (Acanthaceae). *Candollea* 58:101–128.

Stafleu, F. A., and R. S. Cowan. 1979. *Taxonomic literature, vol. II: H-Le*, second ed. *Regum Veg*. 98:1–991.

Steiner, K. E. 1981. Nectarivory and potential pollination by a neotropical marsupial. *Annals of the Missouri Botanical Garden* 68:505–513.

Torre, L. de la, H. Navarrete, P. Muriel M., M. J. Macía, and H. Balslev, eds. 2008. *Enciclopedia de las Plantas Útiles del Ecuador*. Herbario QCA, Quito, Ecuador.

Tripp, E. A. 2010. Taxonomic revision of *Ruellia* section *Chiropterophila* (Acanthaceae): a lineage of rare and endemic species from Mexico. *Systematic Botany* 35:629–661.

Tripp, E. A., and L. A. McDade. 2014. A rich fossil record yields calibrated phylogeny for Acanthaceae (Lamiales) and evidence for marked biases in timing and directionality of intercontinental disjunctions. *Systematic Biology* 63:660–684.

Tripp, E. A., T. F. Daniel, S. Fatimah, and L. A. McDade. 2013. Phylogenetic relationships within Ruellieae (Acanthaceae) and a revised classification. *International Journal of Plant Sciences* 174:97–137.

Vasanthy, G., and S. A. J. Pocock. 1986. Radial through rotated symmetry of striate pollen of the Acanthaceae. *Canadian Journal of Botany* 64:3050–3058.

Vogel, S., I. C. Machado, and A. V. Lopes. 2004. *Harpochilus neesianus* and other novel cases of chiropterophily in neotropical Acanthaceae. *Taxon* 53:55–60.

Wasshausen, D. C. 1970. A synopsis of the genus *Suessenguthia* (Acanthaceae). *Rhodora* 72:119–125.

Wasshausen, D. C. 1992. Acanthaceae. Pages 63–122 *in* J. C. Mutis, *Flora de la Real Expedición del Nuevo Reyno de Granada* (*1783–1816*), vol. 41. Ediciones Cultura Hispánica, Madrid, Spain.

Wasshausen, D. C. 2006. Acanthaceae. Pages 1–141 *in* M. J. Jansen-Jacobs, ed., *Flora of the Guianas, ser. A: Phanerogams*, fas. 23. Royal Botanic Gardens, Kew, England, UK.

Wasshausen, D. C. 2013. Acanthaceae. Pages 225–233 *in* A. I. Piedrahíta et al., eds., *Flora de Antioquia, Catálogo de las Plantas Vasculares*, vol. II. Universidad de Antioquia, Medellín, Colombia.

Williams, L. 1928. Studies of some tropical American woods. *Tropical Woods* 15:14–24.

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# *Odontonema aliciae*, a New Heterostylous Species of Acanthaceae from Panama

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***Odontonema aliciae* is described as a new species of Acanthaceae from southern Panama. It differs from the other species of Panamanian *Odontonema* by the combination of its subauriculate leaves; relatively short and pink corollas; and glabrous internodes, peduncles, and pedicels. Like several other species of the genus, *O. aliciae* is distylous, and its pollen is triaperturate (3-colporate, 6-pseudocolpate). Morphological characters of the species are illustrated in photographs, its distribution is plotted on a map, and the species is compared to putatively related taxa.**

**Se describe *Odontonema aliciae* como una nueva especie de Acanthaceae del sur de Panamá. Se diferencia de las otras especies panameñas de *Odontonema* por la combinación de hojas subauriculatas; corolas relativamente cortas de color rosa; y entrenudos, pedúnculos y pedicelos glabros. Como varias otras especies del género, *O. aliciae* es distila, y su polen es triaperturado (3-colporado, 6-pseudocolpado). Características morfológicas de la especie son ilustradas en fotografías, su distribución es trazada en un mapa, y la especie es comparada con taxones putativamente relacionados.**

*Odontonema* Nees consists of 28 species of shrubs occurring from northern Mexico southward throughout Central America and the West Indies to southeastern Brazil (Daniel, unpublished). Daniel and McDade (1995) recognized four species of the genus from Panama, and provided a key to distinguish them. Several collections from coastal regions of the Azuero Peninsula and nearby islands reveal the presence of a distinctive species of the genus endemic to southern Panama, which we describe below.

### *Odontonema aliciae* T. F. Daniel and J. F. Carrión, sp. nov.

Figure 1.

**Type.**— **Panama: Veraguas**: P.N. Cerro Hoya, Restingue, islote, E800443, N510434, 18 Jul 2011 (flr), *A. Ibáñez, R. Flores, N. León, J. Domínguez, A. Jiménez, L. Vega, & V. Sánchez 6928* (holotype, PMA; isotypes: CAS, MO). Figure 1.

**Diagnosis.**— *Odontonema aliciae* differs from all other Panamanian species of *Odontonema* by the combination of its subauriculate leaves; short (13–20 mm long) and pink corollas; and glabrous internodes, peduncles, and pedicels.

Shrubs to 1.5 m tall. Young stems subquadrate to quadrate, internodes glabrous, nodes pubescent with a line or arc of flexuose to erect eglandular trichomes 0.2–0.7 mm long between petioles, trichomes becoming ± deciduous in fruiting plants. Leaves sessile to subsessile, petiole (if present) to 4 mm long, distal blades elliptic to obovate-elliptic to subpandurate, 90–263 mm long, 24–84

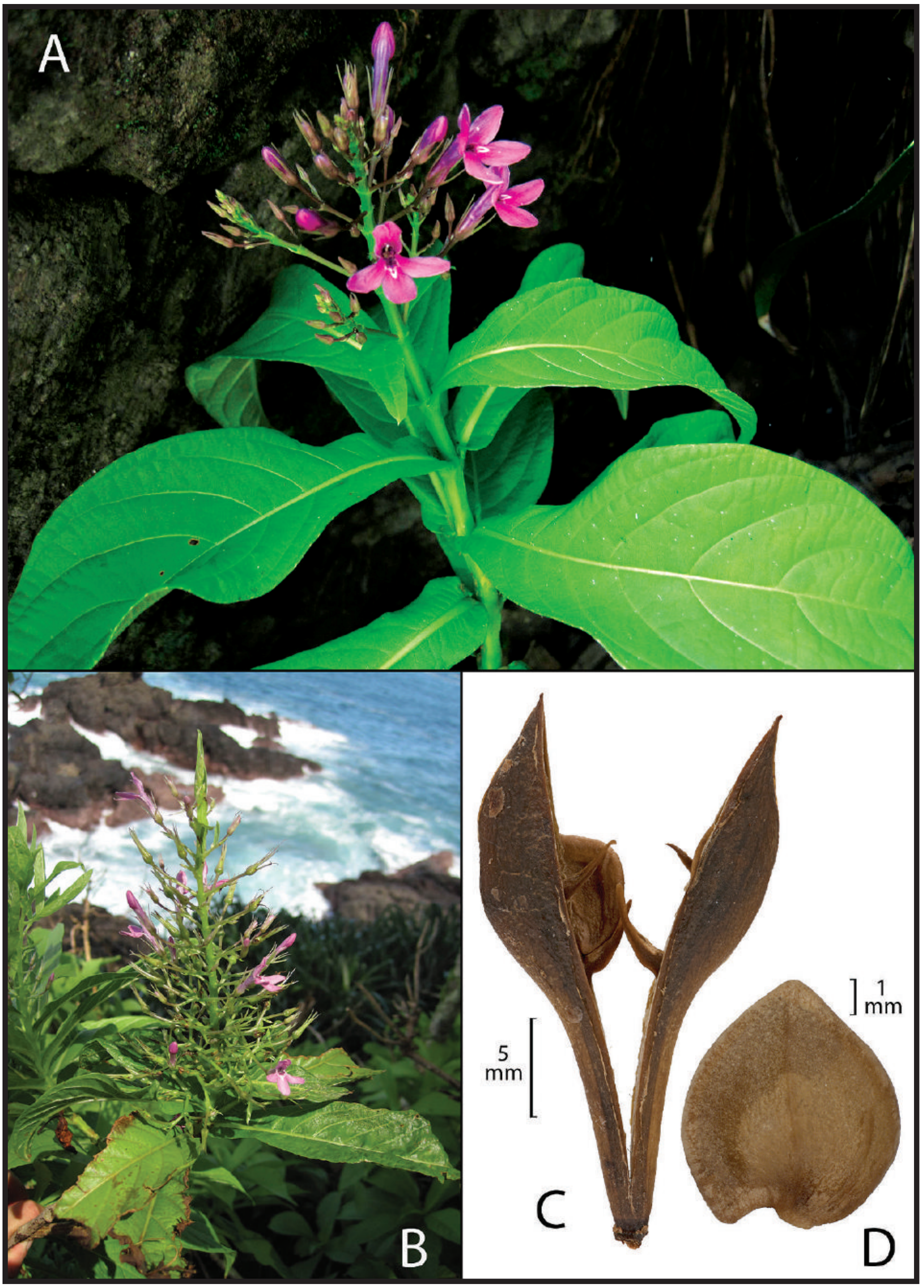

FIGURE 1. *Odontonema aliciae*. A. Habit showing distal leaves with subauriculate bases and inflorescence. B. Habit and habitat. C. Capsule. D. Seed. A, B from the type *A. Ibáñez et al. 6928*, photos by A. Ibáñez, used with permission; C, D from *Nee & Andres 46341*.

mm wide, length:width =2.9–4.5, reduced in size distally to 23 mm long and 3 mm wide, subauriculate at base, attenuate at apex, adaxially glabrous, abaxially pubescent with erect to flexuose eglandular trichomes to 0.7 m long, trichomes sometimes restricted to major veins or deciduous in fruiting plants. Inflorescence of axillary (from distal nodes) and terminal pedunculate thyrses to 115 mm long and 50 mm across near midpoint (including peduncle and excluding corollas/capsules) or sometimes with axillary pedunculate dichasia in axils of some distal leaves, peduncles of thyrses (and dichasia in leaf axils) 11–30 mm long, glabrous, rachis pubescent like young stems, dichasia of thyrses mostly opposite, 2–7 (or more)-flowered, pedunculate, peduncles of dichasia 5–13 mm long, glabrous. Bracts sometimes caducous, lanceolate to subulate, 2.2–8 mm long, 0.4–1.4 mm wide, abaxially glabrous. Bracteoles and secondary bracteoles subulate to lanceolate, 1–3.5 mm long, 0.3–1 mm wide, abaxially glabrous, margin usually ciliate or trichomes deciduous in fruiting plants. Flowers heterostylous, pedicellate, pedicels 4.5–9 mm long, glabrous. Calyx 6.5–9 (–12 in fruit) mm long, tube 0.5–1.5 (–2.5 in fruit) mm long, lobes lanceolate to lance-subulate, 5.5–8 (–10 in fruit) mm long, 0.7–1.1 mm wide, abaxially glabrous. Corolla pink to purple with white marking on lower-central lobe, 13–20 mm long, externally glabrous, internal surface of limb glandular, tube subcylindric 7.5–11 mm long, narrow proximal portion 5–6 mm long, 1.7–2.3 mm in diameter (measured flat), throat inconspicuous, 4–6 mm long, upper lip 6–9.5 mm long, lobes 2.5–3 mm long, lower lip 5.5–11 mm long, lobes 4.8–9.5 mm long. Thrum stamens exserted from mouth of corolla, 5.5–10 mm long, pin stamens included in corolla tube, 3.5 mm long, thecae 2–2.5 mm long, staminodes 2, ca. 1 mm long. Pollen (*Hammel 5472*) spherical to subspheroidal (P:E = 0.97–1.00), 3-colporate, 6-pseudocolpate, colpi and pseudocolpi microverrucate, interapertural surfaces reticulate, polar diameter (P) 30–36 µm, equatorial diameter (E) 31–36 µm. Ovary glabrous, style pubescent with flexuose eglandular trichomes, thrum style 3.8–4.5 mm long, pin style 12–13 mm long, stigma ± 2-lobed, lobes ca. 0.1 mm long. Capsule 20–30 mm long, glabrous, stipe 7–10 mm long, head 13–17 mm long. Seeds flattened (plano-convex to concavo-convex), flattened surfaces subcordate to subcircular to subsquare in outline, longest axis 6–7.8 mm, shortest axis 4.5–6.3 mm, 1.3–1.7 mm thick, surfaces and margin smooth to slightly roughened.

**PHENOLOGY**.— Flowering: July–October; fruiting: December.

**DISTRIBUTION AND HABITAT**.— Panama (Los Santos, Veraguas), on the Azuero Peninsula and islands off the southern coast of Panama to the west of that peninsula (Fig. 2); plants occur on slopes along rocky shoreline and in forests adjacent to beaches at elevations less than 10 m.

**ETYMOLOGY**.— The specific epithet honors Spanish botanist Alicia Ibánez, who has contributed greatly to the knowledge of the Panamanian flora, especially to that of Coiba National Park and neighboring regions. She also collected the type and co-collected two of the paratypes.

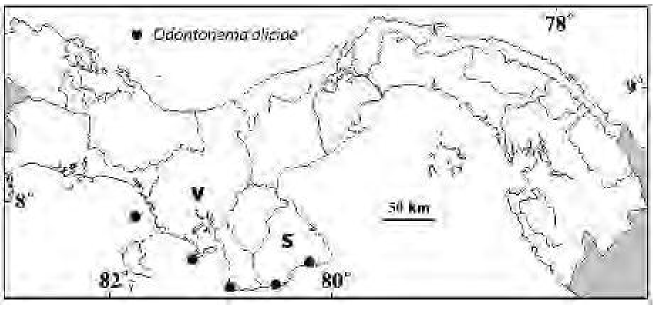

FIGURE 2. Map of Panama showing the distribution of *O. aliciae*
(V and S refer to the provinces of Veraguas and Los Santos, respectively)

**IUCN CONSERVATION STATUS**.— *Odontonema aliciae* is presently known from five relatively recent collections (collected between 1978 and 2012) with an extent of occurrence (EOO) of 4,106 km$^2$ and an area of occupancy (AOO; grid cell area of 4 sq. km) of 20 sq. km. In reality, the terrestrial EOO is considerably less than that calculated because a significant part of the EOO consists of approximately 1,500 sq. km of open ocean (but there is potential habitat on small islands that occur in the oceanic region). The linear distances of occurrence are 170 km west to east and 65 km north to south.

Primary threats to the species consist of seaborne events (e.g., tsunamis, hurricanes) and human-mediated coastal habitat deterioration. Given any of these potential threats, the number of locations of this species is less than five. A potentially mitigating factor that might favor the long-term perpetuation of this species is the occurrence of some plants in protected areas (e.g., *Ibáñez et al. 6928* occurs in Cerro Hoya National Park; *Carrión et al. 543* occurs in Coiba National Park). The other three collections occur in areas lacking official protection, and some of these areas have undergone or will potentially undergo deterioration due to construction of tourist infrastructure in the coastal regions in which the plants occur. According to label information on collections and field observations, at different localities plants varied from the dominant species present (e.g., *Ibáñez et al. 6928*) to occasional (*León et al. 753* ) to rare (*Carrión et al. 543*). Based on the number of locations and an inferred decline in the extent and/or quality of habitat in the range of this species, two of the subcriteria would appear to be met for an assessment of Endangered for *Odontonema aliciae*, given its AOO (i.e., B2, a, b).

**PARATYPES**.— **PANAMA: Los Santos**: Playa Venado, 30 km E of Tonosi on hwy. 50, 30 Oct 1978 (flr), *B. Hammel 5472* (MO, PMA); road along coast, 07°14′N, 80°31′W, 14 Dec 1995 (frt), *M. Nee & T. Andres 46341* (NY, PMA, US). **Veraguas**: PN Coiba, Isla Contreras, Isla Fragata, N416326.62, W866367.81, 11 Jan 2012 (flr), *J. Carrión et al. 543* (PMA); Golfo de Montijo, Cébaco, E472764, N826429, 10 Aug 2011 (flr), *N. León et al. 753* (PMA).

Neotropical relatives of *Odontonema* in the *Pseuderanthemum* lineage of Acanthaceae: Justicieae include several morphologically similar genera: *Chileranthemum* Oerst., *Oplonia* Raf., *Pulchranthus* V.M. Baum, Reveal & Nowicke, and *Pseuderanthemum* Radkl. ex Lindau (McDade et al. 2000). Morphological distinctions among these genera, all of which contain heterostylous species, are largely based on form of the corolla, which likely reflects adaptation to different predominant pollinators (cf. Daniel 1995, especially fig. 1).

A Colombian species originally described as *Odontonema stenostachyum* Leonard (Leonard 1958) and treated as *Pseuderanthemum stenostachyum* (Leonard) V.A.W. Baum by Baum (1982), belongs to the *Pseuderanthemum* lineage. Like *O. aliciae*, it has sessile to subsessile and “more or less subauriculate” leaf blades (Leonard 1958:392). In the protologue of *O. stenostachyum*, the corollas were described as immature and an accompanying illustration shows them as buds only; this condition was verified by studying the type collection at US. Because Baum (1982) did not provide a rationale for transferring this species to *Pseuderanthemum*, and because the differences between these two genera are subtle at best, the generic affinities of *P. stenostachyum* remain suspect. It can be distinguished from *O. aliciae* by the characters in the following couplet:

1a. Internodes of vegetative stems and inflorescence rachis, peduncles, and pedicels glabrous; inflorescence broad (ca. 50 mm across near midpoint) with dichasia pedunculate; calyx 6.5–9 mm long; corolla pink to purple with white markings on lower-central lobe; seeds with longest axis 6.5–7.5 mm. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Odontonema aliciae*

1b. Internodes of vegetative stems and inflorescence rachis, peduncles, and pedicels pubescent; inflorescence narrow (ca. 20 mm across near midpoint) with dichasia sessile to subsessile;

calyx 4–5 mm long; corolla white; seeds with longest axis ca. 3 mm long ............... ............................................ *Pseuderanthemum stenostachyum*

Among Mexican and Central American *Odontonema*, *O. auriculatum* (Rose) T.F. Daniel is also morphologically similar and is perhaps a closer relative of *O. aliciae*. *Odontonema auriculatum* occurs in western Mexico, from Sinaloa to Oaxaca, where plants grow in tropical deciduous and tropical subdeciduous forests at elevations from 60–230 m (Daniel 1995). That species is characterized by the combination of its conspicuously auriculate leaves and red flowers (Daniel 1995). It can be further distinguished from *O. aliciae* by the characters and distributions summarized in the following couplet:

1a. Corolla pink to purple, 13–20 mm long, tube 7.5–11 mm long, subcylindric, throat inconspicuous (i.e., not well differentiated from narrow proximal portion of tube); calyx 6.5–9 mm long, lobes, 5.5–8 mm long; dichasia pedunculate, peduncles 5–13 mm long; leaves sessile to subsessile (i.e., with naked petiole to 4 mm long), subauriculate at base; Panama .... *O. aliciae*
1b. Corolla red, (20–) 25–30 mm long, tube 13–20 mm long, funnelform, throat conspicuous; calyx 2–5 mm long, lobes 1.4–4 mm long; dichasia sessile to pedunculate, peduncles 1–4 mm long; leaves sessile, conspicuously auriculate at base; Mexico ................. *O. auriculatum*

Like many other species of *Odontonema*, *O. aliciae* is distylous with some individuals having long stamens and short styles (thrum flowers; e.g., *Ibáñez et al. 6928* at PMA-plant on left side of sheet) whereas others have shorter stamens and longer styles (pin flowers; e.g., *Hammel 5472* at PMA). Although floral visitors were not observed to *O. aliciae*, the flowers are suggestive of those often pollinated by hummingbirds and/or bees. Corolla color varies from pink (e.g., *Ibáñez et al. 6928*) to purple (e.g., *Carrión et al. 543*). Pollen of *O. aliciae* is of the basic type common to most species of the genus (i.e., 3-colporate, 6-pseudocolpate; Fig. 3) and to the *Pseuderanthemum* lineage (Baum 1982; Daniel 1998; McDade et al. 2000).

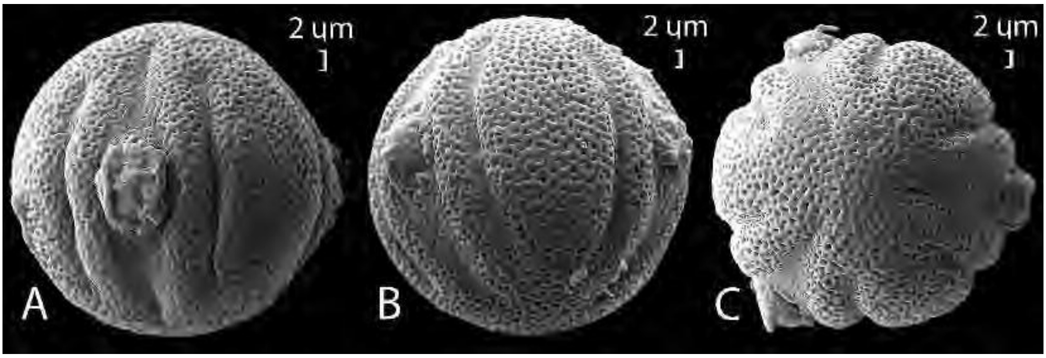

FIGURE 3. Pollen of *Odontonema aliciae* (*Hammel 5472*). A. Equatorial/subapertural view. B. Subequatorial/interapertural view. C. Polar view.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

BAUM, V. M. 1982. A revision of the genus *Odontonema* (Acanthaceae). Unpublished M.Sc. Thesis, University of Maryland, College Park, Maryland, USA.

DANIEL, T. F. 1995. A revision of *Odontonema* (Acanthaceae) in Mexico. *Contributions of the University of Michigan Herbarium* 20:147–171.

DANIEL, T. F. 1998. Pollen morphology of Mexican Acanthaceae: Diversity and systematic significance. *Proceedings of the California Academy of Sciences*, ser. 4, 50:217–256.

DANIEL, T. F., AND L. A. MCDADE. 1995. Additions to the Acanthaceae of Panama. *Annals of the Missouri Botanical Garden* 82:542–548.

LEONARD, E. C. 1958. The Acanthaceae of Colombia, III. *Contributions of the U.S. National Herbarium* 31:323–781.

MCDADE, L. A., T. F. DANIEL, S. E. MASTA, AND K. M. RILEY. 2000. Phylogenetic relationships within the tribe Justicieae (Acanthaceae): Evidence from molecular sequences, morphology, and cytology. *Annals of the Missouri Botanical Garden* 87:435–458.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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# Synopsis of the Grenadier Fishes (Gadiformes; Teleostei) of Taiwan

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## Table of Contents

**Species of grenadier fishes (Order Gadiformes) in Taiwan are reviewed. The species list of Shao et al. (2008) is revised. A total 71 species in 21 genera and 3 families is recognized, including 5 species that are tentatively identified and 5 species, *Coelorinchus hexafasciatus*, *C.* cf. *macrorhynchus*, *C.* cf. *notatus*, *Hymenocephalus papyraceus*, and *Ventrifossa sazonovi,* that are first records for Taiwan. *Ventrifossa fusca* is recognized as a junior synonym of *V. misakia*. Keys to families, genera and species are provided. Species descriptions are based mainly on Taiwanese specimens but supplemented with specimens from various other sources. Figures of species firstly reported by Shao et al. (2008) are provided.**

KEYWORDS: Pisces, taxonomy, Bathygadidae, Macrouridae, Macrouroididae, Taiwan

Grenadiers constitute the largest group of deepwater demersal fishes found at continental-slope depths between 200 m and 4000 m of all oceans. We here use the common name grenadier to include members of four distinct families—Bathygadidae, Macrouridae, Macrouroididae, and Trachyrincidae—of the order Gadiformes, in which the highly valued codfishes of the family Gadidae are a part. Macrouridae is the largest family in the order with more than 350 species classified into about 30 genera. Grenadiers are almost exclusively benthopelagic in habit, with only a few species having taken up a bathypelagic existence. Pelagic captures of some normally benthopelagic species suggest that individuals may on occasion forage well off the bottom, and these forays may be vertical or offshore movements.

Recent deepwater trawl collections from Taiwanese waters have shown an astonishing diversity of benthopelagic fishes, among which the grenadiers are represented by the highest number of species. Shao et al. (2008) recorded 71 species of grenadiers categorized into 19 genera and three families; 33 of those species (in 10 genera) were newly recorded from Taiwan and were captured only since 2001. Our subsequent re-examination and re-evaluation of specimens have changed the composition of the list slightly, but retained the same number of species (70 if *Coelorinchus productus* is accepted to be a synonym of *C. anatirostris*) classified in 21 genera (2 genera formerly treated as subgenera *Hymenogadus* and *Spicomacrurus*). Shao et al. (2008) analyzed the species composition of the group as related to depth and geography in Taiwanese waters and found a distinct separation at 600 m and 1000 m. The principal factors influencing grenadier species composition in the catches were depth, geographic region, and net type.

Documenting the diversity of Taiwan's continental-slope fauna is highly important at this time because of the recently developed deepwater trawl fishery in the country, which has been exploiting the offshore resources heavily. The primary species targeted in this fishery are the shrimps and prawns, with the more valuable food fishes in the catches hand-selected out at the dockside markets. Whatever bycatch remains, and that includes many species of grenadiers, is ground up to be used as feed stock in the country's extensive aquaculture and poultry industries. It is doubtful that such heavy exploitation of these resources can continue without a dramatic depletion of the stocks, owing to the presumed slow growth rate of most deepwater animals. The classic, well-documented depletion of the deepwater orange roughy *Hoplostethus atlanticus* stocks off New Zealand and Australia is mirrored in the North Atlantic by the stocks of roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax*, which by some estimates can be considered as threatened in the northwestern part of the Atlantic (Devine et al. 2006; Devine and Haedrich 2008). Merrett and Haedrich (1997) provide detailed case examples as well as an overview of development, history, and future of deepwater demersal fisheries in their highly informative book *Deep-sea demersal fish and fisheries*.

The many species of grenadiers brought into Taiwanese ports and the difficulty in identifying them have prompted us to develop this identification guide, which we hope will allow its users to accurately identify and document one of the chief components of most deepwater catches. Such identifications are crucial for obtaining accurate statistical information on Taiwan's fishery resources and ultimately to developing regulations that will ensure their sustainablility into the distant future, as well as maintaining that part of the rich biodiversity heritage of the country.

## MATERIAL AND METHODS

Data herein provided are from the specimens we have examined, mostly from Taiwan and Japan, but sometimes from other areas as indicated in the Materials Examined sections. Specimens are primarily from the Academia Sinica, Research Center for Biodiversity (formerly Institute of Zoology) (ASIZ), with supplemental material from the California Academy of Sciences (CAS), Laboratory of Marine Biology, Faculty of Science, Kochi University, Kochi (BSKU); Hokkaido University Museum, Hakodate, Hokkaido (HUMZ); National Museum of Marine Biology and Aquarium (NMMB-P), Kenteng, Taiwan; National Science Museum, Tokyo (NSMT); and United States National Museum of Natural History, Washington DC (USNM). Methods for making counts and measurements follow Iwamoto (1970) and Iwamoto and Sazonov (1988), and further elaborated on by Iwamoto and Williams (1999). The reader is referred to Eschmeyer's *Catalog of fishes* (1998) for complete references to species and generic names. An updated online version can be accessed at <*http//:www.calacademy.org*>. Institutional abbreviations are taken from Fricke and Eschmeyer (2009).

In the **MATERIAL EXAMINED** sections, the ASIZP specimens are grouped by general locality (abbreviated as in following paragraph) and listed by institutional catalog number followed in parentheses by number of specimens, place name or station number, and size range. Collection data for research vessel stations and fishing ports are provided in Appendix 1 (Table 1). The official and unofficial Taiwanese names of Taiwan fishing ports, in English and Chinese, and the geographic coordinates for each locality can be found in Ebert et al. (2013: table 5, fig. 1).

For non-ASIZP specimens more complete data are provided in these sections. The reader should note that characters used in the keys and diagnoses for genera are often not repeated in the descriptions of the species of the particular genus. The **DISTINGUISHING FEATURES** in the species descriptions are usually only those needed to distinguish Taiwan species from others of the genus and may not apply if used with collections from other areas. Distributions are given in more detail for Taiwan records than for other areas. There was no attempt to make the synonymies comprehensive; they are limited to those most applicable to the Taiwanese fauna. Illustrations have been kept to a minimum because a forthcoming book on the codfishes of Taiwan, geared for a general audience, will be fully illustrated with photographs or line drawing of all Taiwan species.

**ABBREVIATIONS**. For measurements and counts: TL, total length; PAL, pre-anal length; HL, head length; 1D, first dorsal fin; 2D, second dorsal fin; P, pectoral fin; V, pelvic fin; A, anal fin; GR-I, gill rakers on first arch, GR-II, gill rakers on second arch; pyl. caeca, pyloric caeca. Other: descr., description; fm, fathom[s]; e., east, eastern; local., locality[ies]; n., north, northern; s., south, southern; spec., specimen[s]; sta., station; w, west, western. Abbreviations for localities in Taiwan follow Shao et al. (2008): ET, eastern Taiwan; NET, northeastern Taiwan; SET, southeastern Taiwan; SWT, southwestern Taiwan; SCS, South China Sea.

## RESULTS

### The Diversity and Current Status of Grenadier Species in Taiwan

In this study, 71 species of grenadiers in 21 genera and 3 families are recognized. Despite a relatively limited coastline (500 nautical miles), the species diversity in Taiwan is very high compared to nearby areas. Of this total, 63 species (of 366, or ca. 17%) are in the family Macrouridae, 7 species (of 27, or ca. 30%) in the family Bathygadidae, and 1 species (of 2) in the family Macrouroididae. The top three largest genera, all in Macrouridae, are *Coelorinchus* (23 species), *Ventrifossa* (9 species) and *Nezumia* (5 species). Six species were described from Taiwan, and three of them (*Coelorinchus leptorhinus, C. sheni* and *C. fuscigulus*) have not been reported elsewhere.

Shao et al. (2008) published a list of grenadier species from Taiwan with a discussion of their distribution pattern.

After our detailed examination of specimens from Taiwan and based on new evidence, we have made the following name changes to Shao et al.'s list: (1) specimens of *Gadomus multifilis* are now recognized as *Gadomus* cf. *multifilis*; (2) records of *Coelorinchus cylindricus* in Taiwan have been replaced by *C. fuscigulus* Iwamoto, Ho & Shao, 2009; (3) the specimen of *Coelorinchus spinifer* is now recognized as *C.* cf. *spinifer*; (4) the specimen of *Coryphaenoides asper* is now recognized as *C.* cf. *asper*; (5) *Hymenocephalus gracilis* has been reassigned to *Hymenogadus* and *Hymenocephalus kuronumai* has been reassigned to *Spicomacrurus*; (6) the western Pacific population of *Malacocephalus laevis* is now recognized as *M. nipponensis*; (7) specimens of *Nezumia coheni* are now recognized as *N.* cf. *coheni*; (8) the specimen of *Nezumia loricata* is now reidentified as *N. proxima*; (9) a specimen of *Pseudocetonurus septifer* is now recognized as *P.* cf. *septifer*; (10) the specimen of *Paracetonurus cetonuropsis* is now reidentified as *Pseudonezumia pusilla*; and (11) *Ventrifossa fusca* is now recognized as a junior synonym of *V. misakia*.

We also report as first records for Taiwan *Coelorinchus hexafasciatus*, *C.* cf. *macrorhynchus*, *C.* cf. *notatus, Hymenocephalus papyraceus,* and *Ventrifossa sazonovi*. Specimens of six species are provided tentative identifications because they showed certain character differences compared with published descriptions. Further study may result in recognizing them as new species or subspecies. Moreover, several specimens of *Bathygadus* could not be confidently identified and were therefore listed with no names: the genus is in great need of revision.

## SYSTEMATICS

### Key to the Grenadier Families in Taiwan

1a. One dorsal fin, no part elevated; head notably inflated; eyes tiny, horizontal orbit diameter more than 10 times in HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Macrouroididae

1b. Two dorsal fins, the first elevated; eyes larger, orbit diameter much less than 10 times in HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Second dorsal fin high, much better developed than anal fin; gill rakers long and lathlike; outer gill slit wholly unrestricted. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Bathygadidae

2b. Second dorsal fin usually much less developed than anal fin; gill rakers short, tubercular; outer gill slit variously restricted by folds of skin connecting gill arch above and below . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Macrouridae

## Family Bathygadidae

### Key to the Genera and Species of Bathygadidae in Taiwan

1a. Chin barbel long, greater than half orbit diameter; elongated ray(s) in 1D, P and V; V 8 (rarely 9) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2 (*Gadomus*)

1b. Chin barbel usually absent, if present, length much less than half orbit diameter; usually no greatly elongated rays except in V, and if present, ray extremely fine distally and usually less than HL; V 8–10 (rarely 11) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4 (*Bathygadus*)

2a. GR-I with blunt tips, 4–6+20–23 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

2b. GR-I with pointed tips, 6+22–26 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *G*. cf. *multifilis*

3a. Chin barbel about 3 times or less into HL; pyl. caeca 24–29. . . . . . . . . . . . . . . . . *G. magnifilis*

3b. Chin barbel about 2 times into HL; pyl. caeca 95–134. . . . . . . . . . . . . . . . . . . . . . . *G. colletti*

4a. Gular membranes scaled; orbit width 1.1–1.2 times into interorbital . . . . . . . . . . . . . . . . . . . 5

4b. Gular membranes wholly naked; orbit width 1.2–2.1 times into interorbital . . . . . . . . . . . . . 6

5a. V 10 (rarely 11); barbel rarely present; pyl. caeca 12–19. . . . . . . . . . . . . . . . . . . *B. nipponicus*

5b. V 9 (rarely 10); rudimentary barbel usually present; pyl. caeca 34–54 . . . . . . . . . . . *B. garretti*

6a.Head bones weak, skin thin and fragile; interorbital width 31–36% HL; pyl. caeca 10–18. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. antrodes*

6b.Head bones relatively strong, skin usually rather stout and thick; interorbital width 26–30% HL; pyl. caeca 20–22 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. furvescens*

### Genus *Bathygadus* Günther, 1878

**DISTINGUISHING FEATURES**.— Chin barbel usually absent; when present barbel tiny and difficult to see without magnification. In some species, 1D, P, and V with a relatively elongated ray, but never extremely long and thickened to degree found in *Gadomus* species.

**REMARKS**.— Identifying some members of this genus has been difficult and uncertain, partly owing to the often poor condition of the specimens. Their delicate bones and integument are easily damaged in trawls, and crucial identification features are often distorted, damaged, or destroyed. The many species described from the broad area encompassing Japan, Taiwan, the South China Sea, Philippines, and Indonesia and our limited knowledge of distributional limits of the species leave the possibility of encountering one or another species wide open. Our study material included a number of specimens for which we could not arrive at a satisfactory identification; such specimens are listed under *Bathygadus* sp. indet. and accompanied by brief remarks.

The genus was reviewed by Howes and Crimmen (1990), but many of their taxonomic conclusions are questionable (see Sazonov 1994:101; Iwamoto and Merrett 1997:479).

#### *Bathygadus antrodes* (Jordan and Gilbert, 1904)

*Melanobranchus antrodes* Jordan and Gilbert, 1904:606–607, pl. 4, fig. 7. (holotype: USNM 50932, 265 TL, Sagami Bay, Japan, 501–749 fm [916–1,370 m], *Albatross* sta. 3696; other spec. from Sagami and Suruga bays, 480–677 fm [878–1238 m]).

*Bathygadus antrodes*: Gilbert and Hubbs, 1916:149–150 (16 spec., 9 local. off Honshu I., Japan; 440–712 fm [805–1,302 m]).— Okamura, 1970:30–33, pl. XI, text-fig. 16 (descr.; 15 spec.; Japan); Okamura, 1984:197, 356, fig. 138 (descr. in Japanese and English; 4 spec.; s. Japan, Okinawa Trough, 792–1,200 m).— Howes and Crimmen, 1990:191 (USNM spec.; s. Japan). Sazonov 1994:100–101, fig. 1 (5 spec., Nintoku Seamount [on Emperor Seamounts chain]; 1120–1160 m).— Chiou et al., 2004b:39. fig. 5 (2 spec., NET; one spec. we currently re-identify as *B. garretti*).— Shao et al., 2008: table 2 (19 spec., NET, SWT, SET, SCS).

**Material examined** (7 spec.).— **NET:** ASIZP 61225 (1, 635 TL); Da-xi. **SCS:** ASIZP 65515 (1, 66.8 HL, 350 TL); CD 322, 1098 m; ASIZP 65633 (2, 150–375+ TL); CD 229, 880–1062 m. **SET**: ASIZ 67033 (1, 78.1 HL, 367+ TL); CP 350, 1148 m; ASIZP 66100 (1, 62 HL, 310 TL); CD 322, 1098 m; ASIZP 66110 (1, 73.1 HL, 377+ TL); CD 322, 1098 m.

**Distinguishing features**.— A species of *Bathygadus* with no scales on gular membrane; chin barbel absent; dorsal profile behind head elevated, nape somewhat humpbacked; 1D II7–9; P i14–i18; V 8–9; GR 5–6+18–20; pyl. caeca 10–18*; interorbital width 31–36% HL; orbit diameter 18–22%; upper jaw length 53–64%; filamentous rays of 1D, P, and V when intact slightly longer than head.* Head bones and integument notably thin and fragile. Color overall dark; fins, head, abdomen, mouth, and gill cavity usually black. (* indicates data from Gilbert and Hubbs, 1916).

**Distribution**.— From n. part of Japan (Tohoku region of Honshu Is.) s. to Taiwan (NET, SET, SCS) and on Emperor Seamounts Chain (at 40°05′N, 170°43′E), from about 800 to 1370 m.

**Remarks**.— Chiou et al. (2004b:39, 42, fig. 5) recorded this species from Taiwan based on two specimens, but we re-identified one of them (ASIZP 61226) as *B. garretti. Bathygadus antrodes* is closely similar to *B. bowersi* (Gilbert, 1905) from Hawaii and to *B. spongiceps* Gilbert and Hubbs, 1920 from the Philippines and Indonesia. Characters used to distinguish the three are minimal and need to be further supported. A closer comparison with many more specimens from throughout the western and central Pacific should prove fruitful.

### *Bathygadus furvescens* Alcock, 1894

Figures 1A–B.

*Bathygadus furvescens* Alcock, 1894:128 (holotype ZSI F13047, “20.5 inches” [ca. 52 cm]; off Maldives, *Investigator* sta. 150; 719 fm [1,315 m]).— Gilbert and Hubbs, 1920:388–391 (descr.; 5 spec., 5 loc., Philippine and Indonesia; 565–976 fm [1033–1785 m]).— Iwamoto and Merrett, 1997:479 (validated position of species in *Bathygadus*).— Iwamoto and Graham, 2001:422–423, fig. 17 (descr., 10 spec., se. coast Australia, “depths between 1,000 and 1, 240 m”).— Shao et al., 2008: table 2 (2 spec., SET, first record for Taiwan).

**Material examined** (10 spec).— **SET:** ASIZP 65510 (1, 91.8 HL, 475+ TL); CP 127, 1263–1268 m. Others questionably assigned to species, but with black head and abdomen, lacking paler areas on head: **SET:** ASIZP 66938 (1, 475 TL); CP 127, 1263–1268 m. **SWT:** ASIZP 66115 (1, 100 HL, 450 TL); CD 322, 1098 m; ASIZP 70215 (1, 345 TL); ASIZP 63788 (4, 118+-380+ TL); CD 192, 1305 m; ASIZP 65530 (2, 280–335 TL); CD 134, 736–1040 m.

**Distinguishing features**.— A species of *Bathygadus* with no scales on gular membrane; chin barbel absent; dorsal profile slightly elevated over nape; 1D II,8–10; P i15–i19; V 8–9; gill-rakers outer arch (5–6) + (18–20); pyl. caeca 20–22. Interorbital width 26–30% HL; orbit diameter 21–23%; suborbital width 14–15%; postorbital length 51–55%; distance orbit to preopercle 48–50%; length upper jaw 56–59%; length P 61–81%; length V 67–83%; length longest gill-raker 13–15%. Fins well developed; outer V ray elongated and distally filamentous. Flesh and head bones relatively firm. Fins black to dark dusky. (After Iwamoto and Graham [2001:479] except for lengths of postorbital and longest gill-raker, the ranges of these were extended by our specimens.)

**Distribution**.— Recorded from Maldives, Indonesia, Philippines, se. Australia, and now off Taiwan, in depths between approximately 1000 m and 1800 m.

**Remarks**.— Howes and Crimmen (1990:195) treated the species as a member of *Gadomus* based on a specimen they erroneously considered a syntype, but which not only was non-type material but also a species different from the holotype (see Iwamoto and Merrett 1997:479). The large Taiwan specimen was similar in most mensurable and count characters to the specimens we called *B. antrodes.* However, its head bones were stouter, integument notably tougher, with scale

FIGURE 1. *Bathygadus furvescens* Alcock, 1894. A. ASIZP 65510, 475+ mm TL, preserved. B. ASIZP 63788, 1 of 4, 380+ mm TL, preserved.

pockets well developed, color overall paler, the interorbital width slightly narrower (27–28% HL), and none of the fin rays longer than the head. The specimen agreed in these respects with *B. furvescens* as circumscribed by Iwamoto and Graham (2001:422–423) and represents the first record of the species from Taiwan waters.

### ***Bathygadus garretti*** **Gilbert and Hubbs, 1916**

*Bathygadus garretti* Gilbert and Hubbs, 1916:151–153, pl.8, fig. 1 (holotype USNM 76863, 513 TL, Suruga Gulf, Japan, *Albatross* sta. 5059, 197–297 fm [360–543 m]).

*Bathygadus* (*Melanobranchus*) *garretti*: Gilbert and Hubbs, 1920:380 (in key).

*Bathygadus garretti*: Okamura, 1970:34–36, pl. 12, text-fig. 17 (descr. based on paratype, USNM 135351); Okamura, 1984:197, 357, fig. 139 (descr. in Japanese and English; 7 spec., Okinawa Trough, 360–650 m).— Chiou et al., 2004b:42, fig. 6 (1 spec., Da-xi, NET).— Shao et al., 2008: table 2 (6 spec., NET, SWT, SCS).

*Bathygadus nipponicus*: Howes and Crimmen, 1990:191 (in part; synonymized *B. garretti* with *B. nipponicus*). Chiou et al., 2004b:42, fig. 7 (1 spec., NET).

MATERIAL EXAMINED (20 spec.).— **NET:** ASIZP 61226 (1, 86.5 HL, 446 TL); Da-xi; ASIZP 61227 (2, 70–77 HL, 362–380 TL); Da-xi; ASIZP 61228 (1, 96.8 HL, 458 TL); Da-xi, ASIZP 64274 (1, 91.3 HL, 365 TL); CP 235, 764 m; ASIZP 70241 (1, 281 TL); Da-xi; ASIZP 70244 (1, 153 TL); Da-xi; ASIZP 70246 (3, 127–175 TL); Da-xi; ASIZP 70249 (3, 360–456 TL); Da-xi; ASIZP 70253 (1, 444 TL); Da-xi. **SWT:** ASIZP 65512 (1, 58.1 HL, 320 TL); CP 130, 709–728 m; ASIZP 65593 (1, 70 HL, 338 TL); CD 140, 280–452 m; ASIZP 65599 (1, 65.6 HL, 291+ TL); CD 137, 316–477 m. **No data:** ASIZP 65580 (1, 71.6 HL, 335+ TL). **Other material**: **Japan:** BSKU 98225 (1, 62.5 HL, 305+ TL) and BSKU 98224 (1, 58.9 HL, 320 TL); Suruga Bay, 520–545 m; 23 Nov. 1978.

**Distinguishing features**.— A species of *Bathygadus* with gular membrane scaled; a rudimentary chin barbel usually present (sometimes absent); dorsal profile behind head relatively low, nape not humpbacked; 1D II8–10; P i15–i18; V 10 (rarely 11); GR-I (5–6) + (17–20); pyl. caeca 34–46 (or more); interorbital width 27–32% HL; orbit diameter 21–26%; upper jaw length 52–58%; none of fins with greatly elongated rays.

**Distribution**.— Southern Japan s. to Taiwan (NET, SWT) in 360–650 m.

**Remarks**.— Our identification of specimens of this species was based on a combination of characters, including the presence of a rudimentary chin barbel. In a few specimens, the barbel was not present, but other characters that we deemed important appeared to confirm our identification. Howes and Crimmen (1990:1910) synonymized *B. garretti* with *B. nipponicus*, stating that the only difference between the two was the presence of a rudimentary chin barbel in the former, a suggestion made earlier by Okamura (1984:358). However, our ASIZ specimens suggest that *B. garretti* almost always has V 10 (11 on one side in a paratype) vs. mostly 9 in *B. nipponicus* (the holotype has 10, *fide* Okamura 1970 and Howes and Crimmen 1990, not 9 as stated in the original description), a slightly larger orbit (1–26% HL vs. 17–22%), and more pyloric caeca (34–46 [5 spec.] vs. 12–19 [5 spec.]). The count of pyloric caeca in the single paratype of *B. garretti* was given as 50 by Gilbert and Hubbs (1916:152), 49 by Okamura (1970:34), and 54 by Howes and Crimmen (1990:191).

Specimen ASIZP 61227, listed in Chiou et al. (2004b) as the first Taiwan record of *B. nipponicus*, was determined by us to be *B. garretti*. One of two specimens of *B. antrodes* (ASIZP 61226) recorded in the same paper is now re-identified as this species.

### *Bathygadus nipponicus* (Jordan and Gilbert, 1904)

*Regania nipponica* Jordan and Gilbert, 1904:605–606, fig. (holotype, USNM 50931, 590+ TL; *Albatross* sta. 3721, Suruga Bay, Japan, 207–250 fm [379–457 m]).

*Bathygadus nipponicus*: Gilbert and Hubbs, 1916:142 (listed).— Okamura, 1970:33 (compiled).— Howes and Crimmen, 1990:191–192 (in part; holotype data; see Remarks under *B. garretti).*— Chiou et al., 2004b:42, fig. 7 (1 spec., NET, re-identified as *B. garretti*).— Shao et al., 2008: table 2 4 spec., NEW, SWT, SCS).

*Bathygadus* (*Melanobranchus*) *nipponicus*: Gilbert and Hubbs, 1920:380 (in key).

**Material examined** (6 spec.).— **SWT:** ASIZP 64117 (1, 60 HL, 210+ TL); CD 193, 821 m; ASZIP 65633 (3, 44–60.2 HL, 150–375 TL) and ASZIP 65634 (1, 66 HL, 264+ TL); CD 229, 880–1062 m. **SCS:** ASIZP 66126 (1, 83.0 HL, 480 TL); CD 320, 731 m.

**Distinguishing features**.— A species of *Bathygadus* with gular membrane scaled; chin barbel absent; dorsal profile behind head relatively low, nape not humpbacked; 1D II,8–10, P i15–i17; V 9 (rarely 10); GR 6+(17–22) (ASIZP 65634 had 2 rudiments and 6 developed rakers on upper arm); pyl. caeca 12–19; interorbital width 27–32% HL; orbit diameter 22–26%; upper jaw length 53–56%; none of fins with greatly elongated finray.

**Distribution**.— Southern Japan to Taiwan (SWT, SCS) in 731–l062 m.

**Remarks**.— Jordan and Gilbert (1904:605) gave the gill raker count as 5+16 in the holotype and only specimen in their original description of the species; this count was confirmed by Howes and Crimmen (1990:191). That the count is lower than the values in our specimens is somewhat unsettling, but we hold to our identification until the time more specimens become available and the holotype can be re-examined by one of us. So far as we can determine, our specimens represent only the second record of the species and the first from Taiwan. Chiou et al. (2004b:42, fig. 7) listed the species as a first record from Taiwan based on ASIZP 61227, but we re-examined that specimen and determined it to be *B. garretti.*

***Bathygadus*** sp. indet.

ASIZP 64268 (1, 39.2 HL, 180+ TL), CD 191, 821 m. This specimen from 821 m in the SCS had interorbital 33% HL, orbit 20%, suborbital 14%, postorbital 56%, orbit-preopercle 49%, upper jaw 62%, and V 10, P 17–18, GR-I 5+19, characters that suggest *B. spongiceps.*

ASIZP 65634 (1, 264+ TL), CD 229, 880–1062 m. This specimen from SWT is in poor condition and most characters are undecipherable. Interorbital 23 mm, orbit 12.7 mm, orbit-preopercle 28 mm; V 9, GR-I 6+19. Head integument relatively tough; orbit too wide to be *B. garretti* or *B. nipponicus*.

ASIZP 66738 (1, 21.3 HL, 92+ TL), CD 324, 1293 m. This small specimen from 1293 m in the SCS had a broad interorbital (38% HL), small orbit (22%), deep suborbital (18%), and GR-I 5+18, characters that suggest *B. antrodes.*

ASIZP 66793 (1, 405 TL); CD 320, 731 m. This specimen from the SCS is in poor condition; it was originally identified as *Bathygadus entomelas*.

## Genus *Gadomus* Regan, 1903

**DISTINGUISHING FEATURES.**— Chin barbel present, usually thick and long. V rays usually 8, rarely 9. Second spinous ray of 1D, upper ray of P, and outermost ray of V usually elongated, in some species extremely long; outer V ray usually rather thick.

**REMARKS.**— The genus was revised by Howes and Crimmen (1990), who based their work mostly on the literature and old, previously recorded specimens (none recently collected). With respect to *Gadomus aoteanus*, they followed McCann and McKnight (1980), who gave an erroneous count of V 9, but examination of the holotype and many other specimens (by TI) of that species showed that there are consistently eight rays in each fin. Gilbert (1905:658) gave a count of V 9 for the holotype (and only type specimen) of *G. melanopterus*; this is the only record of nine rays in a specimen of *Gadomus* that we are aware of. A second non-type specimen (CAS-SU 8545) that he reported in the original description has V 8.

Seven of the 12 described species of *Gadomus* are found in the western Pacific, but there may be others that are new to science. The species from the Indo-Pacific region have, for the most part, been inadequately circumscribed owing to the lack of large series from many localities. A thorough review of the genus using more recently collected material and genetic analyses is badly needed.

### *Gadomus colletti* Jordan and Gilbert, 1904

*Gadomus colletti* Jordan and Gilbert, 1904:603–604 (holotype USNM 50930, Albatross sta. 3721, Suruga Bay, Japan; 207–250 fm [379–457 m]).— Gilbert and Hubbs, 1916:154–155 (descr.; 4 spec., 68–302 TL; Suruga Gulf, 211–293 fm [386–536 m]); Gilbert and Hubbs, 1920:392 (in key).— Okamura, 1970:23–26, pl. I, fig. a; text-fig. 12A, 13 (descr., 44 spec., 177–322 TL); s. Japan, 360–547 m).— Howes and Crimmen, 1990:199 (descr. based on holotype and USNM spec.).— Chiou et al., 2004b:43, fig. 8 (2 spec., NET).— Shao et al., 2008: table 2 (5 spec., NET, SCS).

*Bathygadus colletti*: Weber, 1913:172 (listed).

**Material examined** (6 spec.).— **NET:** ASIZP 61223 (1, 79 HL, 363 TL); Da-xi; ASIZP 61224 (1, 82.7 HL, 382 TL); Da-xi; ASIZP 65636 (1, 68.1 HL, 352 TL); CD 214, 488–1027 m; Da-xi. ASIZP 70251 (1, 90 HL, 346 TL); Da-xi. **SWT:** ASIZP 65513 (1, 200+ TL); CP 130, 709–728 m. **Other specimens: Japan**: HUMZ 37408 (1, 29.8 HL, 146+ TL).

**Distinguishing features**.— A species of *Gadomus* with chin barbel about 2/3 of HL or slightly longer; elongated ray in 1D, P and V often longer than HL; 1D II,10–11; P (i16) i18–i21; V 8; outer gill rakers lathlike but relatively short, bluntly tipped, (4–5)+(8–21) (ASIZP 61224 had 1 rudiment and 5 developed rakers on upper arm, 16 developed and 3 rudiments on lower arm); pyl. caeca small, numerous, about 95 to 165. Interorbital width 14–18% HL; orbit diameter 22–23%; upper jaw length 51–58%; chin barbel 57–91%; 1D spinous ray less than twice HL. Color relatively pale, mouth and gill cavity dark but paler on outer margins; lips and barbel whitish; fins dusky to blackish, dorsal fins lighter basally.

**Distribution**.— Southern Japan to Taiwan (NET, SWT) in 488–1027 m.

**Remarks**.— This species was first recorded from Taiwan by Chiou et al. (2004b:43). Our four specimens appeared to have a somewhat shorter barbel (57–91% of HL) than reported by others. Okamura (1970:24) recorded their length as 0.9–1.2 into HL in 44 specimens from Japan, “about as long as, or a little shorter than, length of head” in 10 specimens from the Kyushu-Palau Ridge and Tosa Bay (Okamura 1982:345), and 75–91% HL in five specimens from the Okinawa Trough (Okamura 1984:356).

### *Gadomus magnifilis* Gilbert and Hubbs, 1920

Figure 2.

*Gadomus magnifilis* Gilbert and Hubbs, 1920:398–401, fig. 4 (holotype USNM 78208; n. Mindanao; *Albatross* sta. 5515 in about 700 fm [1280 m]; 2 paratypes, Philippines; 508–554 fm [929–1014 m]).— Howes and Crimmen, 1990:197 (descr. from type spec.).— Shao et al., 2008: table 2 (1 spec., SWT, first record for Taiwan).

**Material examined**.— **SWT:** ASIZP 65627 (1, 70 HL, 385+ TL); CD 229, 880–1062 m.

**Distinguishing features**.— A species of *Gadomus* with chin barbel about 29–72% of HL; length elongated P ray 2–3 times HL; prolonged ray in 1D and V greater than 1.5 times HL; 1D II,9–10; P i17–i18; V 8; outer gill rakers bluntly tipped, lathlike, short, about half orbit diameter, (5–6)+(21–23); pyl. caeca 24–29; interorbital width 16–17% HL; orbit diameter 21–24%; suborbital depth 10–15%; upper jaw length 55–60%; chin barbel 29–72% (compiled from Gilbert and Hubbs 1920 and ASIZP 65627).

Figure 2. *Gadomus magnifilis* Gilbert and Hubbs, 1920. ASIZP 65627, 385+ mm TL, preserved.

**Distribution**.— Taiwan (SWT) to n. Mindanao, Philippines, in 929–1280 m.

**Remarks**.— Our identification of the single Taiwan specimen is tentative. Its barbel length is somewhat shorter (29% HL cf. 61–72%) and suborbital somewhat deeper (15% HL cf. 10%) than in the type specimens of *G. magnifilis*. The Taiwan specimen appears similar to *G. introniger* in its gill-raker count, barbel length, orbit diameter, and bluntly tipped gill rakers, but differs in having a slightly narrower interorbital (17% cf. 20–23%), slightly deeper suborbital (15% cf. 10–13%), and longer orbit-to-preopercle distance (51% cf. 44–49%). The pyloric caeca could not be counted in our specimen because they had been previously extracted and were unavailable; they may have offered additional clues to the correct identity. Gilbert and Hubbs (1920:396) considered *G. denticulatus* as closely related to *G. magnifilis*, but compared to our specimen, *G. denticulatus* has a much narrower interorbital space (1.5–1.8 into orbit diameter cf. 1.3), slightly larger orbit (23–24% HL cf. 21% in our spec.), and slightly fewer gill rakers (4–6)+(17–22) (23–27 total), cf. 6+23 (29 total).

### *Gadomus* cf. *multifilis* [*sensu* (Günther, 1887)]

Figures 3A–B.

*Gadomus multifilis* (Günther, 1887): Shao et al., 2008: table 2 (4 spec., SWT, first record for Taiwan).

**Material examined** (9 spec.).— **SWT:** ASIZP 64092 (4, 30–50.6 HL, 130+-260+ TL); CD 193, 821 m. **SCS:** ASIZP 66334 (1, 38 HL, 240 TL) and ASIZP 66240 (1, 37.1 HL, 223+ TL), CD 307, 1591 m; ASIZP 66189 (1, 35.1 HL, 170+ TL) and ASIZP 66810 (1, 35.5 HL, 185+ TL); CD 322, 1098 m. **Other specimens:** ASIZP 68056 (1, 34.7 HL, 223 TL); CC2702 Aurora, 944–1004 m, 27 May 2007.

**Distinguishing features**.— A species of *Gadomus* with chin barbel about 50–75% of HL; length elongated P ray 2–3 times HL, prolonged ray in 1D and V much greater than HL; 1D II,8–9, P i16–i19; V 8; outer gill rakers sharply tipped, lathlike (6–7) + (23–26); pyl. caeca 24–29. Interorbital width 16–17% HL, orbit diameter 21–24%; suborbital depth 10–15%; upper jaw length 55–60%; chin barbel 29–72% (compiled from Gilbert and Hubbs, 1920).

**Distribution**.— Taiwan (SWT, SCS) and broadly across Indo-West Pacific, if these specimens are the same as *G. multifilis.*

**Remarks**.— Our identification of nine Taiwan specimens has been problematical, although they for the most part fit the original description and subsequent descriptions of *G. multifilis* by Gilbert and Hubbs (1920) and Howes and Crimmen (1990). However, four of the ASIZ specimens (ASIZP 64092) have a slightly lower count of GR-I (6 + 23) and more pyloric caeca (30–47 in 4 spec.); ASIZP 66334 had more rakers, 7 + 26 rakers. Gilbert and Hubbs (1920:406–408) gave the gill-raker count as 6 + (26–27) and pyloric caeca as 12 and 16. Howes and Crimmen (1990:195–197) counted 6 + 25 gill-rakers for the holotype and eight other specimens, and counts of 25 and 15 pyloric caeca in two of those specimens. The low gill-raker counts and high pyloric caeca counts of ASIZP 64092 agree rather well with those Gilbert and Hubbs (1920:403) gave for *G. introniger* (gill-rakers (5–6) + (20–24) and "pyloric caeca [in several specimens, 35 to 52"]). However, the orbit diameter and interorbital width are less in our specimens and the gill-rakers are pointed, not bluntly tipped, as in *G. introniger.* Similarly, the counts of gill-rakers and pyloric caeca, plus the interorbital and orbit dimensions, agree closely with *G. magnifilis*, but the gill-rakers are also bluntly tipped in that species. We see no resolution to our dilemma without a thorough revision of the genus using extensive material from throughout the Indo-West Pacific, and especially from that critical region around the Philippine Islands and the Malay Archipelago.

Figure 3. *Gadomus* cf. *multifilis* [*sensu* (Ganther, 1887)] A. ASIZP 64092, 260+ mm TL, fresh. B. ASIZP 66334, 240 mm TL, preserved.

## Family Macrouridae

### Key to Genera and Some Species of Macrouridae in Taiwan

(number of species in Taiwan in parentheses after genus)

1a. Six branchiostegal rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
1b. Seven branchiostegal rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

2a. Spinous 1D ray smooth; a stout continuous suborbital ridge terminating posteriorly in a sharp point; V 7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Coelorinchus* (23 spp.)
2b. Spinous 1D ray serrated (sometimes weakly) along leading edge; suborbital ridge not continuous and not ending in a sharp point; V 7–14 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3a. Gill-rakers absent on lateral side of first gill arch; V7 or 8; anus in middle third of distance between V and A . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Mataeocephalus hyostomus*
3b. Gill-rakers present on lateral side of first gill arch; V 7–14; anus usually immediately anterior to A . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Coryphaenoides* (4 spp.)

4a. Abdomen and isthmus with patches of fine black striations with silvery underlayment (especially when fresh); small lens-like light organ on chest connected by black medioventral line to a second lens immediately before anus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

4b. Abdomen and isthmus lacking areas of fine black striations; light organ, if present, not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

5a. Nasal bones forming three flat platelike horizontal processes; gular membrane with net- or mesh-like pattern; prolonged distal portion of outer pelvic fin ray with narrow membranous flange . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Spicomacrurus kuronumai*

5b. Nasal bones not forming horizontal platelike processes; gular membrane with thin black transverse lines at right angle to median line; outer pelvic fin ray tapers evenly to distal tip . . . . 6

6a. First dorsal fin with weakly denticulate spinous ray; gill rakers on inner side of first arch with 12–16 rakers on lower limb; V 7–9, usually 8. . . . . . . . . . . . . . . . . . . . *Hymenogadus gracilis*

6b. First dorsal fin spinous ray entirely smooth along leading edge; gill rakers on inner side of first arch with 15–22 rakers on lower limb; V 7–12. . . . . . . . . . . . . . . . . *Hymenocephalus* (4 spp.)

7a. Anus and urogenital pore within broad black naked area, the periproct, the posterior border of which abuts origin of A and spans most of space between V and A. . . . . . . . . . . . . . . . . . . . 8

7b. Periproct smaller, not occupying most of space between V and A; anus (and urogenital pore) either abuts A origin, or separated from A by several scales rows, sometimes closer to insertion of V than to origin of A . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

8a. Origin of V behind P origin; 2nd spinous ray of 1D smooth . . . . . . . . . . *Trachonurus* (2 spp.)

8b. Origin of V below or anterior to P origin; spinous 1D ray serrated along leading edge . . . . . 9

9a. Head greatly inflated, broad and deep; snout fully scaled; a series of enlarged scales along anterior section of 2D . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cetonurus globiceps*

9b. Head not inflated, moderately compressed; underside of snout naked; no series of enlarged scales along 2D . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Sphagemacrurus* (2 spp.)

10a. Olfactory organ massive, its diameter almost equal to that of orbit . . . . *Macrosmia phalacra*

10b. Olfactory organ small to moderate, much less than orbit diameter . . . . . . . . . . . . . . . . . . . 11

11a. Most of dorsal surface and entire ventral surface of snout naked . . . . . . . . . . *Kumba* (3 spp.)

11b. Dorsal surface of snout fully scaled; ventral surface of snout variously naked. . . . . . . . . . 12

12a. Low jaws bearing enlarged, widely space, fang-like teeth in 1 or 2 rows; spinous 1D ray smooth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Malacocephalus nipponensis*

12b. Lower jaw teeth normal in size, closely spaced, none fang-like, in 2 or more rows to broad band; spinous 1D ray smooth or serrated along leading edge. . . . . . . . . . . . . . . . . . . . . . . . 13

13a. V with 6 rays, placed anterior to P base; anus closer to A origin than to V insertion . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudonezumia pusilla*

13b. V with 7 or more rays, position variable from below 1D to under preopercle; anus removed from A origin, usually closer to V insertion . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

14a. Head broadly inflated, interorbital space about 40% of HL; orbit diameter less than 25% HL; suborbital deep, about 20% HL . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudocetonurus* cf. *septifer*

14b. Head not especially inflated, interorbital space less than 35% HL; orbit diameter usually more than 25% HL, suborbital less than 20% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15

15a. Terminal and lateral snout scutes present, the terminal scute paired; suborbital ridge marked by two rows of coarsely modified scales. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

15b. Terminal and lateral snout scutes generally not well developed, the terminal scute single, if present, not large; no coarsely modified scales along suborbital ridge. . . . . . . . . . . . . . . . . 17

16a. Outer series of rakers on GR-I usually absent (sometimes with a few rudimentary spicules); V 7 or 8 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Mataeocephalus* (2 spp.)

16b. Outer series of rakers on GR-I always present, although sometimes rudimentary; V 7 to 17. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Nezumia* (5 spp.)

17a. Upper jaw extending to below posterior one-third or more of orbit; premaxillary tooth band extends posteriorly beyond maxillary process; inner series of gill rakers on GR-I 14–20 total; no scales on gular or branchiostegal membranes . . . . . . . . . . . . . . . . . . . . *Ventrifossa* (9 spp.)

17b. Upper jaw extending posteriorly to below anterior half of orbit; premaxillary teeth band does not extend beyond maxillary process; gill rakers on inner series of first arch usually less than 14 total; some species with scales on gular or branchiostegal membranes. . . . . . . . . . . . . . 18

18a. Color brown to blackish, no silvery pigmentation; fins uniformly blackish; teeth in broad bands. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Kuronezumia dara*

18b. Color pale to greyish; silvery pigmentation ventrally in fresh specimens; fins often with black blotches or streaks; teeth in relatively narrow bands. . . . . . . . . . . *Lucigadus nigromarginatus*

## Genus *Cetonurus* Günther, 1887

**Distinguishing features**.— A distinctive genus owing to its large, soft, globose head, fully scaled including branchiostegal rays (and gular membrane in some specimens); enlarged scales along dorsal-fin interspace and anterior portion of 2D; interrupted lateral line; BR 7; large periproct region spanning most of the short space between V and A; and serrated spinous 1D ray.

**Remarks**.— Two species recognized, one in our area; genus reviewed by Sazonov and Shcherbachev (1985).

### *Cetonurus globiceps* Vaillant, 1884

Figures 4A–B.

*Macrurus globiceps* Vaillant in Filhol 1884:183, fig. 2 (name and figure, Spanish Sahara; lectotype: MNHN 1886–0092; 7 paralectotypes).

*Hymenocephalus crassiceps* (non Günther, 1878): Vaillant, 1888:214–218, pl. 20, figs. 1, 1a-e (descr.; Atlantic off France, North Africa, and Azores)

*Cetonurus robustus* Gilbert and Hubbs, 1916:207–210, pl. 11, fig. 2 (holotype USNM 76870, Albatross sta. 4971, off central Hondo [Honshu], Japan, 33°23′30″N, 135°34′00″E; 649 fm [1187 m]; 4 paratypes, sta. 4973, 600 fm [1097 m])

*Cetonurus globiceps*: Sazonov and Shcherbachev, 1985 (descr., distr.). Iwamoto and Williams, 1999:169 (7 spec., w. and se. Australia, 792–1030 m).— Iwamoto and Graham, 2001:458 (17 spec., 940–1200 m).— Shao et al., 2008: table 2 (3 spec., SET, SCS, 998–1290 m; first Taiwan record)

**Material examined** (5 spec.).— **SCS:** ASIZP 65559 (1, 170+ TL); CD 136, 998–1211 m; ASIZP 66095 (1, 270+ TL); CD 324, 1293 m. **SWT:** ASIZP 65620 (1, 331 TL); CD 228, 1262–1290 m. **SET:** ASIZP 67020 (1, 310+ TL, 61 HL); CP 353, 1205 m. **Other material:** ASIZP 68059 (1, 390 TL); Aurora, the Philippines.

**Distinguishing features**.— A species of *Cetonurus* with large orbit (24–28% HL); small scales (18–19 rows below 1D and 14–16 rows below 2D); and 3–4 rows of closely spaced teeth on premaxilla. Size to 510 mm TL.

**Distribution**.— This species is widespread in tropical and subtropical waters of the Indo-West Pacific and Atlantic but is absent in the central and e. Pacific. In the w. Pacific it is found off Japan, Taiwan, New Zealand, and Australia. Four specimens were collected in the South China Sea and the s. coast of Taiwan at depths between 998 and 1293 m.

**Remarks**.— The only congener, *C. crassiceps* (Günther, 1878), is a closely similar species that has been recorded from the Kermadecs, Hawaiian Islands, Vanuatu, Loyalty Ridge, Norfolk

FIGURE 4. *Cetonurus globiceps* Valliant, 1884. A. AISZP 67020, 310+ mm TL, fresh. B. ASIZP 65559, 170+ mm TL, preserved.

Ridge, Lord Howe Rise, and in the central and South Atlantic. Characters used by Sazonov and Shcherbachev (1985) to distinguish the only two members of the genus are weak and need to be further tested. Three of the specimens here listed were the basis for Shao et al.'s (2008:fig. 2) first record of the species from Taiwan.

### Genus *Coelorinchus* Giorna, 1810

**DISTINGUISHING FEATURES**.— BR 6; suborbital ridge formed of stout, coarsely spined, modified scales extending continuously from tip of snout to posterior angle of preopercle, ending in a sharp point; second spinous ray of first dorsal fin smooth along leading edge (some juveniles and exceptional adults may have a few spinules near distal tip); ventral light organ variously developed, from small gland anterior to anus not externally visible, to large prominent organ with one or two dermal fossae along ventral midline; no rakers along outer (lateral) side of first gill arch. V almost always 7, rarely 6.

**REMARKS**.— The most diverse genus of family Macrouridae with more than 118 recognized species, categorized by some into as many as seven subgenera; 23 species known from Taiwan. Relationships closest to *Macrourus*, the only significant differences between the two genera the presence of denticulations on spinous second ray of 1D and generally more pelvic fin rays (8 or 9, rarely 7) in *Macrourus.* Preliminary cladistic analysis (e.g., Roa-Varón and Ortí 2009:700) suggests that *Macrourus* is deeply nested within *Coelorinchus*, a situation that could prove to be a nomenclatural nightmare. Greatest diversity found in tropical regions of the Indo-West Pacific. Species most common in upper- to middle-slope waters between 200 and 1000 m, although some species range into shallow continental-shelf depths and others into depths greater than 1000 m. Many species of shallower waters are highly restricted in their geographic distribution. Maximum size attained range from about 20 cm TL to more than 87 cm.

In statements concerning the ventral light organ, Groups I through IV refer to categories assigned by Iwamoto (1990) based on the external development of the dermal window of the light organ.

### Key to the Species of *Coelorinchus* in Taiwan

1a. Light organ with two widely separated, usually blackish fossae, one immediately behind isthmus, the second immediately before anus, both connected by a medioventral line; anus/urogenital opening immediately before A origin; ventral snout surface with a series of overlapping scales at anterolateral margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

1b. Light organ variously developed, from scarcely visible to prominent with a single large fossa between or slightly anterior to V bases; anus/urogenital opening immediately before or separated by several scale rows from A origin; no overlapping series of scales ventrally on anterolateral snout margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

2a. Underside of head behind mouth mostly scaled . . . . . . . . . . . . . . . . . . . . . . . . . *C. formosanus*

2b. Underside of head essentially wholly naked (tiny isolated scales sometimes present above posterior angle of mouth and on preopercle) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Anterior rays of 2D about equal in height to those of A. . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

3b. Anterior rays of 2D decidedly shorter than those of A. . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

4a. Body with prominent dark longitudinal stripes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. hubbsi*

4b. Body with prominent saddles or completely lacking body markings . . . . . . . . . . . . . . . . . . 5

5a. No body markings; snout rather short, broad, depressed, 39–44% HL . . . . . . . . *C. brevirostris*

5b. Prominent saddle marks on body; snout 36–50% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6a. 1D with elongated spinous ray; BR membrane dusky to pale. . . . . . . . . . . . . . . . *C. cingulatus*

6b. No elongated spinous ray in 1D; BR membrane dark to black . . . . . . . . . . . . . . . *C. fuscigulus*

7a. Body covered with bold vermiculations and blotches, more or less aligned in 2 or 3 longitudinal rows; origin of 2D slightly before vertical through A origin; 1D-2D interspace about equal to length base of 1D . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. multispinulosus*

7b. Body immaculate or with irregular, sometimes faint, markings; origin of 2D about on same vertical as, or somewhat behind, A origin; 1D-2D interspace greater than length base of 1D . . 8

8a. Gular and branchiostegal membranes heavily peppered with black pigmentation, chest region relatively dark, underside of head covered with tiny black sensory papillae; spinules on body scales broadly triangular, in irregular, somewhat quincunx pattern . . . . . . . . . . *C. kamoharai*

8b. Underside of head faintly dusky to immaculate, chest region light dusky, sensory papillae on underside of head scattered and inconspicuous; spinules on body scales weak, small, in 6–14 somewhat parallel to divergent rows . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. longissimus*

9a. Snout relatively blunt, not acutely pointed; a distinct curve in anterior portion of suborbital shelf; anus about midway between A origin and base of outer V rays, preceded by large black fossa of light organ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. macrochir*

9b. Snout acutely pointed in lateral view; suborbital shelf lacking distinct curve anteriorly; anus closer to A origin than to base of outer V rays, fossa of light organ present or absent . . . . 10

10a. A blackish round blotch above P; anus removed from A by several scale rows; large fossa of light organ extending forward between V bases . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

10b. No blackish blotch above P; anus immediately before or removed from A origin; light organ situated posterior to V bases . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

11a. Black blotch above P large, spanning 5–7 diagonal rows of scales; gular and branchiostegal membranes black; height 1D 45–54% of pre-vent length . . . . . . . . . . . . . . . . . *C. kishinouyei*

11b. Black blotch above P small, spanning 3 or 4 diagonal scale rows; gular and branchiostegal membranes pale or whitish; height 1D 67% of pre-vent length. . . . . . . . . . . . . . *C.* cf. *notatus*

12a. Underside of head entirely or almost entirely naked (underside of head completely naked except for ventral portion of preopercle in *C. hexafasciatus*) . . . . . . . . . . . . . . . . . . . . . . 13

12b. Underside of head scaled (underside of snout naked in *C. leptorhinus*, but posteriorly head scaly) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

13a. Dark saddles on trunk and tail . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. hexafasciatus*

13b. No saddle marks on body . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

14a. Spinules on body scales below 2D with 3–5 divergent rows of strong, triangular spinules, middle row higher than lateral rows . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. productus*

14b. Spinules on body scales below 2D with 4–11 somewhat parallel to divergent, sharply crest-like rows of narrow, triangular spinules. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15

15a. Scales of median nasal ridge 9–12, spinule rows directed laterally and posteriorly only . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. anatirostris*

15b. Scales of median nasal ridge 6–8, with spinules radiating in all directions . . . . *C. asteroides*

16a. Prominent saddle markings on body; snout tip lacking sharp terminal scute . . . . . . . *C. sheni*

16b. No saddle markings on body; a sharp terminal snout scute present. . . . . . . . . . . . . . . . . . 17

17a. Underside of snout naked (head scaly from above mouth posteriorly) . . . . . . . *C. leptorhinus*

17b. Underside of snout and head fully scaled . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

18a. Anterolateral margin of snout incompletely supported by bone. . . . . . . . . . . . . . . . . . . . . 19

18b. Anterolateral margin of snout completely supported by bone . . . . . . . . . . . . . . . . . . . . . . 20

19a. Body scales with 4–6 parallel rows of strong, high, usually broad-based (i.e., large lateral buttresses) spinules; scales between occipital ridges and on underside of head mostly with one spinule row . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. parallelus*

19b. Body scales with 3–8 somewhat parallel to broadly divergent rows of spinules; scales between occipital ridges with 1–5 spinule rows, on underside of head with 1–3 rows . . . *C. divergens*

20a. Light organ visible only as crescent-shaped area of perianal ring, no separate fossa; most scales between occipital ridges with a single row of spinules . . . . . . . . . . . . . . *C. japonicus*

20b. Light organ with short fossa extending anteriorly almost to or between V fins; scales between occipital ridges with 2–5 rows of spinules . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

21a. Nasal fossa naked; large strong spinules on body scales in 3 divergent rows; scales between occipital ridges with a single row of spinules . . . . . . . . . . . . . . . . . . . . . . . . . *C.* cf. *spinifer*

21b. Nasal fossa usually scaled anteroventrally, seldom naked; spinules on body scales in 4–6 (3–7) divergent rows; scales between occipital ridges with multiple rows (usually 2–4) of spinules . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22

22a. Length 1D base 1.2 times into 1D-2D interspace; nasal fossa densely scaled anteroventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C.* cf. *macrorhynchus*

22b. Length 1D base 1.3–2.0 times into 1D-2D interspace; nasal fossa rather sparsely scaled on anteroventral surfaces, sometimes naked . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. smithi*

### *Coelorinchus anatirostris* Jordan and Gilbert, 1904

*Coelorhynchus anatirostris* Jordan and Gilbert, 1904:619 (holotype: USNM 51471 [ex CAS-SU 8550], 40 cm long; Misaki, Japan).— Okamura, 1970:186–189, pl. VIII, text-fig. 80 (72 spec.; s. Japan, 300–540 m).— Okamura *in* Okamura et al., 1982:171, 352 (2 spec.; s. Japan).— Okamura *in* Masuda et al., 1984:98, pl. 83E.— Yatou *in* Okamura and Kitajima, 1984:233. 368 (4 spec; Okinawa Trough, 300–550 m).

*Coelorinchus anatirostris*: Iwamoto, 1990:141 (compiled).— Shen et al., 1993:168.— Shao et al., 2008: table 2 (5 spec., NET, SWT, 200–441 m).

*Caelorinchus anatirostris*: Iwamoto and Merrett, 1997:486, fig. 6c (7 spec., New Caledonia, Chesterfield and Ballona Plateau, 600–855 m).— Merrett and Iwamoto, 2000:743 (7 spec., Vanuatu, New Caledonia, 450–1160 m).— Chiou et al., 2004b:36, 47 (in key, Taiwan, listed).

**Material examined** (20 spec.).— **NET:** ASIZP 61324 (1, 346 TL), Da-xi; ASIZP 65572 (1, 432 TL), Da-xi; ASIZP 70217 (3, 157–337 TL), Da-xi; ASIZP 70219 (3, 330–358 TL), Da-xi; ASIZP 70698 (1, 79 HL, 272+ TL); Da-xi; CAS 214596 (2); Da-xi; CAS 214728 (4, 215+-325+ TL), Su-ao. **SWT:** ASIZP 65540 (4, 160+-255 TL), CD 138, 441 m. **SCS:** CAS 224495 (ex ASIZP 65594) (1, 63.1 HL, 227 TL), CD 141, 985–1110 m.

**Distinguishing features**.— 1D II 8–10; P i16–i18; GR-I (inner) 5–7 (total). Scales below midbase 1D 3.0–4.5, below 2D 4–6; pyl. caeca 21–30. Snout pointed, length moderate, 38–45% HL, 1.3–1.6 times orbit; preoral length 36–40% HL; anterolateral margin of snout completely supported by bone; orbit 26–31% HL; upper jaw 21–27% HL. Nasal fossa scaled ventrally; underside of head naked except for two small scale patches under orbit and preopercle angle; light organ group II of Iwamoto (1990), fossa narrow and short, not extending to V bases; median rostral ridge scales 9–12, with spinules radiating laterally and posteriorly; body scales covered with narrowly triangular spinules in 4–10 (usually 6–8) slightly divergent, ridgelike rows, median row strongest. Dorsally grayish, ventrally heavily peppered over ivory ground, bluish over abdomen, pale over chest; mouth and gill cavity grayish to blackish; leading edge of 1D black, other fins dusky to pale. Attains about 430 mm TL.

**Distribution**.— Widely distributed in the w. Pacific from s. Japan and East China Sea, Taiwan, New Caledonia, Chesterfield and Bellona Plateau, Vanuatu, and off ne. Australia. Depth range 300–1160 m.

**Remarks**.— An apparent distributional gap in the Philippines and East Indies is somewhat disconcerting; specimens from the sw. Pacific should be carefully compared with those from Taiwan and points north. Specimen CAS 224495 from the SCS has scale spinules that are short and uniform, unlike those in others in the materials examined, and the snout seemed too slender for the species. It is tentatively included here, but should be further compared with other closely related species. Among Taiwan species, *C. anatirostris* is most closely similar to *C. productus* and *C. asteroides*, but the former has stronger and fewer (3–5) divergent rows of spinules on body scales and the latter has fewer scales (6–8) on the median rostral ridge. Fukui et al. (2009) synonymized *C. anatirostris* and *C. productus*, but we have reservations about accepting their conclusion (see discussion in description of *C. productus*).

### *Coelorinchus asteroides* Okamura, 1963

*Coelorhynchus asteroides* Okamura, 1963:21, figs. 1–4 (holotype, FAKU 23801, 7 paratypes; off Owase, Mie Pref., Japan).— Okamura, 1970:189–192, pl. XLI, text-figs. 81, 82 (8 spec., s. Japan, 320–360 m).— Okamura in Masuda et al., 1984:98, pl. 83F.— Yatou *in* Okamura and Kitajima, 1984:235, 369 (5 spec., Okinawa Trough).

*Caelorinchus asteroides*: Chiou et al., 2004b:43, fig. 9 (2 spec., NE, SW Taiwan).

*Coelorinchus asteroides*: Shao et al., 2008: table 2 (3 spec., NET, SWT, 100–452 m).

**Material examined** (8 spec.).— **NET:** ASIZP 61339 (1, 302 TL); Da-xi; ASIZP 65658 (1, 250+ TL); Da-xi. **SWT:** ASIZP 61340 (1, 310 TL); Dong-gang; ASIZP 62194 (2, 224–224 TL); Dong-gang; ASIZP 65560 (1, 230+ TL); CD 140, 280–452 m; ASIZP 70617 (1, 159 TL); Dong-gang. **Other specimens:** ASIZP 68016 (1, 375 TL); Aurora, 909–922 m.

**Distinguishing features**.— 1D II, 7–9; P i15–i19; GR-I (inner) 5–7 (total); scales below midbase 1D. 3.0–4.5, below 2D. 4.0–5.5; pyl.caeca 40–50. Snout fairly broad, tipped with a slender sharp scute, length 39–46% HL, 1.3–1.5 times orbit, preoral length 32–35% HL; anterolateral margin of snout completely supported by bone; orbit 25–31% HL; upper jaw 22–29% HL. Nasal fossa naked ventrally; underside of head naked; median rostral series of scales 6–8, with spinules radiating in all directions; body scales with short, sharp lanceolate to triangular spinules in 4–11 slightly divergent rows, the median row strongest. Light organ group II, fossa narrow and short. Ground color grayish, silvery ventrally, abdomen bluish, paler anteriorly on chest; mouth dark, gill cavity blackish. Attains more than 390 mm TL.

**Distribution**.— Geographically very confined; East China Sea from s. Japan to SCS off Taiwan, in 100–600 m.

**Remarks**.— First recorded from Taiwan by Chiou et al. (2004b). Among the Taiwan members of the genus, *C. asteroides* is most likely to be confused with *C. anatirostris*, but it has fewer platelike scales on the median rostral ridge, and the spinule rows on these scales are arranged radially in all directions, compared to the lateral and posterior orientation of rows in *C. anatirostris.*

### *Coelorinchus brevirostris* Okamura, 1984

*Coelorhynchus brevirostris* Okamura *in* Okamura and Kitajima, 1984:225 (holotype, BSKU 29562; Okinawa Trough, 25°47.4′N, 124°23.4′E, 600 m.).

*Caelorinchus brevirostris*: Chiou et al., 2004b:301 (redescription, 11 spec., Taiwan).

*Coelorinchus brevirostris*: Shao et al., 2008: table 2 (6 spec., NET, ET, SCS, 445–1185 m).

**Material examined** (21 spec.).— **NET:** ASIZP 61350 (1, 175+ TL), Da-xi; ASIZP 61351 (1, 213+ TL), Da-xi; ASIZP 61352 (1, 144 TL), Da-xi; ASIZP 65613 (1, 175+ TL), CP 120, 520–640 m; ASIZP 65518 (1, 183+ TL), 24.66°N, 122.18°E, CD 209, 508–522 m; ASIZP 66806 (1, 44.6 HL, 163+ TL,); CP 315, 509 m; ASIZP 66814 (4, 110–200 TL); CD 311, 516 m; CAS 215542 (2, 51.9 HL, 215+TL); Da-xi; CAS 228339 (1, 215+ TL); Nan-fang-ao. **ET:** ASIZP 65519 (1, 215 TL) and ASIZP 65615 (1, 134+ TL), CD 210, 445–1185 m. **SCS:** ASIZP 65675 (1, 140+ TL), CD 311, 516 m; ASZIP 66170 (1, 196+ TL) and ASIZP 66191 (1, 170+ TL), OCP 313, 513 m; ASIZP 66186 (1, 194+ TL) and ASIZP 66874 (1, 92+ TL), 21.67°N, 117.72°E, CP 314, 506 m; CAS 224494 (ex ASIZP 66182) (1, 185 TL), 21.67°N, 117.72°E; coll. P-F Lee, 17 Aug. 2005.

**Distinguishing features**.— 1D II 7–8; P i14–17; GR-I (inner) 6–8 (total); scales below midbase 1D 4.5–5.5, below 2D 4.5–5.5; pyl.caeca 13–16. Snout rather short, broad, and depressed, 39–44% HL; terminal scute small; anterolateral snout margin incompletely supported by bone; orbit 25–28% HL; 1.5–1.7 in snout length; upper jaw 21–24% HL; body terete. Underside of snout and head naked; nasal fossa scaled; body scales large, with 5–8 parallel spinule rows. Second spinous ray of 1D prolonged, 1.3 times HL; rays of 2D well developed, about as long as opposite rays in A. Light organ group IV (of Iwamoto *in* Cohen et al. 1990), extends from anus to just behind isthmus. Body without prominent markings. Attains about 220 mm TL.

**Distribution**.— East China Sea (Okinawa Trough) n. of Ishigaki Is. to sw. Taiwan in South China Sea at depths of 400–1185 m.

**Remarks**.— The species was originally described from a single specimen taken in the East China Sea in 600 m, but subsequently redescribed by Chiou et al. (2004b) from 11 specimens collected from ne. Taiwan. More specimens were recently collected from the South China Sea at depths between 445 and 1185 m (see Shao et al. 2008: table 2). Our specimens agree well with the original description except that they had fewer P rays (14–17 versus 19) and a shorter barbel (16–20% of orbit versus 24.7%). However, one of us (NN) re-examined the holotype and found P i16–i17 and barbel length 15% of orbit diameter, which is in agreement with our Taiwan specimens.

Among the Taiwan species of *Coelorinchus, C. brevirostris* is likely to be confused only with the recently described *C. fuscigulus* and *C. cingulatus*, but the lack of body markings distinguishes it from other members of the genus having an elevated 2D and long light organ with the anterior fossa just posterior to isthmus.

### *Coelorinchus cingulatus* Gilbert and Hubbs, 1920

*Coelorhynchus cingulatus* Gilbert and Hubbs, 1920:480, fig. 15 (holotype, USNM 78221, South China Sea, near Taiwan, 421 m; paratype, USNM 78223, off n. Luzon, 410 m).

*Coelorinchus cingulatus*: Okamura *in* Okamura and Kitajima, 1984:229, 366 (1 spec., Okinawa Trough, 250 m). Shen 1984:146.— Shao et al., 2008: table 2 (17 spec., NET, SWT, SCS, 236–1211 m).

*Caelorinchus cingulatus*: Iwamoto and Merrett, 1997:493–495, fig. 8 (17 spec., New Caledonia region, e. coast Australia; 480–580 m).— Merrett and Iwamoto, 2000:744 (5 spec., New Caledonia, Vanuatu, 460–525 m).— Chiou et al., 2004b:37, 47 (in key, listed from Taiwan).

**Material examined** (29 spec.).— **NET:** ASIZP 63249 (1, 233 TL), Da-xi; ASIZP 64545 (2, 152–155 TL), Nan-fang-ao; ASZIP 65662 (1, 232 TL), Da-xi; ASIZP 70211 (5, 263–304 TL), Da-xi; ASIZP 70245 (1, 205 TL), Da-xi. **SWT**: ASIZP 65520 (6, 120–173 TL), CD 137, 316–477 m; ASIZP 65582 (2, 195–200 TL), CD 141, 985–1110 m; ASIZP 65583 (5, 175–200 TL), CD 136, 998–1211 m; ASIZP 65605 (2, 160–170 TL), CD 138, 441 m; ASIPZ 66183 (1, 240 TL), OCP 313, 513 m. **Other specimens:** ASIZP 67859 (1, 234 TL), Aurora, 422–431 m; ASIZP 67962 (1, 154 TL), Aurora, 431–493 m; ASIZP 68017 (1, 226 TL), Aurora, 357–367 m.

**Distinguishing features**.— 1D II 8–9; P i16–19; GR-I (inner) 6–8 (total); scales below midbase 1D 3.5–5.5, below 2D 4.5–6.5; pyl.caeca 10–15. Snout sharply pointed, 43–50% HL; terminal scute slender, sharp; anterlateral snout margin incompletely support by bone; orbit 22–26% HL, 1.6–2.2 in snout length; upper jaw 19–24% HL; body somewhat cylindrical, greatest width slightly less than greatest depth. Underside of snout and head naked; nasal fossa naked or sparsely scaled; body scales large, densely covered with 7–15 parallel spinule rows. Second spinous ray of 1D slightly prolonged; rays of 2D well developed, almost as long as opposites in anal fin. Light organ group IV, extends from anus to just behind isthmus. A series of dark saddles on body, anterior two directed obliquely downwards and forward. Attains about 300 mm TL.

**Distribution**.— Originally described from the South China Sea near Taiwan and n. Luzon, but subsequently recorded from Japan (East China Sea), the e. coast of Australia, and the regions around New Caledonia, Vanuatu, and Loyalty Island. It was collected in Taiwan (NET, SWT) at depths between 236 and 1211 m.

**Remarks**.— Specimens from the sw. Pacific show slight differences from those from the n. hemisphere, but we have not been able to tease out any specific characters that would differentiate the populations. The species is most likely to be confused with *C. fuscigulus*, but that species lacks an elongated 1D spinous ray and has differences in body markings.

### ***Coelorinchus divergens*** **Okamura and Yatou, 1984**

Figures 5A–C.

*Coelorincus divergens* Okamura and Yatou *in* Okamura and Kitajima, 1984:236–239 (holotype, BSKU 26865, Okinawa Trough [East China Sea] sw. of Kyushu, Japan, 1000 m; paratype, BSKU 33464, Okinawa Trough, 780–810 m).— Shao et al., 2008: table 2 (15 spec., NET, SCS, SWT, 646–1110 m; first record from Taiwan).

Material examined (17 spec.).— **NET:** ASIZP 64145 (1, 280+ TL), CP 235, 764 m; ASIZP 65575 (1, 286 TL), Da-xi; ASIZP 65577 (1, 245 TL), CP 196, 646–787 m. **SWT:** ASIZP 63799 (1, 338 TL), CD 193, 821 m; ASIZP 65538 (1, 330 TL), CD 141, 985–1110 m. **SCS:** ASIZP 66084 (1, 74 HL, 212+ TL), ASIZP 66788 (2, 260+-295+ TL), and ASIZP 66838 (1, 166+ TL), CD 321, 954 m; ASIZP 66752 (5, 225+-350+ TL) and CAS 224888, ex ASIZP 66752 (2, 323+-385+ TL), CD 320, 731 m. **Other specimens:** ASIZP 68052 (1, 398 TL), Aurora, 944–1004 m.

Distinguishing features.— 1D II, 7–8; P i17–i18; GR-I (inner) 8(total); scales below midbase 1D 4–5, below 2D 4.5–5.5; lateral line scales over distance equal to pre-1D length 30–31; pyl.caeca 9–11. Snout broadly spade-shaped (viewed dorsally), sharply pointed, length 38–45%

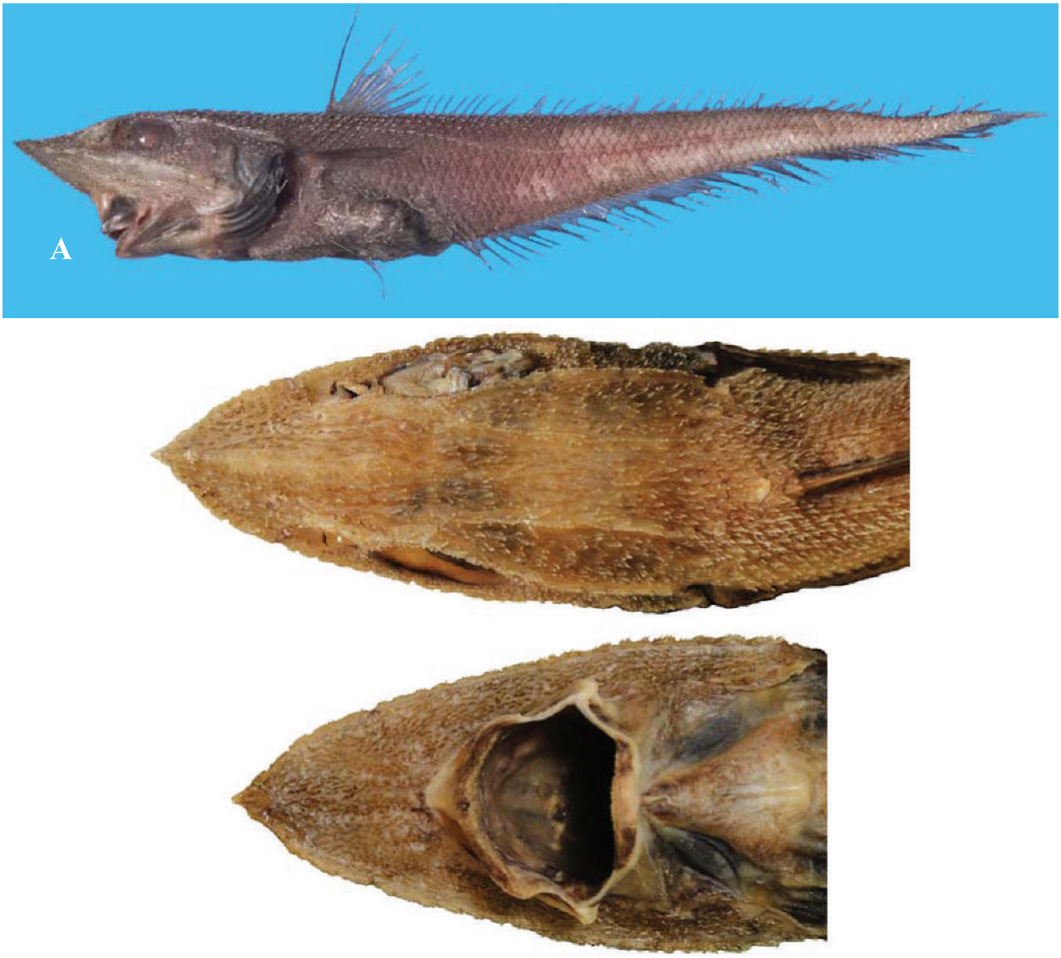

Figure 5. *Coelorinchus divergens* Okamura and Yatou, 1984. A. ASIZP 64145, 280+ mm TL, fresh. B-C. CAS 224888, 385+ mm TL, preserved, dorsal view (B) and ventral view (C) of head.

HL, terminal scute relatively small but pointed, anterolateral margin snout incompletely supported by bone; orbit 24–28(32)% HL, 1.4–1.8 in snout; interorbital 23–27%, postorbital 32–39%, orbit-preopercle 34–37%, upper jaw 26–31%, barbel 8–14%; preanal length 161–163%; height 1D 48–49%; length P 41–42%; isthmus to A 38–40%. Nasal fossa sparsely scaled anteroventrally; scales atop head with 2–5 crestlike rows of spinules in parallel to slightly divergent rows; scales on underside of head with broad, high spinules aligned in one (rarely 2) crestlike row; body scales large, thick, adherent, spinules in about 5 divergent ridgelike rows, middle row enlarged, spinule rows flanking middle row much lower, incomplete, not reaching scale margin. Light organ short, narrow, Group II. Ground color in alcohol brownish or grayish; fins dark or dusky; mouth, gill cavities, branchiostegal membranes, and jaws blackish. Attains at least 40 cm TL.

**DISTRIBUTION**.— Known from East China Sea, Taiwan, and South China Sea in 646–1110 m.

**REMARKS**.— Our specimens (as reported by Shao et al. 2008) represent the first record of the species from Taiwan and the South China Sea. According to Okamura and Yatou (*in* Okamura and Kitajima 1984) this species is very similar to *C. parallelus* Günther and *C. kermadecus* Jordan and Gilbert, but can be distinguished from the former in having 2–5 spinule rows (vs. single row) on scales atop head, slightly shorter snout (38–45% HL vs. 42–48% HL), and longer upper jaw (26–31% vs. 22–26%). *Coelorinchus kermadecus* differs from *C. divergens* in having 3–5 spinule rows (vs. 1 row) on scales on the underside of head, a longer snout (44–48% HL), and shorter upper jaw (23–26%).

### *Coelorinchus formosanus* Okamura, 1963

*Coelorhynchus formosanus* Okamura, 1963(Mar.):37 (holotype FAKU 35856, Da-xi, Taiwan; 4 paratypes, FAKU 35857–60).— Okamura, 1970:161–165, pl. XXXIV, text-figs. 65, 66 (descr. from type specimens).

*Coelorhynchus intermedius* Chu and Lo in Chu, Chan and Chen, 1963 (Aug.):173, fig. 139 (East China Sea).— Xiong, Zhan, and Deng 1988:187–188, fig. 148 (4 spec., 164–238 mm TL; East China Sea off Ryukyu Is., 28°48′N, 127°00′E, 213–285 m).

*Coelorhynchus abbreviatus* Chu and Lo *in* Chu, Chan and Chen, 1963(Aug.):174 (East China Sea).

*Coelorinchus formosanus*: Okamura *in* Masuda et al., 1984:97, pl. 82–J.— Shao et al., 2008: table 2 (9 spec., NET, SCS, SWT, 600–1110 m).

*Caelorinchus formosanus*: Iwamoto, 1990:158 (descr.). Shen et al., 1993 (descr.).— Chiou et al., 2004b:37, 47 (in key, list).

**MATERIAL EXAMINED** (38 spec.).— **NET:** FAKU 35836 (holotype), Da-xi; FAKU 35857 (paratype), Da-xi; ASIZP 57976 (1, 184 TL), Da-xi; ASIZP 61048 (1, 220 TL), Da-xi; ASIZP 61342 (1, 272 TL), Da-xi; ASIZP 65584 (3, juveniles), CP 119, 123–140 m; ASIZP 65650 (1, 251 TL), Da-xi; ASIZP 65661 (1, 260+ TL), Da-xi; ASIZP 65664 (1, 310 TL), Da-xi; ASIZP 61342 (1, 272 TL), Da-xi; ASIZP 70693 (5, 224–333 TL), Da-xi; ASIZP 70714 (1, 154 TL), Da-xi; CAS 214457 (2, 278–297 TL), Su-ao; CAS 224169 (1, 242 TL), Da-xi. **SWT:** ASIZP 65595 (4, 215–305 TL), CD 141, 985–1110 m; ASIZP 65822 (1, 218 TL), Dong-gang; ASIZP 58024 (1, 173 TL), Dong-gang; ASIZP 62195 (1, 168 TL), Dong-gang; ASZIP 62196 (2, 156–160 TL), Kaoshiung; ASIZP 62197 (2, 260–297 TL), Dong-gang; ASIZP 70661 (3, 84–165 TL), Dong-gang. **NT:** ASIZP 61009 (1, 215 TL), Jin-shan; ASIZP 65568 (1, 326 TL), Da-xi. **No data:** ASIZP 65578 (1, 322 TL).

**DISTINGUISHING FEATURES**.— 1D II, 8–10; P i15–i18; GR-I (inner) 7–9 (total); scales below midbase 1D 3.5–4.5, below 2D 3.5–4.5; pyl.caeca 9–12. Snout sharply pointed, length 42–45% HL, anterolateral margin snout incompletely supported by bone; orbit 22–26% HL, 1.5–2.0 in snout; upper jaw 28–35% HL. Nasal fossa and broad areas anteriorly and laterally atop snout almost entirely naked; underside of snout naked except along anterolateral margins where scales broadly overlap edge; underside of head behind mouth and mandibular rami scaly; short triangular spinules on body scales in irregularly quincunx to widely divergent rows. Light organ long, extends forward to near isthmus, Group IV. Ground color brownish to grayish, irregular darker blotches over dorsal portions of body, silvery ventrally; fins dark or dusky; mouth whitish, gill cavities, gular and branchiostegal membranes, and jaws dark dusky; 1D black along leading edge, dark on basal half or so, V and A blackish distally. Attains at least 326 mm TL. (Adapted from Okamura 1970, with additions from current material.)

**Distribution**.— Known from East China Sea e. of Amami Is. (Ryukyu Islands) and Taiwan (NET, SWT, and SCS) in depths between about 100 and 600 m. Most abundant in 100–400 m.

**Remarks**.— *Coelorinchus formosanus* is the most abundant grenadier species in Taiwan in depths less than 600 m (Wu 2002). Among the Group IV species of *Coelorinchus* of Taiwan, it is alone in having a scaly posterior underside of head. Okamura (1970:151) synonymized without comment *C. intermedius* Chu and Lo, 1963 and *C. abbreviatus* Chu and Lo, 1963 with *C. formosanus*. Xiong et al. (1988:148), however, considered *C. intermedius* as distinct, based on lesser amounts of scaly areas under the head and below the nasal fossa in the latter species. We have not been able to verify this with comparative material. They also provided no comment on the status of *C. abbreviatus*, suggesting agreement with Okamura's assessment of the nominal species.

### *Coelorinchus fuscigulus* Iwamoto, Ho, and Shao, 2009

*Coelorinchus fuscigulus* Iwamoto, Ho, and Shao, 2009:40–45, figs. 1–2 (holotype ASIZP 70169, 74.8 mm HL, 322 mm TL; NET, Da-xi, 24.94°N, 121.9°E; 9 paratypes NET and East China Sea).

*Coelorinchus cylindricus* (non Iwamoto and Merrett, 1997): Shao et al., 2008: table 2 (listed, 1 spec. NET, 400–600 m).

**Material examined**.— All type specimens as listed in original description (Iwamoto et al., 2009). ASIZP 70169 (holotype, 74.8 HL, 322 TL), Da-xi,); ASIZP 63249 (1, paratype, 56.1 HL, 233 TL), Da-xi; ASIZP 66922 (1, paratype, 66.2 HL, 286 TL), CP 248, 536 m; ASIZP 66973 (1, paratype, 72.7 HL, 293 TL), Nan-fang-ao; ASIZP 70168 (1, paratype, 77.1 HL, 301+ TL), Da-xi; CAS 228337 ( 2 paratypes, ex. ASIZP 70168, 66.9–74.1 HL, 302+-285+ TL), Da-xi; CAS 228338 (1, paratype, 66.9 HL, 266 TL), Nan-fang-ao; **East China Sea:** ASIZP 63193 (1, paratype, 52.2 HL, 228 TL) and CAS 224492 (1, paratype, ex. ASIZP 63193, 45.4 HL, 190 TL), Diao-yu-tai Archipelago, Yilan, Taiwan.

**Distinguishing features**.— 1D II, 8–9; P i16–i18; GR-I (inner) 7–9 total; scales below midbase 1D 5.5–6.5, below 2D 6.5–7.5; pyl.caeca 19–24. Snout produced and sharply pointed, length 36–41% HL, 1.4–1.7 times orbit; anterolateral margin of snout incompletely supported by bone; orbit 24–25% HL, upper jaw 26–30% HL. Nasal fossa scaled ventrally; underside of head naked except for overlapping scales on anterolateral snout margin; body scales with small, sharp spinules arranged in 10–13 parallel rows. Light organ Group IV of Iwamoto (1990); anterior fossa near isthmus, posterior before anus, no black stripe connecting the two. Rays of 2D well developed, about equal to opposite rays of anal fin. Overall color medium brown to grayish, but in fresh specimens silvery on ventral sides of head and trunk (bluish in preserved specimens); 8–11 prominent saddles on body; fins dusky to blackish; lips and jaws pale; branchiostegal region blackish. Attains at least 322 mm TL.

**Distributions**.— Known only from NET and East China Sea in Diaoyutai Archipelago, Taiwan, in approximately 600 m.

**Remarks**.— *Coelorinchus fuscigulus* was previously confused with *C. cylindricus*, a species known only from the holotype taken off New Caledonia, but that species has a complete bony support of the anterorlateral snout margin. Among the Taiwan members of the genus, *C. fuscigulus* is most similar to *C. brevirostris, C. cingulatus*, and *C. hubbsi.* The body markings easily distinguish the species from *C. brevirostris* and *C. hubbsi*; the blackish branchiostegals that contrast strongly with the pale gular membrane, the fully blackish 1D, and lack of an elongated 1D spinous ray distinguish it from *C. cingulatus.*

### ***Coelorhinchus hexafasciatus* Okamura, 1982**

Figure 6.

*Coelorhynchus hexafasciatus* Okamura in Okamura, Amaoka and Mitani, 1982:173, pl. 104 (Holotype: BSKU 30443; Kyushu-Palau Ridge, 26°45.0′N, 135°19.0′E, 336 m; 31 paratypes from Kyushu-Palau Ridge).

MATERIAL EXAMINED.— ASIZP 71202 (1, 133.3 mm HL, 494+ mm TL), Da-xi.

DISTINGUISHING FEATURES.— 1D II,9; P i17–18; V 7; GR-I (inner) 8; GR-II (outer/inner) 7/9; scale rows below 1D origin 7.5, below midbase 1D 5.5, below 2D origin 6. Snout conical, 40% HL; terminal scute rather blunt; anterolateral margin of snout incompletely support by bone; orbit 23% HL, 1.8 in snout length; mouth large, upper jaw 31% HL; posterior end of rictus scarcely restricted by a lip fold. Premaxillary teeth arranged in wide tapered band; outer series distinctly enlarged. Light organ restricted as a short naked streak before anus. Underside of head completely naked except for lower preopercle; nasal fossa scaled ventrally. Body scales large, adhered, covered with keel-like spinules in 7 widely divergent rows. Second spinous ray of 1D not elongated; 2D poorly developed throughout its length. About 6 dark saddles dorsally on trunk and tail; gill membrane blackish posteriorly; fins generally dark, but outer V ray somewhat paler. Attains at least 70 cm TL.

DISTRIBUTIONS.— Known from the Kyushu-Palau Ridge, s. Japan, and the East China Sea off Taiwan, in about 340–1320 m.

REMARKS.— This species may be confused with *C. sheni* (known only from Taiwan), but the two are readily distinguished by squamation on the head (underside of head mostly naked in *C. hexafasciatus* vs. completely scaled in *C. sheni*). The specimen herein reported represents the first record of the species from Taiwanese waters. The species was originally described from the Kyushu-Palau Ridge, but no additional specimens had been reported after the original description.

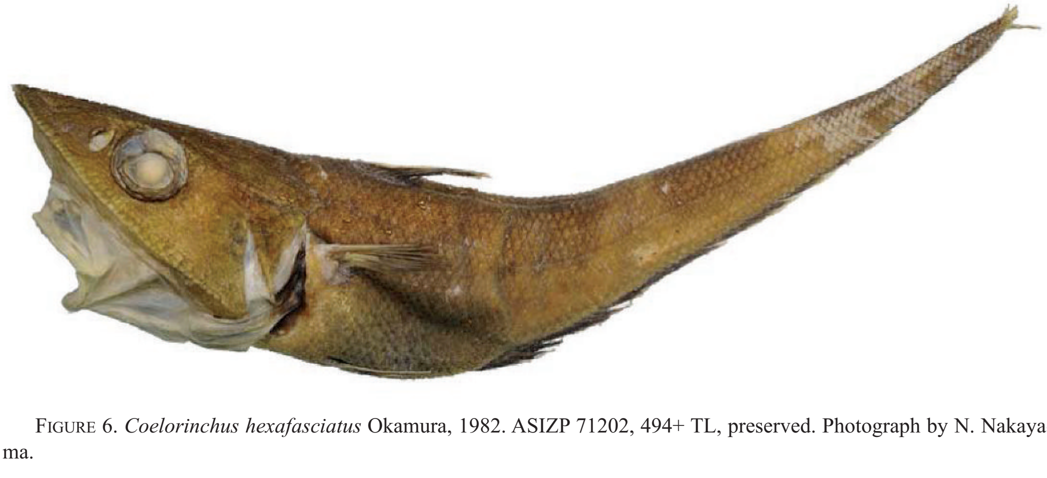

FIGURE 6. *Coelorinchus hexafasciatus* Okamura, 1982. ASIZP 71202, 494+ TL, preserved. Photograph by N. Nakayama.

### *Coelorinchus hubbsi* Matsubara, 1936

*Coelorhynchus hubbsi* Matsubara, 1936:358 (holotype, FAKU. Owase, Mie-ken, Japan, 100–200 fm [about 183–366 m]).— Okamura *in* Okamura et al., 1982:166 (photograph of fresh specimen), 169 (comparison with *C. matsubarai*).

*Coelorinchus hubbsi*: Okamura in Masuda et al., 1984:96, pl. 82–L (photograph).— Shen et al., 1993:169.— Shao et al., 2008: table 2 (2 spec., NET, 100–400 m).

*Caelorinchus hubbsi*: Chiou et al., 2004b:37, 47 (in key, list).

**Material examined** (2 spec.).— **NET:** ASIZP 63189 (1, 260 TL), Diao-yu-tai; ASIZP 64536 (1, 162 TL), Diao-yu-tai.

**Distinguishing features**.— 1D II, 8–10; P i15–i18; GR-I (inner) 8–10 total; scales below midbase 1D 4.0–4.5, below 2D 5.5–6.5; pyl.caeca 20–28. Snout produced and sharply pointed, length 38–45% HL, 1.26–1.65 times orbit; anterolateral margin of snout incompletely supported by bone; orbit 26–32% HL, upper jaw 22–27% HL. Nasal fossa scaled ventrally; underside of head naked except for overlapping scales on anterolateral snout margin; body scales with slender, sharp spinules, arranged in slightly divergent to subparallel rows. Light organ long, extending forward nearly to isthmus, Group IV of Iwamoto (1990). Rays of 2D well developed, about equal to opposites of anal fin. Ground color grayish, silvery on sides of head and trunk; three dark longitudinal streaks on side of body; underside of head and abdomen densely peppered; fins blackish to light dusky; mouth and gill cavities blackish. Attains at least 260 mm TL.

**Distributions**.— Known from s. Japan to ne. Taiwan; restricted in Taiwan to off a small island called "Fishing Island [Uotsuri-shima of the Senkaku Shoto]," at depths less than 400 m.

**Remarks**.— This species has an apparently restricted distribution; it was not captured during the Japanese expeditions off the Kyushu-Palau Ridge (Okamura et al. 1982) and the Okinawa Trough (Okamura and Kitajima 1984). The prominent body stripes on this species distinguish it from all other Taiwan *Coelorinchus.*

### *Coelorinchus japonicus* (Temminck and Schlegel, 1846)

*Macrurus japonicus* Temminck and Schlegel, 1846:256, pl. 112, fig. 2, 2A–B (bays in provinces Oomura and Shimabara, Japan. Lectotype: RMNH 3476. Paralectotypes: RMNH D1405–1406 [2 stuffed]).

*Coelorhynchus japonicus*: Gilbert and Hubbs, 1916:178–179 (5 spec., 158–307 mm TL; Japan).— Okamura, 1970:183–186, pl. XL, text-figs. 78, 79 (93 spec., 138–656 mm TL; range given as "tropic and subtropic regions of Indo-western Pacific including southern part of Japan").— Yatou *in* Okamura et al., 1982:181, photo 106, 353 (8 spec., 438–750 m TL, 300–700 m).

*Coelorinchus japonicus*: Okamura *in* Masuda et al., 1984:98, pl. 83–D.— Yatou *in* Okamura and Kitajima, 1984:231, photo 163, 367 (10 spec., 315–680 mm TL, 560–1000 m).— Xiong, et al., 1988:190–192, fig. 152 (4 spec., 275–373 mm TL; East China Sea, 490–716 m).— Iwamoto, 1990:162–163, fig. 378.— Shen et al., 1993:169 (descr.).— Kim et al,. 2005:172 (Korea).— Shao et al., 2008: table 2 (3 spec., NET, 100–650 m).

*Caelorinchus japonicus*: Chiou et al., 2004b:36, 47 (in key, list).

**Material examined** (7 spec.).— **NET:** ASIZP 56349 (1, 292 TL), Da-xi; ASIZP 65567 (1, 370+ TL), Da-xi; ASIZP 63280 (2, 370–600 TL), Da-xi; ASIZP 70216 (2, 363–450 TL), Da-xi; CAS 214622 (1, 300 TL), Da-xi.

**Distinguishing features**.— 1D II, 8–10; P i16–i20; GR-I (inner) 7–9 total; scales below midbase 1D 4.5–6.0, below 2D 5.5–7.5; pyl.caeca 41–60. Snout produced and sharply pointed, length 40–48% HL; anterolateral margin of snout completely supported by bone; orbit 22–30% HL, upper jaw 23–29% HL. Nasal fossa scaled ventrally; underside of head, including mandibular rami scaly; most head scales with single crestlike spinule row; body scales with broadly triangular spinules lacking strong transverse buttresses, arranged in 3–7 slightly divergent, sharply crestlike rows. Head ridges stout, heavily spinulated. Light organ short, Group I of Iwamoto (1990). Ground color brownish to grayish, paler below, darker over abdomen and gill covers; gular and BR membranes pale, lips white, mouth and gill cavities blackish; fins blackish to light dusky. Attains at least 750 mm TL. (Description mostly after Okamura, 1970.)

**Distribution**.— From s. Japan (including Japan Sea), East China Sea (Okinawa Trough), to ne. Taiwan; 100–1000 m, but most abundant off Japan between 300 and 600 m.

**Remarks**.— A large species with a substantial vertical distribution. One of the few grenadiers recorded as occurring in the Japan Sea, although that record is questionable and must be verified (see Kim et al. 2009:113). Among the Taiwan *Coelorinchus* with short light organ immediately anterior to A origin, *C. japonicus* is distinguished by the combination of anterolateral snout margin completely supported by bone, scales on underside and top of head with spinules in one crestlike row, and body scales with broad spinules in 3–7 sharp crestlike rows.

### *Coelorinchus kamoharai* Matsubara, 1943

*Coelorhynchus kamoharai* Matsubara, 1943:136, fig. 4 (holotype, FAKU 2498 [apparently lost], Kumano-Nada, Japan; paratypes, FAKU 1593–1596 [4], 2496 [1], and 4 other unnumbered lots of 1, 3, 3 and 2 specimens, respectively [apparently lost]).— Okamura, 1970:159–161, text-fig. 64, pl. I, fig. b (111 spec., 115–284 TL; s. Japan)

*Coelorinchus kamoharai*: Okamura *in* Masuda et al., 1984:97.— Iwamoto, 1990:164–165, fig. 382 (compiled).— Yatou in Okamura and Kitajima, 1984:221 (fig. 157 on p. 220), 365 (10 spec.; East China Sea [Okinawa Trough], s. Japan, Taiwan; 220–400 m).— Shen et al., 1993:169 (descr.).— Shao et al., 2008: table 2 (6 spec., NET, 100–650 m).

*Caelorinchus kamoharai*: Chiou et al., 2004b:47 (list).

**Material examined** (9 spec.).— **NET:** ASIZP 61336 (4, 158–211 TL), Da-xi; ASIZP 65796 (1, 176 TL), Da-xi; ASIZP 66336 (1, 221 TL), Nan-Fang-Ao; CAS 56041 (1, 152 TL), Dong-gang; NMMST-P (1, 172 TL), Hsiao-liu-chiu. **Other specimens:** ASIZP 67947 (1, 190 TL), Aurora, 269–277 m.

**Distinguishing features**.— 1D II, 8–10; P i15–i19; GR-I (inner) 9–12 total; scale below midbase 1D 3.5–4.0, below 2D 4.5–5.0; pyl.caeca 7–13. Snout sharply pointed, length 31–37% HL, anterolateral margin snout incompletely supported by bone; orbit 24–29% HL; upper jaw 28–34% HL. Nasal fossa and broad areas anteriorly and laterally atop snout naked; underside of head naked except along anterolateral margin of snout where scales broadly overlap edge; underside of head covered with unpaired black papillae; spinules on body scales short, broad based, in irregularly quincunx order. Light organ long, extends forward to near isthmus, Group IV. Dorsum brownish gray with irregular darker blotches, remainder of body silvery; chest and area around periproct and anal-fin origin blackish or dark; fins dusky; median nasal process black; mouth and gill cavities white; gular and branchiostegal membranes heavily peppered, but underside of snout covered with hair-like black papillae. Attains at least 284 mm TL.

**Distribution**.— Southern Japan, East China Sea, ne. Taiwan, and Philippines, in depths of 100–650 m. The Philippine specimen represents the southernmost record of the species.

**Remarks**.— *Coelorinchus kamoharai* is closely similar to *C. multispinulosus*, *C. formosanus*, and *C. longissimus*, but differs from them in its body markings; in addition, *C. multispinulosus* has slender, dense scale spinules on body scales and sparse, paired papillae under the head, *C. formosanus* has scales posteriorly on underside of head; and *C. longissimus* has scale spinules arranged in definite rows, small scales on nasal fossa, and underside of snout almost immaculate. Five paratypes (FAKU 1593–1596 and 2496) were rediscovered by one or us (NN) from the FAKU collection.

### *Coelorinchus kishinouyei* Jordan and Snyder, 1900

*Coelorhynchus kishinouyei* Jordan and Snyder, 1900:376–377, pl. XX (holotype [unique], USNM 49395; Misaki, Japan.).— Gilbert and Hubbs, 1916:170–172 (7 spec., 192–295 TL, Suruga Gulf, Japan).— Okamura, 1970:172–175, pl. XXXVI, text-fig. 71 (92 spec., 123–362 TL; s. Japan, 250–450 m).

*Coelorinchus kishinouyei*: Okamura *in* Masuda et al., 1984:97.— Iwamoto, 1990:167 (compiled.).— Shen et al., 1993:169 (descr.).— Shao et al., 2008: table 2 (15 spec., NET, SCS, SWT, 227–1211 m).

*Caelorinchus* (*Paramacrurus*) *kishinouyei*: Chiou et al., 2004b:47, table 1 (listed).

Material examined (55 spec.).— **NET:** ASZIP 56351 (4, 109–267 TL), Da-xi; ASIZP 58020 (8, 109–232 TL), Da-xi; ASIZP 58266 (4, 139–158 TL), Da-xi; ASIZP 58633 (2, 105–110 TL), Da-xi; ASIZP 58647 (2, 186–199 TL), Da-xi; ASIZP 60245 (2, 168–248 TL), Da-xi; ASZIP 61049 (1, 181 TL), Da-xi; ASZIP 63148 (1, 160 TL), Da-xi; ASIZP 65082 (1, 181 TL), Da-xi; ASIZP 65645 (1, 256 TL), Da-xi; ASIZP 65654 (1, 309 TL), Da-xi; ASIZP 65655 (1, 222 TL), Da-xi; ASIZP 65656 (1, 222+ TL), Da-xi; ASZIP 65659 (1, 220 TL), Da-xi; ASIZP 65660 (1, 185+ TL), Da-xi; ASIZP 65991 (1, 152 TL), Da-xi; ASIZP 70662 (5, 103–160 TL), Da-xi; ASIZP 70696 (6, 150–212 TL), Da-xi; ASIZP 70732 (1, 210 TL), Da-xi; CAS 214461 (1, 240+ TL), Su-ao; CAS 214612 (2, 192+-213+ TL), Da-xi; CAS 224170 (2, 205–202+ TL), Da-xi. **SWT:** ASIZ 62158 (1, 216 TL), Dong-gang. **SWT:** ASIZP 65555 (1, 188 TL), CD 142, 227–335 m; ASIZP 65585 (1, 205 TL), CD 136, 998–1211 m; ASIZP 65596 (1, 205 TL), CD 141, 985–1110 m; ASIZP 70616 (1, 146 TL), Dong-gang; ASIZP 70660 (1, 210 TL), Dong-gang.

Distinguishing features.— 1D II, 8–10; P i15–i19; GR-I (inner) 9–10 total; scales below midbase 1D 3.5–4.0, below 2D.5–4.5; pyl.caeca 19–26. Snout sharply pointed, sides gently convex, tipped with a blunt scute, length 33–45% HL, anterolateral margin snout completely supported by bone; orbit 31–38% HL; upper jaw 23–29% HL. Nasal fossa and underside of head naked; spinules on body scales short, conical, in 8–17 parallel to slightly divergent rows. Light organ short, extends forward only to base of pelvic fins, Group II. Dorsum brownish, belly blackish, rest of body silvery, a large (⅔ orbit diameter) ocellated dark blotch above pectoral fin; underside of head densely peppered; mandibular rami and gill membranes blackish; fins generally dusky, second 1D spine and tips of rays black; mouth and gill cavities whitish. Attains at least 362 mm TL.

Distribution.— Off s. Japan, South China Sea, and Taiwan (NET, SWT) in 200 m to more than 600 m

Remarks.— *Coelorinchus kishinouyei* was strangely not recorded by Okamura and Kitajima (1984) from the Okinawa Trough, where it would be expected owing to its presence in s. Japan and Taiwan. In this regard, the distribution is similar to that of *C. hubbsi.* It is relatively abundant in landings at Da-xi in ne. Taiwan. This highly distinctive species is closely similar to *C. jordani*, which has a much smaller pectoral blotch and a longer light organ that extends well forward of the pelvic bases and onto the chest. The Taiwan specimens of *C. kishinouyei* appeared to have a slightly longer snout, smaller orbit, darker overall coloration with little or no silvery, with anal fin black overall, and blotch above pectoral fin more obscure and lacking pale outer ring (i.e., not ocellated).

### *Coelorinchus leptorhinus* Chiou, Shao and Iwamoto, 2004

*Caelorinchus leptorhinus* Chiou, Shao and Iwamoto, 2004a:299, figs. 1–3 (holotype, ASIZP 061344 and 23 paratypes, Da-xi, ne. Taiwan, 24°54.63′N, 122°03.49′E, 400–600 m).

*Coelorinchus leptorhinus*: Shao et al., 2008: table 2 (23 spec., NET, SWT, 100–650 m).

Material examined (54 spec.).— **NET:** ASZIP 58636 (1, 146 TL), Da-xi; ASIZP 58648 (2, 285–311 TL), Da-xi; ASIZP 60246 (1, 192 TL), Da-xi; ASIZP 60247 (1, 310 TL), Da-xi; ASIZP 61344 (1, holotype, 800 TL), Da-xi; ASIZP 61345 (1, paratype, 380 TL), Da-xi; ASIZP 61346 (10, paratype, 142–176 TL), Da-xi; ASIZP 61347 (2, paratypes, 480–640 TL), Da-xi; ASIZP 64288 (1, 400 m, 146 TL), Da-xi; ASIZP 65569 (1, 567 TL), Da-xi; ASZIP 65571 (1, 407 TL), Da-xi; ASIZP 65642 (1, 370 TL), KSD sta.4; ASZIP 65646 (1, 230+ TL), Da-xi; ASZIP 65647 (1, 308 TL), KSD sta.4; ASZIP 65649 (1, 261 TL), KSD sta.; ASIZP 65781 (1, 346 TL), Da-xi; ASIZP 66253 (1, 352 TL), Da-xi; ASIZP 66917 (2, 212–224 TL), CP 248, 526 m; ASIZP 66939 (1, 133 TL),Da-xi; ASIZP 70214 (2, 334–394 TL ), Da-xi ; ASIZP 70252 (1, 147 TL), Da-xi; ASIZP 70692 (18, 200–375 TL), Da-xi. **SWT:** ASIZP 66405 (1, 240 TL), Dong-gang; ASIZP 65628 (1, 546 TL), CD 233, 448–526 m.

**Distinguishing features**.— 1D II, 8–9; P i17–i18; GR-I (inner) 6–8 total; scales below mid-base 1D 5.5–7.5, below 2D 5.5–7.5; pyl.caeca 42–48. Snout long, narrow, pointed in lateral view, tip rounded, length 39–46% HL, anterolateral margin of snout completely supported by bone; orbit 16–19% HL; upper jaw 26–29% HL. Nasal fossa scaly, underside of snout naked, but finely scaled posteriorly on head; spinules on body scales in 5–8 sharp, slightly divergent ridge rows. Light organ short, Group II of Iwamoto (*in* Cohen et al. 1990); anus removed from A origin. Ground color brown, bluish on belly and halfway onto chest; underside of head, mouth, and gill cavities dark; fins generally dusky to blackish. Attains more than 850 mm TL.

**Distribution**.— Apparently endemic to Taiwan (NET, SWT, SCS). The species is most abundant in 300–400 m off s. Taiwan and 400–800 m in ne. Taiwan.

**Remarks**.— Shen et al.'s (1993) record of *C. tokensis* was a misidentification of *C. leptorhinus*. The species is abundant in the bycatch of the deepwater trawl fisheries off Da-xi (NET). It is most closely similar to the Philippines species *C. macrorhynchus* Smith and Radcliffe, 1912 in having a notably long snout, long jaws, relatively long barbel, and similar light organ. The main differences between the two species lie in *C. leptorhinus* having the underside of snout naked and having a slightly shorter snout (preoral length 35–40% HL cf 40–45%).

### *Coelorinchus longissimus* Matsubara, 1943

*Coelorhynchus longissimus* Matsubara, 1943:140, fig. 5 (holotype, FAKU 1592 [apparently lost]; Kumano-Nada, Japan).— Okamura, 1970:165–168, pl. XXXV, text-fig. 67 (48 spec., 200–357 mm TL; s. Japan, 280–400 m).

*Coelorinchus longissimus*: Okamura *in* Masuda et al., 1984:97, pl. 82–K (compiled).— Yatou *in* Okamura and Kitajima, 1984:223, 366, fig. 159 (5 spec., 175–325 mm TL; Okinawa Trough).— Shao et al., 2008: table 2 (3 spec., NET, SWT, 100–650 m).— Kim et al., 2005:172 (Korea; compiled).

*Caelorinchus longissimus*: Nakabo, 2003:430 (compiled).— Chiou et al., 2004b:43–44, fig. 10 (2 spec., NET, SWT).

**Material examined** (9 spec.).— **NET:** ASIZP 61337 (1, 202 TL), Da-xi; ASIZP 70695 (2, 212–235 TL), Da-xi. **SWT:** ASIZP 57602 (1, 182 TL), Dong-gang; ASIZP 61338 (1, 262 TL), Dong-gang); ASIZP 70614 (1, 165 TL), Dong-gang. **Other material: Philippines:** ASIZP 68091 (1, 84 TL), Aurora, 184–200; ASIZP 68423 (2, 100–103 TL), Aurora, 184–200 m.

**Distinguishing features**.— 1D II, 8–10; P i16–i20; GR-I (inner) 6–9 total; scales below midbase 1D 3.0–4.5, below 2D 3.5–4.5; pyl.caeca 16–23. Snout sharply pointed, length 42–45% HL, anterolateral margin snout incompletely supported by bone; orbit 24–27% HL; upper jaw 23–28% HL. Most of nasal fossa and broad areas atop snout naked; underside of head naked except along anterolateral margin of snout where scales broadly overlap edge; spinules on body scales short, weak, slender in 6–14 parallel to slightly divergent rows. Light organ long, extends forward to near isthmus, Group IV of Iwamoto (*in* Cohen et al. 1990). Dorsum gray with faint irregular blotches, remainder of body silvery; fins dusky, 1D with blackish membrane behind long spinous ray; median nasal process black; mouth white, gill cavities blackish; gular and branchiostegal membranes heavily peppered; underside of snout clear, mostly lacking melanophores except along outer margins. Attains at least 357 mm TL.

**Distribution**.— Pacific coast of s. Japan from Suruga Bay s. into the East China Sea (Okinawa Trough), ne. Taiwan, the South China Sea off Taiwan, and in the Philippines, in 280–400 m.

**Remarks**.— This species is closely similar to *C. kamoharai*, differing only in the slender scale spinules arrayed in many divergent rows (as compared with short broad spinules in quincunx pattern) and paler, slightly different pattern of blotches on the body.

### *Coelorinchus macrochir* (Günther, 1877)

Figure 7.

*Macrurus macrochir* Günther, 1877:438 (holotype, BMNH 1887.12.7.123; off "Inoshima" [= Enoshima], Japan, *Challenger* sta. 232, 345 fm [631 m]).

*Abyssicola macrochir*: Goode and Bean, 1896:417 (compiled, type-species for new genus *Abyssicola*).— Gilbert and Hubbs, 1916:183–184–186 (36 spec., 91–634 mm TL; Pacific coast of Japan, 129–437 fm [236–799 m]).— Okamura, 1970:145–148, pl. XXXII, text-fig. 58 (136 spec., 173–680 mm TL; Japan: Hokkaido to East China Sea off Kagoshima Prefecture).— Okamura *in* Masuda et al., 1984:96, pl. 82–G (compiled).— Okamura *in* Okamura and Kitajima, 1984:221, 364 (1 spec., 590 mm TL; Okinawa Trough, 820 m).— Nakabo, 2002:429 (compiled).

*Coelorhynchus* (*Abyssicola*) *macrochir*: Gilbert and Hubbs, 1920:425 (in key).

*Coelorinchus macrochir*: Iwamoto, 1990:171 (compiled).— Shao et al., 2008: table 2 (2 spec., NET, 100–650 m; first record from Taiwan).— Honma et al., 2008:65–74 (Japan Sea).— Kim et al., 2009:110–112, fig. 5, table 2 (East Sea [Japan Sea], Korea).

**Material examined** (2 spec.).— **NET:** ASIZP 65574 (1, 424 TL), Da-xi; ASIZP 66972 (1, 570 TL), Da-xi.

**Distinguishing features**.— 1D II, 9–11; P i16–i20; GR-I (inner) 10–12 total; scales below midbase 1D 4.5–6.0, below 2D 5.5–7.0; pyl.caeca 42–48. Snout rather bluntly conical to rounded

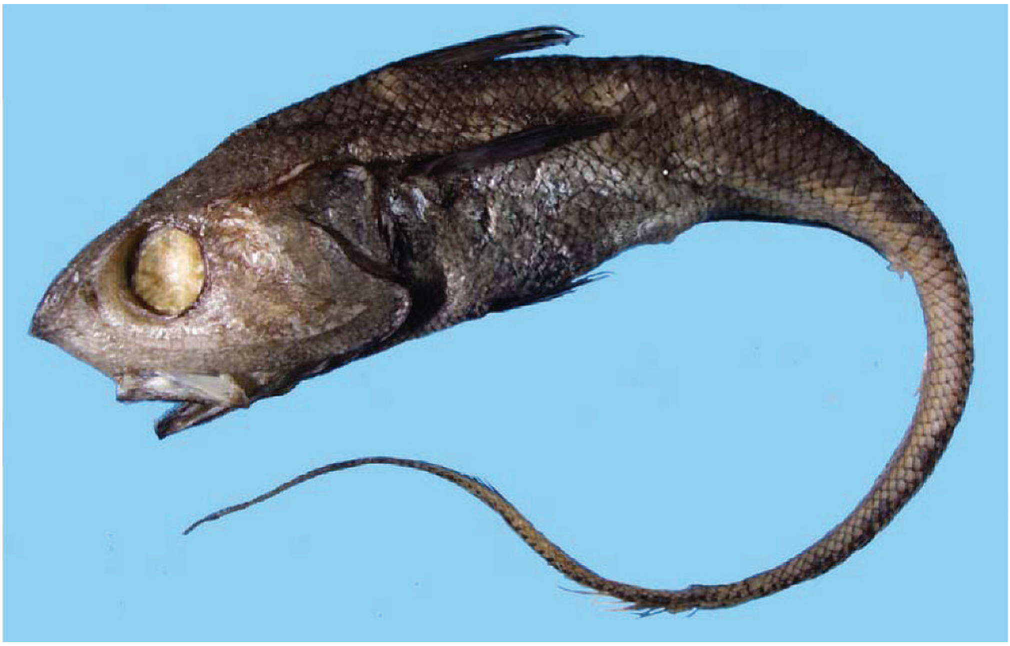

Figure 7. *Coelorinchus macrochir* (Gunther, 1877). ASIZP 55972, 570 mm TL, preserved.

in lateral profile, length 29–36% HL, anterolateral margin of snout incompletely supported by bone; a distinct curve in anterior portion of suborbital ridge; orbit 27–33% HL; mouth relatively large, upper jaw 34–42% HL. Nasal fossa and underside of head scaly; spinules on body scales short, broad, in 4–9 widely divergent rows. Vent about midway between pelvic-fin base and anal-fin origin; naked fossa of light organ close before vent (Group II of Iwamoto, 1990). Ground color brown, bluish ventrally on trunk; mouth and gill cavities blackish; fins dusky to blackish. Attains at least 680 mm TL.

**DISTRIBUTION**.— Pacific coast of Japan (Hokkaido to Kyushu off Kagoshima), s. Okhotsk Sea, East China Sea (including Okinawa Trough), Japan Sea off Niigata, ne. Taiwan, and the Philippines, in 235–830 m.

**REMARKS**.— Shao et al. (2008: table 2) first recorded the species from Taiwan based on the two specimens listed above; they represent the southernmost record (lat. 24.8°N) of the species. Most previous workers have included *Coelorinchus macrochir* in its own genus, *Abyssicola* Günther, based primarily on its dentition: short conical teeth in three series in premaxilla, in two series in dentary. Okamura (1970:143–144) provided a lengthy diagnosis that readily differentiated the species from the 14 then-known Japanese species of *Coelorinchus.* However, when viewed on a worldwide basis of more than 100 species in the genus, the diagnostic characters enumerated by Okamura are shared by one or more species of *Coelorinchus* sensu lato and thus fail to differentiate *Abyssicola.* Fukui et al. (2010) conducted a detailed study of the eggs and larvae of *C. kishinouyei*, and using DNA nucleotide sequences, provided a (*op. cit.* fig. 3) phylogenetic tree which showed *C. macrochir* deeply nested within other Japanese *Coelorinchus*, with its sister group being *C. anatirostris/productus* (which they considered as synonyms: see Remarks under *C. productus*).

### ***Coelorinchus* cf. *macrorhynchus* [*sensu* Smith and Radcliffe, 1912]**

Figure 8.

**MATERIAL EXAMINED**.— **SWT:** ASIZP 65531 (1, 73.0 mm HL, 222 mm TL), CD 138, 441 m.

**Distinguishing feature**.— 1D II 9; P i18–i19; GR-I (inner) 2+6, GR-II (outer/inner) 0+6 / 1+7; scales below midbase 1D 4.5, below 2D 6.5, lateral-line scales over distance equal to pre-D length 47. Snout sharply pointed, slender and spear-shaped in dorsal view, length 51% HL; anterolateral margin of snout completely supported by bone; orbit 23% HL, 2.2 in snout length, upper jaw 23% HL; nasal fossa densely scaled anteriorly and ventrally; underside of head almost fully scaled (scales with 1–3 short rows of spinules). Light organ group II of Iwamoto (1990), fossa narrow and short, not extending to pelvic-fin bases. Anus separated from A origin by 2 or 3 scale rows. Spinules on body scales blade-like in 3–6 sharp, divergent, ridgelike rows, closely overlapping, with height increasing abruptly with posteriormost spinule much larger than anterior ones. Ground color brownish (somewhat faded), bluish over abdomen but not on chest; mouth and gill cavity dark; most fins dark dusky to blackish. Attains more than 44 mm TL.

**DISTRIBUTION**.— Broadly distributed from Philippines to e. and w. coasts of Australia, in 485–1107 m. In Taiwan, the single specimen was collected in 441 m.

**REMARKS**.— This single juvenile was captured in the same haul as two specimens (ASIZP 65523, 250–265 mm TL) that we identified as *C. smithi.* It differed from those specimens in having a more slender and longer snout (orbit 2.2 into snout, cf. 1.3–2.1 in *C. smithi*), slightly narrower internasal and interorbital widths (16% HL and 18% HL, respectively, cf. 17–19% and 19–23% in *C. smithi*) and the nasal fossa was almost fully covered with small scales antero-ventrally (naked to sparsely covered in *C. smithi*). The differences are so slight that we are uncertain whether they simply represent individual variation; thus, our identification must be considered as tentative. The presence of this species in Taiwan waters should not be surprising, however, as it was originally

FIGURE 8. *Coelorhynchus* cf. *macrorhynchus* [*sensu* Smith and Radcliffe, 1912]. ASIZP65531, 222 mm TL. A. lateral view. B. dorsal view of head. C. ventral view of head.

described from captures in the Philippines in the Verde Island Passage off sw. Luzon. If confirmed, this specimen represents the first record of the species from Taiwan.

### *Coelorinchus multispinulosus* Katayama, 1942

*Coelorhynchus multispinulosus* Katayama, 1942:332 (holotype, NSMT-P 18224; Tsuiyama Market, Yogo Pref., Japan [Japan Sea]).— Okamura, 1970:156–158, pl. XXXIII, text-fig. 63 (89 spec., 154–378 mm TL; s. Japan, Japan Sea, East China Sea, 150–300 m).

*Coelorinchus multispinulosus*: Okamura *in* Masuda et al., 1984:97, pl. 82–H (compiled).— Yatou *in* Okamura and Kitajima, 1984:223, fig. 158 (p. 222), 365 (7 spec., 230–325 mm TL; Okinawa Trough in 146–200 m).— Iwamoto, 1990:174–175, fig. 398 (compiled).— Shen et al., 1993:170 (descr.).— Kim et al., 2005:173 (Korea; compiled).— Shao et al., 2008: table 2 (11 spec., NET, 100–650 m).

*Caelorinchus multispinulosus*: Nakabo, 2002:430 (compiled).— Chiou et al., 2004b:37, 47 (in key, list).

MATERIAL EXAMINED (46 spec.).— **NET:** ASIZP 57306 (1, 202 TL), Da-xi; ASIZP 58021 (2, 179–274 TL), Da-xi; ASIZP 58635 (4, 158–255 TL), Da-xi; ASIZP 58699 (2, 179–214 TL), Da-xi; ASZIP 61084 (6, 210–245 TL), Da-xi, 100 m; ASIZP 61104 (1, 135 TL), Da-xi, 50 m; ASIZP 61333 (1, 236 TL), Da-xi; ASIZP 65174 (1, 227 TL), Da-xi; ASZIP 65651 (1, 180 TL), KSD sta. 4; ASZIP 65653 (1, 189 TL), KSD st. 4; ASIZP 66924 (2, 220–255 TL), CP 250, 220 m; ASIZP 61047 (3, 195–230 TL), Da-xi; ASIZP 70663 (13, 195–245 TL), Da-xi; NMMSTP 0183 (2, 208–220 TL), Da-xi; CAS 214597 (6), Da-xi. **NT:** ASZIP 55477 (1, 203 TL), Ye-liou; ASIZP 61215 (1, 215 TL), Jim-shan, 100 m.

**Distinguishing features.**— 1D II, 8–10; P i13–i17; GR-I (inner) 7–10 total; scales below midbase 1D 3.5–4.5, below 2D 3.5–4.5; pyl.caeca 11–20. Snout sharply pointed, length 40–45% HL, scattered paired papillae on underside, anterolateral margins incompletely supported by bone; orbit 22–27% HL; upper jaw 27–31% HL. Most of nasal fossa and broad areas atop snout naked; underside of head naked except along anterolateral margin of snout where scales broadly overlap edge; spinules on body scales weak, slender, in quincunx order. Light organ long, extends forward to near isthmus, Group IV of Iwamoto (1990). Dorsally on body and nape grayish with prominent vermiculations and blotches that extend below lateral midline, laterally mostly silvery, blackish ventrally on trunk, thorax, jaws, and gill membranes; fins dusky to blackish, 1D with blackish membrane behind long spinous ray; mouth white, gill cavities blackish; underside of snout with scattered paired papillae. Attains at least 378 mm TL.

**Distribution.**— Pacific coast of s. Japan to ne. Taiwan, Japan Sea, and East China Sea (Okinawa Trough), in depth less than 400 m. Most abundant in depths less than 200 m.

**Remarks.**— *Coelorinchus multispinulosus* is one of the most abundant grenadier in s. Japan and one of only a few grenadier species known to occur in the Japan Sea (Kim, I.S. et al. 2005; Kim, S.Y. et al. 2009). Its normal depth distribution is also one of the shallowest of all grenadiers from the general region. Its body marking is unique among the Taiwan members of the genus.

### *Coelorinchus* cf. *notatus* [*sensu* Smith and Radcliffe, 1912]

Figure 9.

**Material examined.**— NMMB-P11958 (90++ mm TL, large portion of tail missing, 35.5 mm HL); Taiwan; Nan-fang-ao; ca. 280 m.

**Distinguishing features.**— 1D II, 9; P i16; GR-I (inner) 1+1+6, 8 total; scales below midbase 1D 3.5, below 2D 5.5; pyl.caeca 25. Snout sharply pointed in lateral view, sides gently convex in dorsal view, tipped with a short, broad scute, length 43% HL, anterolateral margin snout completely supported by bone; orbit 28% HL; upper jaw 23% HL. Nasal fossa and underside of head naked; spinules on body scales short, conical, in 5 or 6 almost parallel rows. Light organ short, extends forward slightly anterior to base of pelvic fins, Group II. Belly bluish, ventral aspects of body tail pale; a small (pupil width) ocellated black blotch above pectoral fin; underside of head almost entirely pale to whitish; mandibular rami and gill membranes pale; fins generally dusky, second 1D spine and tips of rays blackish; mouth and gill cavities blackish, but lips pale.

**Distribution.**— Taiwan off Nan-fang-ao (NET) in about 280 m.

**Remarks.**— This single damaged specimen (tail mostly broken off, scales almost entirely missing on body and head) belongs amongst those *Coelorinchus* species that Gilbert and Hubbs (1920:446) included under the subgenus *Paramacrurus* Bleeker. Most of the species in this group have a dark blotch above the base of the pectoral fin, an acute snout slightly longer than diameter of orbit, lateral margins of snout fully supported by bone, snout with convex lateral profile (viewed dorsally), anus removed by a short distance from anal-fin origin, and light organ moderately developed with dermal window extending forward between pelvic-fin bases (and beyond in some species). The subgenus includes *C. kishinouyei* and *C. jordani* from Japan, and at least nine others from the Philippines-East Indies regions, including *C. notatus, C. maculatus, C. velifer, C. sexradiatus, C. triocellatus, C. dorsalis, C. macrolepis, C. argus*, and *C. thurla*. The Taiwan specimen follows very closely the original description and illustration of *C. notatus* Smith and Radcliffe, 1913, as well as the more-extensive description provided by Gilbert and Hubbs (1920:462–465), who in a footnote (*op. cit.* p. 464) stated that none of Radcliffe's "smaller specimens are true *notatus*." Thus, the species is known only from the holotype. NMMB-P11958 differs from *C. notatus*

FIGURE 9. *Coelorinchus cf. notatus* [*sensu* Smith & Radcliffe, 1912], NMMB-P11958, 90+ mm TL.

in having a smaller pectoral blotch, which covers only four diagonal scale rows (cf. six in *C. notatus*) and a snout with a straight dorsal profile (cf. slightly concave). Gilbert and Hubbs (1920:465) stated that "the belly is blackish only in advance of the ventrals," but Radcliffe (1913:137) stated, "belly with blackish shades showing through scales." In NMMB-P11958, the entire underside of the trunk is dark bluish, from the gill membranes to beyond the anal-fin origin. The Taiwan specimen appears to have more saddle markings than does *C. notatus.* A broad dark saddle extends from before the mid-base of 1D to slightly beyond the origin of 2D. This saddle extends one or two scale rows below the lateral line, about to the mid-lateral line of the body; it is not as dark as the pectoral blotch or the short (5 or 6 rows wide) more-posteriorly situated saddle from which it is separated by a pale gap occupying three scale rows wide. A third, longer saddle that does not extend to the lateral line follows a pale gap of three scale rows; this shallow saddle is about 12 scales long and 2.5 to 3 scales deep. A fourth short saddle appears to be developed, although the specimen is so damaged that only parts of the integument remain and the precise limits of the marking could not be confidently acertained. The second and fourth saddles are about in the positions shown for the two saddle marks in the original illustration of the *C. notatus* (Radcliffe, 1913: pl. 30, fig. 3), which does now show the intervening saddles seen in NMMB-P11958. The relatively poor condition of the Taiwan specimen does not allow us to confidently assign the specimen to a species. A judgement awaits the collection and study of additional, better-preserved specimens.

### *Coelorinchus parallelus* (Günther, 1877)

*Macrurus parallelus* Günther, 1877:439 (syntypes, BMNH 1887.12.7.65–68[4], 1887.12.7.69 [1]; MNHN 1890–0125 [ex BMNH] [1]; NMI block reg. no. 114.1899 [1]; off Inoshima, Japan, *Challenger* sta. 232, 345 fm [631 m]. Specimens [4] from New Zealand and Kermadec Islands subsequently renamed *C. kermadecus* Jordan and Gilbert, 1904).

*Coelorhynchus parallelus*: Okamura, 1970:198–200, pl. XLIII, text-fig. 86 (2 spec., 400–450 mm TL; Japan).

*Coelorinchus parallelus*: Kyushin et al., 1977:42 Okamura *in* Masuda et al., 1984:98–99, pl. 83–3 (compiled).— Yatou *in* Okamura and Kitajima, 1984:245, fig. 171 (p. 244), 370 (9 spec., 275–480 mm TL; Okinawa Trough, in 650–990 m).— Iwamoto, 1990:178–179, fig. 404 (compiled).— Iwamoto and Merrett, 1997:500–502, fig.12 (3 spec., New Caledonia region, 412–970 m).— Iwamoto et al., 1999:52.— Merrett and Iwamoto, 2000:746–747, fig. 12 (5 spec., Vanuatu, Norfolk Ridge, Lord Howe Rise, in 764–1124 m). — Shen et al., 1993:170 (descr.).— Shao et al., 2008: table 2 (3 spec., SWT, 100–650 m).

*Caelorinchus parallelus*: Chiou et al., 2004b:36, 47 (in key, list).

*Coelorinchus commutabilis*: Shao et al., 2008: table 2 (1 spec., SCS, 731 m; first record from Taiwan).

**MATERIAL EXAMINED** (6 spec.).— **NET:** ASIZP 65570 (1, 635+ TL), KSD sta.3; ASIZP 70690 (1, 380 TL), Da-xi. **SWT:** ASIZP 65542 (1, 405 TL), CD 138, 441 m; ASIZP 65630 (1, 146 HL, 404 TL) and ASIZP 70271 (1, 430 TL), CD 230, 810–850 m; ASIZP 66108 (1, 350+ TL), OCP 301, 687 m. **SCS:** ASIZP 66785 (1, 62 HL, 210 TL) and CAS 224496 (ex ASIZP 66785) (1, 61 HL, 220 TL), CD 320, 731 m.

**Distinguishing features**.— 1D II, 8–9; P i17–i18; GR-I (inner) 7–8 total; scales below midbase 1D 3.5–4.0, below 2D 4.5–5.5; pyl. caeca about 9. Snout long, sides converge in gentle curve towards sharp spinous scute at tip, length 42–48% HL, anterolateral margin snout incompletely supported by bone; orbit 23–27% HL; upper jaw 22–26% HL. Nasal fossa and underside of snout scaly; body scales large, spinules stout, broad-based, in 1–6 parallel rows; scales of head mostly with spinules arranged in single parallel ridge-row. Light organ short, scarcely visible before vent; Group I of Iwamoto (1990). Color brown, to grayish; mouth and gill cavities dark; fins dusky to blackish. Attains about 450 mm TL.

**Distribution**.— Pacific coast of s. Japan to Taiwan, East China Sea, South China Sea, and sw. Pacific. In Taiwan, specimens were collected from NET and SWT in depths of 441–850 m.

**Remarks**.— *Coelorinchus parallelus* has a reportedly disjunct distribution in the western Pacific. Its apparent absence from the Philippines and Indo-Australian Archipelago and its reported presence on oceanic elevations in the sw. Pacific is suspicious. Specimens from the latter area should be examined in greater detail to confirm their conspecificity with the type specimens. Among the Taiwan *Coelorinchus* species with a simple (Group I) light organ, *C. parallelus* can be distinguished by the combination of broad spinules on body scales arranged in 4–6 parallel rows and its incompletely supported anterolateral snout margin. The two Taiwan specimens previously reported as *C. commutabilis* by Shao et al. (2009) from the SCS are questionably recorded here as this species. In almost all features, they fall in well with *C. parallelus*, but the spinules on their body and head scales are more slender and lack the broadly transverse buttresses characteristic of *C. parallelus.* Also, the nasal fossa is sparsely scaled anteriorly and the snout viewed dorsally is somewhat broader and more convexly curved. That these SCS specimens are relatively small (210+- 220+ mm TL) may account for the differences. A good size series is necessary to confirm these differences.

### *Coelorinchus productus* Gilbert and Hubbs, 1916

*Coelorhynchus productus* Gilbert and Hubbs, 1916:175–177, pl. 9, fig. 1 (holotype, USNM 76865; Suruga Gulf, Japan, 197–297 fm [360–543 m]; paratypes, CAS-SU 22977, USNM 76872, 76873).

*Coelorinchus productus*: Yatou *in* Okamura and Kitajima, 1984:233, fig. 166 (p. 232), 369 (3 spec., 210–270 mm TL; Okinawa Trough, 410–600 m).— Iwamoto, 1990:179–180, fig. 406 (descr.).— Shao et al., 2008: table 2 (3 spec., NET, SWT, 100–650 m).

*Caelorinchus productus*: Chiou et al., 2004b:44, fig.11 (2 spec., NET).

**Material examined** (5 spec.).— **NET:** ASIZP 61326 (1, 296+ TL), Da-xi; ASIZP 61327 (1, 221 TL), Da-xi; ASZIP 65573 (1, 333 TL), Da-xi; ASIZP 65644 (1, 239 TL), Da-xi; ASZIP 65648 (1, 241+ TL), Da-xi.

**Distinguishing features**.— 1D II 8–10; P i16–i18; GR-I (inner) 6–8 total. Scales below midbase 1D 3.5–4.5, below 2D 4–6; pyl.caeca about 27. Snout sharply pointed, length 39–42% HL, 1.5–1.7 times orbit; anterolateral margin of snout completely supported by bone; orbit 26–29% HL, upper jaw 22–23% HL; nasal fossa scaled ventrally; underside of head naked except for occasional small patch below preopercle angle. Light organ group II of Iwamoto (1990), fossa narrow and short, not extending to pelvic-fin bases. Spinules on body scales daggerlike in 3–5 slightly divergent ridgelike rows, middle row strongest. Ground color grayish-brown, silvery ventrally, bluish over abdomen becoming blackish ventrally; mouth and gill cavity blackish; fins dusky to blackish. Attains about 310 mm TL.

**Distribution**.— Pacific coast of s. Japan to ne. Taiwan in 271–651 m.

**Remarks**.— *Coelorinchus productus* has been confused with the closely similar *C. anatirostris*, into which Okamura (1970:186) synonymized the species. However, Yatou (*in* Okamura and Kitajima, 1984:233) treated it as distinct, and Iwamoto (1990:130) and Nakabo (2002:434) provided characters by which the two species could be distinguished. Chiou et al. (2004b) used the specimens here listed to document the first record of the species in Taiwanese waters. In a recent paper, Fukui et al. (2010) re-synonymized *C. productus* with *C. anatirostris* based on examination of two specimens of the former and one of the latter, each collected in Suruga Bay. Their selected measurements and analysis of nucleotide sequences (16S rRNA) showed the two to be the same. However, their measurements do not wholly agree with those we took from our specimens of the two species. Aside from proportional measurements, which can sometimes be misleading because of individual variation, they mention no other character used to distinguish their specimens of each species. This raises the question of whether or not they actually had specimens of *C. productus* (or *C. anatirostris*). Obviously, this problem needs further investigation; in the meantime, we will continue recognition of both species based on characters here given.

### *Coelorinchus sheni* Chiou, Shao, and Iwamoto, 2004

*Caelorinchus sheni* Chiou, Shao and Iwamoto, 2004a:37–39, figs. 1–4 (holotype, ASIZP 061348; off Da-xi, ne. Taiwan, 24°54′63″N, 120°03′49″E, 400–650 m; paratypes: ASIZP 061232 [1], CAS 215541[1]).

*Coelorinchus sheni*: Shao et al., 2008: table 2 (3 spec., NET, SWT, 100–650 m).

**Material examined** (13 spec.).— **NET:** ASIZP 61348 (1, holotype, 420 TL), Da-xi; CAS 215541 (1, paratype, 427 TL), Da-xi; ASIZP 70292 (1, 535 TL), Da-xi; ASIZP 70210 (8, 135–377 TL), Da-xi. BSKU 116417 (1, 578 TL), Da-xi. **SET**: ASIZP 61232 (1, paratype, 937 TL), Lyu-dao.

**Distinguishing features**.— 1D II 8–9; P i18–i19; GR-I (inner) 9–10 total. Scales below midbase 1D 4.5–5.0, below 2D 5–6; pyl.caeca about 27. Snout long, smoothly conical in lateral profile, narrow in dorsal view, its length 41–56% HL, about 2.0 times orbit; anterolateral margin of snout incompletely supported by bone; orbit 20–21% HL, its dorsal margin well below dorsal profile; upper jaw 30–37% HL; nasal fossa scaled anteriorly and ventrally; underside of head fully scaled. Light organ group II of Iwamoto (1990), fossa narrow and short, not extending to pelvic-fin bases. Spinules on body scales sharp, blade-like, in 5–7 slightly divergent, crestlike rows, middle row strongest. Ground color light brown, bluish over abdomen; about 5 prominent saddle marking interspersed with pale narrow bars from trunk to tip of tail; mouth and gill cavity blackish; fins dusky, but pelvic fins blackish except for white outer prolonged ray; margin of A blackish. Attains more than 937 mm TL.

**Distribution**.— Known only from ne. and se. Taiwan in depths of about 100–650 m.

**Remarks**.— *Coelorinchus sheni* appears to be confined to rough-bottom slopes of e. Taiwan where bottom trawls are ineffective; specimens were all captured by longline.

### *Coelorinchus smithi* Gilbert and Hubbs, 1920

*Coelorhynchus smithi* Gilbert and Hubbs, 1920:493–498, fig. 20 (holotype, USNM 78212; Indonesia ne. of Celebes, 298 fm [545 m]; 8 paratypes, Philippines and Indonesia).— Okamura, 1970:179–183, pl. XXXIX, text-figs. 75–77 (63 spec., 144–322 mm TL; s. Japan in 300–610 m).— Okamura *in* Okamura et al., 1982:171, 353, fig. 103 (p.170) (8 spec., 242.5–295 mm TL; Kyushu-Palau Ridge and Tosa Bay, in 300–610 m).

*Coelorinchus smithi*: Okamura *in* Masuda et al., 1984:98, fig. 83C (compiled).— Yatou *in* Okamura and Kitajima, 1984:231, 368, fig. 164 (p. 230) (5 spec., 235–385 mm TL; Okinawa Trough [East China Sea], in 400–600 m).— Shao et al., 2008: table 2 (8 spec., NET, SCS, SWT, 441–1110 m).

*Caelorinchus smithi*: Iwamoto and Williams, 1999:161–164, fig. 22 (10 spec., Java, n. and ne. Australia, 402–731 m).— Iwamoto and Graham, 2001:455, fig. 71 (1 spec., se. Australia, 740 m).— Nakabo, 2003:433 (compiled).— Chiou et al., 2004b:36, 47 (in key, list).

**Material examined** (7spec.).— **NET:** ASIZP 61330 (1, 316 TL), Da-xi; ASIZP 61331 (1, 291 TL), Da-xi. **SWT:** ASIZP 65523 (2, 250–265 TL), CD 138, 441 m; ASIZP 65594 (2, 230–255 TL), CD 141, 985–1110 m; ASIZP 58062 (1, 230+ TL), Tong-Sha Islands, SCS.

**Distinguishing features**.—1D II 7–10; P i15–i19; GR-I (inner) 7–8 total; scales below midbase 1D 3.5–4.5, below 2D 4.5–6.0; pyl.caeca 19–37. Snout sharply pointed, length 39–52% HL; anterolateral margin of snout completely supported by bone; orbit 24–30% HL, upper jaw 20–29% HL; nasal fossa usually sparsely scaled ventrally; underside of head almost fully scaled (scales with 1–3 short rows of spinules). Light organ group II of Iwamoto (1990), fossa narrow and short, not extending to pelvic-fin bases. Spinules on body scales blade-like in 3–7 sharp, divergent, ridgelike rows. Ground color grayish-brown, paler to silvery ventrally, bluish over abdomen but not on chest; mouth and gill cavity dark; most fins dark dusky to blackish. Attains more than 32 mm TL.

**Distribution**.— Broadly distributed from s. Japan to Indonesia and Australia, in 300–750 m. In Taiwan, specimens have been collected between 441 m and 1110 m.

**Remarks**.— Among the *Coelorinchus* of Taiwan, *C. smithi* is most similar to *C. leptorhinus, C. spinifer, C. macrorhynchus*, and *C. japonicus* in having the anterolateral snout margin completely supported by bone. It is distinguishable from *C. leptorhinus* inhaving underside of snout fully scaled (cf. mostly naked) and from *C. spinifer* in having notably stronger, larger scale spinules on body scales, arrayed in three divergent rows with the middle row notably larger, and by having the length of the 1D base entering 1.2 times into the 1D-2D interspace. It differs from *C. japonicus* in having a distinct, though short, naked fossa before the vent (lacking in *C.* japonicus), somewhat fewer scale rows below the midbase of 1D (3.5–4.5 vs. 4.5–6.0) and below 2D origin (4.5–6.0 vs. 5.5–7.5), fewer pyloric caeca (21–37 vs. 41–60), and narrower scale spinules (broad buttresses in *C. japonicus*). Differences from *C. macrorhynchus* are discussed in the description of that species.

### *Coelorinchus* cf. *spinifer* [*sensu* Gilbert and Hubbs, 1920]

*Coelorhynchus spinifer* Gilbert and Hubbs, 1920:516–519, fig. 30 (holoype: USNM 78226, Gulf of Tomini, Sulawesi [Celebes], 762 fm [1440 m]).

*Coelorinchus spinifer*: Shao et al., 2008: table 2 (1 spec., SCS, 1098 m; first record from Taiwan).— Iwamoto et al., 2009:47–48, fig. 4A–B (descr. of Taiwan spec.)

**Material examined** (1 spec.).— **SCS:** ASIZP 66748 (1, 52 HL, 180 TL), CD 322, 1098 m.

**Distinguishing features**.— 1D II, 11; P i16; GR-I 2+7 (inner); GR-II 1+7 (outer); scales below midbase 1D about 7, below 2D 6; lateral line scales over distance equal to predorsal length ca. 43. Snout sharply pointed, about twice orbit diameter, 45–52% HL; anterolateral margin of snout completely supported by bone; orbit 22–23% HL, internasal width 19%, interorbital 25%, orbit to preopercle 30%, postorbital 30%, upper jaw 22%; length 1D base 1.2 times into 1D-2D interspace; underside of head almost fully covered with tiny deciduous scales. Light organ group II of Iwamoto (1990), fossa narrow and short, not extending to pelvic-fin bases. Scales strong and prickly, spinules on body scales in 3 slightly divergent, ridgelike rows, middle row larger. Ground color brownish, blackish over abdomen, opercles, jaws, and gular and branchiostegal membranes; mouth and gill cavity black; most fins dusky, but P and V blackish, outer V ray pale. Attains at least 185 mm TL.

**Distribution**.— Indonesia off Sulawesi and South China Sea off Taiwan in depths of 1440 m and 1098 m, respectively.

**Remarks**.— *Coelorinchus spinifer* is among the deepest-living members of the genus; only a handful of *Coelorinchus* species occur at depths greater than 1000 m. The Taiwan specimen is only the second known of the species (Iwamoto et al. 2009). The notably long and strong spinules on the scales, especially on the head ridges, in the holotype and Taiwan specimen, may reflect a juvenile condition. Until a larger size series is obtained, we are uncertain of its status within the genus. It is otherwise similar in most characters to *C. smithi.*

### Genus *Coryphaenoides* Gunnerus, 1874

Distinguishing features.— BR 6. Spinous second ray of 1D serrated along leading edge. Anus usually immediately before anal fin. No light organ.

Remarks.— *Coryphaenoides* is the second largest genus of Macrouridae, with more than 60 species currently recognized, only four of which are so far known from Taiwan. Six or seven subgenera continue to be recognized, some as full genera, but the circumscription of each of these has not been based on adequate phylogenetic analyses, although some attempts have been made using very limited numbers of species (e.g., Wilson et al. 1991; Wilson 1994), Wilson and Attia (2003) using DNA sequencing, peptide mapping of lactate dehydrogenase, and protein electrophoresis; and Rao-Varón and Ortí (2009) using nuclear and mitochondrial DNA sequences. Most of the species appear to have their primary depth range in mid-continental-slope depths, but many occur at lower-slope depths; a few are primarily found on the continental rise at depths of 2000–4000 m, and the deepest-living grenadier, *C. yaquinae* Iwamoto and Stein, 1974, has been captured in abyssal depths below 6000 m. That species and *C. armatus* (Hector, 1874) can be expected in Taiwan waters deeper than about 4000 m, and other *Coryphaenoides* species are likely to be found when depths greater than 2000 m are more thoroughly sampled. As might be expected from fishes of great depths, many of the species are known from widely separated areas throughout the world oceans. A few of the larger members of this genus are of some commercial importance. The Roundnose grenadier (*C. rupestris*) of the North Atlantic has long been targeted by commercial fishermen and some stocks have become severely depleted. The Pacific grenadier (*Coryphaenoides acrolepis*) is the target of a very limited fishery off northern California.

### Key to the Species of *Coryphaenoides* in Taiwan

1a. V rays 7 or 8; a greatly elongated spinous 1D ray, usually more than 1.5 times HL C. microps
1b. V rays 9–12; spinous 1D ray much less than 1.5 times HL . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Mouth large, upper jaw extends to below posterior margin of orbit or beyond; barbel 10–23% of HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C. rudis*
2b. Mouth moderate to small, upper jaw not extending beyond posterior ⅓ of orbit; barbel 6–14% of HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Interorbital space much smaller than orbit (about 1.3 into); GR-I (inner series) 9–10 total; snout acutely pointed; preopercle ridge forming acute, lobelike angle posteroventrally. . *C. nasutus*
3b. Interorbital space much larger than orbit (about 0.7 into); GR-I (inner series) about 7 total; snout rather bluntly pointed; preopercle ridge forming shallow rounded lobe posteroventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *C.* cf. *asper*

#### *Coryphaenoides* cf. *asper* [*sensu* Günther, 1877]

*Coryphaenoides asper* Günther, 1877:440 (holotype, BMNH 1887.12.7.88; se. of Cape Nojima [se. of Boso Peninsula], Japan, 34°37′N, 140°32′E, 1875 fm [3429 m]). Shao et al., 2008: table 2 (1 spec., Taiwan [SCS], 1982 m; first record from Taiwan).— Iwamoto et al., 2009:45–47, fig. 3 (descr.; Taiwan [SCS] spec.).

**Material examined** (1 spec.).— **SCS:** ASIZP 66107 (1, 92.9 HL, 435+ TL), CD 325, 1982 m.

**Distinguishing features** (figures in square brackets are from original description).— 1D II [9] 11**,** P i19–i21 [25], V 10 [11], GR-I (inner) 2+5; GR-II outer 1+6/1+8; scales below 1D origin 7.5 [6], below midbase 1D 5, below 2D origin 5.5, over distance equal to pre-1D 37. Snout 29% HL, broadly pointed in lateral view, preoral length short, 16%, orbit small, 19%, about 1.5 into snout length, interorbital width 28%, orbit to preopercle 48%, upper jaw 33%, barbel 14% (about 1.3 times in orbit diameter), greatest body depth 81%, 1D-2D interspace 21%, height 1D 91%, length 1D base 26%, length V 83%. Second spine of 1D serrated, produced beyond segmented rays, outer V ray prolonged. Upper jaw extends posteriorly to below middle of orbit. Head fully scaled except over gular and branchiostegal membranes; modified, thickened scales above suborbital ridge; body scales covered with slender spinules in about 5 divergent rows.

**Distribution**.— Known only from two specimens, the holotype taken off Japan in 3429 m and the Taiwan specimen taken in the South China Sea in 1982 m.

**Remarks**.— The ASIZP specimen was first recorded by Shao et al. (2008) and subsequently described in more detail by Iwamoto et al. (2009). If correctly identified, it represents only the second known specimen of the species. The absence of previous captures since the *H.M.S. Challenger* made its historic voyage in 1873–1876 is probably owed to the paucity of trawl hauls made at depths exceeding 2000 m in the area. A few character differences that we found between this Taiwan specimen and the holotype have led to some uncertainty as to it identity; it is for this reason that we consider the identification as tentative.

### *Coryphaenoides microps* (Smith and Radcliffe, 1912)

*Macrourus microps* Smith and Radcliffe *in* Radcliffe, 1912:116–117, pl. 25, fig. 3 (holotype USNM 72934, 42.5 cm long; Philippines, Lagonoy Gulf, se. Luzon, 13°37′30″N, 123°41′09″E; Albatross sta. 5511, 560 fm [1024 m]; 4 paratypes, sta. 5325 off n. Luzon, [CAS-SU 2544])

*Coryphaenoides microps*: Gilbert and Hubbs, 1920:418–419 (descr.; holotype and 4 paratypes, CAS-SU 2246, n. Luzon, Albatross sta. 5325, 224 fm [410 m]).— Shcherbachev and Iwamoto, 1995:300–301.— Chiou et al., 2004a: table 1 (listed from Taiwan).— Shao et al., 2008: table 2 (1 spec., SWT, 687 m).— Kim et al., 2009:108–110, fig. 3 (descr.; type spec., plus others from Philippines, Taiwan [NET], and Korea [East Sea, 115 m; first record])

**Material examined** (53 spec.).— **NET:** ASIZP 58265 (1, 250+ TL, 50.8 HL), Da-xi; ASZIP 60252 (1, 137 TL), Da-xi; ASZIP 61128 (4, 267+-330 TL), Da-xi; ASIZP 63838 (2, 306–413 TL), CP 195, 570 m; ASIZP 65566 (1, 93+ TL), CP 124, 1129–1165 m; ASZIP 65657 (1, 233 TL), Da-xi; ASIZP 66900 (1, 140 TL), CP 247, 480 m. **SWT:** ASIZP 63767 (1, 232+ TL), CD 194, 507 m; ASIZP 63792 (1, 365+ TL) and ASIZP 64144 (1, 268+ TL), CD 193, 821 m; ASIZP 65516 (2, 160–190 TL) and CAS 224886 (1, 175 TL, ex. ASIZP 65516), CD 142, 227–235 m; ASIZP 65526 (2, 150–200 TL), CD 138, 441 m; ASIZP 65535 (4, 130–210 TL), CD 137, 316–477 m; ASIZP 65581 (1, 295 TL), CD 229, 880–1062 m; ASIZP 65591 (8, 160–200 TL), CD 136, 998–1211 m; ASIZP 65603 (1, 359 TL), CD 133, 690–748 m; ASIZP 65617 (1, 174 TL), CD 137, 316–477 m; ASIZP 65624 (1, 395 TL), CD 229, 880–1062 m; ASIZP 65639 (1, 385+ TL), CD 229, 880–1062 m; ASIZP 66099 (1, 295 TL), OCP 301, 687 m; ASIZP 66109 (1, 320+ TL), OCP 301, 687 m; ASIZP 66111 (1, 463+ TL), OCP 301, 687 m; ASIZP 66413 (1, 220+ TL), Dong-gang; ASIZP 66425 (1, 214+ TL), Dong-gang; ASIZP 66427 (1, 166 TL), Dong-gang; ASIZP 66786 (1, 310 TL), OCP 301, 687 m; ASIZP 66799 (1, 188+ TL), OCP 302, 695 m. **No data:** ASIZP 65579 (1, 421 TL). **Other material** (Univ. Philippines, Marine Science Institute, Manila [UPMSI]): UPMSI uncat. (1, 380 TL) (no data, probably MUSORSTOM II); UPMSI uncat. (5) MUSORSTOM II sta.

79, off Luzon, 13°31.6′N, 120°33.7′E, 326–240 m; 1 Dec 1980, 210+–252 TL). **Other specimens:** USNM 72933 (holotype, 82.0 HL, 413+ TL), e. coast Luzon, Philippines, 1024 m; CAS-SU 25446 (2 paratypes, 23.7–39.9 HL, 124+–187+ TL), n. Luzon, 18°34’15″N, 121°51’15″E, 410 m.

**Distinguishing features.**— 1D II 9–10; P i19–i21; V 7–8; GR-I (inner) 9–11 total; GR-II outer/inner 8–10/7–9; scales below midbase 1D 4.5–7.5, below 2D origin 6.0–9.5, over distance equal to snout tip-to-1D 29–35. Snout 28–33% HL, extending less than pupil diameter beyond mouth; preoral steep, short, length 11–16%; internasal narrow, width 15–21%; interorbital 18–26%; orbit 17–25%; postorbital length 47–53%; distance orbit to preopercle 40–47%; upper jaw 30–33%; barbel short, thick 8–14%; greatest body depth 61–96%; 1D-2D interspace 16–38%; second spinous ray of 1D greatly prolonged, 178–388% HL, serrations sparse, reduced or lost in large adults; length V 43–87% HL, outer ray moderately prolonged. Upper jaw extends posteriorly to below anterior ⅓ of orbit, mouth opening restricted laterally. Free margin of preopercle broadly rounded. Head scaly except narrow naked margin under snout and suborbital and all of gular and branchiostegal membranes; a tubercular scale at snout tip; body scales covered with slender reclined spinules in numerous subparallel rows. Color dark brown in adults, paler in young; fins generally pale near base, blackish distally.

**Distribution.**— Off Luzon, Philippine Islands, Japan Sea off Korea, and Taiwan (SCS, NET), in 240–1024 m, but one exceptional capture at 115 m off Korea.

**Remarks.**— Chiou et al. (2004b:47, table 1) listed *C. microps* from Taiwan, indirectly suggesting that the *C. marginatus* recorded by Shen et al. (1993) was an incorrect identification. Kim et al. (2009) recorded the species from the East (Japan) Sea off Korea and provided additional information on the species, comparing it with *C. marginatus*. *Coryphaenoides microps* is closely similar to *C. marginatus*, and the two species have many features in common. They can be separated by a combination of characters including orbit diameter (25–33% HL in *C. marginatus* cf. 17–25% in *C. microps*), postorbital length (42–45% HL cf. 47–56%), distance orbit to preopercle (33–40% cf. 40–47%), and length spinous 1D ray (1.5–2.5 times HL cf 1.8–3.0). The two species belong to what Gilbert and Hubbs (1920:413) describe as “a rather well-marked group of species which agree in possessing a produced dorsal spine, a deep and sharply compressed body, and a dorsal contour horizontal behind the first dorsal fin.” Other species of this group include *C. semiscaber* Gilbert and Hubbs, 1920, *C. macrolophus* (Alcock, 1889), and *C. tydemani* Gilbert and Hubbs 1920.

### *Coryphaenoides nasutus* Günther, 1877

Figures 10A–B.

*Coryphaenoides nasutus* Günther, 1877:440 (2 syntypes, BMNH 1887.12.7.78–79; 1 syntype?, MNHN 1890–0123; “south of Yedo” [Tokyo], Japan, 34°07′N, 138°00′E, *Challenger* sta. 235, 565 fm [1033 m]).— Gilbert and Hubbs, 1916:168 (45 spec., Japan: Hokkaido to e. coast Kyushu; 13 *Albatross* sta., 250–614 fm [457–1123 m]).— Okamura, 1970:140–143, pl. XXXI, text-fig. 56 (38 spec., 155–470 mm TL; Hokkaido to East China Sea, 625–1180 m).— Okamura *in* Okamura et al., 1982:165, 351, fig. 99 (8 spec., 136–234 mm TL; Kyushu-Palau Ridge).— Sawada *in* Amaoka et al. 1983:113, 195, fig. 64 (5 spec., 199–391 mm TL, 815–1100 m).— Okamura *in* Masuda et al., 1984:96, pl. 82F (compiled).— Yatou *in* Okamura and Kitajima, 1984:219, 364, fig. 155 (5 spec., 265–470 TL; Kyushu-Palau Ridge, 815–1000 m).— Iwamoto, 1990:216 (descr.).— Shao et al., 2008: table 2 (5 spec., NET, SET, 979–1268 m; first record from Taiwan).

*Macrurus nasutus*: Günther, 1887:132, pl. 30, fig. B (descr.; type illustrated).

**Material examined** (9 spec.).— **NET:** ASIZP 64113 (2, 240+-338+ TL), CP 242; ASIZP 65576 (1, 288+ TL), CP 197. **SET**: ASIZP 65511 (1, 425 TL), CP 127. **SCS**: ASIZP 65622 (1, 415

FIGURE 10. *Coyphaenoides nasutus* Gunther, 1877. A. ASIZP 64113, 338+ mm TL., fresh. B. ASIZP 65576, 288+ mm TL, preserved.

TL), CD 226. Non-types and possible types: BMNH 1887.12.7.80 [1], BMNH 1889.6.30.8–9 [2], NMI block reg. no. 114.1899 [1].

**DISTINGUISHING FEATURES**.— 1D II 9–11; P i18–i23; V 9–10; GR-I (inner) 1–2+7–9, GR-II outer/inner 1–2+8/1–2+7–8; scales below midbase 1D 4.5–5.5, below 2D origin 7.0–7.5, over distance equal to pre-1D len. 36–40. Snout length 27–32% HL; orbit 24–30%; interorbital width 20–24%; upper jaw 29–36%; barbel 5–8%; greatest body depth 75–97%; interdorsal [1D-2D] space variable 90–114% [2D rays rudimentary anteriorly]; length V 49–69%. Snout acutely pointed, extending short distance in front of mouth. Second spinous ray of 1D serrated, slightly produced (95–125% HL); outer V ray slightly produced. Upper jaw extends posteriorly to below middle of orbit. Head almost fully scaled except for gular and BR membranes; scales above suborbital ridge thickened and modified; a stout conical tubercle at snout tip; body scales covered with needlike spinules in convergent rows.

**DISTRIBUTION**.— Pacific coast of Japan from Hokkaido to East China Sea, and Taiwan from e. coast to South China Sea. Published depth range 625–1180 m, but in Taiwan, specimens collected in 979–1268 m.

**REMARKS**.— Shao et al. (2008) first recorded *C. nasutus* from Taiwan and the South China Sea based on the current specimens. This species is similar in many features to *C. microps* and *C. marginatus* but has a larger, broader head, more strongly pointed snout armed with a stouter terminal scute, V rays 9 or 10 (compared with 7 or 8), and an acute preopercular ridge and angular preopercular margin.

### *Coryphaenoides rudis* Günther, 1878

Figures 11A–C.

*Coryphaenoides rudis* Günther, 1878:24 (lectotype BMNH 1889.12.7.74; Pacific, n of Kermadec I., Challenger sta. 171, 600 fm [1097 m]. BMNH 1887.12.7.75–77 (paralectotypes: 3).— Shcherbachev and Iwamoto, 1995:301 (Indian Ocean).— Iwamoto and Williams, 1999:170 (4 spec., nw. and se. Australia, 1120–1700 m).— Merrett and Iwamoto, 2000:754 (3 spec., New Caledonia region, 1315–1862 m).— Iwamoto and Graham, 2001:467 (descr., 2 spec., NSW, Australia, 1050–1150m).— Shao et al., 2008: table 2 (1 spec., SCS, 1982 m; first record from Taiwan).

*Macrourus paradoxus* Smith and Radcliffe in Radcliffe, 1912:115–116, pl. 25, fig. 1 (holotype, USNM 72932, 585 mm TL, e. Palawan, Philippines, 9°13′00″N, 118°51′15″E, 1105 fm [2021 m]).

*Nematonurus macrocephalus* Maul, 1951:17–22, figs. 3, 4c (holotype, MMF [mounted spec.], 210 HL, taken off Madeira).

**Material examined** (1 spec.).— **SCS:** ASIZP 66117 (1, 132.6 HL), CD 325, 1982 m. **SET:** NMMB-P uncat. (1, 1240 TL), Taitung.

**Distinguishing features**.— 1D II,9–11, P i19, V 9–11, inner GR-I about 10, outer GR-II 8–9 total, scales below 2D 6–7. (Proportional measurements of Taiwan specimen in square bracket): snout length [27] 23–29% HL; preoral [17]10–12%; orbit [20] 16–26%; interorbital [27] 26–30%; upper jaw [38] 37–43%; barbel [20]10–23%; greatest body depth 80–100%; height 1D [76] 43–73%; length V [62] 50–111%. Snout low, bluntly rounded (in adults) to bluntly pointed (juveniles), scarcely extending beyond mouth in adults; no stout angular ridges on head; suborbital region vertical. Second 1D spine serrated (serrations reduced in largest specimens), slightly produced; outer V ray moderately produced. Upper jaw extends to below hind margin of orbit. Premaxillary teeth in narrow tapered band, outer series enlarged; mandibular teeth in about 3 series tapering to one. Head fully scaled except for gular and branchiostegal membranes; modified, thickened scales on suborbital and small tubercles at snout tip and at lateral angles; body scales densely covered with small conical spinules in irregularly divergent rows. (Measurement and count data partly from Shcherbachev and Iwamoto [1995], and Iwamoto and Williams [1999])

**Distribution**.— Possibly worldwide in warm seas; depth range 600–3500 m, but usually 1000–2000 m. One of Taiwanese specimens collected in the South China Sea in 1982 m and another one was taken from off Taitung as depth not less than 400 m.

**Remarks**.— Our specimen is the first collected in Taiwan waters (recorded by Shao et al. 2008: table 2) and one additional specimen was collected from SW Taiwan off Taitung. Its presence is not surprising in that the holotype of *C. paradoxus*, a synonym, was captured off e. Luzon Island in the Philippines.

## Genus *Hymenocephalus* Giglioli, 1882

**Distinguishing features**.— Snout high, relatively rounded, median nasal process forming a weak snout tip (no horizontal platelike process mesially); paired nasal bone in broad contact along median line, without wide gap around nostril cartilage; head much deeper than wide; body relatively compressed; head mucous canals greatly expanded; head covering membranous and often transparent; light organ long, small lens on chest anterior to pelvic-fin bases connected by a black streak to round posterior lens immediately before anus; ventral striae well developed; fine black lines on gular membrane oriented perpendicular to median line, not netlike; inner GR-I, lower limb 12–16; spinous ray of 1D completely smooth; chin barbel present or absent.

**Remarks**.— A genus of about 20 species, four of which are known from Taiwan. Most species do not exceed about 20 cm TL. The highly developed luminescent organ system consisting

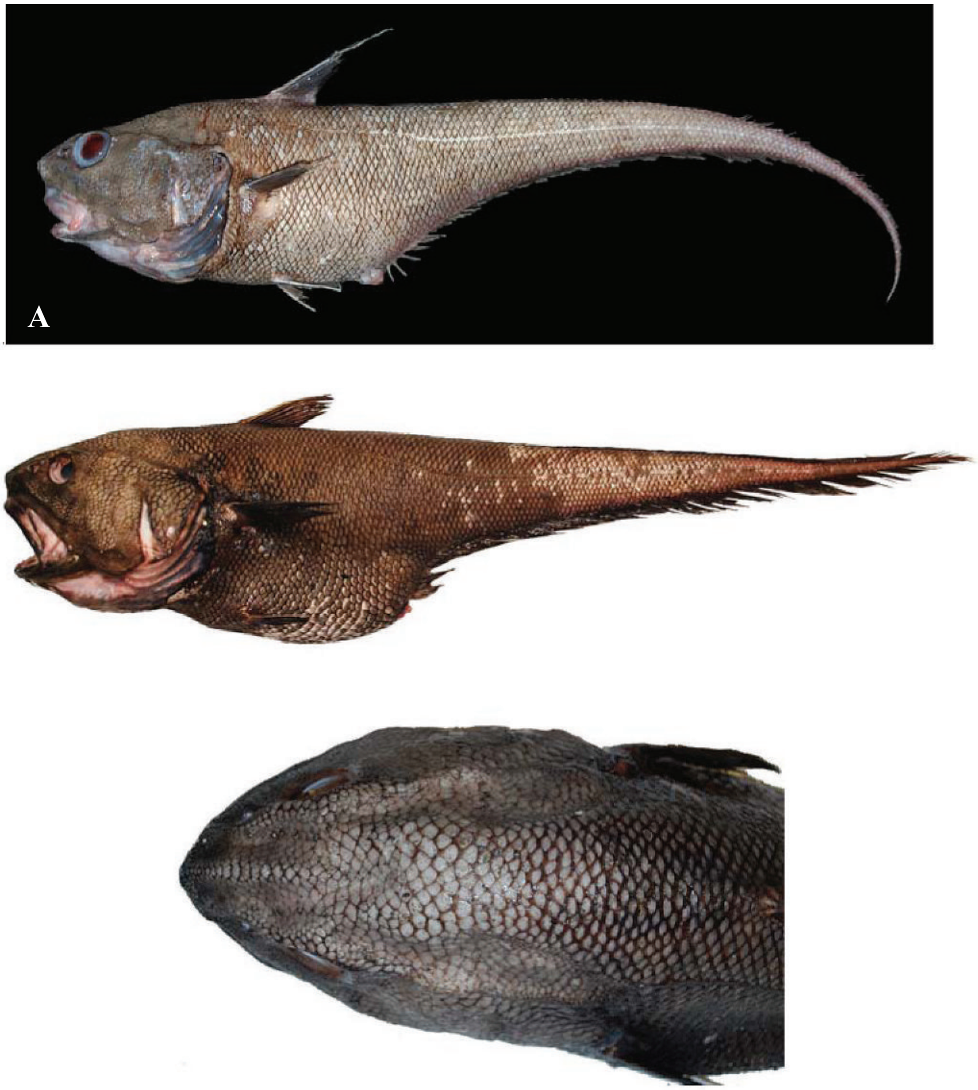

FIGURE 11. *Coryphaenoides rudis* Günther, 1878. A. ASIZP 66117, 133 mm HL, fresh. B. NMMB-P uncat., 1240 mm TL, fresh and C. same specimen, dorsal view of head.

of a network of fine striations ("ventral striae") on the cleithrum, chest, and belly regions is seen in gadiforms only in this genus, its closely related genera *Hymenogadus* and *Spicomacrurus,* and the monotypic genera *Steindachneria* Goode and Bean *in* Agassiz, 1888 and *Lepidorhynchus* Richardson, 1846. The presence of two lens-like bodies of the light organ, one on the chest, the other immediately before the anus, is unique among the grenadiers to *Hymenocephalus, Hymenogadus,* and *Spicomacrurus*. The position of the lenses is similar to that of the ventral fossae of some species of *Coelorinchus*, but so far as we can determine, there are no comparable structures in that or other grenadiers. The delicate, paper-thin head bones and membranous head integument are usually damaged during capture, adding to the difficulties of identifying specimens.

## Key to the Species of *Hymenocephalus* in Taiwan

1a. V 7–9 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
1b. V 11 or 12 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

2a. Barbel long, about 50% HL; orbit diameter 27–31% HL. . . . . . . . . . . . . . . . . . . . *H. longiceps*
2b. Barbel about 11–18% HL; orbit diameter 34–45% HL . . . . . . . . *H. striatissimus striatissimus*

3a. Barbel absent; orbit diameter 28–35% HL; color grayish brown in preservative, somewhat silvery in life . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. lethonemus*
3b. Barbel rudimentary, about 4% HL; orbit diameter 23% HL; color mostly blackish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. papyraceus*

### *Hymenocephalus lethonemus* Jordan and Gilbert 1904

*Hymenocephalus lethonemus* Jordan and Gilbert, 1904:615, text-fig. (holotype, USNM 50936; Sagami Bay, Japan, 120–265 fm [219–485 m]; paratypes, CAS-SU 8641 [3 spec.], USNM 51455 [3 spec.]).— Gilbert and Hubbs, 1916:188–189 (22 spec., s. Japan, East China Sea, 197–440 fm [360–805 m]).— Okamura, 1970:54–56, pl. II, text-fig. 23 (83 spec., 85–140 mm TL; e. coast of s. Japan).— Yatou *in* Okamura et al., 1982:143, 347, fig. 87 (p. 142) (7 spec., 175.5–233 mm TL; Kyushu-Palau Ridge).— Okamura *in* Masuda et al., 1984:94, pl. 80–G (compiled).— Okamura *in* Okamura and Kitajima, 1984:201, 358, fig. 142 (p. 200) (8 spec., 148–180 mm TL; East China Sea [Okinawa Trough]; 570–810 m).— Chiou et al., 2004b:44, fig. 12 (13 spec., ne. Taiwan).— Shao et al., 2008: table 2 (21 spec., Taiwan [NET, SWT, SCS], 441–1040 m).

**Material examined** (36 spec.).— **NET:** ASIZP 61231 (1, 126 TL), Da-xi; ASZIP 64270 (2, 105+-108+ TL), CP 234, 547 m; ASZIP 66974 (12, 112–124 TL), Da-xi. **SWT:** ASIZP 65561 (1, 120+ TL) and ASIZP 65611 (1, 115 TL), CD 203, 634–866 m; ASIZP 65598 (3, 120–155 TL), CD 138, 441 m; ASIZP 65604 (1, 133 TL) and ASIZP 66946 (1, 330 TL), CD 134, 736–1040 m; ASIZP 66731 (1, 97 TL), OCP 317, 515 m; ASIZP 66871 (5, 43–68 TL), OCP 312, 517 m; ASIZP 66872 (1, 78 TL), CD 311, 516 m; ASIZP 66873 (4, 50–80+ TL), OCP 313, 516 m; ASIZP 67582 (2, 75+-95+ TL), CP 348, 395 m. **Other specimens:** ASIZP 67976 (1, 151 TL), Aurora.

**Distinguishing features**.— 1D II 9–11; P i13–i16; V 11 (rarely12); inner GR-I 21–25 total; pyl. caeca 11–16. Head about 5–6 in TL; body depth about 8.0–9.5 TL. Snout high, pointed; mouth large, upper jaw extending posteriorly to below hind margin of orbit; barbel absent; gill openings wide, gill membrane free over isthmus; outer gill slit about as wide as orbit. Attains about 180 mm TL. (Compiled from Okamura [1970] and Gilbert and Hubbs [1916]).

**Distribution**.— Pacific coast of s. Japan, East China Sea off Kyushu Is., Japan, and Taiwan (NET, SWT, SCS), in 360–1040 m.

**Remarks**.— Okamura (1970:56) noted that among members of *Hymenocephalus*, this is the deepest-occurring in Japan.

### *Hymenocephalus longiceps* Smith and Radcliffe, 1912

*Hymenocephalus longiceps* Smith and Radcliffe in Radcliffe, 1912:111–112, pl. 23, fig. 3 (holotype, USNM 72928; off se. Luzon, Philippines, 201 fm [368 m]; paratypes, USNM 149297).— Yatou *in* Okamura et al., 1982:141, 346, fig. 85 (p. 140) (5 spec., 135–225.5 TL; Kyushu-Palau Ridge, 420–555 m).— Okamura *in* Masuda et al., 1984:93, pl. 80–D (compiled).— Okamura *in* Okamura and Kitajima, 1984:199, 357, fig. 140 (p. 198) (5 spec., 184–230 mm TL; East China Sea [Okinawa Trough], 353–490 m).— Shen et al., 1993:171 (descr.).— Chiou et al., 2004b:37, 47 (in key, list).— Shao et al., 2008: table 2 (41 spec., Taiwan [NET, SWT, SCS], 227–1211 m).

*Hymenocephalus* (*Hymenocephalus*) *longiceps*: Gilbert and Hubbs, 1920:525–526 (63 spec., South China Sea off Hong Kong and Taiwan, Philippines, "East Indies," 107–298 fm [196–545 m]).— Okamura, 1970: 45–47, pl. XIV (9 spec., 156–240 m TL; Pacific coast s. Japan, 300–500 m).

**Material examined** (47 spec.).— **NET:** ASIZP 61235 (1, 195 TL), Da-xi; ASIZP 61236 (6, 96–152 TL), Da-xi; ASIZP 66373 (1, 160 TL), Nan-fang-ao. **SCS:** ASIZP 65546 (1, 160+ TL), CD 137, 316–477 m; ASIZP 65554 (1, 200 TL) and ASIZP 65563 (1, 160 TL), CD 142, 227–335 m; ASIZP 65589 (5, 125–155 TL) and ASIZP 65606 (4, 125+-170 TL), CD 136, 998–1211 m. **SWT**: ASIZP 60321 (1, 128 TL), Dong-gang; ASZIP 62270 (2, 100+-130+ TL), Dong-gang. **SCS:** ASIZP 66269 (1, 170+ TL), ASIZP 66797 (13, 87+-118+ TL), and ASIZP 66879 (2, 63+-101+ TL), CD 311, 516 m; ASIZP 66739 (1, 100+ TL), CP 315, 509 m; ASIZP 66836 (1, 26.1 HL, 110+ TL) and ASIZP 66867 (1, 88 + TL), CP 314, 509 m; ASIZP 66837 (1, 168+-177+TL), CD 311, 516 m. **Other specimens:** ASIZP 67841 (1, 200 TL), Aurora, 358–342 m; ASIZP 67949 (1, 90 TL), Aurora, 269–277 m; ASIZP 68031 (1, 120 TL), Aurora, 500–524 m; ASIZP 68192 (1, 166 TL), Auroa, 442–431.

**Distinguishing features**.— 1D II 9–10; P i13–i17; V 8; inner GR-I 18–23 total; pyl. caeca 18–22. Orbit 27–31% HL; upper jaw 53–59%. Head rather low, its length about 5–6.5 in TL; body depth about 7–8 in TL. Snout low, broadly rounded, not projecting beyond mouth; barbel long, more than orbit, about 2 in HL. Attains about 240 mm TL. (Compiled from Okamura, 1970 and Gilbert and Hubbs, 1916).

**Distribution**.— Known from s. Japan to South China Sea, Philippines, Sulu Sea, Bohol Sea, and Celebes Sea, in 196–555 m. The species was taken in 227–1211 m depth off Taiwan.

**Remarks**.— The long barbel and low, rounded snout distinguish this species from all others of the subgenus from Taiwan. It is closely similar to *H. longibarbis* Günther, 1887 and the two may be synonymous.

### *Hymenocephalus papyraceus* Jordan and Gilbert, 1904

Figure 12.

*Hymenocephalus papyraceus* Jordan and Gilbert, 1904:614. fig. (holotype USNM 50935, 147 mm TL; Sagami Bay, Japan, 120–265 fm [219–485 m], *Albatross* sta. 3697).— Okamura, 1970:56–58, pl. XVII, text-fig. 24 (1 spec., 95 mm TL, Pacific coast s. Japan).— Sazonov, 1993:117–121 (fig.) (1 spec., East China Sea; 800–826 m).

*Hymenocephalus* (*Papyrocephalus*) *papyraceus*: Gilbert and Hubbs, 1920:539 (included as one of three species in new subgenus).

*Hymenocephalus papiraceus*: Okamura in Masuda et al., 1984:94, pl. 344–I (species name misspelled; compiled).

**Material examined**.— **NET:** NMMB-P9121 (1, 25.7 HL), Da-xi.

**Distinguishing features**.— 1D II,10; P i14; V 11; GR-I (outer/inner) 0+16/5+17, GR-II 5+17/4+16. Orbit 23% HL, 1.4 into postorbital; interorbital 35%; internasal width 23%; suborbital 19%; postorbital 54%; orbit to preopercle angle 54%; upper jaw 47%; barbel 3.5%; 1D-2D interspace 60%; P length 70%; V length 62%; length outer V to A origin 54%; pre-anal length 144%; length outer gill slit 27%. Head relatively deep and broad; orbit not included in dorsal profile; nape high, beginning slightly behind posterior edge of orbit. Snout with high median nasal ridge, flexible, pointed tip projecting slightly beyond mouth. Posterior end of preopercle ridge narrowly chisel-shaped (or flathead shovel-shaped). Barbel small but distinct. Head color mostly black, but dorsal head bones and snout transparent. Entire trunk to over A origin deeply and heavily peppered; remainder of body covered with large melanophores. Ground color medium brown; A base black anteriorly. Gular and BR membranes black. Attains about 150 mm TL

**Remarks**.— *Hymenocephalus papyraceus* is apparently a rare species, having been recorded only three times previously: the holotype (and only type specimen), a small specimen in poor condition reported by Okamura (1970), and the East China Sea specimen of Sazonov (1993). The Taiwan specimen is the first record from outside Japanese waters.

FIGURE 12. *Hymenocephalus papyraceus* Jordan and Gilbert, 1904. NMMB-P9121, 25.7 mm HL, preserved, photo reserved.

## *Hymenocephalus striatissimus striatissimus* Jordan and Gilbert, 1904

*Hymenocephalus striatissimus* Jordan and Gilbert, 1904:612–613, text-fig. p. 613 (holotype, USNM 50934. Suruga Bay, Japan, 167 fm [305 m]; paratype, CAS-SU 8549 [1]).— Gilbert and Hubbs, 1916:187–188 (22 spec., Pacific coast s. Japan and East China Sea; 360–543 m).— Yatou in Okamura et al., 1982:143, 346, fig. 86 (p. 142) (7 spec., 101–194.5 mm TL; East China Sea [Okinawa Trough], 300–555 m).— Okamura in Masuda et al., 1984:93, pl. 80–E (compiled).— Okamura in Okamura and Kitajima, 1984:199, 358, fig. 141 (p. 198) (25 spec., 148–180 mm TL; Kyushu-Palau Ridge, 425–570 m).— Shen et al., 1993:171 (descr.).— Chiou et al., 2004b:37, 47 (in key, list).

*Hymenocephalus striatissimus striatissimus*: Gilbert and Hubbs, 1920:529–530 (32 spec., South China Sea off Hong Kong, Taiwan, and Luzon, Philippines; 380–494 m; 3 subspecies recognized, including one new [*H. s. aeger*]).— Okamura, 1970:48–50, pl. XV (90 spec., 115–200 mm TL; Pacific coast s. Japan and East China Sea off Kagoshima Prefecture; 300–540 m; new subspecies described [*H. s. hachijoensis*]).— Shao et al., 2008: table 2 (34 spec., Taiwan [NET, ET, SCS], 100–1188 m).

MATERIAL EXAMINED (42 spec.).— **NET:** ASIZP 57973 (1, 206 TL), Nan-fang-ao; ASIZP 61233 (1, 184 TL), Nan-fang-ao; ASIZP 61234 (13, 112–162 TL), Da-xi; ASIZP 64247 (1, 110+ TL), CP 234, 547 m; ASIZP 65564 (1, 125 TL), CP 124, 1129–1165 m; ASIZP 65635 (1, 207 TL), CD 209, 508–522 m; ASIZP 70731 (1, 115 TL), Da-xi. **ET:** ASIZP 65524 (8, 145–200 TL), ASIZP 65528 (2, 160–170 TL), ASIZP 65536 (1, 161 TL), ASIZP 65600 (1, 162+ TL), and ASIZP 65619 (1, 172 TL), CD 210, 445–1185 m; ASIZP 65553 (1, 93+ TL), CD 199, 1134–1188 m. **SCS:** ASIZP 65677 (1, 140 TL), CD 311, 516 m; ASIZP 66834 (1, 117 TL), CP 314, 506 m. **Other locality:** ASIZP 67873 (1, 142 TL), Aurora, 506–542 m; ASIZP 67972 (1, 90 TL), Aurora, 507–540 m; ASIZP 68189 (1, 117 TL), Aurora, 431–442 m; ASIZP 68414 (4, 70–110 TL), Aurora, 507–540 m.

DISTINGUISHING FEATURES.— 1D II 8–10; P i11–i16; V 8 (rarely 7 or 9); inner GR-I 16–22 total; pyl. caeca 10–17. Orbit circular, large 34–45% HL, 0.9–1.0 into postorbital; upper jaw 48–59%. Head deep, length about 6–7 in TL; body depth about 8–9 in TL. Snout bluntly rounded but with short terminal point, barely projecting beyond mouth. Upper jaw extends to vertical through posterior margin of orbit. Barbel about ⅓ orbit. Attains about 200 mm TL.

DISTRIBUTION.— South China Sea off Hong Kong, Taiwan, and Luzon, Philippines, and ne. Taiwan, in 445–1188 m, but mostly between about 300 and 550 m.

**REMARKS**.— Gilbert and Hubbs (1920) recognized three subspecies of this species: *H. striatissimus striatissimus, H. striatissimus aeger, and H. striatissimus torvus.* The last was originally described as a full species by Smith and Radcliffe (*in* Radcliffe 1912). Okamura (1970:50–54) described *H. s. hachijoensis* from two specimens taken off Hachijo, a group of remote islands about 180 nautical miles s. of Tokyo; Okamura *in* Masuda et al. (1984:93) elevated the taxon to full species. Sazonov (1994:101–102) later recorded two additional specimens from the Northwest Pacific Ridge (Emperor seamounts) and one from the Kyushu-Palau Ridge. It is distinguished from *H. s. striatissimus* by "the longer barbel, the larger head, the smaller eye, and the lower snout" (Okamura 1970:53).

## Genus *Hymenogadus* Gilbert and Hubbs, 1920

**DISTINGUISHING FEATURES**.— Snout low, relatively pointed and protruding; paired nasal bones in broad contact along median line, without gap around nostril cartilage; head about as broad as high; body and head somewhat cylindrical; head mucous canals moderately developed; head covering mostly transparent; light organ long, small lens on chest anterior to pelvic-fin bases connected by a black streak to round posterior lens immediately before anus; ventral striae well developed; fine black lines on gular membrane oriented perpendicular to median line, not netlike; inner GR-I, lower limb 10–16; spinous ray of 1D weakly serrated; chin barbel present.

**REMARKS**.— Aside from the low, cylindrical body and head, pointed snout, fewer gill rakers, and the presence of serrations along the leading edge of the first dorsal fin, this genus is otherwise scarcely distinguishable from *Hymenocephalus*, in which it was originally included as a subgenus. Aside from the widely distributed *H. gracilis*, the genus contains only *H. tenuis*, which is known only from the single original record off Hawaii.

### *Hymenogadus gracilis* Gilbert and Hubbs, 1920

*Hymenocephalus* (*Hymenogadus*) *gracilis* Gilbert and Hubbs, 1920:522–525, fig. 31 (holotype, USNM 78227, 96 TL, off s. Luzon, Philippines, 13 28′45″N, 121 01′12″E, 162 fm [296 m]).— Marshall and Iwamoto *in* Marshall, 1973:602–604, fig. 31 (19 spec., nw. Pacific, e. and w. Atlantic; 342–618 m).— Iwamoto and Merrett, 1997:518, fig. 20b.— Shao et al., 2008: table 2 (3 spec., Taiwan [NET, SCS], 100–950 m)

*Hymenogadus gracilis*: Okamura, 1970:61–63, pl. XVIII, text-fig. 27 (60 spec., 91–128 mm TL; s. Japan, 300–500 m).— Okamura *in* Masuda et al., 1984:94, pl. 80H (compiled).— Okamura *in* Okamura and Kitajima, 1984:201, 359, fig. 143 (p. 200) (3 spec., Okinawa Trough [East China Sea], 295–385 m).— Chiou et al., 2004b:44–45, fig. 13 (2 spec., ne. Taiwan).

**MATERIAL EXAMINED** (6 spec.).— **NET**: ASIZP 61229 (1, 118 TL), Nan-fang-ao; ASIZP 61230 (1, 120 TL), Da-xi; ASIZP 65565 (1, 60 TL), Da-xi; ASIZP 70278 (1, 105 TL), Da-xi. **Other specimens:** ASIZP 68334 (2, 96–112 TL), Aurora, 357–367 m.

**DISTINGUISHING FEATURES**.— 1D II9–11; P i14–i17; V 7–9, usually 8; inner GR-I 14–18 total. Body depth 50–60% HL, about 9–10 in TL; barbel long, 20–30% HL. Attains about 130 mm TL.

**DISTRIBUTION**.— Probably circumglobal in warm seas, but not central e. Pacific, central e. Atlantic, and central Pacific (but see Remarks), in 300–450 m.

**REMARKS**.— The taxonomic status of the Hawaiian species *H. tenuis* Gilbert and Hubbs, 1917 has yet to be resolved. It may be a synonym of *H. gracilis*. Okamura (1970:58) recognized *Hymenogadus* as a full genus with two included species, *H. gracilis* and *H. kuronumai*, and by implication, also *H. tenuis*. Okamura also placed *H. kuronumai* into its own subgenus *Spicomacrurus* Okamura, 1970, a taxon that Iwamoto et al. (2011) elevated to full generic status. *Hymenogadus gracilis* appears to be more characteristic of oceanic elevations, such as islands, seamounts, and ridges, than to continental landmasses, and the terete body form is suggestive of a more pelagic, active-swimming lifestyle (not benthic, as proposed by Okamura 1970:60). Surprisingly, the species was not recorded by Okamura (*in* Okamura et al. 1982) from the Kyushu-Palau Ridge. Pelagic captures have been reported (Sazonov and Iwamoto 1992) in the upper 300 m over bottom depths of >1,000 m.

### Genus *Kumba* Marshall, 1973

**Distinguishing features**.— BR 7; anus in middle ⅓ of space between A and V, usually closer to the latter. Luminescent organ with one gland and lens immediately anterior to anus. Most dorsal surface of snout and almost entire ventral surfaces of snout, suborbital, and lower jaw naked. No terminal or lateral snout scute. V 8–12; GR-I (inner) 10–14 total. (After Iwamoto and Sazonov 1994.)

**Remarks**.— The genus was revised by Iwamoto and Sazonov (1994) to include nine species, two of which were described as new. The species are known from few and widely scattered specimens. Three species are recorded from Taiwan, two of these were newly recorded from the area by Shao et al. (2008).

### Key to the Species of *Kumba* in Taiwan

(Adapted from Iwamoto and Sazonov, 1994)

1a. Scaleless areas on dorsal surface of snout extending posteriorly beyond lateral nasal angles; V 9–10; orbit 37–43% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. punctulata*

1b. Scaleless areas on dorsal surface of snout extending posteriorly only to lateral nasal angles; V 10–13; orbit 26–43% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. No pigment spots along A; barbel short, about 7% HL; orbit 26–27% HL, equal or less than interorbital width; V 10–11 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. gymnorhynchus*

2b. Three black pigment spots above mid-length of A; barbel 21–33% HL; orbit 36–43% HL, much greater than interorbital width; V 11–13 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. japonica*

### *Kumba gymnorhynchus* Iwamoto and Sazonov, 1994

*Kumba gymnorhynchus* Iwamoto and Sazonov, 1994:229, figs. 3–4 (holotype, CAS 77313 [ex ZMMU P.17765]; Indian Ocean, West Australian Ridge (Broken Ridge), 30°46′S, 93°20′E, 1260–1370 m; 1 paratype, ZMMU P.17766).— Shao et al., 2008: table 2 (1 spec., Taiwan [SCS], 736–1040 m; first record from Taiwan and SCS).— Iwamoto et al., 2009:48–49, fig. 5 (data and photograph of Taiwan spec., ASIZP 65527).

**Material examined**.— **SCS:** ASIZP 65527 (1, 316 TL), CD 134, 1260–1370 m.

**Distinguishing features** [ASIZP 65527 in square brackets; ranges from types and NMV 23944].— 1D II [10]11; P [i18] i20–i24; V [8] 10–11; inner GR-I [10] 12–13 total, inner GR-II [10] 12–13 total. Snout [27] 27–29% HL; orbit about [26] 25–26%; interorbital [24] 24–31%; suborbital [16] 16–17%; postorbital [40] 48–52%; orbit to preopercle [50] 48–50%; upper jaw [41] 39–43%; barbel [12] about 7–11%; length isthmus to anal-fin origin [44] 58–65%. Head relatively deep and compressed; snout blunt, scarcely protruding beyond wide mouth; upper jaw extends to below posterior ⅓ of orbit; suborbital region flat, without sharp ridge. Spinules on scales short, conical, aligned in 1–3 comblike rows; dorsal snout surface naked to lateral nasal angles but not posteriorly. Spinous second ray of 1D finely serrated. Attains at least 400 mm TL.

**Distribution**.— Originally described from two specimens taken on the West Australian (Broken) Ridge in the e. Indian Ocean in 1260–1370 m. Our specimen was collected from the South China Sea off Taiwan in 736–1040 m.

**Remarks**.— The Taiwan specimen, as reported by Shao et al. (2008), represents the first record of the species from the w. Pacific and only the fourth known specimen. The two type specimens were taken off the West Australian [Broken] Ridge; a third specimen (NMV 23944) was taken off Albany in Western Australia. The species should be expected in intervening areas of the Pacific and Indian oceans. In the Taiwan specimen the counts of the pelvic and pectoral fin rays, and the inner gill rakers on first and second gill arches, and the distance between the isthmus and anal-fin origin were low and must be confirmed when other specimens are captured from the area.

### *Kumba japonica* (Matsubara, 1943)

*Lionurus japonicus* Matsubara, 1943:149, fig. 9 (holotype, FAKU 1951; Kumano-Nada, Japan [not seen in 2007]; 1 paratype, FAKU 1938 [not seen in 2007]).

*Nezumia japonicus*: Okamura, 1970:88–91, pl. XIX, text-fig. 39 (5 spec., 135–157 mm TL; s. Japan).

*Ventrifossa japonica*: Okamura *in* Okamura et al., 1982:147, 349 (10 spec.; s. Japan and Kyushu-Palau Ridge, 550–710 m).— Okamura *in* Masuda et al., 1984:94, pl. 81–F (compiled).— Nakabo, 2002:421 (compiled).

*Kumba japonica*: Iwamoto and Sazonov, 1994:231.— Chiou et al., 2004b:45, fig.14 (2 spec.; sw. Taiwan).— Shao et al., 2008: table 2 (3 spec.; Taiwan [NET, SWT], 100–600 m).

**Material examined** (10 spec.).— **NET:** ASIZP 66371 (1, 93 TL), Nan-fang-ao; ASZIP 66941 (1, 140 TL), CD 210, 445+1185 m; ASIZP 70681 (1, 163 TL), Da-xi. **SWT**: ASIZP 61240 (1, 162 TL), Dong-gang; ASIZP 61241 (1, 156 TL), Dong-gang. **Other materials: Japan:** NSMT-P 58943 (1, 15.8 HL, 115 TL), 65441 (1, 17.4 HL, 113 TL), 65731 (1, 15.2 HL, 110 TL), 65733 (1, 16.0 HL, 99+ TL), 91535 (1, 16.4 HL, 111 TL).

**Distinguishing features**.— 1D II 8–11; P i16–i22; V 9–12; inner GR-I 12–14 total; pyl. caeca 40–52. Snout 21–30% HL; preoral 16–22%; internasal width 17–21%; orbit 36–43%; interorbital 22–28%; upper jaw 37–40%; barbel 18–27%; outer gill slit 17–24%; pre-A 142–155%; isthmus to A 78–96%; body depth 63–89%; height 1D 83–88%; 1D-2D interspace 63–86%; length outer V ray 89–171%. Snout bluntly pointed, relatively high, much shorter than orbit diameter; suborbital ridge prominent; upper jaw extends to below posterior ½ to ¼ of orbit; barbel about two-thirds of orbit. Underside of head entirely naked; naked areas dorsally on snout extend only to transverse line crossing lateral snout angles; pores on mandible large and prominent. V origin under posterior margin of operculum; P origin slightly in advance of 1D origin; A origin behind 1D. Anus located about midway between A origin and inner V bases; ADW rather large, at or slightly ahead of line connecting inner V bases. Spinules on scales short, conical, aligned in 5–8 parallel crest-like rows. Spinous second ray of 1D sparsely serrated. Three small black blotches above mid-length of A. Species small, probably not attaining more than 170 mm TL.

**Distribution**.— Southern Japan, Kyushu-Palau Ridge, and Taiwan, 550–710 m (Taiwan records from 100 to 600 m).

**Remarks**.— The generic placement of this enigmatic species has been problemmatic; its previous allocation to three different genera reflects this. One of the current authors (HCH) visited the FAKU collections in Maizuru in 2007 but was unable to locate the type specimens of this species. The three small black blotches (faint in some specimens) above the A fin are unique and highly characteristic of this species.

### *Kumba punctulata* Iwamoto and Sazonov, 1994

Figures 13A–B.

*Kumba punctulata* Iwamoto and Sazonov, 1994:233–234, figs. 6–7 (holotype, MNHN 1994–0034; off New Caledonia, 20°54′S, 168°21′02″E, 530 m; 1 paratype, ZMMU P.17762 (13.4 HL, 89+ TL; Bismark Sea off New Guinea, 5°20.9′S, 146°16′E; 0–1000 m).— Iwamoto and Merrett, 1997:526, fig. 23 (holotype listed from New Caledonia).— Merrett and Iwamoto, 2000:764 (3 spec.; Vanuatu, 541–577 m).— Shao et al., 2008: table 2 (17 spec.; Taiwan [SCS], 509–516 m. first record for Taiwan).

**Material examined** (17 spec.).— **SCS:** ASIZP 66816 (4, 90+-131 TL), CP 315, 509 m; ASIZP 66861 (1, 95 TL) and ASIZP 66891 (3, 82+-128 TL), OCP 313, 513 m; ASIZP 66877 (2, 105+-118+ TL), CP 314, 506 m; ASIZP 66902 (3, 105–107+ TL), CP 316, 514 m; ASIZP 66942 (1, 90+ TL), CD 311, 516 m; ASIZP 66943 (3, 83+-103+ TL), OCP 317, 515 m.

**Distinguishing features**.— 1D II 9–11; P i18–i22; V 9–10 (rarely 11); inner GR-I 12–13 total. Snout 20–29% HL; orbit 37–43%; interorbital (25)28–35%; upper jaw 40–51%; barbel 13–20%. Snout bluntly pointed, relatively high, much shorter than orbit diameter; suborbital ridge relatively flat, not sharply angular in cross section; upper jaw extends to below of middle one-third orbit; barbel about 1.4–2.2 times into snout length. Underside of head entirely naked; naked areas dorsally on snout extend only to transverse line connecting lateral snout angles. Spinules on scales short, conical, aligned in 5–8 parallel crest-like rows. Spinous second ray of 1D sparsely serrated. Origin of V under opercle, A origin under anterior half of 1D. A small species, probably not attaining more than 150 mm TL.

**Distribution**.— Known from relatively few captures off Vanuatu and New Caledonia in sw. Pacific, but numerous specimens were collected in six trawls from the South China Sea off Taiwan in 509–516 m.

FIGURE 13. *Kumba punctulata* Iwamoto and Sazonov, 1994. A. ASIZP 66877, 1 of 2, 105 mm TL fresh. B. ASIZP 66816, 1 of 4, 131 mm TL, preserved.

**Remarks.**— Our Taiwan specimens (as listed by Shao et al., 2008: table 2) represent the first record of the species from this region and from the nw. Pacific.

### Genus *Kuronezumia* Iwamoto, 1974

**Distinguishing features.**— BR 7. Body and head compressed and deep; snout rounded in profile, almost entirely covered with small uniform, finely spinulated scales; suborbital region vertical, without angular midlateral ridge, covered with small unmodified scales. Teeth in broad villiform bands in both jaws, outer series of upper jaw slightly enlarged. GR-I 8–11 total. Body scales small, adherent, densely covered with long slender spinules. Anus removed from A origin, closer to V bases; a dermal light organ between V bases. Color overall from gray to brown to swarthy; fins uniformly dusky to black. (After Sazonov and Iwamoto, 1994:65–65.)

**Remarks.**— Seven species currently recognized, only one known from Taiwan. The genus was reviewed by Shcherbachev et al. (1992).

#### *Kuronezumia dara* (Gilbert and Hubbs, 1916)

Figure 14.

*Lionurus darus* Gilbert and Hubbs, 1916:197–199, pl. 10, fig. 1 (holotype, 132 mm TL, USNM 76867; Suruga Gulf, Japan, 35°06′N, 138°40′10″E, 197 fm [360 m]).

*Nezumia darus*: Okamura, 1970:101–102 (description from Gilbert and Hubbs, 1916).— Okamura *in* Okamura et al., 1982:161, 349, fig. 95 (p. 160) (2 spec., 130–144 mm TL; Tosa Bay, 355–605 m).— Okamura *in* Masuda et al., 1984:95, fig. 81–J (compiled).— Okamura *in* Okamura and Kitajima, 1984:217, 363, fig. 153 (p. 216) (2 spec., 220–318 mm TL; East China Sea [Okinawa Trough], 560–692 m).— Nakabo, 2002:424 (compiled).

*Kuronezumia darus*: Shao et al., 2008: table 2 (1 spec., Taiwan [SWT], 280–452 m; first record from Taiwan).

*Kuronezumia dara*: Shcherbachev et al., 1992:100–101(mentioned, no additional specimens).

**Material examined** (1 spec.).— **SWT:** ASIZP 65514 (1, 482 TL), CD 140, 280–452 m. **Other specimens: Japan:** BSKU 27666 (1, 49.8 HL, 255+ TL), 26326 (1, 34.6 HL, 209+ TL), 44828 (1, 42.4 HL, 218+ TL), 45036 (60.0 HL, 376+ TL); HUMZ uncat. (1, 22.0 HL, 138+ TL).

**Distinguishing features.**— 1D II, 9–10; P i21–i23; V 10–12, usually11; GR-I (outer/inner) 0+(1–8) / 2+(8–9) , GR-II 1+(7–8) / 1+(7–9); scale rows below 1D origin 12–15, below 2D origin 10.5–11.0; below mid-base 1D 8.5–10; over distance equal to pre-1D 35–42. Snout 24–30% HL; preoral length 15–19%; internasal width 18–19; orbit 25–33%; interorbital 24–25; postorbital length 44–49%; orbit to angle of preopercle 36–42%; upper jaw 30–35%; barbel 20–27%; length outer gill slit 16–20%; greatest body depth 85–97%; pre-A length 139–152%; isthmus to A 57–79%; 1D height 97–98% (3 spec.); 1D base length 28–31; 1D-2D interspace 23–41%; length outer V ray 68–87%. Head compressed, much deeper than wide; snout low, bluntly rounded, scarcely protruding beyond large mouth, lacking stout spinous tubercle at tip; upper jaw extends posteriorly about to below mid-orbit. Barbel moderately long, slender, about 0.5–0.8 of orbit. Scales small, densely covered with slender, conical spinules giving velvety feel to body surfaces; scale ridges on head not especially developed, head contours smoothly rounded. Color medium brown to swarthy, juveniles blackish overall, fins dark (usually black). A moderately large species, probably attaining about 500 mm TL; the current Taiwan specimen is the largest recorded.

**Distribution.**— Pacific coast of s. Japan in 360–692 m and SCS off Taiwan in 280–452 m.

**Remarks.**— Shao et al. (2008) first recorded the species from Taiwan and the South China Sea based on the ASIZP specimen. *Kuronezumia dara* is quite similar in many respects to *K. bubonis* Iwamoto, 1974, which has been recorded from the Atlantic, Pacific, and Indian oceans, includ-

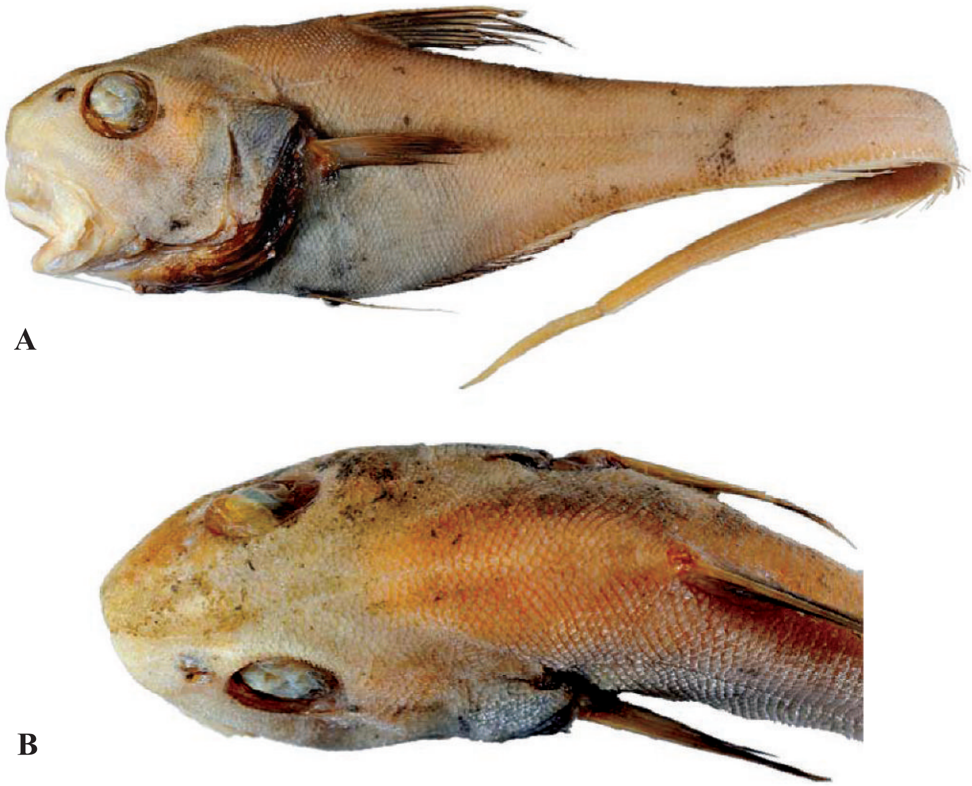

FIGURE 14. *Xuronezumia dara* (Gilbert and Hubbs, 1916). ASIZP 65514, 482 mm TL. A. lateral view. B. dorsal view.

ing the South China Sea off Vietnam (Shcherbachev et al. 1992:99–100). A notable difference is the tubercular swelling housing the light organ in *K. bubonis*, which is absent in *K. dara*.

The species-group name *darus* has been used by most Japanese authors even after the name had been transferred to the genus *Kuronezumia* by Shcherbachev et al. (1992), to which transfer those Japanese authors agree. Gilbert and Hubbs (1916) originally described the species in the masculine genus *Lionurus*, taking the Japanese term *dara* and latinizing it to *darus* to agree in gender with the genus name. When the specific name was combined with the feminine genus *Kuronezumia*, under Article 31.2 of the International Code of Zoological Nomenclature the "species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined" (International Commission on Zoological Nomenclature 1999:38). Thus, the masculine species-group name *darus* must be changed to the feminine *dara*.

### Genus *Lucigadus* Gilbert and Hubbs, 1920

*Lucigadus* Gilbert and Hubbs, 1920:553 (as subgenus of *Ventrifossa*; type species *Macrourus lucifer* Smith and Radcliffe, 1912, by original designation).— Sazonov, 1985:17 (elevated subgenus *Lucigadus* to genus level).

*Lucigadella* Gilbert and Hubbs, 1920:552 (as subgenus of *Ventrifossa*; type species *Macrourus nigromarginatus* Smith and Radcliffe, 1912, by original designation)

**DISTINGUISHING FEATURES.**— BR 7; chin barbel present; spinous ray of 1D serrated; anus removed from A, closer to V bases; light organ well developed, two dermal windows, one before anus, the second between V bases; ventral region of body appearing to have swung far forward so that gill membranes unite below or forward of preopercle, pelvic fins below opercle; suborbital shelf covered with several rows of small relatively unmodified scales, with no sharp ridges; underside of snout mostly or completely scaled; spinules on body scales usually aligned in parallel rows; teeth in both jaws small, in tapered bands, premaxillary band not reaching beyond posterior edge of maxillary process. (Adapted from Iwamoto and Merrett 1997:526).

**Remarks**.— Seven species, only one in Taiwan. Most species smaller than 20 cm TL.

### *Lucigadus nigromarginatus* (Smith and Radcliffe, 1912)

*Macrourus nigromarginatus* Smith and Radcliffe *in* Radcliffe, 1912:114, Pl. 24, fig. 2 (holotype, USNM 72930; near Simaluc I., Philippines, 5°33′15″N, 120°15′30″E, *Albatross* sta. 5569, 303 fm [554 m]).

*Lionurus* (*Nezumia*) *nigromaculatus*: Gilbert and Hubbs, 1916:145, 192 (name only, mispelled).

*Ventrifossa* (*Lucigadella*) *nigromarginata*: Gilbert and Hubbs, 1920:552–553 (44 spec., Philippines, Borneo, Celebes, Java Sea, in 135–392 fm [247–717 m]; new subgenus erected).

*Ventrifossa nigromarginata*: Shen et al., 1993:172 (descr.).— Chiou et al., 2004b:37, 47 (in key, listed from Taiwan).

*Lucigadus nigromarginatus*: Iwamoto and Williams, 1999:185 (mentioned).— Shao et al., 2008: table 2 (2 spec., Taiwan [NET, SWT], 100–600 m).

*Lucigadus lucifer* (*non* Smith and Radcliffe): Chiou et al., 2004b:46–47, fig. 15 (incorrect identification; 1 spec. from Taiwan).

**Material examined** (9 Taiwan spec.).— **NET**: ASIZP 57531 (1, 193 TL), Hsiao-liou-chiou; ASIZP 61308 (1, 110 TL), Nan-fang-ao. **SWT:** ASIZP (1, 158 TL), CD 142, 227–335 m; ASIZP 66322 (1, 153 TL), Dong-gang; ASIZP 67599 (1, 133 TL, 13 HL), CP 347, 305 m. **SCS:** ASIZP 65547 (2, 105–155 TL), CD 134, 736–1040 m. **Other specimens:** ASIZP 67968 (1, 149 TL), Aurora, 507–540 m. The holotype (USNM 72930) and 9 paratypes were previously examined (by TI) at the USNM. ASIZP 61630 (1, 135 TL), New Caledonia, 385–401 m.

**Distinguishing features**.— 1D II,9–11; P i18–i21; V 10–11; inner GR-I 10–12 total, outer GR-II 9–11 total; scales below 1D 14–16, below 2D 7–9.5, lateral line scales over distance equal to pre-1D length 37–42. Snout length 24–28% HL; ventral length of snout 17–20%; orbit 33–36%; interorbital 22–26%; upper jaw 33–39%; barbel 20–26%; outer gill slit 18–21%; body depth 85–94%; height 1D 92–107%. Snout high, smoothly and bluntly rounded; nape with moderate arch; upper jaw extends posteriorly to below mid-orbit; gill openings wide, extending forward under or anterior to posterior margin of orbit; scales small, covered with small, recurved conical spinules in parallel rows, no modified thickened scales on head ridges nor tubercular scutes on snout; 1D with black blotch, anterior portion of A black, no blotches or marking on body. A small species attaining approximately 180 mm TL.

**Distribution**.— Originally recorded from Philippines and Indonesia in 266–718 m; Taiwan records from 100–600 m.

**Remarks**.— Taiwan appears to be the n. limit of *Lucigadus nigromarginatus*. The species is apparently not uncommon in the Philippines and the Indo-Malaysian Archipelago.

## Genus *Macrosmia* Merrett, Sazonov and Shcherbachev, 1983

*Macrosmia* Merrett, Sazonov and Shcherbachev, 1983 (type species *Macrosmia phalacra* Merrett, Sazonov and Shcherbachev, 1983, by original designation).

**Distinguishing features**.— BR 7; V 11–12; pyl. caeca 15–18. Chin barbel present; spinous ray of 1D weakly serrated; anus in small periproct immediately before A; no light organ; V origin anterior to that of P; A origin below hind margin of 1D; head squamation reduced, mostly lacking on snout and underside of head, no scaled ridges on head and snout; teeth in bands in both jaws; olfactory organ massive, posterior nostril about equal to diameter of pupil, 4–5 times in HL. (Adapted from Merrett and Iwamoto 2000:767).

**Remarks**.— Only the single species known. Relationships obscure, but probably most closely related to *Asthenomacrurus* or *Pseudonezumia*. Broad distribution, having been captured in the e. North Atlantic, w. South Atlantic, se. Indian Ocean, and w. Pacific Ocean.

### *Macrosmia phalacra* Merrett, Sazonov and Shcherbachev, 1983

Figures 15A–B.

*Macrosmia phalacra* Merrett, Sazonov and Shcherbachev, 1983:554, figs. 1–2 (holotype, ZMMU P.15390, 31.5 mm HL, 217 mm TL; Ninety East Ridge, se. Indian Ocean, 17°04.8′S, 88°09.0′E, 1650–1660 m; paratype, BMNH 1980.12.31.2, 28.5 HL, 177+ TL; Canary Passage, e. North Atlantic).— Merrett and Iwamoto, 2000:767–768, fig. 25 (1 spec., 207+ TL; Vanuatu, 1160–1220 m).— Shao et al., 2008: table 2 (8 spec., Taiwan [SCS], 1098–1293 m; first record from Taiwan).— Melo et al., 2010:35 (off Brazil).

**Material examined** (9 spec.).— **SCS**: ASIZP 66730 (1, 152+ TL) and ASIZP 66919 (3, 120+-145+ TL) and CAS 224493 (ex ASIZP 66919)(2, 120+-178 TL), CD 322, 1098 m; ASIZP 66775 (1, 150+ TL), CD 324, 1293 m. **Other material.** ASIZP 68275 (1, 128 TL), Aurora, 1262–1360 m.

**Distinguishing features**.— 1D II,9; P i20–i21; V 11–12; total GR-I (outer/inner) 8/10, GR-II 11/10; scales below mid-1D 4, below 2D 6, lateral line scales over distance equal to pre-1D length about 29. Snout length 28–33% HL; preoral 20–22%; interorbital 22–25%; posterior nostril about 16%; orbit 23–29%; suborbital 13–21; orbit-preopercle 45–48%; upper jaw 30–41%; barbel 21–26%. Snout blunt, high; upper jaw extends to below mid-orbit; orbit slightly less than snout

Figure 15. *Macrosmia phalacra* Merrett, Sazonov and Shcherbachev, 1983. A. ASIZP 66919, 145+ mm TL, fresh. B. CAS 224493, 178 mm TL, preserved.

length; suborbital region vertical and rounded; gill openings wide, extending forward to under posterior margin of orbit; scales small, deciduous, entirely absent on underside of head and above snout; pores of cephalic lateral-line system well developed. Coloration mostly black to dark brown. Attains about 220 mm TL.

**Distribution**.— Originally described from the ne. Atlantic and se. Indian Ocean, and subsequently recorded off Vanuatu in the sw. Pacific and off Brazil in the sw. Atlantic, in 1060–1699 m. Our Taiwan specimens are the first from this area and were taken at depths of 1098–1293 m.

**Remarks**.— *Macrosmia phalacra* is turning out to be much more widely distributed than thought when originally described. The lack of specimens from the area between the North Atlantic and e. Indian Ocean leaves a perplexing distributional gap, but it may simply represent a collecting artifact.

### Genus *Malacocephalus* Günther, 1862

*Malacocephalus* Günther, 1862 (type species *Macrourus laevis* Lowe, 1843 by monotypy).

**Distinguishing features**.— BR 7; V usually 8 or 9; inner GR-I 9–14; pyl. caeca 50–100 or more. Snout smoothly rounded; sides of head relatively compressed and vertical; mouth large, usually >45% HL, upper jaws extend to or beyond vertical through posterior edge of orbits; premaxillary teeth in two rows to moderate band, with outer series enlarged; dentary teeth large, widely spaced, in one row laterally; chin barbel present; spinous ray of 1D smooth (subgenus *Malacocephalus*) or serrated (subgenus *Pawnurus*); periproct in middle third of space between V and A, usually closer to V; two dermal windows of light organ, one between V bases, the other within naked periproct region and before anus. Scales densely covered with fine needlelike spinules giving velvety feel to surface; no coarsely scaled ridges or scutes on head and snout; lowermost BR scaled. Gill membranes narrowly united over isthmus, with a free fold; gill openings extend forwards under orbits. Two short, broad retia and two wide but short gas glands.

**Remarks**.— Two subgenera (*Malacocephalus* and *Pawnurus*) and seven species known, but two or three species of subgenus *Malacocephalus* may be synonyms of the widely distributed *M. laevis*.

### *Malacocephalus nipponensis* Gilbert and Hubbs, 1916

*Malacocephalus nipponensis* Gilbert and Hubbs, 1916:189–191, pl. 9, fig. 2 (holotype, USNM 76866, 460 mm TL; e. coast Japan, *Albatross* st. 4967, 244–253 fm [446–463 m].— Okamura *in* Okamura et al., 1982:145, 347, fig. 88 (p. 144) (1 spec., 472 mm TL, Kyushu-Palau Ridge, 453 m).— Okamura *in* Masuda et al., 1984:94, pl. 80–J (compiled).— Okamura *in* Okamura et al., 1984:144, 360, fig. 145 (p. 202) (18 spec., 270–480 mm TL, East China Sea [Okinawa Trough], 420–550 m).— Shen et al., 1993:172 (descr.).— Chiou et al., 2004b:37, 47 (in key, list).— Shao et al., 2008: table 2 (2 spec., Taiwan [SCS], 979–1268 m, first record for Taiwan).

*Malacocephalus laevis*: Okamura, 1970:69–73, pl. IV, text-fig. 29–31(56 spec., 255–520 mm TL; Pacific coast of s. Japan, 350–500 m).— Shao et al., 2008: table 2 (9 spec., NET, ET, SWT).

**Material examined** (20 spec.).— **NET**: ASIZP 60015 (1, 445 TL), Da-xi; ASIZP 61312 (1, 336 TL; Nan-fang-ao; ASIZP 61313 (3, 184–252 TL), Nan-fang-ao; ASIZP 65517 (1, 68 HL, 405 TL), CD 210; ASIZP 70229 (1, 287 TL), Da-xi. **SWT**: ASIZP 61314 (1, 172 TL), Dong-gang; ASIZP 62331 (2, 250+-305+ TL), Fong-gang, 200 m; ASIZP 65517 (1, 405 TL), CD 210, 445–1185 m; ASIZP 65597 (2, 360–370 TL), CD 137, 316–477 m; ASIZP 70615 (1, 196 TL), Dong-gang). **SCS:** ASIZP 58031 (2, 361–389 TL), Tong-sa Islands); ASIZP 66277 (1, 220+ TL), OCP 312, 517 m; ASIZP 66745 (1, 178+ TL), CP 314, 506 m; FRIP 0669 (1, 302 TL), FRI, 630 m; NMMSTP 0907 (1, 290+ TL), Tong-sha Islands, 515 m.

**Distinguishing features.**— 1D II,10–14; P i16–i22; V 9 (8–10); inner GR-I 2–4+7–9; pyl. caeca 107–130. Snout 23–28%; orbit 29–37%; suborbital 11–14%; interorbital 26–31%; orbit-preopercle 42–50%; upper jaw 45–56%; barbel 18–22%. Snout bluntly pointed; mouth large, upper jaw extends to below hind margin of orbit; orbit large, greater than snout length; suborbital region vertical and smoothly curved; gill openings wide, extend forward to under posterior margin of orbit. Scales small, beset with fine, slender spinules; scales uniformly and smoothly cover head and body; no coarsely modified scales on ridges of head or tip of snout, lower branchiostegal rays scaled, but gular membrane naked. Light organ with anterior dermal window relatively small and round, situated between or slightly anterior to V bases; periproct enclosing posterior dermal window and urogenital openings located between V fins, far removed from A origin. Coloration gray to swarthy with silvery sides, blackish ventrally on head and over abdomen; fins dark dusky to black. Attains >520 mm TL. (Mostly after Okamura 1970 and from Taiwan specimens.)

**Distribution**.— Pacific coast of s. Japan, East China Sea [Okinawa Trough], Kyushu-Palau Ridge, and Taiwan off ne., sw. coast and in South China Sea in 316–1185 m.

**Remarks.**— *Malacocephalus nipponensis* was first synonymized into *M. laevis* Lowe, 1843 by Okamura (1970), but later (Okamura *in* Okamura and Kitajima 1982; Okamura *in* Okamura et al. 1984) considered it a valid species based on the absence of scales on the gular membrane (usually present in *M. laevis*) and the small round anterior dermal window (bean-shaped in *M. laevis*). Iwamoto (1979:149) suggested that *M. laevis, M. nipponensis*, and *M. hawaiiensis* Gilbert, 1905 may eventually prove to be the same. Although specimens of this species are available in many collections around the world, no one has yet to comprehensively study these collections. A molecular study may prove the easiest and the most-effective approach to resolving this question of how many species are involved in this clade. We have taken a conservative approach and treat these northwestern Pacific specimens as *M. nipponensis*, following Okamura.

### Genus *Mataeocephalus* Berg, 1898

*Mataeocephalus* Berg, 1898:41 (replacement name for *Coelocephalus* Gilbert and Cramer, 1897, preoccupied).

*Coelocephalus* Gilbert and Cramer, 1897:422 (non Agassiz, 1843) (type species *Coelocephalus acipenserineus* Gilbert and Cramer, 1897, by monotypy.)

**Distinguishing features.**— BR 6 or 7; V 7–9; inner GR-I 6–8, none or few rudiments in outer series; pyl. caeca 8–20. Snout pointed, armed with two tubercular scutes at tip, underside fully scaled to entirely naked; snout protruding well beyond small, almost inferior mouth; upper jaws about ⅓ of HL; chin barbel short; suborbital ridge sharp, angular in cross section, strongly armed with modified scutelike scales. Gill slits restricted by membranes across upper and lower arms; gill membranes broadly attached to isthmus, restricting opercular opening; gular and BR membranes naked. Dentition in both jaws in broad short bands, outer premaxillary series slightly enlarged. Spinous ray of 1D with rudimentary or well-developed serrations. Periproct moderately large, located within middle one-third of space between V and A (but closer to A in one species), rudimentary light organ developed before anus.

**Remarks.**— Sazonov et al. (2003) provided a comprehensive review of the genus and described two new species. They also removed *Macrourus hyostomus* Smith and Radcliffe, 1912 from either *Coryphaenoides* or *Hyostomus* and included it as a subgenus of *Mataeocephalus*. Six species, two of which are found in Taiwan waters, although two others (*M. adustus* and *M. accipenserinus*) could be expected, based on their presence in the SCS, and for the latter, in n. Philippine Islands.

### Key to Species of *Mataeocephalus* in Taiwan

1a. BR 6; body scales densely covered with slender somewhat flattened, reclined spinules in somewhat convergent to divergent rows . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *M. hyostomus*

1b. BR 7; body scales with needle-like spinules in 12–18 parallel rows, middle row slightly enlarged . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *M. cristatus*

### *Mataeocephalus* (*Mataeocephalus*) *cristatus* Sazonov, Shcherbachev and Iwamoto, 2003

Figures 16A–C.

*Mataeocephalus cristatus* Sazonov, Shcherbachev and Iwamoto, 2003:290–291, figs. 3–4 (holotype, 48 mm HL, 215 mm TL; ZMMU P.15345, Ninety East Ridge, 11°31′S, 88°55′E, 1600–1700 m;19 paratypes, 152–271 mm TL; w. tropical Pacific and Indian Ocean, 1000–1720 m).— Shao et al., 2008: table 2 (2 spec., Taiwan [SCS], 227–1010 m; first record from Taiwan).

**Material examined** (3 spec.).— **SCS**: ASIZP 66077 (1, 188 TL) and ASIZP 66912 (1, 216+ TL), CD 322, 1098 m. **SET:** ASIZP 67386 (1, 52 HL, 262 TL), CP 366, 1032 m.

**Distinguishing features**.— BR 7; P i17–i21; V 7. Snout 35–41% HL, 1.4–2.0 times larger than orbit; orbit 21–25% HL, about equal to interorbital space; orbit to angle of preopercle 33–38% HL. Snout depressed, narrowly pointed in lateral view, broadly triangular in dorsal view, tipped with stout spiny scutes; mouth small, underslung, U-shaped; underside of head fully scaled; spinous second ray of 1D weakly serrated, slightly prolonged, its height usually 60–84% HL; body scales with needle-like spinules in 12–18 parallel rows, middle row slightly enlarged; window of light organ absent; periproct relatively small, about midway between V and A. Attains at least 271 mm TL.

**Distribution**.— Broadly distributed in the w. tropical Pacific and Indian Ocean in 1000–1720 m. Our two specimens were collected from the South China Sea off Taiwan in 1032–1098 m.

**Remarks**.— Shao et al. (2008: table 2) first recorded the species from Taiwan based on the current specimens. *Mataeocephalus cristatus* is quite distinct from *M. hyostomus*, its congener in Taiwan, which is classified in a separate subgenus. The two species can be distinguished by a combination of characters including BR 7 (vs. 6 in *M.* hyostomus), V ray count (7 vs. 7–8, rarely 9, in *M. hyostomus*), height of spinous 1D ray (<HL in *M. cristatus*, greatly elongated, 145–295% HL in *M. hyostomus*), snout length (35–41% HL vs. 30–36%), orbit-preopercle (33–38% HL vs. 40–44%), and length upper jaw (20–27% HL vs. 28–31%). *Mataeocephalus accipenserinus* and *M. adustus* are distinguished from *M. cristatus* by their naked underside of snout. (Mostly adapted from Sazonov et al., 2003.)

### *Mataeocephalus* (*Hyostomus*) *hyostomus* (Smith and Radcliffe, 1912)

Figures 17A–B.

*Macrourus hyostomus* Smith and Radcliffe *in* Radcliffe, 1912:121–122, pl. 27, fig. 1 (holotype, 280 mm TL, USNM 72938, Lagonoy Gulf, Luzon I., Philippines; *Albatross* sta. 5470, 560 fm [1024 m]; paratypes from Sibuku Bay, Borneo, 750 m, and Buton Strait, Celebes, 1022 m).

*Coryphaenoides* (*Hyomacrurus*) *hyostomus*: Gilbert and Hubbs, 1920:422–424 (redescription of types; described new subgenus *Hyomacrurus*).

*Hyomacrurus hyostomus*: Marshall, 1973:565 (listed).

*Mataeocephalus* (*Hyomacrurus*) *hyostomus*: Sazonov et al., 2003:294–296, fig. 6 (7 spec. [including holotype], 36.5–65.5 HL, 160+–283 TL; Philippines, 760–1100 m).— Shao et al., 2008: table 2 (2 spec., Taiwan [SWT, SCS], 227–1040 m; first record from Taiwan).

FIGURE 16. *Mataeocephalus* (*Mataeocephalus*) *cristatus* Sazonov, Shcherbachev and Iwamoto, 2003, ASIZP 66386, 262 mm TL. A. lateral view. B. dorsal view of head.

FIGURE 17. *Mataeocephalus* (*Hyostomus*) *hyostomus* (Smith and Radcliffe, 1912), ASIZP65550, 220 mm TL. A. lateral view. B. dorsal view of head.

**Material examined** (2 spec.).— **SCS**: ASIZP 65541 (1, 180+ TL), CD 142, 227–335 m; ASIZP 65550 (1, 220 TL), CD 134, 736–1040 m.

**Distinguishing features**.— BR 6; P i16–i20; V 7–8; inner GR-I 5–8; scales below mid-1D 5.0–7.5; pyl. caeca 8–13. Snout 30–36% HL; orbit 22–25%; interorbital 22–26%; orbit to angle of preopercle 40–44%. Snout broad, moderately pointed and protruding; upper jaws extend posteriorly to below posterior ¼ to ⅓ of orbit; spinous second ray of 1D weakly serrated near base, prolonged, 1.5 or more times HL; body scales densely covered with slender, slightly flattened, reclined spinules in somewhat convergent to divergent rows; underside of head almost fully scaled; window of light organ scarcely discernible from exterior; periproct relatively moderate in size, situated between V and A but closer to former. Attains at least 283 mm TL. (Adapted from Sazonov et al. 2003.)

**Distribution**.— Known only from the Philippines, Indonesia, and Taiwan in 227–1100 m.

**Remarks**.— Our two specimens collected in the South China Sea in 227–1040 m were first recorded from Taiwan and the South China Sea by Shao et al. (2008: table 2). *Mataeocephalus hyostomus* is closely similar to *M. kotlyari* Sazonov, Shcherbachev, and Iwamoto, 2003, which is found in the sw. Pacific, but *M. hyostomus* has more pyl. caeca (16–19 cf. 8–13 in *M. kotlyari*), V 7, rarely 6 vs. 7–8, rarely 9, and shorter 1D (88–119% HL vs. 124–295%).

## Genus *Nezumia* Jordan, 1904

*Nezumia* Jordan, 1904:620 (type species *Nezumia condylura* Jordan and Gilbert, 1904, by original designation).

**Distinguishing features**.— BR 7; V 7–17 or more; inner GR-I usually 12 or fewer; mouth subterminal, upper jaw usually <40% HL; chin barbel present; spinous ray of 1D serrated; anus removed from A, closer to V bases; periproct located between V and A, usually closer to V; light organ well developed, a small dermal window between V bases; V base usually under P base; suborbital shelf with two rows of coarsely modified scutelike scales; underside of snout scaled or naked; spinules on body scales variable, from conical to broadly triangular, in parallel to widely divergent rows; teeth in both jaws in tapered bands, outer premaxillary tooth series slightly enlarged and not extending beyond maxillary process. Ground color usually light brown to blackish to bluish; ventral and abdominal area of trunk generally dark, often underlain with blue integument.

**Remarks**.— A diverse genus with approximately 48 species, but some of these may be allocated to other genera in future; others are yet to be described. There are five species represented in Taiwan waters.

### Key to the Species of *Nezumia* in Taiwan

1a. V 8–10; 1D usually overall dusky to blackish, without prominent black blotch . . . . . . . . . . . 2
1b. V 13–17; 1D with distinct black distal tip contrasting with pale proximal part of fin . . . . . . 4

2a. Underside of head mostly scaled except under snout; length second spinous 1D ray usually < HL; body scales with narrowly triangular to broadly lanceolate spinules . . . . . . . . . . . . . . 3
2b. Underside of head almost entirely naked; length second spinous 1D ray > 95% HL; body scales densely covered with needle-like spinules . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *N. spinosa*

3a. V 8 or 9, rarely 10; underside of snout naked only along median line . . . . . . . . . . . *N. proxima*
3b. V 10; underside of snout virtually entirely naked . . . . . . . . . . . . . . . . . . . . . . . . . *N.* cf. *coheni*

4a. V 13–15; scale rows below mid-1D 7.0–7.5, below 2D origin 8.5–10.0; length outer V ray 66–127% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *N. evides*

4b. V 13–17; scale rows below mid-1D 8.0–9.5, below 2D origin 10.0–13.0; length outer V ray 68–81% HL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *N. condylura*

### *Nezumia condylura* Jordan and Gilbert, 1904

*Nezumia condylura* Jordan and Gilbert *in* Jordan and Starks, 1904:620–621, pl. 4, fig. 2 (holotype, 195 mm TL, USNM 50937; Suruga Bay, Japan, 207–257 fm [379–470 m]; paratypes, CAS-SU 8551).— Okamura, 1970:85–88, pl. VII, text-fig. 38 (71 spec., 153–207 mm TL; Pacific coast s. Japan, 360–720 m).— Okamura *in* Okamura et al., 1982:161, 350, fig. 96 (p. 160) (7 spec., 152–200 mm TL; Kyushu-Palau Ridge).— Okamura *in* Masuda et al., 1984:95, pl. 81–G (compiled).— Okamura *in* Okamura and Kitajima, 1984:215, 362, fig. 151 (5 spec., 170–204 mm TL; Okinawa Trough [East China Sea], 510–760 m).— Iwamoto, 1990:269–370, fig. 625–626 (descr. compiled).— Chiou et al., 2004b:45, fig.16 (25 spec.; Taiwan [NET, ET, SCS], 400–1211 m).

*Lionurus condylura*: Gilbert and Hubbs, 1916:195–197 (29 spec., 103–204 mm TL; Pacific coast s. Japan, 197–440 m).

**Material examined** (33 spec.).— **NET:** ASIZP 61238 (1, 186 TL), Nan-fang-ao; ASIZP 61239 (8, 116–124 TL), Nan-fang-ao; ASIZP 64104 (1, 193 TL), CP 235, 764 m; ASIZP 65552 (1, 110 TL) and ASIZP 65607 (2, 114+-162+ TL); CD 210, 445–1185 m; ASIZP 65625 (2, 139–153 TL), CD 211, 517–529 m; ASIZP 65631 (1, 168 TL), CD 209, 508–522 m; ASIZP 65638 (1, 164 TL), CD 214, 488–1027 m; ASZIP 65643 (1, 132 TL), Da-xi; ASIZP 65663 (1, 192 TL), Da-xi; ASIZP 70683 (3, 25–28 HL), Da-xi. **SCS:** ASZIP 58022 (2, 131–133 TL), Tong-sha Islands; ASIZP 65587 (1, 155+ TL), CD 136, 998–1211 m; ASIZP 66803 (3, 27.8–33.0 HL, 160+-210+ TL); CD 320, 731 m; ASIZP 66831 (2, 20–23.6 HL, 105+-117+ TL); CP 315, 509 m; ASIZP 66894 (2, 16.8–22.8 HL, 82+-130+ TL), OCP 312, 517 m. **Other specimen**: ASIZP 68038 (1, 120+ TL; Aurora, 500–524 m).

**Distinguishing features**.— 1D II,10–13; P i18–i22; V 13–17; inner GR-I 8–11 total; scale rows below midbase 1D 8–9.5, below 2D 10–13; pyl. caeca 25–28. Snout length 27–30% HL; interorbital 23–27%; orbit 29–36%; upper jaw 29–33%; barbel 14–21%. Body relatively deep, about equal to HL; head 6.4–6.7 in TL; snout short, high, projecting slightly beyond mouth, with stout tubercles at tip and lateral angles; mouth rather small, upper jaw extends posteriorly to under posterior margin of pupil; barbel well developed, about ⅔ orbit diameter; suborbital ridge sharp, beset with two rows of thickened scales; underside of head naked except along peopercle; pores of cephalic lateralis system prominent; body scales densely covered with short, conical spinules arranged in 4–16 parallel rows. Spinous 1D ray about equal to HL, with slender, widely spaced serrations. Anterior dermal window of light organ small, situated between inner V-fin bases; anus closer to A than to outer base of V. Color yellowish gray to grayish brown, trunk, gill and gular membranes purplish-black; mouth and gill cavities dark; 1D with black tip, V and anterior portion of A black, other fins pale. Attains about 210 mm TL.

**Distribution**.— Pacific coast of s. Japan, East China Sea, and South China Sea in 360–910 m, and off Taiwan in 400–1211 m.

**Remarks**.— Differences between *N. condylura* and *N. evides* are slight and need to be more adequately determined. Iwamoto (1990:281) differentiated the two based on V fin-ray count, length P, and position of anus relative to V and A, but in the same volume (1990:270) said "this species may be the same as *N. propinqua*." Okamura (1984) cited "the shorter distance between the vent and the origin of anal fin, dense outer premaxillary teeth, etc." to distinguish *N. condylura* from *N. propinqua.*

### *Nezumia evides* (Gilbert and Hubbs, 1920)

Figure 18.

*Lionurus evides* Gilbert and Hubbs, 1920:557, fig. 39 (holotype, USNM 78231; near Sibuko Bay [Celebes Sea], Borneo, 4°12′10″N, 118°38′08″E, 260 fm [475 m]; 7 paratypes).

*Nezumia evides*: Iwamoto, 1990:262, fig. 614 (in key).— Iwamoto and Williams, 1999:201 (mentioned).— Shao et al., 2008: table 2 (5 spec., Taiwan [NET, SCS], 488–1027 m; first record from Taiwan).

MATERIAL EXAMINED (17 spec.).— **NET:** ASIZP 65641 (4, 147–175+ TL), CP 214, 488–1027 m; ASIZP 70699 (2, 156–162 TL), Da-xi. **SCS:** ASIZP 66830 (1, 127+ TL), OCP 317, 515 m. **Other specimens**: CAS-SU 25467 (4 paratypes, 19.6–27.5 HL, 104+-146+ TL), off Borneo, 475 m; CAS-SU 25468 (3 paratypes, 22.8–23.5 HL, 12–132+ TL), Molucca Sea off Halmahera [Gillolo], 545 m; and Aberdeen Fishery Station, Hong Kong uncat. (3, 22.3–27.5 HL, 120–160 TL), SCS s. of Hainan Is., 200–400 fm [366–732 m].

DISTINGUISHING FEATURES.— 1D II,9–13; P i16–i21; V 13–15; inner GR-I 8–11 total; scale rows below midbase 1D 7.0–7.5, below 2D 8.5–10; pyl. caeca about 25. Snout length 27–33% HL; interorbital 24–29%; orbit 31–36%; orbit to angle of preopercle 32–36%; upper jaw 29–34%; barbel 13–18%; length outer ray V 83–127%. Body relatively deep, 82–92% HL; head 4.1–5.8 in TL; snout short, high, projecting slightly beyond mouth, with stout tubercles at tip and lateral angles; mouth rather small, upper jaw extends posteriorly to under posterior margin of pupil; barbel well developed, about ⅖ to ½ orbit diameter; suborbital ridge with coarsely modified scales; underside of head to end of upper jaw and mandibular rami naked; body scales densely covered with short, conical spinules arranged in 8–13 parallel rows. Spinous 1D ray about equal to HL, denticulation on leading edge widely spaced; outer V ray extends to 10th to 20th A ray. Anterior dermal window of light organ small, situated between inner V bases; anus between V and A, but usually closer to inner V bases. Color in alcohol overall brownish, opercle and abdomen blackish with silvery sheen, abdomen underlain with bluish; mouth and gill cavities dark; 1D with distinct black tip. A small species, probably not much >160 mm TL.

DISTRIBUTION.— From Taiwan, South China Sea, Philippines, Celebes Sea, Molucca Sea, in 475–1027 m; the Taiwan specimens were collected in 517 m (NET) and 488–1027 m (SCS).

REMARKS.— Our specimens represent the northernmost record, and the first record (as reported by Shao et al. 2008) from Taiwan and the South China Sea. *Nezumia evides* closely resembles *N. condylura* and *N. propinqua* in having similar head shape, high V counts, naked underside of snout and mandibles, black-tipped 1D, and scale size and spinulation. The slightly lower counts of V rays, somewhat longer outer V ray, slightly fewer scales below mid-1D and below 2D origin (7–7.5 vs. 8–9.5 and 8.5–10 vs. 10–13, respectively), shorter body (HL 4.1–5.9 in TL vs. 6.4–6.7), and possibly smaller size attained distinguish *N. evides* from the two.

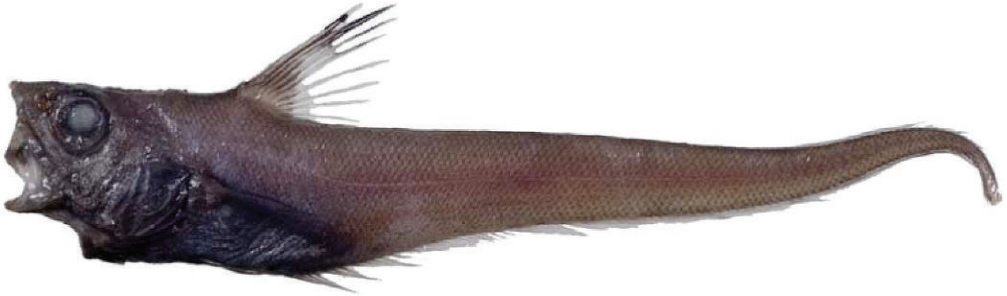

FIGURE 18. *Nezumia evides* (Gilbert and Hubbs, 1920). ASIZP 66830, 127 mm TL, fresh.

### *Nezumia proxima* (Smith and Radcliffe, 1912)

Figure 19.

*Macrourus proximus* Smith and Radcliffe *in* Radcliffe, 1912:119–120, pl. 26, fig. 2 (holotype, 292 mm TL, USNM 72936; Sogod Bay, Leyte I., Philippines, 10°12′00″N, 125°04′10″E, 502 fm [918 m]; paratypes, USNM 135338–39).

*Macrourus nasutus* [non *Coryphaenoides nasutus* Günther, 1877]: Jordan and Gilbert, 1904:618 (spec. from off Izu, Japan).

*Lionurus proximus*: Gilbert and Hubbs, 1916:201–202 (11 spec. [excluding 3 types]; East China Sea, Pacific coast of s. Japan, 361–544 fm [660–995 m]).

*Lionurus* (subgenus *Nezumia*) *proximus*: Gilbert and Hubbs, 1920:554 (3 spec. [including holotype], Philippines).

*Lionurus abei* Matsubara, 1943:146–147, fig. 7, 8 (holotype, 160.7 mm TL, cat. no. 4909, Kumano-nada, Japan; "Sigenkagaku Fish Coll. No. 7").

*Nezumia proximus*: Okamura, 1970:94–98, pl. XXI, text-fig. 41(17 spec., 174–370 mm TL; e. coast s. Japan, East China Sea; 420–910 m; synonymized *Lionurus spinosus* Gilbert and Hubbs, 1916 with *N. proxima*).

*Nezumia proxima*: Okamura *in* Okamura et al., 1982:163, 351, fig. 98 (p. 162) (1 spec., 160 mm TL; Kyushu-Palau Ridge).— Sawada *in* Amaoka et al., 1983:107, 192, fig. 58 (p. 106) (4 spec., 269.6–346.4 mm TL; Ibaragi [central Honshu, ca. 37°N], Japan, 1100 m).— Okamura *in* Masuda et al., 1984:95, pl. 81–I (compiled).— Okamura *in* Okamura and Kitajima, 1984:217, 362, fig. 152 (p. 216) (8 spec., 186–350 mm TL; Okinawa Trough [East China Sea], 820–932 m).— Iwamoto, 1990:281–282, fig. 645–646 (compiled).— Nakabo, 2002:424 (compiled).— Shao et al., 2008: table 2 (2 spec., Taiwan [ET, SCS], 488–1098 m; first record from Taiwan).

**Material examined** (2 spec.).— **NET**: ASIZP 65632 (1, 377+ TL), CP 214, 488–1027 m. **SCS**: ASIZP 66187 (1, 32 HL, 163+ TL); CD 322, 1098 m. **SWT:** ASIZP 65529 (1, 282+ TL), CD 142, 227–335 m.

**Distinguishing features**.— 1D II,9–11; P i17–i21; V 9, rarely 10; inner GR-I 9–11 total; scale rows below midbase 1D 5–7.5, below 2D 7–8.5; pyl. caeca 24–31. Snout length 23–31% HL; interorbital 18–25%; orbit 28–33%; suborbital 14–17%; upper jaw 31–34%; barbel 15–23%. Body relatively slender, compressed; head in TL about 6–7 times; snout conical, protruding well beyond mouth, with stout tubercles at tip and lateral angles; suborbital ridge sharp and beset with stout modified scales; underside of head mostly scaled except for broad naked median swath on underside of snout; body scales densely covered with recumbent narrowly triangular to lanceolate spinules. Long spinous ray of 1D about 70–100% HL, serrations strong, sharp, widely spaced. Anterior dermal window of light organ small, situated between inner V-fin bases; anus about midway between V and A. Color overall dark brown, abdominal region bluish to black; gill cover, gill membranes black; mouth dusky; fins dark dusky to black. Attains at least 380 mm TL.

**Distribution**.— Broadly distributed from east-central Japan and East China Sea to South China Sea off Taiwan and the Philippines; recorded depth range 355–1100 m. The sw. Taiwan specimen was taken in 227–335 m; the ne. Taiwan specimen in 488–1027 m, and the SCS specimen in 1098 m.

**Remarks**.— The 133 mm specimen listed in the table in Gilbert and Hubbs (1916:202) as *N. proxima* from *Albatross* sta. 4918 is deposited at CAS [cat. no. CAS-SU 22941]; we have determined that it represents *N. spinosa*, a species that is closely similar to *N. proxima* and with which it has been mistaken in the past. However, the underside of head of *N. spinosa* is almost wholly naked, compared with only the median portion of snout in front of the mouth naked in *N. proxima*. The spinous 1D ray is also longer in *N. spinosa*, the scale spinules needle-like and not flattened (viz., not lanceolate or spear-shaped), and the outer premaxillary dentition is larger than in *N. proxima*.

FIGURE 19. *Nezurnia proxima* (Smith and Radcliffe, 1912), ASIZP 66187, 163+ mm TL, fresh (A) and preserved (B).

### *Nezumia spinosa* (Gilbert and Hubbs, 1916)

Figures 20A–B.

*Lionurus spinosus* Gilbert and Hubbs, 1916:199–200, pl. 10, fig.2 (holotype, USNM 76868, East China Sea off Japan, 427 fm [781 m]).— Gilbert and Hubbs 1920:554 (4 spec., off Luzon, Philippines).— Okamura, 1970:94 (in part; in synonymy of *Nezumia proximus*).

*Nezumia spinosa*: Okamura *in* Masuda et al., 1984:95, pl. 345–A (compiled).— Iwamoto, 1990:254, fig. 582 (in key).— Iwamoto and Anderson, 1994:18–19 (22 spec., 26.3–44.2 HL; 117–255 mm TL, s. Africa and Mozambique, 560–1000 m).— Iwamoto and Merrett, 1997:542–545, fig. 29b (8 spec., 20–54.2 HL, 133–319 TL; sw. Pacific, Japan, South China Sea, 660–900 m).— Iwamoto and Williams, 1999: 202–204, fig. 43b (8 spec., 33.3–51.1 HL, 140–260+ TL, Western Australia, 420–853 m).— Merrett and Iwamoto, 2000:772–773 (1 spec., 45 HL, 250+ TL; Norfolk Ridge [sw. Pacific], 640–740 m).— Shao et al., 2008: table 2 (3 spec., Taiwan [SWT, SCS], 316–720 m; first record from Taiwan).

**MATERIAL EXAMINED** (6 spec.).— **SWT:** ASIZP 65545 (1, 170 TL), CD 137, 316–477 m; ASIZP 67586 (2, 105+-160+TL), CP 338, 569 m; ASIZP 67591 (1, 34 HL, 159+ TL); CP 338, 569 m. **SCS:** ASIZP 66747 (1, 216+ TL), CD 320, 731 m; ASIZP 66817(1, 127+ TL), CP 315, 509 m.

**DISTINGUISHING FEATURES**.— 1D II,9–10 (rarely 8 or 12); P i18–i22; V 8–9; inner GR-I 9–12 total; scale rows below midbase 1D 6.5–9, below 2D 7.5–11; lateral line scales over distance equal to predorsal length 35–42; pyl. caeca 15–16 (13–14 fide Iwamoto and Anderson 1994:18). Snout

FIGURE 20. *Nezumia spinosa* (Gilbert and Hubbs, 1916). A. ASIZP 67586, 105 mm TL, fresh. B. ASIZP66817, 127+ mm TL, preserved.

length 28–32% HL; preoral length 18–29%; interorbital 18–24%; orbit 29–31%; orbit to preopercle 34–40%; suborbital 12–14%; upper jaw 27–33%; barbel 9–18%. Body relatively slender, compressed; head about 5–6 in TL; snout conical, protruding well beyond mouth, with stout tubercles at tip and lateral angles; suborbital ridge sharp and beset with stout modified scales; underside of head almost completely naked, with large pores; body scales densely covered with long, needle-like spinules in parallel to convergent rows. Long spinous ray of 1D 96–156% HL, serrations widely spaced. Anterior dermal window of light organ prominent, situated between V-fin bases. Color overall light brown, blackish over abdomen; gill cover, gill membranes dark; mouth and gill cavities black; 1D blackish proximally, pale to whitish distally, V black, P and A dusky. Attains about 320 mm TL.

**DISTRIBUTION**.— A widespread Indo-Pacific species; s. Japan through Philippines, Indonesia, s. to New Caledonia region, w. coast of Australia, and s. Africa, in 316–1000 m. Our Taiwan specimens were taken in 316–731 m.

**REMARKS**.— Shao et al. (2008) first recorded the species from Taiwan based on the current specimens.

### *Nezumia* cf. *coheni* [*sensu* Iwamoto and Merrett, 1997]

Figure 21A–C.

*Nezumia coheni* (not of Iwamoto and Merrett, 1997): Shao et al., 2008: table 2 (3 spec., SWT, 1305 m; first record from Taiwan).

**MATERIAL EXAMINED** (3 spec.).— **SWT:** ASIZP 63791 (3, 290+-333+ TL), CD 192, 1305 m.

**DISTINGUISHING FEATURES**.— 1D II,9–11; P i19–i21; V9–10; GR-I (inner) 2+7, total GR-II (outer /inner) 8–9 / 9–10; scale rows below 2D origin 7.0–8.5, under midbase of 1D 6.5; lateral-line scales over distance equal to predorsal length 33–35. Snout conical with smoothly rounded dorsal and ventral profiles, length 31–33% HL, interorbital flat, its width 22–24%, orbit 27–32%, suborbital almost vertical, gently rounded, depth 17–19%; upper jaw 33–35%; barbel 15–20%; outer gill slit 12–16%; pre-A length 165–186%; outer V to A origin 44–50%; body depth about

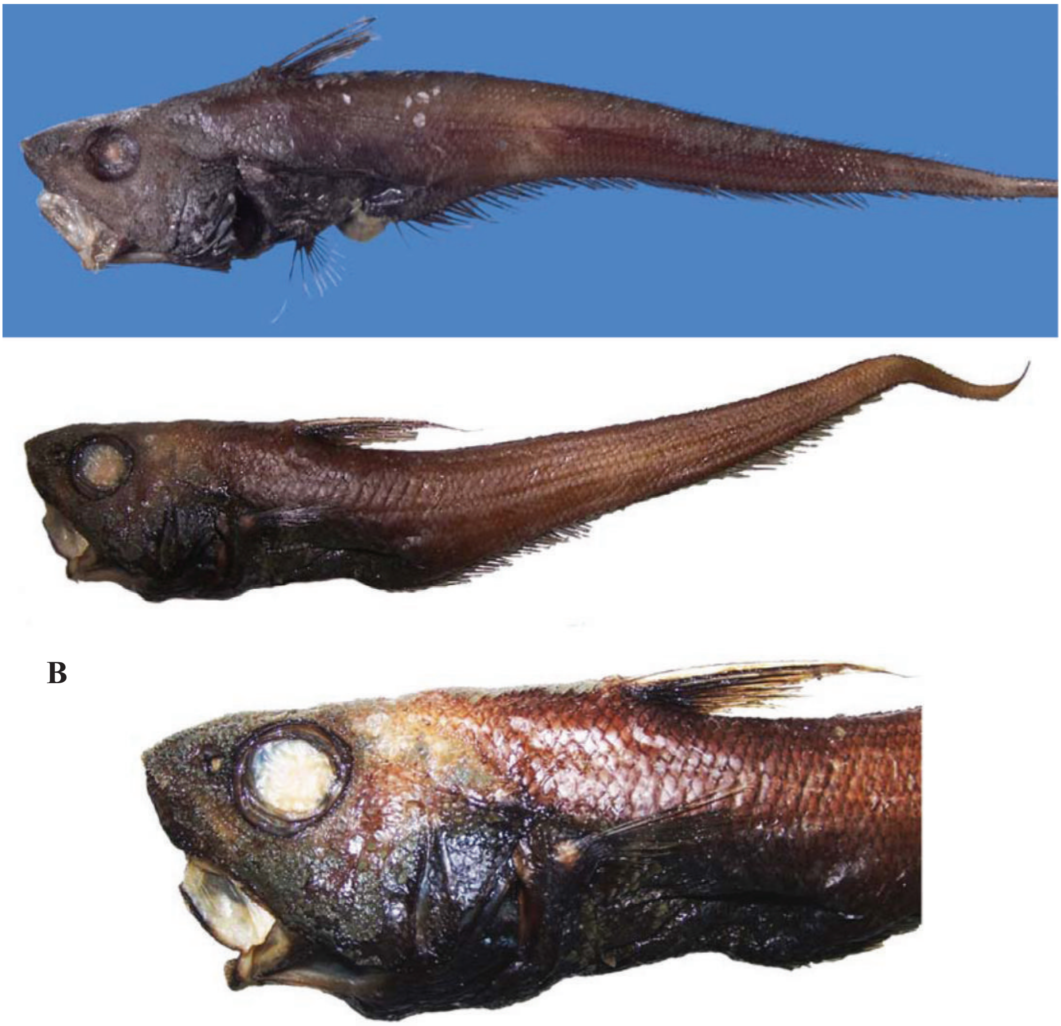

FIGURE 21. *Nezumia* cf. *coheni*. A. ASIZP 63791, 1 of 3, 333+ mm TL, fresh. B-C. ASIZP 63791, 1 of 3, 290+ mm TK. B. lateral view. C. lateral view of left head.

77–92%; 1D-2D interspace 38–52%; height 1D 94–98%; length 1D base 24–30%; length P 51–61%; length outer V 49–54%. Underside of snout mostly naked; underside of head becoming increasingly covered with scales ventrally and posteriorly from about vertical through nasal fossa; pores and sensory papillae of cephalic lateralis system densely arrayed on underside of head, especially under snout and mandibles, producing a roughened surface texture; scales densely covered with broadly lanceolate spinules. All fins dark, blackish; dermal window of light organ relatively small and located between inner margins of V bases. Color in alcohol overall dark brownish; abdomen, gill covers, and gill membranes blackish; mouth dark but somewhat pale along outer margins; gums pale. Attains at least 333 mm TL.

**DISTRIBUTION**.— Known from the South China Sea off the sw. coast of Taiwan in 1305 m.

**REMARKS**.— Shao et al. (2008) first recorded these specimens as *Nezumia coheni* Iwamoto and Merrett, 1997, but on closer examination, certain character disparities suggested that the Taiwan specimens may represent a different species. The pelvic fin-ray count of 9 or 10 contrasts with the usually 11 (rarely 9 or 10) of *N. coheni.* Certain proportional measurements differed slightly: suborbital depth 17–19% HL cf. 15–16% in *N. coheni*; preanal length 165–186% cf 143–166%; and barbel length into orbit diameter 1.3–1.6 times cf. 1.6–2.0 times. The spinules on body scales also have rather broadly convex tips in the Taiwan specimens compared with the more attenuated and sharp tips of *N. coheni.* Although the three Taiwan specimens are in excellent condition, they were all collected together and are all of relatively the same size and likely do not show the range of variation in the species. The similarities in most features suggest a close relationship between *N. coheni* and these Taiwan specimens, if indeed they are different. We must await collection and study of more specimens of different sizes to confirm or reject the notion of their being different species.

### Genus *Pseudocetonurus* Sazonov and Shcherbachev, 1982

*Pseudocetonurus* Sazonov and Shcherbachev, 1982:5–6 (type species *Pseudocetonurus septifer* Sazonov and Shcherbachev, 1982 by monotypy).

**Distinguishing features**.— BR 7; V 9 or 10, rarely 8; inner GR-I 13–18 total; pyl. caeca 22–34. Head enlarged, notably broad and deep, preopercle and suborbital bones deep and large; orbit small in adults, proportionally larger in young, diameter 19–31% HL; interorbital width 33–44% HL. Snout high, bluntly pointed, little protruding beyond mouth; mouth large, upper jaw 41–49% HL; chin barbel small, 7–10%; gill opening wide, extending ventrally to below end of maxilla. Spinous ray of 1D smooth proximally, finely serrated distally; abdominal area short, periproct between V and A, closer to V bases. Light organ developed: a small round dermal window between V bases. Head fully scaled except for gular and gill membranes; small, awl-shaped spinules on body scales, no reticulations on anterior field; grooved lateral line scales over trunk present or absent. Teeth small, in narrow band on premaxillary, in single series in dentary. Ground color black to dark brown overall.

**Remarks**.— This genus is closely similar to *Ventrifossa* and would likely be categorized in that taxon except for its very dark color, greatly expanded head, and commensurately expanded bones of the opercular series. Only the single species known.

### *Pseudocetonurus* cf. *septifer* [*sensu* Sazonov and Shcherbachev, 1982]

*Pseudocetonurus septifer*: Chiou et al., 2004b:46, fig. 17 (1 spec., ASIZP 61237, 147 mm TL; Da-xi, Taiwan [NET]).— Shao et al., 2008: table 2 (3 spec., Taiwan [NET]).

**Material examined** (1 spec.).— **NET**: ASIZP 61237 (1, 147 TL), Da-xi.

**Distinguishing features**.— 1D II,8–12, usually 9 or 10**;** P i16–i20; GR-I (outer/inner) 7–12/13–18, GR-II 14–18/14–17. Snout length 25–34% HL; preoral length 19–27%; postorbital 47–59%; orbit to preopercle 53–64%; suborbital 19–26%; outer gill slit 23–31; body depth 75–95; V-A 12–38%; height 1D 52–66%; length V 41–63%. Head about 5.0–5.5 in TL; greatest width about 1.5 into greatest depth; interorbital about 2.3–3.0 into HL; suborbital deep, almost vertical and lacking modified scutelike scales; Mouth large, upper jaw extends to below midorbit. Barbel almost rudimentary, <0.5 orbit. Sensory canals of head greatly expanded, but sensory pores small; free neuromasts poorly developed. Grooved lateral line present.

**Distributions**.— So far known only from the nw. Pacific off Taiwan.

**Remarks**.— Based on the presence of a grooved lateral line, this specimen is probably an undescribed species. The only other member of the genus, *P. septifer* Sazonov and Shcherbachev, 1982, known from the Saly-Gomez and Nazca ridges in the southeastern Pacific and off Hawaii, lacks a grooved lateral line.The Taiwan species was first recorded as *P. septifer* by Chiou et al. (2004b) and subsequently by Shao et al. (2008).

## Genus *Pseudonezumia* Okamura, 1970

*Pseudonezumia* Okamura, 1970:38–39 (type-species *Pseudonezumia japonicus* Okamura, 1970 by original designation).

*Paracetonurus* Marshall, 1973:615–616 (type-species *Macrourus parvipes* Smith and Radcliffe, 1912 by original designation).

**Distinguishing features.**— BR 7 or 8; V 6, rarely 5 or 7, situated below posterior end of head; P 16–18; anus slightly removed from A; head much deeper than wide (*P. japonica*) to relatively broad and deep (other spp.); sensory canals expanded, well developed; head and body almost fully scaled; body scales small, exposed field with erect awl-shaped spinules in subparallel to slightly divergent rows, reticulations on scales; suborbital ridge without modified scales; snout broad, tip and lateral angles lacking tubercles; teeth in narrow bands, somewhat enlarged in outer premaxillary and inner dentary series. No apparent light organ developed.

**Remarks.**— We are treating the genus *Paracetonurus* Marshall, 1973 as a synonym, although this has not been adequately confirmed. Sazonov and Shcherbachev (1982:11) provided a good diagnosis and discussion of relationships of the genus (as *Paracetonurus*); they listed four species as belonging to the genus, including *P. flagellicauda* (Koefoed, 1927), *P. parvipes* (Smith and Radcliffe, 1912), and *P. cetonuropsis* (Gilbert and Hubbs, 1916), and their new one *P. pusillus*, but not *P. japonica* Okamura, 1970. Of the five species, only one is known from Taiwan.

### *Pseudonezumia pusilla* (Sazonov and Shcherbachev, 1982)

Figures 22A–B.

*Paracetonurus pusillus* Sazonov and Shcherbachev, 1982:12–14, fig. 4 (holotype, ZMMU P.15306, Indian Ocean, Ninety-East Ridge, 11°24.3′S, 88°50′E, 1500–1600 m; 17 paratypes, Indian Ocean and w. Pacific off New Guinea; 1380–2000 m)

*Paracetonurus cetonuropsis* (non Gilbert and Hubbs, 1916): Shao et al., 2008: table 2 (3 spec., Taiwan [SCS], 1098 m).

*Pseudonezumia pusilla*: Iwamoto and Williams, 1999:208–209, fig. 45 (1 spec., off Western Australia, w. of NW Cape; 1460–1500 m).

**Material examined** (5 spec.).— **SCS:** ASIZP 66945 (3, 137–163 TL) and ASIZP66424 (1, 234 TL), CD 322, 1098 m. **Other material**: CAS 224176 (1, 28.6 HL; 175+ TL), SCS, off Vietnam, 15°38′N, 111°54′E; *MV Stranger*, NAGA Exped., sta. 60–67, GVF Reg. no. 2083, 28 Feb. 1960.

**Distinguishing features.**— 1D II,8–9; P 17–18; V 6 or rarely 7; total GR-I (outer/inner) 10–12/10–11; GR-II 10–12/10–11; pyl. caeca 7–12. Snout length 29–32% HL; preoral length 21–22%; internasal width 23–26%; interorbital 30–33%; orbit 29–31%; posterior nostril 12–16%, 2.2–2.7 times into orbit; suborbital 14–18%; postorbital 41–46%; orbit to preop. 35–42%; upper jaw 34–40%; barbel 12–20%; outer gill-slit 12–20%; pre-A 122–138%; isth. to A 57–72%; outer V to A 35–52%; 1D-2D 22–46%; length base 1D 21–29%. Head relatively compressed, deeper than wide; snout pointed, rather broad, internasal width about ¼ HL; interorbital ⅓ HL, slightly greater than orbit diameter; suborbital about half orbit; barbel relatively long, slender. Margin of preopercle broadly rounded, almost vertical posteriorly, preopercle ridge rounded at angle. Origin of V under posterior margin of preopercle; vent slightly removed from origin of A, under anterior ¼ of 1D. Posterior end of upper jaw below mid-orbit. Scale spinules 2–9, awl-shaped, erect to slightly reclined. Periproct small, slightly removed from A origin. Paired fins small, weak; 1D spine with weak, widely spaced denticles. (In part from Sazonov and Shcherbachev 1982:12–13.)

**Distribution.**— Known from the holotype and 17 paratypes taken in the Indian Ocean and

FIGURE 22. *Pseudonezumia pusilla* (Sazonov, and Shcherbachev, 1982). ASIZP66424, 234 mm TL. A. fresh. B. lateral view of left head, preserved.

w. Pacific off New Guinea (Bismark Sea); one specimen from off the NW Cape of Australia; and the current Taiwan specimens from the South China Sea, which extend the range of the species into the w. North Pacific. Depth range 1098–2000 m; the Taiwan specimens represent the shallowest recorded at 1098 m.

**REMARKS**.— Shao et al. (2008: table 2) first recorded the Taiwan specimens as *Pseudonezumia cetonuropsis,* a species known only from the holotype and small paratype taken off central Japan. That species differs from *P. pusilla* in having a much shorter barbel (6% HL), longer snout (35%), and smaller orbit (27%).

### Genus *Sphagemacrurus* Fowler, 1925

**DISTINGUISHING FEATURES**.— BR 7; ventral region of short head and short trunk shifted forward, gill membranes united under orbit, V usually under opercle, anus under origin of 1D, A origin under hind margin of 1D; snout blunt, high, tip of snout with small, spiny tubercle, on level with upper margin of pupil, naked areas, if present, confined to lower surfaces; jaws oblique; 1D spine with saw-tooth serrations on leading edge, 1D base somewhat elevated; naked periproct region broad, occupying ⅓ or more of space between V and A, usually immediately before A origin; inner GR-I 15 or fewer; length barbel 1.7 to > 2.0 into orbit diameter. A well-developed suborbital shelf composed of two parallel rows of stout, spiny, modified scales. Body scales with 5–9 subparallel rows of short, awl-shaped, slightly reclined spinules.

**REMARKS**.— A small genus of six species, two of which are recorded from Taiwan. Iwamoto and Williams (1999:211–212) noted differences in recorded values and features of specimens identified as *S. pumiliceps* from the Indian and Pacific oceans and stated that there are unresolved problems with the species in the genus. There is overlap in many characters between the *Sphagemacrurus* specimens we have examined, making identification difficult. The genus is in need of further study.

### Key to the Species of *Sphagemacrurus* in Taiwan

1a. Rays of V 11–14; inner GR-I 8–11; barbel length 15–24% HL; interorbital width 23–28%. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. pumiliceps*

1b. Rays of V 9–11; inner GR-I 11–13; barbel length 13–16% HL; interorbital width 28–32% . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. richardi*

### *Sphagemacrurus pumiliceps* (Alcock 1894)

Figures 23A–B.

*Macrurus pumiliceps* Alcock 1894:125 (Laccadive Sea; 1,315 m).

*Lionurus pumiliceps*: Gilbert and Hubbs, 1920:559, 560 (Philippine and East Indies, 732–1646 m).

*Sphagemacrurus pumiliceps*: Iwamoto, 1990:288 (in key).— Iwamoto and Merrett, 1997:549 (28 spec., sw. Pacific).— Iwamoto and Williams, 1999:210 (descr., 4 spec., Western Australia, 882–1880 m).— Merrett and Iwamoto, 2000:773 (24 spec., sw. Pacific).— Iwamoto et al., 2004:199 (1 spec., Walters Shoals, sw. Indian Ocean, 1310–1265 m).— Shao et al., 2008: table 2 (listed; Taiwan [ET, SCS], 736–1188 m).

**Material examined** (6 spec.).— **NET:** ASIZP 65551 (1, 36.9 HL, 265+ TL), CD 199, 1134–1188 m. **SCS:** ASIZP 65558 (1, 26.6 HL, 140+ TL), CD 134, 736–1040 m; ASIZP 66905 (3, 23.8–29.0 HL, 112+-202+ TL), CD 322, 1098 m.

**Distinguishing features.**— 1D II,10–11; P i20–i23; V 11–14; inner GR-I 8–11 total; scale rows below 2D 7–10; pyl. caeca 10–12. Snout length 29–37% HL; interorbital 23–27%; orbit 31–37%; suborbital 18–21%; postorbital 40–44%; orbit-preopercle 36–43; upper jaw 36–39%; barbel 17–20%. Body relatively deep, about equal to HL; head about 7.5 in TL [all our specimens have a broken tail]; mouth rather small, upper jaw extends posteriorly to under midorbit; barbel well developed, about half diameter of orbit; underside of head mostly scaled except ventrally on snout and suborbital margin; body scales with short fine spinules arranged in about 5–8 parallel rows. Outer ray of V slightly prolonged, its tip extending to A origin or substantially beyond (to as far as 10th A ray). Periproct broad, abutting A origin posteriorly, spanning about ⅔ distance between V and A. Attains about 27 cm TL. (Data from Taiwan specimens only.)

**Distribution.**— Widely distributed in the w. Pacific from se. Australia to Taiwan, in 732–1880 m; also found through most of Indian Ocean, where species was originally described. The ASIZ specimens, captured in 736–1188 m off Taiwan, were the first recorded from the area (Shao et al., 2008) and extend the range to n. of the Philippines.

**Remarks.**— The reportedly wide distribution of this species and the variation in certain features found by Iwamoto and Williams (2001:211–212) suggest that more than one species may be currently recognized under this name.

### *Sphagemacrurus richardi* (Weber, 1913)

Figures 24A–B.

*Macrurus richardi* Weber, 1913:154 (28 syntypes: FMNH 52442 ex cm 700 [1 spec.] Flores Sea; MOM 0091–1766 [1, disintegrated]; ZMA 110456 [1], 110447–49 [18, 1, 3], 110464 [1]; Makassar Strait; Celebes [Sulawesi] Sea; Ceram Sea; Flores Sea; *Siboga* sta. 85, 122, 170, 314, and 316; 538–1260 m).

FIGURE 23. *Sphagemacrurus pumiliceps* (Alcock, 1894). A. ASIZP 66905, 198 mm TL, fresh. B. ASIZP 65551, 265+ mm TL, preserved.

*Sphagemacrurus richardi*: Iwamoto, 1990:288, fig. 658 (in key).— Iwamoto and Williams, 1999:212 (mentioned).— Iwamoto and Graham, 2001:493 (56 spec., se. Australia; 880–1100m).

**MATERIAL EXAMINED** (6 spec.).— **SCS:** ASIZP 65621 (1, 29.3 HL, 176 TL), CD 203; ASIZP 66087 (1, 32.7 HL, 165+ TL), CD 320; ASIZP 66184 (1, 35.5 HL, 186+ TL), CD 320; ASIZP 66192 (1, 32.9 HL, 176 TL), CD 320; ASIZP 66910 (1, 34.5 HL, 190+ TL), CD 321; ASIZP 66944 (1, 127 TL), CD 321.

**DISTINGUISHING FEATURES**.— 1D II,9–10; P i19–i21; V 10–11(12); inner GR-I 11–14 total; scale rows below 2D 8–9; pyl. caeca about 10. Snout length 35–37% HL; interorbital 30–34%; orbit 28–34%; suborbital 19–21%; postorbital 40–43%; orbit-preopercle 40–41%; upper jaw 37–39%; barbel 13–16%. Body relatively deep, about equal to HL; head about 5.3–6.0 in TL; mouth rather small, upper jaw extends posteriorly to under midorbit; barbel well developed, about half orbit diameter; underside of head mostly scaled except ventrally on snout and suborbital margin; body scales with short fine spinules arranged in about 7–9 parallel rows. Outer ray of V slightly prolonged, its tip extending to or somewhat beyond A origin. Periproct broad, abutting A origin posteriorly, spanning about ⅔ distance between V and A; anus closer to A than to outer base of V. Attains about 23 cm TL. (Data from Taiwan specimens only.)

**DISTRIBUTION**.— The ASIZ specimens captured in 634–954 m off Taiwan were the first recorded from the area (Shao et al. 2008) and extend the range to northward from Indonesia where it was first described.

**REMARKS**.— Our specimens represent the first record for Taiwan. In his original description of the species, Weber (1913) gave 8 as the count of V rays, but one of the current author's (TI) examination of what was probably the illustrated syntype (ZMA 110.456) had 10 rays in each fin. No other specimen of the species that we know of had such a low count, and we suspect it to be erroneous. *Sphagemacrurus decimalis* (Gilbert and Hubbs, 1920) has a low V count of 10, similar to *S. richardi*, but it differs in a number of morphometric features (as enumerated in the original description), including a somewhat lower count of rakers on the lower limb of GR-I (7 cf. 9–12); shorter snout (26–28% HL cf. 35–37%); shorter upper jaw (28–29% cf. 40–41%; shorter orbit-pre-

FIGURE 24. *Sphagemacrurus richardi* (Weber, 1913). A. ASIZP 66910, 190+ mm TL, fresh. B. ASIZP 65621, 176 mm TL, preserved, photo reversed laterally.

opercle distance 33–34% cf. 40–41%; and shorter barbel (9–11% cf. 13–16%). *Sphagemacrurus richardi* differs from *S. pumiliceps* in having slightly fewer V rays (10–11, rarely 12, vs. 11–14), shorter barbel (13–16% vs. 16–21%), and somewhat wider interorbital (30–34% vs. 24–28%) (*S. pumiliceps* data from Iwamoto and Graham 2001:493).

## Genus *Spicomacrurus* Okamura, 1970

**DISTINGUISHING FEATURES**.— Snout low, pointed and slightly protruding, median and lateral processes of nasal bone forming broad horizontal plates; head about as broad as high; body and head cylindrical; head mucous canals moderately developed; head covering mostly transparent; light organ long, small lens on chest anterior to pelvic-fin bases connected by a black streak to elongated posterior lens immediately before anus; ventral striae well developed; inner GR-I, lower limb, 10–12; spinous ray of 1D completely smooth; chin barbel present; gular region with netlike epidermal cover; outer pelvic ray with narrow membranous flange that is somewhat expanded distally near tip.

**REMARKS**.— *Spicomacrurus* was originally treated as a subgenus of *Hymenogadus*, but Iwamoto et al. (2011) elevated the subgenus to full generic status. Although obviously related to members of the genera *Hymenocephalus* and *Hymenogadus,* the four species of *Spicomacrurus* are readily differentiated from them by the broad horizontal plates of their nasal bones, elongated posterior lens of the light organ, netlike gular covering, and membranous flange of the outer pelvic fin ray. *Spicomacrurus kuronumai* is the only member of the genus found in Taiwan.

### *Spicomacrurus kuronumai* (Kamohara, 1938 )

*Hymenocephalus kuronumai* Kamohara, 1938:70, fig. 40 (Mimase, Kochi Pref., Japan; neotype: BSKU 4333, invalid according to ICZN).— Shao et al., 2008: table 2 (1 spec., NET, 100–650 m; first record from Taiwan).

*Hymenogadus* (*Spicomacrurus*) *kuronumai*: Okamura, 1970:64–67, pl. III, text-figs. 25, 26–28 (79 spec., 143–200 mm TL; Pacific coast of s. Japan, in about 350–450 m).

*Hymenogadus kuronumai*: Okamura *in* Masuda et al., 1984:94, pl. 80–I (compiled). Okamura *in* Okamura and Kitajima, 1984:203, 359, fig. 144 (p.202) (3 spec., 135–194 mm TL, Okinawa Trough [East China Sea], 400–510 m.

*Spicomacrurus kuronumai*: Iwamoto et al., 2011:513–530, fig. 1A–C (subgenus elevated to genus).

**MATERIAL EXAMINED** (2 spec.).— **NET:** ASIZP 65232 (1, 165 TL), Da-xi. ASIZP 70247 (1, 97 TL), Da-xi.

**DISTINGUISHING FEATURES**.— 1D II 9–12; P i18–i22; V 8; inner GR-I 12–15 total; pyl. caeca 11–18. Snout depressed, nasal bones developed into three horizontal platelike processes; body subcylindrical; outer V ray produced and expanded distally. Attains 240 mm TL.

**DISTRIBUTION**.— Pacific coast of s. Japan, and ne. Taiwan. in 350–650 m.

**REMARKS**.— Shao et al., (2008: table 2) first recorded the species from Taiwan based on ASIZP 65232. The species is apparently relatively abundant off Japan, as suggested by the 95 specimens (143–211 mm TL) recorded by Okamura (1970b:4, table 1), who treated it as a subgenus of *Hymenogadus*. Kamohara (1961) designated a neotype for the species but not in a revisory work, which renders the designation invalid (*fide* Eschmeyer 1998:852).

## Genus *Trachonurus* Günther, 1887

**DISTINGUISHING FEATURES**.— BR 7; origin of V well behind P base and under posterior one-quarter of 1D base; V-A distance short, less than orbit diameter; broad periproct region spanning most of distance between V and A; second spinous ray of 1D smooth, rounded in cross-section, slightly longer than adjacent segmented ray; head smoothly rounded, without sharp ridges, almost fully scaled; scale patches usually present on branchiostegals; chin barbel short; body scales strongly adherent, with short, conical, relatively erect spinules; V 6 or 7; color uniformly gray to dark brownish black, fins dark, usually black.

**REMARKS**.— At least six species, two of which are found off Taiwan. The species in this genus are closely similar and differences between them are difficult to find. The widespread distributions reported for certain species (especially *T. villosus* and *T. sentipellis*) beg closer scrutiny.

### Key to the Species of *Trachonurus* in Taiwan

1a. Body scales relatively large and coarsely spinulated; 8 or 9 scale rows between V base and gill cover . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *T. sentipellis*

1b. Body scales smaller, finer spinulated; about 10–14 scale rows between V base and gill cover . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *T. villosus*

### *Trachonurus sentipellis* Gilbert and Cramer, 1897

Figures 25A–C.

*Trachonurus sentipellis* Gilbert and Cramer, 1897:429 (syntypes SU 3140 and USNM 51689; Hawaiian Is., 21°12′00″N, 157°38′30″W, *Albatross* sta. 3474, 375 fm [686 m]).— Iwamoto, 1997:945.— Iwamoto and Merrett, 1997:551.— Iwamoto and Williams, 1999:213 (descr., w. and se. Australia).— Merrett and Iwamoto, 2000:775 (6 spec., New Caledonia, 764–1,050 m).— Iwamoto and Graham, 2001:495 (3 spec., se Australia, 940–1130 m).— Shao et al., 2008: table 2 (7 spec., Taiwan [SWT, SCS], 441–1040 m).

**Material examined** (10 spec.).— **SWT:** ASIZP 64232 (2, 54.6–61.0 HL, 265+-295+ TL), CD 193, 821 m; ASIZP 65539 (1, 59.9 HL, 305 TL), CD 134, 736–1040 m; ASIZP 65543 (1, 150 TL), CD 138, 441 m; ASIZP 65544 (1, 175 TL) and ASIZP 65548 (1, 135 TL), CD 203, 634–866 m; ASIZP 65637 (1, 310+ TL), CD 229, 880–1062 m. **SCS**: ASIZP 66150 (1, 49 HL, 250+ TL), CD 321, 954 m; ASIZP 66743 (2, 21–32 HL, 105+-170+ TL), CD 320, 731 m.

**Distinguishing features.**— 1D II,6–8; P 15–16 (rarely 18); V 7; total GR-I (inner) 11–13; scale rows below origin 2D usually 6–7, below midbase 1D 5–7; lateral line scales over distance equal to pre-1D length 26–34; scale rows between V base and gill cover 8–9; pyl. caeca 9–13, short, thick. Snout length 23–26% HL; interorbital width 26–33%; orbit diameter 27–37%; suborbital width 8–12; postorbital length 38–53%; orbit-preopercle 26–33; upper jaw 28–37%; barbel 8–11%; 1D-2D interspace 11–29%. Grooved lateral line present; body scales relatively large, coarsely covered with stout, erect spinules. Jaw teeth all small. Attains more than 31 cm TL. (Adapted from Iwamoto 1997.)

**Distribution.**— Hawaii, Australia, New Caledonia, and Taiwan in 441–1130 m. Specimens from Taiwan were all taken from the South China Sea in 441–1040 m; they represent the first record of the species from the w. North Pacific.

**Remarks.**— *Trachonurus sentipellis* is closely similar to *T. robinsi* Iwamoto, 1997 from the Philippines, but that species shows differences in some meristic values: P rays 10–14 vs. 15–16; inner GR-I 9–11 vs. 11–13; scales below 2D origin 4–6 vs. 5–8 (usually 6–7). Also, where *T. sentipellis* almost invariably has V 7, in *T. robinsi* the count is more often 6 than 7, and the maximum size in *T. robinsi* probably does not exceed 25 cm, whereas *T. sentipellis* exceeds 31 cm.

### *Trachonurus villosus* (Günther, 1877)

Figure 26.

*Coryphaenoides villosus* Günther, 1877:441 (holotype BMNH 1887.12.7.105; s. of Tokyo, Japan).— Günther, 1887:142 (second specimen BMNH 1887.12.7.106 [non-type] from s. of the Philippines added).

*Trachonurus villosus*: Okamura *in* Masuda et al., 1984:95 (compiled).— Okamura *in* Amaoka et al., 1990:193.— Iwamoto, 1997:944–947 (comparison with T. robinsi).— Iwamoto and Williams, 1999:212 (mentioned).— Shao et al., 2008: table 2 (5 spec.; Taiwan [SCS], 634–954 m).

**Material examined** (4 spec.).— **SWT:** ASIZP 65626 (2, 175–255+ TL), CD 203, 634–866 m. **SCS**: ASIZP 66094 (1, 60 HL, 345+ TL) and ASIZP 66909 (1, 155+ TL), CD 321, 954 m.

**Distinguishing features.**— 1D II,8; P 14–17; V 7; total GR-I (inner) 9–13; scale rows below origin 2D 5–9, usually 6–7, below midbase 1D 5–7; lateral line scales over distance equal to pre-1D length 26–34; scale rows between base of V and gill cover 10–14; pyl. caeca 9–13, short, thick. Grooved lateral line present; body scales relatively small, finely covered with erect spinules. Jaw teeth all small. Snout length 23–27% HL; interorbital width 31–34%; orbit diameter 29–30%; suborbital width 11–12%; postorbital length 38–42%; orbit-preopercle 29–33%; upper jaw 30–33%; barbel 6+–11%; 1D-2D interspace 20–22%. (Adapted from Iwamoto 1997.)

**Distribution.**— Known from Japan to Taiwan and the Philippines. In Taiwan, specimens were taken from the South China Sea in 634–954 m.

**Remarks.**— More specimens of this species must be examined from near the type locality off Japan to properly circumscribe the species and determine its difference from other described species.

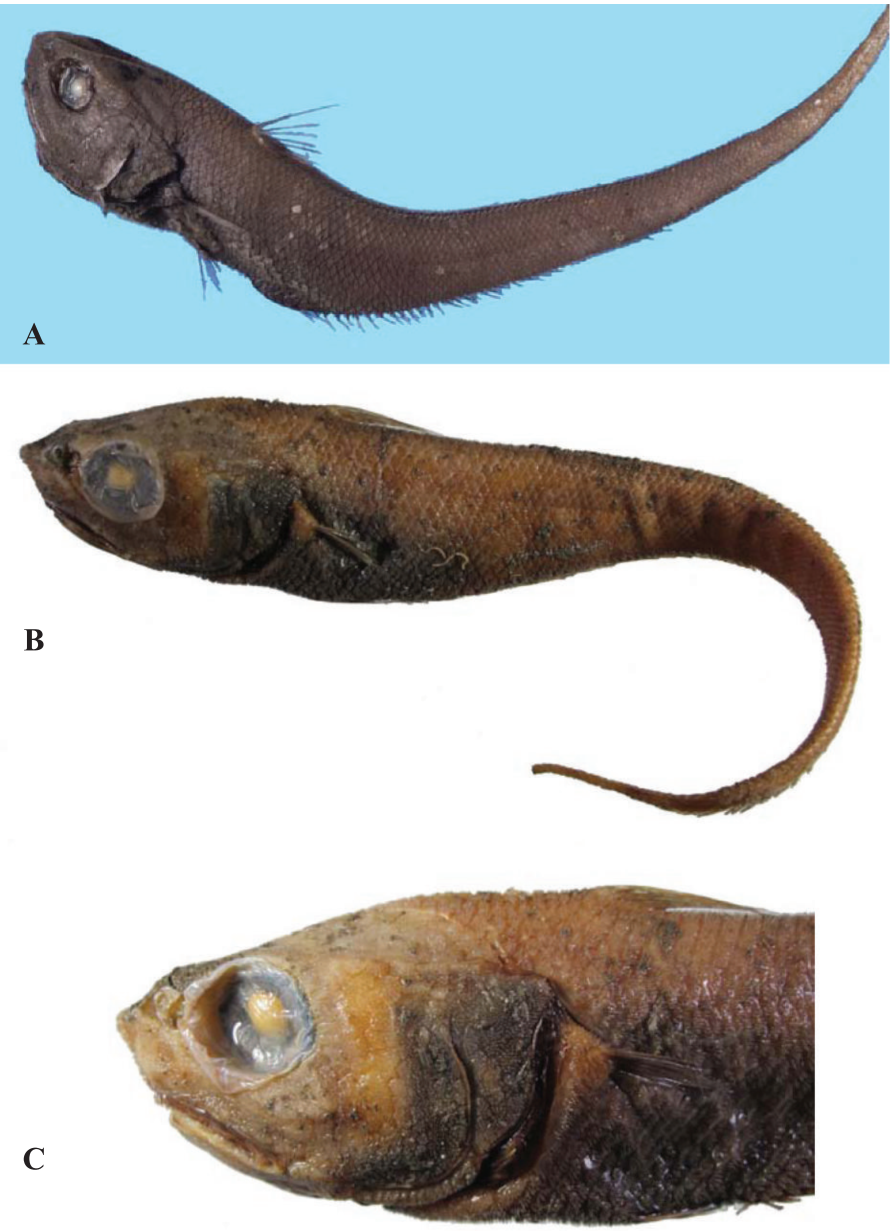

FIGURE 25. *Trachonurus sentipellis* Gilbert and Cramer, 1897. A. ASIZP 64232, 295+ mm TL. B. ASIZP 65539, 305 mm TL. C. ASIZP 65539, lateral view of right head, photo reversed laterally.

## Genus *Ventrifossa* Gilbert and Hubbs, 1920

**DISTINGUISHING FEATURES.**— BR 7. Head and body relatively compressed; gill membranes narrowly united over isthmus and under midorbit; snout blunt to pointed and moderately protruding beyond mouth; tubercular scale lacking on snout tip except in *V. misakia;* no thickened modified scales on suborbital region; head uniformly and fully scaled except gular and BR membranes;

FIGURE 26. *Trachonurus villosus* (Günther, 1877). ASIZP 66909, 155+ mm TL. A. fresh. B. lateral view, preserved. C. dorsal view of head.

upper jaws generally more than 40% HL (35–42% in *V. misakia*), beset with long band of small teeth, outer series slightly enlarged; teeth on lower jaw all small, in one or two series to long narrow band; chin barbel usually well developed. Second spinous 1D ray smooth or finely serrated; V 8–10; no fin with greatly prolonged rays. Inner series GR-I 14–20 total. Periproct oval to teardrop shaped, connected anteriorly to small dermal window of light organ lying between V bases; anus much closer to V bases than to A origin. Pyloric caeca more than 30. Color often silvery along sides; lips usually black; leading edge of snout, suborbital shelf, dorsal snout ridges, gill and gular membranes usually black or blackish. (Adapted from Iwamoto and Graham, 2001:496.)

**REMARKS.**— There are more than 25 species in this genus; nine are here recorded from Taiwan. There are likely to be other species still undiscovered, especially in Indonesia and the Indian Ocean. Because of the often fragile nature of their integument and bones, smaller individuals of the genus are often severely damaged in capture. Features distinguishing species of *Ventrifossa* are often subtle, requiring relatively intact specimens, which add to the difficulties in their identification.

## Key to the Species of *Ventrifossa* in Taiwan

1a. Second spinous ray of 1D smooth. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
1b. Second spinous ray of 1D finely serrated along leading edge . . . . . . . . . . . . . . . . . . . . . . . . 3

2a. Pectoral fin long, 1.3–1.5 into HL; no enlarged spinules on scales along 2D base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *V. macroptera*
2b. Pectoral fin moderate to short, about 1.7 into HL; scales along 2D base with enlarged spinules . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *V. sazonovi*

3a. Scales extremely small and finely spinulated, scaled surfaces almost velvety when stroked fore and aft; scale rows below 2D origin 9–10 a small tubercular scale at snout tip; suborbital shelf greatly constricted below anterior quarter of orbit . . . . . . . . . . . . . . . . . . . . . . . . . *V. misakia*
3b. Scales moderate in size with spinules of variable size, skin surface not velvety smooth; scale rows below 2D origin 5–8; no terminal snout scute; suborbital shelf not greatly constricted anteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4a. Spinules on body scales broad, short, and triangular (V 8–9, usually 8; 1D dusky to clear, without a distinct black blotch) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *V. garmani*
4b. Spinules on body scales narrowly lanceolate to conical (V 8–10; 1D dusky to blackish, some species with a black blotch) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5a. Body color uniformly brown except swarthy over abdomen (underlain by bluish) and no silvery reflections, suborbital uniformly dark brown, no black shelf; snout rather blunt in lateral view, scarcely protruding beyond mouth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *V. saikaiensis*
5b. Body color light grayish-brown dorsally, silvery along sides, suborbital with black shelf; snout moderately pointed to rather blunt and prominently to scarcely protruding beyond mouth. . 6

6a. Barbel less than 24% of HL; lateral-line scale rows 43 or less; 1D with prominent black blotch or broad midlateral streak . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
6 b. Barbel 25% or more of HL; lateral-line scale rows 45 or more; 1D uniformly dusky or with midlateral black streak . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

7a. Rays of V 9 or 10; mesial GR-I 15–17 total, lateral GR-II 14–17 total; length upper jaw usually 43–46% HL; black distal margin anteriorly on A fin . . . . . . . . . . . . . . . . *V. rhipidodorsalis*
7b. Rays of V 8 or 9; mesial GR-I 13–15 total, lateral GR-II 12–14 total; length upper jaw 40–43% HL; no black margin on A fin. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *V. nigrodorsalis*

8a. 1D usually uniformly dusky or somewhat darker proximally . . . . . . . . . . . . . . . . . *V. divergens*
8b. 1D dark or black midlaterally, distally pale or dusky . . . . . . . . . . . . . . . . . . . . *V. longibarbata*

### *Ventrifossa divergens* Gilbert and Hubbs, 1920

Figure 27.

*Ventrifossa divergens* Gilbert and Hubbs, 1920:549 (holotype, USNM 78230, Celebes Sea near Sibuko Bay, Borneo, 4°12′44″N, 118°27′44″E, *Albatross* sta. 5592, 305 fm [558 m]; 59 paratypes).— Iwamoto, 1990: 299–300, fig. 676–677 (descr.).

Material examined (21 spec.).— **SWT:** ASIZP 66928 (1, 62 HL, 320+ TL), PCP 339, 846 m; ASIZP 66255 (1, 67 TL), OCP 303, 807 m. **SCS:** ASIZP 66781 (4, 59–64 HL, 297+-330+ TL), and ASIZP 66782 (2, 58–59 HL, 275+-310+ TL), CD 320, 731 m; ASIZP 66784 (2, 41–47 HL, 205+-217+ TL), OCP 317, 515 m. **Other specimens** (all from *Albatross* Philippines Expedition of 1907–1909): **Indonesia:** USNM 78230 (holotype, 48.4 mm HL, 271 mm TL). USNM 122917 (paratypes, 3, 34.2–40.3 HL), Molucca Sea, 545 m, sta. 5621. **Philippines:** USNM 122916 (paratypes, 2, 142+-469+ TL), off ne. tip of Luzon, 410 m, sta. 5325; USNM 122919 (41.5 HL,

FIGURE 27. *Valtrifossa divergens* Gilbert and Hubbs, 1920. ASIZP 66928, 320+ mm TL, fresh. B. ASIZP 66781, 292+ mm TL, preserved, photo reserved laterally.

222 TL), off ne. Mindoro, 623 m. USNM 148988 (paratype, 53.0 HL, 281 TL), off Balayan Bay, Batangas, sw. Luzon, sta. 5116 or 5115. USNM 149361 (paratype, 24.7 HL, 140 TL), off sw. Luzon, 315 m, sta. 5289. USNM 149363 (paratype, 53.2 HL, 250 TL) and USNM 150400 (paratype, 19.5 HL, 105 TL), off sw. Luzon, 391 m, sta. 5290.

**DISTINGUISHING FEATURES** (from 11 USNM specimens, holotype data with asterisk*).— 1D II,9–11(10*); P i18–i25 (21–22*); V 8*–9; total GR-I (mesial) (12*)15–18, GR-II (lat.) 14*–15(17); scale rows below 1D 10–12, below midbase 1D (10*), below 2D 8–9* (11); lateral line scales over distance equal to predorsal length (48*). Snout length (29*) 26–31% HL; preoral length (15*) 14–19%; internasal 19*–25%; interorbital (24*) 30–37%; orbit (31*) 30–38%; suborbital (11*) 13–15%; postorbital (44*) (38) 41–47%; orbit to preopercle (45*) 40–46%; upper jaw 43*–49%; barbel (28*) 26–35%; outer gill slit (19*) 24–28%. Color in alcohol silvery on sides, brown dorsally but darker anteriorly, blackish ventrally on head and trunk; lips, lower jaw and gill membranes black; leading edge of snout blackish; mouth and gill cavity as in others of genus; 1D dusky proximally, paler distally; V dusky to black; base and axil of P black. Attains more than 47 cm TL.

**DISTRIBUTION**.— From South China Sea off Taiwan and Hong Kong; Philippines (e., n. and w. Luzon, off n. Mindoro, Sulu Sea off Panay); Celebes Sea off e. Borneo; Molucca Sea off Halmahera. Depth range about 183 to 807 m. Records of the species from s. Africa were misidentifications of a species that was subsequently described as *V. mystax* Iwamoto and Anderson, 1994.

**REMARKS**.— Chiou et al., (2004b:46, fig. 19) recorded this species from Taiwan based on two specimens, ASIZP 61309 and 61310, which we re-identified as *V. saikaiensis*. However, new specimens were collected off Taiwan at depths of 515–807 m. Based on examination (by TI) of many

USNM specimens, there may actually be more than one species represented in the type series. The holotype (USNM 78230) had several characters that appeared to be outside the normal range of other specimens. These characters include a low GR-I count of 12 total (mesial side) cf. 15–18 in others examined, narrower interorbital (24% cf. 26–32%), narrower suborbital (11% cf. 13–15%); shorter upper jaw (43% cf. 43–49%); and shorter outer gill slit (19% cf. 24–28%). Other measurements appear to be at one or another extreme in the range. The relatively sharply pointed snout and high anterior dorsal profile also differ in degree with other specimens. Among other *Ventrifossa* species from Taiwan, the one most similar is *V. longibarbata*, and so far as our limited study material allow, the two species overlap or are essentially identical in their counts and measurements. The snout in *V. divergens* appears to be slightly more pointed and protruding, and the broad black stripe across the 1D in *V. longibarbata* is generally prominent, compared to the difuse duskiness of that fin in *V. divergens*. A more in-depth study may reveal other distinguishing characters. The overall brownish color of *V. saikaiensis*, its longer postorbital length (44–49% HL), and fewer scale rows below the 2D (6.0–6.5 cf. 8–9 in *V. divergens*), among other characters, distinguish that species from *V. divergens*. Compared with *V. rhipidodorsalis*, *V. divergens* has a longer preoral (15–19% cf. 11–15% of HL), somewhat broader interorbital (26–32% cf. 21–26%), somewhat larger orbits (with overlap, 29–38% cf. 27–32%), and somewhat shorter postorbital (with overlap, 38–44% cf. 43–48%); *V. rhipidodorsalis* also has a somewhat higher average number of V rays (9–10) and more prominent black blotches on 1D.

### *Ventrifossa garmani* (Jordan and Gilbert, 1904)

Figures 28A–B.

*Coryphaenoides garmani* Jordan and Gilbert *in* Jordan and Starks, 1904:610 (holotype USNM 50933, Sagami Bay, Japan, 110–259 fm [201–474 m]; paratypes ANSP 114108 [1 spec.], CAS-SU 8548 [5 spec.], USNM 51415 [9 spec.]).

*Ventrifossa garmani*: Matsubara, 1955:1315.— Kamokara, 1964:96.— Okamura, 1970:74.— Iwamoto, 1979: 152.— Okamura *in* Okamura et al., 1982:145, 348.— Okamura *in* Masuda et al., 1984:94.— Okamura *in* Okamura and Kitajima, 1984:213, 360.— Iwamoto, 1990:300–301, fig. 678–679 (descr.).— Shen et al., 1993:172 (desc.).— Chiou et al., 2004b:37, 47 (in key, list).— Shao et al., 2008: table 2 (2 spec., SWT).

**Material examined** (8 spec.).— **SWT:** ASIZP 61306 (1, 260+ TL), Dong-gang. ASIZP 65586 (1, 235 TL), CD 140, 280–452 m. **Other materials: Japan**: USNM 50933 (holotype, 52.8 HL, 292 TL), *Albatross* sta. 3695, Sagami Bay, 201–474 m. USNM 51415 (5 of 9 paratypes, 32–46.1 HL, 180–250+ TL), Suruga Bay, *Albatross* sta. 3738, 305 m.

**Distinguishing features**.— 1D II,10–11; P i19–i22; V 8, rarely 9; inner GR-I 16–17 total, outer GR-II 16–17; scale rows below midbase 1D 7.5–9.0, below 2D 4.5–5.0; lateral line scales over distance equal to predorsal length 38–42. Snout length 25–27% HL; preoral length 18–19%; interorbital 29–32%; orbit 30–35%; suborbital 11–15%; orbit to preopercle 41–45%; upper jaw 42–47%; barbel 23–29%; outer gill slit 24–27%. Head and body relatively compressed; snout relatively short, high, forming obtuse angle viewed dorsally. Body scales covered with broad-based, triangular spinules in quincunx arrangement. Spinous ray of 1D usually less than HL, leading edge finely sawtoothed. Periproct occupying about half anterior space between V and A, close behind V bases, dermal window of light organ extends forward between V bases. Gill membranes narrowly united over isthmus and under midorbit. Color in preservative light to medium gray-brown overall, silvery over most of head, trunk, and anteriorly on sides of tail, but not over dorsum; jaws, gill membranes, and below suborbital ridge blackish; mouth pale, gill cavities blackish posteriorly; leading edge of snout blackish; 1D dusky, somewhat darker midlaterally; V blackish; P and A clear to dusky. Attains about 30 cm TL.

FIGURE 28. *Ventrifossa garmani* Jordan and Gilbert, 1904. ASIZP 61306, 260+ mm TL, preserved. A. lateral view of whole fish. B. lateral view of right head, photo reversed laterally.

**DISTRIBUTION**.— From s. Japan to sw Taiwan [SCS], in 280–452 m.

**REMARKS**.— This is one of the most abundant species of macrourid in Japan, but it is not particularly common off Taiwan. The broadly triangular scale spinules on body scales are unique among the Taiwan members of this genus.

### *Ventrifossa longibarbata* Okamura, 1982

*Ventrifossa longibarbata* Okamura in Okamura et al., 1982:157–159, pl. 94 (holotype BSKU 29494; Tosa Bay, Japan, 32°58.0′N, 133°32.0′E, 605 m; 4 paratypes, Tosa Bay, Suruga Bay, and Okinawa Trough, in 382–620 m).— Okamura *in* Masuda et al., 1984:94.— Okamura *in* Okamura and Kitajima, 1984:215, 361.— Iwamoto and Williams, 1999:228 (comparisons with V. nigrodorsalis et al.).— Chiou et al., 2004b:48, fig.20 (2 spec.; sw. Taiwan).

**MATERIAL EXAMINED** (45 spec.).— **NET:** ASIZP 65609 (1, 301 TL), CD 209, 508–522 m; ASIZP 70242 (1, 133 TL), Da-xi. **SWT:** ASIZP 61242 (1, 272 TL), Dong-gang; ASIZP 61243 (2, 182–268 TL), Dong-gang and CAS 224884 [ex ASIZP 61243] (1, 238+ TL), Dong-gang; ASIZP 64114 (5, 185–225+ TL) and ASIZP 66950 (5, 53–55 TL), CD 194, 507 m; ASIZP 65532 (1, 290 TL) and ASIZP 65556 (1, 180 TL), CD 137, 316–477 m; ASIZP 65602 (1, 185 TL), CD 138, 441 m; ASIZP 65629 (1, 155 TL), CD 233, 448–526 m; ASIZP 65537 (1, 260 TL), CD 133, 690–748 m. **SCS:** ASIZP 66102 (1, 58 HL, 285+ TL), CP 315, 509 m; ASIZP 66257 (1, 35.5 HL, 155+ TL), ASIZP 66267 (1, 31.6 HL, 140+ TL), and ASIZP 66779 (7, 23–36 HL, 110+-180+ TL), CD 311, 516 m; ASIZP 66948 (2, 150–210 TL), CD 136, 998–1211 m; ASIZP 66263 (1, 37 HL, 200+ TL), CD 310, 364 m; ASIZP 66749 (3, 25–31 HL, 110+-170+ TL),) and ASIZP 66778 (2, 30–37 HL, 150+-160+ TL), CP 314, 506 m; ASIZP 66777 (2, 145–145+ TL, 24–30 HL; CP 313, 513 m;

ASIZP 66812 (2, 24–25.5 HL, 120+-130+ TL), OCP 317, 515 m; ASIZP 66829 (2, 100+-130+ TL), CP 315, 509 m.

**Distinguishing features (**data from six Taiwan specimens**)**.— 1D II,10–11; P i18–i21; V 8–9; total GR-I (lat/mesial) 10–12/15–17, GR-II 14–17/14–16; scale rows below midbase 1D 4.5–7.5, below 2D 5.0–6.5(9.0); lateral line scales over distance equal to predorsal length 37–41. Snout length 26–28% HL; preoral length 16–17%; interorbital 25–31%; orbit 29–36%; suborbital 12–14%; postorbital 42–48%; orbit to preopercle 41–46%; upper jaw 40–47%; barbel 28–39%; outer gill slit 26–28%. Color in life (from Okamura *in* Okamura et al., 1982:159) dark gray or swarthy dorsally, silvery on sides of head and body, black over gular region, lips, lower jaw, gill membranes, chest and ventrally on trunk; abdomen bluish under silvery reflections, suborbital region and ventral and posterior margin of gill cover blackish; mouth pale, gill cavities blackish posteriorly; leading edge of snout blackish; 1D with wide dusky to blackish midlateral section, but pale distally and along base; V black; P blackish; base of P silvery but with black distal edge and mesial lunate area. Attains at least 31 cm TL.

**Distribution**.— From s. Japan to Taiwan (SWT) and South China Sea in 382–1211 m.

**Remarks**.— This species closely resembles *V. garmani* in general physiognomy but differs in having a slightly longer barbel (28–39% HL vs. 21–29%), a darker midlateral region of 1D, more pyloric caeca (about 70 vs. <53 *fide* Okamura 1970:77), slender scale spinules (vs. triangular), and possibly darker V (black vs. dusky or blackish) and P (which appears to be blackish in Okamura's [*in* Okamura et al., 1982:156] photograph of the holotype vs. "light" in *V. garmani* [Okamura, 1970:77]). The six Taiwan specimens from which the above measurements and counts were taken agree closely with the original description of *V. longibarbata* except for slight differences in interorbital width (25–31% HL cf. 21–26.5%), postorbital length (42–48% cf. 39–44%), P ray count (i18–i21 cf. i21–i26"), and scale rows (below 1D origin 7–12 cf. 12–14, below mid-base 1D 4.5–7.5 cf. 8.5–11.5, and below 2D origin 5.0–9.5 cf. 9.0–10.0). The 1D was also almost entirely dusky, with only faint trace of a midlateral stripe. Four additional examples taken off Kochi, Japan (BSKU 12919, 12920, 12922, and 12923) were examined by TI many years ago; they agree well with the original description of the species.

### *Ventrifossa macroptera* Okamura, 1982

*Ventrifossa macroptera* Okamura *in* Okamura et al., 1982:149 (holotype BSKU 32185, Kyushu-Palau Ridge, 27°55.1′N, 134°44.8′E, 685–710 m; paratypes BSKU 30432 [1 spec.], 30435–36 [2], 30467–69 [3], 29429 [1], 32153–84 [31], 32186–89 [4], 32192–200 [8]).— Okamura *in* Masuda et al., 1984:94 (compiled).— Iwamoto, 1990:303, figs. 682–683 (descr.).— Chiou et al., 2004:48, fig. 21 (2 spec.; Tungkang, Taiwan [SWT]).

*Ventrifossa atherodon* (not of Gilbert and Cramer, 1897): Chiou et al., 2004b:46, fig. 18 (ASIZP 61311 (1 spec., Da-xi, Taiwan [NET]).

**Material examined** (103 Taiwan spec.).— **NET:** ASIZP 60253 (1, 286 TL), Da-xi; ASIZP 65533 (1, 190 TL), CD 210, 445–1185 m; ASIZP 61311 (1, 245 TL), Da-xi; ASIZP 70682 (1, 47 HL), Da-xi; ASIZP 70729 (1, 254 TL), Da-xi. **SWT:** ASIZP 61244 (1, 199 TL), Dong-gang; ASIZP 61245 (1, 202 TL), Dong-gang; ASIZP 65525 (3, 170–190 TL0, CD 142, 227–335 m; ASIZP 66947 (2, 235–250 TL), CD 140, 280–452 m; ASIZP 67596 (3, 118–143 TL), CP 348, 395 m; ASIZP 70254 (1, 180 TL), Dong-gang. **SCS:** ASIZP 65522 (18, 90–185 TL), ASIZP 65590 (41, 143–221 TL), ASIZP 65612 (5, 175–225 TL), and ASIZP 65614 (4, 111–132 TL), CD 136, 998–1211 m; ASIZP 65534 (1, 280 TL), CD 137, 316–477 m; ASZIP 65623 (1, 208 TL), CD 233, 448–526 m; ASZIP 65640 (1, 218 TL), CD 233, 448–562 m; ASIZP 65679 (1, 21 HL, 97+ TL), CP 315, 509 m; ASIZP 66751(1, 125 TL), OCP 312, 517 m; ASIZP 66764 (2, 35–38 HL, 130+-160+

TL), CP 314, 506 m; ASIZP 66798 (6, 20–38 HL, 110–180+ TL), CD 311, 516 m; ASIZP 66804 (2, 125–255 TL), OCP 317, 515 m; ASIZP 66808 (1, 180 TL), CP 314, 506 m; ASIZP 66832 (1, 143 TL), CP 315, 509 m; ASIZP 66949 (2, 130+-144 TL), CP 234, 547 m.

**Other specimens: Japan (**all from Kyushu-Palau Ridge). HUMZ 75049 (330+ TL); 75050 (325+ TL); 75051 (328+ TL); 75052 (332+ TL); 75053 (250+ TL); 75054 (338+ TL); 75055 (290+ TL); 75056 (356+ TL); 75057 (295 TL). CAS 52971 (3 paratypes, ex. BSKU spec.; 60.0–73.0 HL, 290+-376+ TL); CAS 52972 (7 paratypes, ex. BSKU; 58.2–70.3 HL, 235+-360+ TL).

**DISTINGUISHING FEATURES**.— 1D II,9–10(11); P i19–i23; V 9–10; GR-I (outer/inner) (10) 13–15 / 16–18 total, GR-II (outer/inner) 16–18 / 16–18; scale rows below 1D origin 9.5–11.0 (12.0), below midbase 1D 6.0.0–7.5, below 2D 7.5–10.0; lateral line scales over distance equal to predorsal length 48–57. Snout length 27–32% HL; preoral length 12–17%; internasal 23–27%; interorbital 29–32%; orbit 26–31%; suborbital 12–15%; postorbital 42–48%; orbit to preopercle 45–52%; upper jaw 47–51%; barbel 20–27%; outer gill slit 26–33%. Second spinous ray of 1D smooth. Snout rather blunt, little protruding beyond mouth; suborbital shelf narrowly constricted anteriorly below posterior nostril. Premaxillary tooth band broad; outer series of recurved, canine-like teeth with arrowhead-shaped tips; lower jaw teeth in two series. Color overall dark, head swarthy to black, somewhat silvery on sides of head and body, blackish over gular region and chest, de-scaled areas on trunk and anterior part of tail bluish; mouth pale, gill cavities blackish posteriorly; gill arches dark; leading edge of snout blackish; fins blackish; broad lunate area mesial to P base black. Attains about 40 cm TL.

**DISTRIBUTION**.— Kyushu-Palau Ridge to Taiwan and the South China Sea. In Taiwan, specimens were collected off NET, SWT, and SCS, mostly at depths between 280 and 516 m, but one collection (CD 136) from 998–1211 m.

**REMARKS**.— Chiou et al. (2004b:46, fig. 18) recorded a specimen referred to *V. atherodon* that is now re-identified as *V. macroptera*. Okamura (*in* Okamura et al. 1982:151) considered this species to be the most dominant of the grenadiers off the Kyushu-Palau Ridge. It appears to be similarly abundant in the South China Sea. In respect to the smooth spinous 1D ray, the low blunt snout, and dentition, *V. macroptera* resembles *V. atherodon* (Gilbert and Cramer, 1897), *V. macrodon* Sazonov and Iwamoto, 1992 from the se. Pacific, and *V. sazonovi* Iwamoto and Williams, 1999 from w., nw., and ne. Australia and the South China Sea. The last species is notable in having enlarged spinules on scales of the dorsum below the anterior portion of the 2D.

### *Ventrifossa misakia* Jordan and Gilbert, 1904

Figure 29.

*Coryphaenoides misakius* Jordan and Gilbert, 1904:611–612 (holotype, CAS-SU 8107, 340 mm TL; Misaki, Japan).

*Macrourus asper* (not of Günther): Jordan and Thompson, 1914:306, pl. 38, fig. 2 (“Misaki in deep water;” no description.)

*Lionurus misakius*: Gilbert and Hubbs, 1916:194–195 (1 spec., 113+ mm TL).

*Ventrifossa misakia*: Okamura, 1970:78–81, pl. VI, text-fig. 35 (47 spec., 150–260 mm TL; s. Japan).— Iwamoto, 1990:304–305, fig. 684–685 (descr.).— Sazonov and Shcherbachev, 1997:529–533 (comparisons; synonymized *V. fusca* with *V. misakia*).— Nakabo, 2002:423 (compiled).

*Ventrifossa fusca* Okamura *in* Okamura et al., 1982:153–155, fig. 93, A-D (p. 152) (holotype, BSKU 26067, female, 612 mm TL; Kyushu-Palau Ridge, 27°55′N, 134°39′E, 700 m; paratypes [same locality], BSKU 26068 [female, 526 TL], 26069 [male, 434+ TL], 26115 [male, 468 TL]).— Okamura *in* Masuda et al., 1984:94, pl. 81–B (compiled).— Nakabo, 2002:422 (compiled).— Shao et al., 2008 (6 spec., SCS; first record for Taiwan).

**Material examined** (6 spec. from Taiwan).— **SCS:** ASIZP 66783 (6, 157–380+ TL), CD 320, 731 m. **Other specimens: Japan**: CAS-SU 8107 (holotype, 60 HL, 340 TL), Sagami Bay near Misaki, Japan. USNM 51421 (3 paratypes, 54–76 HL, 165+-380 TL), Misaki. BSKU 12002 (1, 50 HL, 240 TL); Tosa Bay. BSKU 12953 (1, 46 HL, 225+ TL), Tosa Bay. BSKU 12955 (1, 28 HL, 157 TL). NSMT P49952 (1, 42.7 HL, 198+ TL), Suruga Bay, 440 m. NSMT P78960 (1, 44.3 HL, 230+ TL) and P78961 (1, 43.0 HL, 230+ TL), Suruga Bay, 376 m. FAKU 5270 (1, 36.8 HL, 197+ TL), M7634 (1, 42 HL, 221 TL), M7651 (1, 38 HL, 190+ TL), and M7655 (39.5 HL, 194 TL), Chiba Pref., off Choshi.

**Distinguishing features**.— 1D II,10–12; P i19–i23; V 8 (rarely 9); total GR-I (lateral/mesial) 11–12 / 13–16 total, (lateral/mesial) GR-II 14–15 / 12–15; scale rows below midbase 1D 8.5–10.5, below 2D 9–10; lateral line scales over distance equal to predorsal length 57–76. Snout length 27–33% HL; preoral length 20–27%; internasal 22–29%; interorbital 29–35%; orbit 32–38%; postorbital 36–44%; orbit to preopercle 40–45%; suborbital 12–15%; upper jaw 37–42%; barbel 4–9%; outer gill slit 18–24%; 1D-2D interspace 40–56%. Head broad, body relatively compressed; snout conical, protruding well beyond mouth, with a small tubercle at tip; suborbital area gently rounded, ridge defined but lacking stoutly modified scales, suborbital shelf abruptly constricted anteriorly; head fully scaled, but lacking large pores; body scales covered with slender, needle-like spinules in quincunx pattern. Color in alcohol light to medium gray-brown with silvery reflections along sides; bluish black over abdomen and chest; gill cover and gill membranes blackish; mouth and gill cavities pale, but blackish posteriorly; tip of snout (and in young along leading edge) blackish; 1D dusky, V black, P and A dusky. Attains about 40 cm TL.

**Distribution**.— From se. coast Japan to the East China Sea and South China Sea off sw. Taiwan, in 200 to 731 m.

**Remarks**.— We have been informed by Dr. Hiromitsu Endo of Kochi University that specimen BSKU 28596 recorded by Okamura (*in* Okamura and Kitajima 1984:213) as *V. misakia* is actially a specimen of *V. johnboborum*. We follow Sazonov and Shcherbachev (1997:529) in synonymizing *V. fusca* Okamura with *V. misakia.* It is rather peculiar that Okamura (*in* Okamura et al. 1982) failed to recognize specimens of his new species as representing *V. misakia* or a species very similar, knowing that he had examined many specimens of *V. misakia* for his work on the Japanese macrourids in the *Fauna Japonica* book series (Okamura 1970:78) and treating both species in

Figure 29. *Ventrifossa misakia* Jordan and Gilbert, 1904. ASIZP66783, 1 of 6, 380+ mm TL, preserved.

Masuda et al. (1984). The first author (TI) has examined two paratypes of *V. fusca* (BSKU 26068, 99 mm HL, 526 mm TL, and 26069, 106 HL, 434+ TL [large pseudocaudal]), both of which are much larger than any other we have seen. They are nonetheless identical in every feature with our smaller Tawian representatives of *V. misakia,* so far as we can tell. Sazonov and Shcherbachev (1997:532) pointed out that Okamura compared his species with *Kuronezumia macronema* (Smith and Radcliffe, 1912), a very different species that has been classified in another genus. The close similarity of *V. misakia* and *V. johnboborum* Iwamoto, 1982 was also recognized by Iwamoto (1982:59–60; 1990:305) and Sazonov and Iwamoto (1992:80). Sazonov and Shcherbachev (1997:529) compared specimens of *V. johnboborum* from the w. Indian Ocean, e. and w. Australia, the South China Sea, the Sala y Gomez Ridge (se. Pacific), and the holotype taken in the Bismarck Sea. They found these populations "differing in a few morphometric indices while retaining several common characters not peculiar to *V. misakia* (including *V. fusca*)." Among the different populations, that from the South China Sea was most similar to *V. misakia*, but they were unable to arrive at any conclusions as to "the independence of *V. johnboborum.*" Accordingly, we continue recognition of *V. johnboborum* while awaiting a more detailed analysis, perhaps using DNA information. Our specimens represent the first record of *V. misakia* from Taiwan and the South China Sea and also the deepest record at 731 m.

### *Ventrifossa nigrodorsalis* Gilbert and Hubbs, 1920

*Ventrifossa nigrodorsalis* Gilbert and Hubbs, 1920:546 (holotype, USNM 83627; n. coast Mindanao, Philippines, 391 m; 168 paratypes from Formosa [Taiwan], Philippines, and East Indies, 290–868 m). Iwamoto, 1990:307–309, fig. 690 (descr.).— Iwamoto and Merrett, 1997:559 (New Caledonia and vicinity).— Iwamoto and Williams, 1999:224–225, 228, fig. 54 (descr., e. and w. Australia).— Iwamoto and Graham, 2001:497–498, fig. 112 (descr., se. Australia, 300–790 m).— Chiou et al., 2004b:47 (listed, Taiwan, Table 1).

**MATERIAL EXAMINED** (3 Taiwan spec.).— **NET:** ASIZP 66903 (1, 197 TL), CP 248, 536 m; ASIZP 70715 (1, 188 TL), Da-xi. **SCS:** ASIZP 57974 (1, 183+ TL), Tong-sa Islands. **Other specimens:** USNM 8362 (holotype, 41.5 HL, 214 TL), Philippines, Mindanao Sea; 8˚37'37″N, 124˚35′E, 391 m, *Albatross* sta. 5502, 4 Aug. 1909. USNM 149302 (paratypes, 4, 32.3–36.0 HL, 125+-195+ TL), same data as for holotype; CAS 64574 (5, 30–9–36.6 HL, 499+-193+ TL), SCS off Vietnam; 15˚40'00″N, 109˚47′E, 479 m. CAS 221057 (38.5 HL, 210+ TL), Philippines, e. coast Luzon, 14˚41'04″N, 123˚24'07″E, 435–451 m, *Fishery Researcher I*, field no. TI95–12, 27 Sept. 1995.

**DISTINGUISHING FEATURES.**— 1D II,9–10; P i19–i23; V 8–9; total GR-I (lateral/mesial) 9–13/13–15, GR-II 13–14 /13–14; scale rows below 1D 8–9, below 2D 7–9; lateral line scales over distance equal to predorsal length 36–43. Snout length 29–30% HL; preoral length 19–21%; internasal 22–23%; interorbital 23–28%; orbit 28–34%; postorbital 42–44%; orbit to preopercle 39–42%; suborbital 13–16%; upper jaw 37–41%; barbel 17–26%; outer gill slit 21–25%; 1D-2D interspace 39–66%. Body and head moderately deep and compressed, nape somewhat elevated; snout slightly protruding beyond mouth, acutely pointed in lateral view, broadly obtuse in dorsal view. Body scales covered with small, needle-like spinules in wide chevron-like rows; small area of spinuleless scales along and behind 1D base. Color in alcohol grayish-brown dorsally on trunk, becoming paler along 2D base to form a dorsolateral stripe on tail; top of head and snout pale, integument translucent; faint silvery reflections along sides of head and ventrally on trunk and tail; underlying silvery pigmentation abdomen and chest bluish-black, tail pale with light peppering; gill cover and gill membranes mostly black; mouth and gill cavities pale, but dark in gullet; black margins on suborbital shelf, leading edge of snout, and supranarial ridges; 1D with black blotch or blackish over middle third or so of fin but pale distally and along base; V black, sometimes paler distally and near base; P and A dusky, but base of P black with lateral surface mostly silvery. Lips, jaws, and gill cavity as in others of genus. Attains about 25 cm TL in Taiwan region, possibly more elsewhere.

**Distribution**.— Known from off Australia, New Caledonia region, and Indonesia n. to the Philippines, Taiwan (NET), and the South China Sea.

**Remarks**.— Okamura (*in* Okamura et al. 1982:147, 348, fig. 90) initially recorded this species from two specimens collected in Tosa Bay. He later (Okamura et al. 1984) treated those specimens as representatives of his new species *V. rhipidodorsalis*, and used the photograph of one of the specimens (fig. 146C; BSKU 29495, 172 mm TL) to illustrate another example of the new species. *Ventrifossa nigrodorsalis* is an apparently broadly distributed species abundant in the Philippines, Indonesia, and the warm-water regions of Australia, as well as the sw. Pacific off New Caledonia, Vanuatu, and near regions, but it was scarce off Taiwan. Characters that have been used to distinguish species of *Ventrifossa* are often subtle and dependent on well-preserved specimens to observe. The existence of seemingly widely scattered populations of *V. nigrodorsalis* heighten the possibility that other species lie hidden under the cloak of that species name as currently circumscribed, and they may be unveiled after closer study of more specimens. The description provided above is from specimens collected off Taiwan, the South China Sea, and the Philippines in the Mindanao Sea between Mindanao and Cebu.

### *Ventrifossa rhipidodorsalis* Okamura, 1984

*Ventrifossa rhipidodorsalis* Okamura *in* Okamura and Kitajima, 1984:205 (Okinawa Trough, 28°42.0′N, 127°09.0′E, 500–535 m (holotype, BSKU 27695; 23 paratypes, Okinawa Trough and Tosa Bay, 500–650 m [but 1 spec. at 220 m]).— Okamura *in* Masuda et al., 1984:94 (compiled).— Iwamoto and Williams, 1999:228 (mentioned).— Chiou et al., 2004b:48, fig.22 (13 spec.; Nanfangao, Taiwan [NET]).

? *Ventrifossa nigrodorsalis*: Okamura in Okamura et al., 1982:147, 348, fig. 90 (2 spec.; BSKU 29495, later identified as *V. rhipidodorsalis* by Okamura *in* Okamura and Kitajima, 1984: fig. 146C).

**Material examined** (70 Taiwan spec.).— **NET:** ASIZP 61246 (1, 170 TL), Nan-fang-ao; ASIZP 61247 (12, 142–168 TL), Nan-fang-ao; ASIZP 62331 (2, 126+-162+ TL), Fong-kang, 200 m; ASIZP 64236 (3, 110+-215 TL) and CAS 224885 (ex. ASIZP 64236) (2, 121+~161 TL), CP 234, 547 m; ASIZP 65549 (1, 160+ TL), CP 124, 1129–1165 m; ASIZP 70231 (2, 109–113 TL), Da-xi; ASIZP 70248 (9, 98–180 TL), Nan-fang-ao; ASIZP 70250 (1, 125 TL), Da-xi; ASIZP 70685 (1, 40 HL), Da-xi; ASIZP 70733 (1, 196 TL), Da-xi. **SWT:** ASIZP 62388 (1, 181 TL), Dong-gang, 300 m; ASIZP 66322 (1, 153 TL), Dong-gang. **SCS:** ASIZP 65521 (11, 100–142 TL) and ASIZP 65592 (18, 105–165 TL), CD 136, 998–1211 m; ASIZP 65588 (3, 140–155 TL), CD 141, 985–1110 m. **SET:** ASIZP 66104 (1, 65 HL, 285+ TL), CP 299, 799 m. **Other specimens:** BSKU 27695 (holotype) and six paratypes, BSKU 27123, 27191, 27660, 27696, 27861, 27865, Okinawa Trough. CAS 88668 (5, 51.6–58.7 HL, 233+-312+ TL), Philippines, off se coast Luzon; 14˚50.46′N, 123˚17.30′E, 760–770 m; *R/V Fishery Researcher I* sta. TFRI-Ph1–12–95, 27 Sep. 1995.

**Distinguishing features**.— 1D II,10–12; P i19–i23; V 9–10; total GR-I (lateral/mesial) 10–13/15–17 total, (lateral/mesial) GR-II 14–17/(13)15–17; scale rows below midbase 1D 5.5–7.5, below 2D 7–8.5; lateral line scales over distance equal to predorsal length 36–43. Snout length 25–32% HL; preoral length 11–15%; internasal 18–23%; interorbital 21–27%; orbit 26–34%; postorbital 42–48%; orbit to preopercle (38) 41–44%; suborbital 11–14%; upper jaw (39) 42–47%; barbel (16) 19–26%; outer gill slit 22–28%; 1D-2D interspace 45–62%. Body moderately deep and compressed; snout low, blunt in adults, somewhat more pointed and protruding in young; suborbital area gently rounded. Body scales covered with small, slender, needle-like spinules in wide chevron-like rows; an area of spinuleless scales along and behind 1D base. Color in alcohol overall dark, with faint silvery reflections along sides of head and trunk; bluish-black over abdomen and chest; gill cover and gill membranes mostly black; mouth and gill cavities pale, but dark in gullet; black margins on suborbital shelf, leading edge of snout, suparnarial ridges, and a V-shaped stripe joined at apex to black nape stripe before 1D; 1D black except distal third or less white, base dusky to pale; V black, P dusky but base black with bulk of lateral face of base silvery, A dark dusky overall but with narrow black distal margin anteriorly. Lips, mouth, jaws, and gill cavity as in others of genus. Attains about 33 cm TL.

**DISTRIBUTION**.— From s. Japan to sw. Taiwan (SCS) in 400–1211 m.

**REMARKS**.— Among the Taiwanese grenadiers, *V. rhipidodorsalis* is most similar to *V. nigrodorsalis*, but that species has 8 or 9 V rays (cf. 9 or 10), overall paler coloration; paler, more silvery sides; slightly sharper, more protruding snout; generally narrower black streak on 1D; and shorter upper jaw (37–41% HL). In its overall dark color and V count of 9–10, it resembles *V. macroptera*, but that species has a smooth 1D spinous ray and differences in dentition. Another species with a black streak across the 1D is *V. longibarbata,* but that species has slightly lower average number of V rays (8–9), much longer barbel (28–39% HL cf. 19–26%), slightly longer preoral length (16–17% cf. 11–15%), and somewhat fewer scale rows below 2D (5.0–6.5 cf. 7.0–8.5).

### *Ventrifossa saikaiensis* Okamura, 1984

*Ventrifossa saikaiensis* Okamura *in* Okamura and Kitajima, 1984:209 (holotype, BSKU 28004; Okinawa Trough, 28°50.0′N, 127°14.0′E, 700–740 m; 11 paratypes, Okinawa Trough).— Chiou et al., 2004b: 48–49, fig. 23 (19 spec.; Taiwan [NET]).

*Ventrifossa divergens* (not of Gilbert and Hubbs, 1920): Chiou et al., 2004b:46, fig.19 (2 spec.; Da-xi, Taiwan [NET]).

**MATERIAL EXAMINED** (58 Taiwan spec.).— **NET:** ASIZP 61248 (1, 250 TL), Da-xi; ASIZP 61249 (14, 102–168 TL), Da-xi; ASIZP 61307 (1, 224 TL), Da-xi; ASIZP 61310 (1, 182 TL), Da-xi; ASIZP 64094 (1, 53 HL, 260+ TL), CP 235, 764 m); ASIZP 63271 (1, 144 TL), Da-xi; ASIZP 64094 (1, 260+ TL), CP 235, 764 m; ASIZP 65608 (1, 145+ TL), CP 120, 520 m; ASIZP 65602 (1, 295+ TL), CD 138 m; ASIZP 70223 (1, 60 HL), Da-xi; ASIZP 70225 (2, 270+-395 TL), Da-xi; ASIZP 70730 (1, 170 TL), Da-xi. **SWT:** ASIZP 61242 (1, 272 TL), Dong-gang; ASIZP 61309 (1, 220 TL), Dong-gang; ASIZP 64119 (1, 278+ TL) and ASIZP 64253 (1, 200+ TL), CD 193, 821 m; ASIZP 65601 (2, 285 TL) and CAS 224887 (ex. ASIZP 65601, 1, 299 TL), CD 139, 718–852 m; ASIZP 65608 (1, 145+ TL), CP 120, 520–640 m; ASIZP 65616 (1, 185 TL), CD 138, 441 m; ASIZP 70273 (1, 295 TL), CD 138, 441 m; ASIZP 71146 (1, 267 TL), CD 271, 700–800 m. **SCS:** ASIZP 64562 (1, 275 TL) and ASIZP 65562 (1, 275 TL), CD 140, 280–452 m; ASIZP 65522 (18, 90–185 TL), CD 136, 998–1211 m; ASIZP 61242 (1, 272 TL), Dong-gang. **Other specimens** (all from Okinawa Trough, East China Sea)**:** BSKU 28004 (holotype, 305+ TL); BSKU 27576 (paratype, 285+ TL); BSKU 28005–28008 (4, 180+–290 TL).

**DISTINGUISHING FEATURES**.— 1D II,9–11; P i18–i22; V 8–9; total GR-I (lateral/mesial) 12–16 / 16–18, GR-II 15–18 /15–18; scale rows below midbase 1D 5.5–7.0, below 2D 6.0–7.5; lateral line scales over distance equal to predorsal length 33–44. Snout length 28–31% HL; preoral length 14–19%; internasal 21–26%; interorbital 27–32%; orbit 27–32%; postorbital 44–48%; orbit to preopercle 43–46%; suborbital 14–16%; upper jaw 45–50%; barbel 27–35%; outer gill slit 27–30%; 1D–2D interspace 43–68%. Body and head moderately deep and compressed; snout low, rather blunt and protruding little beyond large mouth; barbel long, slender. Body scales densely covered with slender, reclined, needle-like spinules in wide chevron-like rows; no spinuleless scales around 1D base. Color in alcohol medium brownish, lacking silvery reflections; blackish over gill cover;

bluish-black over abdomen and chest; gill and gular membranes black; mouth and gill cavities pale, but dark in gullet; margins on suborbital shelf and leading edge of snout faintly blackish or not distinguished; barbel pale, but base dark; 1D uniformly dusky; V blackish; P and A dark dusky, but base of P black along distal margin. Coloration of lips, mouth, jaws, teeth, and gill cavities as in others of genus. Attains more than 31 cm TL.

**Distribution**.— Known only from the Okinawa Trough (in East Sea), Taiwan (NET, SWT), and the South China Sea in 280–1211 m.

**Remarks**.— Chiou et al. (2004b:46, fig.19) recorded two specimens (ASIZP 61309 and 61310) as *V. divergens*, but we re-identified them as *V. saikaiensis*. Among the Taiwan grenadiers, *V. saikaiensis* is most similar to *V. divergens* in having a uniformly dusky 1D, but it is easily distinguished from that species (and all other Taiwan members of *Ventrifossa*) in having a uniformly brownish overall coloration, with little or no silvery reflections on the sides, and dark brown scale pockets. In these color features and in its general appearance, the species resembles certain members of the genus *Nezumia,* especially *N. atlantica* (Parr, 1946) and *N. africana* (Iwamoto, 1970). However, the dentition, squamation, luminescent organ, gill rakers and arches, and other features clearly support its position within *Ventrifossa.*

### ***Ventrifossa sazonovi*** Iwamoto and Williams, 1999

Figure 30.

*Ventrifossa sazonovi* Iwamoto and Williams, 1999:231, fig. 56 (holotype: CAS 13564, South China Sea, off Vietnam, 15°48′N, 109°47′E, depth 479 meters; 15 paratypes, n. and w. Australia).

**Material examined**.— SWT: BSKU 98976 (1, 38.5 mm HL, 202+ mm TL), Dong-gang Fish Market, ca. 200–300 m depth, bottom trawl, coll. by H.-C. Ho, 16 Nov. 2007.

**Distinguishing features**.— 1D II,10; P i21–22; V 9; GR-I (outer/inner) 13/17; GR-II (outer/inner) 18/17. Snout 27% HL; preoral 10% HL; interorbital 25% HL; orbit 33% HL; suborbital 11% HL; orbit to preopercle 45% HL; upper jaw 47% HL; barbel 21% HL; outer gill slit 27% HL. Head and body moderately compressed; snout relatively short, barely protruding beyond upper jaw; suborbital shelf somewhat constricted anteriorly; chin barbel fairly developed; pectoral fin rather short, 1.7 in HL. Branchiostegal membranes narrowly united over isthmus; gill opening extending forward to below hind ⅓ of orbit. Periproct situated just behind V insertions, occupying about ⅓ of V–A interspace; dermal window of light organ small, reaching on a line passing through outer V bases. Premaxillary teeth in broad tapered band; outer series distinctly enlarged; dentary teeth aligned in irregular 2 rows. Spinules on body scales needle-like, arranged in quincunx order; those on scales along 2D base prominently enlarged. No modified scutes on snout. 1D smooth along its leading edge. Color in preservative light brown overall, but dark over ventral parts of head and abdomen; prominent blackish streaks along leading edge of snout, upper suborbital shelf, and

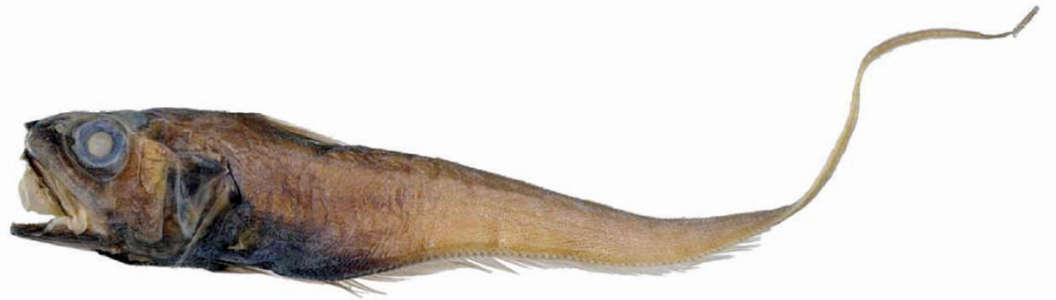

Figure 30. *Ventrifossa sazonovi* Iwamoto and Williams, 1999. BSKU 98976, 202+ mm TL, preserved.

median nasal ridge; lips and chin barbel pale; oral cavity immaculate; 1D darker proximally, paler distally; V blackish; other fins dusky overall. Attains at least 34 cm TL.

**Distribution**.— Known from the South China Sea off Vietnam and Taiwan, and northern coasts of Australia from Western Australia to Queensland, in about 200–610 m.

**Remarks**.— This species is readily distinguished from other Taiwanese congeners except *V. macroptera* in having a smooth leading edge of 1D. It further differs from *V. macroptera* in having enlarged spinules on scales along 2D base. The Taiwanese specimen is the shallowest captures (previously known only below 420 m) and the northernmost record of the species.

## Family Macrouroididae

**Distinguishing features**.— Head huge, rounded, with consistency of water-filled balloon; eyes tiny, diameter about 10 times into head length, placed forward of upper jaws; dorsal fin single, low; A long low; V absent (*Macrouroides*) or tiny with five short rays (*Squalogadus*); chin barbel absent; outer GR-I somewhat lathlike; first (outer) gill slit not restricted dorsally and ventrally by opercular membrane.

**Remarks**.— Two genera, each with one widespread species, found in most tropical and temperate oceans.

### Genus *Squalogadus* Gilbert and Hubbs, 1916

**Distinguishing features**.–V present but tiny, five rays, none prolonged; other features as for family.

### *Squalogadus modificatus* Gilbert and Hubbs, 1916

Figure 31.

*Squalogadus modificatus* Gilbert and Hubbs, 1916:156 (Bungo Channel, 32°32′N, 132°25′E, off Kyushu, Japan, *Albatross* sta. 4956, 720 fm [1317 m]; holotype USNM 76864, paratypes SU 22928).— Marshall, 1973:517–518.— Okamura, 1970:16–18, pl. IX (Sagami Bay and off Choshi, Japan).— Shiobara, 1982:143–146, figs. 1–3 (2 spec., 261–397 mm TL; Suruga Bay, Japan).— Sawada *in* Amaoka et al., 1983:105, 192, fig. 57 (HUMZ 78126, 1 spec., off Miyagi, Tohoku district, 1110 m).— Okamura *in* Masuda et al., 1984:93.— Endo et al., 1994:332 (HUMZ 121632, 1 spec., Sea of Okhotsk off ne. Hokkaido, 1393 m; n. record).— Okamura and Amaoka, 1997:129 (photograph of living individual).— Shinohara et al., 1996:170 (7 spec., east-central Honshu, Japan; 967–4867 m).— Shinohara et al., 1997:290 (listed).— Shinohara et al., 2001:306 (1 spec., Tosa Bay, 765–823 m).— Amaoka, 2009:177, fig. 304 (photo of fresh specimen). See also Shao et al. (2008: table 1, 1 spec., SCS) first record for Taiwan.

*Squalogadus intermedius* Grey, 1959:330–333, fig. 53 (holotype USNM 185606, n. Gulf of Mexico, R/V *Oregon* sta 1426, 1098 m; 5 paratypes, FMNH 64489).

**Material examined**.— **SCS:** ASIZP 64070 (1, 330+ TL), CP 178, 1241 m.

**Distinguishing features**.— As for genus.

**Distribution**.— Widespread in tropical and southern temperate seas, but absent in e. Pacific. In nw. Pacific, known off Japan, from Hokkaido to Kyushu and Taiwan.

**Remarks**.— A single specimen collected from SCS off sw. Taiwan in 1241 m represents the first record from Taiwan.

FIGURE 31. *Squalogadus modificatus* Gilbert and Hubbs, 1916. ASIZP 64070, 330+ mm TL, preserved.

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## LITERATURE CITED

ALCOCK, A. 1894. Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator,' Commander C. E. Oldham, R. N., commanding. Series 2, No. 11. An account of a recent collection of bathybial fishes from the Bay of Bengal and from the Laccadive Sea. *Journal of the Asiatic Society of Bengal* 63(pt. 2)(2):115–137, pls. 6–7.

AMAOKA, K. 2009. Deep-sea fishes-monsters of underworld. Bookman-sha Co. Ltd, Tokyo, Japan. 223 pp.

AMAOKA, K., K. NAKAYA, H. ARAYA, AND T. YASUI. 1983. Fishes from the north-eastern sea of Japan and the Okhotsk Sea off Hokkaido. *The intensive research of unexploited fishery resources on continental slopes.* Japan Fisheries Resource Conservation Association, Tokyo, Japan. 371 pp.

ARAI, T., AND T. IWAMOTO. 1979. A new species of the macrourid fish genus *Coelorinchus* from off Tasmania, New Zealand, and the Falkland Islands. *Japanese Journal of Ichthyology* 26:238–246.

BARNARD, K. H. 1925. Descriptions of new species of marine fishes from S. Africa. *Annals and Magazine of Natural History,* ser. 9, 15:498–504.

BERG, C. 1898. Substitucion de nombres genéricos. *Comunicaciones del Museuo Nacional de Historia Natu-*

*ral Bernardino Rivadavia Buenos Aires* 1:41–43.

Cohen, D. M., T. Inada, T. Iwamoto, and N. Scialabba. 1990. *FAO Species Catalogue. Vol. 10. Gadiform fishes of the world* (*Order Gadiformes*). *An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis no. 125.* FAO, Rome, Italy. 442 pp.

Chiou, M.-L, K.-T. Shao, and T. Iwamoto. 2004a. New species of *Caelorinchus* (Macrouridae, Gadiformes, Teleostei) from Taiwan, with a redescription of *Caelorinchus brevirostris* Okamura. *Copeia* 2004(2):298–304.

Chiou, M.-L, K.-T. Shao, and T. Iwamoto. 2004b. A new species, *Caelorinchus sheni*, and 19 new records of grenadiers (Pisces: Gadiformes: Macrouridae) from Taiwan. *Zoological Studies* 43:35–50.

Chu, Y.-T., C.-L. Chan, and C.-T. Chen. 1963. *Ichthyofauna of East China Sea*, i-xxviii + 1–642. (In Chinese.)

Devine, J. A., K. D. Baker, and R. L. Haedrich. 2006. Fisheries: Deep-sea fishes qualify as endangered. *Nature* (*London*) 439:29.

Devine, J. A., and R. L. Haedrich. 2008. Population trends and status of exploited Northwest Atlantic grenadiers, *Coryphaenoides rupestris* and *Macrourus berglax*. Pages 463–484 *in* A. Orlov and T. Iwamoto, eds., *Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries.* American Fisheries Society, Symposium 63, Bethesda, Maryland, USA. 484 pp.

Ebert, D. A., H.-C. Ho, W. T. White, and M. R. de Carvalho. 2013. Introduction to the systematics and biodiversity of sharks, rays, and chimaeras (Chondrichthyes) of Taiwan. *Zootaxa* 3752 (1):5–19.

Endo, H., D. Tsutsui, and K. Amaoka. 1994. Range extensions of two deep-sea macrourids *Coryphaenoides filifer* and *Squalogadus modificatus* to the Sea of Okhotsk. *Japanese Journal of Ichthyology* 41(3): 330–333.

Eschmeyer, W. N. 1998. *Catalog of Fishes*. 3 vols. California Academy of Sciences, San Francisco, California, USA. 2905 pp.

Filhol, H. 1884. Explorations sous-marines—Voyage du “Talisman.” *Nature* (*Paris*) (558):182–186, figs. 1–3.

Fricke, R., and W. N. Eschmeyer. 2009. *A Guide to Fish Collections in the Catalog of Fishes*. On-line version of 13 March 2009. Available at: *<http://research.calacademy.org/research/ichthyology/catalog/collections.asp>*.

Gilbert, C. H. 1905. The deep-sea fishes of the Hawaiian Islands. Pages 575–713, figs. 230–276, pls. 66–101 *in* D. S. Jordan and B. W. Evermann, eds., The Aquatic Resources of the Hawaiian Islands. *Bulletin of the United States Fish Commission for 1903*, 22(pt. 2, sect. 2).

Gilbert, C. H., and F. Cramer. 1897. Report on the fishes dredged in deep water near the Hawaiian Islands, with descriptions and figures of twenty-three new species. *Proceedings of the United States National Museum* 19:403–435.

Gilbert, C. H., and C. L. Hubbs. 1916. Report on the Japanese macrouroid fishes collected by the United States fisheries steamer “Albatross” in 1906, with a synopsis of the genera. *Proceedings of the United States Museum* 51(2149):135–214, pls. 8–11.

Gilbert, C. H., and C. L. Hubbs. 1920. The macrourid fishes of the Philippine Islands and the East Indies. *United States National Museum Bulletin 100*, 1 (pt. 7):369–588.

Gilbert, C. H., and W. F. Thompson, *in* Thompson, W. F. 1916. Fishes collected by the United States Bureau of Fisheries steamer “Albatross” during 1888, between Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. *Proceedings of the United States National Museum* 50:401–476.

Goode, G. B., and T. H. Bean. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world. *Smithsonian Contributions to Knowledge* 30(9810:1–553 [text], 1–26, pls 1–123, figs. 1–417. (Also *United States National Museum Special Bulletin* 2, and *Memoirs of the Museum of Comparative Zoology, Harvard* 22.)

Grey, M. 1959. Deep sea fishes from the Gulf of Mexico with the description of a new species *Squalogadus intermedius* (Macrouroididae). *Fieldiana Zoology* 39(29):323–346.

Günther, A. 1877. Preliminary notes on new fishes collected in Japan during the expedition of H.M.S. “Challenger.” *Annals and Magazine of Natural History,* ser. 4, 20:433–447.

GÜNTHER, A. 1878. Preliminary notices of deep-sea fishes collected during the voyage of H.M.S. "Challenger." *Annals and Magazine of Natural History,* ser. 5, 2:17–28.

GÜNTHER, A. 1887. Report on the deep-sea fishes collected by H. M. S. "Challenger" during the years 1873–76. *Report of the scientific results of the voyage of H.M.S. "Challenger"* 22:1–268.

HONMA, Y., Y. NAKAMURA, H. IMURA, T. SHOJI, R. HONMA, AND N. INOUE. 2008. Further additions to a list of the fishes collected in the Province of Echigo including Sado Island (XVIII). Kashiwaaki City Museum (22):65–74. (In Japanese with English abstract.)

HOWES, G. J., AND O. A. CRIMMEN. 1990. A review of the Bathygadidae (Teleostei: Gadiformes). *Bulletin of the British Museum* (*Natural History*) (*Zool.*) 56(2):155–203.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. *International Code of Zoological Nomenclature*, 4th edition. The International Trust for Zoological Nomenclature, London, England, UK. 306 pp.

IWAMOTO, T. 1970. The R/V Pillsbury Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65. 19. Macrourid fishes of the Gulf of Guinea. *Studies in Tropical Oceanography* 4:316–431.

IWAMOTO, T. 1974. *Nezumia* (*Kuronezumia*) *bubonis*, a new subgenus and species of grenadier (Macrouridae: Pisces) from Hawaii and the western North Atlantic. *Proceedings of the California Academy of Sciences* ser. 4, 39(22):507–516.

IWAMOTO, T. 1979. Eastern Pacific macrourine grenadiers with seven branchiostegal rays (Pisces: Macrouridae). *Proceedings of the California Academy of Sciences*, ser. 4, 42(5):135–179.

IWAMOTO, T. 1982. *Ventrifossa johnboborum*, a new grenadier from the western Pacific (Macrouridae: Pisces). *Australian Zoologist* 21(10):55–61.

IWAMOTO, T. 1997. *Trachonurus robinsi*, a new species of grenadier (Gadiformes, Macrouridae) from the Philippines. *Bulletin of Marine Science* 60(3):942–949.

IWAMOTO, T. 1990. Family Macrouridae. Pages 90–317 *in* D. M. Cohen, T. Inada, T. Iwamoto, and N. Scialabba, *FAO Species Catalogue. Vol. 10. Gadiform fishes of the world* (*Order Gadiformes*)*. An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis no. 125.* FAO, Rome, Italy. 442 pp.

IWAMOTO, T., AND M. E. ANDERSON. 1994. Review of the grenadiers (Teleostei: Gadiformes) of southern Africa, with descriptions of four new species. *Ichthyological Bulletin, J.L.B. Smith Institute of Ichthyology* (61):1–28.

IWAMOTO, T., AND M. E. ANDERSON. 1999. New species of *Coelorinchus* (Macrouridae, Gadiformes, Teleostei) from the Indian Ocean. *Copeia* 1999(4):1079–1083.

IWAMOTO, T., D. GOLANI, A. BARANES, AND M. GOREN. 2006. Two new grenadiers (Teleostei, Gadiformes, Macrouridae) from the Seychelles and Mascarene Ridge, Western Indian Ocean. *Proceedings of the California Academy of Sciences*, ser. 4, 57(13):433–442.

IWAMOTO, T., AND K. J. GRAHAM. 2001. Grenadiers (families Bathygadidae and Macrouridae, Gadiformes, Pisces) of New South Wales, Australia. *Proceedings of the California Academy of Sciences*, ser. 4, 52(21):407–509.

IWAMOTO, T., H.-C. HO, AND K.-T. SHAO. 2009. Description of a new *Coelorinchus* (Macrouridae, Gadiformes, Teleostei) from Taiwan, with notable new records of grenadiers from the South China Sea. *Zootaxa* 2326:39–50.

IWAMOTO, T., P. MCMILLAN, AND YU. N. SHCHERBACHEV. 1999. A new grenadier, genus *Caelorinchus*, from Australia and New Zealand (Pisces, Gadiformes, Macrouridae). *New Zealand Journal of Marine and Freshwater Research* 33:49–54.

IWAMOTO, T., AND N. R. MERRETT. 1997. Pisces Gadiformes: taxonomy of grenadiers of the New Caledonian region, southwest Pacific. Pages 473–570 *in* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, vol. 18. *Mémoires du Muséum national d'Histoire naturelle* 176.

IWAMOTO, T., AND YU. I. SAZONOV. 1988. A review of the southeastern Pacific *Coryphaenoides* (sensu lato) (Pisces, Gadiformes, Macrouridae). *Proceedings of the California Academy of Sciences*, ser. 4, 45(3):35–82.

IWAMOTO, T., AND YU. I. SAZONOV. 1994. Revision of the genus *Kumba* (Pisces, Gadiformes, Macrouridae), with description of three new species. *Proceedings of the California Academy of Sciences* ser. 4, 48(11):221–237.

IWAMOTO, T., K.-T. SHAO, AND H.-C. HO. 2011. Elevation of *Spicomacrurus* (Gadiformes: Macrouridae) to generic status, with descriptions of two new species from the southwestern Pacific. *Bulletin of Marine Science* 87(3):513–530.

IWAMOTO, T., YU. N. SHCHERBACHEV, AND B. MARQUARDT. 2004. Grenadiers (Gadiformes, Teleostei) of Walters Shoals, southwestern Indian ocean, with description of a new "West-Wind Drift" species. *Proceedings of the California Academy of Sciences*, ser. 4, 55(10):190–207.

IWAMOTO, T., AND A. WILLIAMS. 1999. Grenadiers (Pisces, Gadiformes) from the continental slope of western and northwestern Australia. *Proceedings of the California Academy of Sciences*, ser. 4, 51(3):105–243.

JORDAN, D. S., AND C. H. GILBERT. 1904. Macrouridae. Pages 602–621 *in* D. S. Jordan and E. C. Starks, List of fishes dredged by the steamer *Albatross* off the coast of Japan in the summer of 1900, with descriptions of new species and a review of the Japanese Macrouridae. *Bulletin of the United States Fish Commission (1902*) 22:577–630, pls. 1–8.

JORDAN, D. S., AND C. L. HUBBS. 1925. Record of fishes obtained by David Starr Jordan in Japan, 1922. *Memoirs of the Carnegie Museum* 10(2):93–346, pls. V-XII.

JORDAN, D. S., AND J. O. SNYDER. 1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with description of fourteen new species. *Proceedings of the United States National Museum* 23(1213):335–380, pls. 9–20.

JORDAN, D. S., AND E. C. STARKS. 1904. List of fishes dredged by the steamer *Albatross* off the coast of Japan in the summer of 1900, with descriptions of new species and a review of the Japanese Macrouridae. *Bulletin of the United States Fish Commission* 22(1902):577–630, 52 textfigs., pls. 1–8.

JORDAN, D. S., AND W. F. THOMPSON. 1914. Record of the fishes obtained in Japan in 1911. *Memoirs of the Carnegie Museum* 6(4):205–313, pls. 24–42.

KAMOHARA, T. 1938. *On the offshore bottom-fishes of Prov. Tosa, Shikoku, Japan*. Maruzen Kobushiki Kaisha, Tokyo, Japan. 86 pp.

KAMOHARA, T. 1961. Notes on type specimens of fishes in my laboratory. *Reports of the Usa Marine Biological Station* 8(2):1–9, pls. 1–7.

KAMOHARA, T. 1964. Revised catalogue of fishes of Kochi Prefecture, Japan. *Reports of the Usa Marine Biological Station* 11(1):1–99.

KATAYAMA, M. 1942. A new macrourid fish from the Japan Sea. *Zoological Magazine* 54(8):332–334, fig. 1.

KIM, I. S., Y. CHOI, C. L. LEE, Y. J. LEE, B. J. KIM, AND J. H. KIM. 2005. *Illustrated Book of Korean Fishes*. Kyo-Hak Publishing Co., Seoul, Korea. 615 pp.

KIM, S.-Y., T. IWAMOTO, AND M. YABE. 2009. Four new records of grenadiers (Macrouridae, Gadiformes, Teleostei) from Korea. *Korean Journal of Ichthyology* 21(2):106–117.

KOEHLER, R. 1896. Résultats scientifiques de la Campagne du "Caudan" dans le Golfe de Gascogne, Aout-Septembre 1895. Poissons. *Annales de l'Université de Lyon* 26:475–526.

MARSHALL, N. B. 1973. Family Macrouridae. Pages 496–665 *in* D. M. Cohen, ed., Fishes of the western North Atlantic. *Memoirs of the Sears Foundation for Marine Research*, no. 1, part 6.

MASUDA, H., K. AMAOKA, C. ARAGA, T. UYENO, AND T. YOSHINO. 1984. *The fishes of the Japanese Archipelago*. Tokai University Press, Tokyo, Japan. 437 pp., 370 pls.

MATSUBARA, K. 1936. On two new species of fishes found in Japan. *Annotationes Zoologicae Japonenses* 15:355–360.

MATSUBARA, K. 1943. Ichthyological annotations from the depth of the Sea of Japan, VIII-IX. *The Journal of the Sigenkagaku Kenkyusyo* 1(2):131–152.

MATSUBARA, K. 1955. *Fish Morphology and Hierarchy,* Part II. Ishizaki-Shoten, Tokyo, Japan. (In Japanese.)

MAUL, G. 1951. Monographia dos peixes do Museum Municipal do Funchal. Familia Macrouridae e Merlucciidae. *Boletim do Museu Municipal do Funchal* (5)(art. 12):5–55.

MCCANN, C., AND D. G. MCKNIGHT. 1980. The marine fauna of New Zealand: Macrourid fishes (Pisces: Gadida). *New Zealand Oceanographic Institute Memoir* 61:1–91.

MCMILLAN, P., AND T. IWAMOTO. 2008. Two new species of *Coelorinchus* (Teleostei, Gadiformes, Macrouridae) from the Tasman Sea. *Proceedings of the California Academy of Sciences*, ser. 4, 60(4):39–51.

MELO, M. R. S., A. C. BRAGA, G. W. A. NUNAN, AND P. A. S. COSTA. 2010. On new collections of deep-sea Gadiformes (Actinopterygii: Teleostei) from the Brazilian continental slope, between 11° and 23°S.

*Zootaxa* 243:25–46.

Merrett, N. R., and R. L. Haedrich. 1997. *Deep-sea Demersal Fish and Fisheries*. Chapman and Hall, London, England, UK. 282 pp.

Merrett, N. R., and T. Iwamoto. 2000. Pisces Gadiformes: grenadier fishes of the New Caledonian region, southwest Pacific Ocean. Taxonomy and distribution, with ecological notes. Pages 723–781 *in* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, vol. 21. *Mémoires du Muséum national d'Histoire naturelle*, 184.

Merrett, N. R., Yu. I. Sazonov, and Yu. N. Shcherbachev. 1983. A new genus and species of rattail fish (Macrouridae) from the eastern North Atlantic and eastern Indian ocean, with notes on its ecology. *Journal of Fish Biology* 22:549–561.

Nakabo, T., ed. 2002. *Fishes of Japan with pictorial keys to the species*, English edition [vol.] I. Tokai University Press, Tokyo, Japan. 866 pp.

Okamura, O. 1963. Two new and one rare macrourid fishes of the genera *Coelorhynchus* and *Lionurus*, found in Japan waters. *Bulletin of the Misaki Marine Biological Institute* 4:21–35.

Okamura, O. 1970. *Fauna Japonica, Macrourina* (*Pisces*). Academic Press, Tokyo, Japan. 216 p.

Okamura, O., and K. Amaoka. 1997. *Sea Fishes of Japan*. Yama-Kei Publishers, Tokyo, Japan. 784 pp. (In Japanese.)

Okamura, O., K. Amaoka, and F. Mitani, eds. 1982. *Fishes of the Kyushu-Palau Ridge and Tosa Bay. The Intensive Research of Unexploited Fishery Resources on Continental Slopes*. Japan Fisheries Resource Conservation Association, Tokyo, Japan. 435 pp.

Okamura O., and T. Kitajima, eds. 1984. *Fishes of the Okinawa Trough and the Adjacent Waters. I. The Intensive Research of Unexploited Fishery Resources on Continental Slopes*. Japan Fisheries Resource Conservation Association, Tokyo, Japan. 414 pp.

Radcliffe, L. 1912. Descriptions of a new family, two new genera, and twenty-nine new species of anacanthine fishes from the Philippine Islands and contiguous waters. *Proceedings of the United State National Museum* 43(1924):105–140, pls. 22–31.

Roa-Varón, A., and G. Ortí. 2009. Phylogenetic relationships among families of Gadiformes (Teleostei, Paracanthopterygii) based on nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution* 52:688–704.

Sazonov, Yu. I. 1985. Two new macrourid species (Gadiformes) from northern Pacific seamounts. *Voprosy Ikhtiologii* 25(5):719–727. (In Russian; English version in *Journal of Ichthyology* 25:13–21.)

Sazonov, Yu. I. 1993. Discovery of a rare grenadier species, *Hymenocephalus papyraceus* (Gadiformes, Macrouridae), in the East China Sea. *Voprosy Ikhtiologii* 33(3):446–448. (In Russian; English version in *Journal of Ichthyology* 33(8):117–121.)

Sazonov, Yu. I. 1994. Additions to the list of macrourids (Gadiformes, Bathygadidae and Macrouridae) from the Northwest Pacific Ridge. *Journal of Ichthyology* 34(5):98–115. (Also published as *Voprosy Ikhtiologii* 34(2), 1994:149–160.)

Sazonov, Yu. I., and T. Iwamoto. 1992. Grenadiers (Pisces, Gadiformes) of the Nazca and Sala y Gomez ridges, southeastern Pacific. *Proceedings of the California Academy of Sciences*, ser. 4, 48(2):27–95.

Sazonov, Yu .I., and Yu. N. Shcherbachev. 1982. A preliminary review of grenadiers related to the genus *Cetonurus* Günther and *Kumba* Marshall. *Voprosyi Ikhtiologii* 22(5):707–721, figs. 1–4. (In Russian, with English summary; also English translation *Journal of Ichthyology* 22(5):1–15.)

Sazonov, Yu. I., and Yu. N. Shcherbachev. 1985. Preliminary review of grenadiers of the *Cetonurus* group (Gadiformes, Macrouridae). II. The genus *Cetonurus* Günther: taxonomic characters of the group. *Journal of Ichthyology* 25(3):12–27.]

Sazonov, Yu. I., and Yu. N. Shcherbachev. 1997. The composition and some problems pertaining to the variability of species of subgenus *Sokodara* (genus *Ventrifossa*, Macrouridae). *Journal of Ichthyology* 37(7):529–533.

Sazonov, Yu. I., Yu. N. Shcherbachev, and T. Iwamoto. 2003. The grenadier genus *Mataeocephalus* Berg, 1898 (Teleostei, Gadiformes, Macrouridae), with descriptions of two new species. *Proceedings of the California Academy of Sciences*, ser. 4, 54(17):279–301.

Shao, K.-T., T. Iwamoto, H.-C. Ho, T.-Y. Chen, and C.-Y. Chen. 2008. Species composition and distribution pattern of grenadiers (family Bathygadidae, Macrouridae and Macrouroididae) from Taiwan. Pages 17–29 *in* A. Orlov and T. Iwamoto, eds., *Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries.* American Fisheries Society, Symposium 63, Bethesda, Maryland, USA. 484 pp.

Shcherbachev, Yu. N., and T. Iwamoto. 1995. Indian Ocean grenadiers of the subgenus *Coryphaenoides*, genus *Coryphaenoides* (Macrouridae, Gadiformes, Pisces). *Proceedings of the California Academy of Sciences*, ser. 4, 48(14):285–314.

Shcherbachev, Yu. N., Yu. I. Sazonov, and T. Iwamoto. 1992. Synopsis of the grenadier genus *Kuronezumia* (Pisces: Gadiformes: Macrouridae), with description of a new species. *Proceedings of the California Academy of Sciences*, ser. 4, 48(3):97–108.

Shen, S.-C., S.-C. Lee, K.-T. Shao, H.-C. Mok, C.-H. Chen, C.-C. Chen, C.-S. Tzeng, eds. 1993. *Fishes of Taiwan.* National Taiwan University, Taipei, Taiwan. 960 pp. (In Chinese.)

Shinohara, G., H. Endo, and K. Matsuura. 1996. Deep-water fishes collected from the Pacific coast of northern Honshu, Japan. *Memoirs of the National Science Museum*, *Tokyo* (29):153–185.

Shinohara, G., H. Endo, K. Matsuura, Y. Machida, and H. Honda. 2001. Annotated checklist of the deep-water fishes from Tosa Bay, Japan. Pages 283–343 *in* T. Fujita, H. Saito, and M. Takeda, eds., Deep-Sea Fauna and Pollutants in Tosa Bay. *National Science Museum Monographs* (20).

Shinohara, G., and K. Matsuura. 1997. Annotated checklist of deep-water fishes from Suruga Bay, Japan. *National Science Museum Monographs* (12):269–318, pls. 1–2.

Shinohara, G., T. Sato, Y. Aonuma, H. Horikawa, K. Matsuura, T. Nakabo, and K. Sato. 2005. Annotated checklist of deepwater fishes from the waters around the Ryukyu Islands, Japan. Pages 385–452 *in* K. Hasegawa, G. Shinohara, and M. Takeda, eds., Deep-Sea Fauna and pollutants in the Nansei Islands. *National Science Museum Monographs* (29).

Shiobara, Y. 1982. A deep-sea macrouroid fish, *Squalogadus modificatus* from the inshore areas of Suruga Bay, Japan. *Annual Report of the Marine Science Museum of Tokai University* (10):143–146.

Smale, J. M., G. Watson, and T. Hecht. 1990. Otolith atlas of southern African marine fishes. *Ichthyological monographs of the JLB Smith Institute of Ichthyology* 1:1–253.

Smith, H. M. and L. Radcliffe. *in* Radcliffe, L. 1912. Descriptions of a new family, two new genera, and twenty-nine new species of anacanthine fishes from the Philippine Islands and contiguous waters. *Proceedings of the U.S. National Museum* 43:105–140.

Steindachner, F., and L. Döderlein. 1887. Beiträge zur Kenntniss der fische Japan's. (IV. *Denkschr. Akademisch Wissenschaft Wien* 49(1. Abth.):257–296, pls. 1–4. 295 pp.

Temminck, C., and H. Schlegel. 1842. *Fauna Japonica. 2. Pisces*. Leiden, Netherlands. 345 pp., 143 pls.

Weber, M. 1913. Die Fische der SIBOGA-Expedition. *Siboga Expedition* 57:1–179, pls. 1–12.

Wilson, R. R., Jr. 1994. Interrelationships of the subgener of *Coryphaenoides* (Gadiformes: Macrouridae): comparison of protein electrophoresis and peptide mapping. *Copeia* 1994(1):42–50.

Wilson, R. R., Jr., and P. Attia. 2003. Interrelationships of the subgenera of *Coryaenoides* (Teleostei: Gadiformes: Macrouridae): synthesis of allozyme, peptide mapping, and DNA sequence data. *Molecular Phylogenetic and Evolution* 27:343–347.

Wilson, R. R., Jr., J. F. Siebenaller, and B. J. Davis. 991. Phylogenetic analysis of species of three subgenera of *Coryphaenoides* (Teleostei: Macrouridae) by peptide mappin of homologs of LDH-$A_4$. *Biochemical Systematics and Ecology* 18:565–572.

Xiong, G., H. Zhan, and S. Deng. 1988. Gadiformes, Beryciformes. Pages 166–219 *in* Li Chuan Jing, ed., [and Deep water fishes of the East China Sea Editorial Subcommittee], *The Deep Water Fishes of the East China Sea.* Xue Lin Publishing House, Shanghai, China. 356 pp. (In Chinese.)

# Appendix

TABLE 1. Collection data for station of research vessels and commercial trawls operating out of nine fishing ports. Abbreviations: CD—otter trawl station; OCP—ORE-type beam trawl station and CP—the French type beam trawl station.

| Station/Location | Longitude and Latitude | Region | Date | Depth (m) |
|---|---|---|---|---|
| CP 119 | 122°01′E, 24°56′N | NET | 7/31/01 | 123–140 |
| CP 120 | 122°02′E, 24°51′N | NET | 7/31/01 | 520–640 |
| CP 124 | 122°17′E, 24°58′N | NET | 8/1/01 | 1129–1165 |
| CP 127 | 121°03′E, 22°08′N | SET | 8/21/01 | 1263–1268 |
| CP 130 | 120°07′E, 22°19′N | SCS | 8/22/01 | 709–728 |
| CD 133 | 120°08′E, 22°15′N | SCS | 11/21/01 | 690–748 |
| CD 134 | 120°06′E, 22°16′N | SCS | 11/22/01 | 736–1040 |
| CD 136 | 120°00′E, 22°07′N | SCS | 11/22/01 | 998–1211 |
| CD 137 | 120°25′E, 22°12′N | SWT | 11/23/01 | 316–477 |
| CD 138 | 120°20′E, 22°13′N | SWT | 11/23/01 | 441 |
| CD 139 | 120°14′E, 22°10′N | SWT | 11/23/01 | 718–852 |
| CD 140 | 120°22′E, 22°11′N | SWT | 11/23/01 | 280–452 |
| CD 141 | 119°59′E, 22°12′N | SCS | 11/24/01 | 985–1110 |
| CD 142 | 120°13′E, 22°21′N | SWT | 11/24/01 | 227–335 |
| CP 178 | 119°55′E, 22°25′N | SCS | 8/25/02 | 1241 |
| CD 191 | 118°22′E, 21°41′N | SCS | 8/28/02 | 1621–1630 |
| CD 192 | 120°01′E, 22°17′N | SWT | 8/29/03 | 1305 |
| CD 193 | 120°06′E, 22°22′N | SWT | 8/29/02 | 821 |
| CD 194 | 120°24′E, 22°11′N | SET | 8/29/02 | 507 |
| CP 195 | 122°03′E, 24°52′N | NET | 9/11/02 | 570 |
| CP 196 | 122°03′E, 24°51′N | NET | 9/11/02 | 646–787 |
| CP 197 | 122°17′E, 24°51′N | NET | 9/11/02 | 1040–1141 |
| CD 199 | 122°12′E, 24°25′N | ET | 9/12/02 | 1134–1188 |
| CD 203 | 120°28′E, 22°00′N | SCS | 5/29/03 | 634–866 |
| CD 209 | 122°11′E, 24°40′N | NET | 5/30/03 | 508–522 |
| CD 210 | 122°12′E, 24°28′N | ET | 5/31/03 | 445–1185 |
| CD 211 | 122°11′E, 24°40′N | NET | 8/26/03 | 517–529 |
| CD 214 | 122°12′E, 24°28′N | ET | 8/27/03 | 488–1027 |
| CP 214 | 122°13′E, 24°29′N | NET | 8/27/03 | 488 |
| CD 226 | 121°04′E, 22°18′N | SET | 8/29/03 | 1174–1212 |
| CD 228 | 121°01′E, 22°08′N | SET | 8/30/03 | 1262–1290 |
| CD 229 | 120°01′E, 22°13′N | SWT | 8/30/03 | 880–1062 |
| CD 230 | 120°03′E, 22°19′N | SWT | 8/30/03 | 810–850 |
| CD 233 | 120°19′E, 22°11′N | SWT | 8/31/03 | 448–526 |
| CP 234 | 122°31′E, 25°22′N | NET | 7/22/04 | 547 |
| CP 235 | 122°43′E, 25°23′N | NET | 7/23/04 | 764 |

TABLE 1. Continued.

| Station/Location | Longitude and Latitude | Region | Date | Depth (m) |
|---|---|---|---|---|
| CP 242 | 122°29′E, 25°08′N | NET | 7/23/04 | 979 |
| CP 247 | 122°02′E, 24°52′N | NET | 8/28/04 | 480 |
| CP 248 | 122°02′E, 24°51′N | NET | 8/28/04 | 536 |
| CP 250 | 122°04′E, 24°55′N | NET | 8/28/04 | 220 |
| CD 271 | 120°.8′E, 22°19′N | SWT | 12/28/04 | 700–800 |
| CP 299 | 122°03′E, 22°19′N | SET | 8/11/05 | 799 |
| OCP 301 | 120°06′E, 22°20′N | SET | 8/11/05 | 687 |
| OCP 302 | 120°06′E, 22°21′N | SET | 8/11/05 | 695 |
| OCP 303 | 120°15′E, 22°10′N | SWT | 8/15/05 | 807 |
| CD 307 | 118°14′E, 21°35′N | SCS | 8/16/05 | 1591 |
| CD 310 | 117°17′E, 21°35′N | SCS | 8/17/05 | 364 |
| CD 311 | 117°43′E, 21°40′N | SCS | 8/17/05 | 516 |
| OCP 312 | 117°43′E, 21°40′N | SCS | 8/17/05 | 517 |
| OCP 313 | 117°43′E, 21°40′N | SCS | 8/17/05 | 513 |
| CP 314 | 117°43′E, 21°40′N | SCS | 8/17/05 | 506 |
| CP 315 | 117°43′E, 21°40′N | SCS | 8/17/05 | 509 |
| CP 316 | 117°43′E, 21°40′N | SCS | 8/17/05 | 514 |
| OCP 317 | 117°43′E, 21°40′N | SCS | 8/17/05 | 515 |
| CD 320 | 117°27′E, 20°50′N | SCS | 8/17/05 | 731 |
| CD 321 | 117°33′E, 20°43′N | SCS | 8/19/05 | 954 |
| CD 322 | 117°39′E, 20°44′N | SCS | 8/19/05 | 1098 |
| CD 324 | 117°45′E, 20°40′N | SCS | 8/20/05 | 1293 |
| CD 325 | 118°03′E, 20°40′N | SCS | 8/20/05 | 1982 |
| CP 338 | 120°20′E, 22°10′N | SCS | 3/7/06 | 569 |
| CP 339 | 120°15′E, 22°10′N | SCS | 3/7/06 | 846 |
| CP 347 | 120°13′E, 22°25′N | SCS | 3/9/06 | 305 |
| CP 348 | 120°12′E, 22°22′N | SCS | 3/9/06 | 395 |
| CP 350 | 121°08′E, 22°21′N | SET | 6/2/06 | 1148 |
| CP 353 | 121°04′E, 22°15′N | SET | 6/2/06 | 1205 |
| CP 366 | 121°10′E, 22°01′N | SET | 8/24/06 | 1302 |
| Da-xi | 121°54′E, 24°56′N | NET | | ca. 100–650 |
| Diao-yu-tai | 123°30′E, 25°43′N | NET | | ca. 100–400 |
| Hsiao-liou-chiou | 120°22′E, 22°20′N | SWT | | ca. 100–400 |
| Fong-kang | 120°41′E, 22°11′N | SWT | | ca. 100–200 |
| Jin-shan | 121°55′E, 25°33′N | NT | | ca. 100 |
| Lyu-dao | 121°29′E, 22°38′N | ET | | ca. 400 |
| Nan-fang-ao | 121°52′E, 24°35′N | NET | | ca. 100–600 |
| Dong-gang | 120°26′E, 22°27′N | SWT | | ca. 100–400 |
| Tong-sa Islands | 116°51′E, 20°41′N | SCS | | ca. 100–600 |

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# Mosses New for Mindanao Island, Republic of the Philippines

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**Twelve new moss records are reported for Mindanao; two of these, *Fissidens pallidinervis* Mitten and *Symphysodon longicuspis* (Brotherus) Brotherus are new records also for the Philippine moss flora. The re-classification of moss taxa from the phytogeographical category of Taiwan-Philippine (Luzon) endemics to Wallacean endemics is noted.**

KEYWORDS: Asian mosses, bryophyte inventory, species distribution, Philippines, Mindanao Island, new records

The moss flora of Mindanao has gained the interest of bryologists in recent years (Tan et al. 2000; Lubos 2007; Linis 2010; Tan and Shevock 2014). The new focus on the Mindanao biota, including the mosses, is brought by the increasing knowledge of tectonic history of this island which plays an important role in the evolution of the biotic diversity of the Philippines and the adjacent island groups in Malesia (Hall 1998; Michaux 1991; Tan 1992). Today, the island of Mindanao at 104,630 km$^2$ harbors a significant number of Gondwana species of plants in the Philippines that are not found in other island groups in the country (Linis and Tan 2008; Tan and Shevock 2014).

Fortunately, Mindanao still has, at present, plenty of mossy forests left on its high mountain peaks that preserve much of the bryophyte diversity in the country (figs. 1–2). Furthermore, the island has a small group of active resident botanists documenting the local plant diversity. They have collected, over the years, a number of new and noteworthy moss specimens representing hitherto unreported taxa from various provinces on the island. We report below twelve new moss records for Mindanao; two of these, *Fissidens pallidinervis* Mitten and *Symphysodon longicuspis* (Brotherus) Brotherus are new records also for the Philippine moss flora. Serving as Part II of Tan and Shevock (2014), the present report follows the same format and style in the listing of new species records of Mindanao mosses.

### 1. *Clastobryopsis robusta* (Brotherus) M. Fleischer [Sematophyllaceae]

This is widespread Malesian moss species, reported here for the first time from Mindanao, is characterized by having many expanded, somewhat complanate, and attenuated branch terminals that produce plenty of filamentous propagules in leaf axils. This species is rather large in plant size among its congeners and can be recognized further by having broad, decurrent leaf bases, recurved upper leaf margins with strong marginal teeth, and, a heterophylloid alar organization (cf. Tan and Jia 1999). In the Philippines, *Clastobryopsis robusta*, which is an epiphyte of small branches in forest canopy, is also widespread on Luzon Island and islands of the Visayan group.

FIGURE 1. In Mindanao typical mossy forests are primarily restricted to steep mountainous areas generally exceeding 1500 m in elevation. At this elevation, ample precipitation forms cloud forest environments ideal for bryophyte cover. The amount of water retained by bryophytes in such forests can be significant. Photo by J. Shevock.

FIGURE 2. High quality cloud forest habitat draped in bryophyte cover. Collecting in high quality forests is primarily limited to existing roads and trails. Cross-country travel is difficult and slow due to dense forest vegetation and steep slopes. Bryophytes colonize a wide variety of habitats from soil, litter, rotten wood, and boulders on the forest floor to shrubs, tree trunks, to small branches and twigs up in the forest canopy. Inventory efforts to document the diversity of species present at any location need to sample all of the available microhabitat conditions. Photo by J. Shevock.

**Specimen examined**.— Bukidnon Province. Mt. Kitanglad Range Natural Park, on branch in forest, 6 Sep 2007, *Azuelo et al. s.n.* (CMUH, UC).

### 2. *Dendrocyathophorum paradoxum* (Brotherus) Dixon [Hypopterygiaceae]

The genus and the species are easy to identify in the family Hypopterygiaceae. The complanate and dendroid plant with irregular branches and leaves arranged in three rows characterizes *Dendrocyathophorum*. Treated as a monotypic genus in the recently published *Flora of China* (English Version) (Jia et al. 2002), our report extends the local range of *D. paradoxum* from Luzon to Mindanao in the country. The species has a scattered distribution across tropical and subtropical Asia, including Malesia.

**Specimen examined**.— Misamis Oriental Province. Mt. Balatukan near Gingoog City, on tree trunk, 22 Oct 2005, *Padayao 22 b* (CMUH 02, UC).

### 3. *Elmeriobryum philippinense* Brotherus [Hypnaceae]

[syn. *Gollania philippinensis* (Brotherus) Noguchi, *Elmeriobryum assimile* Brotherus, *Elmeriobryum brotheri* R.S. Williams ex Brotherus]

In a very recent revision, the genus *Elmeriobryum* Brotherus was shown to consist of two species in Asia, namely, *E. philippinense* found in continental China (Guangdong Province), Taiwan and the Philippines, and *E. wilhemense* (E.B. Bartram) W.R. Buck & B.C. Tan, restricted to Papua New Guinea (Buck and Tan 2007; Higuchi 1985). The two species were stated to differ diagnostically in their plant size and altitudinal range (Buck and Tan 2007). A good illustration of *Elmeriobryum philippinense* is shown in Higuchi (1985, as *Gollania philippinensis*).

For many years, *E. philippinense* was known only from northern Luzon, which is geographically close to Taiwan and mainland China, representing an example of the "Taiwan-Philippine (Luzon)" endemics. Yet, *E. philippinense* is now shown to be present also in Mindanao. See the report of *Trachypus longifolius* Noguchi below for a similar distribution pattern.

**Specimens examined**.— Bukidnon Province. Mt. Kitanglad Range Natural Park, on tree trunk, 25 Apri 2009, *Azuelo s.n.* (CMUH, UC); ibid, epiphytic, 7 Sep 2007, *Azuelo s.n.* (CMUH 30, UC).

### 4. *Fissidens pallidinervis* Mitten [Fissidentaceae]

[syn. *F. garberi* Lesquereux & James, *F. minutus* Thwaites & Mitten, *F. rizalensis* E.B. Bartram]

*Fissidens pallidinervis* is a nearly pantropical and a micro-*Fissidens* species that is characterized by having pluripapillose laminal cells, obtuse to round leaf apices, and limbidia restricted to vaginant laminae. In many recent publications, Philippine specimens of *Fissidens* with pluripapillose laminal cells, obtuse leaf apices and a percurrent leaf costa are treated as one broad taxon, *F. microcladus* Thwaites & Mitten (see Tan and Iwatsuki 1991). Pursell et al. (1993) made a clarification of the species concept of this confused group of taxa and regrouped them into two separate species, i.e., *F. pallidinervis* and *F. gardneri* Mitten (syn. *F. microcladus*). The main difference of these two segregated species lies in the size of the two vaginant laminae on the leaf (Pursell et al. 1993). Good illustrations of the two species are presented by Pursell (2007).

The new Mindanao collection reported here is identified as *Fissidens pallidinervis*. It is a new species record for Mindanao. Because of the past taxonomic confusion, its distribution in Luzon and Visayan Island groups needs a clarification.

**Specimen examined**.— Bukidnon Province. Mt. Kitanglad Range Natural Park, on soil, *Azuelo et al. s.n.* (CMUH).

### 5. *Holomitrium cylindraceum* (P. Beauvois) Wijk & Margadant [Dicranaceae]

[syn. *H. vaginatum* (Hooker) Bridel, *H. javanicum* Dozy & Molkenboer]

The genus is distinctive in the family Dicranaceae in having rather large perichaetial leaves enfolding ⅓ the length of the seta. The leaves have round to oval, thick-walled laminal cells, and the leaf alar consists of numerous quadrate, also thick-walled and colored cells. The habit illustration of this species in Gao et al. (1999, Plate 49) with long acuminate leaf apices is misleading. Accurate illustrations of this species are found in Fleischer (1904, as *Holomitrium javanicum*), Bartram (1939, as *H. vaginatum*) and Eddy (1988, as *H. vaginatum*). The species has a wide distribution from eastern Africa to Malesia and Polynesia (Eddy 1988). Before the present report of this species from Mindanao, *Holomitrium cylindraceum* had been reported from Luzon and Mindoro (Tan and Iwatsuki 1991).

SPECIMENS EXAMINED.— Bukidnon Province. Mt. Kitanglad Range Natural Park, on trail to Mt. Kitanglad, 17 Nov 2008, *Azuelo 112* (CAS, CMUH); Mt. Kalatungan, San Guinto, Barangay Bacusanon, on decayed log, 27–29 Dec 2012, *Segumpan, Roble & Octaviano s.n.* (CMUH).

### 6. *Leiomela javanica* (Renauld & Cardot) Brotherus [Bartramiaceae]

This is a genus in Bartramiaceae that has long setaceous leaves with prorate leaf cells, sessile capsules, and reduced peristome teeth. Only one species is known in Malesia, based on a Philippine record from Luzon (Tan and Iwatsuki 1991). There are no previously published records for its occurrence on Mindanao until the present report.

SPECIMEN EXAMINED.— Bukidnon Province. Mt. Kitanglad Range Natural Park, mid slope along trail toward Mt. Kitanglad, on trunk of tree fern, 26 Apr 2009, between 2100–2610 m, *Azuelo 178* (CAS, CMUH).

### 7. *Mniomalia semilimbata* (Mitten) Müller Hal. [Phyllodrepaniaceae]

This is a very distinctive moss characterized by asymmetrical leaf shape with a one-sidedly located midrib. *Mniomalia semlimbata* grows preferably on moist shaded substrates in forest. In the Philippines, this widely scattered Malesian moss previously had been reported from a few locations on Luzon (Tan and Iwatsuki 1991).

SPECIMEN EXAMINED.— Agusan del Sur Province. Philsaga Mining Corporation, Brgy. Bayugan, Rosario, on moist rock, Feb 2014, 200–500 m, *Raganas s.n.* (CMUH).

### 8. *Rhacocarpus alpinus* (C.H. Wright) Paris [Rhacocarpaceae]

The species can be recognized by the dull, yellowish brown coloration of the specimens. The appressed, thick and leathery leaves are also distinctive. It was known previously from only one locality in the Philippines, Mt. Halcon in Mindoro (Tan and Mandia 2001). Its presence in Mindanao fills in the distribution gap of this widespread Gondwana taxon in the country.

SPECIMENS EXAMINED.— Bukidnon Province. Mt. Kitanglad Range Natural Park, on summit ridge of Mt. Dulang-Dulang, boggy ridge along saddle, 9 Jun 2007, *Azuelo s.n.* (CMUH, UC); ibid, in small bog with *Sphagnum* and *Campylopus*, 2740 m, 24 Apr 2014, *Shevock, Fritsch & Opiso 44868* (CAS, CMUH, NY, PNH, UC).

### 9. *Symphyodon copelandii* Brotherus [Symphyodontaceae]

The genus is distinctive with its echinate capsules. Without the capsule, specimens of *Symphyodon* can be mistaken for *Chaetomitrium* or *Neckera* because of the prorate laminal cells and the short double leaf costae. *Symphyodon copelandii* is the second species of the genus reported from Mindanao after *S. perrottetii* Montagne. The two species differ in the outline of their leaf apices being acute to bluntly and shortly acuminate in the former, and gradually acuminate in the latter. Good illustrations of these two species are found in He and Snider (2000). As currently documented, *Symphyodon copelandii* has a Wallacean range found in the Philippines and central part of Indonesia (Sulawesi and Lesser Sunda Islands).

**Specimen examined.**— Bukidnon Province. Mt. Kalatungan, San Guinto, Barangay Bacusanon, on tree trunk at ca 2000 m, 28 Dec 2012, *Segumpan et al. s.n* (CMUH, UC).

### 10. *Symphysodon longicuspis* (Brotherus) Brotherus [Pterobryaceae]

The genus *Symphysodon* is recognized easily by its dendroid plant habit with attenuate branches. The leaves are concave, unicostate and with acuminate apices. *Symphysodon longicuspis* differs from its congeners in having a large plant size and slightly concave and narrowly lanceolate leaves with gradually narrowed and long acumen that is bordered with strong dentation. Its closest relative is alleged to be *Symphysodon neckeroides* (see Hyvönen 1989), which differs from this species in having a smaller stature and more strongly concave leaves with an abruptly narrowed short to long, toothed acumen.

*Symphysodon neckeroides* Dozy & Molkenboer var. *tjibodensis* M. Fleischer (1908) was noted to differ from var. *neckeroides* in having larger plant size with leaves having a gradually, not abruptly, narrowed long acumen. We suspect that the var. *tjibodensis* is a synonym of *S. longicuspis*.

*Symphysodon longicuspis* is reported to be an endemic of Papua New Guinea (Hyvönen 1989). Herein we report this as a new record for the Philippine moss flora. Its presence in Mindanao indicates the New Guinea connection of the Philippine moss flora.

**Specimens examined.**— Bukidnon Province. Mt. Kiamo, on tree trunk in lower montane forest by a deeply shaded stream, 7 May 2014, *Tan 2014-271* (UC), *Shevock & Tan 45161* (CAS, CMUH, MO, UC).

### 11. *Trachypodopsis serrulata* (P. Beauvois) M. Fleischer var. *crispatula* (Hooker) Zanten [Trachypodaceae]

The taxon is characterized by having a robust plant size with subpinnate branches forming brownish mats on forest floor. The leaves are longitudinally plicate, unipapillose, unicostate, with long acuminate apex and strongly cordate leaf bases with marked alar differentiation (Zanten 1959).While the species is widespread in Malesia and in Luzon of the Philippine archipelago, the record is new to Mindanao Island both as a variety, species and genus.

**Specimens examined.**— Bukindon Province. Mt. Kitanglad Range Natural Park, on tree trunk, 7 Sep 2007, *Azuelo s.n.* (CMUH, UC); upper slope of Dulang-Dulang, on litter, snag and base of hardwood trunks, 2620 m, 22 Apr 2014, *Shevock 44819* (CAS, CMUH, MO, UC), 23 Apr 2014, *Shevock 44863* (CAS, CMUH, UC) and 2875 m, 24 Apr 2014, *Shevock, Fritsch & Opiso 44881* (CAS, CMUH, NY, UC).

### 12. *Trachypus longifolius* Noguchi [Trachypodaceae]

Among the species of *Trachypus* Reinwardt & Hornschuch, this species has a distinctive oblong-lanceolate leaf blade with very long, narrow and acuminate acumen (van Zanten 1959). Its previous Philippine record is from northern Luzon (Tan and Iwatsuki 1991). The range extension of this species from northern Luzon to southern part of the Philippines, and notably its presence in

Mindanao, suggests that it does not belong to the phytogeographical category of Taiwan-Philippine (Luzon) endemic group. Indeed, additional searches among the neighboring island groups south of Mindanao may show that this species actually has a broader range, representing, instead, the Wallacean biota or Central Malesian phytogeographical group (Vallejo 2011; van Welzen et al. 2011; Vane-Wright 1990).

**SPECIMENS EXAMINED**.— Bukidnon Province. Mt. Kalatungan, San Guinto, Barangay Bacusanon, on tree trunk at ca 2000 m, 19 May 2013, *A. Azuelo 23* (CMUH, UC); North Catabato Province. Kidapawan City. Mandarangan Trail along slope from Site B of Geothermal Production Field of EDC to Agco Mahomanoy Mountain Resort, on hardwood tree trunk, 1430 m, *Shevock & Tan 45067* (CAS, CMUH, UC).

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## LITERATURE CITED

BARTRAM, E. B. 1939. Mosses of the Philippines. *Philippine Journal of Science* 68:1–437.

BUCK, W. R., AND B. C. TAN. 2007. A review of *Elmeriobryum*. *Telopea* 12:251–256.

EDDY, A. 1988. *A Handbook of Malesian Mosses. Vol. 1. Sphagnales to Dicranales*. British Musuem (Natural History), London, England, UK.

FLEISCHER, M. 1904. *Die Musci der Flora von Buitenzorg,* Bd. 1, pp. xxxi + 379. E.J. Brill, Leiden, Netherlands.

FLEISCHER, M. 1908. *Die Musci der Flora von Buitenzorg*, Bd. 3, pp. xxiv + 645–1103. E.J. Brill, Leiden, Netherlands.

GAO, C., D. H. VITT, AND S. HE. 1999. Dicranaceae. Pages 90–241 *in* C. Gao and M. R. Crosby, eds., *Moss Flora of China* (English Version). *Vol. 1. Sphagnaceae-Leucobryaceae*. Science Press, Beijing, China and Missouri Botanical Garden Press, St. Louis, Missouri, USA.

HALL, R. 1998. The plate tectonics of Czenozoic SE Asia and the distribution of land and sea. Pages 99–131 *in* R. Hall and J. D. Holloway, eds., *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, Netherlands.

HE, S., AND J. A. SNIDER. 2000. A taxonomic revision of *Symphyodon* (Musci: Symphyodontaceae). *Bryologist* 103:52–81.

HIGUCHI, M. 1985. A taxonomic revision of the genus *Gollania* Broth. (Musci). *Journal of Hattori Botanical Laboratory* 59:1–77.

HYVÖNEN, J. 1989. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXVI. Pterobryaceae (Musci). *Acta Botanica Fennica* 137:1–40.

JIA, Y., Z.-H. LI, AND P-C. WU. 2002. Hypopterygiaceae. Pages 43–64 *in* P.-C. Wu and M. R. Crosby, eds., *Moss Flora of China* (English Version). *Vol. 6. Hookeriaceae-Thuidiaceae*. Science Press, Beijing, China and Missouri Botanical Garden Press, St. Louis, Missouri, USA.

LINIS, V. C. 2010. The moss flora of Camiguin Island, Philippines and their floristic relations to some adjacent islands in the archipelago. *Telopea* 12(4):525–542.

LINIS, V. C., AND B. C. TAN. 2008. Progress of studies on phytogeography and biodiversity of Philippine moss flora from 1991 to 2006. Pages 13–22 *in* H. Mohamed, B. B. Baki, A. Nasrulhaq-Boyce, and P. K. Y. Lee, eds., *Bryology in the New Millennium*. University of Malaya, Kuala Lumpur, Malaysia.

LUBOS, L. C. 2007. New records of Philippine mosses from Mindanao Island. *Liceo Journal of Higher Education Research* 5:1–8.

MICHAUX, B. 1991. Distributional patterns and tectonic development in Indonesia: Wallace reinterpreted. *Australian Systematic Botany* 4:25–36.

PURSELL, R. A. 2007. Fissidentaceae. *Flora Neotropica Monograph* 101:1–278.

PURSELL, R. A., M. A. BRUGGEMAN-NANNENGA, AND Z. IWATSUKI. 1993. The identity of *Fissidens gardneri* and *Fissidens minutus*. *Bryologist* 96:626–628.

TAN, B. C. 1992. Philippine Muscology (1979–1989). *Bryobrothera* 1:137–141.

Tan, B. C., and Z. Iwatsuki. 1991. A new annotated Philippine moss checklist. *Harvard Papers in Botany* 3:1–64.

TAN, B. C. AND Y. JIA. 1999. A preliminary revision of Chinese Sematophyllaceae. *Journal of Hattori Botanical Laboratory* 86:1–70.

TAN, B. C., L. C. LUBOS, AND U. SCHWARTZ. 2000. New and biogeographically noteworthy records of Philippine mosses from Mindanao Island. *Tropical Bryology* 18:27–37.

TAN, B. C., AND E. H. MANDIA. 2001. New and noteworthy records of mosses from Mindoro, the Philippines, and their biogeographical implication. *Gardens' Bulletin Singapore* 53:315–322.

TAN, B. C. AND J. R. SHEVOCK. 2014. Noteworthy mosses collected from the 2014 joint expedition of CAS and CMU new to Mindanao Island of the Philippines. *Bryophyte Diversity and Evolution* 38:22–30.

VALLEJO, B. JR. 2011. The Philippines in Wallacea. Pages 27–42 *in* D. Telnov, ed., *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea*, Vol. 1. The Entomological Society of Latvia, Riga, Latvia.

VAN WELZEN, P. C., J. A. N. PARNELL, AND J. W. F. SLIK. 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? *Biological Journal of Linnean Society* 103: 531–545.

VAN ZANTEN, B. O. 1959. Trachypodaceae, a critical revision. *Blumea* 9:477–575.

VANE-WRIGHT, R. I. 1990. The Philippines — key to the biogeography of Wallacea? Pages 19–34 *in* W. J. Knight and J. D. Holloway, eds., *Insects and the Rainforests of Southeast Asia*. Royal Entomological Society of London, London, England, UK.

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# Morphology and Systematics of *Kalophrynus interlineatus-pleurostigma* Populations (Anura: Microhylidae: Kalophryninae) and a Taxonomy of the Genus *Kalophrynus* Tschudi, Asian Sticky Frogs

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**Sticky Frogs, *Kalophrynus* Tschudi, are a small group of Southeast Asian species with their greatest diversity in Borneo. Two species, *K. interlineatus* (Blyth) and *K. pleurostigma* Tschudi, were proposed as residents of Myanmar (Burma), northern and southern populations respectively. An analysis of morphological variation in Burmese specimens and comparison with small samples from throughout the distribution of the *interlineatus-pleurostigma* group of species demonstrates variable levels of regional differentiation, which I interpret as evidence of speciation. This interpretation recommends the restriction of *K. pleurostigma* to Sumatra populations and *K. interlineatus* to peninsular Myanmar and adjacent mainland Southeast Asian populations. The northern Borneo populations have the largest body size of any members of this group and represent a new species, *K. meizon*. The Philippine populations, *K. sinensis* Peters, are confirmed as unique as proposed recently by Ohler and Grosjean (2005). The populations from northern Myanmar also represent a distinct taxon, *K. anya*, and differ from *K. orangensis* (India and Bangladesh) and *K. interlineatus* (peninsular Myanmar and Southeast Asia). To assist the on-going discovery of new species of this cryptic frog group, I provide a taxonomic resumé of all currently recognized species of the genus *Kalophrynus* and a diagnostic key to all species of *Kalophrynus*.**

KEYWORDS: nomenclature, anatomy, morphometrics, tropical Asia, Myanmar, Thailand, Sumatra, Borneo, Philippines, Amphibia, *Kalophrynus*

Tschudi (1838) recognized the uniqueness of the Sticky Frogs with the erection of a new genus, *Kalophrynus*. Simultaneously he described *K. pleurostigma* for a specimen from Sumatra, thereby establishing this taxon as the type species of *Kalophrynus*. The Sumatran origin has not been questioned, although few Sumatran specimens are available to provide a thorough examination of variation of topotypic *K. pleurostigma* in the broadest sense of all Sumatran populations.

The scarcity of Sumatran specimens and the widespread occurrence of presumably similar appearing frogs from southern Myanmar through Southeast Asia to Borneo and the Philippines led to the name *pleurostigma* being applied to the larger-bodied Sticky Frogs in this area. This concept of *K. pleurostigma* had its foundation in Parker's review (1934) of the Microhylidae. Therein, he recognized four of the eight species of *Kalophrynus* described prior to his review. He considered the broadly distributed *K. pleurostigma* as consisting of two subspecies (nominate and *interlineatus*). This concept persisted for sixty years until Matsui et al. (1996) recognized the two subspecies as full species with *K. interlineatus* for the northern populations and *K. pleurostigma* for the southern ones.

During our Myanmar Herpetological Survey's (MHS) country-wide survey of the composition and distribution of the herpetofauna of Myanmar, I noted the absence of populations of any *Kalophrynus* species in central Myanmar (between 18° to 23°N). This area was visited repeatedly between 1997 and 2009 by our MHS teams. This absence and a preliminary examination and comparison of a few individuals from northern and peninsular Myanmar encouraged me to examine more closely the morphology of Burmese *Kalophrynus*. That examination led me to broaden the investigation to include samples of *interlineatus-pleurostigma* frogs from throughout the range of these two species. The first part of this report details the results of that study. My literature review for the preceding morphological analysis informed me of the scattered nature of the published records on the species of *Kalophrynus* and the absence of consistent characterization of the now 25 species of this genus. I have attempted a review of the *Kalophrynus* literature and offer a series of standardized species accounts for every recognized species of this genus through September 2014.

Owing to the long term adoption of *K. pleurostigma* as a broadly distributed Asian species with two subspecies, I assumed at the beginning of my analysis of Burmese *interlineatus-pleurostigma* populations that these populations represented a single clade. The Asian-wide populations are not a single clade as I will demonstrate later in a discussion of recent molecular phylogenetic studies. Nevertheless, my focus remains on these populations as they have been historical treated as a single species, which had not undergone a detailed morphological examination, i.e., the major goal of this study. For convenience, I refer to these broadly distributed populations as the *interlineatus-pleurostigma* group, a phenetic paradigm and not a clade.

## MATERIALS AND METHODS

The morphometric characters are standard ones for the study of frog morphology and are defined in the Appendix 2. *Character definitions*. Sex and maturity for the frogs examined were determined by dissection. I note my preference again for abbreviated labels, such as HeadL and SnEye, for character names versus the usual initial abbreviations, i.e., HL and SE, which are uninformative to all but frog specialists. I developed a set of color pattern characters for the Sticky Frogs. Although I am not totally satisfied with these defined traits, I argue that this qualitative approach to the major features of *Kalophrynus* coloration is less subjective than verbal descriptions and, further, allows statistical examination of intra- and interpopulational variation.

Whether descriptive or qualitative, recording coloration (i.e., both color and pattern) of preserved specimens remains subjective owing to the varying degrees of fading, manner of original preservation, and other factors. Our recent MHS specimens, their field descriptions, and, in some cases, photographs give me confidence in my coding and recording of coloration traits for them but leaves me much less confident of my data from older specimens (extra-Myanmar) from other collections. The erection of a coding scheme for documenting the various features of color pattern attempts to overcome some of the subjectivity resulting from preservation related changes in coloration (I use coloration to include the color of an individual and the pattern of color marks, e.g., stripes, blotches, spots, etc.). The coding reduces the arbitrariness of recording and analysis of pattern, but problems remain; these are noted in the analysis of coloration traits.

The samples are identified in Appendix 1. *Specimens examined*. Although the impetus for this project was Burmese frogs, perusal of the literature and my initial examination of specimens from outside of Myanmar indicated the necessity of a wider geographic exploration of morphological variation and eventually encompassed the entire range of the *interlineatus-pleurostigma* group (also see Ohler and Grosjean 2005). Although my study encompasses the entire range of this group, I limited my sampling to seven sites within the group's total range. With the exception of the Thai-Indochina sample, the samples each derives from a limited geographic area (see Appendix 1). All statistical analyses were performed with SYSTAT version 12. Students' *t* tests determined whether adult females and males were significantly different ($P = 0.05$); body proportions were arcsine-transformed to approximate normal distributions for each sample. Proportions are reported in the text as the original proportions, not their arcsine-transformed values. I use the standard leaf-shape definitions, commonly illustrated in botanical text, for describing the outline shape of head and body.

Because *K. pleurostigma* has been identified as the species of southern peninsular Myanmar and the remainder of the Malayan Peninsula, this study needed to characterize *K. pleurostigma* in a broader geographic area than Myanmar and further to confirm that *K. pleurostigma* from this mainland area was the same as the Sumatra population, i.e., the topotypic population. The available Sumatra specimens are few, and I discovered from a colleague, H. Kaiser, that the type specimen of *K. pleurostigma* had deteriorated badly. *Kalophrynus pleurostigma* is the type-species of the genus, hence the designation of a neotype has been proposed (Zug and Kaiser 2013). I provide a description of the neotype herein and a brief diagnosis of the genus *Kalophrynus*. Although this detour is seemingly extraneous to a study of Burmese frogs, it has become evident during the past decade that the majority of the presumed widespread tropical Asian frog species are multi-species complexes. To resolve the nomenclature for a narrow regional sample frequently creates uncertainty in the taxonomic identity of populations elsewhere in the range of the former pan-Asian species.

## Results

### Morphology and Variation

*Sexual dimorphism*.— Five of the regional samples are sufficiently large to test for sexual dimorphism in adults: northern Myanmar (Sagaing only; 5 females, 4 males); central peninsular Myanmar (Tanintharyi; 7, 4); Thai-Indochina (Thailand, Laos, Vietnam, Cambodia; 4, 7); north-central Sarawak (Samarahan & Sri Aman; 11, 7); and Philippines (Bohol; 9, 17). Of the Myanmar samples, only two proportions, SnEye/SVL (38 % females, 42 % males) and EyeD/HeadL (32 %, 35 %), were significantly dimorphic in the northern sample. In contrast, the central peninsular sample had no dimorphic measurements or proportions, although the coloration trait HeadMid was dimorphic with median head stripe usually distinct in females and absent or indistinct in males. The Thai-Indochina, Sarawak, and Philippine samples are strongly size dimorphic with females as the larger sex. All measurements except Tymp are dimorphic in the Philippine samples; tympanum width averages larger (3.6 mm) in females than in males (3.4 mm) but with strong overlap and high variance. All measurements are dimorphic in Sarawak frogs, and all but TarsL in the Philippine individuals. Of the proportions, HndlL/SVL is also significantly different in all three samples with shorter legs in Sarawak and Philippine females (means 142 % females, 150 % males; 153 %, 157 % Philippines; respectively) and slightly longer in Thai-Indochina females (134 %, 133 %). Sarawak females also have significant shorter tarsi (54 %, 58 % TarsL/ThghL). Of the non-metric traits, Philippine males have significantly stronger webbing of the hindfoot (1.8, 2.6 WebIII2) but no other significantly dimorphic traits. The Sarawak frogs have males with darker sides of the trunk (LatTrnk) and all other traits are monomorphic. Thai-Indochina frogs display no dimorphism in non-metric traits. The type series of *K. orangensis* contains five adults; they fall in a narrow size of range of 35 to 38 mm SVL, suggesting an absence of sexual dimorphism; no traits could be tested for dimorphism owing to small sample size and absence of trait quantification.

*Morphometrics*.— Although small, the Burmese samples reveal similar size ranges for adults from the three geographic areas: north Myanmar (Sagaing and Kachin); southeast main Myanmar (Mon, limited to five immature individuals); and central peninsular Myanmar (Tanintharyi). Additionally, the adult females and males are of equal size. The females' mean SVLs (Table 1) are the same in the north and south samples, although the north (Sagaing) sample has a broader range, which encompasses the minimum and maximum SVLs of the southern sample. Male SVL ranges of both Myanmar samples are also contained within the size range of their respective female samples. Body measurements are typically considered to be highly correlated with SVL. Such is not the case in the Tanintharyi sample. For the Tanintharyi adult sample ($n = 11$), only HeadL, SnEye, and ThghL have correlation coefficients greater than 0.50, $R = 0.70$, 0.71, 0.66, respectively. This low correlation probably results from the limited size range (i.e., absence of juveniles) of the sample and the sample's small size.

In spite of the similarities in body length in the northern and southern Burmese samples, the southern sample averages larger than the northern one in all measurements and strikingly so in all segments of the hindlimb; thus, hindlimbs are distinctly longer in the southern sample. This difference in limb length is evident in the HndlL/SVL proportion (Table 1). The proportional lengths of the components, however, do not differ; CrusL is 90 % and 87 % of total hindlimb length, north and south, respectively, and the ranges are nearly identical. The same proportional similarities exist for TarsL and HndfL. The Mon sample includes only juveniles, and it shows the same pattern of differences from the north sample as the southern sample. The Mons' mean HndlL/SVL is the highest (Table 1) of the three Burmese samples but that may result from the comparison of a sample of juveniles to samples of adult females.

TABLE 1. Select morphometric features of adult females from several geographic areas within distribution of the *Kalophrynus interlineatus-pleurostigma* species group. Character abbreviations are defined in the Appendix. The values are mean±standard deviation, minimum and maximum values; mm for SVL and percent for proportions.

| **Sample** | **SVL** | **HeadL/SVL** | **SnEye/HeadL** | **Tymp/EyeD** | **HindlL/SVL** | **CrusL/ThghL** | **HndfL/ThghL** |
|---|---|---|---|---|---|---|---|
| **Location** | | | | | | | |
| Sagaing<br>*n* = 5 | 41.2±4.46 | 27.2±1.4 | 37.7±2.2 | 74.8±13.7 | 117±5.3 | 90.0±5.3 | 87.3±8.2 |
| | 36.4–47.1 | 24.9–28.9 | 35.2–40.8 | 60.6–92.5 | 110–125 | 81.2–95.9 | 78.5–95.5 |
| Mon<br>*n* = 5 immatures | 32.2±2.17 | 33.7±2.4 | 37.3±7.0 | 80.6±10.3 | 147±5.9 | 88.1±7.8 | 88.0±5.5 |
| | 29.6–34.5 | 31.3–36.8 | 27.5–44.7 | 67.6–93.8 | 142–154 | 79.5–100.8 | 82.0–96.6 |
| Tanintharyi<br>*n* = 7 | 40.9±1.52 | 30.6±0.8 | 39.7±1.1 1 | 85.1±10.0 | 139.5±5.2 | 87.3±4.4 | 87.6±2.2 |
| | 39.3 -43.7 | 29.6–31.9 | 38.2–41.3 | 72.1–100.0 | 132–147 | 82.6–93.1 | 84.9–90.9 |
| Thai-Indochina<br>*n* = 4 | 44.7±1.68 | 31.7±2.9 | 39.3±2.3 | 81.2±4.0 | 133±6.5 | 87.2±2.6 | 86.2±4.3 |
| | 42.8–46.4 | 29.3–35.7 | 35.9–41.0 | 76.2–84.8 | 127–142 | 84.9–90.0 | 82.6–92.2 |
| Sumatra<br>*n* = 1 neotype | 34.5 | 28.7 | 41.4 | 89.7 | 152 | 80.7 | 65.9 |
| Sarawak<br>*n* = 11 | 54.8±3.95 | 32.0±1.5 | 41.1±6.20 | 101±7.0 | 141.7±6.6 | 88.8±1.7 | 77.9±4.1 |
| | 48.2–60.2 | 29.0–34.7 | 36.2–46.4 | 89.5–112.0 | 136–157 | 85.2–91.0 | 71.2–86.6 |
| Philippines<br>*n* = 9 | 42.3±1.82 | 30.6±1.9 | 40.4±2.5 | 83.0±6.1 | 153.5±6.1 | 93.1±8.3 | 88.0±8.5 |
| | 39.4–45.7 | 28.1–34.2 | 36.6–45.2 | 54.8–104 | 142–163 | 76.9–106.3 | 79.8–104.4 |

HeadL and the other head measurements are slightly smaller in the northern sample (Table 1). The proportion HeadL/SVL illustrates this difference (Table 1). The other head proportions are also less in the northern sample, and again the Mon sample is similar to the southern (Tanintharyi) sample.

Comparisons of extra-Myanmar samples show the Thai-Indochina sample's metrics overlap broadly the ranges of most Tanintharyi sample traits, although the hindfoot proportion (HndfL/ThghL) is smaller in the Thai-Indochina sample. The mean HndlL/SVL proportion of Thai-Indochina is intermediate between that of Sagaing and Tanintharyi, although its range largely overlaps Tanintharyi. The single Sumatra adult female is smaller than adult females from any other locality (Table 1), although not smaller than some adult males from elsewhere. The Sumatra female has proportionately longer hindlimbs (HndlL/SVL) than any adult Burmese female, although this proportion is within the ranges of Borneo and Philippine females. The Sumatra female differs strikingly from all other females in its relative small hindfoot length (HndfL/ThghL; Table 1). Borneo females average significantly larger than females from any other area, and for my samples, there is no overlap in SVL ranges. Relative hindfoot length of Borneo females is intermediate between that of Sumatra and Burmese females. Philippine females match the Tanintharyi and Thai-Indochina ones in all body metrics, although they average larger in relative hindlimb and crus lengths; ranges of these latter two proportions, however, overlap with those of the Tanintharyi and Thai-Indochina samples.

Only SVL and head metrics are available for *K. orangensis*. The body size of the three adult females overlaps the lower range of adult Burmese females. I am unable to compare the head morphometrics of the *K. orangensis* type series owing to a presumed error in the reported measurements of head dimensions (Dutta et al. 2000: table 1). Accepting their SVL data as correct, their HeadL measurements are too small, and SnEye and NarEye too large; HeadW and EyeD appear correct. This conclusion derives from a comparison with the samples from Myanmar and elsewhere. The problem is highlighted by adding SnEye and EyeD from their table; the resulting sum equals or exceeds HeadL. HeadL should equal roughly the sum of these two values plus Tymp. The other aspect indicating an error in their head length measurements is that HeadL/SVL proportions for their data range 20–23 % in contrast to 28–36 % for my combined samples. TarsL of *K. orangensis* was measured although these data were not reported in the description.

*External morphology*.— The shape or dorsal outline of all *K. interlineatus-pleurostigma* group-members is a cordate to conical/triangular body with a smooth transition from of head and neck to the body. Limbs are of moderate length and sturdy. The dorsal surface from nape to trunk is strongly glandular, consisting of compact skin with contiguous columnar epidermal glands (Fig. 1A–B). These glands appear structurally similar to those of the parotoid glands of *Rhinella marina*, hence they are likely granular glands with a syncytial cellular column surrounding a narrow lumen or duct that opens to the exterior. This dorsal glandular sheet of skin is like a cloak and extends from the middle of the head to above the vent and laterally onto the sides of the body, apparently with glandular tissue columns gradually decreasing in height and becoming less compact, and merges into the thinner, although still glandular, skin of the sides. The merger of the thicker, glandular trunk skin with the dorsal head skin is smooth in most populations; only in the Borneo specimens is the transition marked by a slight transverse ridge. Some researchers (e.g., Parker 1934) report the presence of parotoid glands; however, there is no delineation of the skin on the posterodorsal surface of the head and the supra-axillary region into an elevated gland. In contrast to the trunk, the thick skin ends abruptly dorsolaterally on the head and ventrolaterally in the preaxillary region thereby creating a distinct supratympanic fold continuous with a broad preaxillary fold (Fig. 1C). A white to cream stripe (commonly mislabeled a dorsolateral fold) extends from the tip

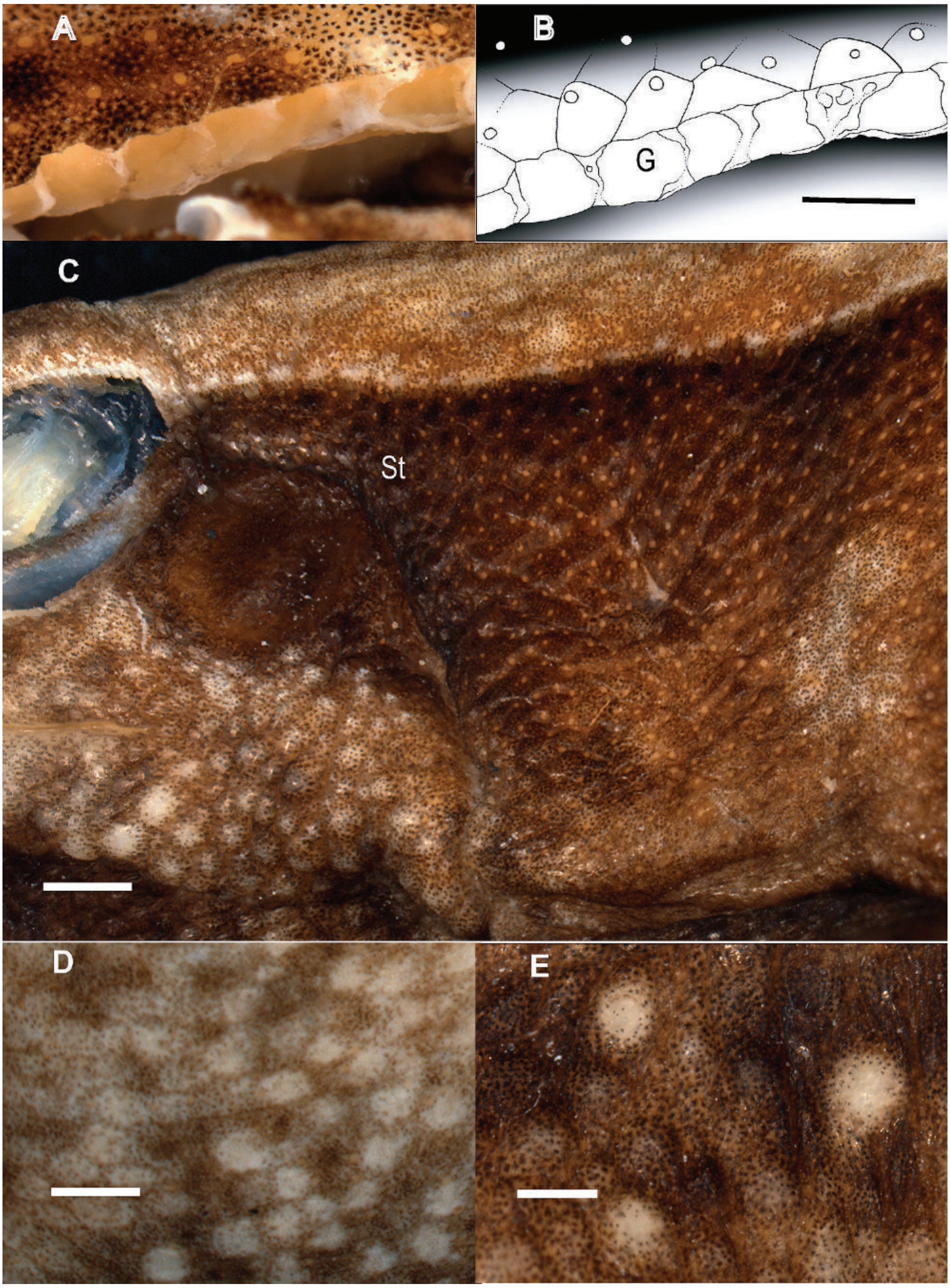


FIGURE 1. Morphology of the glandular skin of a northern Myanmar *Kalophrynus* individual (USNM 537421). (A) compact, columnar macroglands comprising the skin in the dorsolateral pre-inguinal region; (B) sketch of the preceding image A to assist the identification of structures; incision is immediately below and parallel to white diagonal dorsolateral stripe; tile-like pattern on dorsal surface identifies individual macroglands, each with a single duct opening (lighter area in each tile); (C) lateral view of head and neck displaying the abrupt termination of thick glandular skin, equivalent to a supratympanic fold; (D) belly pebbly skin just anterior to pubic area; (E) white glandular epidermal patches on chest. Abbreviations: D, dorsolateral stripe; G, columns of glandular tissue; St, supratympanic fold. Scale bars equal 1 mm in figures B, D, E, and 10 mm in C.

of the snout to the inguinal region, running diagonally on the side of the trunk from dorsolateral on the shoulder angling downward to a mid-lateral position at inguina. It is not a discrete glandular ridge or fold, as its tissue composition is identical to the skin on either side of this light stripe. The entire surface of the glandular cloak bears small flattened circular tubercles of two sizes, small and smaller. The dorsal surface of the head lacks the thickened columnar skin and its surface bears numerous tiny spiculate tubercles. Ventrally, the skin's surface is tuberculate with small, flattened, circular tubercles (Fig. 1D) from chin to rear of the chest and the abdomen (belly) paved with large flattened tubercles; a few small, white 'macroglands' (Fig. 1E) are scattered from chin to pelvis. Although histological data are lacking, these 'macroglands' appear to be unpigmented tubercles, otherwise they are the same as other ventral tubercles. The preceding description is applicable to all adults from all samples.

The appearance of the head is similar in individuals of all samples. The tip of the snout usually bears a short pointed proboscis. The canthus rostralis is sharply defined and the loreal or lore is a flat vertical surface. The nares lie anteriorly on the lower edge of the canthus, about one-third of the distance from snout tip to the anterior border of orbit, although this character is variable within a locality and with differences in the mean position (NarEye/SnEye) among the samples. In the Mon juveniles, Tanintharyi adults, and the two Sumatran specimens, the nares are nearest the midpoint (55, 56, 56 %, respectively), whereas they are somewhat closer to the snout in the northern Myanmar, Borneo, and Philippine samples (59, 58, 59 %, respectively) and closest (64 %) to the tip of the snout in the Thai-Indochina sample; all samples have broad ranges (~15 %) of the measurement. The NarEye/HeadL means (22–25 %) are similar in all samples and less variable than NarEye/SnEye. Eyes are moderately large (means ~30 % EyeD/HeadL) with horizontal, elliptical pupils. Tympanum is exposed and visible; it is modest sized, its diameter usually smaller than the diameter of the orbit (Table 1). The tympanum averages smallest in the northern Myanmar sample and largest (i.e., equals eye diameter) in the Borneo sample (Tymp/EyeD, Table 1). The upper annulus (rim) of the tympanum is usually partly covered by the bottom edge of the supratympanic fold.

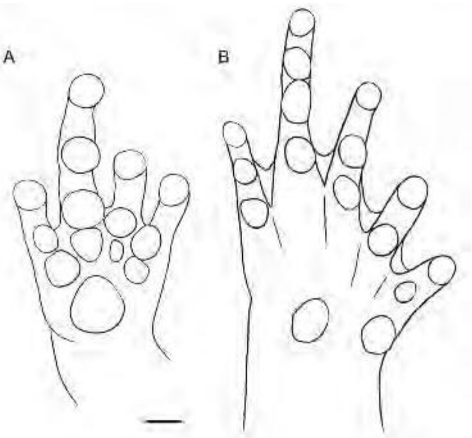


FIGURE 2. Schematic ventral view of the right (A) fore- and (B) hindfoot of *Kalophrynus anya* sp. nov. (USNM 537420). Scale bar equals ~1 mm.

Fore- and hindlimbs are well-developed, moderately slender, and of moderate length, hindlimbs are about twice the length of forelimbs. Forefeet are web-free. Finger tips are bluntly rounded. Fingers are of moderate length, and most individuals in all populations have a phalangeal formula of 3>2≈1>4 or 3>2≈1≈4, although a few individuals have the first finger slightly longer than second one. The underside of forefoot has well-developed tubercles (Fig. 2A). A large round to oblong outer palmar tubercle occupies most of the palm and is encircled distally by four well-developed tubercles at the base of each finger. All four digits bear large basal or proximal subarticular tubercles, and the third digit has a second, well-developed subarticular tubercle beneath the proximal phalanx, thus a subarticular formula of 1 1 2 1 from first to fourth finger. In two Laos individuals, the third finger had a third small tubercle distally, i.e., 1 1 3 1. Hindlimbs are moderately robust, and the crus is slightly shorter than the thigh (Table 1); the hindfoot and crus are commonly equal-sized or nearly so. The ankle (tarsus) is the shortest segment of the hindlimb, slightly more than half the length of the thigh (average 55–59 % TarsL/ThghL for all populations). Hindfoot is modestly webbed (Fig. 2B) with webbing varying in development between toes, basal between the first and second and second and third digits, and moderate between the third and fourth and fourth and fifth digits. The webbing formulae (means) for extent of webbing on the fourth toe vary among populations (Table 2): WebIII2 averages 1.0 (north Myanmar), 2.3 (Tanintharyi), 2.0 (Indochina), 2.1 (Borneo), and sexually dimorphic for the Philippine sample with 1.8 (female) and 2.6 (male); WebIV2 averages 0.9, 1.7, 1.2, 1.3, respectively and 1.8 (female) and 2.2 (male) for the Philippine sample. Thus, Philippine males have the most extensive webbing and Tanintharyi adults next, although in no population is the hindfoot fully webbed. The two Sumatran specimens display 1.5 WebIII2 and 1.0 WebIV1, values within the range of the other populations. Toes are of moderate length, tips bluntly rounded, and all populations share a 4>3>5>2>1 phalangeal formula. The plantar surface bears moderate sized, round inner and outer metatarsal tubercles, usually of similar size although occasionally the inner is half the size of the outer. The five distal plantar tubercles at the base of the toes are variously developed, although always evident. Each toe except the fifth has a well-developed basal subarticular tubercle. First and second toe have only the basal tubercle; third toe usually has a second more distal tubercle, uncommonly a third one (two Laos specimens); fourth toe usually has a third distal tubercle, uncommonly a fourth one (two Laos specimens). The condition of subarticular tubercles on the fifth toe is variable. One tubercle is the most prevalent condition and typically it is moderately developed; however, about a third of the Sarawak toads had no tubercle and where present, the tubercle was small, weakly developed. In Philippine specimens, a single tubercle was always present, although weakly developed in some. For the northern and peninsular Myanmar, and Thai-Indochina frogs, slightly more than half had two tubercles and the remainder one tubercle; tubercles ranged from weakly to moderately well-developed. The Sumatran adult female had a single tubercle and it was distal rather than basal as in most specimens examined. The toes' most common subarticular tubercle formulae are 1 1 2 3 1 and 1 1 2 3 2.

TABLE 2. Select morphological features of adults from the regional samples of the *Kalophrynus interlineatus-pleurostigma* species group. Character abbreviations are defined in the Appendix. The values are means.

| **Sample** | **Hindfoot** | **Webbing** | **Roof of Mouth** | **Coloration** | | | | |
|---|---|---|---|---|---|---|---|---|
| **Location** | **WebIII2** | **WebIV2** | **Buccal Fold** | **HeadMid** | **DorsNap** | **IngSpt** | **HndlBr** | **Chin** |
| Sagaing<br>*n* = 5 | 0.9 | 0.9 | rectangular edged | 1 | 0.8 | 1.2 | 0.2 | 1.3 |
| | 0.5–1 | 0.5–1 | | 0–2 | 0–2 | 0–2 | 0–2 | 0–2 |
| Mon<br>*n* = 5 immatures | 1.7 | 0.9 | rectangular edged | 0.8 | 0.2 | 2 | 0.6 | 0.6 |
| | 1–2 | 0.5–1 | | 0–2 | 0–1 | 2–2 | 0–2 | 0–2 |
| Tanintharyi<br>*n* = 7 | 2.3 | 1.6 | rectangular edged | 1.1 | 1.4 | 2 | 1.4 | 1.7 |
| | 2–3 | 1–2 | | 0–2 | 0–2 | 2–2 | 0–2 | 1–2 |
| Thai-Indochina<br>*n* = 4 | 2 | 1.25 | rectangular edged | 0.7 | 0.7 | 1.8 | 1.4 | 1.5 |
| | 2–2 | 1–2 | | 0–2 | 0–2 | 0–2 | 0–2 | 0–2 |
| Sumatra<br>*n* = 1 neotype | 2 | 1.5 | denticulate edged | 0 | 1 | 2 | 0 | . |
| Sarawak<br>*n* = 11 | 2.1 | 1.2 | blunt-lobed edged | 0 | 0.1 | 2 | 0.7 | 0.3 |
| | 2–2.5 | 1–2 | | 0–0 | 0–1 | 2–2 | 0–1 | 0–1 |
| Philippines<br>*n* = 9 | 1.8 | 1.8 | blunt-lobed edged | 0.1 | 1.3 | 1.5 | 0.7 | 0.8 |
| | 1–3 | 1–2.5 | | 0–1 | 0–2 | 1–3 | 0–1 | 0–1 |

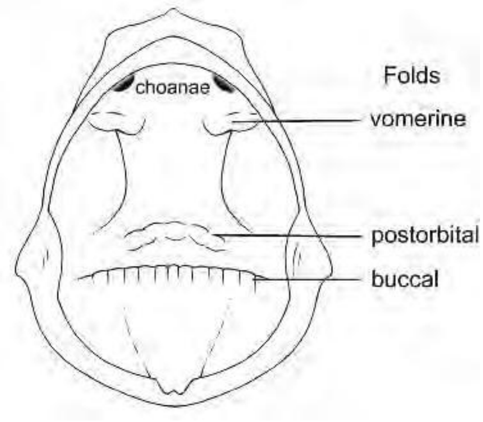


FIGURE 3. Schematic depiction of the roof of the mouth of a *Kalophrynus anya* sp. nov., emphasizing the palatal folds. Only the basal portion of the tongue is shown, epiglottis and esophageal opening are not shown, and lower jaw is foreshortened.

*Oral morphology*.— The tongue is moderately large, broadly oblong to obovate in outline, smoothly truncated on its rear edge, and variably attached. In the Sumatra and some Borneo frogs, the posterior quarter or less of the tongue is free, about half is free in Borneo and Philippine individuals, and half to two-thirds is free in north and south Burmese and Thai-Indochina specimens. The roof of the mouth (Fig. 3) bears three transverse folds (dermal pharyngeal folds of Parker 1934) (Fig. 3; also see Fei et al. 2005:fig. 349). These folds appear to be edentulous in all individuals examined and lack underlying bony support (not evident in a small series of x-rays). The anterior-most fold is the vomerine fold; the second fold (postorbital) extends transversely between the posterior quarter of the orbits; and the third fold (buccal) lies transversely just behind the orbits. Size and shape of these folds vary among the different populations (Table 2). In the Sumatran specimens (*K. pleurostigma* sensu stricto), the vomerine fold is pair of long, straight-edged folds extending from the labial edge of the mouth to near the midline, with a short gap between the left and right folds. The postorbital fold is a low, smooth-edged fold and is followed closely by the high, edentulous buccal fold which has a strongly serrated free edge. Each serration has the shape of a tri-crowned tooth, although there is no evidence of dentine or enamel in these ‘denticles.’ I recommend the use of the term palatal folds as the folds lie on the primary palate and are anterior to the epiglottal opening into the pharynx.

In the northern Myanmar sample, the vomerine fold is a broad, smooth-edged double flap and somewhat undulatory; left and right sides are separated by moderate gap. This morphology is largely shared by the Mon, Tanintharyi, Thai-Indochina, Borneo, and Philippine specimens. The left and right folds are narrowly separated in the Borneo and Philippine specimens. Owing to various states of preservation, observed relative size and undulation of the folds may be considered tentative observations. The extent of the medial hiatus appears more consistent within regional samples. Differences in the morphology of the postorbital folds seem more robust. The northern Myanmar specimens have a moderately broad flap divided into five or six unequal-sized lobes; the fold is paired in Tanintharyi individuals and distinctly separated at the midline, the left and right sides each with two or three lobes. In the Indochinese specimens, morphology is similar to Tanintharyi although it ranges from a short lobular fold of well-separated lobes to left and right lobular folds separated medially. Borneo individuals have a moderately wide, continuous lobular fold, and there is a similar morphology in Philippine specimens with the folds ranging from strongly undulatory to broad lobes. The buccal fold extends across the entire breadth of the buccal cavity in all specimens from all localities. Regional differences occur in the relative height and lobular shape of the fold. Height or its appearance may possibly be influenced by preservation, whereas the lobular nature of the fold probably not. Northern Myanmar individuals have a buccal fold of ten or more closely abutting rectangular lobes; Tanintharyi individuals have a similar morphology although the lobes appear shorter and more round-edged. Borneo and Philippine frogs have folds comprised of variously shaped, short blunt lobes.

The apex of the lower jaw is similar in individuals from all localities. The lower jaw has a smooth, labial margin and anteriorly curves downward forming a concave edge with a small blunt odontoid process in the middle (tip of the jaw). It is edentulous. The upper jaw lies rearward of the tip of snout, producing a distinctly under-hung (subterminal) jaw. The upper jaw bears tiny teeth, often hidden by the labial mucosa.

*Coloration*.— The color characters were analyzed for sexual dimorphism. No differences in the frequency between females and males were observed for any of the eleven color traits in the five regional samples large enough for statistical testing. Thus, these data indicate that no population of the *interlineatus-pleurostigma* group displays sexual dichromatism.

Only two color traits (HeadMid, DlatSt) were invariant within any regional samples. No color trait was uniform across all regional samples. IngSpt was present in all individuals of the Mon, Tanintharyi, and Borneo samples, and was present in most individuals in each of the other samples; however, this spot was absent in a few individuals. Further, it was of variable size in most samples, and the white outer edge was also of variable distinctiveness. This latter variation can result from variable quality of preservation and time in preservative, although it appears to exist in living individuals from the same population. The dorsal head stripe (HeadMid) was absent in all Borneo individuals and most Philippine frogs; otherwise it occurred at about a 50 % frequency in the other samples (Table 2). DlatSt occurred as a bold stripe in all Mon frogs, and as a distinct or bold stripe in individuals of all other samples, except the Philippines where it was more commonly indistinct or absent.

Distinct parasagittal head stripes (HeadPsag) occurred in less than 50 % of the individuals in all samples. Presence-absence frequency is more variable for DorsNap. The nape stripe was present in the majority of individuals of the Tanintharyi and Philippines samples, rarely occurred in Mon and Borneo frogs, and present in about a third of the northern Myanmar and Thai-Indochina samples. The parasagittal stripes (DorsPsag) occurred in 50 % of Mon and Tanintharyi individuals, about a third of northern Myanmar and Philippines ones, and rarely in Tanintharyi and Borneo. Face coloration (Loreal) is typically darker than the top of head, but the degree of darkness beneath the distinct dark canthal ridge is variable and difficult, at times, to discriminate between character states 1 and 2; nonetheless, my data indicate that most individuals in the Tanintharyi, Thai-Indochina, and Borneo samples have uniformly dark faces. Lateral trunk coloration from fore- to hindlimbs (LatTrnk) is dark in most individuals in all samples. Barring or banding of the upper surface of the thigh (HndlBr) is present in the majority of the Tanintharyi, Thai-Indochina, and Philippine samples, in about a third of the individuals of Mon and Borneo samples, and rare in northern Myanmar frogs. Half or more individuals in all samples, except Borneo, have distinct chin markings; most Borneo frogs have dusky throats without markings. Chest markings (Chest) are less common in all samples and nearly absent in Mon, Borneo, and Philippine samples.

No single coloration trait uniquely delimits any population with the possible exception of the nape-anterior trunk hourglass blotch in *K. pleurostigma*. The few *K. pleurostigma* examined prevents an unequivocal declaration to the uniqueness of this pattern. Additionally, few color traits are invariant within a sample or population. As noted above, only the presence of inguinal spots (IngSpt) was invariant in the Mon, Tanintharyi, and Borneo samples, absence of middorsal head stripe (HeadMid) was invariant in the Borneo sample, and presence of distinct dorsolateral trunk stripes (DlatSt) was invariant in the Mon sample. The variation in the two largest samples (Borneo, Philippines) is no greater or less than the variation in the smaller samples, thereby indicating that small samples of eight or more individuals encompass most coloration variation.

## Taxonomic Discussion and Conclusions

Not surprising, the pan-Asian concept of *Kalophrynus pleurostigma* is incorrect. Matsui and associates (1996) began the current recognition of multiple species by elevating the two subspecies (*K. pleurostigma pleurostigma*, *K. pleurostigma interlineatus*) to specific status. Their concept of the two taxa was based primarily on the morphology of north-central Thai and Borneo specimens and the difference in call structure of these two populations. They did not examine the holotypes of either taxon. The proposed distributions of the two taxa from their map (Matsui et al. 1996: fig. 3) placed *K. interlineatus* as a northern Southeast Asian species and *K. pleurostigma* as a southern species from southern Thailand, Malaysia and Sumatra eastward into the Philippines. This paradigm was the one with which I began my study of the Burmese populations of *Kalophrynus*. This paradigm was also the one that led me to conceptualize the larger *Kalophrynus* species as the *pleurostigma* species group and a clade. Once I began a thorough review of the literature, I discovered that the earliest molecular phylogeny (Matsui et al. 2011) did not support the monophyly of this species group. I will discuss the genetic relationships later, but first, a discussion of my analysis of the morphology of the larger members of the *interlineatus-pleurostigma* populations

*Kalophrynus pleurostigma* and *K. interlineatus* and the earlier inclusive *K. pleurostigma* (i.e., pre-Matsui et al., 1996) have been variously mentioned in diagnoses of new *Kalophrynus* species, but the first analysis of geographic variation awaited Ohler and Grosjean's (2005) analysis of the advertisement call structure of a Vietnamese population of *K. interlineatus*. They demonstrated that the call of their Vietnamese population differed little from that of the Thai population analyzed by Matsui et al. (1996). They interpreted this similarity to indicate that the two populations were conspecific. They (Ohler and Grosjean 2005) also examined coloration, noting that variation occurred in the reverse V-striped dorsal pattern, although it usually remained recognizably distinct from the dorsal pattern of *pleurostigma* sensu Matsui et al. With their coloration data, they compared type specimens of *Kalophrynus stellatus* Stejneger (Basilan, Philippines) and *Calophrynus pleurostigma* var. *Sinensis* Peters (correcting the type locality to Mindanao, Philippines) and concluded that the names were synonyms of and available for the Philippine populations of *K. pleurostigma* sensu Matsui et al. 1996. They also considered that the description of *K. orangensis* did not sufficiently differentiate it from *K. interlineatus* and proposed it as a synonym of the latter, even though they performed no analysis to support their decision. Matsui and colleagues (2009, 2011, 2012) continued to recognize *K. orangensis*.

Ohler and Grosjean (2005) suggested that the dorsal reverse-V pattern (my DorsNap character) of northern Vietnam-China displayed differences from that of Thai individuals. Further, in their discussion of dorsal color pattern of Southeast Asian *pleurostigma*, they emphasized constancy of pattern at a local intrapopulational level and interpopulational differences on a broader geographic scale. My observations indicate a higher level of intrapopulational variation. Relative to the presence of the reverse V-stripe, it is present in the majority (> 80 %) of the Philippine and Tanintharyi samples, and usually absent in the Borneo and Mon samples, and roughly half of the other samples. It is important to note that my coding and scoring of this trait differ from their evaluation owing to their consideration of the 'wholeness' and fragmentation of the arms of the stripe; furthermore, my Thai-Indochina sample contains individuals from both eastern and western localities. Ohler and Grosjean's recognition of pattern difference between northern Vietnam and Thailand is suggestive of regional differentiation even though they found no differences in the structure of Thai and Vietnamese vocalizations. My Thai-Indochina sample combines these areas and the variation within characters is no greater than the geographically more restricted samples of the Philippines, Borneo, and Tanintharyi, suggesting, although not verifying, the presence of a single species in this area.

Do the Thai-Indochina sample and the Tanintharyi one represent a single species? Given that there are no striking differences in coloration (Table 2) and morphology (Table 1), I propose that they represent the same species. The decision on the specific status of populations in peninsular Myanmar is less certain, although I propose that the Mon and the Tanintharyi populations represent the same species. The most striking difference is the relative hindlimb length (HndlL/SVL; Table 1) between these two samples; however because the former sample is composed entirely of juveniles and the latter of adults, I interpret this difference as an ontogenetic one. Accepting them as representatives of a single species attaches the name *Kalophrynus interlineatus* (Blyth 1855) to the peninsular Myanmar population and further to the populations of Thailand, Laos, Vietnam, Cambodia, and southern China (composition of my Thai-Indochina sample). I do not have a sample representing the Peninsular Malaysia and Singapore populations; however, Chan et al. (2014) recognized the uncertainty of the distribution of *K. palmatissimus* and *K. interlineatus* (= their *pleurostigma*) and gave their characters for differentiation of these two. They demonstrated that *K. interlineatus* occurred widely through central and southern Peninsular Malaysia and that *K. palmatissimus* occurred at only three locations and sympatric with *K. interlineatus* at only one locality. Their Malaysian *interlineatus* localities are the ones mapped in Fig. 4.

The preceding morphological analysis of *Kalophrynus* specimens reveals modest regional differentiation of populations. Although modest, I interpret the differences to indicate speciation and propose the recognition of multiple species within the *interlineatus-pleurostigma* populations. Molecular data and analyses for the postulation of phylogenetic relationships among *Kalophrynus* species are accumulating slowly and largely as "out-group" taxa for the examination of relationships of other microhylid genera or species complexes. This situation handicaps the interpretation of relationship based on DNA sequence data because of the incomplete representation of *Kalophrynus* species. Four studies (Kurabayashi et al. 2011; Matsui et al. 2011; de Sa et al. 2012; Vassilieva et al. 2014) provide information on relationships, and all four demonstrate that *Kalophrynus* populations are a monophyletic group. This monophyly is the only information that can be drawn from the Kurabayashi group's results as their two *Kalophrynus* samples derive from pet-trade specimens with questionable locality data. The phylogeny of Matsui and collaborators is more useful in portraying interpopulational relationships. Their samples represent eight different taxa (each a single individual) with broad geographic coverage. The resulting phylogenetic analysis identifies the Sumatran sample (*pleurostigma*) as the basal branch of the *Kalophrynus* phylogeny. The Philippine sample is the next branch and without a close relative. Subsequent branching has the Southeast Asian *K. interlineatus* embedded in a cluster of the smaller West Malaysian species and the northern Myanmar (Chatthin) individual shows sister relationships to the Borneo *K. heterochirus*. In an analysis of American microhylids, de Sa and associates had four *Kalophrynus* samples and similarly place the Sumatran sample as basal on the *Kalophrynus* tree. The northern Myanmar sample is sister group to two Thai *K. interlineatus,* one of which is a Kurabayashi pet-trade specimen. The phylogeny of Vassilieva and colleagues (2014) was generated specifically to examine relationships among Vietnamese *Kalophrynus* (a third of their genetic sample) and those with other *Kalophrynus* taxa. Their two new species and the Vietnamese, southern China, and northern Myanmar *interlineatus* form a clade as the final branch in their phylogram. The northern Myanmar individual is the basal branch in the latter clade. The other *interlineatus-pleurostigma* populations/species are distributed elsewhere throughout the phylogram. Their *pleurostigma* clade includes a Borneo specimen as a sister group to a Sumatra-West Malaysia pair. The Philippine sample is a pet-trade specimen without reliable locality data.

I interpret the preceding molecular data as demonstrating: 1) monophyly of the *Kalophrynus* species; 2) polyphyly of a *interlineatus-pleurostigma* group; 3) genetic uniqueness of northern

Myanmar population; 4) strong indication that the Sumatran *pleurostigma* and the Philippine *sinensis* are each distinct genetic entities.

In summary, I propose that the morphological differences support the recognition of six species in the polyphyletic *interlineatus-pleurostigma* species group. I recommend the continuing recognition of *K. orangensis*. Ohler and Grosjean (2005) correctly observed that the proposed diagnostic features of this taxon were inadequate to differentiate the Assam population from other *pleurostigma* group populations; however, comparison of the Assam sample to its closest geographic congener identifies some differences. Adult *K. orangensis* are smaller than the northern Myanmar population, and they display no sexual dimorphism of SVL. The largest female *orangensis* is 3.0 mm smaller (SVL) than the smallest mature Myanmar female. The northern Myanmar population differs in several traits from the peninsular Myanmar populations of *K. interlineatus* as well as being distantly geographically isolated from the latter. Our current distributional data indicates that *K. interlineatus* is widespread throughout Southeast Asia although with a spotty occurrence. Sumatran specimens of *Kalophrynus* are rare; the few available ones demonstrate some striking morphological differences and support the uniqueness of this island's *Kalophrynus*. The large size and other features emphasize the distinctiveness of the Borneo "*pleurostigma*" populations. Similarly, the "*pleurostigma*" populations of the Philippines differ morphologically from the Borneo and other populations thus also represent a separate species, *K. sinensis*. The following section provides a detailed taxonomic and nomenclatural summary of my conclusions.

## TAXONOMY OF *KALOPHRYNUS*

Species are arranged alphabetically. The two new species described herein are *Kalophrynus anya* from northern Myanmar and *K. meizon* from Borneo. Those two taxa and the members of *interlineatus*-*pleurostigma* group of populations (i.e., *K. interlineatus*, *K. pleurostigma*, *K. sinensis*; Fig. 4) have more detailed descriptive synopses than the other species in order to present the morphological details from the preceding analysis. Morphological details for the remainder (and majority) of the *Kalophrynus* species derive entirely from published information, as I examine no types or other specimens of these taxa. Measurements and proportions are for adults unless noted otherwise. NA indicates that data were not available in any published studies.

### *Kalophrynus* Tschudi, 1838

Sticky Frogs

Type species: *Kalophrynus pleurostigma* Tschudi, 1838.

**DEFINITION**.— Small to medium-sized microhylid frogs (adults, 17–60 mm SVL) with deltoid to ovate dorsal body outline, narrowest anteriorly, and well-developed, moderate-length fore- and hindlimbs. Dorsal skin thick, surface typically granular, often spiny, and strongly glandular.

Skull with prevomer divided and postchoanal portion absent; palatine absent; ethmoids small or absent. Pectoral girdle with well-developed clavicles and procoracoids reaching ventral midline cartilage and laterally the scapulae; omosternum small, cartilaginous; sternum large, cartilaginous. Terminal phalanges T-shaped.

Pupil round to slightly horizontal elliptical. Tongue oblong to obovate, posterior edge blunt to rounded, and half to two-thirds free. Palate with two to three transverse ridges or folds, anterior one (vomerine) smooth, usually medially interrupted, and adenticulate just behind choanae, middle one (postorbital) smooth and adenticulate between posterior edges of orbits, and posterior one (buccal) variably segmented and adenticulate lying about halfway between rear of orbits and epiglottis.

TABLE 3. Select characteristic of currently recognized species of *Kalophrynus*.

| Species | Range of adult SVL | | Inguinal spots | | Ocellus | Forefoot | Hindfoot |
|---|---|---|---|---|---|---|---|
| | Females | Males | Present | color | | digit formula | webbing |
| *Kalophrynus anya* sp nov.[1]<br>North Myanmar | 36–47 | 34–41 | yes, occasionally absent | black | light-edged | 3>2≈1>4 | at base |
| *Kalophrynus baluensis* [2]<br>Borneo | to 47 | to 36 | yes | yellow | None or dark brown-edged | 3>2>1>4 | at base or slightly beyond |
| *Kalophrynus barioensis* [3]<br>Borneo | 21 | 18–20 | yes | black | none | 3>2>1>4 | at base or slightly beyond |
| *Kalophrynus bunguranus* [4]<br>Great Natuna Isl. | 25–27 | 22–23 | yes | black | none | 3>2>1>4 | at base |
| *Kalophrynus calciphilus* [5]<br>Borneo | 35–39 | 29–30 | no | none | none | 3>2>1>4 | at base |
| *Kalophrynus cryptophonus* [6]<br>Vietnam | 23 | 28–30 | yes | black | none | 3>2>4>1 | at base |
| *Kalophrynus eok* [7]<br>Borneo | ? | 26 | no | none | none | 3>2>1>4 | at base |
| *Kalophrynus heterochirus* [8]<br>Borneo | 30–33 | 24–27 | yes | bluish-white | none | 3>2>1>4 | one-third |
| *Kalophrynus honbaensis* [9]<br>Vietnam | ? | 27–37 | yes | black | light-edged | 3>2>4>1 | one-third |
| *Kalophrynus interlineatus* [10]<br>SE Asia | 35–46 | 34–45 | yes, occasionally absent | black | light-edged | 3>2≈1>4 | one-third |
| *Kalophrynus intermedius* [11]<br>Borneo | 38–41 | ? | no | none | none | 3>2>1>4 | ~ two-thirds |
| *Kalophrynus limbooliati*[12]<br>West Malaysia | ? | 26–29 | yes | dark | none | 3>2>1>4 | at base or slightly beyond |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Kalophrynus meizon* sp nov.[13]<br>Borneo | 35–60 | 37–50 | yes | black | light-edged | 3>2≈1≈4 | one half to two-thirds |
| *Kalophrynus menglienicus* [14]<br>China | ? | 20–23 | yes | none | none | 3>4>2>1 | slight to none |
| *Kalophrynus minusculus* [15]<br>Java & Sumatra | to 35 | to 25 | no | none | none | ? | ? |
| *Kalophrynus nubicola* [16]<br>Borneo | 21–24 | 19–20 | no | none | none | 3>2>1>4 | ~ one-third |
| *Kalophrynus orangensis* [17]<br>NE India | 35–38 | 36–38 | yes | black | light-edged | 3>2>1>4 | at base |
| *Kalophrynus palmatissimus*[18]<br>West Malaysia | 31–39 | 31–39 | no | none | none | 3>2>1=4 | two-thirds |
| *Kalophrynus pleurostigma* [19]<br>Sumatra | 34–35 | ? | yes | black | light-edged | 3>2≈1>4 | ~ one-third |
| *Kalophrynus punctatus* [20]<br>Borneo | ? | 22–27 | no | none | none | 3>2≈1>4 | at base |
| *Kalophrynus robinsoni* [21]<br>West Malaysia | 18+ | 17–18 | no | none | none | 3>2>1>4 | one-third |
| *Kalophrynus sinensis* [22]<br>Philippines | 39–46 | 35–42 | yes, occasionally absent | black | light-edged | 3>2≈1>4 | variable, one-third to two-thirds |
| *Kalophrynus subterrestris* [23]<br>Borneo | 26–27 | 21–23 | yes, occasionally absent | black | none | 3>2>1>4 | one-third |
| *Kalophrynus tiomanensis* [24]<br>West Malaysia | 25–26 | 26 | yes | dark brown | yes | 3>2≈1>4 | at base or slightly beyond |
| *Kalophrynus yongi* [25]<br>West Malaysia | ? | 29–31 | yes | black | none | 3>2>1>4 | at base |

DATA RESOURCES. 1, this study; 2, Kiew, 1984b, Malkmus et al., 2002; 3, Matsui & Nishikawa, 2011; 4, Günther, 1895, Inger, 1966; 5, Dehling, 2011, Inger, 1966; 6, Das & Haas, 2003; 7, Vassilieva et al., 2014; 8. Boulenger, 1900, Inger, 1966; 9, Vassilieva et al., 2014; 10, this study; 11, Inger, 1966; 12, Matsui et al,. 2012; 13, this study, Inger, 1966; 14, Yang & Su, 1980, Fei, 1999, Fei et al., 2010; 15, Iskandar, 1998; 16, Dring, 1983; 17, Dutta et al., 2000; 18, Dehling, 2011, Kiew, 1984a; 19, this study; 20, Inger, 1966; 21, Dehling, 2011, Smith, 1922; 22, this study, Inger, 1954, Taylor, 1921; 23, Inger, 1966; 24, Chan et al., 2011; 25, Matsui, 2009.

A "?" denotes that datum is not available.

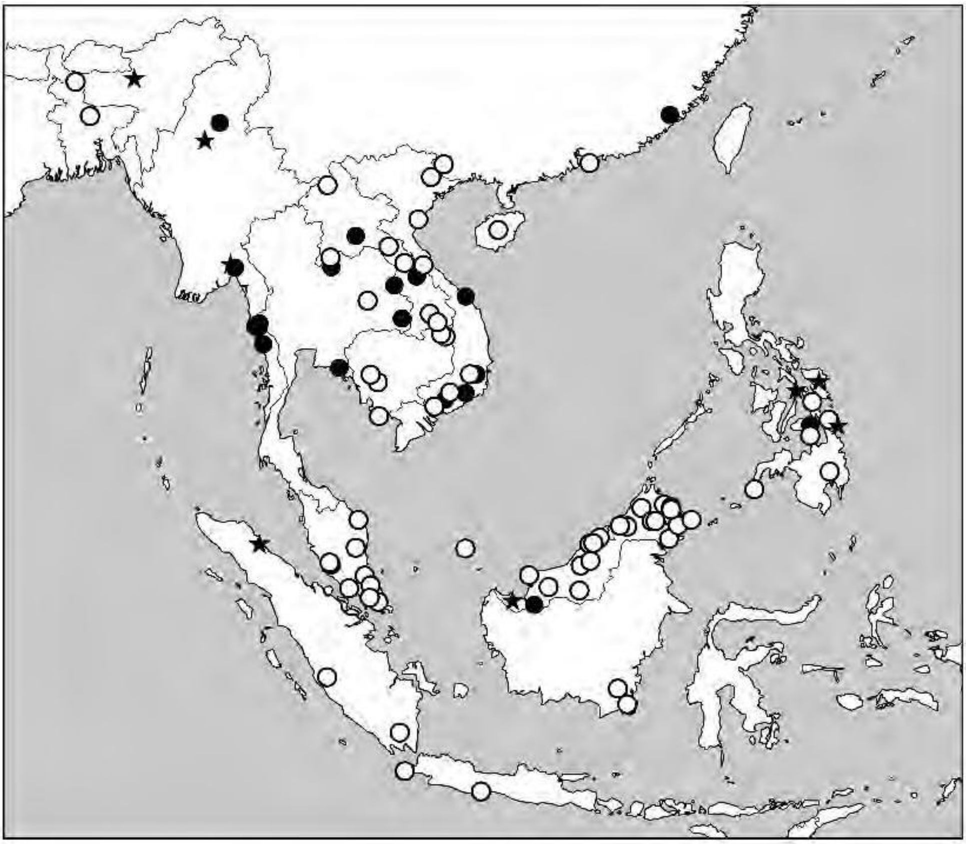


FIGURE 4. General distribution of the *Kalophrynus interlineatus-pleurostigma* group. Solid circles denote specimens examined in this study; open circles are literature records and museum records of specimens not seen; stars represent type localities of available names. Source of the locality records are in Appendix Specimens examined section.

Tympanum always visible, although posterodorsal edge often partially overlapped by edge of thick glandular dorsal skin. Digit well-developed and not expanded distally. Forefoot usually without webbing or slight basal webbing, basal to moderate webbing on hindfoot. Both fore- and hindfeet with numerous subarticular tubercles. Commonly, snout with short, pointed proboscis.

**CONTENT**.— Twenty-five species (Table 3) with the greatest diversity in Borneo (ten endemic species).

**DISTRIBUTION**.— Northeast India (Assam, West Bengal) and northern Bangladesh (Rajshahi), north-central Myanmar (Sagaing, Kachin), peninsular Myanmar (Mon, Tanintharyi), Southeast Asia (Laos, Thailand, Vietnam, Cambodia), southern China (Yunnan, Guangxi, Hainan, Guangdon, Fujian), Sumatra, Java, Borneo (Kalimantan, Sarawak, Brunei, Sabah), and Philippines (southeastern islands). See Fig. 4.

### *Kalophrynus anya* Zug, sp. nov. Northern Burmese Sticky Frog

Figure 5, 11A–B.

**TYPE MATERIAL**.— HOLOTYPE: USNM 537420, adult male from Chatthin Wildlife Sanctuary, San Maung Camp (~23°35′57″N, 95°31′13″E) elevation ~200 m, approximately 2 km WNW of Chatthin (town), Sagaing Division, Myanmar, collected 5 September 1998 by Htun Win.

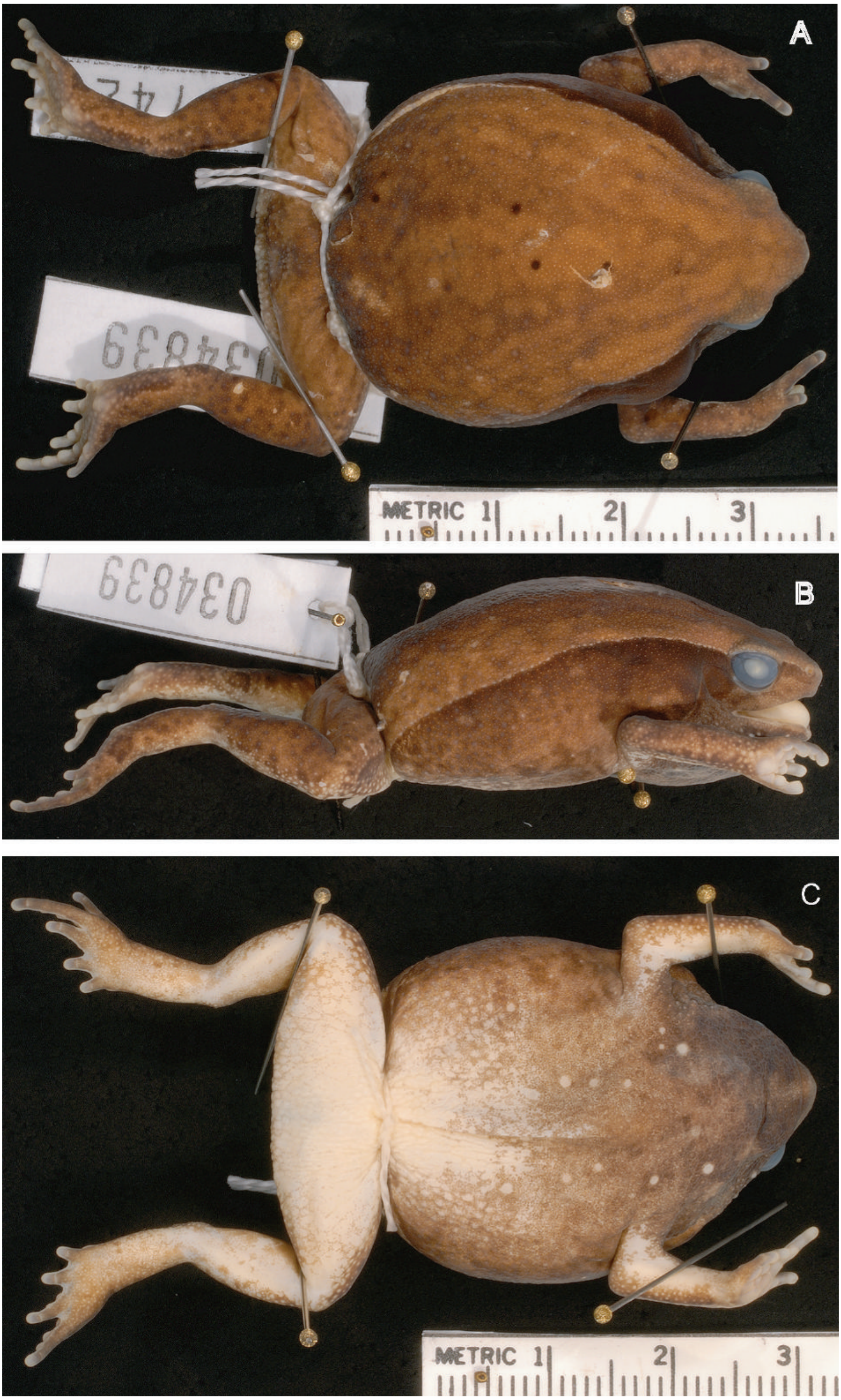
**Paratypes**: CAS 232488, Moenyini, Indawgyi Wildlife Sanctuary headquarters (24°44′55.7″N 96°20′52.6″E) elevation 799 ft [~242 m], Kachin State, Myanmar; USNM 520321, 523964–965 locality same as holotype; USNM 523966 Chatthin Wildlife Sanctuary, approximately 5 km WNW (~23°36′06″N, 95°31′13″E) of Chatthin (town), Sagaing Division, Myanmar; USNM 537419, 537421–422 locality same as holotype.

**Definition**.— Adult *K. anya* can be distinguished from all congeners by the following combination of characters: no size dimorphism, adults 34–47 mm SVL; HeadL/SVL 30–32 %; tympanum about equal eye diameter, Tymp/EyeD 72–100 %; moderate short hindlimbs, HndlL/SVL 132–147 %; short hindfoot, HndfL/ThghL 85–91 %; dimorphism of SnEye/HeadL (35–43 %) and EyeD/HeadL (31–37 %) with females smaller; strong supratympanic ridge dorsoposteriorly overhanging tympanic annulus; paired vomerine folds, each broad, smoothly undulatory with modest medial separation; single postorbital fold with five or six undulatory lobes; single broad buccal fold comprised of ten or more abutting rectangular lobes; forefeet without webbing; hindfeet webbed at base, highest between 3rd and 4rd toe, usually to base of 2nd subarticular tubercle of 4rd toe; head pattern variably with HeadMid 50 % present and DorsNap 33 % present; chin usually with paired, broad longitudinal bars; hindlimbs (HndlBr) seldom barred.

**Description of holotype**.— Moderately robust-bodied male (39.7 mm SVL) with well-developed, moderate-length fore- and hindlimbs (45 % ForarmL+HandL/SVL, 119 % HndlL/SVL); head ovate (25 % HeadL/SVL, 30 % HeadW/SVL) and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: HeadL 10.1 mm; HeadW 11.8 mm; SnEye 4.3 mm; NarEye 2.3 mm; EyeD 3.5 mm; Tymp 3.1 mm; ForarmL 9.8 mm; HandL 8.1 mm; ThghL 14.4 mm; CrusL 13.0 mm; TarsL 7.5 mm; HndfL 12.8 mm. Eye distinctly larger than tympanum (89 % Tymp/EyeD).

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, smooth surface, thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; posteriorly glandular cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular folds; chest and abdominal skin glandular and pebble-like with scattered unpigmented ‘pebbles’ on chest. Tongue large, elliptical, posterior two-thirds free. No vomerine teeth. Three sets of palatal folds on roof of mouth: vomerine paired, each long with smooth undulatory free edge and distinctly separated medially; postorbital single, indistinct, and free-edge undulatory; buccal, single continuous fold of 15 to 16 rectangular, abutting lobes, medial lobes larger than lateral ones. Fingers and toes well-developed and tips bluntly rounded; hand web free; foot basally webbed (WebIII.2 = 1, WebIV.1 = 0.5). Subarticular tubercles well developed on hand and foot (Fig. 2A–B); large, nearly circular palmar tubercle with small tubercle at base of each finger and only third finger with tubercle of free portion of digit; no nuptial pads or asperities evident; paired moderate-sized, circular metatarsal tubercles on edges, inner slightly smaller than outer; each toe with basal subarticular tubercle; third toe with single tubercle on free portion of digit, fourth with two tubercles, and fifth with one (hence total of two tubercles on fifth toe). Digital length formulae, hand 3>2≈4=1, foot 4>3>5>2>1.

**Coloration in preservative**.— Dorsum from tip of snout to thigh medium rufous brown with faded brown middorsal stripe on head, bifurcating at nape into diagonally diverging stripes; parasagittal stripes from nape to trunk also diagonal; laterally neck and trunk dark brown, fading ventrally; narrow white dorsolateral stripe evident only on neck and shoulder; face (loreal) dark brown at canthus rostralis, lighter brown to mouth; vague banding on dorsal of thighs. Venter dark brown to nearly black on chin to mid throat, fading gradually thereafter to creamy white in prepubic area; vague lighter longitudinal stripe from chin to anterior chest.


A
034839
METRIC 1 2 3
B
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C
METRIC 1 2 3

**Description and intrapopulational variation**.— Moderate-sized adults, not sexually dimorphic although females average larger (mean 41.6, 36.4–47.1 mm SVL) than males (40.7, 34.0–41.3 mm). These differences are reflected in the other measurements: HeadL 9.9–13.8 mm ♀♀, 9.6–10.7 mm ♂♂; HeadW 10.5–14.8mm ♀♀, 10.3–12.0 mm ♂♂; SnEye 3.7–5.0 mm ♀♀, 3.8–4.4 mm ♂♂; NarEye 2.2–3.5 mm ♀♀, 2.2–2.7 mm ♂♂; EyeD 3.3–4.6 mm ♀♀, 3.2–4.0 mm ♂♂; Tymp 2.0–3.9 mm ♀♀, 2.5–3.3 mm ♂♂; ForarmL 9.3–12.1 mm ♀♀, 9.0–10.6 mm ♂♂; HandL 7.0–10.7 mm ♀♀, 8.1–9.1 mm ♂♂; ThghL 13.1–17.8 mm ♀♀, 11.7–15.5 mm ♂♂; CrusL 11.7–15.8 mm ♀♀, 12.1–13.3 mm ♂♂; TarsL 7.0–10.5 mm ♀♀, 6.9–8.4 mm ♂♂; HndfL 11.3–14.9 mm ♀♀, 10.3–13.4 mm ♂♂. Body proportions differ between females and males, although not greatly so (all values are percent): HeadL/SVL 25–32 ♀♀, 25–28 ♂♂; HeadW/HeadL 97–118 ♀♀, 105–117 ♂♂; SnEye/HeadL 35–41 ♀♀, 40–43 ♂♂; NarEye/SnEye 56–65 ♀♀, 50–61 ♂♂; EyeD/HeadL 31–33 ♀♀, 34–37 ♂♂;Tymp/EyeD 61–93 ♀♀, 78–89 ♂♂; Forarm/SVL 24–26 ♀♀, 22–26 ♂♂; Forarm/CrusL 73–85 ♀♀, 69–80 ♂♂; HndlL/SVL 110–125 ♀♀, 119–122 ♂♂; CrusL/SVL 30–32 ♀♀, 32–33 ♂♂; CrusL/ThghL 81–96 ♀♀, 86–103 ♂♂; TarsL/ThghL 52–62 ♀♀, 52–59 ♂♂; HndfL/SVL 27–32 ♀♀, 30–32 ♂♂; HndfL/ThghL 79–96 ♀♀, 82–88 ♂♂.

Tongue large, obovate, posterior half to two-thirds free. Vomerine teeth absent. Palatal fold morphology is moderately variable although these data are not quantified. The vomerine folds range from smooth-edged, undulatory folds to folds with broad lobular appearance (USNM 523964, 537419, 537422); usually folds moderately separated on midline, rarely narrowly separated. Postorbital folds are usually well developed and higher than buccal folds; also most variable of three palatal folds and usually continuous although uncommonly narrow separated at midline; fold free edge ranges from smooth, undulatory to broad, round-edged lobes. Buccal fold is low, continuous with ten to 14 smooth-edged rectangular lobes.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercles are well developed on digits; only third finger bears subarticular tubercle on free portion of digit (low on fifth); all fingers have a tubercle at their base and another row between a large, usually circular (rarely elliptical), nearly medial outer palmar tubercle. Nuptial pads not present. For hindfoot, each toe has a basal subarticular tubercle, third and fifth toes have an additional tubercle on free portion of digit, two tubercles on fourth toe (fifth toe of USNM 523965 lacks tubercles). Inner and outer metatarsal tubercles are present; inner is small to moderate-sized, nearly circular to elliptical; outer moderate-sized, circular to elliptical; inner and outer tubercles equal-sized to outer larger than inner. Toes lightly webbed WebIII2 median 1.0 (0.5–1.0), WebIV1 1.0 (0.5–1.0). Digit lengths nearly constant for fore- and hindfeet; finger formula 3>1≈2>4; toe formula 4>3>5>2>1.

Color pattern variation statistics for adults are (median and range): HeadMid 1, 0–2; HeadPsag 1, 0–2; DorsNap 1, 0–2; DorsPsag 1, 0–2; IngSpt 2, 0–2; HndlBr 0, 0–2; DlatSt 2, 1–2; Loreal 1, 0–2; LatTrnk 2, 0–2; Chin 1, 0–2; Chest 1, 0–2. *Kalophrynus anya* is highly variable, commonly with distinct middorsal stripe and faded parasagittal stripes on head, faded to distinct nape stripe in most individuals and bifurcating and quickly fragmenting or disappearing; inguinal spot almost always present and usually as ocelli, dorsolateral narrow white stripe rarely absent or indistinct, hindlimbs uncommonly barred, loreal area and lateral trunk usually uniformly dark, chin and throat always dusky and often with pair of darker longitudinal bars, and chest commonly dusky.

**Etymology**.— All readers of Burmese cultural history are familiar with the country's division into Upper and Lower Burma. This species occurs in the more northern portion of Upper Burma, and the Burmese *a-nya tha* refers to the human inhabitants of Upper Burma (*auk tha*,

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Figure 5 (left). Images of holotype of *Kalophrynus anya* (USNM 537420, male, 39.7 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

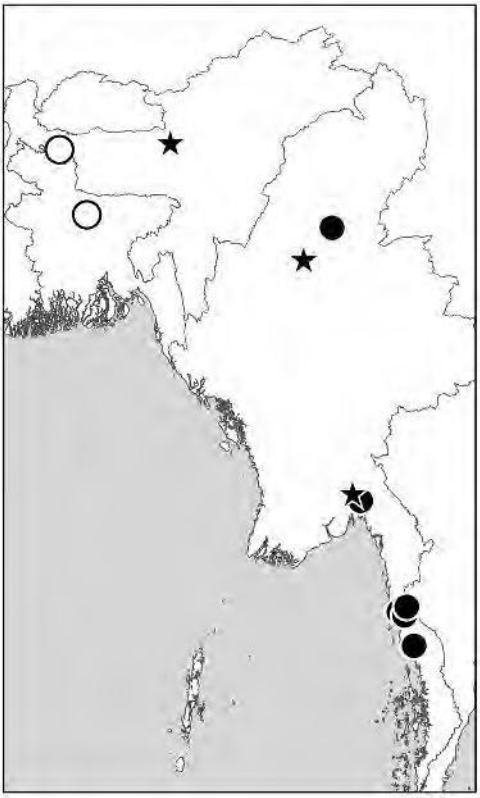

FIGURE 6. Burmese distribution of voucher specimens of *Kalophrynus anya* sp. nov. in northern Myanmar and *K. interlineatus* in southern and peninsular Myanmar. The three reported localities of *K. orangensis* are also shown; all lie within the Brahmaputra river valley. Solid circles denote specimens examined in this study; open circles are literature or unexamined museum records; and stars represent type localities of available names.

Lower Burma inhabitants). Because *tha* references human populations, I have taken the liberty of subverting the meaning of *a-nya* to the region of Upper Burma, hence the name for this Upper Burma endemic species.

**DISTRIBUTION.**— Myanmar. *Kalophrynus anya* is presently known from recent vouchers in east-central Sagaing Division (Chatthin) and south-central Kachin State (Indawgyi) (Fig. 6). Bourret (1942) reported specimens from Bhamo and Teinzo in Upper Burma. I have not located the source of these records; see discussion in the distribution section of the *K. interlineatus* account.

**NATURAL HISTORY.**— Many authors (e.g., Fei et al. 2010, Ohler and Grosjean 2005) report *K. interlineatus* and *K. pleurostigma* as a common frog and regularly calling in choruses. Our (MHS teams) observations found *K. anya* an uncommon species, and we heard no choruses. Our assessment is that it is an uncommon species. We found individuals in open In (*Dipterocarpus tuberculatus*) forest with slight to moderate ground vegetation (grass), seasonally with heavy leaf litter.

### ***Kalophrynus baluensis* Kiew, 1984** **Balu Sticky Frog**

*Kalophrynus baluensis* Kiew, 1984a, *Malayan Nature Journal* 38:152 [type locality: "Kamborangoh at 7,200 feet, Mount Kinabalu", Sabah, Malaysia].

**TYPE MATERIAL.**— HOLOTYPE: BMNH 1929. 12. 22. 51, by original designation.

**DEFINITION.**— Small, adult females 24.7–25.8* mm SVL (*n* = 2), adult males 25.8– 26.3* mm SVL (*n* = 2) [*see Comments]; head moderately long 31–33 % HeadL/SVL; head slightly wider than long 104–106 % HeadW/HeadL; naris closer to snout than to eye 59–72 % NarEye/SnEye; eye moderately large 36–37 % EyeD/HeadL; tympanum visible and smaller than eye 77–79 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, 39–40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth absence; palatal fold morphology not reported; tongue size and shape not reported.

Fingers no webbing; lengths 3>2>1>4; tips rounded and slightly dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes moderately webbed, web extending to distal subarticular tubercle of toe 3 and between proximal and middle tubercle of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles present, number and shapes not reported; oval inner and round outer metatarsal tubercles poorly developed.

Color in life not known; dorsum brown with darker brown hour-glass mark from between eyes to mid-trunk with broad brown stripes radiating rearward , no inguinal ocelli (see Comments); loris dark brown; dark brown dorsolateral stripe from above eye to anterior trunk; sides of trunk dark spotted; venter tannish with numerous small dark spots from chin to pelvis.

**ETYMOLOGY**.— The name *baluensis* derives from the frog's origin in the high montane forest of Mount Kinabalu.

**DISTRIBUTION**.— Sabah, Borneo. Known only from upper slopes of Mount Kinabalu.

**NATURAL HISTORY**.— *Kalophrynus baluensis* is a high-elevation, forest-floor frog living in the leaf-litter of oak-chestnut forest between 1400–1800m a.s.l. It calls predominantly at night and typically from burrows or forms. It appears to have an unique handstand defensive posture.

**COMMENTS**.— Preceding information extracted from Kiew (1984a). The description of this species in Malkmus et al. (2002) differs substantially from Kiew's original description, and the former's characterization is summarized below. I accept their characterization as mostly correct and attribute the differences to Kiew's data as a result of Kiew having juveniles and their examination of a larger series of adults.

Moderate-sized, adult females to 47 mm SVL, adult males to 36 mm SVL; head wider than long; tympanum smaller than eye 50–75 % Tymp/EyeD, supratympanic fold present (their fig. 114); tips of fingers round, not dilated, finger length 3>2>1>4; hindlimbs moderately long 39–45 % CrusL/SVL; toes webbed at base; subarticular and metatarsal tubercles weakly developed; one to two yellow inguinal "ocelli" (not clear whether just spots or dark-edged spots).

### *Kalophrynus barioensis* Matsui and Nishikawa, 2011 Bario Sticky Frog

*Kalophrynus barioensis* Matsui and Nishikawa, 2011, *Current Herpetology* 30:146 [type locality: "Jln. Arul Dalan trail to New Dam, Bario, State of Sarawak, Malaysia (03°45′N, 115°26′E, 1141 m asl)"].

**TYPE MATERIAL**.— HOLOTYPE: Sarawak Museum MU455.16, by original designation. PARATYPE: Kyoto University Graduate School 53128–129, 5371.

**DEFINITION**.— Small, adult female 20.5 mm SVL (*n* = 1), adult males 17.5–19.8 mm SVL (*n* = 5); head moderately long 33–36 % HeadL/SVL; head width equals length 33–36 % HeadW/SVL; naris closer to snout than to eye 15–21 % NarEye/SVL; eye moderately large 15–20 % EyeD/SVL; tympanum visible and about equal to eye 60–140 % Tymp/EyeD; slender moderately long forelimb 56–63 % Forelimb/SVL; hindlimb moderately long 126–141 % HndlL/SVL, 42–47 % CrusL/SVL.

Vomerine teeth presence or absence not reported; palatal folds present, morphology not reported; tongue entire.

Fingers with slight basal web; lengths 3>2>1>4, 4th very short; tips rounded and not dilated; subarticular tubercles round, indistinct, and one on digit 2, two on 3; outer palmar tubercle large, inner indistinct; no nuptial excrescences on fingers. Toes slightly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>2>5>1; tips rounded, not dilated; subarticular tubercles indistinct and one on digit 2, two on 3, three on 4, and none on 1 and 5; oval inner and no outer metatarsal tubercles.

Color in life, dorsum orangish brown with faint brown hour-glass mark from between eyes to suprascapular area and largely immaculate from mid-trunk rearward; body; large black inguinal spot, no light edge; loris and temporal area to inguina dark brown, fading ventrally; yellowish white oblique stripe from above eye to lower inguinal area; chin and chest dark brown with indistinct lighter bands, posterior chest and belly yellowish white with scattered black spots anteriorly.

**Etymology**.— The name *barioensis* derives from the town of Bario in the Kelabit Highlands of Sarawak.

**Distribution**.— Sarawak, Borneo. Presently, *K. barioensis* is known only from the vicinity of the type locality.

**Natural History**.— These frogs are ground-dwelling residents of broad-leaf and bamboo forest. All specimens were collected in mid August from the leaf litter along forest trails. Males, hidden beneath the leaf litter, were calling in scattered small chorus and chorused in late afternoon and early evening whether it rained or not.

**Comments**.— The extreme variance of the Tymp/EyeD data suggest an error in the measurement of one individual.

Preceding information extracted from Matsui and Nishikawa (2011).

### *Kalophrynus bunguranus* (Günther, 1895) Natuna Sticky Frog

*Diplopelma bunguranum* Günther, 1895, *Novitates Zoologicae* 2:501 [type locality: “Bunguran, or Great Natuna [Island]”, Indonesia].

**Type material**.— Syntypes: number and deposition not noted in original publication, presumably BMNH; British Museum of Natural History 1947.2.11.38–41 (formerly 95.5.1.105–108) according to R. F. Inger (in Frost, 1985).

**Definition**.— Small, adult females 25–27 mm SVL, adult males 22–23 mm SVL; head medium length 28 % HeadL/SVL; head slightly wider than long 113 % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 45 % EyeD/HeadL; tympanum visible and smaller than eye 61 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long HndlL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 85 % HndfL/CrusL.

Vomerine teeth presences or absence not reported; palatal fold morphology not reported; tongue large, subelliptical and entire behind.

Fingers without web; lengths 3>2≈1>4 (nub-like); tips rounded; subarticular tubercles not reported; palmar tubercle not repored; spiny nuptial excrescences dorsally on base of fingers 1 to 3 and adjacent hand of males (fide Parker; see comment). Toes weakly webbed, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles indistinct, numbers on toes not reported; indistinct inner and outer metatarsal tubercles.

Color in life unknown. Dorsum purplish brown, no mark mentioned; large dark brown , oval black inguinal spot without light border; loris edged with reddish rose that extends posteriorly above eye and onto and widening on trunk to inguina and hindlimbs; loris, chin to anterior chest black fading to yellowish.

**Etymology**.— Great Natuna Island is also called Bunguran, whence the name of the species as a resident of Bunguran.

**Distribution**.— Great Natuna Island.

**Natural History**.— Günther considered it a common frog owing to its abundance in collections.

**Comments**.— Preceding information extracted from Günther (1895) and Parker (1934). Parker considered *C. heterochirus* Boulenger as a synonym of *K. bunguranus* and may have included traits of the former in the description of the latter. Parker reported nuptial pads on dorsum of fingers; Inger (1966: table 16) specifically noted their absence.

### *Kalophrynus calciphilus* Dehling, 2011 Limestone Sticky Frog

*Kalophrynus calciphilus* Dehling, 2011, *Zootaxa* 2737:51 [type locality: "close to the northern entrance of Gua Bulansusu (Moonmilk Cave) on Batu Bungan, ca. 200 m a.s.l., Gunung Mulu National Park, Sarawak, Malaysia"].

**Type material.**— Holotype: Naturhistorisches Museum der Burgergemeinde Bern 1056261. Paratypes: BMNH 1978.1611–1615, FMNH 171777, NMBE 1056262–263. All by original designation.

**Definition.**— Small, adult females 35.5–38.8 mm SVL (*n* = 2), adult males 29.7–30.1 mm SVL (*n* = 2); head moderately long 31 % HeadL/SVL; head wider than long 119 % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 38 % EyeD/HeadL; tympanum visible and distinctly smaller than eye 54 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb slender and long 183 % HndlL/SVL, 43 % CrusL/SVL, and 96 % CrusL/ThghL; hindfoot well developed 84 % HndfL/CrusL. Proportions from holotype only.

Vomerine teeth absence; vomerine fold paired and crenulated, condition of other palatal fold morphology not reported; tongue broad and not bifurcated. Adult males with series of spiny tubercles on rear half of mandible.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles. No nuptial pad or asperities present. Toes modestly webbed not extending to proximal subarticular tubercle of toe 4, lengths 4>3>5>2>1; tips rounded, slightly dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, three on 4, none on 5; large, elongate inner and small, round outer metatarsal tubercles.

In life and at night, dorsum and sides of head and body black from tip of snout to end of trunk; narrow white oblique stripe from tip of snout, passing above eye and tympanum to lower inguinal area; venter from chin to anterior belly fading to dusky thereafter; chest and anterior belly with scattered white spots. During day, dorsum and sides lighten to a medium brown.

**Etymology.**— The specific name derives from the Latin *calx* for limestone and the Latinized Greek suffix *philus* for "who is attracted to" combined to denote this species affinity to karst forest.

**Distribution.**— Sarawak, Borneo. Known only from the karst forest in Gunung Mulu National Park, Sarawak.

**Natural History.**— *Kalophrynus calciphilus* is a terrestrial species, apparently confined to karst forest. It calls day and night from the entrance of small burrows in the soil and owing to the absent of standing water in the karst forest, it is hypothesized that eggs are laid in these burrows and possibly "guarded" by the male.

**Comments.**— Preceding information extracted from Dehling (2011).

### *Kalophrynus cryptophonus* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014 Lam Dong Bamboo Sticky Frog

*Kalophrynus cryptophonus* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014, *Zootaxa* 3769(3):410 [type locality: "Loc Bao, Lam Dong Province, Vietnam (coordinates 11°44′17″N, 107°42′25″E, elevation 800 m a.s.l.)"].

**Type material.**— Holotype: Zoological Museum of the Lomonosov Moscow University (ZMMU) A-4944. Paratypes: ZMMU A-4858–59. Original designations.

**Definition**.— Small, adult female 23.4 mm SVL (*n* = 1), adult males 27.9– 30.4 mm SVL (*n* = 5); head moderately long 28–32 % HeadL/SVL; head wider than long 105–122 % HeadW/HeadL; naris closer to snout than to eye 59–68 % NarEye/SnEye; eye moderately large 35–42 % EyeD/HeadL; tympanum visible and smaller than eye 55–77 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb slender and moderate length 129–140 % HndlL/SVL, 40–43 % CrusL/SVL, and 89–98 % CrusL/ThghL; hindfoot well developed 77–96 % HndfL/CrusL.

Vomerine teeth absence; three palatal folds, vomerine one continuous, postorbital short and low, buccal continuous and crenulated; tongue rounded free end. Skin on margin of mandible with longitudinal series of short triangular spines in males.

Fingers rudimentary webbing; lengths 3>2>4>1; tips rounded and not dilated; subarticular subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large oval palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3; fine-spined asperities dorsally covering fingers 2, 3, and 4 from base to end of penultimate phalanx. Toes modestly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles moderate, oval and one on digits 1, 2, two on 3, three on 4, two on 5 (only distal one prominent); moderate oval inner and small, round outer metatarsal tubercles.

In life, dorsum ranging from dark brown at night to diurnal pinkish beige with faint darker reticulation from between eyes to end of trunk and reverse Y-mark with base on crown and nape and arms extending to rear of trunk; body; narrow, orangish dorsolateral stripe from tip of snout and edge of canthus rostralis above eye running diagonally to mid inguina, bordered below by dark brown that fades ventrolaterally; small round, black inguinal spot, not light edged; venter pale yellowish-pink, chin to mid chest with dark marking , belly largely immaculate.

**Etymology**.— Because this species was only discovered by the males' vocalization from hollow bamboo stems, the authors highlight this behavior with Greek *cryptos* for hidden or mystery and *phonus*, voice, thus hidden voice.

**Distribution**.— Vietnam. *Kalophrynus cryptophonus* is known only from the vicinity of the type locality.

**Natural History**.— This sticky frog lives in a mid-montane evergreen tropical forest (secondary) with abundant bamboo clumps. It was discovered in mid April by the males' vocalization from inside cut bamboo stems. The water inside the bamboo stems serve as egg-deposition and larval development sites (phytotelm breeding).

**Comments**.— Preceding information extracted from the original description by Vassilieva and colleagues (2014).

### *Kalophrynus eok* Das and Haas, 2003 Eok Sticky Frog

*Kalophrynus eok* Das and Haas, 2003, *Raffles Bulletin of Zoology* 51:110 [type locality: "Long Re (03°42′2″N; 115°32′06″E), east of Bario along forest trail to Kalimantan border, Sarawak, East Malaysia (Borneo)"].

**Type material**.— Holotype: Sarawak Biodiversity Centre Zoological Museum A.00310, by original designation.

**Definition**.— Small, known from single adult male 26.3 mm SVL; head moderate length 20 % HeadL/SVL; head wider than long 132 % HeadW/HeadL; naris closer to snout than to eye 78 % NarEye/SnEye; eye large 55 % EyeD/HeadL; tympanum visible and smaller than eye 62 % Tymp/EyeD; with exception of CrusL, limb measurements not reported, 44.8 % CrusL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue size and shape not reported.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial pad on base of fingers 2 and 3. Toes lightly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, 5, and three on 4; round inner and outer metatarsal tubercles.

In life, dorsum brick-red with brown interorbital bar, brown inverted V-shaped mark on posterior head to suprascapular area, and brown traverse bar at midbody; no inguinal ocelli; lores and temporal area to axilla dark brown, trunk side reddish brown; venter pinkish white, sides of throat light red, scattered white spots of chest and anterior belly.

**ETYMOLOGY**.— This small frog lives in the Kelabit language area of Borneo, and the Kelabit word *eok* meaning tiny.

**DISTRIBUTION**.— Borneo, Sarawak. This species is known currently only from the vicinity of the type locality.

**NATURAL HISTORY**.— The only known specimen is a male that was discovered calling from a water-filled node of a fallen bamboo trunk in primary submontane evergreen forest.

**COMMENTS**.— Preceding information extracted from Das and Haas (2003) and Frost (2014).

### *Kalophrynus heterochirus* Boulenger, 1900 Short-fingered Sticky Frog

*Calophrynus heterochirus* Boulenger, 1900, *Proceedings of the Zoological Society, London* 1900:186 [type locality: "Borneo (no precise locality)"].

**TYPE MATERIAL**.— HOLOTYPE: Sarawak Museum according to the original description. Parker (1934) reported BMNH 1909.8.18.6–7 (now 1947.2.11.38–41) as syntypes; see Comments.

**DEFINITION**.— Small to medium size, adult females 30.5–32.9 mm SVL ($n$ = 6), adult males 24.1–27.2 mm SVL ($n$ = 10); head moderately long NA % HeadL/SVL; head slightly wider than long NA % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye ~50 % Tymp/EyeD; slender forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately slender NA % HndlL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold transverse interrupted medially, morphology of others not reported; tongue large and ovate.

Fingers not webbed; lengths 3>2>1>4, fourth nub-like; tips rounded and not dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes one-third webbed, web extending to distal subarticular tubercle of toe 3, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles present, number and shapes not reported, except none of fifth; inner and outer metatarsal tubercles poorly developed.

Color in life, dorsum purplish brown and largely immaculate, no inguinal ocelli, rather one or more bluish white spots; narrow white stripe extending from canthus rostralis above eye and tympanum diagonally to mid inguina; venter whitish immaculate or variously dusky on throat and anterior chest.

**ETYMOLOGY**.— Boulenger did not explain his selection of *heterochirus*. The Greek *heteros* for other or different and *cheir* for hand, i.e., different hand, likely to highlight the small, nub-like fourth finger of this species.

**Distribution**.— Borneo. Inger (1966) reports it from western Sarawak and northeastern West Kalimantan.

**Natural History**.— All *K. heterochirus* have been found on the floor of hilly primary forest.

**Comments**.— Preceding information extracted from Boulenger (1900), Smith (1922), and Inger (1966). Parker's (1934) listing of syntypes in The Natural History Museum, London (= BMNH) is in error. Boulenger (1900) specifically stated "Type in Sarawak Museum." thereby indicating only a single type. Additionally, no one has demonstrated that the type and other specimens were transferred from Sarawak to London.

### *Kalophrynus honbaensis* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014
**Hon Bao Sticky Frog**

*Kalophrynus honbaensis* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014, *Zootaxa* 3769(3):422 [type locality: "vicinity of the Yersin station on Hon Ba Mountain, Hon Ba Nature Reserve, Cam Lam District, Khanh Hoa Province, Vietnam (coordinates 12°07′16″N, 108°56′55″E, elevation 1500 m a.s.l.)"].

**Type material**.— Holotype: Zoological Museum of the Lomonosov Moscow University (ZMMU) A-4941. Paratype: ZMMU A-4943.

**Definition**.— Small to medium size, adult males 26.7– 36.8 mm SVL (*n* = 2); head moderately long 30–32 % HeadL/SVL; head wider than long 122–129 % HeadW/HeadL; naris closer to snout than to eye 62–71 % NarEye/SnEye; eye moderately large 34–37 % EyeD/HeadL; tympanum visible and smaller than eye 76–78 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb slender, moderately long 129–135 % HndlL/SVL, 39 % CrusL/SVL, and 95–97 % CrusL/ThghL; hindfoot well developed 86–99 % HndfL/CrusL.

Vomerine teeth absence; three palatal folds, vomerine one indistinct, postorbital small and smooth, buccal continuous and crenulated; tongue with rounded free end. Skin on margin of mandible smooth in males.

Fingers basal webbing; lengths 3>2>4>1; tips rounded and not dilated; subarticular tubercles prominent, round, and one on digits 1, 2, 4, and two on 3; one small oval palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3; no nuptial pad on dorsal surface of hand. Toes modestly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, slightly dilated; subarticular tubercles moderate, oval and one on digits 1, 2, two on 3, three on 4, two on 5 (only distal one prominent); moderate oval inner and small, round outer metatarsal tubercles.

In life, dorsum orangish yellow and immaculate, except for inguinal spot; body; dark brown laterally from snout through loris above tympanum onto trunk narrowing at midtrunk and ending before inguina; ventrolaterally fading to yellowish pink of venter; small round, black inguinal spot with faint light border; venter pale yellowish-pink, chin to mid chest dusky , belly largely immaculate.

**Etymology**.— The specific name derives from its presence in the Hon Ba Mountains.

**Distribution**.— Vietnam. Known only from the type locality.

**Natural History**.— *Kalophrynus honbaensis* was found on the ground in a small patch of montane evergreen forest.

**Comments**.— Preceding information extracted from Vassilieva et al. (2014).

### ***Kalophrynus interlineatus*** **(Blyth, 1855)** **Striped Sticky Frog**

Figures 7, 11C.

*Engystoma* (?) *interlineatum* Blyth, 1855, *Journal of the Asiatic Society of Bengal* [1854] 23:732 [type locality: "Pegu", Myanmar; see Comments below].

**Type material.**— Lectotype: Natural History Museum United Kingdom, formerly British Museum of Natural History 68.4.3.128, recataloged as 1947.2.31.26. Paralectotype: NHMUK/BMNH 68.4.3. 129, recataloged as 1947.2.31. 27. See discussion on the assignment of type specimens in the Comments section below.

**Description and intrapopulational variation.** Moderate-sized adults, not sexually dimorphic although females average larger (mean 41.5, 35.0–46.4 mm SVL) than males (39.2, 33.7–44.6 mm). These differences are reflected in the other measurements: HeadL 11.2–15.3 mm ♀♀, 10.3–13.4 mm ♂♂; HeadW 12.7–15.1 mm ♀♀, 11.3–13.5 mm ♂♂; SnEye 4.3–5.7 mm ♀♀, 3.8–5.3 mm ♂♂; NarEye 2.8–3.7 mm ♀♀, 2.3–3.8 mm ♂♂; EyeD 3.6–4.5 mm ♀♀, 3.4–4.5 mm ♂♂; Tymp 3.1–3.8 mm ♀♀, 2.6–3.5 mm ♂♂; ForarmL 9.0–13.2 mm ♀♀, 8.7–12.2 mm ♂♂; HandL 8.4–11.3 mm ♀♀, 7.7–10.0 mm ♂♂; ThghL 13.7–18.6 mm ♀♀, 14.1–17.7 mm ♂♂; CrusL 13.0–16.2 mm ♀♀, 12.0–15.6 mm ♂♂; TarsL 8.5–10.4 mm ♀♀, 7.9–10.8 mm ♂♂; HndfL 13.0–16.6 mm ♀♀, 11.7–15.8 mm ♂♂. Body proportion means differ between females and males, although not greatly so (all values are percent): HeadL/SVL 29–36 ♀♀, 28–31 ♂♂; HeadW/SVL 31–36 ♀♀, 29–36 ♂♂; HeadW/HeadL 95–11 ♀♀, 95–116 ♂♂; SnEye/HeadL 36–41 ♀♀, 36–45 ♂♂; NarEye/SnEye 56–66 ♀♀, 54–78 ♂♂; EyeD/HeadL 28–36 ♀♀, 30–37 ♂♂; Tymp/EyeD 72–100 ♀♀, 71–79 ♂♂; Forarm/SVL 25–31 ♀♀, 24–31 ♂♂; Forarm/CrusL 69–83 ♀♀, 65–86 ♂♂; HndlL/SVL 127–147 ♀♀, 122–148 ♂♂; CrusL/SVL 34–40 ♀♀, 30–39 ♂♂; CrusL/ThghL 83–95 ♀♀, 81–96 ♂♂; TarsL/ThghL 51–62 ♀♀, 53–63 ♂♂; HndfL/SVL 30–40 ♀♀, 30–40 ♂♂; HndfL/ThghL 84–95 ♀♀, 80–93 ♂♂.

I noted earlier in the Morphometric section that the Tanintharyi sample displayed no significant sexual dimorphism and that females were significantly larger in the SE Asia sample. When the samples are combined, the overall size dimorphism declines, although a few traits remain dimorphic. Females have larger heads than males; HeadL, HeadW, and SnEye average larger, but none of the other head metrics do, and there are no proportional differences in the head or body metrics. There is strong dimorphism in ForarmL and HndfL with females being larger in both.

In their amphibian atlas, Fei et al. (2010) reported Chinese males as 32–38 mm SVL and females to 40 mm. These adult lengths are smaller, likely significantly so, than my sample which is comprised of frogs from more southern locations. Karsen et al. (1986) did not give a range or mean for Hong Kong *K. interlineatus* and his "up to 6 cm long", contrasts sharply with Fei's lengths and is much larger than the maximum SVL in our sample or that reported for this species elsewhere. Bourret (1942) gave single value adult sizes of 38 mm SVL for males and 44 mm for females. Berry (1975) gave total lengths of Peninsular Malaysia *K. interlineatus* as 47–58 mm. I interpret his total length as SVL, hence his size data are greater than the range for my Tanintharyi and Thai-Indochina samples and more closely match the size of *K. meizon*. Although I do not reject his data, I am uncertain how to interpret it and have not included his values in Table 3. Manthey and Grossmann (1997), in contrast, gave 35–41 mm SVL for males and 38–46 mm for females from Peninsular Malaysia, matching my adult size range for the Tanintharyi and Thai-Indochina samples. A more recent study of Malaysian *K. interlineatus* (Chan et al, 2011) reported 33.7–38.1 mm SVL for adult males ($n$ = 7) and 41.1–47.3 mm SVL for adult females ($n$ =10); these values also match my values for the more northern Thai-Indochinese sample.

Tongue is broadly obovate, posterior edge smooth; vomerine teeth are absent; palatal fold morphology appears relatively uniform among individuals although these data are not quantified. Vomerine folds are smooth-edged flaps, one adjacent to each choanae and widely separated from its opposite. Postorbital folds are more variable; in Tanintharyi frogs, a pair of folds is separated on the midline, and each side has two or three. Variation in the Thai and Indochina frogs is described in the morphology section. Buccal fold is a continuous lobular fold with abutting lobes and each lobe a low, round-edged rectangle. See Fei et al. (2005) for an illustration of the buccal cavity of a Chinese *K. interlineatus*.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, circular, nearly medial outer palmar tubercle. For the hindfoot, each toe has a basal subarticular tubercle, third and fifth toes have an addition tubercle on free portion of digit, two tubercles on fourth toe. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer small to nearly absent and circular. Toes modestly webbed WebIII2 median 2.0 (1.0–3.0), WebIV1 1.0 (0.5–2.0). Digit lengths nearly constant for fore- and hindfeet; finger formula 3>2≈1>4; toe formula 4>3>5>2>1.

Color pattern variation statistics for entire sample of juve-

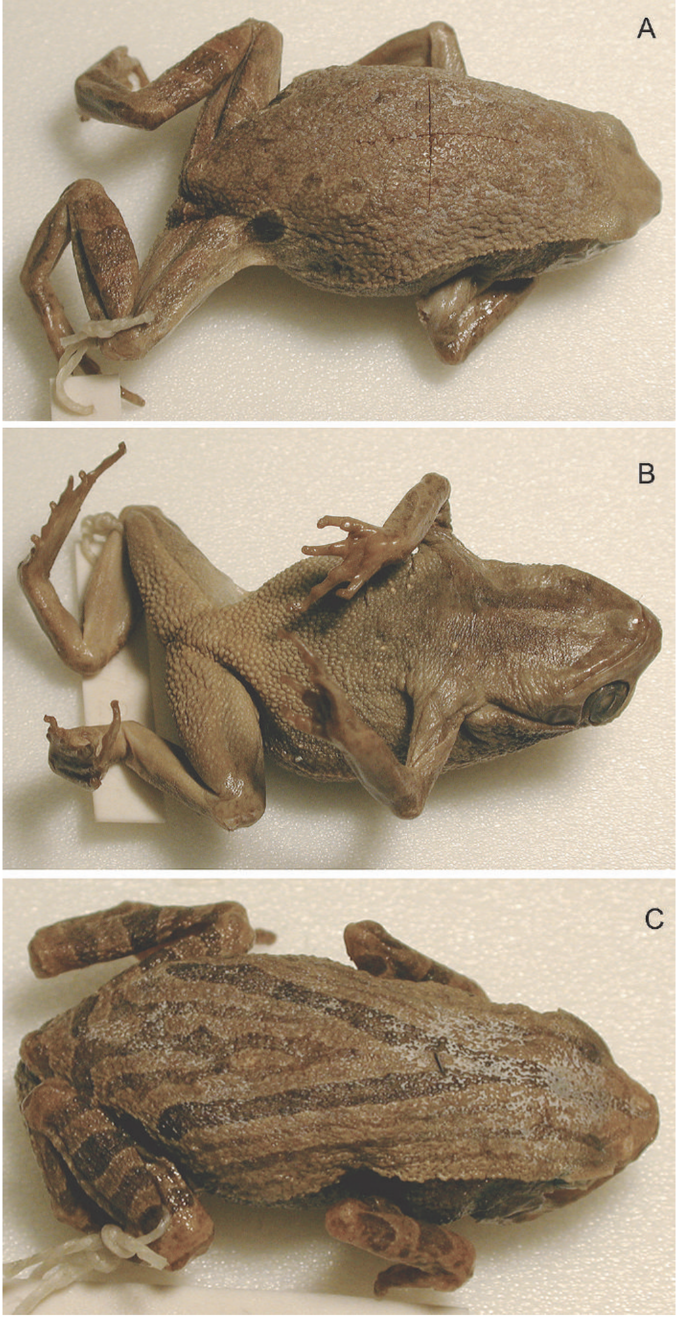

FIGURE 7. Images of lectotype of *Kalophrynus interlineatus* (NHMUK/BMNH 1947. 2.31.26, female) in (A) dorsal and (B) ventral views, and of paralectotype (NHMUK/BMNH 1947. 2.31.27, male) in (C) dorsal view [photographer G.R. Zug].

nile and adults are (median and range): HeadMid 1, 0–2; HeadPsag 0, 0–2; DorsNap 1, 0–2; DorsPsag 1, 0–2; IngSpt 2, 0–2; HndlBr 2, 0–2; DlatSt 2, 1–2; Loreal 2, 0–2; LatTrnk 2, 0–2; Chin 2, 0–2; Chest 1, 0–2. In summary, *K. interlineatus* usually has a faded to distinct middorsal stripe and no parasagittal stripes on head, distinct nape stripe in about half of the individuals continuing into bilateral (parasagittal) stripes, inguinal spot almost always present and usually as ocelli, dorsolateral narrow white stripe rarely absent or indistinct, hindlimbs almost always distinctly barred, loreal area and lateral trunk usually uniformly dark, chin and throat always dusky and usually with pair of darker longitudinal bars, and chest commonly dusky. Dorsal ground color is variable, ranging from a light beige or tan to medium or rufous brown, occasional individuals are rose to pink; sides from lore to inguinal are usually shades of medium to dark brown.

Fei et al. (2010) provided color images of five living individuals whose dorsal coloration ranged from unicolor [*n* = 1 individual] to strongly patterned with all six of my dorsal pattern characters strongly developed [*n* = 5]. The dorsal stripe pattern of Chinese *K. interlineatus* has the same layout/arrangement; however, the stripes differ markedly in being broader with strongly scalloped edges and fragmented, especially the DorsPsag ones. Karsen et al. (1986) pictured a Hong Kong striped individual that matched those of Fei et al. Additionally Fei's photographs showed well-developed white dorsolateral stripes that were strongly speculate in all individuals. The single individual depicted for Cambodia (Thy and Holden 2008) had a well-developed dorsal pattern similar to the western populations, although the white dorsolateral stripe was narrow and appeared interrupted. Ohler and Grosjean (2005) reported distinct pattern difference between "western" and Vietnamese frogs. The former depicted by a Laos individual (O&G 2005: figs. 1a,c,e) has straight-edged dorsal stripes, the latter (2005: figs. 1b,d,f) has the scalloped and fragmented stripes of the Chinese individuals. The preceding summary confirms Ohler's and Grosjean's observations of color pattern differences between west (Thailand) and east (Vietnam) and, as they noted, hints at the possibility of speciation between eastern and western populations. Chan and collaborators (2011) noted that half of their sample of Malaysian *K. interlineatus* (= their *pleurostigma*) lacked inguinal spots on one or both sides and concluded that "populations in Peninsular Malaysia are not conspecific" with mainland Asia populations. Their interpretation may be correct, although I suspect that there is no genetic discontinuity between these Malaysian population and those of peninsular Myanmar and Thailand.

**ETYMOLOGY**.— Blyth (1855) offered no explanation for his name, presumably using *interlineatus* to note the longitudinal lines on the dorsum, hence a derivation from the Latin *inter*, between, and *lineatus*, from Latin *lineo*, drawing lines, and *linearis, lineatus*, of a line, linear.

**DISTRIBUTION**.— *Kalophrynus interlineatus* as here defined has the broadest geographic range of the *pleurostigma* group, extending eastward from northern-most Peninsular Myanmar, eastward through northern Thailand, Laos, Cambodia, and Vietnam, southward through Peninsula Malaysia, and also in southern China from southeastern Yunnan to Hong Kong and adjacent Guangdong.

Bourret's (1942) concept of *K. interlineatus* was as a subspecies with a northern distribution from Myanmar through northern Thailand to Vietnam and adjacent China to Hong Kong. He had only a single male specimen (38 mm SVL) of questionable locality (probably Tonkin, Vietnam) in Indochina. He listed four Burmese localities: Bhamo, Teinzo, Palon, Toungo (credited to Oates [Toungo] and Fea [diverse localities]). The first two records are potential localities for *K. anya*, the latter two are potential localities for *K. interlineatus*. Toungo (= Taungo, 20°56′N 95°24′E) is in the upper Sittaung River valley. MNHN 1893.492 is identified as *Kalophrynus interlineatus* from Palon; I did not examine this specimen to confirm its presence or identification. Palon (7°41′N 97°31′E), Kayin State, is identified as a Pegu locality in the British natural history museum specimen register but represented by only one gecko and one *Micryletta inornata*. This record highlights the broad geographic concept of Pegu by the British in late 19th century.

Thy and Holden (2008) stated that *K. interlineatus* was a common frog and suggested that it occurred throughout Cambodia.

**Natural History**.— In Cambodia, Thy and Holden (2008) reported it as a common species living in grassland, scrub forest adjacent to villages, and deciduous forest. The recent Burmese individuals derived from the soil surface in mixed deciduous-evergreen secondary growth forest (Mon) and from evergreen forest abutting a clear-cut (weedy) pipeline (Tanintharyi).

**Comments**.— The type locality "Pegu" is commonly interpreted by biologists as equivalent to the present Myanmar division of Bago (formerly called Pegu). Nineteenth century Pegu encompassed a much broader area than the present political division. The older Pegu encompassed the area from the Arkan (roughly equivalent to the present state of Rakhine) eastward to the Sittang River drainage. This broad Pegu likely encompassed northernmost Mon State, hence my placement of the type locality straddling the Bago-Mon border. This broad Pegu is emphasized by a NHMUK/BMNH specimen from Palon, Kayin state, that was geographically labeled as Pegu.

Ohler and Grosjean (2005) reported examining the holotype of *Engystoma interlineatum* Blyth, a specimen (ZSI 9853) from Mergui, Myanmar. The British Museum has two specimens (NHMUK/BMNH 68.4.3.128–129, recataloged as 1947.2.31.26–27, an adult female and male, respectively) collected by Theobald in Pegu. I believe that the latter two Pegu specimens of Theobald's (Fig. 7) are the individuals on which Blyth based his description of *interlineatum*, and they were subsequently sent to London. The precision of ZSI locality indicates that someone arbitrarily selected a *Kalophrynus* specimen and designated it as a ZSI holotype. Mergui was never recognized as part of Pegu and is in Tenasserim. Because both Blyth (1855:720) and Theobald (1882: 192) specifically noted having two specimens, I recommend recognizing one of them as a lectotype and select BMNH 1947.2.31.26, the female, because this specimen is presently in the best physical condition. BMNH 1947.2.31.27 is then a paralectotype. Because Pegu is not sufficiently delimited, I recommend a more precise, yet not overly restrictive, type locality: Bago Division-Mon State border in the lower Sittaung River valley, Myanmar (~17°35′24″N 96°53′33″E).

### *Kalophrynus intermedius* Inger, 1966 — Mengiong Sticky Frog

*Kalophrynus intermedius* Inger, 1966, *Fieldiana, Zoology* 52:131 [type locality: "Nanga Tekalit, Mengiong River, Third Division, Sarawak", Malaysia (Borneo)].

**Type material**.— Holotype: Field Museum of Natural History 139348. Paratypes: FMNH 138070, 144298. By original designation.

**Definition**.— Medium size, adult females 37.9–40.5 mm SVL ($n = 2$), no males known; head moderately long NA % HeadL/SVL; head wider than long NA % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye ~66 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, 38–41 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth, presence or absence not reported; palatal fold morphology, vomerine fold not described, postorbital fold short and notched medially, and buccal fold long and crenulated; tongue size and shape not reported.

Fingers not webbed; lengths 3>2>1>4, fourth nub-like; tips rounded, not dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes two-thirds webbed, web extending to distal subarticular tubercle of toe 3 and between proximal and middle tubercle of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles present, number and shapes not reported, distinct on toes 1–4, barely visible on 5; inner and outer metatarsal tubercles poorly developed.

Color in life not known; dorsum brown to purplish brown with obscure darker markings on back , no inguinal ocelli; sides cream or yellow; venter cream, pinkish on throat and pair of dark bars on throat and scattered small dark spots on chest.

**ETYMOLOGY**.— The choice of the name *intermedius* was not stated, presumably it is in reference to this frog's size between that of two smaller Bornean *Kalophrynus heterochirus*, *punctatus*¸ and *subterrestris* and the larger *K.* "*pleurostigma*".

**DISTRIBUTION**.— Borneo, Sarawk. Known only from the type localitye.

**NATURAL HISTORY**.— The three known specimens were collected on the floor of primary rain forest at less than 300 m a.s.l.

**COMMENTS**.— Preceding information extracted from Inger (1966).

### *Kalophrynus limbooliati* Matsui, Nishikawa, Belabut, Ahmad, and Yong, 2012

**Johor Tiny Sticky Frog**

*Kalophrynus limbooliati* Matsui, Nishikawa, Belabut, Ahmad, and Yong, 2012, *Zootaxa* 3155:39 [type locality: "Gunung (= Mt.) Pulai, Kpg. (Kampung = village) Sri, Kulai, State of Johor, Peninsular Malaysia (01°36′N, 103°32′E, 457 m a.s.l.)"].

**TYPE MATERIAL**.— HOLOTYPE: Universiti Kebangsaan Malaysia Herpetological Collection 705. PARATYPES: Kyoto University Health & Environment 53314–315, 52061. All by original designation

**DEFINITION**.— Small, no adult females, adult male 26.2–28.7 mm SVL (*n* =3); head long 32 % HeadL/SVL; head width subequal length 32–34 % HeadW/SVL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 13–17 % EyeD/SVL; tympanum visible and smaller than eye 8–9 % Tymp/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 129–136 % HndlL/SVL, 41–42 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 33–36 % HndfL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue entire, i.e., presumably end rounded and not notched.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles large, round, and two on digits 1, 2, 4, and three on 3; outer palmar tubercle fleshy and large, inner indistinct; asperities (nuptial pad) absent on hand. Toes lightly webbed to below level of proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded; subarticular tubercles variously developed, none on digit 5, one on 1, 2, two on 3, and three on 4, tubercles prominent only on fourth toe (distal and middle one); large, oval inner metatarsal tubercle, indistinct outer tubercle.

In life, dorsum variable from light orange brown to dark brown with obscure darker hourglass mark from interorbital to shoulders and scattered small dark spots posteriorly on trunk; light colored narrow stripe from tip of snout above eye and tympanum, then diagonally to mid inguina; dark inguinal spot without light border; loris and temporal area to axilla dark brown, trunk side as dorsum; venter pinkish gray with scattered white spots.

**ETYMOLOGY**.— The specific name honors Dr. Lim Boo Liat, a pioneer of field zoology in Malaysia.

**Distribution**.— Southern Peninsular Malaysia (Johor, Negeri Sembilan, and possibly Pahang but unconfirmed) and Singapore.

**Natural History**.— *Kalophrynus limbooliati* is a forest-floor resident in a variety of forests, secondary broad-leafed and bamboo. Males call from beneath leaf litter.

**Comments**.— Preceding information extracted from Matsui et al. (2012).

### *Kalophrynus meizon* Zug, sp. nov. Borneo Big Sticky Frog

Figures 8, 11D.

**Type material**.— Holotype: Field Museum of Natural History 267881, adult male from Samarakan Nursery (2°56′N 113°05′E), Bintulu Division, Sarawak, collected by Robert F. Inger on 29 Nov 2004 (Fig. 8). Paratypes: FMNH 267873, 267875–880, same locality as holotype; FMNH 269668–670, 269673, 269675 Sg Mina, Kakus District, Sarawak; 273260–262 same locality as holotype; FMNH 273264, 273266 Penyaria, Bintulu Division, Sarawak; USNM 197671 (formerly FMNH 157676) Tabua Camp on Sungei Pesu, Bintulu District, Sarawak.

**Definition.—** Adult *K. meizon* can be distinguished from all congeners by the following combination of characters: size dimorphic, adults female 48–60 mm, males 44–50 mm SVL; proportion not dimorphic (except for TarsL/ThghL and HndlL/SVL; females smaller), HeadL/SVL 29–35 %; tympanum about equal eye diameter, Tymp/EyeD 84–112 %; moderately long hindlimbs, HndlL/SVL 136–157 %; short hindfoot, HndfL/ThghL 71–87 %; strong supratympanic ridge dorsoposteriorly overhanging tympanic annulus; paired vomerine folds, each broad smoothly undulatory with narrow medial separation; single postorbital fold of broad undulatory lobes; single broad buccal fold comprised of numerous abutting short blunt lobes; forefeet without webbing; hindfeet moderately webbed, highest between 3rd and 4th toe, usually to base of 2nd subarticular tubercle of 4th toe; head without median head stripe (HeadMid 0 %) uncommonly with parasagittal ones (HeadPsag 11 % present) and DorsNap (11 % present); chin seldom with paired, broad longitudinal bars; hindlimbs (HndlBr) weakly or inconspicuously barred (50 %) and commonly (>50 %) with light horizontal stripe on rear of thighs.

**Description of the holotype**.— Moderately robust-bodied male (47.5 mm SVL) with well-developed, moderate-length fore- and hindlimbs (51 % ForarmL+HandL/SVL, 147 % HndlL/SVL); head ovate ( 33 % HeadL/SVL, 30 % HeadW/SVL) and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: HeadL 15.8 mm; HeadW 14.2 mm; SnEye 6.2 mm; NarEye 3.4 mm; EyeD 4.1 mm; Tymp 3.7 mm; ForarmL 13.2 mm; HandL 11.0 mm; ThghL 22.7 mm; CrusL 17.9 mm; TarsL 11.9 mm; HndfL 17.2 mm. Eye distinctly larger than tympanum.

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, surface with numerous small white conical spines in adult males; skin thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; distinct diagonal dorsolateral ridge from eye to inguina, below cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular areas and surface mostly smooth; chest skin smooth, abdominal skin glandular and pebble-like; chest without small unpigmented glands. Nuptial pad of dense fine spines on bases second and third fingers. Tongue large, spatulate, posterior one half free. Vomerine teeth absent. Three sets of palatal folds on roof of mouth: vomerine paired, each long with low smooth free edge and narrowly separated medially; postorbital single, continuous, composed of 10 to 12 rectangular lobes; buccal slightly lower than postorbital and single continuous fold of 15 to 16 rectangular, abutting lobes, medial lobes larger than lateral ones. Fingers and toes well-developed and tips bluntly rounded; hand web free; asperities dorsally on base of second and third fingers; foot moderately webbed (WebIII.2 = 2.5, WebIV.1 = 1.5). Subarticular tubercles well-developed on hand and foot; large, elliptical palmar tubercle with moderately large tubercle at base of each finger and only third finger with tubercle of free portion of digit; on foot, paired moderate-sized, elliptical metatarsal tubercles on edges, inner slightly smaller than outer; each toe with basal subarticular tubercle; third toe with single tubercle on free portion of digit, fourth with two tubercles, and fifth with one (hence total of two tubercles on fifth toe, both low). Digital length formulae, hand 3>1≈2≈4, foot 4>3>5>2>1.

Coloration in preservative (Fig. 8). Dorsum from tip of snout to between eyes uniform light brown thereafter to end of body dusky brown; dorsum largely without marking aside from numerous white spine; distinct dark centered ocelli in light brown inguinal pocket; dorsolateral ridge light brown bordered immediately below by narrow 'stripe' of dark brown quickly fading to medium brown ventrolaterally; face (loreal) dark brown at canthus rostralis, lighter brown to mouth; no banding on dorsal of thighs although light brown horizontal stripe from vent to behind knees. Venter light brown from chin to thighs, somewhat dusky from chin to base of throat; no stripes or bars on venter.

**Description and intrapopulational variation.**— Large adults, strongly sexually

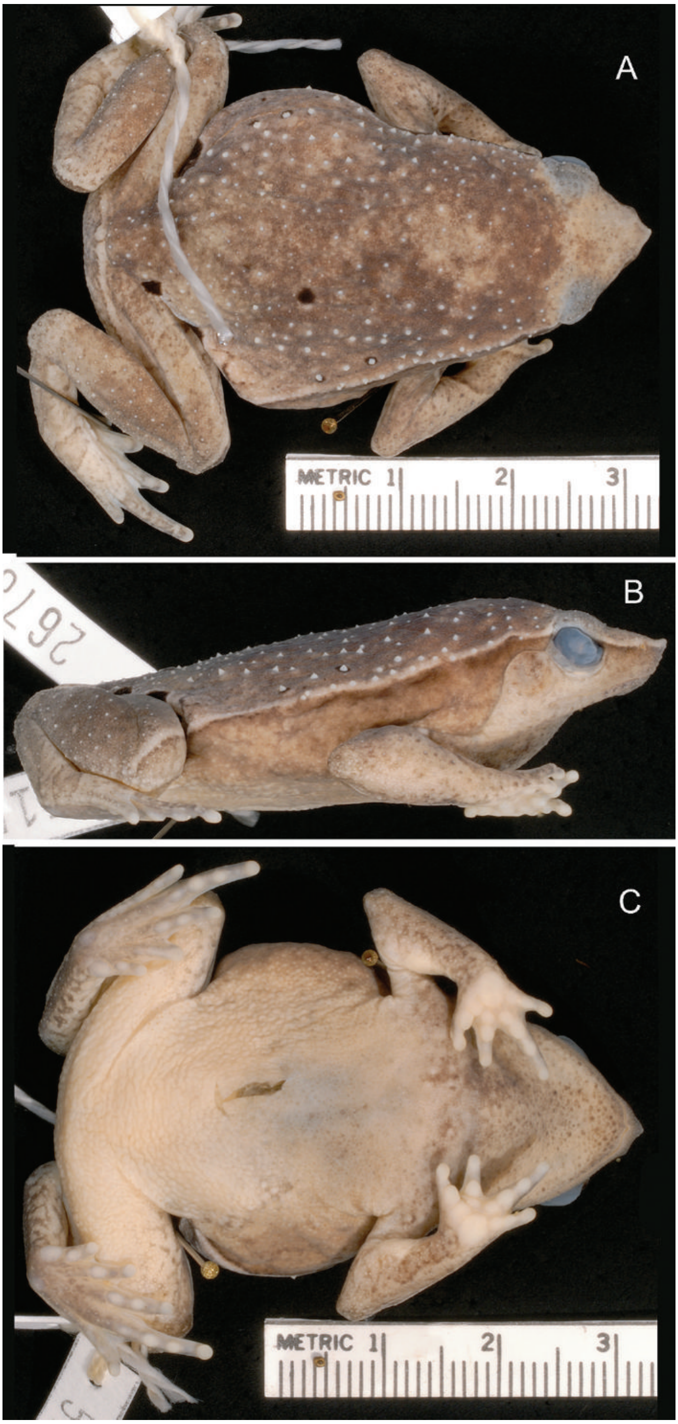

FIGURE 8. Images of holotype of *Kalophrynus meizon* (FMNH 267881, male, 47.5 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

dimorphic with females averaging larger (54.8 mm, 48.2–60.2 mm SVL) than males (45.6 mm, 44.1–47.5 mm). These size differences occur in all other measurements: HeadL 16.0–19.2 mm ♀♀, 13.4–15.8 mm ♂♂; HeadW 16.3–21.1 mm ♀♀, 14.1–16.9 mm ♂♂; SnEye 6.4–8.4 mm ♀♀, 5.1–6.2 mm ♂♂; NarEye 3.5–4.8 mm ♀♀, 5.1–6.2mm ♂♂; EyeD 3.5–4.8 mm ♀♀, 4.0–4.9 mm ♂♂; Tymp 4.4–5.6 mm ♀♀, 3.7–4.6 mm ♂♂; ForarmL 14.9–18.3 mm ♀♀, 12.4–14.3 mm ♂♂; HandL 11.3–13.4 mm ♀♀, 10.0–11.9 mm ♂♂; ThghL 21.6–27.1 mm ♀♀, 19.8–22.7 mm ♂♂; CrusL 19.5–231. mm ♀♀, 17.9–19.7 mm ♂♂; TarsL 12.1–14.9 mm ♀♀, 11.4–12.5 mm ♂♂; HndfL 17.1–19.8 mm ♀♀, 15.4–18.0 mm ♂♂. Body proportions do not differ between females and males, except for TarsL/ThghL and HndlL/SVL (all values are percent): HeadL/SVL 29–35 ♀♀, 30–34 ♂♂; HeadW/SVL 31–36 ♀♀, 30–36 ♂♂; HeadW/HeadL 97–117 ♀♀, 90–108 ♂♂; SnEye/HeadL 36–46 ♀♀, 36–45 ♂♂; NarEye/SnEye 52–62 ♀♀, 53–67 ♂♂; EyeD/HeadL 27–30 ♀♀, 26–31 ♂♂; Tymp/EyeD 90–112 ♀♀, 84–105 ♂♂; Forarm/SVL 26–32 ♀♀, 26–32 ♂♂; Forarm/CrusL 66–76 ♀♀, 66–76 ♂♂; HndlL/SVL 136–157 ♀♀, 144–156 ♂♂; CrusL/SVL 38–43 ♀♀, 38–43 ♂♂; CrusL/ThghL 85–91 ♀♀, 79–93 ♂♂; TarsL/ThghL 51–59 ♀♀, 52–62 ♂♂; HndfL/SVL 31–38 ♀♀, 35–39 ♂♂; HndfL/ThghL 71–87 ♀♀, 76–83 ♂♂. The dimorphism between TarsL/ThghL and HndlL/SVL indicates that the tarsus is longer in males than in females, although the differences are significant, the proportions strongly overlap.

All individuals dorsally with thick cloak of glandular skin from behind eyes to vent; unlike other *pleurostigma* group members surface texture and dorsolateral ridge/fold are sexually dimorphic, latter distinctly elevated in males; surface dimorphic, smoothly rugose in females, spiny rugose in males. Most males, perhaps sexually active ones, have numerous small white, sharp-tipped, conical spines from nape to vent, spines more numerous on posterior third of males' trunks; in females, most individuals are spine free, when present, spines rounded (dome-shaped) and widely scattered on posterior third of trunk. Ventrally, males and females have similar surface morphology, smoothly rugose from chin to chest, abdomen large, pebble-like rugose. All adult males have asperities on bases of second and third finger, but of variable development.

Oral morphology is relatively uniform among individuals although these data are not quantified. Tongue broadly ovate, about ½ free. No vomerine teeth. Vomerine folds are elongate smooth-edged flaps, nearly in contact on midline. Postorbital folds are well developed and continuous across midline and consist of six to eight abutting rectangular lobes. Buccal fold is low continuous fold with low abutting rectangular lobes.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, elliptical to oblong, nearly medial outer palmar tubercle. Second and third fingers bear asperities on dorsal surface of distal end of the metacarpal and first phalanx. For the hindfoot, each toe has a basal subarticular tubercle, third toe with addition tubercle on free portion of digit, two tubercles on free portion of fourth toe, and fifth toe with basal and midlevel tubercles often poorly developed to nearly absent. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer circular and small to nearly absent. Toes moderately webbed WebIII2 median 2.0 (2.0–2.5), WebIV1 1.0 (1.0–2.0). Digit lengths nearly constant for fore- and hindfeet; finger formula 3>1≈2≈4; toe formula 4>3>5>2>1.

Color pattern variation statistics for adults are (median and range): HeadMid 0, 0–0; HeadPsag 0, 0–2; DorsNap 0, 0–1; DorsPsag 0, 0–2; IngSpt 2, 2–2; HndlBr 1, 0–2; DlatSt 2, 1–2; Loreal 1, 1–2; LatTrnk 1, 1–2; Chin 0, 0–1; Chest 0, 0–1. In preservative, most *K. meizon* are dull, muddy colored (light to moderate grayish brown) frogs from dorsal view. Most individuals are unicolor dorsally or with few widely scattered, small, dark brown spots. Dorsolateral white stripe is well developed in all individuals and extends from snout tip above orbit to inguina, bordered below by dark brown fading to light brown ventrally. Inguinal dark-centered ocelli present in all individuals and uncommonly unilateral, smaller ocellus posteromedial to main ocellus. Venter is typically without pattern, dusky from chin through chest and light brown to cream on abdomen. Hindlimb commonly lack thigh banding and about half of individuals with horizontal light stripe continuously across rear of thighs. One individual (FMNH 267879) possesses the hourglass dorsal pattern of neotype of *K. pleurostigma*; pattern is outlined by narrow cream edge.

**ETYMOLOGY**.— Of the twenty-one species of *Kalophrynus*, this species has the largest average size, and the Greek adjective *meizon* for larger or greater denotes this feature.

**DISTRIBUTION**.— *Kalophrynus meizon* is potentially widespread in Borneo; however, the specimens or records available to me, of which I can confidently identify, indicate a predominantly northern Borneo distribution (Fig. 9) extending from northern West Kalimantan to northeastern Sabah with outlying occurrence in southern South Kalimantan.

**NATURAL HISTORY**.— In the Mt. Kinabalu area (Malkmus et al. 2002), this Sticky Frog occurs on the floor of primary dipterocarp forest between 500 to 800 m. Breeding males commonly vocalized from body pits beneath leaf litter or at edge of shallow, ephemeral, forest pools. Eggs are deposited in clusters and develop quickly with metamorphosis in about 16 days. Diet is principally ants although other small invertebrates are eaten.

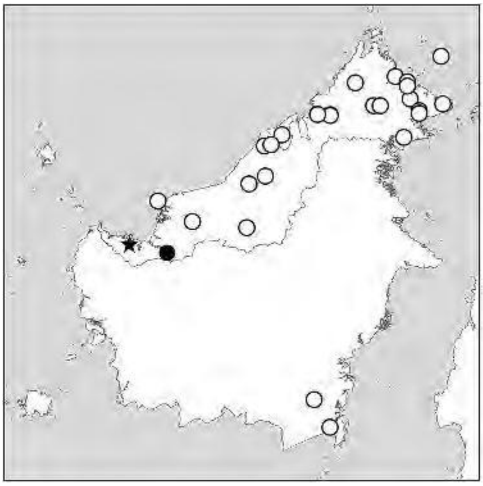

FIGURE 9. Distribution of *Kalophrynus meizon* (Borneo). Solid circle denote specimens examined in this study; open circles are literature records and museum records of specimens not examined.

Earlier, Inger (1966) observed that individuals occurred on the forest floor of primary forest and mainly beneath leaves. He also confirms small pools in logs and road ruts as breeding sites. Between 1984 and 2005, Inger (field data – *in litt*., August 2013) observed more than 125 *K. meizon* at 11 field sites (340–700 m asl) in Sabah and Sarawak. The following is my summary of his data sheets. The majority (>75 %) of the frogs were found on midstream bars or tree snags in intermittent streams in primary forest. During morning searching, he and his team found ~30 % of the total frogs observed and all but few were beneath dry to moist leaf litter or other forest litter; at night, the frogs were exposed and most were sitting on the surface of the leaf litter. A few (4; ~3 % of total observations) were sitting on vegetation hanging over the stream bed, one individual at 8 m, the others at ~2 m.

**COMMENTS**.— Inger (1966: table 6) gave a smaller adult size for both the female (35 mm) and male (37 mm) *K. pleurostigma* from northern Borneo. It is unclear how he sexed his specimens (I suspect externally through darkened throats in male and egg-swollen abdomens in females). Although his maturity identifications are likely correct, I have retained the minimum adult size as determined by my examination of the gonads for the specimens available to me for this account, but use his broader range of sizes in Table 3.

### ***Kalophrynus menglienicus*** **Yang and Su, 1980** **Menglien Dwarf Sticky Frog**

*Kalophrynus menglienicus* Yang and Su, 1980, *Zoological Research, Kunming* 1:257 [type locality: "Menglien, Yunnan, altitude 1040 m", China.]

**TYPE MATERIAL.**— HOLOTYPE: Kunming Institute of Zoology 75I377. PARATYPES: KIZ, 32 males without number. All by original designation.

**DEFINITION.**— Small, no adult females, adult males 19.7– 23.4 mm SVL ($n = 16$); head long 31–33 % HeadL/SVL; head width subequal length NA % HeadW/SVL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 14 % EyeD/SVL; tympanum visible and subequal to eye 14 % Tymp/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 133–134 % HndlL/SVL, 44–45 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 44–46 % HndfL/SVL.

Vomerine teeth absence; palatal fold morphology diagrammatically illustrated; tongue moderately large, oblong and rounded posteriorly.

Fingers not webbed; lengths 3>4>2>1; tips rounded and not dilated; subarticular tubercles apparently present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes not webbed, lengths 4>3≈5>2>1, first toe nub-like; tips rounded, not dilated; subarticular tubercles presence, number and shapes not reported; inner and outer metatarsal tubercles not reported.

Coloration not described. A color illustration is presented in Fei's (1999:305) field guide to Chinese amphibians.

**ETYMOLOGY.**— This frog takes its specific name from its origin at Menglien.

**DISTRIBUTION.**— Known only from the vicinity of its type locality.

**NATURAL HISTORY.**— Not reported; however, I note that it is a high elevation frog.

**COMMENTS.**— Preceding information extracted from Yang and Su (1980). Mensural data from their table; however, owing to the column headings in Chinese, I may have misinterpreted the data.

### ***Kalophrynus minusculus*** **Iskandar, 1998** **Dwarf Sticky Frog**

*Kalophrynus minusculus* Iskandar, 1998, *The Amphibians of Java and Bali* p.53 [type locality: "Cigeunteur, Ujung Kulon, West Java", Indonesia].

**TYPE MATERIAL.**— HOLOTYPE: Museum Zoologicum Bogoriense 367. PARATYPES: MZB 265–66, 375–76, MZB 2339, MZB 2924, and possibly ten other specimens not designated by museum number. All specimens by original designation.

**DEFINITION.**— Small, adult females to 35 mm SVL ($n = 1$), adult males to 25 mm SVL ($n = 10$); head modest length NA % HeadL/SVL; head wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye NA % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL; limb measurements not reported.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue morphology not reported.

Hand and foot morphology not reported.

In life, dorsum brownish black with darker bands and stripes.

**ETYMOLOGY.**— The specific epithet *minusculus* refers to small size of adults relative to the larger *K. interlineatus-pleurostigma* frogs.

**DISTRIBUTION**.— This species appears to be fairly common on Peucang Island and on the mainland of Ujung Kulon National Park, Java. It is also reported to occur in southern Sumatra (Lampung Province).

**NATURAL HISTORY**.— *Kalophrynus miniscuslus* occurs only in forest at low altitudes in West Java. Females bear 30 to 50 eggs which hatch into nonfeeding tadpoles.

**COMMENTS**.— Preceding information extracted from Iskander (1998).

### *Kalophrynus nubicola* Dring, 1983 Blue-spotted Sticky Frog

*Kalophrynus nubicola* Dring, 1983, *Amphibia-Reptilia* 4:103 [type locality: "camp four 1800 m, Gunung Mulu [National Park], Fourth Division, Sarawak", Malaysia, Borneo].

**TYPE MATERIAL**.— HOLOTYPE: British Museum of Natural History 1978.69. PARATYPES: BMNH 1978.66–68, 1978.1553–1558; Sarawak Museum not numbered/tagged. All by original designation.

**DEFINITION**.— Small, adult females 21.4–24.1 mm SVL ($n = 3$) adult male 19.3–20.1 mm SVL, sexually dimorphic in size but proportions do not differ; head modest length 30 % HeadL/SVL; head wider than long 37 % HeadW/SVL; snout moderately broad 9 % SnW/SVL; naris closer to snout than to eye 5 % NarEye/SVL; eye moderately large 12 % EyeD/SVL; tympanum indistinct and smaller than eye 40 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % NA % HndlL/SVL, 40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold not reported, postorbital fold short and crenulated, buccal fold bony with fleshy crenulated edge; tongue size and shape not reported.

Fingers with weak fleshy web extending along edge of fingers as ridge; lengths 3>2>1>4, fourth nub-like; tips rounded and slightly flatten; subarticular tubercles indistinct or absent; palmar tubercle indistinct or absent; no nuptial pad on hand. Toes about one-third webbed, lengths 4>3≈5>2>1; tips not reported; subarticular tubercles absent or single flesh pad covering length of toe; large oval inner metatarsal tubercle, outer absent.

In life, dorsum brown with faint dark mottling, yellow chevron edged with dark brown on snout in some individuals; no inguinal ocelli, occasionally with yellowish patches in groin; lores and temporal area not darker than dorsum; ventrally throat and chest orange with dark brown mottling, posteriorly belly and underside of thighs with light blue spots on brown background.

**ETYMOLOGY**.— The specific epithet derives from the Latin *nubicolus* for sky-dwelling and refers to its high elevation occurrence.

**DISTRIBUTION**.— This species occurs widely in upper slopes of Gunung Mulu, Sarawak.

**NATURAL HISTORY**.— *Kalophrynus nubicola* is a terrestrial frog of the high-elevation forest, oak-laurel or ericaceous. It appears to chorus only during the day.

**COMMENTS**.— Preceding information extracted from Dring (1983).

### *Kalophrynus orangensis* Dutta, Ahmed, and Das, 2000 Indian Striped Sticky Frog

Figure 6.

*Kalophrynus orangensis* Dutta, Ahmed, and Das, 2000, *Hamadryad* 25:68 [type locality: "Orang National Park (26°30′N; 92°15′E), Darrang District, Assam, north-eastern India"].

**TYPE MATERIAL**.— HOLOTYPE: Zoological Survey of India, Kolkata A9087. PARATYPES: ZSI A9088–91. All specimens by original designation.

**Definition**.— Medium-sized, adult females to 35–38 mm SVL (*n* = 3), adult males 36–38 mm SVL (*n* = 2); head modest length NA % HeadL/SVL; head wider than long 118–133 % HeadW/SVL; snout moderately broad ?38–43 % SnW/HeadL; naris closer to snout than to eye NA ?72–80 % NarEye/SnEye; eye moderate ?42–44 % EyeD/HeadL; tympanum visible and nearly as large as eye ?83–94 % Tymp/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL; limb measurements not reported. Question marks preceding data indicate uncertainty of original data.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers not webbed; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles round, one beneath fingers 1, 2 and 4, two beneath finger 3; fleshy palmar tubercle, size and shape not reported. Toes webbed at base, lengths 4>3>5>2>1; tips rounded, not dilated; large round subarticular tubercles, one of 1 and 2, two on 3 and 5, and 3 on 4; small, round inner and outer metatarsal tubercles.

In life, dorsum reddish brown to cream with dark brown reverse-Y shaped mark with base between eyes, bifurcating on nape and limbs extending diagonally to top of hindlimbs, distinct narrow white stripe from above eyes to shoulder and extending diagonally to mid inguina; black white-edged inguinal ocellus. Venter yellowish cream with black speckled throat and anterior chest.

**Etymology**.— The specific name derives from the type locality, Orang National Park.

**Distribution**.— (Fig. 6) Presently known from the type locality in Orang National Park (26°30′N, 92°15′E) in central Assam, India, and two other localities: West Bengal, India (Paul et al. 2007); Mymensignh, Bangladesh (Mahony and Ali Reza 2007). All three localities are within the lower middle portion of the Brahmaputra River drainage.

**Natural History**.— The individuals from the type series were found on the ground [litter] in grassland adjacent to dry deciduous forest [secondary] or among trees at forest edging on grassland. Breeding occurred in this area in June with females depositing eggs in small puddles; males called beneath vegetation overhanging these puddles. The West Bengal individual was found 60 cm high in a bush in a primary semi-evergreen forest. No habitat data are available for the Bangladesh specimen.

**Comments**.— Preceding information extracted from Dutta et al. (2000). Question marks in the Definition indicate my uncertainty on the accuracy of the proportions.

*K. orangensis* is recently described and is based on five adult specimens, three females and two males. Because the variation in head striping and outer metatarsal tubercle size, the two major diagnostic features identified by Dutta et al. (2000), were encompassed in a wider sample of Thai and Vietnamese *K. interlineatus*, Ohler and Grosjean (2005) proposed that Assam and Indochinese specimens were conspecific; they thus considered *K. orangensis* a junior synonym of *K. interlineatus*. Matsui and colleagues (2009, 2011, 2012) continued to recognize *K. orangensis* as a valid species. An additional difficulty in evaluating the status of this species is presumed errors in the measurements of the head of the type series (Dutta et al. 2000: table 1; see comments in *Morphometric* subsection of the above *Morphology and Variation* section). I have not examined any specimens of this population, and even though, this taxon is poorly characterized in its original description, I hesitate to consider it a synonym without a thorough comparison. Additionally, recent molecular analyses have demonstrated considerable genetic diversity in *Kalophrynus*, hence the geographic isolation of the Indian populations likely will be matched by their genetic uniqueness.

### ***Kalophrynus palmatissimus* Kiew, 1984 Web-footed Sticky Frog**

*Kalophrynus palmatissimus* Kiew, 1984b, *Malayan Nature Journal* 37:146 [type locality: "lowland dipterocarp forest at about 75 m a.s.l. at the Pasoh Forest Reserve in Negeri Sembilian", Malaysia (Malaya).

**Type material.**— Holotype: British Museum of Natural History 1982.1508. Paratypes: BMNH 1982.1509–1523, FMNH two unnumbered (now 216461–462), University of Malaysia one unnumbered. All by original designation.

**Definition.**— Medium-sized, adults 31.2– 38.3 mm SVL (*n* = 19, not sexed); head moderately large 29–34 % HeadL/SVL; head slightly broader than long 102–116 % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 36–48 % EyeD/HeadL; tympanum visible and smaller than eye 55–70 % Tymp/EyeD; moderate length forelimb 24–28 % Forarm/SVL and forearm shorter than crus length 56–66 % Forarm/CrusL; hindlimb moderate NA % HndlL/SVL, crus moderate length 41–46 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers without web; lengths 3>2>1=4; tips rounded and not dilated; subarticular tubercles prominent, number beneath each finger not reported; palmar tubercle not reported. Toes strongly although not fully webbed, web between toes 3 and four to tip of 3, toe lengths 4>3>5>2>1; tips rounded; subarticular tubercles prominent on digits 1, 2, 3, 4, none beneath 5; oval inner and small indistinct outer metatarsal tubercles.

In life, dorsum light brown to reddish brown with darker brown blotch extending from between eyes and extending posteriorly and breaking into patches on trunk; no inguinal ocelli; lores and temporal area to axilla dark brown, trunk side reddish brown; venter yellowish with two faint longitudinal dusky bars on throat and gray mottling on sides and posterior of abdomen.

**Etymology.**— The specific epithet *palmatissimus* refers to the strongly webbed hindfeet, the greatest amount of webbing seen in the genus *Kalophrynus*.

**Distribution.**— This species is a resident of southern Peninsular Malaysia and presently know from only three localities in the provinces of Selangor, Negri Sembilan, and Johor.

**Natural History.**— *Kalophrynus palmatissimus* is a terrestrial frog of lowland dipterocarp forests. Kiew (1984) provides details on breeding and tadpole development and morphology.

**Comments.**— Preceding information extracted from Kiew (1984), Chan et al. (2011), and Dehling (2011).

### ***Kalophrynus pleurostigma* Tschudi, 1838 Rufous-sided Sticky Frogs**

Figures 10, 11F.

*Kalophrynus pleurostigma* Tschudi, 1838, *Classification der Batrachier, . . . Abteilung der Reptilien*: 86 [type locality: "Sumatra", Indonesia]

**Type material.**— Neotype: United States National Museum 36645, an adult female from "Aru Bay, East Sumatra", collected by Dr. W.L. Abbott on 9 December 1905. This Indonesia, Sumatra locality was identified by Lyon (1908) as "about longitude 98°15′East, and latitude 4°10′N", which places it in present-day Sumatera Utar province, on the island Pulau Sembilan, NNW of Medan.

**Definition.—** Definition is based on two specimens, a 34.5 mm SVL adult female (neotype) and a 25.4 mm juvenile male; both collected prior to 1934 and both from northeastern Sumatera Utar. Moderate sized *Kalophrynus*, adults estimated 30–36 mm SVL, sexual dimorphism unknown. Additional information is available below in the description; data for the juvenile (MCZ

A22499) are in brackets when different from neotype. *K. pleurostigma* is the smallest member of the *interlineatus-pleurostigma* group and differs from other members by the morphology of its oral folds, proportionately longer hindlimbs yet proportionately smaller hindfeet, and coloration

**Description of neotype.—** Moderately robust-bodied female frog with well-developed, moderate-length fore- and hindlimbs; head ovate and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: SVL 34.5 [25.4]; HeadL 9.9 mm [8.1 mm]; HeadW 10.1 mm [7.9 mm]; SnEye 4.1 mm [3.2 mm]; NarEye 2.3 mm [2.0 mm]; EyeD 2.9 mm [2.6 mm]; Tymp 2.6 mm [2.3 mm]; ForarmL 8.9 mm, [7.1 mm]; HandL 8.5 mm [6.4 mm]; ThghL 14.7 mm [12.0 mm]; CrusL 12.7 mm [12.3 mm]; TarsL 8.3 mm [8.1 mm]; HndfL 13.2 mm [8.7]. Body proportions are (all values are percent): HeadL/SVL 29 [31]; HeadW/SVL 29 [30];HeadW/HeadL 102 [96]; SnEye/HeadL 41 [41]; NarEye/HeadL 23 [25];NarEye/SnEye 56 [63];NarEye/SnEye 56 [63]; EyeD/HeadL 29 [33]; Tymp/EyeD 90 [89]; Forarm/SVL 28 [28]; Forarm/CrusL 67 [58]; HndlL/SVL 152 [162]; CrusL/SVL 41 [48]; CrusL/ThghL 81 [103]; TarsL/ThghL 52 [68]; HndfL/SVL 34 [34]; HndfL/ThghL 66 [73].

No vomerine teeth present. Tongue obovate and about half free. Palatal fold morphology is similar for the two specimens. Vomerine folds are smooth, straight-edged flaps behind choanae, each extending from labial edge of mouth to near midline, separated by short gap from its opposite fold. Postorbital fold is single, medial smooth edged fold, closely followed by broad buccal fold; this latter fold is strongly serrate. Each serration has shape of tri-crowned tooth, but there is no evidence of dentine or enamel on these closely packed ‘denticles.’

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on digits; all digits bear subarticular tubercle on proximal phalanx, third finger also with subarticular tubercle on second phalanx; large, oblong to ovate, nearly medial outer palmar tubercle; digital formula 3>2≈1>4. On hindfoot, each toe has one or more subarticular tubercles, one each on first, second and fifth toes, on proximal phalanx of first two toes, on penultimate phalanx of fifth toe; two tubercles on third toe, three on fourth toe (first low and elongate). Inner and outer metatarsal tubercles are present; inner is largest, nearly circular to oval; outer small (neotype) to nearly absent (juvenile) and circular. Toes moderately webbed WebIII2 1.5 [2.5], WebIV1 1.0 [1.5]. Digit lengths for hand differ for neotype and MCZ juvenile, toe lengths same in both, formula 4>3>5>2>1.

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, light granular surface, thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; posteriorly glandular cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular folds; chest and abdominal skin glandular and pebble-like with scattered unpigmented ‘pebbles’ on chest.

Coloration in both is faded to near medium brown dorsum and tan venter. Juvenile (MCZ 22495) is nearly unicolor; dark inguinal spots persist with light encircling border; portions of narrow, light dorsolateral stripes remain, and face or loreal area appears nearly uniformly dark brown. Pattern is more evident in neotype (USNM 36645) although faded and does not match the longitudinal dorsal striping of other members of *interlineatus-pleurostigma* group, presumably owing to preservative induced fading. Dark centered inguinal ocelli and uniformly dark loreal area persist. Dorsally, head is unicolor; dorsally double vague hourglass-shape pattern extends from behind eyes to shoulder then repeated and more elongate from shoulders to mid-ilial area. Diagonal dorsolateral stripe and pattern on dorsal surface of hindlimbs are not evident. Venter is uniformly light grayish brown from tip of chin to end of body.

For color in life see Fig. 11F of an individual recently collected in western Sumatra; dorsum light brown to tannish yellow, faint nape hourglass-shaped blotch, distinct white “dorsolateral stripe from tip of snout to inguinal, tan to yellow side of face, lemon yellow side of trunk, and no dark bars on top of thighs.

**Etymology**.— Tschudi did not explain his choice of *pleurostigma*, although it likely refers to the inguinal or lateral (from Greek *pleura* for side, from *pleuron* for rib) spot (Greek *stigma*, for mark, brand or spot).

**Distribution**.— Presently known from northeastern coastal (Sumatera Utar) and west central (Jambi) Sumatra. I assume that the GenBank *K. pleurostigma* sample (MZB A.15298) from Lampung is the same taxon as the northern populations, thus giving this species a Sumatra-wide distribution.

**Natural History**.— Not reported.

**Comments**.— Specimens of *K. pleurostigma* are rare in collections. *K. pleurostigma* survives in Sumatra, although their abundance and actual distribution are unknown.

I tentatively identify the Javan populations as *K. pleurostigma* owing to their nearness to Sumatra, although I suspect that they represent a distinct species. The Javan occurrence relies on a single specimen from Nusa Kambangan Island (Iskandar 1998) and the report of it being a common species in Ujung Kulon National Park (Crampton 1990). Crampton (1990) further noted that it was an abundant frog in leaf litter near water throughout Ujung Kulon, Java; the individuals observed were SVL to 35 mm. Crampton may have mistaken *K. minusculus* for *K. pleurostigma* as both have adults in the same size range.

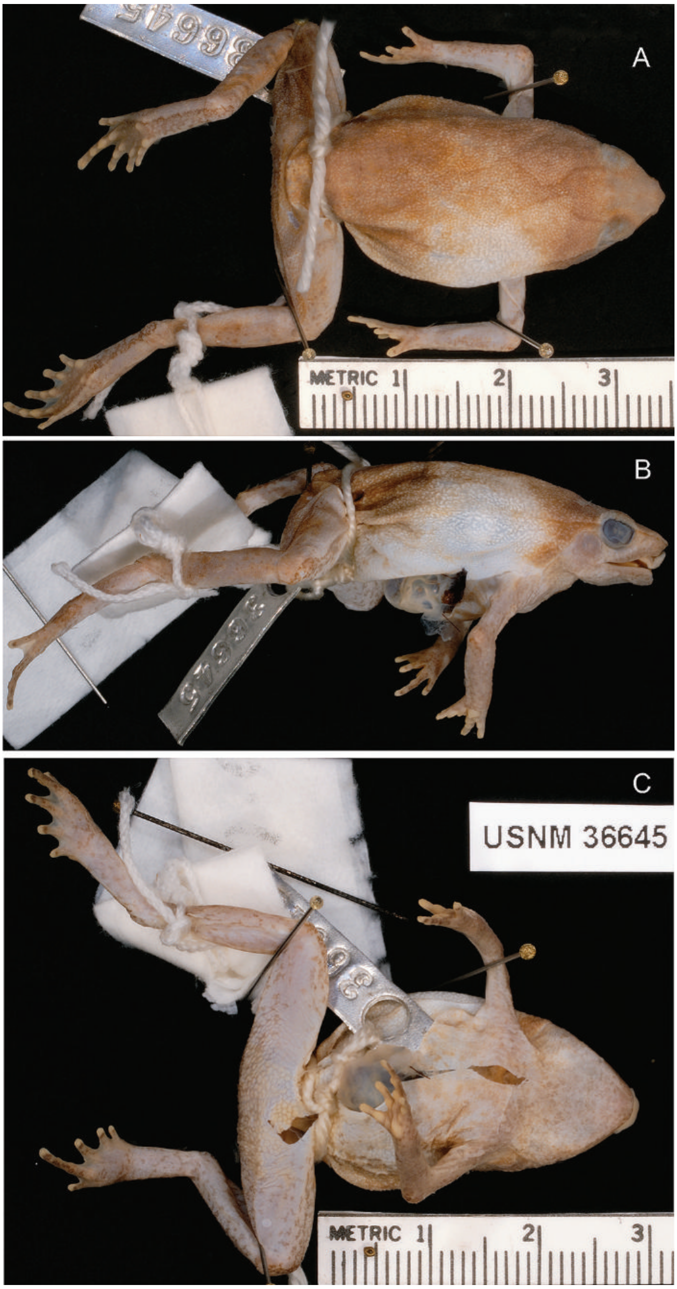

Figure 10. Images of neotype of *Kalophrynus pleurostigma* (USNM 36645, female, 34.5 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

### *Kalophrynus punctatus* Peters, 1871 Spotted Sticky Frog

*Calophrynus punctatus* Peters, 1871, *Monatsberichte der Königlichen Preussichen Akademie der Wissenschaften zu Berlin* 1871:579 [type locality: "Sarawak", East Malaysia (Borneo)].

**Type material.**— Holotype: Museo Civico di Storia Naturale di Genova 29130, according to *Annali del Museo Civico di Storia Naturale di Genova*, ser. 2, 3, 69:219.

**Definition.**— Small, adult males 22–27 mm SVL (*n* = 2); head modest length 26 % HeadL/SVL; head wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible but obscured by skin and smaller than eye 50 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 137 % HndlL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue shape and size not reported.

Fingers without web; lengths 3>2≈1>4; tips rounded and not dilated; subarticular tubercles prominent, number of tubercle on each finger not reported; fleshy palmar tubercle. No asperities on dorsum of fingers. Toes lightly webbed to below level of proximal subarticular tubercles of toe 4, lengths 4>3≈5>2>1; tips rounded, not dilated; subarticular tubercles prominent and four on 4, not reported for toes 1, 2, 3,5; rounded inner metatarsal tubercle and no outer one.

Dorsum reddish brown, back with or without small black spots; side of head, neck and trunk dark brown; venter pale yellowish white, chin and anterior throat with dark band, scattered black spots posteriorly.

**Distribution.**— Borneo (Kalimatan and Sarawak). See comment below.

**Natural History.**— Not reported.

**Comments.**— Preceding information extracted from Peters (1871) and predominantly from Inger (1966). Peters' description is brief and incomplete for diagnostic purposes. Inger's account is detailed and includes a second adult male that he discovered in the Rijksmuseum in Leiden. The latter specimen also had specific locality information, "Semedum," which the holotype did not.

In a 1894 report on a small herpetological collection from one of the Mentawei Islands. Boulenger identified a juvenile specimen (23 mm SVL) and declared that it closely matched Peters' description of *K. punctatus*. I believe this identification is erroneous and highly unlikely for a Borneo frog to occur in the distant Mentawei Islands.

### *Kalophrynus robinsoni* Smith, 1922 Pahang Mountain Sticky Frog

*Kalophrynus robinsoni* Smith, 1922, Journal of the Federated Malay States Museums 10:280 [type locality: "Wray's camp", Pahang, Malaysia].

**Type material.**— Holotype. BMNH 1923.5.14.29, according to R.F. Inger in Frost, 1985:383.

**Definition.**— Small, juveniles female 18 mm SVL, males 17–18 mm SVL (*n* = NA); head modest length NA % HeadL/SVL; head width , not reported NA % HeadW/HeadL; snout short and truncate NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye 66 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and NA % Forarm/CrusL; hindlimb moderate length NA % HndlL/SVL, NA % CrusL/SVL and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold V-shaped and broadly separated on the midline, condition of postorbital fold not reported, buccal fold strong and denticulate; tongue elliptical and entire.

Fingers presumably without basal web; lengths 3>2>1>4, first and second very short, fourth nub-like; presumably tips rounded and not dilated; subarticular tubercles low and indistinct; fleshy palmar tubercle; aspersities on fingers 1–3. Toes one-third webbed, lengths 4>3>5>2=1; tips bluntly pointed; subarticular tubercles low and indistinct; small oval inner and larger round outer metatarsal tubercles.

Dorsum light brown with elongated X-shaped mark, anterior arms extend to eyelids, posterior arms to groin; no inguinal ocelli; loris through side of trunk dark brown, no light dorsolateral stripe; venter yellowish with spots and speckles of brown.

**ETYMOLOGY**.— Malcolm Smith named the frog for Mr. Herbert Robinson, director of the Federated Malaya States Museum in appreciate for his opportunity to examine the herpetological collection made in association with a meteorological survey.

**DISTRIBUTION**.— Western Malaysia on side of Gunung Tahang.

**NATURAL HISTORY**.— Not reported.

**COMMENTS**.— Preceding information extracted from Smith (1922) and Dehling (2011). Smith consider the specimens to be juveniles; Dehling noted the presence of asperities on at least one of the males, thereby suggesting sexual maturity.

### *Kalophrynus sinensis* Peters, 1867 Philippine Sticky Frog

Figure 11E.

*Calophrynus pleurostigma* var. *Sinensis* Peters, 1867, *Monatsberichte der Königlichen Preussichen Akademie der Wissenschaften zu Berlin* 1867:33 [type locality: "Hongkong"; in errore; actually "Dapa, Siargao [Island]", 9°45′39.23″N, 126°03′26.27″E, Province Surigao del Norte, Philippines]. See Comment below.

*Calophrynus acutirostris* Boettger 1897, *Zoologischer Anzeiger* 20:165 [type locality: "Philippinen, entweder von Culion oder von Samar"].

*Kalophrynus stellatus* Stejneger, 1908, *Proceedings of the United States National Museum* 33:575 [type locality: "Basilan, Philippines Islands"].

**TYPE MATERIAL**.— HOLOTYPE: Museum für Naturkunde, Berlin 5696, see Comments on identity and assignment of holotype.

**DESCRIPTION AND INTRAPOPULATIONAL VARIATION.** The following characterization derives largely from my Bohol Island sample. Moderate-sized adults, sexually dimorphic with females averaging larger (42.4, 39.4–45.7 mm SVL) than males (37.9, 34.9–41.6 mm). These size differences are reflected in the other measurements: HeadL 12.0–14.1 mm ♀♀, 10.6–12.6 mm ♂♂; HeadW 13.0–14.0 mm ♀♀, 10.6–13.7 mm ♂♂; SnEye 4.8–5.6 mm ♀♀, 4.3–5.0 mm ♂♂; NarEye 2.7–3.6 mm ♀♀, 2.2–3.2 mm ♂♂; EyeD 3.9–4.8 mm ♀♀, 3.5–3.-4.5 mm ♂♂; Tymp 2.3–4.8 mm ♀♀, 2.7–3.9 mm ♂♂; ForarmL 10.2–13.0 mm ♀♀, 9.6–11.5 mm ♂♂; HandL 10.2–11.9 mm ♀♀, 8.8–10.9 mm ♂♂; ThghL 14.8–21.3 mm ♀♀, 15.1–19.9 mm ♂♂; CrusL 16.0–19.0 mm ♀♀, 14.9–17.8 mm ♂♂; TarsL 9.8–15.2 mm ♀♀, 9.3–11.4 mm ♂♂; HndfL 15.4–18.2 mm ♀♀, 13.2–18.6 mm ♂♂. Body proportions differences are not significantly different between adult females and males (all values are percent): HeadL/SVL 28–34 ♀♀, 29–32 ♂♂; HeadW/HeadL 98–120 ♀♀, 96–114 ♂♂; HeadW/SVL 31–35 ♀♀, 30–35 ♂♂; SnEye/HeadL 37–45 ♀♀, 37–44 ♂♂; NarEye/SnEye 52–69 ♀♀, 47–67 ♂♂; EyeD/HeadL 31–36 ♀♀, o-o ♂♂; Tymp/EyeD 55–104 ♀♀, 68–92 ♂♂; Forarm/SVL 24–30 ♀♀, 24–32 ♂♂; Forarm/CrusL 63–69 ♀♀, 55–77 ♂♂; HndlL/SVL 142–163 ♀♀, 150–170 ♂♂; CrusL/SVL38–44 ♀♀, 39–46 ♂♂; CrusL/ThghL 77–100 ♀♀, 88–111 ♂♂; TarsL/ThghL 52–73 ♀♀, 53–74 ♂♂; HndfL/SVL 36–43 ♀♀, 37–51 ♂♂; HndfL/ThghL 80–104 ♀♀, 79–123 ♂♂.

Dorsal skin forms thick, glandular cloak from behind eyes to vent; dorsolateral ridge on trunk variously defined from smooth transition to sides to distinct ridge or fold from shoulder to inguina. Dorsal surface lightly rugose to granular rugose, latter rugosity especially evident on posterior third of trunk; no spiny tubercles although lightly pigmented dome-like tubercles common on posterior third of trunk. Ventrally surface is lightly rugose from chin to chest, abdomen large pebbly rugose; some females with numerous unpigmented short tubercles on base of neck and chest.

Vomerine teeth absent. Tongue is moderate to large, usually oblong, and posterior half to two-thirds free. Palatal fold morphology appears relatively uniform although these data are not quantified. Pair of low vomerine folds nearly in contact on midline, free edge, smooth edged and lightly undulatory; postorbital folds short, low and continuous across midline, composed of four to eight irregular width lobes; buccal fold long, medium height, continuous with 14 to 18 abutting rectangular lobes.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercles are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, circular to elliptical, nearly medial outer palmar tubercle. Second and third fingers bear asperities on dorsal surface of distal end of the metacarpal and first phalanx. For the hindfoot, each toe has a basal subarticular tubercle although often poorly developed and low on fourth toe, low or absent on fifth toe; third and fifth toes with addition tubercle on free portion of digit, two tubercles on free portion of fourth toe. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer small to nearly absent and circular. Toes modestly webbed WebIII2 median 2.5 (1.0–3.0), WebIV1 2.0 (1.0–3.0). Digit lengths nearly constant for fore- and hindfeet; finger formula 3>2≈1>4; toe formula 4>3>5>2>1.

Color pattern variation statistics for entire sample of juvenile and adults are (median and range): HeadMid 0 0–1, HeadPsag 0 0–2, DorsNap 1 0–2, DorsPsag 1 0–2, IngSpt 2 0–2, HndlBr 1 0–2, DlatSt 1 0–2, Loreal 1 0–2, LatTrnk 1 0–2, Chin 1 0–2, Chest 0 0–1. In preservatives, *K. sinensis* varies from dorsally uniformly colored to well-marked pattern of longitudinal stripes. Some striped individuals have a middorsal stripe extending from snout to neck, there bifurcating; most lack middorsal snout stripe, instead have pair of medially converging diagonal stripes or reverse triangle mark on rear of head; on rear of neck stripe of triangle bifurcates as pair of narrow (usually), diverging trunk stripes; latter stripes rarely fragmented although of variable sharpness; parasagittal trunk stripes regularly present although faded; narrow, light-colored dorsolateral trunk stripe usually present, regularly faded, and narrowly edged below from eye to mid trunk by dark brown border; inguinal ocelli rarely absent, occasionally with smaller ocellus (unilateral) to rear of main ocellus. Thigh banding evident in majority of individuals. Venter in majority is light brown or tan, uniform from chin to thighs, except most individual show pair of broad, dark, longitudinal stripes on throat (usually faded, but visible).

**ETYMOLOGY.**— Although a Philippine species, the original (holotype) was thought to derive from China. Peters designated the species as Chinese, hence *sinensis* derives from the Latin *Sinae*, the Chinese, and used broadly in English as the prefix Sino- in the sense of Chinese or of/from China.

**DISTRIBUTION.**— *Kalophrynus sinensis* occurs in the southern islands of Samar, Leyte, Dinagat, Siargao, Bohol, Camiguin, Mindanao, and Basilan.

**NATURAL HISTORY.**— This species is a forest floor and dry stream bed denizen, hiding under the leaf and other litter during the day and foraging on the surface at night. It also breeds in small, shallow pools of water.

**COMMENTS.**— Bauer et al. (1996) identified a single specimen in the Berlin collection as the

FIGURE 11. Coloration of living representatives of *pleurostigma-interlineatus* group. (A) Dorsolateral view of a *K. anya* (USNM 520321) from the Chatthin Wildlife Sanctuary, Sagaing, Myanmar [photographer, C. Hansen]; (B) dorsolateral view of a *K. anya* (USNM 523966) from the Chatthin Wildlife Sanctuary, Sagaing, Myanmar [photographer, G.R. Zug]; (C) dorsolateral view of a *K. interlineatus* (CAS) from the Tanintharyi National Park, Tanintharyi, Myanmar [photographer, J.V. Vindum]; (D) dorsolateral view of a *K. meizon* (FMNH 242796) from Poring Station, Mt. Kinabulu Park, Ranua District, Sabah [photographer, R.F. Inger]; (E) dorsolateral view of a *K. sinensis* (UK 333148) from Agusan del Norte, Mindanao, Philippines [photographer, R.M. Brown]; (F) dorsolateral view of a *K. pleurostigma* (UK 333148) from Gunung Kunyit, Jambi, Sumatra [photographer, E.N. Smith].

syntype of *K. sinensis* and, based on W. Peters' handwritten note in the ZMB catalog identifying the specimen as the type and corrected the locality to "Dapa, Siargao". Ohler and Grosjean (2005) accepted the existence of two syntypes and identified the type locality as Mindanao, Philippines, based on a bottle label of a supposed syntype in the Vienna collection. I accept the interpretation of a single specimen, and it being the Berlin specimen. Either way, the correction of the syntypic locality makes *sinensis* the senior synonym for the Philippine populations. Inger (1954) noted that the type locality of *C. acutirostris* is most likely Samar.

This study does not examine the possibility of multiple species in the Philippine Islands. Inger (1954) noted differences in toe webbing of males in samples from Basilan and Mindanao; however, a statistical test did not reveal the differences to be significant. Taylor (1921) accepted the specific status of the Basilian species *stellatus* (using his Mindanao sample for his detailed description) and Boettger's description of the Samar species *acutirostris*. He noted: "It is not improbable that *Kalophrynus stellatus* and *K. acutirostris* are merely variations of the same species."

Stejneger (1908) reported that the buccal fold was strong denticulate in his description of *K. stellatus*. My examination of the Basilan specimens available to him showed the lobes to be mostly blunt rectangular, occasionally with an irregular free edge.

### ***Kalophrynus subterrestris* Inger, 1966 Labang Sticky Frog**

*Kalophrynus subterrestris* Inger, 1966, *Fieldiana, Zoology* 52:137 [type locality: "Sungei Seran, Labang, Bintulu District, Fourth Division, Sarawak", East Malaysia (Borneo)].

**Type material**.— Holotype: Field Museum of Natural History 150421. Paratypes: FMNH 140238, 154022–026, 157652–656. All by original designation.

**Definition**.— Small, adult females 25.8–27.0 mm SVL (*n* = 4), adult males 21.0– 23.4 mm SVL (*n* = 6); head moderately long NA % HeadL/SVL; head slightly wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA NA NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye 50–66 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, 40–45 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 85 % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology, vomerine fold not reported, postorbital fold angular and strongly notched, buccal fold crenulated; tongue size and shape not reported.

Fingers with slight basal web; lengths 3>2>1>4, fourth nub-like; tips rounded and not dilated; single subarticular tubercle between palmar tubercle and tip of finger 4, number of subarticular tubercles not reported for other fingers; fleshy palmar tubercle. Toes lightly webbed to center of distal subarticular tubercles of toe 3, lengths 4>3>5>2>1; tips rounded; conspicuous subarticular tubercles on first four toes, number not reported, none on toe 5; low inner and outer metatarsal tubercles.

In life, dorsum dark gray without darker or lighter markings; usually no light diagonal line of side or dorsolaterally on head; inguinal region with or without a dark spot, if present without light border; side of body orange in groin; venter dusky mottling anteriorly, white belly.

**Etymology**.— The name *subterrestris* was selected because two individuals were discovered in burrows.

**Distribution**.— This species occur broadly, if not commonly in northern Borneo (Sarawak and Sabah).

**Natural History**.— Most individuals of this species derived from the floor of primary rain forest in hillside situations, and most were found beneath the floor litter and two in long burrows.

**Comments**.— Preceding information extracted from Inger (1966).

### ***Kalophrynus tiomanensis*** **Chan, Grismer, and Grismer, 2011** **Tioman Sticky Frog**

*Kalophrynus tiomanensis* Chan, Grismer, and Grismer, 2011, *Zootaxa*, 3123:62 [type locality: "outside Gua Tengkuk Air (= Tengkuk Air Cave), Gunung Kajang, Tioman Island, Pahang at 810 m elevation (2°46′ 12.22″N 104°9′15.75″E)", Western Malaysia].

**Type material.**— Holotype: La Sierra University Herpetological Collection 5024. Paratypes: LSUHC 4682, 5154, 5558, 6147. All by original designation.

**Definition.**— Small, adult females 24.7–25.8 mm SVL (*n* = 2), adult males 25.8– 26.3 mm SVL (*n* = 2); head moderately long 31–33 % HeadL/SVL; head slightly wider than long 104–106 % HeadW/HeadL; naris closer to snout than to eye 59–72 % NarEye/SnEye; eye moderately large 36–37 % EyeD/HeadL; tympanum visible and smaller than eye 77–79 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndlL/SVL, 39–40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth absence; palatal fold morphology not reported; tongue size and shape not reported.

Fingers with slight basal web; lengths 3>2≈1>4; tips rounded and slightly dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3. Toes modestly webbed not extending to proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, slightly dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, three on 4, none on 5; oval inner and no outer metatarsal tubercles.

Dorsum yellowish brown with dark brown hour-glass mark from between eyes to suprascapular area and small dark brown irregularly shaped spots from mid-trunk rearward; body; large dark brown, white-edged inguinal ocelli; loris and temporal area to axilla dark brown, fading to tan ventrally; yellowish white oblique stripe from above eye to lower inguinal area; venter light brown, chest and belly with scattered white spots.

**Etymology.**— The specific epithet derives from this species type locality on Tioman Island.

**Distribution.**— *Kalophrynus tiomanensis* has been found only on Gunung Kajang, Tioman Island, West Malaysia.

**Natural History.**— Like most other species of *Kalophrynus*, *K. tiomanensis* is a terrestrial frog, living mostly beneath leaf litter and foraging on the latter's surface in hill dipterocarp forests.

**Comments.**— Preceding information extracted from Chan et al. (2011).

### ***Kalophrynus yongi*** **Matsui, 2009** **Cameroon Highland Sticky Frog**

*Kalophrynus yongi* Matsui, 2009, *Zoological Science* 26:580 [Type locality "near the top of Gunung Brinchang, 04°51′N, 101°38′E, 1954 m a.s.l., Cameron Highlands, Pahang, Peninsular Malaysia"].

**Type material.**— Holotype: Kyoto University Humanities and Environment 15531. Paratypes: KUHE 566, 52446. All by original designation.

**Definition.**— Small to medium-sized, adult males 28.8–31.0 mm SVL (*n* = 3); head moderate length 29 % HeadL/SVL; head wider than long 32–33 % HeadW/SVL; snout moderately broad 7–8 % SnW/SVL; naris closer to snout than to eye 4–5 % SnNar/SVL; eye moderately large 13–14 % EyeD/SVL; tympanum visible and smaller than eye 8–9 % Tymp/SVL; moderately long and stout forelimb 65–67 % Foreleg/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 135–148 % HndlL/SVL, 38–43 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 43–47 % HndfL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles large, round, and one on digits 1, 4, two on 2, and three on 3; fleshy outer palmar tubercle and no inner one; nuptial pad with conical tubercles present; weakly developed but externally protruding spine on proximal end of humerus. Toes with weak basal webbing, lengths 4>3≈5>2>1; tips rounded; subarticular tubercles large, round and one on digits 1, 2, two on 3, 5, and three on 4; prominent round inner and indistinct round outer metatarsal tubercles.

In life, dorsum changes from light orangish brown to dark brown; in lighter phase, ill-defined darker stripe from tip of snout to transverse interorbital bar, obscure shoulder chevrons and transverse bars on trunk; black spot in inguina without light border; laterally from loris to inguina darker than dorsum and demarcated from latter by a narrow darker dorsolateral stripe; dusky cream venter with darker throat and scattering of small spots on limbs.

**ETYMOLOGY**.— This species was named to honor Dr. Yong Hoi-Sen of the University of Malaya for his contributions to Malaysian zoology.

**DISTRIBUTION**.— Presently this species is known from only from the vicinity of the type locality on Gunung Brinchang, Cameron Highlands, Malaysia.

**NATURAL HISTORY**.— Eggs and larvae occurred on the internal walls of large pitcher plants. Males called from the inside of the pitchers as well. The pitcher plants and frogs live in the dense moss forests on the mountain side.

**COMMENTS**.— Preceding information extracted from Matsui (2009).

## Diagnostic traits for the identification of adults of *Kalophrynus*

1a. Adult SVL equal or greater than 32 mm . . . . . . . . . . 2

1b. Adult SVL equal or less than 32 mm . . . . . . . . . . 14

2a. Moderate to large spot of contrasting color in inguinal area . . . . . . . . . . 6

2b. No moderate to large spot in inguinal area . . . . . . . . . . 3

3a. No light-colored diagonal dorsolateral stripes on trunk; adult size 37–41 mm SVL; subarticular tubercles beneath fingers and fourth finger nub-like; hindfoot two-thirds webbed with small indistinct inner and outer metatarsal tubercles [Borneo, Sarawak] . . . . . . . . . . *K. intermedius*

3b. Light-colored diagonal dorsolateral stripes on trunk . . . . . . . . . . 4

4a. Hindfoot strongly webbed, web extending half to two-thirds length of fourth toe; adult size 31–38 mm SVL; fingers with distinct subarticular tubercles; indistinct, flatten oval inner metatarsal tubercle, small indistinct outer tubercle [Peninsular Malaysia] . . . . . . . . . . *K. palmatissimus*

4b. Hindfoot webbed basally or one-third or less . . . . . . . . . . 5

5a. Moderately broad, light-colored diagonal dorsolateral stripes on trunk; adult size 29–39 mm SVL; large subarticular tubercles on all fingers, two beneath third, one beneath other three fingers; large oval inner and small round outer metatarsal tubercle [Borneo, Sarawak] . . . . . . . . . . *K. calciphilus*

5b. Presumed narrow, light-colored diagonal dorsolateral stripes on trunk; adult size 20–35 mm SVL; morphology of hand and hindfoot not described [Java]. . . . . . . . . . *K. minusculus*

6a. Inguinal spot not dark brown or black, with or without a light border . . . . . . . . . . 7

6b. Inguinal spot dark, usually black, and light edged (ocellus) . . . . . . . . . . 8

7a. Inguinal spot bluish white and neither light or dark edged; adult size 24–33 mm SVL; distinct subarticular tubercles on all fingers, fourth finger nub-like; hindfeet about one-third webbed; inner and outer metatarsal tubercles weakly developed [Borneo, Kalimantan & Sarawak] . . . . . . . . . . *K. heterochirus*

7b. Inguinal spot yellow; adult size 36–47 mm SVL; finger morphology not reported; hindfeet webbed at base; inner and outer metatarsal tubercles poorly developed [Borneo, Sabah] . . . . . . . . . . *K. baluensis*

8a. Hindlimbs short, 110–125 % HndlL/SVL; adult size 34–47 mm SVL; distinct subarticular tubercles on all finger, two beneath third, one beneath other three fingers; hindfeet less than one-third webbed; moderate sized, round inner and outer metatarsal tubercles, outer often smaller; dorsal coloration variable, usually a dark nape stripe [northern Myanmar]. . . . . . . . . . *K. anya*

8b. Hindlimbs moderate length, 130–160 % HndlL/SVL; distinct subarticular tubercles on all finger, two beneath third, one beneath other three fingers . . . . . . . . . . 9

9a. Outer palmar tubercle small and oval; adult size 27–37 mm SVL; hindfeet modestly webbed, about one-third; medium-sized, oval inner metatarsal tubercle, outer small and round; dorsum immaculate except for inguinal ocelli [Vietnam] . . . . . . . . . . *K. honbaensis*

9b. Outer palmar tubercle moderate to large and round. . . . . . . . . . 10

10a. Toes with only basal webbing; small round metatarsal tubercles; adult size 35–38 mm SVL; middorsal or parasagittal stripes always present on head [Bangladesh, NE India] . . . . . . . . . . *K. orangensis*

10b. Toes modestly webbed; moderate to large, oval or round outer metatarsal tubercle. . . . . . . . . . 11

11a. Toes modestly webbed, one-third to one half between third and fourth toe; adult size 44–60 mm SVL; distinct subarticular tubercles on most toes, one beneath first and second fingers, two on third, three on fourth, one or two indistinct tubercles on fifth; never a middorsal head stripe, dorsum of trunk commonly unicolor [Borneo] . . . . . . . . . . *K. meizon*

11b. Toes modestly webbed, one-third or less between third and fourth toe; distinct subarticular tubercles beneath all toes . . . . . . . . . . 12

12a. Faint hour-glass mark on dorsum of nape and trunk; buccal fold continuous series of abutting denticulate-like lobes; adult size 34–35 mm SVL [Sumatra]. . . . . . . . . . *K. pleurostigma*

12b. Dorsum from nape to at least midtrunk usually with whole or broken reverse Y-shaped mark, occasionally dorsum near immaculate; buccal fold continuous series of abutting abutting rectangular lobes . . 13

13a. Middorsal or parasagittal stripes on head of many individual; adult size 35–46 mm SVL [southern Myanmar, SE Asia] . . . . . . . . . . *K. interlineatus*

13b. No middorsal or parasagittal stripes on head; adult size 37–46 mm SVL [Philippines] . . . . . *K. sinensis*

14a. Moderate to large spot of contrasting color in inguinal area . . . . . 15

14b. No moderate to large spot of contrasting color in inguinal area; no spots or scattered small spots . . . 23

15a. Inguinal spot light colored and not contrastingly edged . . . . . 16

15b. Inguinal spot dark, usually black, with or without a light border . . . . . 17

16a. Inguinal spot yellow; adult size 24–26 mm SVL; finger morphology not reported; hindfeet moderately webbed, about one third; oval inner and round outer metatarsal tubercles poorly developed [Borneo, Sabah] . . . . . *K. baluensis*

16b. Inguinal spot bluish-white without dark or lighter edge: adult size 24–33 mm SVL; distinct subarticular on all fingers, fourth finger nub-like; hindfeet about one-third webbed; inner and outer metatarsal tubercles weakly developed [Borneo, Kalimantan & Sarawak] . . . . . *K. heterochirus*

17a. Black inguinal spot without light border (no ocellus) . . . . . 19

17b. Dark inguinal spot with light border (ocellus) . . . . . 18

18a. Outer palmar tubercle small and oval; adult size 27–37 mm SVL; hindfeet modestly webbed, about one-third; medium-sized, oval inner metatarsal tubercle, outer small and round; dorsum immaculate except for inguinal ocelli [Vietnam] . . . . . *K. honbaensis*

18b. Dark brown inguinal spot with light border; adult size 24–26 mm SVL; subarticular tubercles on hand distinct, one on fingers 1, 2, 4 and two on 3; large outer palmar tubercle; feet modestly web, less than one third; oval inner metatarsal tubercle, no outer one [Peninsular Malaysia] . . . . . *K. tiomanensis*

19a. Fourth finger very short and nub-like. . . . . . 20

19b. Fourth finger short but not nub-like . . . . . 22

20a. Toes modestly webbed, about one-third between third and fourth toes; adult size 21–27 mm SVL; toes with subarticular tubercles except fifth toe; inner and outer metatarsal tubercles present; diagonal, light dorsolateral stripe usually absent [Borneo, Sabah & Sarawak]. . . . . . *K. subterrestris*

20b. Toes weakly webbed at base; subarticular tubercle variably present, occasionally indistinct. . . . . . 21

21a. Tympanum size variable from smaller than eye to larger than eye 60–140 % Tymp/EyeD; faint hourglass mark on dorsum from eyes to suprascapular area; adult size 17–21 mm SVL; subarticular tubercle usually absent or indistinct on first and fifth toe [Borneo, Sarawak]. . . . . . *K. barioensis*

21b. Tympanum alwasys smaller than eye ~60 % Tymp/EyeD; dorsum usually immaculate; adult size 22–27 mm SVL [Great Natuna Isl.]. . . . . . *K. bunguranus*

22a. Large subarticular tubercles on hand, two on first, second and fourth fingers and three on third; adult size 26–29 mm SVL; distinct subarticular tubercles on first through fourth toe, none of fifth; diffuse hourglass-shaped mark on dorsum between eyes and suprascapular area [West Malaysia] . . . *K. limbooliati*

22b. Distinctiveness of subarticular tubercles on all fingers variable, round and elevated to flat or absent . . . . . . . 23

23a. Distinct subarticular tubercles on finger, one on first and fourth, two on second and three on third; adult size 28–31 mm SVL; hindfoot webbing slight, basally between all toes; modest round inner metatarsal tubercle, small round outer one; dorsally suprascapular area with dark chevron marks [West Malaysia] . . . . . *K. yongi*

23b. Indistinct or absent subarticular tubercles on fingers. . . . . . 24

24a. Distinct subarticular tubercles on fingers, one on first, second and fourth, two on third finger . . . . . . 30

24b. Subarticular tubercles on fingers indistinct or condition not reported. . . . . . 25

25a. Distinct to faded light diagonal dorsolateral stripe from behind head to inguina . . . . . 26

25b. No light dorsolateral stripe on head and trunk; adult size 17–18 mm SVL; hand with short first and second fingers, third longest, fourth nub-like; subarticular tubercles of hand and feet weak and indistinct; dorsum brown with dark X-shaped mark on back of head to pelvis [West Malaysia] . . . . . *K. robinsoni*

26a. Toes without webs; first toe very short, nub-like; adult size 19–23 mm SVL [China, Yunnan]. . . . . . . . . . . *K. mengliensis*

26b. Toes webbed, at least at base . . . . . 27

27a. Hindfoot strongly webbed, web extending half to two-thirds length of fourth toe; adult size 31–38 mm

SVL; fingers with distinct subarticular tubercles; indistinct, flatten oval inner metatarsal tubercle, small indistinct outer tubercle [Peninsular Malaysia] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. palmatissimus*

27b. Toes weakly to modestly webbed, one-third or less between third and fourth toe . . . . . . . . . . . . . . . . 28

28a. Hands web free; subarticular tubercles absent on all toes except fourth with one tubercle; adult size 22–27 mm SVL; round inner metatarsal tubercle, no outer one; reddish brown dorsum with or without scattered black spots [Borneo, Kalimantan & Sarawak] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. punctatus*

28b. Slight or shallow webbing between fingers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29

29a. Fourth finger of hand short, nub-like; adult size 19–24 mm SVL; subarticular tubercles on hand and palmar tubercle indistinct or absent; subarticular tubercles on toes indistinct or as single flattish pad extending length of toe [Borneo, Sarawak] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. nubicola*

29b. Fourth finger short, but not nub-like; adult size 26 mm SVL; distinct round subarticular tubercles, one on first, second and fourth, two on third finger; distinct subarticular tubercles on all fingers; round inner and outer metatarsal tubercles [Borneo, Sarawak] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. eok*

30a. Distinct subarticular tubercles on fingers, one on first, second and fourth, two on third; adult size 23–30 mm SVL; hindfoot webbing modest, less than quarter height between third and fourth toe; moderate-sized oval inner metatarsal tubercle, small round outer one; reverse Y-shaped pattern from back of head to midtrunk [Vietnam] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. cryptophonus*

30b. Subarticular tubercles present on all toes, faint to strong . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 31

31a. Diagonal, light dorsolateral stripe usually absent; toes modestly webbed, about one-third between third and fourth toes; adult size 21–27 mm SVL; toes with subarticular tubercles except fifth toe; inner and outer metatarsal tubercles present; [Borneo, Sabah & Sarawak] . . . . . . . . . . . . . . . . . . . *K. subterrestris*

31b. Light-colored diagonal dorsolateral stripes on trunk . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 32

32a. Presumed narrow, light-colored diagonal dorsolateral stripes on trunk; adult size 20–35 mm SVL; morphology of hand and hindfoot not described [Java]. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *K. minusculus*

32b. Moderately broad, light-colored diagonal dorsolateral stripes on trunk; adult size 29–39 mm SVL; large subarticular tubercles on all fingers, two beneath third, one beneath other three fingers; large oval inner and small round outer metatarsal tubercle [Borneo, Sarawak] . . . . . . . . . . . . . . . . . . . . . . *K. calciphilus*

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## LITERATURE CITED

BAUER, A. M., R. GÜNTHER, AND H. E. ROBECK. 1996. An annotated type catalogue of the hemisotid, microhylid, myobatrachid, pelobatid and pipoid frogs in the Zoological Museum, Berlin (Amphibia: Anura: Hemisotidae, Microhylidae, Myobatrachidae, Pelobatidae and Pipidae). *Mitteilungen aus dem Zoologischen Museum in Berlin* 72:259–275.

BERRY, P. Y. 1975. *The Amphibian Fauna of Peninsular Malaysia*. Tropical Press, Kuala Lumpur.

BLYTH, E. 1855. Various notabilia contained in the collections presented by Capt. Berdmore and Mr. Theobald. *Proceedings of the Asiatic Society of Bengal* 1855(7):713–723.

BOETTGER, O. 1897. Neue Reptilien und Batrachier von den Philippinen. *Zoologischer Anzeiger* 20:165

BOULENGER, G. A. 1894. A list of the reptiles and batrachians collected by Dr. E. Modigliani on Sereinu (Sipora), Mentawei Islands. *Annali del Museo Civico di Storia Naturale di Genova*, ser. 2, 14:613–618.

BOULENGER, G. A 1900. Description of new reptiles and batrachians from Borneo. *Proceedings of Zoological Society of London* 1900:182–187.

Bourret, R. 1942. Les Batraciens de l'Indochine. *Mémoires de l'Institut Océanographique de l'Indochine* 6:1–547.

Chan, K. O., L. L. Grismer, and J. Grismer. 2011. A new insular endemic frog of the genus *Kalophrynus* Tschudi, 1838 (Anura: Microhylidae) from Tioman Island, Pahang, Peninsular Malaysia. *Zootaxa* 3123:60–68.

Crampton, W. 1990. *The Oxford University Herpetological Expedition to West Java. Preliminary Report Bogor Sept 1990*. Unpublished report. 25 pp.

Das, I., and A. Hass. 2003. A new species of *Kalophrynus* (Anura: Microhylidae) from the highlands of north-central Borneo. *The Raffles Bulletin of Zoology* 51(1):109–113.

Dehling, J. M. 2011. A new karst-dwelling species of *Kalophrynus* (Anura: Microhylidae) from Gunung Mulu National Park, Borneo, Malaysia. *Zootaxa* 2737: 49–60.

Dring, J. 1983. Some new frogs from Sarawak. *Amphibia-Reptilia* 4:103–115.

de Sa, R., J. W. Streicher, R. Sebonyela, M. C. Forlani, S. P. Loader, E. Greenbaum, S. Richards, and C. F. B. Haddad. (2012). Molecular phylogeny of microhylid frogs (Anura: Microhylidae) with emphasis on relationships among New World genera. *BMC Evolutionary Biology* 12:1–17.

Dutta, S. K., Ahmed M. F., and I. Das 2000. *Kalophrynus* (Anura: Microhylidae), a new genus for India, with the description of a new species, *Kalophrynus orangensis*, from Assam State. *Hamadryad* 25(2):67–74.

Fei, L. 1999. *Zhongguo liang qi dong wu tu jian* [Atlas of Amphibians of China]. Zhengzhou Shi, Henan.

Fei, L., C. Ye, J. Jiang, and F. Xie. 2005. *Zhongguo liang qi dong wu . . . tu jian* [An Illustrated Atlas of Chinese Amphibians]. Sichuan Publishing Group, Chengdu.

Fei, L., C. Ye, and J. Jiang. 2010. *Zhongguo liang qi dong wu cai se tu jian* [Colored Atlas of Chinese Amphibians]. Sichuan Publishing Group, Chengdu.

Frost, D. R., ed. 1985. *Amphibian Species of the World: a Taxonomic and Geographical Reference*. Association of Systematics Collection, Lawrence, Kansas

Frost, D. R. 2014. *Amphibian Species of the World: an Online Reference. Version 6.0* (*September 30, 2014*). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Günther, A. 1895. The reptiles and batrachians of the Natuna Islands. *Novitates Zoologicae* 2(4):499–502.

Inger, R. F. 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana: Zoology* 33(4):389–424.

Inger, R. F. 1966. The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana: Zoology* 52:1–402.

Iskandar, D. J. 1998. *The Amphibians of Java and Bali*. Research and Development Centre for Biology – LIPI, Indonesia [no city given].

Karsen, S. J., M. W. Lau, and Bogadek. 1986. *Hong Kong Amphibians and Reptiles*. Urban Council, Hong Kong.

Kiew, B. H. 1984a. A new species of sticky frog (*Kalophrynus palmatissimus* n. sp.) from Peninsular Malaysia. *Malayan Nature Journal* 37:145–152.

Kiew, B. H. 1984b. A new species of frog (*Kalophrynus baluensis* n. sp.) from Mount Kinabalu, Sabah, Malaysia. *Malayan Nature Journal* 38:151–156.

Kurabayashi, A, M .Matsui, D. M. Belabut, H-S. Yong, N. Ahmad, A. Sudin, M. Kuramoto, A. Hamidy, and M. Sumida. 2011. From Antarctica or Asia? New colonization scenario for Australian-New Guinean narrow mouth toads suggested from the findings on a mysterious genus *Gastrophrynoides*. *BMC Evolutionary Biology* 11/175:1–12.

Lyon, M. W., Jr. (1908) Mammals collected in eastern Sumatra by Dr. W. L. Abbott during 1903, 1906, and 1907, with descriptions of new species and subspecies. *Proceedings of the United States National Museum* 34(1626):619–679.

Mahony, S., and A. H. M Ali Reza. 2007. *Kalophrynus interlineatus* (Striped Sticky Frog). *Herpetological Review* 38(3):348.

Malkmus, R, U. Manthey, G. Vogel, P. Hoffmann, and J. Kosuch. 2002. *Amphibians & Reptiles of Mount Kinabalu (North Borneo)* A.R.G. Gantner Verlag, Ruggell.

MANTHEY, U., AND W. GROSSMANN. 1997. *Amphibien & Reptilien Südostasiens*. Natur und Tier, Münster.

MATSUI, M. 2009. A new species of *Kalophrynus* with a unique male humeral spine from Peninsular Malaysia (Amphibia, Anura, Microhylidae). *Zoological Science* 26:579–585.

MATSUI, M., T. CHAN-ARD, AND J. NABHITABHATA. 1996. Distinct specific status of *Kalophrynus pleurostigma interlineatus* (Anura, Microhylidae). *Copeia* 1996(2):440–445.

MATSUI, M., A. HAMIDY, D. M. BELABUT, N. AHMAD, S. PANHA, A. SUDIN, W. KHONSUE, H-S. OH, J-P. JIANG, AND K. NISHIKAWA. 2011. Systematic relationships of Oriental tiny frogs of the family Microhylidae (Amphibia, Anura) as revealed by mtDNA genealogy. *Molecular Phylogenetics and Evolution* 61:167–176.

MATSUI, M., AND K. NISHIKAWA. 2011. A new tiny *Kalophrynus* (Amphibia, Anura, Microhylidae) from northern Sarawak, Malaysian Borneo. *Current Herpetology* 30(2):145–153.

MATSUI, M., K. NISHIKAWA, D. M. BELABUT, A. NORHAYATI, AND H-S.YONG. 2012. A new species of *Kalophrynus* (Amphibia, Anura, Microhylidae) from southern Peninsular Malaysia. *Zootaxa* 3155:38–46.

OHLER, A., AND S. GROSJEAN. 2005. Color pattern and call variation in *Kalophrynus* from south-east Asia. *Herpetofauna* 18 (3/4):99–106.

PARKER, H. W. 1934. *A Monograph of the Frogs of the Family Microhylidae*. The Trustees of the British Museum, London.

PAUL, S., M. C. BISWAS, AND K. DEUTI. 2007. *Kalophrynus orangensis* (Orang Sticky Frog). *Herpetological Review* 38(1):97–98.

PETERS, W. 1867. Herpetologische Notizen. *Monatsberichte der Königlichen Preussichen Akademie der Wissenschaften zu Berlin* 1867:13–37.

PETERS, W. 1871. Über neue Reptilien aus Ostafrica und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genoa. *Monatsberichte der Königlichen Preussichen Akademie der Wissenschaften zu Berlin* 1871:566–580.

SMITH, M. A. 1922. On a collection of reptiles and batrachians from the mountains of Pahang, Malaya Peninsula. *Journal of the Federated Malay States Museum* 10(4):263–282.

STEJNEGER, L. 1908. Two new species of toads from the Philippines. *Proceedings of the United States National Museum* 33(1578):573–576

TAYLOR, E. H. 1921. Philippine Amphibia. *Philippine Journal of Science* 16(3):213–359.

THEOBALD, W. 1882. *Burma, Its People and Productions; Notes on Fauna, Flora and Minerals of Tenasserim, Pegu and Burma by Rev. F. Mason, D.D., M.R.A.S. Vol. I. Geology, Mineralogy and Zoology*. Stephen Austin & Sons, Hertford.

THY, N., AND J. HOLDEN. 2008. *A Field Guide to the Amphibians of Cambodia*. Fauna & Flora International, Phnom Penh.

TSCHUDI, J. J. 1838. *Classification der Batrachier, mit Berücksichtigung der Fossilen Thiere dieser Abtheilung der Reptilien*. Buchdruckerei von Petitpierre, Neuchâtel, Switzerland.

VASSILIEVA, A. B., E. A. GALOYAN, S. S. GOGOLEVA, AND N. A. POYARKOV, JR. 2014. Two new species of *Kalophrynus* Tschudi, 1838 (Anura: Microhylidae) from the Annamite mountains in southern Vietnam. *Zootaxa* 3796(3):401–434.

YANG, D, AND C. SU. 1980. A new species of the family Microhylidae frog from Yunnan [in Chinese]. *Zoological Research* 1(3):257–260.

ZUG, G. R., AND H. KAISER. 2013. *Kalophrynus* Tschudi, 1838 (Amphibia Anura, Microhylidae): proposed conservation by designation of a neotype for its type species *Kalophrynus pleurostigma* Tschudi, 1838. *Bulletin of International Commission for Zoological Nomenclature* 70(2):86–88.

# Appendicies

## APPENDIX 1. Specimens examined

*Kalophrynus anya*: Myanmar, Kachin CAS 232488; Sagaing USNM 520321, 523964–966, 537419–422.

*Kalophrynus interlineatus*: Myanmar, Bago-Mon(“Pegu”) NHMUK/BMNH 1947.2.31.26–27; Mon CAS 240327–331; USNM 587070; Tanintharyi CAS 229825, 243687, 243749, 243927, 245699–5700, 255733, 245749, 245895, 245941, 246333–334, 246685, 247889, 247917, 247923, 247932, 247937, 247981, 247995, 249946. Cambodia FMNH 270637. China FMNH 176352. Laos FMNH 270357, NCSM 79833. Thailand FMNH 265845, 265847. NCSM 76409–410, 79833, USNM 103422, 103450. Vietnam CAS 115821, FMNH 261613, NCSM 80324–325.

*Kalophrynus meizon*: Borneo, Sarawak CAS-SU A23030, FMNH 267873, 267875–881, 269668–670, 269673, 269675, 273260–262, 273264, 273266, USNM 197671.

*Kalophrynus pleurostigma*: Indonesia, Sumatra, Sumatera Utara MCZ A22499, USNM 36645.

*Kalophrynus sinensis*: Philippines, Biliran USNM 318371; Bohol CAS 22063–078, 22080–083, 21967–969, 21972–973, 21980, 21982; Camiguin USNM 305724; Leyte USNM 160015–016.

Data for the maps derives from the preceding specimens. Additional distributional data were extracted from the electronic databases of CAS, FMNH, KU, MCZ, and MVZ. Literature records derive from Chan et al. (2011), Crampton (1990), Das and Hass (2003), Dutta et al. (2000), Fei (1999), Günther (1895), Iskandar (1998), Karsen et al. (1986), Mahony and Ali Reza (2007), Matsui et al. (2011), Ohler and Grosjean (2005), Parker (1934), Paul et al. 2007, and Vassilieva et al. (2014). Recent Sumatra voucher locality (Gunung Kunyit, Jambi Prov. @ 1242 m) is from A. Hamidy and E. N. Smith, University of Texas Arlington.

## APPENDIX 2. Character definitions

MEASUREMENTS. [mm; all bilateral measurements recorded from right side.]

**Crus length** (CrusL): Straight-line distance from knee to ankle.

**Eye diameter** (EyeD): Horizontal diameter of eye [exposed surface] from anterior to posterior.

**Hand length** (HandL): Distance from base of palm (proximal edge of medial outer palmar tubercle) to tip of third finger.

**Forearm length** (ForarmL): Straight-line distance from elbow to wrist.

**Head length** (HeadL): Straight-line, horizontal distance from tip of snout to posterior corner of jaw.

**Head width-posterior** (HeadW): Straight-line, transverse distance from left to right edges of rear corner of jaws.

**Hindfoot length** (HndfL): Straight-line distance from heel to tip of fourth toe.

**Hindlimb length** (HndlL): Sum of ThghL, CrusL, TarsL, and HndfL.

**Snout width or internarial distance** (SnW): Distance between left and right nares.

**Snout-eye distance** (SnEye): Distance between tip of snout and anterior corner of orbit.

**Snout-vent length** (SVL): Distance from tip of snout to vent. Measurement is taken with frog’s venter adpressed against a flat, firm surface.

**Naris-eye distance** (NarEye): Distance between naris and anterior corner of orbit.

**Tympanum diameter** (Tymp): Horizontal diameter of tympanum from outer edge of annulus.

**Thigh length** (ThghL): Straight-line distance from vent to knee.

**Tarsus or ankle length** (TarsL): Straight-line distance from crus-ankle joint to heel.

MERISTIC.

Hindfoot webbing

Webbing is recorded only in halves and whole numbers using the subarticular tubercles as integers, e.g., basal tubercle is 1. Toes are identified by Roman numerals, and inner (anterior) and outer (posterior) edges by integers; for example, the inside edge of third toes is **III1**, its outside edge **III2**.

**WebIII2**: location at which web joins outside edge of third toe.

**WebIV1**: location at which web joins inside edge of fourth toe.

Subarticular tubercles

**Fifth toe, number of** (Toe5Sub): number of subarticular tubercles on fifth digit of hindfoot.

COLOR PATTERN. These traits are coded arbitrarily in a numerical sequence. All observations on color pattern derive from preserved specimens.

Dorsal Patterns

**Head, middorsal stripe** (HeadMid) three states: absent [0]; faded and/or fragmented [1]; sharply defined, often from tip of snout [2].

**Head, parasagittal stripes** (HeadPsag) three states: absent [0]; faded [1]; sharply defined, usually extend from supraorbital area onto trunk [2].

**Dorsum, nape stripe** (DorsNap), three states: absent [0]; single, faded [1] or bold [2] middorsal stripe, bifurcating on shoulders.

**Dorsum, parasagittal stripes** (DorsPsag), three states: absent [0]; indistinct, possibly fragmented, lacks narrow white borders [1]; bold, dark stripes with narrow white borders [2].

**Inguinal spots** (IngSpt) three states: absent [0]; small to large, without light border [1]; ocellus, narrow light encircling border [2].

**Hindlimb barring** (HndlBr): three states: absent [0]; indistinct, without light edging [1]; bold on thigh and crus, usually light edged [2].

Lateral Pattern

**Dorsolateral stripe** (DlatSt) three states: absent [0]; indistinct, narrow, faded light stripe, at least from supraorbital to mid trunk [1]; bold, narrow light stripe from snout to inguinal [2].

**Loreal color** (Loreal) three states: lightly shaded with or without thin dark subcanthal stripe [0]; broad dark subcanthal stripe, lighter below canthus stripe to upper lip [1]; dark from canthus to mouth [2].

**Lateral trunk color** (LatTrnk) three states: lightly shaded from supratypmpanic fold to inguinal [0]; dark from fold to mid trunk, faded thereafter [1]; dark from fold to inguinal [2].

Ventral Pattern

**Chin & throat** (Chin) three states: dusky without distinct markings [0]; dusky with ill-defined blotches or vague pair of longitudinal stripes [1]; pair of bold, dark longitudinal stripes, usually narrowly edged in white [2].

**Chest** (Chest): three states: dusky without markings [0]; dusky with vague dark spots or blotches [1]; dusky with distinct dark spots and blotches [2].

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# Three New Species of Aglajid Cephalaspidean Mollusks from the Tropical Indo-Pacific of the Verde Island Passage

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**Three new species of aglajid opisthobranchs are described from the Verde Island Passage of the Philippines. *Philinopsis buntot* sp. nov. is found from two localities in Batangas, Luzon. It is immediately recognizable and distinct from all other aglajids by its medial projection that extends from the posterior end of the posterior shield. Its penis has a lobate prostate and a bilobed penial papilla with a basal collar. The collar and the lobes of the papilla bear small spines around their margins. *Philinopsis aliciae* sp. nov., known only a single specimen from the Philippines, is similar to *P. buntot,* but lacks the distinctive tail or any posterior medial appendage. It has a simple penis, which lacks any trace of penial spines. *Chelidonura alexisi* sp. nov. is characterized by its black body, often with minute opaque white spots. It has a simple penis with two cuticularized conical papillae, one situated near the middle and the other near the apex. This species is known from four specimens and a photo of a fifth specimen, also observed in the Philippines, on the southern side of the Verde Island Passage.**

KEYWORDS: Aglajidae, Indo-Pacific, new species, biodiversity

The Aglajidae is a diverse clade of Cephalaspidean heterobranch gastropods with more than 60 species (Camacho-García et al. 2014). The greatest diversity of species is found in the Indo-Pacific tropics with a concentration of species within the Coral Triangle, encompassing most of the Philippines, Indonesia and Papua New Guinea, where nearly half of the members of the family are found (Gosliner et al., 2008). Recently, six new species of aglajids were described (Gosliner 2011). The systematic relationships of the family have been reviewed by Rudman (1972a, 1972b, 1972c, 1974, 1978), Gosliner (1980), and Baba (1985) and the first molecular phylogeny of the group was published by Camacho-García et al. (2014). This preliminary phylogeny provides the systematic framework for a revision of the family, but no major realignment of taxonomic boundaries was proposed, pending the sampling of additional genes and taxa to produce a more robust phylogeny.

Since Gosliner's (2011) description of six new agalajids, several additional species have come to light, largely through the 2011 Hearst Philippine Biodiversity Expedition launched jointly by the California Academy of Sciences, the University of the Philippines, the National Museum of the Philippines and the Bureau of Fisheries and Aquatic Resources. Holotypes are deposited in the National Museum Philippines (PNM) and paratypes are deposited in the invertebrate zoology collections of the California Academy of Sciences (CASIZ).

## METHODS

Over the last few years, new specimens of aglajids were collected from Batangas Province, Luzon Island, Philippines. Specimens were preserved in either 10% formalin for proper preservation of anatomical structures, or preserved entirely in 95% ethanol for later molecular study. Prior to preservation of any specimen in formalin, a tissue sample was taken from the animal and preserved in 95% ethanol for later molecular study.

Upon return to the California Academy of Sciences, dissections were completed, and drawings of anatomical structures were accomplished using a Nikon SMZ-U binocular microscope with drawing tube. Specimens of copulatory organs were mounted on stubs and air-dried. Structures were then coated with gold/palladium using a Denton Desk II vacuum sputter coater. Scanning electron micrographs were produced by a LEO 1450 VP scanning electron microscope. Specimens and dissected structures were deposited at the Philippine National Museum (PNM) or the California Academy of Sciences in the Invertebrate Zoology Department collection (CASIZ).

The methodology for molecular study of two of these species was described in Camacho García et al. (2014). Phylogenetic analyses for these species are included in that paper.

## Species Descriptions

### Family Aglajidae Pilsbry, 1895

### Genus *Philinopsis* Pease, 1860

Type species: *Philinopsis speciosa* Pease, 1860, by monotypy

***Philinopsis buntot* Gosliner, sp. nov.**
Figures 1C–E, 2A, 3, 4.

**Material examined**.— Holotype: PNM 41060, 5 m depth, subsampled for molecular study, Anilao Harbor, Mabini, Batangas Province, Luzon, Philippines, 13.75994°S, 120.83036°E, 30 April 2011, E. Jessup. Paratype: CASIZ, 185780, one specimen, 5 m depth, Anilao Harbor, Mabini, Batangas Province, Luzon, Philippines, 13.75994°S, 120.83036°E, 24 May 2011, T. M. Gosliner. CASIZ 185942, one specimen, dissected, 7 m depth, Cemetery Beach, Tingloy, Batangas Province, Luzon, Philippines, 13.68433°S, 120.82993°E, 19 May 2011, T. M. Gosliner. CASIZ 185777, two specimens, 7 m depth, Cemetery Beach, Tingloy, Batangas Province, Luzon, Philippines, 13.68433°S, 120.82993°E, 19 May 2011, T. M. Gosliner.

**Geographical distribution**.— Thus far, known only from southern Luzon Island, Philippines.

**Etymology**.— The name "buntot" is the Tagalog word for tail, referring to the distinctive posterior appendage of this species.

**Natural history**.— This species is found crawling on clean sand where it is nocturnally active. It has not been observed diurnally and may remain buried in the sand during the day.

**Description**.— *External morphology*: The living animals are 7 to 12 mm in length and 3–6 mm wide. The general body color of the living animal (Figs. 1C–E) is translucent white with varying amounts of reticulated brown pigment on the dorsal surface. In specimens with sparse brown pigment patches of opaque white may also be present. The brown pigment frequently surrounds small yellow spots on the dorsal surface. Larger yellow spots are evident along the margins of the cephalic and posterior shields and on the margins of the parapodia.

Living animals are elongate, and relatively slender. The anterior end of the cephalic shield is blunt and quadrangular. The cephalic shield is roughly rectangular and terminates posteriorly with a rounded edge. No upturned papilla was observed on the end of the cephalic shield. The posterior shield is slightly rounded anteriorly and terminates in a medial elongate, digitiform posterior projection that is well-elevated from the base of the shield. This appendage is rounded at the apex

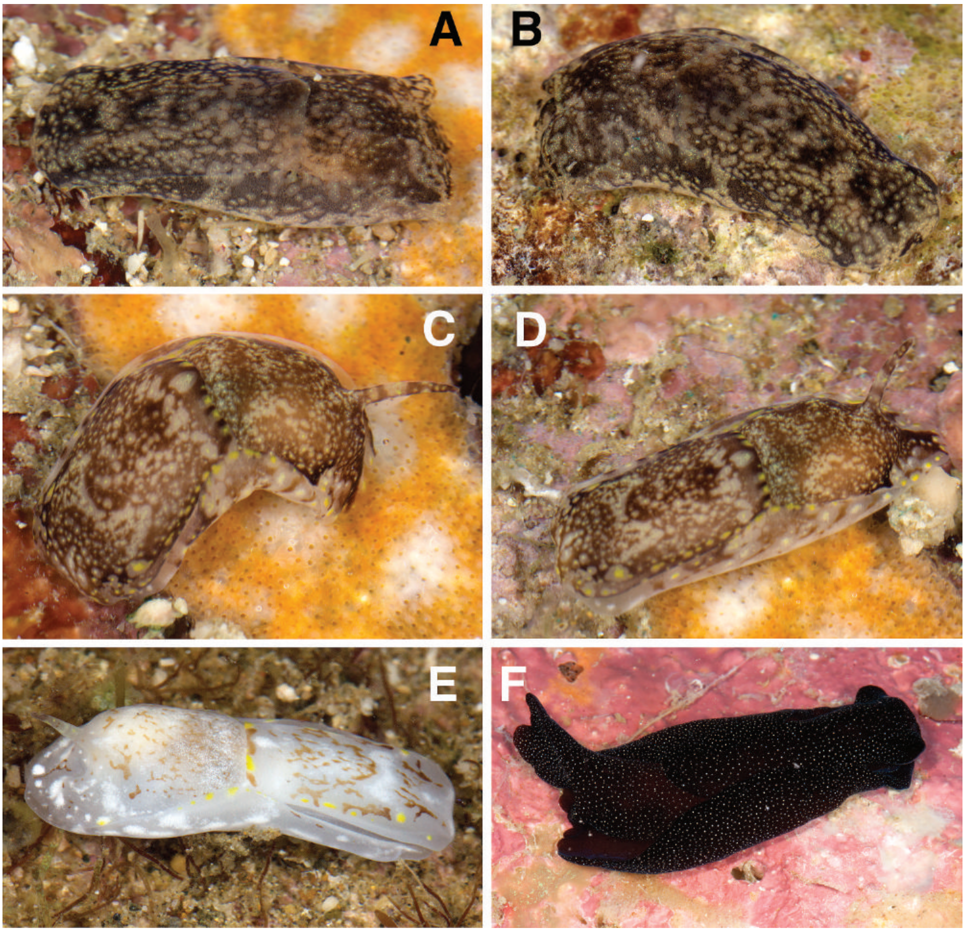

FIGURE 1. Living animals A–B. *Philinopsis aliciae* sp. nov., holotype, PNM 41061, Mabini, Philippines. C. *Philinopsis buntot* sp. nov., holotype, PNM 41060, Mabini, Philippines, ventral view showing markings on foot. D. *Philinopsis buntot*-paratype, CASIZ 185942, Tingloy, Philippines. E. *Chelidonura alexisi* sp. nov., holotype, PNM 41062, Mabini, Philippines.

and is often held upright in actively crawling individuals. The posterior end of the posterior shield is much lower that the area with the projection and two relatively flat lateral posterior lobes are short and simply rounded. The parapodia are relatively short, leaving most of the cephalic and posterior shields visible. The gill is simply plicate consisting of 12 primary folds and is situated ventrally on the right posterior end of the animal.

*Shell* (Fig. 2A): The shell is relatively thickly calcified and consists of a narrow band that occupies the posterior extreme of the animal. There is a membranous periostracum that is slightly more extensive anteriorly than the calcified portion. The area at the base of the shell near the protoconch is more thickly calcified that the rest of the shell.

*Digestive system*: The buccal mass is large, highly muscularized and slightly elongate posteriorly and occupies the body cavity for the entire length of the cephalic shield. The buccal bulb entirely lacks any vestige of a radula. There is a large ventral oral gland and a smaller dorsal oral gland. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, wider than the buccal bulb. The crop narrows pos-

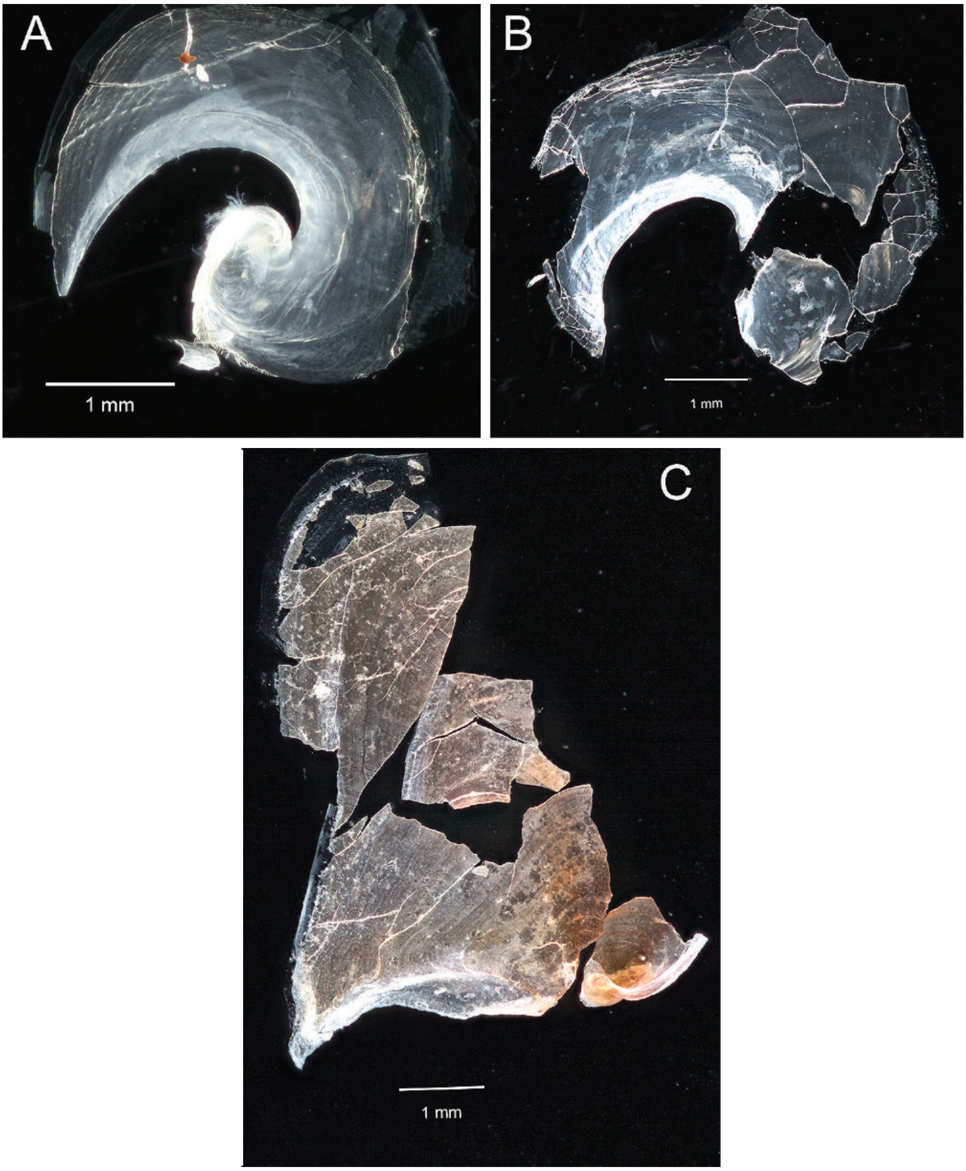

FIGURE 2. Shells. A. *Philinopsis buntot.* sp. nov., paratype, CASIZ 185942, Tingloy, Philippines. B. *Philinopsis aliciae* sp. nov., holotype, PNM 41061, Mabini, Philippines. C. *Chelidonura alexisi* sp. nov., holotype, PNM 41062, Mabini, Philippines.

teriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 3A): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, whereas the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which has a distinct genital ganglion. The buccal ganglia can be seen near the middle of the ventral surface of the buccal mas and are somewhat separated from each other.

*Reproductive System* (Figs. 3B–C, 4): The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands (Fig. 3C). From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the receptaculum seminis and enters the short, coiled albumen and membrane glands by means of a single duct. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The outer margins of both lobes bear a rounded margin with numerous tooth-shaped lobes. The hermaphroditic duct then joins the duct of the receptaculum seminis and continues to the genital atrium, where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens until its widest portion at the genital atrium. The genital atrium is large and muscular. The atrium also has a lobate vestibular gland situated on its ventral surface. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Figs. 3B, 4) consists of a penial sac and a thick, curved, irregularly-shaped prostate gland that is joined to the penial sac by a narrow duct. Within the penial sac is an elongate penial papilla (Figs. 3B, 4A). The papilla has a bilobed apex with an expanded outer collar. The collar (Figs. 4A–C) is ornamented with undivided and bifid penial spines as are the inner (Fig. 4D) and outer (Fig. 4E) lobes of the penial papilla.

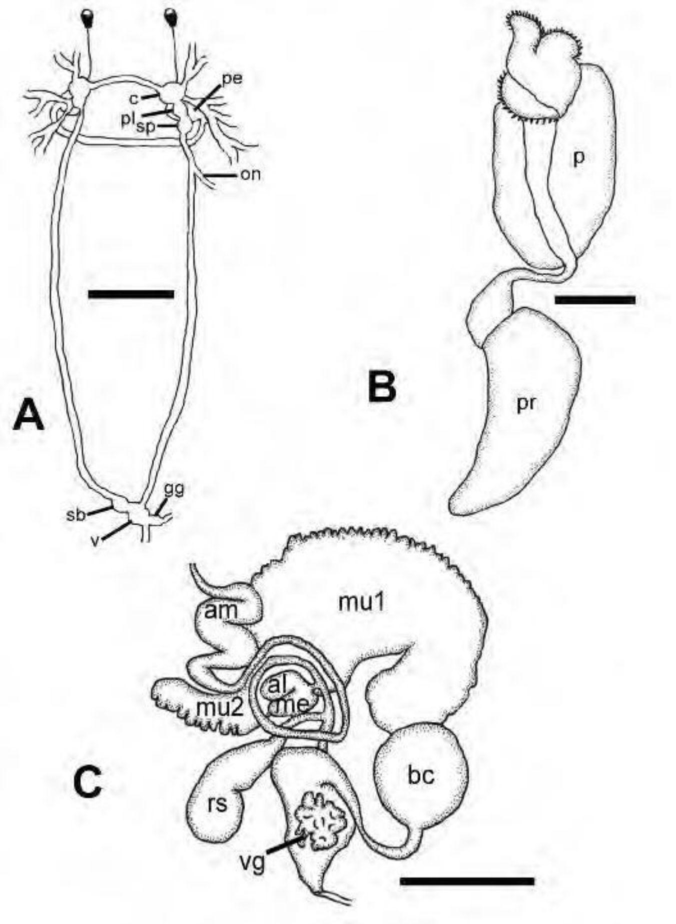

Figure 3. Internal anatomy, *Philinopsis buntot.* sp. nov., paratype, CASIZ 185942, Tingloy, Philippines. A. Central nervous system c-cerebral ganglion, gg–genital ganglion, on–osphradial nerve, pe–pedal ganglion, pl–pleural ganglion, sp–supraintestinal ganglion, su–subintestinal ganglion, v–visceral ganglion, scale = 1 mm. B. Penis, p–penial papilla, pr–prostate, scale = 0.75 mm. C. Posterior reproductive organs, al–albumen gland, am–ampulla, bc–bursa copulatrix, me–membrane gland, mu1–mucous gland large, mu2–mucous gland small, rs–receptaculum seminis,vg–vestibular gland, scale = 1 mm.

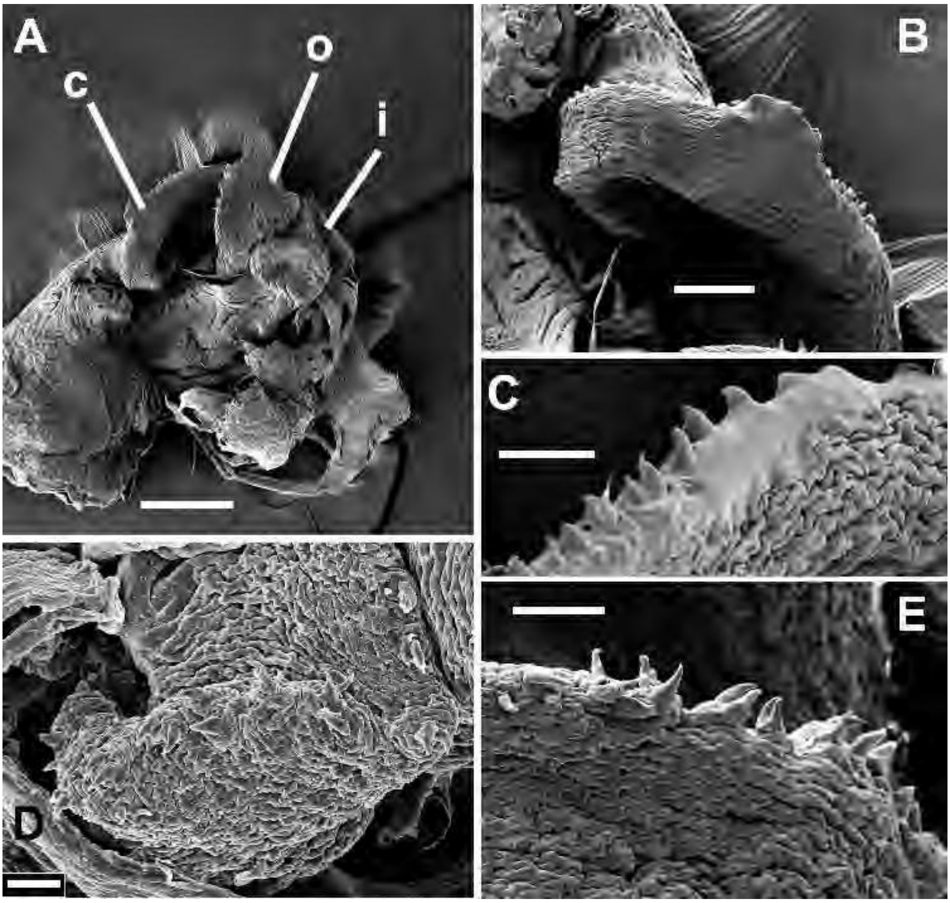

FIGURE 4. *Philinopsis buntot.* sp. nov., paratype, CASIZ 185942, Tingloy, Philippines, scanning electron micrographs of penis. A. Entire penial papilla, c-collar. i-inner lobe, o-outer lobe, scale = 150 µm. B. Collar, scale = 80 µm. C. Collar showing detail of spines, scale = 20 µm. D. Inner lobe, scale = 20 µm. E. Outer lobe, 20 µm.

**REMARKS**.— The presence of a quadrangular anterior end of the body, a posterior lobe of the cephalic shield, a large muscular bulb, the single branch of the hermaphroditic duct to the albumen and membrane glands, a bilobed mucous gland are all characteristics of species of *Philinopsis* (Rudman, 1972a). *Philinopsis buntot* lacks the elevated posterior extension of the cephalic shield but has all the other characteristics of *Philinopsis*. The anatomy of *P. buntot* differs significatntly from other described members of the genus. The most obvious morphological attribute that distinguishes *P. buntot* is the presence of the elongate posteromedial appendage on the posterior shield. The penis is also similar to that described for *P. falciphallus* Gosliner, 2011 and *P. coronata* Gosliner, 2011. These two species also have a oblong prostate that is connected to the penial sac by means of a thin duct. In all three species, the penial papilla is armed with spines, whereas no other species of *Philinopsis* are known to have an armed penis. In *P. falciphallus*, the base of the penis has a series of spines and a large chitinous sickle-shaped spine near the apex, whereas *P. coronata* has a ring of spines around the apex of the penial papilla and a ring of larger spines at the base of the penial papilla with a second ring of larger spines above the penial papilla. The arrangement of spines along the margins of the two penial papilla lobes and spines along a basal collar in *P. buntot* is unique to this species.

In his review of *Philinopsis*, Rudman (1972a) indicated there were two distinct groups of species. Members of the first group are characterized by having a large quadrangular head, a bulbous buccal mass and a specialized penis with a basal elongate penial papilla and a short prostate (Marcus and Marcus 1967: fig. 12) or a simple penis in *P. depicta* (Renier, 1807) (Gosliner 1980). Members of the second group of species have a rounded head with an elevated bulbous region (that resembles the front end of a Boeing 747) with prominent eyes visible at the base of the bulb, an elongate, tubular buccal bulb and a simple penis.

In the molecular study by Camacho-García et al. (2014) (Fig. 7), these two groups are largely upheld, but two additional groups of taxa being included in the same clade as the taxa with a tubular buccal bulb. *Philinopsis orientalis* (Baba, 1949) and *P. petra* (Marcus and Marcus, 1976) are sister to the clade of species with the tubular buccal mass. *Philinopsis coronata* Gosliner, 2011, together with *P. buntot* (as *P*. sp. CASIZ 185779), is sister to the remainder of the members of this clade. *Philinopsis falciphallus*, which has very similar morphology to *P. buntot* and *P. coronata*, surprisingly nests with *Aglaja regiscorona* Bertsch, 1972, and several species of *Chelidonura*. This relationship requires additional study as the COI mitochondrial gene was not able to be amplified for *P. falciphallus*. The morphological distinctions of *P. buntot*, *P. coronata* and *P. falciphallus* are discussed above, but the molecular data suggesting a sister species relationship between *P. buntot* and *P. coronata* is consistent with their morphological similarity.

### ***Philinopsis aliciae* Gosliner, sp. nov.**

Figures 1A–B, 2B, 5.

**Material examined.**— Holotype: PNM 41061, dissected, 5 m depth, subsampled for molecular study, Anilao Harbor, Mabini, Batangas Province, Luzon, Philippines, 13.75994°S, 120.83036°E, 30 April 2011, A. Hermosillo.

**Geographical distribution.**— Known only from the southern Luzon Island, Philippines (present study).

**Etymology.**— The name “aliciae” honors my good friend and colleague, Alicia Hermosillo, who collected this specimen. Ali’s keen eye and infectious enthusiasm brighten up any field trip and produce a wealth of remarkable new observations and species.

**Natural history.**— This species is found in the same habitat and at the same locality as the preceding species on a sandy bottom in 5 m depth. Little else is known about its biology.

**Description.**— *External morphology*: The living specimen was 11 mm in length and 4 mm wide. The general body color of the living animal (Figs. 1A–B) is mottled dark chocolate brown. Between the brown regions are clear areas of transparent white, which contain minute flecks of light green. The living animal is elongate and wide. The anterior end of the cephalic shield is uniformly round but blunt and quadrangular. The cephalic shield is roughly rectangular and terminates posteriorly with a medial, rounded knob. The posterior shield is slightly rounded anteriorly and terminates in a rounded lobe without any extension. The two lateral posterior lobes of the posterior shield are short and simply rounded. They are about equal in length. The parapodia are very short, leaving most of the cephalic and posterior shields visible. The gill is simply plicate consisting of 13 primary folds and is situated on the right posterior side of the animal.

*Shell* (Figs. 2B, 5A): The shell is relatively thickly calcified and consists of a thicker band that occupies the posterior extreme of the animal. There is a thin membranous periostracum that is slightly more extensive anteriorly than the calcified portion. The area at the base of the shell near the protoconch is more thickly calcified that the rest of the shell and a posterior lobe is present on the left side of the shell. The shell was fractured into several pieces prior to dissection.

*Digestive system*: The buccal mass is large, highly muscularized and slightly elongate posteriorly. It occupies the entire length of the cephalic shield. The buccal bulb lacks any vestige of a radula. There is a large ventral oral gland and the small dorsal oral glands were indistinct. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, as wide as the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

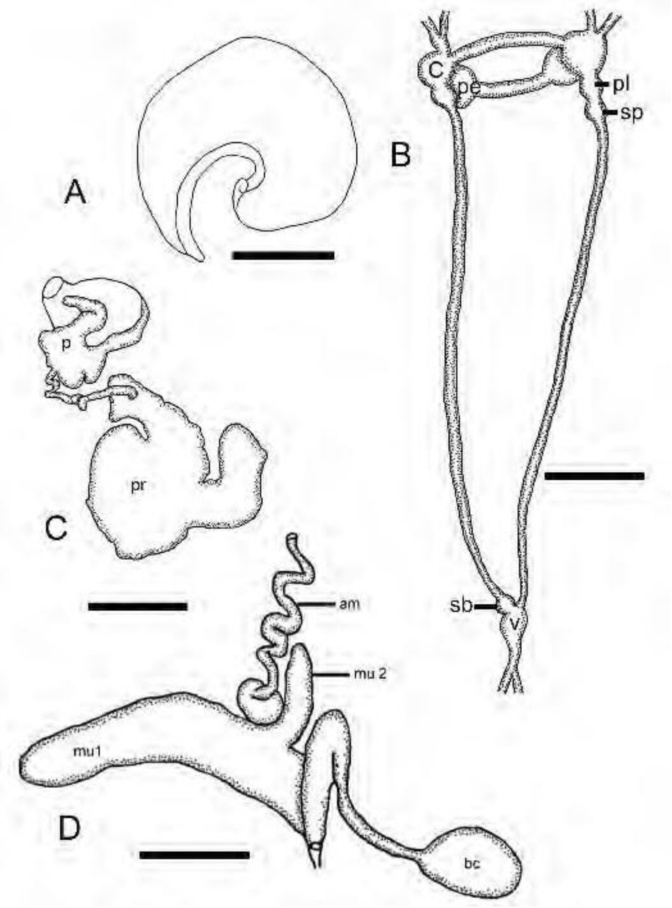

FIGURE 5. *Philinopsis aliciae* sp. nov., holotype, PNM 41061, Mabini, Philippines. A. Shell, scale = 1.5 mm. B. Central nervous system c–cerebral ganglion, pe–pedal ganglion, pl–pleural ganglion, sp–supraintestinal ganglion, su–subintestinal ganglion, v–visceral ganglion, scale = 1 mm. C. Penis, p–penial papilla, pr–prostate, scale = 0.75 mm. D. Posterior reproductive organs, am–ampulla, bc–bursa copulatrix, mu1–mucous gland large, mu2–mucous gland small, scale = 1 mm.

*Central Nervous System* (Fig. 5B): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, whereas the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which lacks a distinct genital ganglion. The buccal ganglia can be seen near the middle of the ventral surface of the buccal mas and are somewhat separated from each other.

*Reproductive System* (Figs. 5C–D): The posterior reproductive organs are not well preserved. The arrangement of reproductive organs is monaulic (Fig. 5D) with a single branch to the albumen and membrane glands. From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, curves around female glands and has a single branch to the short, coiled albumen and membrane glands. A distinct receptaculum seminis could not be distinguished. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The hermaphroditic duct continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens until its widest portion at the muscularized genital atrium. From the genital atrium, the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 5C) consists of a penial sac and a lobate prostate gland that is joined to the penial sac by a narrow duct. Within the penial sac is a large, curved penial papilla, which appears to be devoid of spines.

**Remarks**.— *Philinopsis aliciae* is very similar in its external coloration to some specimens of *P. buntot*, described above. Most significantly, it lacks the distinct "tail-like" posterior appendage of the posterior shield, which characterizes *P. buntot*. Internally, there are also significant differences, as well. The central nervous system of *P. buntot* contains a distinct genital ganglion (Fig. 3A) at the posterior end of the central nervous system, which is absent in *P. aliciae*. The general shape of the penis is similar in the two species, with a well-developed prostate separated form the penis by a thin duct. In *P. buntot*, the prostate is oblong in shape, whereas in *P. aliciae* it is more irregular in shape. The penis of *P. buntot* has a series of undivided and bifurcate spines on the the penial collar and two lobes of the penial papilla. In *P. aliciae*, the penis contains a single simple lobe, lacks a penial collar and lacks any armature on the penial papilla. Both *P. buntot* and *P. aliciae* are sympatric and were collected from the same dive site on the same dive. The two species avoided eachother when placed in the same container. When multiple specimens of *P. buntot* were observed together they aggregated and were observed mating with each other. Both species have marked genetic differences and *P. aliciae* does not cluster with other species of *Philinopsis* (unpublished data), likely owing to the lack of amplification of the 16S and H3 genes for this species. This species is tentatively described as a species of *Philinopsis*, based on anatomical characters, but verification of its systematic position must await additional molecular study.

## Genus *Chelidonura* A. Adams, 1850

Type species: *Bulla hirundinina* Quoy and Gaimard, 1832, by monotypy

### *Chelidonura alexisi* Gosliner, sp. nov.

Figures 1E, 2C, 6.

**Material examined**.— Holotype: PNM 41062, dissected, sub-sample removed for molecular study, 20 m depth, crawling on sandy slope, Mainit Bubbles, Mabini, Batangas, Philippines, 13.68651°S 120.89533°E, 18 May 2009, Alexis Principe. Paratypes: CASIZ 204580, 3 specimens, not dissected, 17 m depth, crawling on sandy slope, Shipyard, Puerto Galera Bay, Mindoro Oriental, Philippines, 13.516026°S 120.965622°E, 27 March 2015, T. Gosliner and Kelly Markello.

**Geographic range**.— Known only from southern Luzon Island, Philippines (present study) and Puerto Galera (northern Mindoro Island) (Carole Harris, pers. comm., unpublished data).

**Etymology**.— The name *alexisi* is named for dive guide and photographer Alexis Principe who found the only specimen of this species. Alexis has made many new discoveries and has a great passion for the unique biodiversity of the Philippines.

**Natural history**.— This species was found crawling on the surface of silty sand in the open in 20 m of water.

**Description**.— *External morphology*: The living animal is 30 mm in length. The general body color of the living animal (Fig. 1E) is uniformly black with numerous minute punctations of opaque white. This pigment pattern is found on the cephalic and posterior shields and parapodia,but opaque white spots are absent from the foot. One specimen observed in Puerto Galera (unpublished data) lacked opaque white spots. The living animals are elongate, and narrow. The anterior end of the cephalic shield is quadrilobate. Fine sensory appendages are evident along the anterior margin of the head and in the preserved specimen individual nerve cells appear to be found at the base of each bristle-like appendage. The cephalic shield is elongate making up almost two-thirds of the body length. It is triangular, broadest anteriorly and terminates posteriorly with a short rounded lobe. The posterior shield is well rounded anteriorly and terminates in a long bilobed appendage on the left side and a short, broad posterior lobe on the right The parapodia are relatively wide, largely covering most of the cephalic shield at its widest part. The gill is plicate with 8 primary folds.

*Shell* (Figs. 2C, 6A): The shell is relatively thinly calcified and has a shiny brownish tinge. It occupies most of the posterior shield. The shell is thin and brittle and fragmented into four pieces when it was removed from the holotype. There is a broad anteriorly-directed wing and an elongate extension that is deeply embedded in the posterior shield right to the end of the left posterior lobe. The protoconch is visible at the base of the shell.

*Digestive system*: The buccal mass is small, highly muscularized, occupying the anterior one-fourth of the cephalic shield. The buccal bulb entirely lacks any vestige of a radula. There is a small dorsal oral gland and a large ventral one. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is small and saccate, about the same width as the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 6B): The circumesophageal nerve ring consists of paired cerebral, pedal, pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both short with poorly separated ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, whereas the right lateral nerve enters the visceral ganglion posterior to its junction with the subintesinal ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which lacks a distinct genital ganglion.

*Reproductive System* (Figs. 6C–D): The arrangement of reproductive organs is a modified monaulic arrangement (Fig. 6C). From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves along the inner face of the receptaculum seminis and enters short, coiled albumen and membrane glands. It appears to have only a single entrance to these glands. The larger mucous gland is curved with a massive single lobe. The hermaphroditic duct then joins the duct of the long receptaculum seminis and continues to the genital atrium where it joins the thick, muscular genital atrium. The bursa copulatrix is large and spherical. Its duct is wide and short and widens slightly at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 6D) consists of a penial sac and an elongate, curved prostate gland that is joined to the penial sac by a short, narrow duct. Within the penial sac is a large penial papilla that is ribbed, lobed and blunt. At the base of the papilla are about 5–7 small glandular structures that have a small chitinous hook extending outward from the glandular base (Fig. 6D). The primary lobe of the penial papilla has a conical protuberance near the middle of its length. A second protuberance is found near the apex of the papilla.

**REMARKS.**— This species is similar in external color pattern to *Chelidonura inornata* Baba, 1955 and some color variants of *C. sandrana* Rudman, 1973 (Gosliner et al. 2008). In *C. inornata* the body is black with small opaque white spots, but white spots are absent from the cephalic shield and posterior shield whereas in *C. alexisi* the spots are present on the entire body except for the inside of the parapodia. Additionally, specimens of *C. inornata* have a broad anterior opaque white band with smaller orange lines or spots in front of the white band near the margins anterior end of the head shield. The posterior end of the cephalic shield usually has a thin opaque white margin. The head of *C. inornata* has three distinct lobes, whereas *C. alexisi* has four lobes. In both species, the left lobe of the posterior shield is longer than right one and in *C. inornata* they may be markedly unequal or subequal. The internal anatomy of *C. inornata* remains largely undescribed (Rudman 1970). Rudman illustrated the penis as having a short prostate with a simple penial papilla. A specimen of *C. inornata* examined here (CASIZ 179987), has a simple penis devoid of any cuticular hooks or conical warts. *Chelidonura inornata* is generally found on hard substrate often associated with living coral colonies, whereas *C. alexisi* inhabits sandy areas.

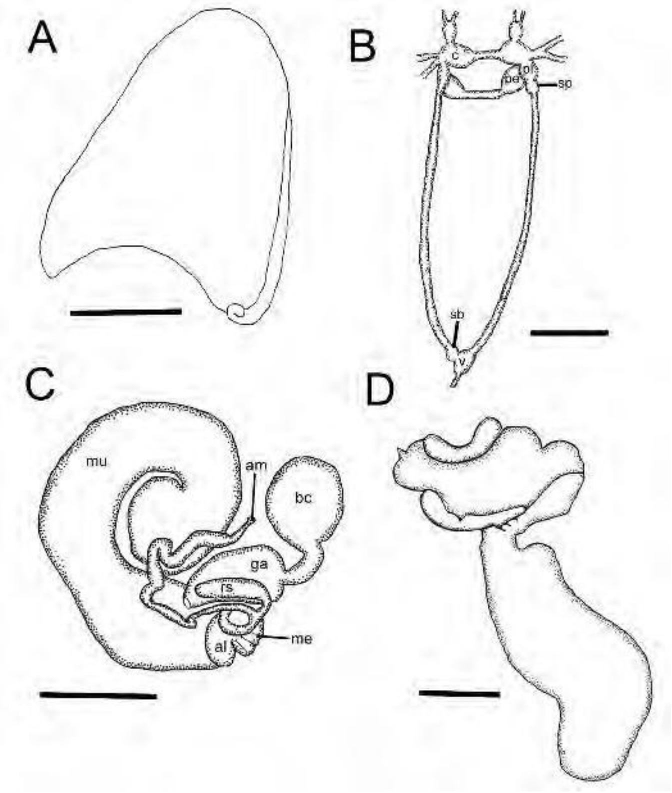

FIGURE 6. *Cheilidonura alexisi* sp. nov., holotype, PNM 41062, Mabini, Philippines. A. Shell, scale = 1 mm. B. Central nervous system c–cerebral ganglion, pe–pedal ganglion, pl–pleural ganglion, sp–supraintestinal ganglion, su–subintestinal ganglion, v–visceral ganglion, scale = 1 mm. C. Posterior reproductive organs, al–albumen gland, am–ampulla, bc–bursa copulatrix, genital atrium, me–membrane gland, mu–mucous gland large, rs–receptaculum seminis, scale = 0.75 mm. D. Penis, scale = 0.5 mm.

*Chelidonura sandrana* also has some similarities to *C. alexisi*. As mentioned above, some color variants have a black body with opaque white spots. In *C. sandrana*, the right lobe of the posterior shield is very truncated and simple rounded, whereas in *C. alexisi* it is longer and lobate or acutely pointed. The penis of *C. sandrana* has a simple short prostate and a conical penial papilla that lacks any armature or warty protrusions (Rudman, 1973). In *C. alexisi*, the penis has distinct chitinous hooks and two warty protrusions. *Chelidonura alexisi* is about twice the size of the largest speciemens of *C. sandrana*.

In the molecular phylogenetic analysis of the aglajids (Camacho-García et al. 2014), *C. alexisi* (as *C.* sp. CASIZ 181278) is sister to a clade composed of *C. mandroroa* and *C. inornata* (Fig. 7). Both *C. inornata* and *C. mandroroa* have a tribloate head whereas it is quadrilobate in *C. alexisi*. The penis of *C. mandroroa* has a single apical cuticular spine whereas *C. alexisi* has two cuticular warts and several basal chitinous spines and *C. inornata* has an entirely unarmed penis (Rudman 1970; present study). This clade of three species is sister to a clade containing the *C. sandrana* species complex and *C. pallida* Risbec, 1951.

*Chelidonura alexisi* can be clearly distinguished from all other alglajids by its quadrolobate anterior margin of the head and its unique color pattern of a black body with or without small opaque white spots. The shape of the anterior portion of the body is most similar to *C. inornata*,

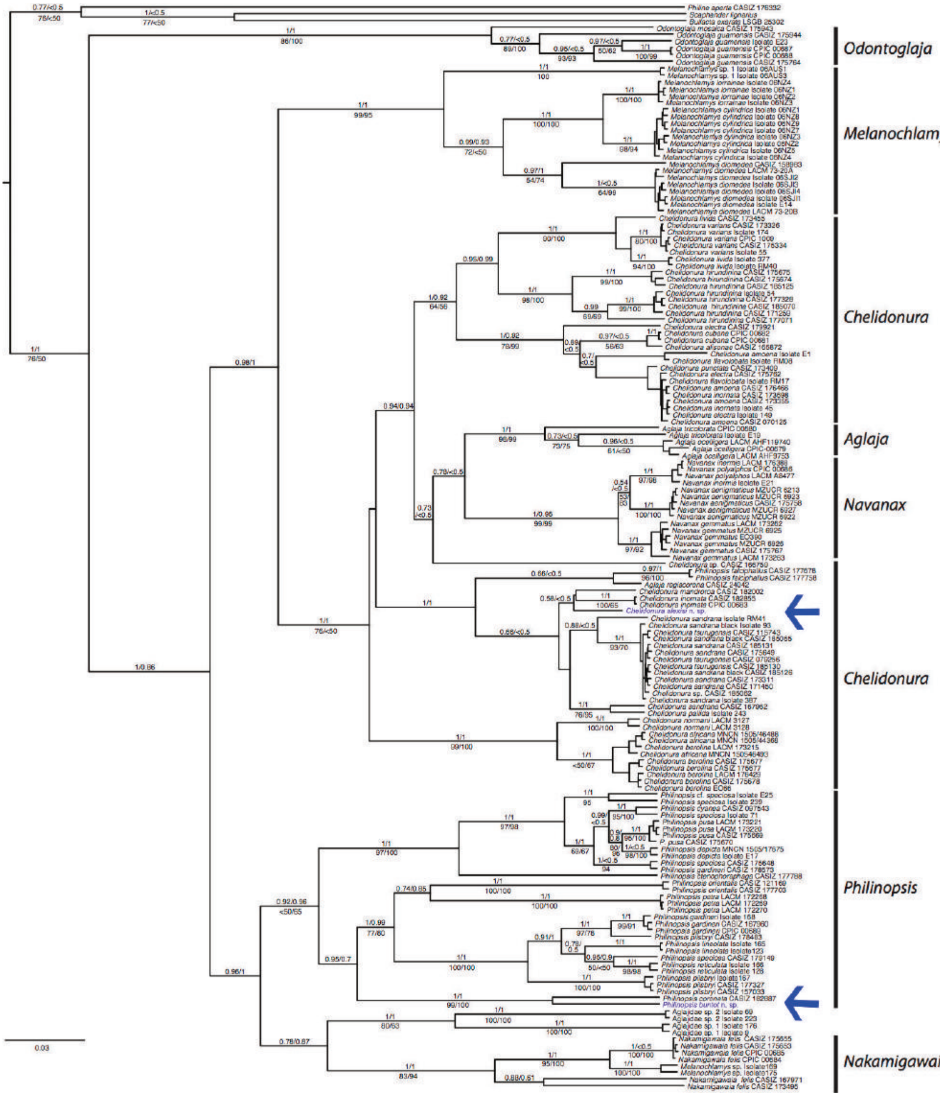

FIGURE 7. Bayesian maximum credibility tree showing all taxa included for the analysis of the combined H3, 16S, and COI sequence alignments (after Camacho et al. 2014). Posterior probabilities areindicated above each branch (for the analysis without COI third positions on the left, and for the analysis with COI third positions on the right) and bootstrap values areindicated below each branch. Branch lengths are also shown here indicating the proportion of substitutions. Species names are color-coded according to their range, blue forIndo-Pacific, red for Atlantic and green for Eastern Pacific. The phylogenetic positions of *Philinopsis buntot* sp. nov. and *Chelidonura alexisi* sp. nov. are indicated by arrows on the tree.

*C. mandroroa* and *C. sandrana,* but all of these species have differences in external and internal morphology, as well as genetic differences.

## DISCUSSION

The Verde Island Passage (VIP) separating southern Luzon Island from northern Mindoro Island in the northern Philippines, has been shown to represent the center of the center of marine biodiversity (Carpenter and Springer 2005; Gosliner et al. 2008) for both shore fishes and opisthobranchs. Gosliner (2011) described six new aglajid species, three of which were found in the VIP: *Philinopsis ctenophorophaga*, *P. falciphallus* and *P. coronata*. With the descriptions of three new species of agaljids in this paper: *P. buntot*, *P. aliciae* and *Chelidonura alexisi*, all recorded only from the VIP, this area has the richest known diversity for this family, with 25 species being found in these waters. Camacho-García et al. (2014) demonstrated that other cryptic species complexes of aglajids are found in the Indo-Pacific region and the total diversity of aglajids might be even greater.

Aglajid cephalaspideans are predators on a wide variety of other opisthobranchs, ctenophores, flatworms and annelid worms (Gosliner et al. 2008). Many of them appear to be highly specialized predators and this trophic diversification might have driven the diversification of aglajids in the Coral Triangle and in the VIP, more specifically. Little is known about the natural history and prey specificity of the species described in the present paper and far more detailed observations of the natural history of aglajids are required to better understand the causal factors that have contributed to their diversification in the VIP. The two closely related species, *C. alexisi* and *C. inornata* that are found sympatrically in the VIP are found in different habitats. *Chelidonura alexisi* is known only from sandy and silty habitats, whereas *C. inornata* is associated with living corals. *Philinopsis buntot* and *P. coronata* are sister species and there appears to be some habitat differences as to where they are found. *Philinopsis buntot*, inhabits clean shallow water sand flats whereas *P. coronata* is found on silty slopes in deeper water.

Ortea et al. (2014) described a new genus, *Migaya* Ortea, Caballer, Moro and Espinosa, 2014, for *Aglaja felis* Marcus and Marcus, 1970, based on the phylogeny presented by Camacho-García et al., 2014. *Aglaja felis* was considered as a member of the genus *Nakamigawaia* Kuroda and Habe in Habe, 1961, by Camacho-García et al. (2014). Ortea et al. noted that the type species of *Nakamigawaia, N. spiralis* Kuroda and Habe in Habe, 1961, was not included in Camacho-García et al.'s analysis and that *N. spiralis* has a distinct planispiral shell and lacks sensory bristles around the head (Baba 1985). Ortea et al. also removed *Spinoaglaja* Ortea, Moro and Espinosa, 2007, from synonymy with *Philinopsis* Pease, 1860, based on the phylogeny of Camacho-García et. al. and the fact that members of one subclade have a distinctive shell morphology. Ortea et al. (2014:94) stated that "if the shell is really a valid character to separate genera within the family Aglajidae, each genus should have a typical kind of shell." Despite the obvious circularity of this statement, the authors continue to state *Melanochlamys* Cheeseman, 1881 and *Philinopsis* do not have distinctive shell morphology. The same is true for *Navanax* Pilsbry, 1895 where species can have either a simple calcified shell or a calcified portion with an expanded conchiolin wing (Gosliner 1980). Interestingly, *Chelidonura* A. Adams, 1850 has a consistent shell morphology, with minor variation, but has been shown not to be monophyletic Camacho-García et al. (2014). whereas shell morphology may ultimately prove to be an informative systematic character in the higher classification of aglajid cephalaspideans, neither a comprehensive phylogeny nor a complete review of shell morphology has been undertaken for members of the family. Thus, it is premature and imprudent to make additional systematic changes in the classification of aglajids, based exclusively on differences in shell morphology and other minor morphological differences that require verification. whereas the paper by Ortea et al. raises some intriguing suggestions about character evolution, it raises more questions than answers in providing an understating of how morphological attributes are distributed across the aglajid phylogeny. Future studies require greater taxon sampling to establish systematic partitioning of aglajid cephalaspideans as suggested by Gonzales and Gosliner (2014), where some taxa previously assigned to Philinidae appear to cluster with members of the Aglajidae.

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All these specimens were collected under our Gratuitous Permits (GP-0059-11, GP-0077-14) from the shallow waters of the municipalities of Mabini and Tingloy. This is part of the joint DA-NFRDI-CAS Memorandum of Agreement for the on-going implementation of the NSF-funded biodiversity expedition in the Verde Island Passage. The specimens were collected in accordance with the terms and conditions of the gratuitous permit and under the supervision of our partners from BFAR FRQD and NFRDI.

## LITERATURE CITED

BABA, K. 1985. Anatomical review of a cephalaspidean mollusk, *Nakamigawaia spiralis* Kurdoa & Habe in Habe 1961, (Aglajidae), from Japan. *Special Publication of the Mukaishima Marine Biological Station*, 1985:1–5.

CAMACHO-GARCÍA, Y. E., E. ORNELAS-GATDULA, T. M. GOSLINER, AND Á. VALDÉS. 2014. Phylogeny of the family Aglajidae (Pilsbry, 1895) (Opisthobranchia: Cephalaspidea) inferred from mtDNA and nDNA. *Molecular Phylogenetics and Evolution* 71:113-126.

CARPENTER, K., AND V. G. SPRINGER. 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environmental Biology of Fishes* 72:467–480.

GONZALES, C., AND T. GOSLINER. 2014. Six new species of *Philine* (Opisthobranchia: Philinidae) from the tropical Indo-Pacific. The Coral Triangle: the 2011 Hearst Biodiversity Expedition. Special Publication of the California Academy of Sciences: 351-383.

GOSLINER, T. M. 1980. Systematics and phylogeny of the Aglajidae (Opisthobranchia: Mollusca). *Zoological Journal of the Linnean Society* 68:325–360.

GOSLINER, T. 1994. Gastropoda: Opisthobranchia. Pages 235–355 *in* F. Harrison and A. Kohn, eds., *Microscopic Anatomy of Invertebrates*. V. 5. Mollusca, ch. 5. John Wiley & Sons, New York, New York, USA.

GOSLINER, T. 2011. Six new species of aglajid opisthobranch mollusks from the tropical Indo-Pacific. *Zootaxa* 2751:1-24.

Gosliner, T. M., D. Behrens, and Á. Valdés. (2008) *Indo-Pacific Nudibranchs and Sea Slugs*: *a Field Guide to the World's Most Diverse Fauna*. Sea Challengers, Gig Harbor, Washington, and California Academy of Sciences, San Francisco, California, USA. 426 pp.

Marcus, Ev., and Er. Marcus. 1967. American opisthobranch mollusks Part I, Tropical American opisthobranchs. *Studies in Tropical Oceanography, Miami* 6:1-137.

Ortea, J., M. Caballer, L. Moro and J. Epinosa. 2014. What the shell tells in Aglajidae: A new genus for Aglajafelis (Opisthobranchia: Cephalaspidea). *Revista de la Academia Canaria de Ciencias* 26: 83-119.

Rudman, W. B. 1970. *Chelidonura inornata* Baba and *C. electra* sp. nov. from the Solomon Islands (Opisthobranchia, Aglajidae). *Journal of the Malacological Society of Australia* 2:7–12.

Rudman, W. B. 1972a. On *Melanochlamys* Cheeseman, 1881, a genus of the Aglajidae (Opisthobranchia: Gastropoda). *Pacific Science* 26:50–62.

Rudman, W. B. 1972b. A comparative study of the genus *Philinopsis* Pease, 1860. (Aglajidae, Opisthobranchia). *Pacific Science* 26:381–399.

Rudman, W. B. 1972c. Structure and functioning on the gut of the Bullomorpha (Opisthobranchia). Part 4. Aglajidae. *Journal of Natural History* 6:547–560.

Rudman, W. B. 1973. On some species of *Chelidonura* (Opisthobranchia: Aglajidae) from Zanzibar and Fiji. *Zoological Journal of the Linnean Society* 52:201-215.

Rudman, W. B. 1974. A comparison of *Chelidonura, Navanax* and *Aglaja* with other genera of the Aglajidae (Opisthobranchia, Gastropoda). *Zoological Journal of the Linnean Society* 54:185–212.

Rudman, W. B. 1978. A new species and genus of the Aglajidae and the evolution of the philinacean opisthobranch molluscs. *Zoological Journal of the Linnean Society* 62:89–107.

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# A Revision of the *rhopalocerus* Species Group of *Bembecinus* Costa (Hymenoptera: Crabronidae: Bembicinae)

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**Eight new species of *Bembecinus* of the *rhopalocerus* species group are described and illustrated: *damarensis* F. Gess and Pulawski, *gariepensis* F. Gess and Pulawski, *helicicola* Pulawski, *inexspectatus* Pulawski, *karasanus* F. Gess and Pulawski, *namaquensis* Pulawski, *namibius* Pulawski, and *omaruru* Pulawski. *Bembecinus ruficaudus* Bohart, 1997 is herein referred to the synonymy of *Bembecinus mutabilis* (Arnold, 1929). *Bembecinus quadristrigatus somalicus* (Arnold, 1940) is raised to the full species status, with *B. quadristrigatus dubiosus* (Guiglia, 1941) recognized as its synonym. Geographical distributions based on available records are presented for all seventeen species of the *rhopalocerus* species group: *Bembecinus damarensis* F. Gess and Pulawski, *gariepensis* F. Gess and Pulawski, *gilvus* R. Bohart, *helicicola* Pulawski, *hyperocrus* (Arnold), *inexspectatus* Pulawski, *karasanus* F. Gess and Pulawski, *mutabilis* (Arnold), *namaquensis* Pulawski, *namibius* Pulawski, *omaruru* Pulawski, *pakhuisae* R. Bohart, *quadristrigatus* (Arnold), *rhopaloceroides* (Arnold), *rhopalocerus* (Handlirsch), *somalicus* (Arnold), and *zebratus* R. Bohart. According to the current knowledge, all species are restricted to sub-Saharan Africa, and most occur in the semi-arid to arid Succulent Karoo and Nama-Karoo of South Africa and Namibia. Three species (*gilvus, omaruru* and *quadristrigatus*) penetrate the Namib Desert along the courses of drainage channels and one (*somalicus*) is known only from Ethiopia, Kenya, and northeast Tanzania. A summary of flower associations, nesting and prey is provided for those species for which data are available. Flowers visited are principally small, clustered in heads, and of the families Zygophyllaceae, Molluginaceae, Amaranthaceae and Asteraceae. All known prey are Homoptera: Cicadellidae, Flatidae, Issidae, and Nogodinidae.**

*Bembecinus* is a cosmopolitan genus with 188 currently recognized species (Pulawski 2014). Of these, 61 species have been recorded from the Afrotropical Region, and 49 from southern Africa.

Considering the size of the genus it is not surprising that several authors have attempted to divide it into species groups. Arnold (1929) in his account of the southern African *Bembecinus* (treated by him, as previously by Handlirsch, as belonging to *Stizus*) divided the species then known to him into eight species groups. These groups were based upon those proposed by Handlirsch (1892) and were generally in agreement with them. The only divergence was with respect to Handlirsch's *clavicornis* group (based upon *Stizus clavicornis* Handlirsch, 1892, a junior synonym of *Larra cinguliger* F. Smith, 1856). From the *clavicornis* group, renamed by him the *cinguliger* group, Arnold removed *rhopalocerus* Handlirsch to form a new species group, the *rhopalocerus* group, consisting of *rhopalocerus* and his four allied, newly described species (*hyperocrus, mutabilis, quadristrigatus* and *rhopaloceroides*). A further species group, the *oxydorcus* group, was created by Arnold (1929) to separate off *B. oxydorcus* Handlirsch, a species sharing many characteristics with *cinguliger* Smith.

Bohart and Menke (1976) in their overview of the world genera suggested somewhat wider group limits than those proposed by either Handlirsch or Arnold. With respect to the Afrotropical fauna the consequent reduction in the number of species groups was in part achieved by considering the *cinguliger* group to include Arnold's *rhopalocerus* and *oxydorcus* groups.

Bohart (1997) further reduced the number of groups to three, the *Bembecinus caffer* group with two subgroups*,* the *Bembecinus rhopalocerus* group with two subgroups, *B. rhopalocerus* subgroup and *B. oxydorcus* subgroup, and *Bembecinus tridens* group with seven subgroups. Rather than giving a key he listed the groups with their subgroups giving diagnostic characters to distinguish them.

It was the opinion of the first author (FWG, here supported by WJP), however, that there are sufficient differences, both morphological and biological, between the *B. rhopalocerus* and *B. oxydorcus* subgroups for these to be treated as full groups.

Bohart (1997) thought that *Bembecinus lomii* (Guiglia) was a member of the *rhopalocerus* group, but this opinion is certainly erroneous. Guiglia's original description (1941) clearly mentions an emarginate margin of the propodeal declivity. She says, in the Latin diagnosis: *Margine declivi segmenti mediani incisione profunda et angusta praedito*, and later in the Italian description: *L'incisione ai margini declivi del segmento mediano è piuttosto stretta e profonda*. In addition, the illustration of the whole insect and that of the propodeum in profile clearly show an emargination. This character decidedly excludes the possibility of *B. lomii* being part of the *rhopalocerus* group, in which the posterior propodeal declivity is non-emarginate.

For some years prior to 1992 Friedrich Gess had been working towards a revision of the *rhopalocerus* species group as defined by him in his unfinished manuscript of 1992, which was set aside whilst he engaged himself in revisions of the masarine genera, meanwhile making a partial revision following Bohart (1997) and collecting together and determining more specimens of *Bembecinus,* thus adding to the knowledge of geographical distributions and flower associations. Regrettably, due to his ill health over many years and his subsequent death on 6 August 2013, his revision was not completed. The present contribution is a further revision and expansion of the 1992 manuscript. It is based on the examination of 1,423 specimens.

Friedrich's descriptions of two new species and recognition of a third have been checked and the descriptions completed by Wojciech Pulawski, who has also added and described five additional new species, a key to the species, Recognition sections under all species, photographs of morphological characters, and whole body photographs of some species.

Photographs of a pair of specimens of most species*,* maps depicting the known geographical distributions, comments on the geographical distributions of the species, and of their flower associations, nesting and prey have been added by Sarah Gess.

Clearly, although the contribution is based on the work of Friedrich Gess, it has not been checked or approved by him and therefore should errors be found he should not be held responsible for them.

Members of the *rhopalocerus* group occur in Africa south of Sahara. When discussing their distributions, the terms Nama-Karoo, Succulent Karoo, Namib Desert, Savanna and Kalahari have been used. The terms follow the categorization of biomes in southern Africa by Rutherford (in Cowling et al. 1997). Each of the biomes (Fig. 1) is by no means uniform and can be divided into types related, amongst other factors, to latitude, altitude, geology and rainfall patterns (Cowling et al. 1997).

The Nama-Karoo is the largest of the three biomes included in the Karoo-Namib Region. Its annual rainfall varies but as a generalization can be said to decrease from east to west with the areas of very low precipitation being in the rain shadows of major mountain ranges. Rainfall is bimodal or strongly seasonal and, for some areas, relatively high in summer.

The Succulent Karoo is characterized by predominantly winter rainfall and, as its name suggests, a remarkably high diversity of succulents.

The Namib Desert stretches for 2,000 km in a north-south direction. It is adjacent to the Nama-Karoo and Succulent Karoo biomes and may be considered from many perspectives to comprise the most arid portions of these biomes.

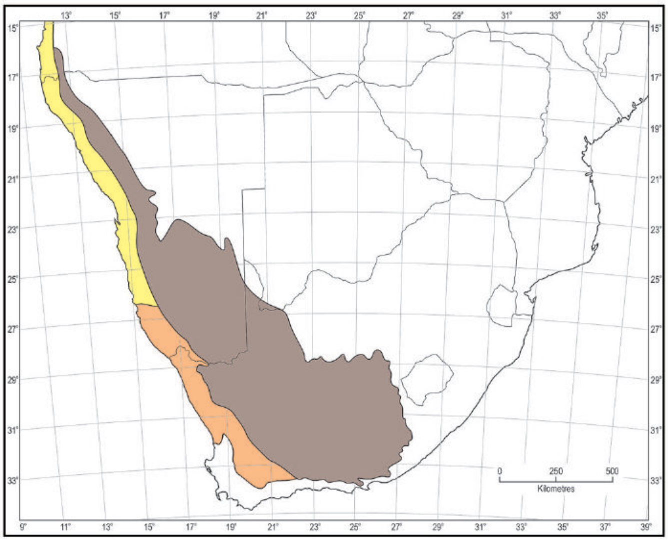

FIGURE 1. Southern Africa. The distribution of Succulent Karoo (orange), Nama-Karoo (brown) and middle and northern Namib Desert (yellow) after Rutherford (1997).

Savanna is a tropical biome, which grades into the arid shrublands of the Nama-Karoo in the Eastern and Northern Cape provinces of South Africa and in Namibia.

The Kalahari does not constitute a separate biome but to the south is considered to be arid Nama-Karoo and to the north arid Savanna. The Kalahari basin is characterized by its infilling being the single largest body of wind-blown sand in the world.

The term *ocular index*, as used in the present paper, is defined as the interocular distance on the vertex divided by the interocular distance at the base of the clypeus. The term *streptaulus* indicates a transverse pronotal sulcus that extends between the bases of the pronotal lobes and that separates the collar from the anterior pronotal rim.

For plotting the distribution maps ArcMap 10.1 GIS by ESRI was used with the coordinates in decimal degrees. Coordinates given as label data have been included in the 'Material examined' species sections. Those not given as label data have been obtained from relevant websites or in the instances where the label data gives the collection locality as a number of kilometres or miles from a fixed point the coordinates have been calculated from maps (Gazetteer as an Appendix compiled by SKG).

Acronyms for institutions in which material is housed follow Evenhuis (2013) The names of the persons responsible for the loans follow in parentheses. These are:

AEIC = American Entomological Institute, Gainesville, Florida (the late Henry K. Townes to FWG).
AMGS = Albany Museum, Grahamstown, South Africa (John Midgley to WJP).
AMNH = American Museum of Natural History, New York, USA (Jerome G. Rozen to FWG).
BMNH = Natural History Museum, London, United Kingdom, formerly British Museum, Natural History (David G. Notton to WJP).
CAS = California Academy of Sciences, San Francisco, California, USA (Wojciech J. Pulawski to FWG).
MHNG = Muséum d'Histoire Naturelle de Genève, Switzerland (Bernard Landry to WJP).

MS = Maximilian Schwarz, Ansfelden, Austria (personal collection, to WJP).
MSNG = Museo Civico di Storia Naturale di Genova, Italy.
NMBZ = Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe, formerly National Museum of Southern Rhodesia (Hamish G. Robertson, SAMC to FWG).
OÖLM = Oberösterreichisches Landesmuseum, Linz, Austria (Fritz Gusenleitner to WJP).
PPRI = Plant Protection Research Institute, Pretoria, South Africa (Connal D. Eardley to WJP).
SAMC = South African Museum, Iziko Museums of Cape Town, South Africa (Hamish G. Robertson to FWG; Dawn Larson to WJP).
TMSA = Transvaal Museum, now National Museum of Natural History, Ditsong Museum, Pretoria, South Africa (Robert W. Toms to FWG).
UCDC = University of California, Davis, R.M. Bohart Museum of Entomology, California, USA (Lynn S. Kimsey to FWG; Steven L. Heydon to WJP).
USNM = United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (Brian Harris to WJP).
ZMB = Museum für Naturkunde, Institut für Systematische Zoologie, Berlin, Germany (Michael Ohl, to FWG and WJP).
ZMUC = Zoological Museum, University of Copenhagen, Copenhagen, Denmark (Lars Vilhelmsen, to WJP).

## Key to Species Groups of *Bembecinus*

(based on Bohart, 1997, with modifications derived from the manuscript key of F. Gess)

1a. Male flagellomere IX produced into a spine beneath . . . . . . . . . . . . . . . . . . . . *B. tridens* group (including *discolor, irwini, loriculatus*, *meridionalis, peregrinus, spinicornis,* and *tridens* subgroups)

1b. Male flagellomere IX simple . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Male flagellum relatively slender; male sterna simple; female foretarsus with apical tarsomere and arolium not unusually large. Afrotropical and Australian Regions. . . . . . . . *B. caffer* group (including *caffer* and *inermis* subgroups)

2b. Male and female flagellum moderately to strongly clavate; male sterna mainly simple, with prong on sternum II in *cinguliger* (F. Smith), *escalerae* (Turner), and *flavopictus* (Arnold); female foretarsus with apical tarsomere and arolium much larger than on other legs. Afrotropical Region. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Flagellum moderately clavate (Fig. 2b); lateral margin of propodeal declivity only slightly compressed, not excised (Fig. 2c); clypeus sub-triangular, only slightly wider than long (Fig. 2a); length of labrum about 0.7–1.0 × its width (Fig. 2a); female forebasitarsus with a sand rake composed of a small number of long spines; male sternum II simple. Nesting in friable (sandy) soil; nest excavation by means of the raking of dry sand; burrow entrance without a turret (F. Gess and S. Gess 1971; F. Gess 1981) . . . . . . . . . . . . . . . . . . . . . . . *B. rhopalocerus* group

3b. Flagellum conspicuously clavate; lateral margin of propodeal declivity strongly compressed, widely and deeply excised; clypeus more than twice as wide as long; length of labrum about 0.3–0.4 × its width; female forebasitarsus with dense row of short cilia; male sternum II simple in *oxydorcus* Handlirsch, with prong in *cinguliger* (F. Smith), *escalerae* (R. Turner), and *flavopictus* (Arnold). Nesting in non-friable (clayey) soil; nest excavation aided by use of water; burrow entrance surmounted by turret (F. Gess and S. Gess, 1975; S. Gess, 1981) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. oxydorcus* group

FIGURE 2. Species group characters exemplified by *Bembecinus rhopalocerus*: a – female clypeus and labrum, b – female antenna, c – non-emarginate posterolateral edge of propodeum.

## Key to Species of *Bembecinus rhopalocerus* Group

♀♀

Unknown and not included: *Bembecinus namaquensis*

1a. Forefemur conspicuously expanded basoventrally, its dorsal margin almost straight (Fig. 20b); clypeus near base roundly angulate in profile (Fig. 20a) . . . . . . . . *rhopalocerus* (Handlirsch)
1b. Forefemur not expanded, somewhat expanded basoventrally in *damarensis*, in which dorsal margin is shallowly concave basally and clypeus is evenly arcuate in profile . . . . . . . . . . . 2

2a. Labrum with large punctures (Fig. 12a), larger than those on scutum, averaging about one diameter apart. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***karasanus* F. Gess and Pulawski, sp. nov.**
2b. Labrum with punctures smaller than or equal to those on scutum, averaging several diameters apart . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Scutum with pair of admedian yellow stripes extending through most of scutum length, and gaster yellow and black; interocellar area yellow (partly so in some *gilvus*). . . . . . . . . . . . . 4
3b. Scutum all black mesally or, if with yellow admedian stripes (*omaruru*, many *mutabilis*, some *gariepensis*), then gaster ferruginous (at least with ferruginous apical fasciae on terga), with or without yellow apical fasciae on terga; interocellar area black or with minute yellow spot between midocellus and hindocellus in some *mutabilis* . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

4a. Terga II-V each with pair of submedian black stripes (Fig. 22) that extend beyond tergal midlength or with pair of black spots near tergal middle . . . . . . . . . . . . . . *somalicus* (Arnold)
4b. Terga II-V with narrow black fascia basally or with single median black stripe that extends beyond tergal midlength . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5a. Scape with erect setae along its entire length (except basally) . . ***namibius* Pulawski, sp. nov.**
5b. Scape without erect setae or with erect setae at apex only . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6a. Labrum microscopically reticulate between punctures; forebasitarsus barely broadened (Fig. 8a); lower metapleuron closely, microscopically punctate; length 6.0–10.0 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *gilvus* R. Bohart
6b. Labrum unsculptured between punctures, at least along midline; forebasitarsus broadened (Fig. 18a); lower metapleuron microscopically areolate; length 9.5–14.0 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *quadristrigatus* (Arnold)

7a. Tergum II laterally with erect setae (Fig. 10b), longest setae about 0.5 × midocellar width . 8
7b. Tergum II without erect setae or setae markedly shorter . . . . . . . . . . . . . . . . . . . . . . . . . . 10

8a. Gastral terga ferruginous, without apical yellow fasciae . . . . . . . . . . . . . . *hyperocrus* (Arnold)
8b. Gastral terga with pale yellow apical fasciae (fasciae ill-defined in *omaruru* with golden tan gaster) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

9a. Clypeus all yellow, practically not angulate near base; minimum interocular distance equal to 2.2 × that between antennal scrobe and base of clypeus . . . . . . . ***omaruru* Pulawski, sp. nov.**
9b. Clypeus black basally, roundly angulate near base in profile (Fig.11a); minimum interocular distance equal to 3.2 × that between antennal scrobe and base of clypeus . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***inexspectatus* Pulawski, sp. nov.**

10a. Terga all ferruginous or with apical ferruginous fasciae (apical terga may be all or partly black), in some species with yellow apical fasciae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11
10b. Terga black and yellow. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

11a. Terga largely ferruginous or with ferruginous, apical fasciae, but without yellow apical fasciae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *mutabilis* (Arnold)
11b. Terga with yellow apical fasciae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

12a. Hindtibial arolium about as long as 0.5 × inner claw; mid- and hindtarsal claws slightly curving inwards at base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***helicicola* Pulawski, sp. nov.**
12b. Hindtibial arolium about as long as 0.25 × inner claw; mid- and hindtarsal claws straight (indistinguishable morphologically, but can be determined by association with topotypical males) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13

13a. Southern Namibia, Eastern and Western Cape Provinces of South Africa. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *rhopaloceroides* (Arnold)
13b. Southern Namibia, northwestern part of Northern Cape Province of South Africa. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***gariepensis* F. Gess and Pulawski, sp. nov.**

14a. Dorsal surface of tergum I yellow except for median, black, nearly rectangular marking (Fig. 6b) that does not attain posterior margin; scape without erect setae; dorsal margin of forefemur somewhat concave basally, ventral margin slightly expanded basally (Fig. 6a) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***damarensis* F. Gess and Pulawski, sp. nov.**
14b. Tergum I black except for narrow, yellow apical fascia; scape apically with several erect setae (setal length at least 0.5 × midocellar width); dorsal margin of forefemur practically straight, ventral margin not expanded basally. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15

15a. Clypeus all or partly black, mesopleuron black. . . . . . . . . . . . . . . . . . . . . *pakhuisae* R. Bohart
15b. Clypeus all yellow, mesopleuron partly yellow. . . . . . . . . . . . . . . . . . . . *zebratus* R. Bohart

♂♂

Unknown and not included: *Bembecinus helicicola*

1a. Punctures of labrum larger than those of scutum (Fig. 12a). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***karasanus* F. Gess and Pulawski, sp. nov.**
1b. Punctures of labrum smaller than or equal to those on scutum . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Foretibia incrassate in profile (Figs 7b, 19c) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2b. Foretibia not incrassate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

3a. Foretibial inner surface with oblique impression that is visible in dorsal view as an emargination at tibia's basal third (Fig. 19b). . . . . . . . . . . . . . . . . . . . . . . . . . *rhopaloceroides* (Arnold)
3b. Foretibia with inner surface flat or nearly so, without emargination in dorsal view (Figs 7a and b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***gariepensis* F. Gess and Pulawski, sp. nov.**

4a. Tergum II with erect setae (Fig. 10c), at least laterally; longest setae about 0.5 × midocellar width. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
4b. Tergum II without erect setae or setae markedly shorter . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

5a. Clypeus, supraclypeal area, and stripes along orbit pale yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***inexspectatus* Pulawski, sp. nov.**

5b. Clypeus, supraclypeal area, and frons all black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6a. Gastral terga without pale yellow apical fasciae; tergum VII shorter, rounded (Fig. 10d) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *hyperocrus* (Arnold)

6b. Gastral terga with pale yellow apical fasciae (fasciae ill defined in specimens with golden tan gaster); tergum VII longer, roundly triangular (Fig. 16) . . . . . . . ***omaruru*** **Pulawski, sp. nov.**

7a. Apical flagellomere curved, excavated posteriorly, only slightly so in *pakhuisae* (Fig. 17b) . 8

7b. Apical flagellomere not curved, not excavated posteriorly or insignificantly excavated. . . . 11

8a. Gastral terga largely ferruginous (tergum I black basally, following terga all ferruginous or narrowly black basally) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *mutabilis* (Arnold)

8b. Gastral terga yellow and black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

9a. Tergum VII longer, roundly triangular (Fig. 6d); apical flagellomere markedly curved and excavated (Fig. 6c) . . . . . . . . . . . . . . . . . . . . . . . . . . ***damarensis*** **F. Gess and Pulawski, sp. nov.**

9b. Tergum VII shorter, roundly trapezoid (Fig. 17c); apical flagellomere slightly curved and excavated (Fig. 17b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

10a. Apical flagellomere less curved (Fig. 17b); yellow apical fascia of tergum II slightly shorter to longer than black, basal part, at least mesally . . . . . . . . . . . . . . . . . . . *pakhuisae* R. Bohart

10b. Apical flagellomere in most specimens more curved (Fig. 23a); yellow apical fasciae of tergum II shorter than black, basal part . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *zebratus* R. Bohart

11a. Gastral terga largely ferruginous . . . . . . . . . . . . . . . . . . . . . ***namaquensis*** **Pulawski, sp. nov.**

11b. Gastral terga yellow and black (with some ferruginous on tergum I in *rhopalocerus*) . . . . 12

12a. Terga II-V with pair of submedian black stripes that extend beyond tergal midlength or with pair of black spots near tergal middle (Fig. 22) . . . . . . . . . . . . . . . . . . . . . *somalicus* (Arnold)

12b. Tergum II-V with narrow black fascia basally or with single median black stripe that extends beyond tergal midlength . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13

13a. Scape with erect setae along its entire length (except basally) . ***namibius*** **Pulawski, sp. nov.**

13b. Scape without erect setae or with erect setae at apex only. . . . . . . . . . . . . . . . . . . . . . . . 14

14a. Distance between clypeus and antennal scrobe equal to about 0.3 × least interocular distance (Fig. 8b); lower gena without erect setae between mandibular base and occipital carina; length 7.0–9.2 mm. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *gilvus* R. Bohart

14b. Distance between clypeus and antennal scrobe equal to 0.6–0.7 × least interocular distance; lower gena with erect setae between mandibular base and occipital carina; length 12.1–14.6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15

15a. Clypeus roundly angulate basally (best seen in profile, Fig. 20a); tergum VII broadly rounded (Fig. 20c); scutum black mesally . . . . . . . . . . . . . . . . . . . . . . . *rhopalocerus* (Handlirsch)

15b. Clypeus evenly arcuate in profile; tergum VII less rounded, more prominent mesally (Fig. 18d); scutum with pair of admedian yellow stripes . . . . . . . . . . . . . *quadristrigatus* (Arnold)

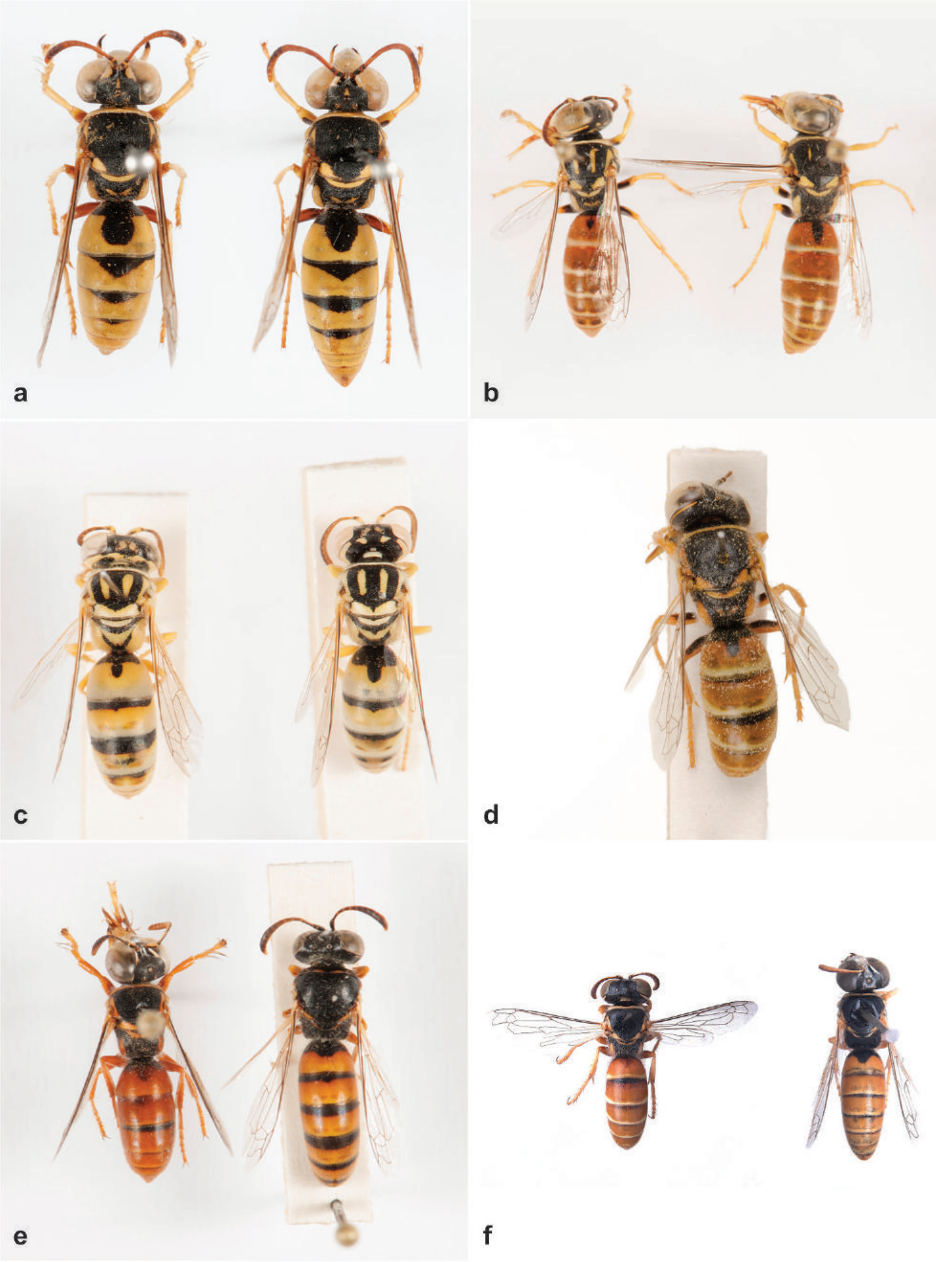

FIGURE 3. *Bembecinus* spp.: a – *damarensis*, female, male, b – *gariepensis*, female, male, c – *gilvus*, female, male, d – *helicicola*, female; e – *hyperocrus*, female, male, f – *inexpectatus*, female, male. (approximate lengths of females: a. 12 mm, b. 11.5 mm, 9 mm, d. 10 mm, e. 10 mm, f. 9.2 mm).

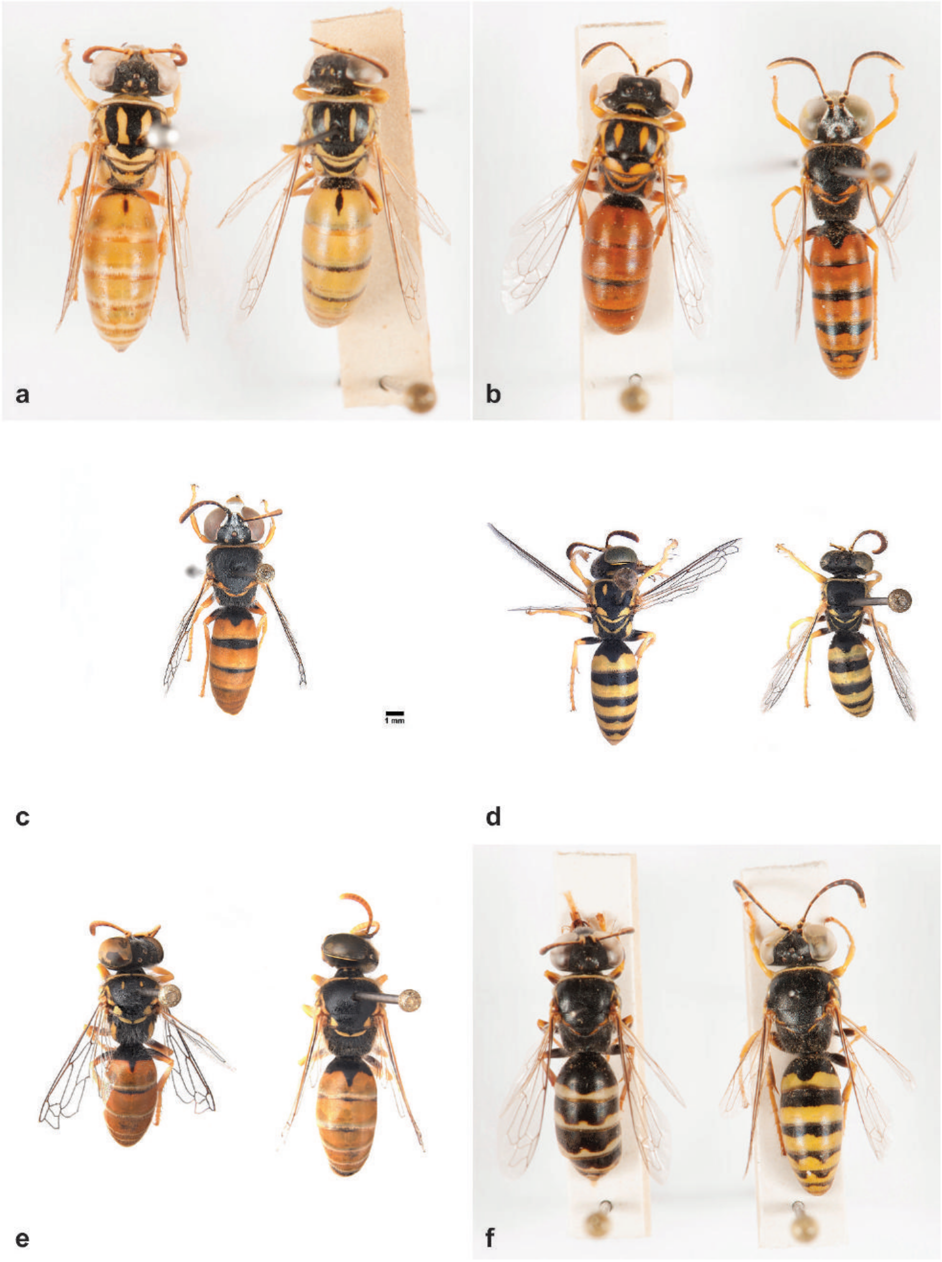

FIGURE 4. *Bembecinus* spp.: a – *karasanus*, female, male, b – *mutabilis*, female, male; c – *namaquensis,* male; d – *namibius*, female, male; e – *omaruru*, female, male; f – *pakhuisae*, female, male.(approximate lengths of females: a. 11 mm, b. 10.5 mm, c. male 11.8 mm, d. 9.7 mm, e. 11.3 mm, f. 15 mm).

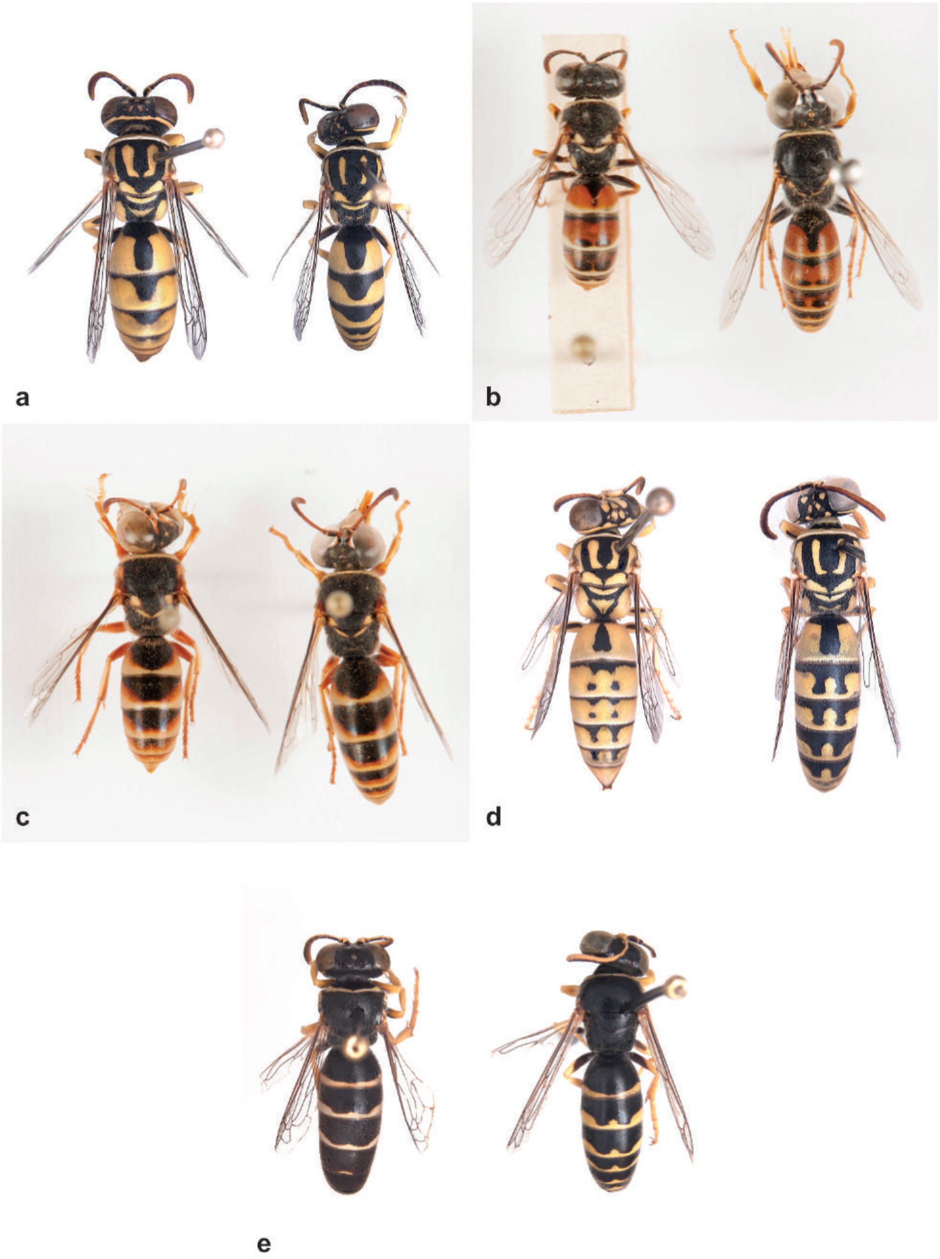

Figure 5. *Bembecinus* spp.: a – *quadristrigatus*, female, male; b – *rhopaloceroides*, female, male; c – *rhopalocerus*, female, male; d – *somalicus*, female, male; e – *zebratus*, female, male (approximate lengths of females: a. 11.5 mm, b. 11.5 mm, c. 13 mm, d. 11.8 mm, f. 10.5 mm).

### ***Bembecinus damarensis*** **F. Gess and Pulawski, sp. nov.**

Figures 3a, 6a-d.

*Bembecinus* sp. nov. A (*rhopalocerus* species group): S. Gess and F. Gess, 2003:117 (floral records).

**NAME DERIVATION.**— The name, a newly coined Neolatin adjective, is derived from the geographical name, Damaraland, a historic province of Namibia, and refers to the provenance of the holotype.

**RECOGNITION.**— *Bembecinus damarensis* has the scutum black mesally, the mesopleuron largely yellow, and the terga largely yellow (at least terga I-III black basally), without ferruginous color. In the female, the length of the hindtibial arolium is about 0.5 × of the inner claw. The females of *pakhuisae* and *zebratus* are similar, but *damarensis* differs in having the dorsal surface of tergum I yellow except for the median, black, nearly rectangular marking (Fig. 6b) that does not attain posterior margin and the scape without erect setae. Also, the dorsal margin of the forefemur is somewhat concave basally and the ventral margin slightly expanded basally. In the other two species, tergum I is black except for narrow, yellow apical fascia, the scape apically has several erect setae (setal length at least 0.5 × midocellar width), and the dorsal margin of the forefemur is practically straight and the ventral margin is not expanded basally. The shape of the forefemur is similar in the female of *rhopalocerus*, in which, however, the clypeus is roundly angulate basally (best seen in profile), whereas evenly convex in *damarensis*.

The male of *damarensis* shares with that of *mutabilis* a conspicuously curved and excavated apical flagellomere (Fig. 6c), markedly more so than in *pakhuisae* and *zebratus*. It differs from that of *mutabilis* in having the scutal punctures averaging about one diameter apart, the mesopleuron yellow, the gastral terga mostly yellow (partly black), tergum VII elongate, roundly triangular (Fig. 6d), and the length of 12.7–14.7 mm. In *mutabilis*, the scutal punctures, near center, average about two diameters apart, the mesopleuron is all or predominantly black, the gaster is ferruginous (with some parts black), tergum VII is short, trapezoid, with apical margin nearly straight (Fig. 13d), and the length is of 10.5–11.5 mm.

FIGURE 6. *Bembecinus damarensis*: a – female forefemur, b – female tergum I showing color pattern, c – apical flagellomere of male, d – male tergum VII.

**Description**.— Head black, with the following yellow: mandible except apex, labrum, clypeus, face below antennae and narrowly up to midheight along orbit, streak on frons in midline below anterior ocellus, occasionally small spot touching posterior ocellus anteromedially, gena narrowly above and widely below, cardo, stipes, galea, both pairs of palps, scape except for dorsal black streak, underside of pedicel and of flagellomere I. Rest of antennae ferruginous except for black dorsal surface of pedicel and of flagellomeres VI–IX. Thorax black with the following yellow: entire pronotum except for black streptaulus, a C-shaped marking apically on each propleuron, lateral streak on scutum, tegula, triangular area on each side of scutellum, metanotum except narrowly black basally, and mesopleuron largely. Propodeum black, with the following yellow: anterior third of lateral surface, posterolateral margin, and a pair of spots on preapical part of enclosure. Gaster yellow with the following black: anterior declivity of tergum I, extending posteriorly into subrectangular, median marking on disk, basal transverse band expanded posteriorly in the middle on tergum II, and similar but often less developed markings on terga III and IV. Female legs yellow with the following light ferruginous: outer and inner surface of fore- and midtrochanters and fore- and midfemora and almost entire hindtrochanter and hindfemur, streaks on lower surface of all tibiae, tarsomeres to a variable degree. Male legs predominantly yellow with only the inner surface of hindfemur light ferruginous, inner surface of fore- and midfemora marked with black, and inner surface of hindfemur with ferruginous area marked with black. Wings hyaline, Sc + R black, other veins brown.

Clypeus, face below antennae and halfway up along sides densely covered with decumbent silvery pubescence, rest of face more sparsely so.

♀: Length 12.2–14.7 mm (average of 13: 13.3 mm; holotype:12.3 mm). Ocular index 1.9–2.0 (average of 13 = 1.9). Minimum interocular distance equal to 2.9–3.2 × that between antennal scrobe and base of clypeus (average of 8 = 3.0); distance between posterior ocelli 1.4 × ocellocular distance. Clypeus impunctate, markedly convex, fairly evenly curved from base to free margin, its high point near center of disk, its width at insertion of mandibles 1.8–1.9 × its median length (average of 13 = 1.85). Labrum triangular, markedly shiny, with small, widely separated punctures, sparsely microsculptured unlike clypeus which is densely microsculptured; its width at base subequal to median length. Dorsal margin of forefemur somewhat concave basally, ventral margin slightly expanded basally (Fig. 6a)

♂: Length 12.7–14.7 mm (average of 6 = 13.9 mm). Ocular index 1.9–2.1 (average of 6 = 2.0). Minimum interocular distance equal to 2.1–2.6 × that between margin of antennal scrobe and base of clypeus (average of 6 = 2.26 ); distance between posterior ocelli 1.4 × ocellocular distance; width of clypeus at insertion of mandibles 1.5–1.7 × its median length (average of 6 = 1.6). Flagellomere XI curved, excavate below, hook-like (Fig. 6c). TergumVII triangular, rounded apically (Fig. 6d).

**Material examined**.— Holotype: ♀, **Namibia: Otjozondjupa Region**: Osire, 24.xii.1974, H.N. Empey (AMGS). Paratypes: **Namibia: Otjozondjupa Region**: 44 km SW Otjiwarongo at 20°37′S 16°22′E, 4.iii.1990, W.J. Pulawski (1 ♀, CAS); Osire, 24.xii.1974, H.N. Empey (8 ♀, 6 ♂, AMGS); 70 km N Okahandja, 16.iii.1990, W.J. Pulawski (2 ♀, 1 ♂, CAS); Okahandja, 2–4.ii. 1972, BMNH Southern African Expedition (2 ♀, 8 ♂, BMNH). **Kunene Region**: Kamanyab (sic, = Kamanjab), iii.1925, Mus. Exped. (2 ♀, 1 ♂, SAMC, det. Arnold as *Stizus rhopalocerus* Handl.), same label data (1 ♀, SAMC ex NMB). **Erongo Region**: 17–19 km E Usakos, 18.iii.1976, J.G. and B.L. Rozen (1 ♀, AMNH); 11 km N Karibib, 27.ii.1990, W.J. Pulawski (1 ♀, CAS); 26 km N Karibib, 6.ii.1993, J. Gusenleitner (2 ♀, OÖLM). **Khomas Region**: between Rehoboth and Gamsberg Pass at 23°09.43′S 16°41.97′E, 11.iii.1999, F.W. and S.K. Gess (1 ♀, 1 ♂, AMGS), visiting flowers of *Hermstaedtia odorata* (Burch.) T. Cooke, Amaranthaceae; 18 km W junction 1237 and

C26 at 23°09′S 16°42′E, 11.iii.1999, F.W. and S.K. Gess (1 ♀, 1 ♂, AMGS), visiting flowers of *Hermbstaetia* sp., Amaranthaceae; Narebis (sic = Naribis?), iii.1921, K.H. Barnard (1 ♀, SAMC, det. Arnold as *Stizus rhopalocerus* Handl.). **Omaheke Region**: Gobasis [= Gobabis], 17.xii.1933, J. Ogilvie (1 ♀, BMNH); Gobabis District, 40 km W Witvlei, 16.ii.1990, W.J. Pulawski (1 ♀, 2 ♂, CAS) and M. Schwarz (2 ♂, CAS; 3 ♂, MS). **Hardap Region**: SW Gibeon at 25°19.76′S 17°28.85′E, 8.iii.1999, F.W. and S.K. Gess (2 ♂, AMGS), one visiting flowers of *Limeum sulcatum* (Klotsch) Hutch., Molluginaceae; SW Gibeon at 25°19.76′S 17°28.85′E, 10.iii.1999, F.W. and S.K. Gess(4 ♂, AMGS), visiting flowers of *Limeum sulcatum* (Klotsch) Hutch., Molluginaceae; SW Gibeon 41 km on 1089 at 25°20′S 17°29′E, F.W. and S.K. Gess, 8.iii.1999 (2 ♂, AMGS), one visiting flowers of *Limeum* sp., Molluginaceae, 10.III.1999 (5 ♂, AMGS), four visiting flowers of *Limeum* sp., Molluginaceae, 24.iii.1999 (1 ♀, AMGS). **SOUTH AFRICA: Northern Cape**: 11 km from Twee Rivieren on Nossob road at 26°24′S 20°41′E, 8–11.iii.1990, F.W. and S.K. Gess (5 ♂, AMGS), visiting flowers of *Limeum aethiopicum* Burm., Molluginaceae.

**GEOGRAPHICAL DISTRIBUTION**.— Known from the Nama-Karoo/Savanna fringe in Northern Namibia to the Nama-Karoo in southern Namibia and the southern Kalahari to the north of Twee Rivieren (Fig. 24a)

**FLORAL ASSOCIATIONS**.— Visiting flowers of two families: Molluginaceae (*Limeum sulcatum* (Klotsch) Hutch. and *Limeum aethiopicum* Burm.) and Amaranthaceae (*Hermbstaedtia odorata* Burch.) (label data, see Material Examined; S. Gess and F. Gess 2003).

**NESTING**.— Unknown.

**PREY**.— Unknown.

### *Bembecinus gariepensis* F. Gess and Pulawski, sp. nov.

Figures 3b, 7a, b.

**NAME DERIVATION**.— The name, a newly coined Neolatin adjective, is derived from Gariep, the Khoi name for the Orange River, on the raised southern bank of which, at Upington, the majority of the specimens were collected.

**RECOGNITION**.— *Bembecinus gariepensis* is similar to *rhopaloceroides.* See that species for differences.

**STATUS OF THE SPECIES**.— *Bembecinus gariepensis* and *rhopaloceroides* differ only by the shape of the male foretibia (as discussed under the latter species), whereas the females are indistinguishable morphologically. We have considered the possibility of the two being just individual or geographic variants of one species. We have rejected this hypothesis, because we have found no intermediate males, and because identical females occur in a number of species within the genus.

**DESCRIPTION**.— Head black with the following yellow: mandible except apex, labrum, clypeus, face below antennae and narrowly up to midheight along orbit, gena along orbit narrowly dorsally and widely ventrally, stipes laterally, scape (except black dorsally), pedicel and flagellomere I ventrally (rest of antenna ferruginous), in female also sublateral spot on each side immediately below level of anterior ocellus and transverse spot behind each posterior ocellus. Thorax black with the following yellow: pronotal collar, pronotal lobe, and pronotum ventrally of lobe, propleuron with small spot posterolaterally and a pair of small, transverse spots adjacent to posterior margin, adlateral streak and in many specimens pair of admedian streaks on scutum, large part of tegula, triangular lateral spot on scutellum, metanotum (except basally), most of mesopleuron. Propodeum black, with yellow posterolateral margin and yellow spot on lateral surface anteriorly extending top to bottom in female, slightly above midcoxal base in male, in female also with pair of spots toward apex of enclosure. Gaster ferruginous, terga I-V with pale yellow apical fascia, female tergum VI pale yellow except laterally, male terga VI and VII pale yellow (except tergum

VII mesally), and following is black: basal declivity of tergum I and narrow median streak extending through most of its dorsal surface. Legs pale yellow except posterior surface of femora largely black, foretibial venter with black streak, and mid- and hindtibial venters with ferruginous streaks. Wings hyaline, Sc+R black, other veins brown.

♀: Length 11.2–11.7 mm. Ocular index = 2.25–2.52. Minimum interocular distance equal to 2.1–2.2 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.3–1.5 × ocellocular distance. Width of clypeus at mandibular insertion 1.69–1.70 × its median length.

♂: Length 10.2–12.3 mm. Ocular index 2.22–2.47 (average of 17 = 2.36). Minimum interocular distance equal to 1.8–2.1 × that between margin of antennal scrobe and baseof clypeus (average of 17 = 2.0); distance between posterior ocelli 1.3–1.7 × ocellocular distance (average of 17 = 1.5). Width of clypeus (measured near mandibular insertion) 1.56–1.70 × midlength (average of 17 = 1.63). Foretibia incrassate (Fig. 7).

FIGURE 7. *Bembecinus gariepensis*: a – male foretibia in profile, b – male foretibia dorsally.

MATERIAL EXAMINED.— HOLOTYPE: ♀, **SOUTH AFRICA: Northern Cape Province**: Richtersveld 2816 BB at Road Khubus-Ochta, near Vyfsusters Mountain, 7.x.1987, M. Struck, on flowers of *Psilocaulon subnodosum* (Berger) N.E.Br., Mesembryanthemaceae (Aizoaceae) (AMGS). PARATYPES: **NAMIBIA: !Karas Region**: Aus, 11.ii.1990, W.J. Pulawski (1 ♀, CAS); Aus at 26°40′S 16°15′E, 3.iii.2000, F.W. and S.K. Gess (2 ♀, AMGS); Klinghardtberge, 20.x.1974, R.A. Watmough (1 ♂, PPRI); road 727 80 km S Aus, 8.xii.1994, M. Kuhlmann (1 ♂, ZMB); 16 km S Rosh Pinah at 28°04′S 16°51′E, F.W. and S.K. Gess, 13.x.2000 (2 ♂, AMGS), one visiting flowers of Mesembryanthemaceae, 14.x.2000 (1 ♀, AMGS), visiting flowers of Mesembryanthemaceae, 15.x.2000 (1 ♂, AMGS). **SOUTH AFRICA: Northern Cape Province**: Richtersveld 2816 BB [Degree Refeence System (Leistner and Morris 1976) = 28°45′–49′S 16°01′–15′E] at Road Khubus-Ochta, near Vyfsusters Mountain, 7.x.1987, M. Struck (2 ♂, AMGS), on flowers of *Psilocaulon subnodosum* (Berger) N.E.Br., Mesembryanthemaceae [Aizoaceae]; 60 km N Port Nolloth 28°47′S 16°38′E, 27.ix.1997, F.W. and S.K. Gess (1 ♀, 1 ♂, AMGS); Upington, 10–12.x.1966, F.W. and W.H.R. Gess (14 ♂, SAMC).

GEOGRAPHICAL DISTRIBUTION.— Known from the winter rainfall Succulent Karoo of southern Namibia and the Northern Cape Province, South Africa. (Fig. 24b).

FLORAL ASSOCIATIONS.— Visiting flowers of Aizoaceae (Mesembryanthema, *Psilocaulon subnodosum* (Berger) N.E.Br.) (label data, see Material Examined).

NESTING.— Unknown.

PREY.— Unknown.

## ***Bembecinus gilvus*** **R. Bohart**

Figures 3c, 8a, b.

*Bembecinus gilvus* R. Bohart, 1997:168, Fig. 3, ♀. Holotype: ♀, Namibia: Gobabeb (USNM), examined by W. Pulawski.— S. Gess and F. Gess, 2003:115 (floral records); Pulawski, 2014:12 (in catalog of world Sphecidae *sensu lato*).

**Recognition**.— *Bembecinus gilvus* has the gaster mainly yellow with some black, but without ferruginous color. It also has a pair of admedian yellow stripes on the scutum and a yellow marking between the midocellus and each hindocellus (the two separated in the midline). It differs from similar species (*quadristrigatus*, *somalicus*) in lacking the erect setae along the hypostomal carina (at most a few such setae are present next to the occipital carina), the lower metapleuron closely, microscopically punctate, the body length of 6.0–10.0 mm (rather than 9.5.0–14.0), the female forebasitarsus barely broadened (Fig. 8a), and in the male the distance between the clypeus and the antennal scrobe equal to about 0.3 × least interocular distance rather than 0.6–0.7 ×.

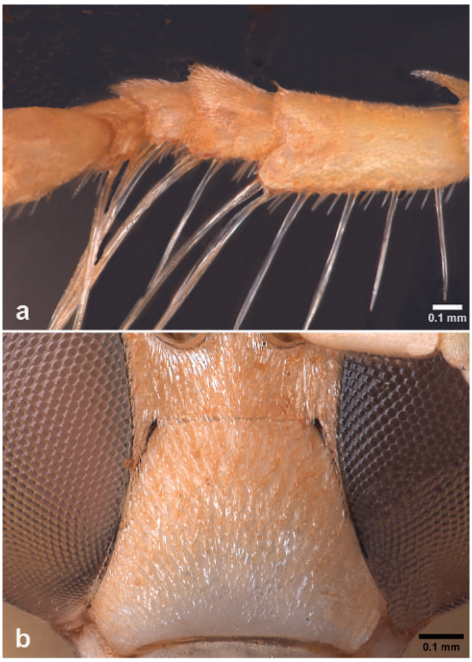

Figure 8. *Bembecinus gilvus*: a – female forebasitarsus, b – male clypeus.

**Material examined**.— **Namibia: Kunene Region:** on road 3245 E Skeleton Coast Park (20°14′S 13°53′E), F.W. and S.K. Gess, visiting yellow flowers of *Zygophyllum simplex* Linnaeus, Zygophyllaceae (5 ♀, AMGS); 12 km E Springbokwaater at 20°15′S 13°44′E, F.W. and S.K. Gess, visiting flowers of *Zygophyllum simplex* L., Zygophyllaceae, 13.x.2000 (1 ♀, AMGS), 14.x.2000 (1 ♀, AMGS), 11.iv.2002 (3 ♀, 7 ♂, AMGS). **Erongo Region**: 20 km NE Hentiesbaaai at 21°58′S 14°22′E, 10.xii.1996, W.J. Pulawski (2 ♀, 2 ♂, CAS); 5 km E Swakopmund, 4.ii.1978, O. Lomholdt (1 ♀, ZMUC); 63 km E Swakopmund at 22°45′S 15°02′E, 15.ii.1996, W.J. Pulawski (1 ♀, 1 ♂, CAS); 11 km E Walvis Bay at 22°59′S 14°37′E, 6.xii.1996 (2 ♂, CAS); between Kuiseb and Gaub passes (23°27′S 15°46′E) 22.iii.1999, F.W. and S.K. Gess (1 ♀, AMGS); Gaub Pass (23°30′S 15°46′E), 19.iii.1997, F.W. and S.K. Gess, on yellow flowers of *Zygophyllum simplex* Linnaeus, Zygophyllaceae (1 ♀, 1 ♂, AMGS); Kuiseb River bed at Rooibank (23°11′S 14°39′E), 10.iv.1998, F.W. and S.K. Gess (2 ♀ and 1 ♂ visiting yellow flowers of *Zygophyllum simplex* Linnaeus, Zygophyllaceae, 2 ♀ visiting yellow flowers) (4 ♀, 2 ♂, AMGS); Rooibank Desert Park, 15.xii.1977, Empey (3 ♂, AMGS); 5 km N Gobabeb, Wharton, 31.xii,1978, on *Zygophyllum simplex* Linnaeus (1 ♀, PPRI) and 2.i.1979 (1 ♀, PPRI); Kuiseb-Naukluft Bridge in Namibpark, 15.v.1973, M.F. Johannsmeier (4 ♀, PPRI); Kuiseb Naukluft Bridge, Namib Park, 16.v.1973, M.F. Johannesmeier (2 ♂, AMGS); Gobabeb [Namib Desert Research Station] 6.i.1980, R. Wharton (1 ♀, UCDC, holotype of *Bembecinus gilvus*); Namib Desert Research Station [Gobabeb] at 13°33′45″S 15°02′38″E, I. Kapofi and M.E. Irwin, 14–26.ii.1997 (1 ♀, CAS), 8–15.ix.1997 (1 ♀, CAS), 24.xi.1997 ( 10 ♀, CAS), 1–8.xii.1997 (4 ♀, CAS), 15–22.xii.1997 (3 ♀, CAS), 22–29.xii.1997 (3 ♀, CAS), 29.xii.1997 (3 ♀, CAS), 5–12.i.1998 (1 ♀, CAS), 17–24.ii.1998 (13 ♀, CAS); 8 km S Gobabeb, 12.ii.1978 (2 ♂, ZMUC); 88 mi. E [147 km] Walvis Bay, 2.x.1967, E.S. Ross and A.R. Stephen (1 ♀, CAS). **!Karas Region**:

SW Gibeon 41 km on 1089 (25°20′S 17°29′E) 10.iii.1999, F.W. and S.K. Gess (8 ♀ and 10 ♂, AMGS), visiting white flowers of *Limeum* sp., Molluginaceae (11 ♀, 15 ♂, AMGS); SW Gibeon 41 km on road 1089 (25°20′S 17°29′E) 24.iii.1999, F.W. and S.K. Gess (2 ♂, AMGS); 16 km S Rosh Pinah at 28°04′S 16°51′E, F.W. and S.K. Gess, 13.x.2000 (1 ♀, AMGS), visiting flowers of *Tripteris*, Asteraceae, 15.x.2000 (1 ♂, AMGS); Great Fish River, Aiais [Ai-Ais], Mus. Staff, xi.1939 (1 ♀, SAMC). **SOUTH AFRICA: Northern Cape Province**: Goodhouse, xi.1936, Museum Staff [SAMC] (4 ♀, SAMC). **Western Cape**: 11 km W Clanvilliam on road to Graafwater, 1.xii. 1989, F.W. and S.K. Gess (1 ♂, AMGS).

**GEOGRAPHICAL DISTRIBUTION.**— Known from Namibia, from the Desert/Nama-Karoo fringe in the north, penetrating the Namib Desert along the courses of the Swakop and Kuiseb rivers, to the Nama-Karoo in the south and across the Orange River into South Africa, with a single record from 11 km west of Clanwilliam in arid sandy Fynbos (Fig. 24c). This record so far south is surprising, however, it is of interest that the specimen was collected in the dry summer month of December, an unusual collecting time for this winter rainfall area which is most commonly visited by insect collectors in the spring, when flowering is at its height. It is clear that summer collecting in the winter rainfall area north to the Orange River is required to establish the complete distribution of this species.

**FLORAL ASSOCIATIONS.**— Visiting flowers of four plant families: Zygophyllaceae (*Zygophyllum simplex* Linnaeus), Molluginaceae (*Limeum* sp.), Asteraceae (*Tripteris* sp.) and Vahliaceae (label data, see Material Examined; S. Gess and F. Gess 2003).

**NESTING.**— Unknown.

**PREY.**— Unknown.

### *Bembecinus helicicola* Pulawski, sp. nov.

Figures 3d, 9.

*Bembecinus* sp. of *rhopalocerus* species group: F. Gess and S. Gess, 1999:147.

**NAME DERIVATION.**— The name *helicicola* is derived from two Latin words: *helica*, *a snail shell*, and the suffix *-cola*, *a dweller*; with reference to this species habit of seeking shelter in the empty shells of the snail *Trigonephrus* sp., Dorcasiidae.

**RECOGNITION.**— Like *rhopaloceroides* and *gariepensis*, *helicicola* has the gastral terga ferruginous, with pale yellow apical fasciae (tergum I black basally). It differs from these two species in having the claws of the mid- and hindtarsi slightly curving inward at base, and in having the hindtarsal arolium about as long as 0.5 × inner claw. In the other two species, the mid- and hindtibial claws are straight, and the hindtarsal arolium is about as long as 0.25 × inner claw.

FIGURE 9. *Bembecinus helicicola*: apical hindtarsomere.

**DESCRIPTION.**— Head black, with the following pale yellow: mandible except apex, labrum (black basomedially in holotype), clypeus, face below antenna, narrow stripe along eye orbit up to level of midocellus, gena narrowly along orbit, scape and pedicel ventrally; flagellum brownish yellow ventrally, dark brown dorsally; palpi brown. Thorax black with the following yellow: pronotal collar, pronotal lobe, narrow adlateral streak on scutum, tegula anteriorly (ferruginous posteriorly), triangular lateral spot on scutellum, posterior half of metanotum, and spot of varying size on mesopleuron. Propodeum black, with the following yellow: enclosure posteriorly, posterolateral margin mesally, and small spot on lateral surface anteroventrally. Gaster ferruginous, with pale yellow apical bands on terga; anterior declivity of tergum I black. Legs yellow, femora black dorsally (except apex). Wings hyaline, vein Sc+R dark brown, other veins light brown.

♀: Length 9.4–10.5 mm. Ocular index 2.20–2.30. Minimum interocular distance equal to 2.2–2.5 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.6–1.8 × distance between posterior ocellus and eye margin. Clypeus evenly arcuate in profile, its width at insertion of mandibles 1.6 × its midline. Labrum roundly triangular, its greatest width about 1.2 × midlength. Hindtarsal arolium about as long as 0.5 × of inner claw.

♂: Unknown.

**Material examined**.— Holotype: ♀, **South Africa: Northern Cape Province**: Richtersveld W Brandkaros at 28°29′S 16°40′E, 15.ix.1996, F.W. Gess, S.K. Gess, and R.W. Gess (AMGS). Paratypes: same data as holotype (1 ♀, CAS); 60 km N Port Nolloth at 28°47′S 16°38′E, 27.ix.1996, F.W. Gess and S.K. Gess (1 ♀, AMGS)

**Geographical distribution**.— Known from two adjacent localities in the Northern Cape Province of South Africa (Fig. 24d).

**Snail shell association**.— All three specimens were collected from empty shells of the snail *Trigonephrus* sp., Dorcasiidae, in which they were found sheltering. In windswept desertic areas snail shells provide shelter for various species of aculeates. Furthermore, some species use shells, sand-filled or empty, as secure nesting sites (F. Gess and S. Gess 1999; S. Gess and F. Gess 2008).

**Floral associations**.— Unknown.

**Nesting**.— Unknown.

**Prey**.— Unknown.

### *Bembecinus hyperocrus* (Arnold)

Figures 3e, 10a–c.

*Stizus hyperocrus* Arnold, 1929:295, ♀ (as Brauns's MS name). Holotype or syntypes: ♀, South Africa: Cape Province: Willowmore (TMSA).— Arnold, 1930:20 (in checklist of Afrotropical Sphecidae).— As *Bembecinus hyperocrus* (Arnold): R. Bohart and Menke, 1976:531 (new combination, in checklist of world Sphecidae); S. Gess and F. Gess, 2003:115–116 (floral records), 2006:14 (floral records); Pulawski, 2014:18 (in catalog of world Sphecidae *sensu lato*).

**Recognition**.— *Bembecinus hyperocrus*, *inexspectatus*, and *omaruru* are the only species within the *rhopalocerus* group having the erect setae on tergum II, although in the female these setae are short dorsally and distinct only laterally (Fig. 10b). In all three species, the gastral terga are mostly ferruginous with some parts black (golden tan in several *omaruru*), and in the males of *hyperocrus* and *omaruru* the clypeus (all or nearly so), the supraclypeal area, and the frons are all black. Unlike *inexspectatus* and *omaruru*, the gastral terga of *hyperocrus* have no pale yellow apical fasciae (the yellow fasciae are ill defined in *omaruru* with golden tan gaster). Subsidiary recognition features of *hyperocrus* are: the female clypeus black basally and markedly roundly angulate in profile (Fig. 10a), the male clypeus and the frons ventrally of the antennal socket are covered with dense, appressed vestiture, partly covering integument (no such vestiture in *omaruru*, the integument easily visible).

**Material examined**.— **Namibia: !Karas Region**: Aus, 8–30.xi.1929, R.E. Turner (1 ♀, SAMC ex NMBZ); Aus (Pad C13) 8.xii.1994, M. Kuhlmann (1 ♀, ZMB)]. **South Africa: Northern Cape Province**: Namaqualand, Richtersveld: Die Koei, 2–5.x.1991, M.W. Mansell (1 ♂,

FIGURE 10. *Bembecinus hyperocrus*: a – female clypeus in profile (arrow indicates the roundly angular portion), b – left side of female terga I and II, c – dorsal parts of male terga I and II in profile, d – male tergum VII.

PPRI); Naib or Boesmanland, between Springbok and Pella, Mus. Staff, x.1939 (2 ♀, 2 ♂, SAMC); Btw. Kamieskroon and Springbok, Namaqualand, Mus. Staff, x.1939 (1 ♀, SAMC); Skouerfontein, 28 17 Cc, 6.x.80, [V.] Whitehead (1 ♂, SAMC); Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve, 27.ix.1986, M. Struck (I ♂, AMGS); same locality, 15–21.x.1987, F.W. and S.K. Gess (3 ♀, 10 ♂, AMGS), same locality, 10–12.x.1988, F.W. and S.K. Gess (1 ♀, AMGS), same locality and dates, D.W. Gess (1 ♀, AMGS); Namaqualand, 70 km E Port Nolloth, 26.xi.1974, J.G. and B.L. Rozen (1 ♀, AMNH); Namaqualand, Anenous, 11–13.x.1988, F.W. and S.K. Gess (3 ♀, AMGS), same locality and dates, D.W. Gess (2 ♀, AMGS); Exteenfontein at 28°49.5′S 17°14.4′E, 9.x.2008, B.N. Danforth (1 ♂, CAS), on flowers of *Lebeckia*, Fabaceae; Namaqualand, Concordia, 21.xi.1990, R. Miller and L. Stange (1 ♀, UCDC); Namaqualand, 14 km N Concordia at 29°25.9′S 17°57.2′E, 15.x.2008, B.N. Danforth (1 ♀, CAS); Namaqualand, Farm Arkoep 6 km N Kamieskroon at 30°19′S 17°56′E, 1–2.x.1990, C.D. Eardley (1 ♂, PPRI); Calvinia, 2 Nov., T.D.A. Cockerell (1 ♀, BMNH), 11–16.xi.1931, J. Ogilvie (1 ♀, BMNH); Augustfontein (Calvinia), ix.1947, Museum Expedition [SAMC] (1 ♂, SAMC); Murraysburg District, xi.1935, Museum Staff [SAMC] (4 ♀, 1 ♂, SAMC). **Western Cape Province**: [Knersvlakte] Moedverloorn [Moedverloren Nature Reserve] Dorn [rivier] River (1 ♀, UCDC);Tankwa Karoo, Renoster River, xi.1952, Museum Expedition [SAMC] (2 ♀, SAMC); Matjesfontein, R.E. Turner, 1–6.xi.1928 (2 ♀, BMNH), 7–13.xi.1928 (1 ♀, BMNH), 14–27.xi.1928 (1 ♀, BMNH); Matjiesfontein, R.E. Turner, 1–6.xi.1928 (2 ♂, UCDC), 7–13.xi.1928, (1 ♀, SAMC ex NMBZ); Moordenaars Karoo, Lamerfontein, x.1952, Museum Expedition [SAMC] (4 ♀, 4 ♂, SAMC); Dikome, Merweville, Koup, x.1952, Museum Expedition [SAMC] (2 ♀, SAMC); Koup Siding, xi.1939, Museum Staff [SAMC] (1 ♀, SAMC); 18 m. E Touws River to Hondewater, xii.1962, S.A.M. [SAMC staff] (1 ♂, SAMC); Lammerkraal, Prince Albert District, ix.1947, Museum Expedition [SAMC] (1 ♂, SAMC); Prince Albert District, Tierberg, 26.i.-5.xii.1987, F.W., S.K. and R.W. Gess (2 ♀, AMGS); 31.x.1967, C. Jacot-Guillarmod (3 ♀, AMGS); Prince Albert District, Tierberg Research Station, 16.xi.1994, V. Mauss (1 ♀, 1 ♂, AMGS). **Eastern Cape Province**: Willowmore, xi.1912, Brauns (1 ♀, SAMC ex NMBZ).

**Geographical distribution**.— Known principally from the winter rainfall Succulent Karoo from southern Namibia southwards through Namaqualand in South Africa and from the southern Nama-Karoo in South Africa from the Moordenars Karoo in the west to Willowmore in the east (Fig. 24e).

**Floral associations**.— Visiting flowers of four families: Amaranthaceae (*Hermbstaedtia glauca* (Wendl. Reichb. Ex Steud.), Zygophyllaceae (*Zygophyllum prismatocarpum* E. Mey. ex Sond., Campanulaceae (*Wahlenbergia* sp. (label data, see Material Examined; S. Gess and F. Gess 2003, 2006), and Fabaceae (*Lebeckia*) (label data, see Material Examined).

**Nesting**.— Nesting in level, compacted, friable soil in the Goegap Reserve, near Springbok. Two nests were investigated (S. Gess). Burrows sloping, nest 87/88/61 not yet with a cell, nest 87/88/60 with a single sub-horizontal cell containing a larva and prey. Shaft diameter 5 mm, cell diameter 6 mm, depth of cell 55 mm. (F. Gess and S. Gess, field notes 87/88/60 and 87/88/61, AMSG).

**Prey**.— Cicadellidae (Homoptera), adults (5 specimens double mounted on pins labeled 87/88/60, AMSG).

### *Bembecinus inexspectatus* Pulawski, sp. nov.

Figures 3f, 11a, b.

**Name derivation**.— *Inexspectatus* is a Latin adjective meaning *unexpected*; with reference to the fact that the specimens became unexpectedly available to WJP at the very end of this study.

**Recognition**.— Like *hyperocrus* and *omaruru, inexspectatus* has erect setae on tergum I (although these setae are well defined only on the tergum's side), and subsidiary recognition features are: scape with erect setae along its entire length (except basally), gastral terga predominantly ferruginous, female hindtarsal arolium about 0.25 × length of inner claw. Both sexes differ from *hyperocrus* in having a yellow apical fascia on terga (which is lacking in *hyperocrus*), the male also by an all yellow clypeus (rather than all or partly black) and the absence of setae on most of tergum I and on tergum II dorsally (erect setae present in *hyperocrus*), although this may be a secondary loss due to abrasion. Unlike *omaruru*, the female of *inexspectatus* has the clypeus black basally (rather than all yellow), whereas the reverse is true for the males: the clypeus is all yellow in *inexspectatus*, and nearly all black in *omaruru*. Also, the minimum interocular distance of the female equals 3.2 × that between antennal scrobe and base of clypeus in *inexspectatus*, while 2.2 × in *omaruru*, the female clypeus of *inexspectatus* is roundly angulate near the base in profile (practically

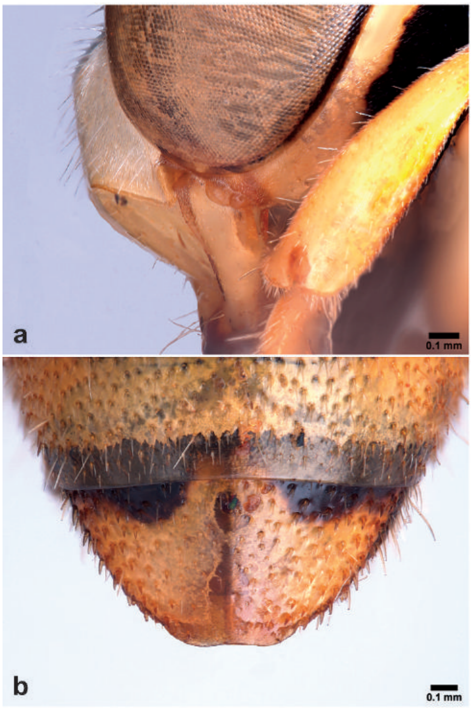

Figure 11. *Bembecinus inexspectatus*: a – female clypeus in profile, b – male tergum VII.

not angulate in *omaruru*), and male tergum VII is markedly more rounded in *inexspectatus* than it is in *omaruru* (compare Figs. 11b and 16).

**DESCRIPTION**.— Head black, with the following yellow: mandible except apex, labrum, clypeus (with black, basal spot in female), face below antenna, narrow strip along eye orbit up to level of midocellus, gena narrowly along orbit, scape, pedicel, and flagellomere I (all three black dorsally), remaining flagellum yellowish brown, brown dorsally; palpi brown. Thorax black with the following yellow: pronotal collar, pronotal lobe, narrow adlateral streak on scutum, tegula, triangular lateral spot on scutellum, posterior half of metanotum, and spot on mesopleuron (large in female, in male dorsoventrally elongate, its height equal 1.5 × of midocellar width). Propodeum black, with posterolateral margin yellow mesally. Gaster ferruginous, with pale yellow apical bands on terga; anterior declivity of tergum I black, expanded posteromesally in male. Legs yellow, posterior surface of forefemur black in male (except dorsally, ventrally, and apically). Wings hyaline, vein Sc+R dark brown, other veins light brown.

Scape covered with erect setae along its entire length (except basally). Setae of tergum II erect laterally (as in Fig. 10b).

♀.— Length about 9.1–9.3 mm. Ocular index 2.4–2.7. Minimum interocular distance equal to 3.2 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.1–1.2 × distance between posterior ocellus and eye margin. Clypeus roundly angulate near base in profile, its width at insertion of mandibles 1.8 × its midline. Labrum roundly triangular, its greatest width about 1.0 × midlength. Hindtarsal arolium as long as one quarter of inner claw.

♂.— Length about 11.2 mm. Ocular index 2.5. Minimum interocular distance equal to 2.3 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.6 × distance between posterior ocellus and eye margin. Width of clypeus at insertion of mandibles 1.6 × its midline. Labrum roundly triangular, its greatest width 1.1 × midlength. Apical flagellomere simple. Tergum VII obtusely rounded (Fig. 11b).

**MATERIAL EXAMINED**.— HOLOTYPE: ♀, **SOUTH AFRICA: Northern Cape Province**: Putsonderwater, October 1939, Mus. Staff [SAMC] (SAMC). PARATYPES: same data as holotype (1 ♂, SAMC; 1 ♀, CAS).

**GEOGRAPHICAL DISTRIBUTION**.— Known from one locality in the Nama-Karoo of the Northern Cape Province of South Africa (Fig. 24f).

**FLORAL ASSOCIATIONS**.— Unknown.

**NESTING**.— Unknown.

**PREY**.— Unknown.

### ***Bembecinus karasanus*** **F. Gess and Pulawski, sp. nov.**

Figures 4a, 12a, b.

**NAME DERIVATION**.— The name, a newly coined Neolatin adjective, is derived from the Nama word !Karas (meaning Quiver Tree, or *Aloe dichotoma* Masson) as incorporated in the town name, Karasburg, and in the mountains, the Groot Karasberge, which are situated within the triangle formed between the three localities, Karasburg, Keetmanshoop and Aroab, from which the Namibian specimens were obtained.

**RECOGNITION**.— *Bembecinus karasanus* differs from the other species of the *haplocerus* group in having the punctures of the labrum large, larger than those on the scutum. In the other species, the labrum punctures are fine, either smaller than those on the scutum (most specimens) or as large as those on the scutum.

**DESCRIPTION**.— Labrum with large punctures (larger than those on scutum), in female aver-

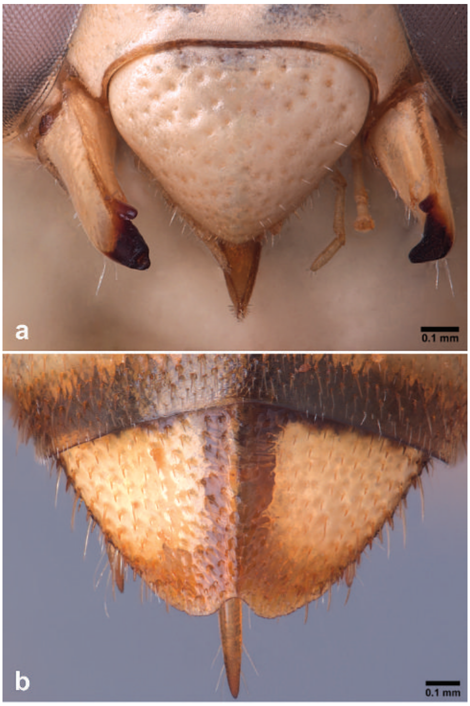

FIGURE 12. *Bembecinus karasanus:* a - female labrum, b – male tergum VII.

aging less than one diameter apart. Head black with the following yellow: mandible excepting apex, labrum, clypeus, face below antenna and narrowly up to midheight along orbit, spot on each side of frons below level of anterior ocellus in some females, spot between anterior and posterior ocellus (not reaching anterior ocellus in some specimens, absent in many males), in female spot behind posterior ocellus (in some specimens spots joining mesally, forming posteriorly curved band), gena narrowly above and widely below, stipes, galea, both pairs of palpi, scape, pedicel and flagellomere I ventrally; rest of antennae more or less ferruginous with dorsal side darker than ventral side. Thorax black with the following yellow: pronotum except black mesally (narrowly so in female, broadly in male), propleuron except brown anteriorly, scutum adlaterally and a pair of admedian longitudinal streaks (broad in female, narrow in male), tegula, scutellum except variably shaped basomedian area, metanotum except extreme base, mesopleuron except anterior, posterior and dorsal edges. Propodeum in female yellow with the following black: narrow basal band, spot on each side of enclosure (except basally), and in some specimens long streak extending above spiracle and continuing to side of gastropropodeal articulation; in male black with the following yellow: posterolateral margin, anterior half of lateral surface, and enclosure except basally (in some specimens only a pair of small spots on enclosure ventrally are yellow). Color of gaster: see below. Legs yellow or inner surface of mid- and hindfemora light ferruginous, also mid- and hindtarsomeres. Wings hyaline, Sc+R black, other veins brown.

Base and sides of clypeus, face below antennae and halfway up sides covered with inconspicuous, decumbent, silvery pubescence.

♀: Length 9.7–11.8 mm long (average of 14 = 10.4 mm; holotype 11.2 mm). Ocular index 2.2–2.3 (average of 12 = 2.3). Minimum interocular distance equal to 2.0–2.2 × that between antennal scrobe and base of clypeus (average of 3 = 2.1). Distance between posterior ocelli 1.4–1.5 × distance between posterior ocellus and eye margin (average of 12 = 1.5). Clypeus moderately convex, unevenly curved, its highest point close to its base, apical area flattened medially, sparsely and insignificantly punctured; its width at insertion of mandibles 1.7–1.8 × its midlength (average of 12 = 1.7). Labrum triangular, its greatest width 1.1 × midlength. Gaster mostly yellow except the following are whitish: preapical transverse bands (widened laterally on terga I-V), most of tergum VI and most of sterna; testaceous are: apical margins of terga I-VI; and black are: anterior declivity of tergum I ventrally and, in some specimens median, short streak on disk of tergum I and preapical spot on tergum VI.

♂: Length 10.5–11.0 mm (average of 4 = 10.75 mm). Ocular index 2.1–2.2 (average of 5 = 2.15). Minimum interocular distance equal to 2.1–2.3 × that between antennal scrobe and base of clypeus (average of 3 = 2.2). Distance between posterior ocelli 1.4–1.6× distance between posterior ocellus and eye margin (average of 4 = 1.5). Width of clypeus at insertion of mandibles 1.7 × its midline. Labrum triangular, its greatest width 1.2 × its midlength. Gaster mostly yellow or light brownish, terga I-III to I-V with whitish or yellow preapical fasciae, sterna whitish or yellow, apical fasciae of terga brown or light ferruginous, anterior declivity of tergum I black, extending into median streak on disk. Apical flagellomere simple. Tergum VII subtriangular, narrowly emarginated apically (Fig. 12b).

**Material examined**.— Holotype: ♀, **Namibia: !Karas Region**: Karasburg, 14.xii.1974, H.N. Empey (AMGS). Paratypes: **Namibia: !Karas Region**: Karasburg, 15.i.1975, H.N. Empey (4 ♀, AMGS); Aroab, 4.i.1975, H.N. Empey (1 ♀, AMGS); Keetmanshoop, 15.xii.1974, H.N. Empey (1 ♀, AMGS); 16 km S Rosh Pinah at 28°04′S 16°51′E, 15.x.2000, F.W. and S.K. Gess (2 ♀, AMHS, CAS). **South Africa: Northern Cape Province**: Vioolsdrif on Orange River, Namaqualand, 4–6.x.1966, F.W. Gess and W.H.R. Gess (2 ♂, SAMC); Goodhouse, xi.1936, Museum Staff [SAMC] (7 ♀, SAMC).

**Geographical distribution**.— Known from the southern Nama-Karoo of Namibia and the south bank of the Orange River, neighboring on Namibia (Fig. 25a).

**Floral associations**.— Unknown.

**Nesting**.— Unknown.

**Prey**.— Unknown.

### *Bembecinus mutabilis* (Arnold)

Figures 4b, 13a–d.

*Stizus mutabilis* Arnold, 1929:295, Figs 48, 48a and b, ♀, ♂. Lectotype: ♂, South Africa: Western Cape Province: Montagu (BMNH), designated by W. Pulawski: **present designation**.— Arnold, 1930:20 (in checklist of Afrotropical Sphecidae).— As *Bembecinus mutabilis*: R. Bohart and Menke, 1976:531 (new combination, in checklist of world Sphecidae); S. Gess, 1996:277, 280 (floral records); S. Gess and F. Gess, 2003:116 (floral records); Pulawski, 2014:24 (in catalog of world Sphecidae *sensu lato*).

*Bembecinus ruficaudus* R. Bohart, 1997:170, Fig. 6, ♀, ♂. Holotype: ♂, South Africa: Western Cape Province: Doorn River at Moedverloor, now Moedverloren Nature Reserve (UCDC), examined by W. Pulawski. **New synonymy by W. Pulawski**.— Pulawski, 2014:33 (in catalog of world Sphecidae *sensu lato*).

**Recognition**.— *Bembecinus mutabilis* has a gaster either largely ferruginous (tergum I black basally, several or all following terga all ferruginous or narrowly black basally) or (one female from Montague) with ferruginous apical fascia, but without yellow apical fasciae on terga, and with setae appressed on gastral tergum II. *B. hyperocrus* is similar, but *mutabilis* has the following: the face below the antenna and the clypeus are all yellow in most specimens (the clypeus is black basally in the single female from Upington), male flagellomere XI is markedly curved and excavated (Fig. 13b), male tergum VII is trapezoidal, with apical margin truncate, widely, shallowly emarginate mesally (Fig. 13d), and the ocular index is 2.68–2.92 in the female and 2.67–2.90 in the male. In *hyperocrus*, the setae of tergum II are erect (only laterally so in the female), the face below the antenna and the clypeus basally are black (the entire clypeus and labrum are black in some males), male flagellomere XI is simple (not curved and not excavated), male tergum VII is rounded with the apical margin convex and narrowly emarginate mesally (Fig. 10d), and the ocular index is 2.13–2.26 in the female and 2.08–2.27 in the male. Also similar is *inexspectatus*, which has pale yellow apical fasciae on gastral terga and the apical flagellomere of the male simple (not curved and not emarginate); the apical flagellomere is also simple in the male of *namaquensis* (the female is unknown).

**Lectotype Selection**.— Arnold described *mutabilis* from one female and three males. He labeled the female and one male as Types, and the remaining two males as paratypes.W. Pulawski has designated the male labeled Type as a lectotype, and the female as a paralectotype.

**Justification of new synonymy.**— Both the holotype male and the female paratypes of *Bembecinus ruficaudus* are identical to *mutabilis*, and the former name is clearly a junior synonym of the later. It should be noted that Bohart's (1979) illustration 6c of the apical flagellomere of the male *ruficaudus* is misleading, as it does not show its curvature. In reality, this flagellomere is markedly more curved and excavated in the holotype than represented, just as in the other males of *mutabilis*.

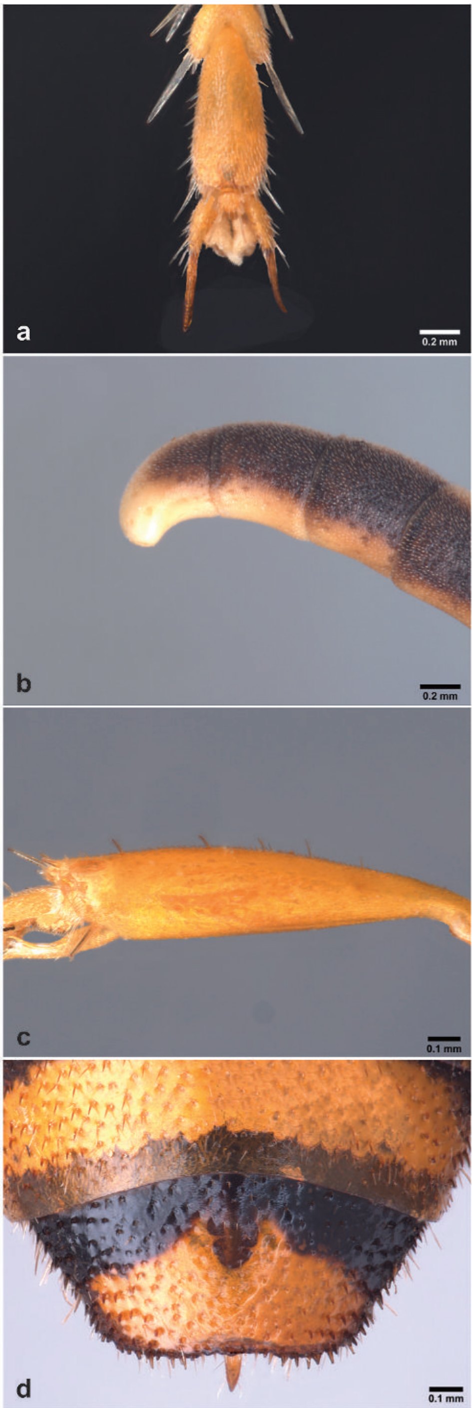

Figure 13. *Bembecinus mutabilis*: a – apical hindtarsomere of female showing length of arolium, b – male apical flagellomeres, c – male foretibia in profile, d – male tergum VII.

**Material examined.**— South Africa: **Northern Cape Province**: Naib or Boesmanland, between Springbok and Pella, Mus. Staff, x.1939 (1 ♀, SAMC); Namaqualand, 67 km E Port Nolloth, 17.x.1972, J.G. Rozen and C. Thompson (2 ♀, AMNH); Namaqualand, Anenous, 11–13.x.1988, F.W. and S.K. Gess (26 ♀, 2 ♂, AMGS), same locality and dates, D.W. Gess (22 ♀, 1 ♂, AMGS), same locality, 12.x.1989, F.W. and S.K. Gess (2 ♀, AMGS); 10 km W Steinkopf [Anenous], 10.xi.19960, R. Miler (1 ♀, UCDC, paratype of *Bembecinus ruficaudus*); Namaqualand, Eksteenfontein, 2817CD, 9.x.1980, V. Whitehead (1 ♂, SAMC); Namaqualand, 42 km S Eksteenfontein at 29°06.8′S 17°26.6′E, 9.x.2008, B.N. Danforth (1 ♀, CAS), on flowers of *Grielum*, Neuradaceae; 53 km S Vioolsdrift at 29°10′S 17°50′E, 12.x.2000, F.W. and S.K. Gess (1 ♀, AMGS); Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve, 15–21.x.1987, F.W. and S.K. Gess (1 ♀, AMGS), same locality, 10–12.x.1988, D.W. Gess (2 ♂, AMGS), same locality, 10–11.x.1989, D.W. Gess (7 ♀, AMGS); Springbok, Voelklip, 2 and 7.x.1994, F.W. and S.K. Gess (3 ♀, AMGS); Kamieskroon, Bakleikraal, 9–11.x.1994, F.W. and S.K. Gess (1 ♂, AMGS); Moedverloren Nature Reserve, Knersvlakte, 8.x.1975, R.M. Bohart (1 ♂, UCDC, holotype of *Bembecinus ruficaudus*); Augustfontein (Calvinia), ix.1947, Museum Expedition [SAMC] (1 ♀, SAMC); Niewoudtville, 18–22.xi.1931, J. Ogilvie (2 ♀, BMNH); Van Rhyn's Pass, 11–21.xi.1931, J. Ogilvie (1 ♀, BMNH).**Western Cape Province**: Doringboos NE Clanwilliam, 11.x.1999, M. Halada (10 ♀, OÖLM); Bulshoek, Klaver-Clanwilliam, x.1950, Museum Expedition (8 ♀, 3 ♂, SAMC); Pakhuis Pass, 7.x.1975 (2 ♀, UCDC, paratypes of *Bembecinus ruficaudus*); 12 miles [19.31 km] N

Clanwilliam, 4.xi.1966, J.G. Rozen (1 ♂, AMNH); Clanwilliam, 20.x.1968, J.G. Rozen and E. Martinez (1 ♂, AMNH); 5 km W Clanwilliam on road to Graafwater, 12.x.1987, F.W. and S.K. Gess (5 ♂, AMGS), same locality, 5–6.x.1988, F.W. and S.K. Gess (1 ♀, AMGS), same locality and dates, D.W. Gess (4 ♂, AMGS); 11 km W Clanwilliam on road to Graafwater, 2–8.x.1990, F.W. and S.K. Gess (1 ♀, 3 ♂, AMGS), 1 ♂ on flowers of *Helichrysum hebelepis* DC., Asteraceae; Clanwilliam Dam , 3–7.x.1988, F.W. and S.K. Gess (6 ♀, 6 ♂, AMGS), 1 ♂ on flowers of *Limeum africanum*, Aizoaceae; same locality and dates, D.W. Gess (3 ♀, 5 ♂, AMGS); E Clanwilliam, 10.x.1999, M. Halada (6 ♀, 1 ♂, OÖLM); Clanwilliam Dam, Caleta Cove, 19–20.x.1989, F.W. and S.K. Gess (1 ♀, AMGS), same locality and dates, D.W. Gess (1 ♀, AMGS); 4 miles [6.44 km] S Clanwilliam on old road to Citrusdal, 6.x.1991, D.W. Gess (1 ♂, AMGS); 10 km S Clanwilliam at 32°13’39″S 18°50′50″E, 5–25.x.2004, M.E. Irwin, F.D. Parker, M. Hauser (3 ♀, 2 ♂, ZMB; 16.5 km S Clanwilliam on old road to Citrusdal, 13.x.1990, F.W. and S.K. Gess (9 ♀, 11 ♂, AMGS), 2 ♀ and 1 ♂ on flowers of *Athanasia trifurcata* (Linnaeus) Linnaeus, Asteraceae; 15 km S Clanwilliam on old road to Citrusdal, 14.xi.1992, D.W. Gess (1 ♀, AMGS); 19 km S Clanwilliam on old road to Citrusdal, 14.xi.1992, D.W. Gess (3 ♀, AMGS); 20 km S Clanwilliam on old road to Citrusdal, 15.x.1994, F.W. and S.K. Gess (1 ♀, AMGS); Olifants River between Citrusdal and Clanwilliam, x-xi.1931, Museum Staff [SAMC] (16 ♀, 16 ♂, SAMC); 20 km N Citrusdal, 27.x.1999, M. Halada (1 ♀, CAS) (4 ♀, 1 ♂, OÖLM); 8 miles [12.88 km] N Citrusdal, ix.1961, SAM (1 ♂, SAMC); Citrusdal District, xi.1948, Museum Expedition [SAMC] (3 ♂, SAMC); Groenkloof, between Clanwilliam and Algeria, 19.x.1989, D.W. Gess (1 ♂, AMGS); Paleisheuwel, xi.1948, Museum Expedition [SAMC] (4 ♀**,** SAMC), 6.x.1990, F.W. and S.K. Gess (2 ♂, AMGS); Het Kruis, x.1947, Museum Expedition [SAMC] (2 ♂, SAMC); 25 km E Velddrif, 23.x.1972, J.G. Rozen *et al*. (1 ♂, AMNH); Upper Sources, Olifants River, Ceres, xii.1949, Museum Expedition [SAMC] (1 ♀, SAMC); 43 km ENE of Ceres on road to Sutherland, 2–3.xii.1989, F.W. and S.K. Gess (1 ♀, AMGS); Montagu, 1–21.x.1924, R.E. Turner (2 ♀, 6 ♂, BMNH, including lectotype, paralectotype, and 2 paratypes), same locality and dates, R.E. Turner (labeled *Stizus mutabilis* Arn., det. R.H.R. Stevenson and clearly the same material from which the types were drawn) (2 ♀, SAMC ex ZMHB); 18 miles [28.97 km] E Touws River [on road] to Hondewater, xii.1962, SAM [staff] (2 ♀**,** SAMC); Laingsburg at 33°12′S 20°51′E, 25.xii.1996, W.J. Pulawski (1 ♀, CAS); Koup Siding, Laingsburg, xi.1939, Museum Staff [SAMC] (2 ♀, SAMC); Moordenaars Karoo, Swanepoel, x.1952, Museum Expedition [SAMC] (2 ♂, SAMC); Prince Albert District, Tierberg, 26.xi.-5.xii.1987, F.W., S.K. and R.W. Gess (1 ♀, AMGS); 60 km N Cape Town, 9.xi. 1999, M. Halada (2 ♀, 1 ♂, OÖLM). **Eastern Cape Province**: Willowmore, 12.i.1965, H. Empey (1 ♀, AMGS), 18.x.1970, H. and M. Townes (1 ♀, AEI), 5.x.1971, C. Jacot-Guillarmod (1 ♀, AMGS), same locality, 7.x.1971, F.W. Gess (1 ♂, AMGS); Waterford, 29.x.1967, C. Jacot-Guillarmod (1 ♀, AMGS); Rietbron, 11.i.1965, H. Empey (1 ♀, AMGS).

**GEOGRAPHICAL DISTRIBUTION**.— Known only from South Africa, widely distributed from the winter rainfall Succulent Karoo of Namaqualand, south through the Olifant’s River Valley and eastwards to Willowmore in the Nama-Karoo (Fig.25b).

**FLORAL ASSOCIATIONS**.— Visiting flowers of four plant families: Asteraceae (*Helichrysum hebelepis* DC. and *Athanasia trifurcata* (Linnaeus) Linnaeus, Amaranthaceae (*Hermbstaedia glauca* (Wendl.) Reichb. Ex Steud.), Aizoaceae (non-Mesembryanthema, *Limeum africanum* Linnaeus) (label data, see Material Examined; S. Gess and F. Gess 2003), and Neuradaceae (*Grielum*) (label data, see Material Examined).

**NESTING**.— Nesting in friable soil of a stabilized dune mole rat ‘hillock’ in an area of dry Fynbos to the west of Clanwilliam. One nest was investigated (S. Gess). Burrow entrance was in sloping side of ‘hillock’, burrow sloping downwards for 84 mm, shaft ending in sub-horizontal cell, diameter of entrance and shaft 5 mm, diameter of cell 7.5 mm, length of cell 25 mm, depth of cell 56 mm. Female opens and closes the burrow on entering and leaving the nest. Cell containing larva and prey (F. Gess and S. Gess, field notes 90/91/124, AMGS).

Prey.— Cicadellidae (Homoptera) nymphs and adults from nest 90/91/124 (8 specimens in gelatin capsule on same pin as female 90/91/124, AMGS).

### *Bembecinus namaquensis* Pulawski, sp. nov.

Figures 4c,14a, b.

Name derivation.— The name, *namaquensis*, a newly coined Neolatin adjective, is derived from the Nama people of South Africa, Namibia and Botswana, and also from Namaqualand of South Africa, where the holotype was collected.

Recognition.— *Bembecinus namaquensis* has a ferruginous gaster (basal terga black basally), without pale yellow apical fasciae, a character shared with *mutabilis*.The female is unknown, but the male differs from *mutabilis* in having the apical flagellomere simple (not curved and not emarginate), and from *gariepensis* and *rhopaloceroides* in lacking yellow, apical fasciae on the terga and in having the foretibia not incrassate (incrassate in the lateral view in the other two species).

Description.— Head black, with the following yellow: mandible except apex, labrum, clypeus, face below antenna and narrowly up to level of midocellus along orbit, gena narrowly along orbit, both pairs of palpi, scape and pedicel ventrally (black dorsally), flagellum ventrally (almost black dorsally). Thorax black with the following yellow: pronotal collar, pronotal side and ventral part of right pronotal lobe, narrow adlateral streak on scutum, tegula, triangular lateral spot on scutellum, posterior half of metanotum, and small spot on mesopleuron (spot size less than midocellus). Propodeum black, with posterolateral margin yellow mesally. Gaster ferruginous, tergum I black in about basal half, black area widened mesally; terga II and III with narrow basal band. Legs yellow, with the following black: coxae posteriorly, foretrochanter dorsally and posteriorly, mid- and hindtrochanters dorsally, mid- and hindfemora dorsally. Wings hyaline, vein Sc+R black, other veins brown.

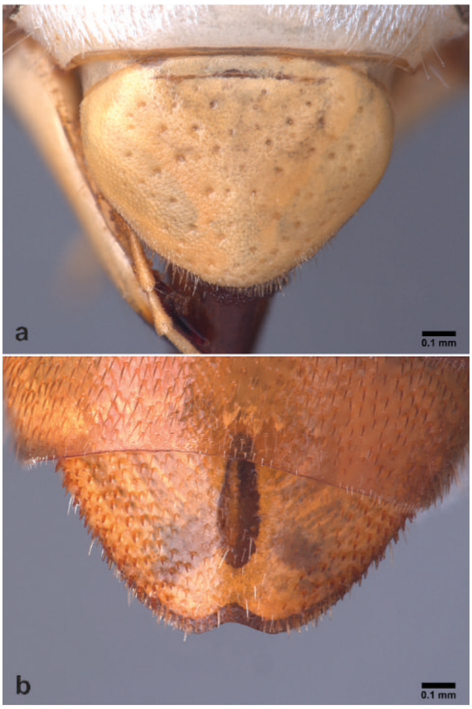

Figure 14. *Bembecinus namaquensis*: a – male labrum, b – tergum VII of male.

♂: Length 11.8 mm. Ocular index 2.1. Minimum interocular distance equal to 2.1 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.8 × distance between posterior ocellus and eye margin. Width of clypeus at insertion of mandibles 1.6 × its midline, its apical area flattened, asetose. Labrum roundly triangular (Fig. 14a), its greatest width 1.25 × its midlength. Apical flagellomere simple. Tergum VII rounded, shallowly emarginate apically (Fig. 14b).

Material examined.— Holotype: ♂, **South Africa: Northern Cape Province**: 23 km S Alexander Bay at 28°46′S 16°37′E, 11.x.2000, F.W. and S.K. Gess (AMGS). Paratypes: **South**

**AFRICA: Northern Cape Province**: Richtersveld W Brandkaros at 28°29′S 16°40′E, 15.ix.1996, F.W. Gess, S.K. Gess, and R.W. Gess (1 ♂, AMGS; 1 ♂, CAS).

**GEOGRAPHICAL DISTRIBUTION.**— Known from two localities in the arid Succulent Karoo of northwestern South Africa (Fig. 25c).

**SNAIL SHELL ASSOCIATION.**— The two specimens from Brandkaros were collected from empty shells of the snail *Trigonephrus* sp., Dorcasiidae, in which they were found sheltering. In windswept desertic areas snail shells provide shelter for various species of aculeates. Furthermore, some species use shells, sand-filled or empty, as secure nesting sites (F. Gess and S. Gess 1999; S. Gess and F. Gess 2008).

**FLORAL ASSOCIATIONS.**— Unknown.

**NESTING.**— Unknown.

**PREY.**— Unknown.

### ***Bembecinus namibius*** **Pulawski, sp. nov.**

Figures 4d, 15a, b.

**NAME DERIVATION.**— The name, a newly coined Neolatin adjective, is derived from the geographic name *Namib* and the Greek word *βιος*, *life*; with the reference of the species occurrence in the Namib Desert.

**RECOGNITION.**— *Bembecinus namibius* has erect setae on the whole length of the scape (except basally), a character shared with *hyperocrus* and *omaruru*. In *namibius*, however, the terga are yellowish greenish (black basally), the setae of tergum II are appressed, the clypeus is yellow and evenly rounded in profile. In *hyperocrus* and *omaruru*, the terga are ferruginous (black basally, with pale yellow apical fasciae in *omaruru*), the setae of tergum II are erect (short dorsally, distinct laterally in the female), the male clypeus is black (at least in the basal half), and in *hyperocrus* the female clypeus in profile is roundly angulate basally.

FIGURE 15. *Bembecinus namibius*: tergum VII of male.

**DESCRIPTION.**— Head black, with the following yellow: mandible except apex, labrum, clypeus, face below antennae and narrowly up to midheight along orbit in female, up to level of midocellus in male, gena narrowly, in female small spot between midocellus and hindocellus, scape, pedicel (black dorsally), flagellum ventrally (black dorsally). Thorax black with the following yellow: pronotal collar, scutum laterally and with pair of short admedian streaks (admedian streak absent in one male), tegula, triangular lateral spot on scutellum, metanotum except basally, and mesopleuron largely (with only small spot yellow in one male). Propodeum black, with enclosure along lateral margin and lateral margin yellow. Gastral terga yellowish-greenish, black basally (black on tergum I about as long as yellowish part, gradually diminishing on following terga). Femora, tibiae, and tarsi pale yellow, with the following black: forefemur basodorsally, mid- and hindfemora dorsally (except apex yellow) and in the female also anterior surface basally. Wings hyaline, vein Sc+R black, other veins brown.

Scape covered with erect setae along its entire length (except basally).

♀: Length 8.8–10.2 mm. Ocular index 2.7–2.9. Minimum interocular distance equal to 2.1–2.2 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.4 × distance between posterior ocellus and eye margin. Clypeus slightly, evenly convex in profile, narrowly asetose and shiny along free margin mesally; its width at insertion of mandibles1.5–1.6 × its midlength. Labrum roundly triangular, its greatest width 1.0–1.3 × midlength.

♂: Length 9.2–10.0 mm. Ocular index 2.5–2.6. Minimum interocular distance equal to 1.8–1.9 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.5–1.6 × distance between posterior ocellus and eye margin. Width of clypeus at insertion of mandibles 1.4–1.5 × its midline. Labrum roundly triangular, its greatest width 1.1–1.2 × midlength. Apical flagellomere simple. Tergum VII subtrapezoidal (Fig.15b).

**Material examined**.— Holotype: ♀, **Namibia: !Karas Region**: Klinghardtberge (= Klinghardt Mountains, Sperrgebiet, a National Park since 2004), 5.ix.1980, V.B. Whitehead (AMGS). Paratypes: same locality and collector, 3.iv.1980 (1 ♀, CAS), 5.ix.1980 (1 ♂, AMGS; 1 ♂, CAS).

**Geographical distribution**.— Known from a single locality in the arid Succulent Karoo of the southern Namib Desert, Namibia (Fig. 25d).

**Floral associations**.— Unknown.

**Nesting**.— Unknown.

**Prey**.— Unknown.

### *Bembecinus omaruru* Pulawski, sp. nov.

Figures 4e, 16.

**Name derivation**.— Named after the Omaruru River, near which the holotype was collected; a noun in apposition to the generic name.

**Recognition**.— Like *hyperocrus* and *inexspectatus*, *omaruru* has erect setae on tergum II, although in the female these setae are short dorsally and distinct only laterally (as in Fig. 10c). The males of both *hyperocrus* and *omaruru* have the clypeus, supraclypeal area, and the frons all black (in *inexspectatus*, the clypeus, supraclypeal area, and stripes along the orbits are pale yellow). In *hyperocrus*, however, the gastral terga are ferruginous and have no pale yellow apical fasciae, whereas in *omaruru* the terga are either ferruginous or golden tan, with pale yellow apical fasciae (the fasciae are ill defined in golden tan specimens); in the female of *omaruru*, the clypeus is all yellow and practically not angulate in profile (in *inexspectatus* and *hyperocrus*, it is black basally, and roundly angulate in profile); in addition, in the female of *omaruru,* the minimum interocular distance is equal to 2.2 × that between antennal scrobe and base of clypeus, while 3.2 × in *inexspectatus*. In the male of *omaruru*, the clypeus and the frons ventrally of the antennal socket have no dense, appressed vestiture and the integument is thus easily visible (in *hyperocrus* the clypeus and the frons ventrally of the antennal socket are covered with dense, appressed vestiture, partly covering integument). The scape covered with erect setae along its entire length (except basally) is a subsidiary recognition feature of this species.

Figure 16. *Bembecinus omaruru*: tergum VII of male.

**Description**.— Head black, with the following yellow: mandible except apex, labrum, narrow stripe on gena adjacent to orbit, and in the female also clypeus, face below antennae and narrowly along orbit up to about one third of frons height, scape, pedicel, flagellomeres I and II (remaining flagellomeres yellowish brown, apical flagellomeres dark dorsally); in male, narrow stripe along clypeus free margin yellow, scape and pedicel yellow ventrally, black dorsally, flagellum yellow. Thorax black, with the following yellow: pronotal collar, pronotal lobe, scutum laterally, tegula, triangular lateral spot on scutellum, metanotum except basally, in female also pair of short admedian streaks and mesopleuron anteriorly. Propodeum black, with lateral margin yellow. Gastral terga either ferruginous or golden tan, with apical pale yellow fasciae (fasciae ill defined in golden tan specimens), basal declivity of tergum I black, black extending mesally on horizontal part, tergum II and in male also tergum III narrowly black basally. Coxae black basally, yellow apically; trochanters yellow ventrally, black dorsally; femora yellow, black basodorsally; tibiae and tarsi yellow. Wings hyaline, vein Sc+R black, other veins brown.

Scape covered with erect setae along its entire length (except basally). Setae of tergum II erect, in female short dorsally, distinct laterally (as in Fig. 10c). Hindtarsal arolium as long as one quarter of hindtarsal claw.

♀: Length 10.3–12.8 mm. Ocular index 2.3. Minimum interocular distance equal to 2.2 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 1.5 × distance between posterior ocellus and eye margin. Width of clypeus at insertion of mandibles 1.7 × its midline. Labrum roundly triangular, its greatest width 1.0–1.3 × midlength.

♂: Length 11.4–15.5 mm. Ocular index 2.1. Minimum interocular distance equal to 2.4 × that between antennal scrobe and base of clypeus. Distance between posterior ocelli 2.0 × distance between posterior ocellus and eye margin. Width of clypeus at insertion of mandibles 1.6 × its midline. Labrum roundly triangular, its greatest width 1.3 × midlength. Apical flagellomere simple. Tergum VII subtriangular (Fig. 16).

**MATERIAL EXAMINED.**— HOLOTYPE: ♀, **NAMIBIA: Erongo Region**: 20 km NE Hentiesbaai at 21°58′S 14°22′E, 10.xii.1996, W.J. Pulawski (CAS). PARATYPES: **NAMIBIA: ERONGO REGION**: 20 km NE Hentiesbaai at 21°58′S 14°22′E, 10.xii.1996, W.J. Pulawski (1 ♂, CAS); **!Karas Region**: Aus, xii.1929, R.E. Turner (1 ♀, 1 ♂, BMNH).

**GEOGRAPHICAL DISTRIBUTION.**— Known from two widely separated localities in Namibia: one associated with the drainage channel of the Omaruru River in the northern Namib Desert and the other from the eastern edge of the northern limit of the winter rainfall southern Namib (Fig. 25e).

**FLORAL ASSOCIATIONS.**— Unknown.

**NESTING.**— Unknown.

**PREY.**— Unknown.

### *Bembecinus pakhuisae* R. Bohart

Figures 4f, 17a-c.

*Bembecinus pakhuisae* R. Bohart, 1997:168, ♀ ♂. Holotype: ♂, SouthAfrica: Western Cape Province: Pakhuis Pass (UCDC), examined by W. Pulawski.— S. Gess and F. Gess, 2003:116 (floral records), 2014:210 (nest situation); Pulawski, 2014:26 (in catalog of world Sphecidae *sensu lato*).

**RECOGNITION.**— *Bembecinus pakhuisae* has the scutum all black mesally, an all black mesopleuron, and the gastral terga black with yellow apical fasciae, without ferruginous gastral terga (in some males, yellow tergal fasciae may occupy most of tergal length). The female can be recognized by its all or partly black clypeus except for a narrow yellow stripe basally (unlike that of *hyperocrus* in which the clypeus has no basal yellow stripe and, in addition, the terga are ferruginous). In the male, the apical flagellomere is curved and excavated (Fig. 17b), but markedly less so than in *damarensis* and *mutabilis* (see Figs 6c and 13b). For differences with *zebratus*, see the latter species.

**MATERIAL EXAMINED.**— **SOUTH AFRICA: Northern Cape Province**: Namaqualand: Richtersveld National Park, Koeroegabvlakte at 28°11′S 17°03′E, 3.x.1995, F.W., S.K. and R.W. Gess (5 ♀, 6 ♂, AMGS), same locality, 17–21 and 24.ix.1995, F.W., S.K. and R.W. Gess (2 ♂ on deep pink

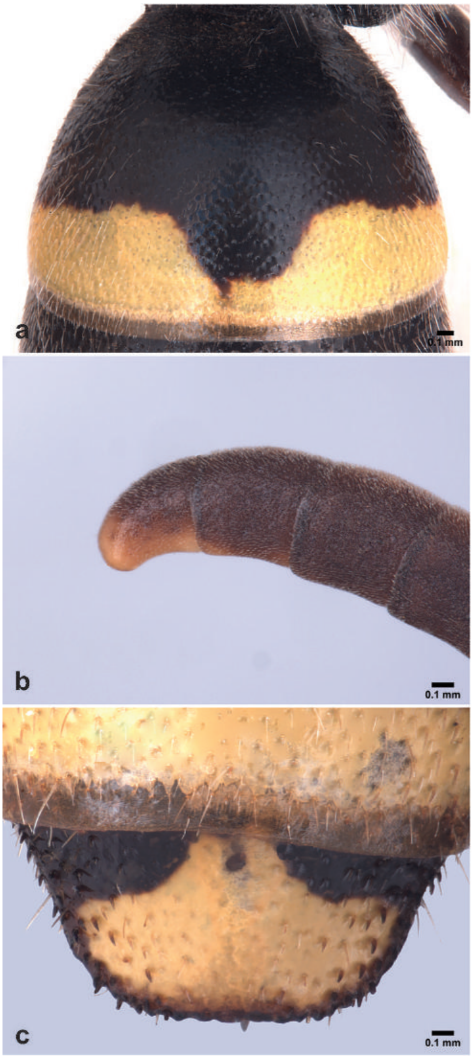

FIGURE 17. *Bembecinus pakhuisae*: a – female tergum I showing color pattern, b – apical flgellomeres of male, c – male tergum VII.

flowers of *Hermbstaedtia glauca* (Wendl.) Reichb. ex Steudl., Amaranthaceae) (7 ♀, 9 ♂, AMGS), same locality, 6.ix.1996, F.W., S.K. and R.W. Gess (1 ♀, 21 ♂, AMGS); Bloukrans Farm near Springbok at 29°43′S 17°55′E, 7.x.1974, R.H. Watmough (7 ♀, 2 ♂, PPRI); [Springbok], Hester Malan [now Geogap] Nature Reserve at 29.17Db [Degree Reference System (Leistner and Morris 1976) = 29°30′–45′S 17°35′–49′E], M. Struck, 4.x.1987 (1 ♀, PPRI) and 15–18.x.1987 (1 ♂, PPRI); Springbok, Hester Malan [now Goegap] Nature Reserve, 17.ix.1983, V. B. Whitehead (1 ♂, SAMC), same locality, 4.ix.1986, M. Struck (2 ♂, AMGS), same locality, 5.ix.1986, M. Struck (I ♀, AMGS), same locality, 20.x.1986, M. Struck (one stylopized) (2 ♀, AMGS), same locality, 17.xi.1986, M. Struck (1 ♀, AMGS), same locality, 10.x.1987, M. Struck (1 ♀, 1 ♂, AMGS), same locality, 31.x.1987, M. Struck (1 ♂, AMGS), same locality, 15–21.x.1987, F.W. and S.K. Gess (1 ♀ stylopized, 1 ♀ from nest, prey in gelatin capsule on separate pin, Issidae (Homoptera), adults and nymphs) (9 ♀, 9 ♂, AMGS), same locality, 10–12.x.1988, F.W. Gess and S.K. Gess (1 ♀ stylopized) (7 ♀, 5 ♂, AMGS), same locality and dates, D.W. Gess (3 ♀ stylopized) (23 ♀, 16 ♂, AMGS), same locality, 10–11.x.1989, F.W. Gess and S.K. Gess (2 ♀ stylopized) (8 ♀, 13 ♂, AMGS), same locality and dates, D.W. Gess (I ♀ stylopized) (2 ♀, 12 ♂, AMGS); Anenous, 12.x.1989, F.W. and S.K. Gess (1♀, AMGS); Nababeep, 12–13.x.1089, F.W. and S.K. Gess (1 ♂, AMGS); W end of Wildeperdehoek Pass, 14.x.1989, F.W.and S.K. Gess (1 ♂, AMGS); Mesklip, 1.x.1985, F.W. and S.K. Gess (1 ♂, AMGS); between Kamieskroon and Springbok, x.1939, Mus. Staff (2 ♂, SAMC); Farm Arkoep 6 km N Kamieskroon at 30°19′S 17°56′E, 1–2.x.1990, C.D. Eardley (6 ♀, 1 ♂, PPRI); Farm Dassiefontein near Kamieskroon at 30°09’ S 17°59′E, 1.x.1990, C.D. Eardley (2 ♂, PPRI); Bowesdorp, ix.1941, Museum Staff [SAMC] (9 ♂, SAMC); Kamieskroon, ix.1930, Museum Staff [SAMC] (5 ♀, 7 ♂, SAMC); Garies, 27.ix.1970, H. and M. Townes (2 ♂, AEI), same locality, 30.ix.1970, H. and M. Townes (1 ♂, AEI); 15 km N the on road to Loriesfontein, 3–8.x.1989, D.W. Gess (1 ♂, AMGS); Augustfontein (Calvinia), ix.1947, Museum Exedition [SAMC] (1 ♀, 1 ♂, SAMC); Niewoudville Flower Reserve at 31°22′18.4″S 19°08′58.2″E, 26.ix.2006, K. Timmermann (1 ♀, BMNH). **Western Cape Province**: Pakhuis Pass, 7.x.1975, R.M. Bohart (23 ♀, 40 ♂, UCDC, holotype and paratypes of *Bembecinus pakhuisae*); E Pakhuis Pass, ix.1947, Museum Expedition [SAMC] (1 ♂, SAMC); 5 km W Clanwilliam on road to Graafwater, 12.x.1987, F.W. and S.K. Gess (2 ♂, AMGS); Clanwilliam Dam, 3–7.x.1988, D.W. Gess (3 ♂, AMGS); Clanwilliam Dam, Caleta Cove, 19–20.x.1989, F.W. and S.K. Gess (on flowers of *Athanasia trifurcata* (Linnaeus) Linnaeus, Asteraceae) (1 ♀, AMGS); Moordenaars Karoo, Lammerfontein, x.1952, Museum Expedition [SAMC] (1 ♂, SAMC).

**GEOGRAPHICAL DISTRIBUTION**.— Known from the winter rainfall Succulent Karoo from the Richtersveld, Namaqualand south through Namaqualand and the Olifant's River Valley, east into the Cederberg and west into the sandveld, and from the Moordenaars Karoo (Fig. 25f).

**FLORAL ASSOCIATIONS**.— Visiting flowers of two families: Asteraceae (*Athanasia trifurcata* (Linnaeus) Linnaeus) (label data, see Material Examined; S. Gess and F. Gess 2003) and Amaranthaceae (*Hermbstaedtia glauca* (Wendl.) Reichb. ex Steudl.) (label data, see Material Examined).

**NESTING**.— Nesting in friable soil in the sides of runoff channels in Goegap Reserve, near Springbok. Six nests were investigated (S. Gess). Burrows sloping, with single sub-horizontal cell, angle of slope varied between nests, cell leaves shaft at an angle. Diameter of shaft 5.0–5.5 mm, diameter of cell 8 mm, length of cell 25 mm, cell depths 35–55 mm. Tumulus of excavated sand 20 mm from entrance, 45 mm long, 25 mm across. On entering and leaving the nest female opens and closes burrow. Cell of nest 87/88/20 provisioned. In cell of completed nest 87/88/23 cocoon, shaft filled with sand. (F. Gess and S. Gess, field notes 87/88/20–25, AMGS).

**PREY**.— Issidae (Homoptera), nymphs and adults (17 specimens in gelatin capsule, pinned with same data as nest builder 87/88/20, AMGS).

### *Bembecinus quadristrigatus* Arnold

Figures 5a, 18a-d.

*Stizus quadristrigatus* Arnold, 1929:297, Figs 49 and 49a, ♀. Holotype: ♀, Namibia: Kunene Region Kamanyab [= Kamanjab] (SAMC), photographs examined by W. Pulawski.— Arnold, 1930:20 (in checklist of Afrotropical Sphecidae).— As *Bembecinus quadristrigatus* (Arnold): R. Bohart and Menke, 1976:532 (new combination, in checklist of world Sphecidae); S. Gess and F. Gess, 2003:117 (floral records); Pulawski, 2014:29 (in catalog of world Sphecidae *sensu lato*).

**RECOGNITION**.— *Bembecinus quadristrigatus* has the terga yellow with black, but without ferruginous. It has the scutum with a pair of admedian yellow stripes extending through most of scutum length, and the interocellar area yellow between midocellus and hindocellus. Unlike *gilvus*, the lower gena of *quadristrigatus* has a row of erect setae along the hypostomal carina and the lower metapleuron is microareolate (rather than closely, microscopically punctate). In the female, the labrum is unsculptured between the punctures, at least along midline (microscopically reticulate between the punctures in *gilvus*), and the forebasitarsus is broader than in that species (compare Figs18a and 8a).

**VARIATION**.— *Bembecinus quadristrigatus* has two color forms, apparently identical morphologically, both of which occur in Namibia, and one in Angola and South Africa. In the first (including the type of *quadristrigatus*), the metapleuron is all black, and tergum II has a median, subrectangular black mark that is rather well differentiated from the black, basal fascia and that extends beyond the tergal midlength. This form occurs in Namibia, in the Okahandja, Omaruru, Otjiwarongo, and Outjo areas. In the second form, known from Namibia, from the Aus, Karibib, Khorixas, and Usakos areas, and also from the Northern Cape Province of South Africa and from Angola, the metapleuron is all (most specimens) or partly yellow, and the black area on tergum II is (most specimens) reduced to a narrow, basalfascia, or the fascia is semicircularly broadened, also extending beyond the tergal midlength.

**MATERIAL EXAMINED**.— **NAMIBIA** (typical form)**: Kunene Region**: Kamanjab (Arnold, 1929); Khorixas, 4.iii.1990, W.J. Pulawski (1 ♀, CAS); 38 km W Khorixas, 4.iii.1990, W.J.

Pulawski (1 ♀, CAS); **Erongo Region**: Omaruru/Usakos at 21°41′S 15°59′E, 26.iv.2002, F.W. and S.K. Gess (1 ♀, AMGS); 30k S Omaruru on road to Karibib, 21°41′S 15°59′E, 24.iii.1997, F.W. and S.K. Gess (4 ♂, AMGS), visiting deep pink flowers of *Hermbstaedtia odorata* (Burch.) T. Cooke, Acanthaceae. **Angola** (yellow form)**:** Pedive ca 36 mi. E Porto Alexandre, 24–27.vi. 1954, J. Balfour-Browne (8 ♀, BMNH). **Namibia** (yellow form)**: Otjozondjupa Region**: Leeu River 9 km W Okahandja at 21°58′S 16°50′E, 13.ii.1996, W.J. Pulawski (1 ♀, 1 ♂, CAS); 70 km N Okahandja 16.iii.1990, W.J. Pulawski (1 ♀, CAS); Otjiwarongo, 1.i.1975, Empey (1 ♂, AMGS); 44 km SW Otjiwarongo at 20°37′S 16°22′E, 4.iii.1996, W.J. Pulawski (1 ♀, CAS); 3 km NE Kalkfeld, 2.iii.1990, W.J. Pulawski (1 ♀, CAS); 25 km NE Kalkfeld at 20°41′S 16°18′E, 27.ii.1996, W.J. Pulawski (2 ♀, CAS). **Erongo Region**: western end of Grootberg Pass at 19°47′S 14°17′E, 19.iii.2004, F.W. and S.K. Gess (1 ♂, AMGS), visiting flowers of *Emelia mariothina* (O. Hoffm.) C. Jeffrey, Asteraceae; 7 km N Palmwag at 19°51′S 13°54′E 26.iii.2004. F.W. and S.K. Gess (1 ♀, AMGS); near Two Palms, Uniab River at 19°53′S 13°54′E, 27.iii.2004, F.W. and S.K. Gess (1 ♀, AMGS), visiting flowers of *Zygophyllum simplex* L., Zygophyllaceae; 120 km from Khorixas on road to Palm at 20°17′S 14°05′E, 8.iv.1998, F.W. and S.K. Gess (2 ♀, 1 ♂, AMGS); 5 km N Khorixas Rest Camp at 20°20′S 14°55′E, 17.iii.2004, F.W. and S.K. Gess (1 ♀, AMGS), visiting flowers of *Sesamum*, Pedaliaceae; 15 km from Khorixas on road to Palm at 20°26′S 14°54′E, 1.iv.1997, F.W. and S.K. Gess (1 ♀, AMGS); D2344 WNW Omatjete at 20°57′S 15°14′E, 15.iii.2004, F.W. and S.K. Gess (1 ♂, AMGS); Uis to Omaruru at 21°14′S 15°00′E, 14.iii.2004, F.W. and S.K. Gess (2 ♂, AMGS), one visiting flowers of *Heliotropium tubulosum* E. Mey ex Benth, Boraginaceae; 6 km N Omaruru at 21°27′S 15°59′E, 22.ii.1996, W.J. Pulawski (1 ♀, CAS); 23 km N Karibib, 27.ii.1990, W.J. Pulawski (2 ♀, CAS); 15 km W of Karibib, 26.ii.1990, W.J. Pulawski (6 ♀, 5 ♂, CAS); same data but 28.ii.1990 (4 ♀, 4 ♂, CAS); Uis/Henties Bay at 21°27′S 14°45′E, 17.iv.2002, F.W. and S.K. Gess (1 ♀, AMGS), visiting flowers of Acanthaceae; Omaruru/Usakos at 21°41′S 15°59′E,

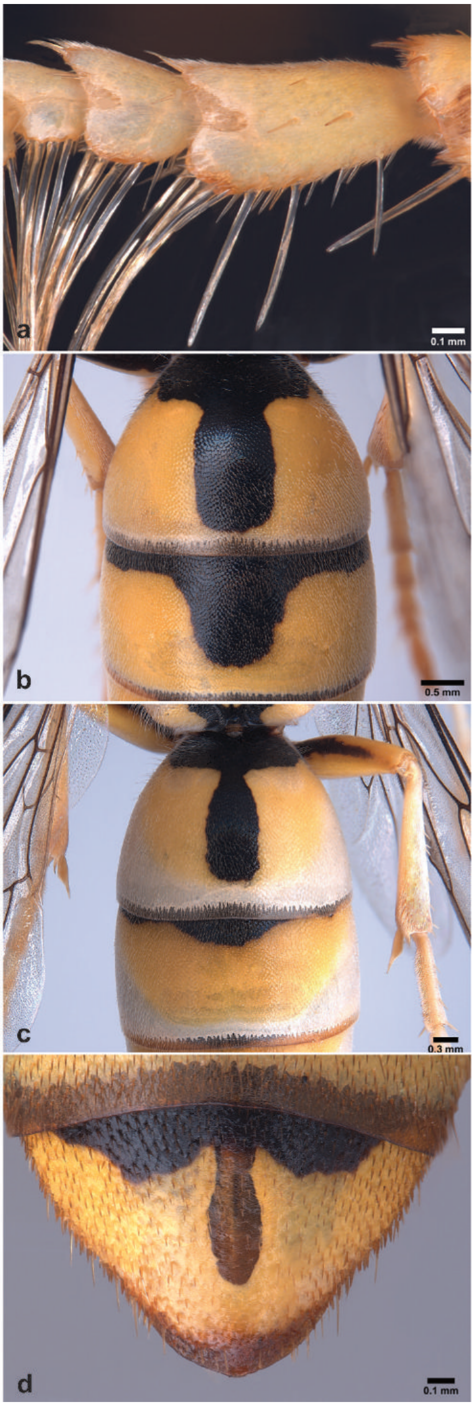

FIGURE 18. *Bembecinus quadristrigatus*: a – female foretarsomere I, b – tergum I of typical form, c – tergum I of yellow form, d – male tergum VII.

26.iv2002, F.W. and S.K. Gess (1 ♀, 1 ♂, AMGS), visiting flowers of *Hermbstaedtia odorata* (Burch.) T. Cooke, Amaranthaceae; Karibib/Omaruru at 21°51′S 15°55′E, 12.iii.2004, F.W. and S.K. Gess (5 ♀, 1 ♂, AMGS); 15 km W Karibib at 21°56′S 15°42′E, 5.iv.1998, F.W. and S.K. Gess (11 ♀, 2 ♂, AMGS), visiting white flowers; 8 km W Usakos at 21°59′S 15°31′E, 15 Feb 1996, W.J. Pulawski (2 ♀, CAS); 117 km from Swakopmund on road to Usakos at 22°02′S 15°17′E, 16.iii.2000, F.W. and S.K. Gess (1 ♀, AMGS); 34 km SW Usakos at 22°02′S 15°17′E, F.W. and S.K. Gess (17 ♀, AMGS), visiting flowers of *Petalidium lanatum* (Engl.) C.B.Cl., Acanthaceae; between Kuiseb and Gaub passes, F.W. and S.K. Gess, at 23°24′S 15°50′E, 22.iii.1999 (1 ♀, AMGS) and 23°27′S 15°46′E, 22.iii.1999 (1 ♀, AMGS);1–5 km E Usakos at 21°58′S 15°36′E, 14.iii.2014, J. Halada (2 ♀, 3 ♂, OÖLM); 25 km NEE Usakos at 21°52′S 15°19′E, 17.iii.2014, J. Halada (1 ♂, OÖLM); 5 km N Gobabeb, 26.ii.1979, Wharton (1 ♀, PPRI). **!Karas Region**: Aus, xii.1929, R.E. Turner (1 ♀, 1 ♂, BMNH); Onze Rust at 24°09′S 18°02′E, 17–18.v.1973, C. Jacot-Guillarmod (1 ♀, AMGS); Nomtsas Farm at 24°25′S 16°51′E, 18.iii.1997, F.W. and S.K. Gess (1 ♀, AMGS), visiting flowers of *Sesuvium sesuvioides* (Fenzl) Verdc, Aizoaceae; Nomtsas at 24°25′S 16°51′E, 18.iii.1997, F.W. and S.K. Gess (1 ♂, AMGS), visiting flowers of *Limeum argute-carinatum* Wawra and Peyr, Aizoaceae 5 km S Mariental at 24°40′S17°57′E, 31.iii.2000, F.W. and S.K. Gess (1 ♀, AMGS); SW Gibeon 41 km on 1089 at 25°20′S 17°29′E, F.W. and S.K. Gess, 8.iii.1999 (1 ♂, AMGS), 10.iii.1999 (1 ♀, 13 ♂, AMGS), visiting flowers of *Limeum* sp., Molluginaceae, and 24.iii.1999 (1 ♀, AMGS). **South Africa** (yellow form)**: Northern Cape Province**: Kalahari Gemsbok National Park, Nossob River bed 11 km NNE Twee Rivieren, 8–11.iii.1990, F.W. and S.K. Gess (5 ♂, AMGS), visiting flowers of *Limeum aethiopicum* Burm., Aizoaceae; Twee Rivieren in Kalahari Gemsbok National Park at 26°28′S 20°37′E, 30.x. 1990, M.W. Mansell (1 ♂, PPRI); 123 km N on road 360 from Upington to Kgalagadi at 27°30′S 20°48′E, 6.iv.2000, F.W. and S.K. Gess (1 ♀, AMGS): 61 km N on road 360 from Upington to Kgalagadi at 27°58′S 20°59′E, 6.iv.2000, F.W. and S.K. Gess (1 ♀, AMGS).

**Geographical distribution**.— Known from the Nama Karoo from southern Angola, Namibia and the southern Kalahari in South Africa, and in northern Namibia penetrating the Namib Desert via the drainage channels (Fig. 26a).

**Floral association**.— Visiting flowers of seven families: Acanthaceae (*Petalidium lanatum* (Engl.) C.B.Cl.), Aizoaceae (non-Mesembryanthema, *Sesuvium sesuvioides* (Fenzl) Verdc), Amaranthaceae (*Hermbstaedtia odorata* (Burch.) T. Cooke, Asteraceae (*Emelia mariothina* (O. Hoffm.) C. Jeffrey), Boraginaceae (*Heliotropium tubulosum* E. Mey ex Benth.), Molluginaceae (*Limeum aethiopicum* Burm. and *Limeum argute-carinatum* Wawra and Peyr), and Pedaliaceae (*Sesamum*) (label data, see Material Examined; S. Gess and F. Gess 2003).

**Nesting**.— Unknown.

**Prey**.— Unknown.

### *Bembecinus rhopaloceroides* (Arnold)

Figures 5b, 19a-c.

*Stizus rhopaloceroides* Brauns, 1911:92 (sleeping on *Datura*). Nomen nudum.

*Stizus rhopaloceroides* Arnold, 1929:294, Figs 47 and 47a, ♀, ♂ (authorship attributed to Brauns). Syntypes: South Africa: Eastern Cape Province: Willowmore (TMSA).— Arnold, 1930:20 (in checklist of Afrotropical Sphecidae); Handcock, Chawanda, and Mhlanga, 1995: 40 (syntypes in NMZB].— As *Bembecinus rhopaloceroides* (Arnold): Evans, 1966:135 (new combination, observations by Brauns, 1911); R. Bohart and Menke, 1976:532 (in checklist of world Sphecidae); S. Gess, 1996:273 (floral records); S. Gess and F. Gess, 2003:117 (floral records), 2006:14 (floral records); Pulawski, 2014:33 (in catalog of world Sphecidae *sensu lato*).

**Recognition**.— The female of *B. rhopaloceroides* shares with *gariepensis* the ferruginous terga (at least terga I and II) with pale yellow apical fasciae. *Bembecinus inexspectatus* and *omaruru* share this color pattern, but in *inexspectatus* the length of hindtarsal arolium is about 0.5 × of the inner claw, whereas about 0.25–0.30 × in *rhopaloceroides* and *gariepensis*; in *omaruru* the setae of tergum II are erect at least laterally, where as they are appressed in the females of the other two species. Some *karasanus* are also similar, but in that species the labrum punctures are larger than those on the scutum, where as markedly smaller in the other two species.

The females of *gariepensis* and *rhopaloceroides* are identical morphologically and can only be identified by association with the topotypical males. The geographic distribution is of some help: *rhopaloceroides* occurs in the Eastern, Western, and Northern Cape Provinces of South Africa as well as in southern Namibia, whereas *gariepensis* is found in the Northern Cape Province of South Africa as well as in southern Namibia (in other words, *gariepensis* is unknown from the Eastern and Western Cape Provinces).

The male of *rhopaloceroides* shares with *gariepensis* an incrassate foretibia, with the dorsal margin convex in profile (Fig. 19c, 7a). They differ as follows: in *gariepensis*, the foretibial inner surface is flat or nearly so, without emargination in the dorsal view (Fig. 7b); in *rhopaloceroides*, it has an oblique impression that in the dorsal view looks like an emargination at the tibia's basal third (Fig. 19b).

Figure 19. *Bembecinus rhopaloceroides*: a – apical hindtarsomere of female showing length of arolium, b – male foretibia in dorsal view, c – male foretibia in profile

**Variation**.— In most of the specimens examined, terga II and III are ferruginous or with insignificantly narrow black fascia basally and the pale yellow apical fascia not broadened laterally, in some females with a pair of black spots in the middle. The specimens from Aus, Namibia, have the pale yellow apical fasciae of terga broadened laterally; in the female, tergum II has a conspicuous black basal fascia and tergum III has only a minimum of ferruginous (anterior to the pale yellow apical fascia).

In most males, the gaster is all or largely ferrugineus (except for the yellow apical fasciae), but all black (except for the apical fasciae) in some specimens; some intermediate specimens have a small amount of ferruginous color on tergum I, just anterior to the yellow apical band.

In the vast majority of specimens, the setae are appressed on tergum II, but they are erect laterally in the single male from Aus, Namibia, up to 0.5 × midocellar width.

**Material examined**.— **Namibia:** Aus, xii.1929, R.E. Turner (1 ♀, 1 ♂, BMNH). **South Africa: North West Province**: Constable, xii.1962, SAM (1 ♀, SAMC). **Northern Cape**

**Province**: Namaqualand, Springbok, Hester Malan Reserve [now Goegap], 3–7.xi.1987, M. Struck (1 ♂, PPRI); Bloukrans near Calvinia, 17.xi.1931, J. Ogilvie (1 ♀, 2 ♂, BMNH); Pofadder, Bushmanland, Mus. Staff, x.1939 (1 ♀, SAMC). **Western Cape Province**: Doringbos [NE of Clanwilliam], 3.xi.1966, J.G. Rozen (1 ♂, AMNH); Clanwilliam, F.W. Gess and S.K. Gess (2 ♂, AMGS); 43 km ENE Ceres on road to Sutherland, 2–3.xii.1989, R.W. Gess (1 ♀, 1 ♂, AMGS), ♀ on flowers of mauve-white "mesem", Mesembryanthemaceae (Aizoaceae); 18 miles [28.98 km] E Touws River to Hondewater, xii.1962, SAM [staff] (7 ♀, 123 ♂, SAMC); 18 miles [28.98 km] southeast Touwsrivier, 12.xi.1966, J.G. Rozen (3 ♂, AMNH); Koup at 33°07′S 21°17′E, 26.xii.1996, W.J. Pulawski (1 ♀, CAS); Koup Siding, Laingsburg, xi.1939, Museum Staff [SAMC] (1 ♀, SAMC); Dikbome, Merweville, Koup, x.1952, Museum Expedition [SAMC] (1 ♂, SAMC); Laingsburg at 33°12′S 20°51′E, 25 and 26.xii.1996, W.J. Pulawski (4 ♀, CAS); Oudtshoorn, Onverwacht, 9–12.xii.1986, F.W. and S.K. Gess (3 ♀, 1 ♂, AMGS), 1 ♀ and 1 ♂ on flowers of *Zygophyllum retrofractum* Thunb., Zygophyllaceae. **Eastern Cape Province**: Willowmore, no date, H. Brauns (2 ♀, SAMC ex NMZB; 1 ♂, UCDC), same locality, 20.i.1903, H. Brauns (1 ♀, SAMC), same locality, 25.ix.1909, H. Brauns (1 ♂, SAMC), same locality, 1.xii.1909, H. Brauns (1 ♂, SAMC), same locality, 15.i.1910, H. Brauns (1 ♀, SAMC ex NMZB), same locality, 10.i.1912, H. Brauns (1 ♀, SAMC ex NMZB), same locality, ii.1914 (1 ♀, UCDC), same locality, xi.1916, H. Brauns (1 ♀, 1 ♂, AMGS), same locality, 1.xii.1917, H. Brauns (1 ♂, SAMC ex NMZB), same locality, xii.1920, H. Brauns (1 ♀, AMGS), same data (1 ♀, SAMC ex NMZB), same locality, 12.i.1965, H. Empey (1 ♀, 1 ♂, AMGS); near Fullerton, C. Jacot-Guillarmod (3 ♂, AMGS); 4 miles [6.44 km] E Waterford, 29.x.1967, C. Jacot Guillarmod (1 ♀, AMGS).

GEOGRAPHICAL DISTRIBUTION.— Known from southwestern Namibia, the Northern, Western and Eastern Cape Provinces of South Africa. It appears to have a southern distribution from the Succulent Karoo in the west to the Nama-Karoo in the east (Fig.26b).

FLORAL ASSOCIATIONS.— Visiting flowers of three plant families: Asteraceae (*Athanasia trifurcata* (Linnaeus) Linnaeus) (S. Gess and F. Gess 2003), Zygophyllaceae (*Zygophyllum retrofractum* Thunb.) and Aizoaceae (Mesembryanthema) (label data, see Material Examined; S. Gess and F. Gess 2003, 2006).

NESTING.— Unknown.

PREY.— Unknown.

### *Bembecinus rhopalocerus* (Handlirsch)

Figures 5c, 20a-c, 21.

*Stizus rhopalocerus* Handlirsch, 1895:986, Pl. 11, Figs 4 and 7, ♀. Holotype: ♀, South Africa: Cape Colony = Cape Province: no specific locality (MHNG), examined by W. Pulawski.— Dalla Torre, 1897:529 (in catalog of world Sphecidae); Brauns, 1911:92 (sleeping aggregations on *Datura*); Arnold, 1929:293, Figs 46, 46 a-d, ♀, ♂, Cape Province [Eastern Cape], Willowmore (in revision of southern African Sphecidae).— As *Bembecinus rhopalocerus* (Handlirsch): Evans, 1966:135 (new combination, observations by Brauns, 1911); R. Bohart and Menke, 1976:532 (new combination, in checklist of world Sphecidae); S. Gess, 1996:281 (floral records); S. Gess and F. Gess 2003:117 (floral records), 2014:210 (nest situation),214 (prey); Pulawski, 2014:33 (in catalog of world Sphecidae *sensu lato*).

RECOGNITION.— *Bembecinus rhopalocerus* has the clypeus roundly angulate basally (best seen in profile (Fig. 20a), whereas it is evenly arcuate in the other species except the female of *B. hyperocrus*. The female has the forefemur unusually broadened ventrally, whereas the dorsal margin is straight or nearly so (Fig. 20b). The female of *B. damarensis* is similar, but has the clypeus evenly arcuate in profile, the ventral broadening of the forefemur less prominent, and the dorsal margin slightly concave (Fig. 6a). The male of *B. rhopalocerus* has the apical flagellomere straight (neither curved nor emarginate), the setae appressed on tergum II, and the gastral terga yellow and black (except for some ferruginous on tergum I). Unlike *gilvus*, it has a row of erect setae between the mandibular base and the occipital carina. It is similar to *B. quadristrigatus* and *B. somalicus*, but differs, in addition to the shape of the clypeus, in having tergum VII broadly rounded apically (less so in the other two species) and the scutum all black mesally (with a pair of admedian yellow stripes in the other two).

Material examined.— **Namibia: !Karas Region**: Aus, 8–30.xi.1929, R.E. Turner (3 ♀, 2 ♂, SAMC ex NMZB, 6 ♀, 6 ♂, BMNH); Aus, xii.1929, R.E. Turner (1 ♂, BMNH); Keetmanshoop, 15.xii.1974, H. Empey (1 ♀, AMGS); 30 miles [48.28 km] SE Keetmanshoop, 23.x.1968, J.G. Rozen and E. Martinez (1 ♀, AMNH). **No specific locality**: no date, as S.W. Africa, R.E. Turner (1 ♂, UCDC). **South Africa: North West Province**: Constable, xii.1962, SAM [staff] (1 ♀, SAMC). **Northern Cape Province**: Namaqualand, Hester Malan [now Goegap] Nature Reserve, 4.xi.1986, M. Struck (1 ♂, AMGS); Upington, 10–12.x.1966, SAM [F.W. and W.H.R. Gess] (33 ♂, SAMC); Doorn River Falls, xi.1931, A. Mackie (1 ♂, BMNH); Doringbos at 31°59′S 19°14′E, 17.xi.1984, C.D. Eardley (1 ♀, PPRI); Britstown, 28.xii.1970, H. and M. Townes (1 ♀, AEI). **Western Cape Province**: 17.5 km from Clanwilliam on road 363 to Klawer, 9.x.1990, F.W. and S.K. Gess, on flowers of *Athanasia trifurcata* (Linnaeus) Linnaeus, Asteraceae (1 ♂, AMGS); 31.5 km from Clanwilliam on road to Klawer, 9–10.x.1990, F.W. and S.K. Gess, on flowers of *Athanasia trifurcata* (Linnaeus) (2 ♂, AMGS); 24 km NE Clanwilliam, 14.xi.1996, M.A.Metz (1 ♀, CAS); 38 km NE Clanwilliam, 12.xi.1996, M.A. Metz (1 ♀, CAS); Olifants River between Citrusdal and Clanwilliam, x-xi.1931, Museum Staff (2 ♀, 9 ♂, SAMC); 19 km S Clanwilliam on old road to Citrusdal, 14.xi.1992, D.W. Gess (1 ♀, AMGS); Leipoltville, xi.1956, SAM [staff] (6 ♀, SAMC); 43 km ENE of Ceres on road to Sutherland, 2–3.xii.1989, F.W. and S.K. Gess

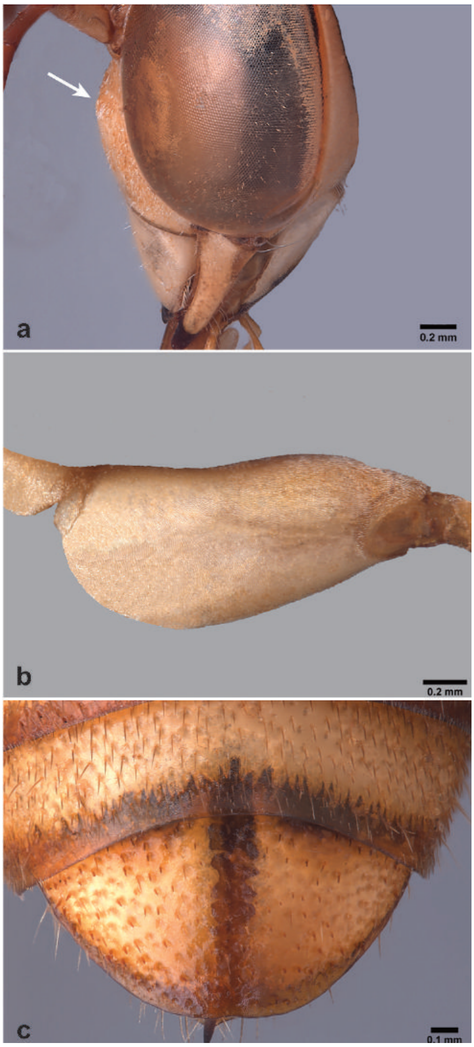

Figure 20 (left). *Bembecinus rhopalocerus*: a – ventral part of female head in profile (arrow indicates the roundly angular portion of clypeus), b – female forefemur, c – male tergum VII.

Figure 21. *Bembecinus rhopalocerus* at nest entrance.

(1 ♀, AMGS); Hex River, i.1884, no collector, det. Arnold (2 ♀, SAMC); Matijesfontein, 1–18.xii.1928, R.E. Turner (1 ♀, UCDC, det. *Bembecinus mutabilis* by R. Bohart); Whitehill, 26.xi, T.D.A. Cockerell (1 ♀, BMNH); Tankwa Karoo, i.1949, Zinn-Hesse Museum Expedition [SAMC] (1 ♀, SAMC); 18 miles [28.97 km] E of Touws River to Hondewater, xii.1962, SAM [staff] (I ♂, SAMC); Oudtshoorn, Onverwacht, 9–12.xii.1986, F.W., S.K., H.W. and R.W. Gess (1 ♀; from nests Homoptera prey in dry collection and larvae in wet collection; Gess and Gess fieldnotes 86/87/18 and 86/87/23) (13 ♀, 2 ♂, AMGS); Rietbron, 11.i.1965, H. Empey (1 ♀, 1 ♂, AMGS). **Eastern Cape Province**: Willowmore, 25.ii.1905, H. Brauns (1 ♂, SAMC ex NMZR), same locality, 4.xii.1917, H. Brauns (1 ♀, SAMC ex NMZR), same locality, 21.i.1965, H. Empey (1 ♀, 1 ♂, AMGS); 9 km E Willowmore at 33°15′S 23°34′E, 28.i.1996, W.J. Pulawski (1 ♀, CAS); near Fullarton, 30.x.1967, C. Jacot Guillarmod (1 ♂, AMGS).

GEOGRAPHICAL DISTRIBUTION.— Known from the Succulent Karoo and Nama-Karoo of southern Namibia south through the Succulent Karoo of Namaqualand, the Olifant's River valley, the Tankwa Karoo and east to Willowmore in the Nama-Karoo (Fig. 26c).

FLORAL ASSOCIATIONS.— Visiting flowers of Asteraceae (*Athanasia trifurcata* (Linnaeus) Linnaeus) (label data, see Material Examined; S. Gess and F. Gess 2003).

NESTING.— Nesting in friable soil on a vegetated flood plane in an area of karroid scrub, Onverwacht, Oudtshoorn (Fig. 21). Three single-celled nests were investigated (S. Gess). Burrows sloping, diameter circa 5 mm, reaching a depth of 47–98 mm, ending in a cell circa 9 mm in diameter and circa 23 mm in length; temporary closure maintained within entrance, cells of nests 86/87/18 and 86/87/23 provisioned, provisioning progressive (Gess and Gess, field notes 86/87/15, 86/87/18 and 86/87/23, AMGS).

PREY.— Two species of Homoptera, *Telmosias cf. crito* Fennah (Nogodinidae) and *Sajuba reversa* (Melichar) (Flatidae), all adults, prey extracted from nests 86/87/18 and 86/87/23 (AMGS).

### *Bembecinus somalicus* (Arnold), new status

Figures 5d, 22.

*Stizus quadristrigatus* race *somalicus* Arnold, 1940:116, Fig. 11 ♀. Holotype ♀, Somalia: Warderi, now Ethiopia: Werder (SAMC), examined by W. Pulawski.— As *Bembecinus qudristrigatus somalicus* (Arnold): R. Bohart and Menke, 1976:532 (new combination, new status, in checklist of world Sphecidae); Pulawski, 2014:30 (in catalog of world Sphecidae *sensu lato*.

*Stizus quadristrigatus* var. *dubiosus* Guiglia, 1941:78, ♀. Holotype: ♀, Ethiopia: Gabredarre, now Kebri Dehar (MSNG). **New synonymy by W. Pulawski**.— As *Bembecinus quadristrigatus dubiosus* (Guiglia): R. Bohart and Menke, 1976:531 (new combination, new status, in checklist of world Sphecidae); Pulawski, 2014:29 (in catalog of world Sphecidae *sensu lato*).

RECOGNITION.— *Bembecinus somalicus* has a color pattern unique within the *rhopalocerus* group: terga II-V each have a pair of submedian black stripes that extend beyond tergal midlength, as in *B. loriculatus* (F. Smith), or a pair of black spots near the tergal middle.

JUSTIFICATION OF NEW SYNONYMY.— The original description and the illustration of *B. dubiosus* clearly show the unique color pattern identical to that of *B. somalicus*. These two names are therefore synonyms. In addition, the holotypes of the two species originate from adjacent localities that are less than 100 km apart, both in the Somali Region of Ethiopia.

MATERIAL EXAMINED.— **ETHIOPIA: Somali Region**: El Rago, 9.xii.1953, Desert Locust Survey, D.J. Greathead (1 ♀, AMGS); Gabredarre, now Kebri Dehar (Guiglia, 1941); Warderi, now Wereder (1 ♀, SAMC, holotype of *somalicus*). **KENYA: Eastern Province**: Archer's Post at Ewaso Ngiro River, 12.xii.1969, E.S. Ross (5 ♀, 6 ♂, CAS; 1 ♀, 1 ♂, UCDC); 5 km NNE Isiolo at

0°24.3′N 37°35.7′E, 8–10.vi.2000, M.H. Bourbin, V.F. Lee, and W.J. Pulawski (2 ♀, CAS); near Ewaso Ngiro River opposite Archer's Post at 0°38.1′N 37°40.4′E, 2–8.xii.2002, W.J. Pulawski (14 ♀, CAS); same locality, M.A. Prentice, 2–8.xii. 2002 (7 ♂, CAS) and 19–20.xii.2002 (1 ♀, 2 ♂, AMGS; 1 ♀, 3 ♂, CAS). **Coast Province**: Taveta on Lumi River, xii.1912, collector unknown (1 ♀, BMNH); **TANZANIA**: **Tanga Region**: 2 km NE Mkomazi at 4°37.8′S 38°05.5′E, 29–31.xii.2002, M.A. Prentice (1 ♀, CAS) and W.J. Pulawski (1 ♀, CAS).

**GEOGRAPHICAL DISTRIBUTION**.— Known from semi-arid to arid areas of the Somali Region of Ethiopia, Kenya, and northeast Tanzania (Fig. 26d).

**FLORAL ASSOCIATIONS**.— Unknown.

**NESTING**.— Unknown.

**PREY**.— Unknown.

FIGURE 22. *Bembecinus somalicus*: female tergum II showing color pattern.

### *Bembecinus zebratus* R. Bohart

Figures 5e, 23.

*Bembecinus zebratus* R. Bohart, 1997:171, Fig. 7, ♀, ♂. Holotype: ♂, South Africa: Western Cape Province: Worcester (UCDC according to original description, but apparently lost). Neotype: ♂, South Africa: Western Cape Province: Worcester, paratype of *B. zebratus* (UCDC) designated by W. Pulawski.— Pulawski, 2014:44 (in catalog of world Sphecidae *sensu lato*).

**RECOGNITION**.— *Bembecinus zebratus* has the scutum all black mesally, and terga black, not ferruginous, with narrow, yellow apical fasciae. It differs from *damarensis* in having tergum I mostly black except for the narrow, yellow apical fascia, the dorsal margin of the female forefemur practically straight and the ventral margin not expanded basally, the apical flagellomere of the male only slightly curved and excavated (Fig. 23a), and tergum VII is short, trapezoid (Fig. 23b). In *damarensis,* the dorsal surface of tergum I is yellow except for the median, black, nearly rectangular marking that does not attain posterior margin (Fig. 6b), the female forefemur is somewhat concave basally and the ventral margin is slightly expanded basally (Fig. 6a), the apical flagellomere of male is markedly curved and excavated, and tergum VII is significantly longer, roundly triangular (Fig. 6d).

Differences between *zebratus* and *pakhuisae* are slight. In the female of *zebratus*, the clypeus is all yellow and the mesopleuron has a vertical yellow

FIGURE 23. *Bembecinus zebratus*: a – apical flagellomeres of male, b – male tergum VII.

marking (yellow marking present or absent in the male); in most males, the apical flagellomere is slightly more curved and excavated (Fig. 23a) than in *pakhuisae*, but about the same in the specimen from Niewoudtville, and the yellow, apical fasciae on the terga are markedly narrower (e.g., the fascia of tergum II is markedly shorter than the black, anterior portion). In the female of *pakhuisae*, the clypeus is all or partly black and the mesopleuron is all black (as it is in the male); in the male, the apical flagellomere is slightly less curved and excavated (Fig. 17b), and the yellow apical fasciae on terga are markedly broader (e.g., the fascia of tergum II is slightly shorter to longer than the black, anterior portion).

**DESIGNATION OF NEOTYPE**.— The holotype of *Bembecinus zebratus* was deposited in UCDC according to the original description, but Steven L.Heydon, Senior Museum Scientist, could not find it there, neither in the type collection nor in the general collection. Apparently, the holotype has been lost, and W. Pulawski designated as a neotype one of the existing paratypes, a male.

**MATERIAL EXAMINED**.— **SOUTH AFRICA: Northern Cape**: Niewoudtville Flower Reserve, 24.ix.2006, K. Timmermann (1 ♂, BMNH). **Western Cape Province**: Worcester, ix-x.1931, R.E. Turner (1 ♀, BMNH); Worcester, x.1975, R.M. Bohart (9 ♀, 13 ♂, UCDC, neotype and paratypes of *zebratus*).

**GEOGRAPHICAL DISTRIBUTION**.— Known from the winter rainfall area of South Africa from one locality in southeastern Namaqualand and one in the Western Cape Province of South Africa (Fig. 26e).

**FLORAL ASSOCIATIONS**.— Unknown.

**NESTING**.— Unknown.

**PREY**.— Unknown.

## DISCUSSION OF GEOGRAPHICAL DISTRIBUTIONS, FLORAL ASSOCIATIONS, NESTING, AND PREY

The distribution records here assembled for the Bembecinus rhopalocerus species group (Figs. 24–26) make possible the recognition of geographical patterns for some species; for others, however, the number of records remains too few, drawing attention to species, which require purposeful collecting.

Current knowledge of the distributions of the species suggests that most are restricted to southern Africa and within southern Africa to the semi-arid to arid Succulent Karoo and Nama-Karoo (Fig. 26f). Three species (*gilvus, omaruru* and *quadristrigatus*) penetrate the Namib Desert along the courses of drainage channels and one (*somalicus*) is known only from Ethiopia, Kenya, and northeast Tanzania.

*Bembecinus* visit plants not only to obtain nectar for adult nourishment but also when hunting their Homoptera prey. Records of actual visits to flowers by members of the *rhopalocerus* species group are surprisingly few. Records are for 11 families: Asteraceae, Zygophyllaceae, Amaranthaceae, Molluginaceae, Fabaceae, Neuradaceae, Aizoaceae (Mesembryanthema and non-Mesembryanthema), Boraginaceae, Campanulaceae, Pedaliaceae and Vahliaceae. Most commonly the flowers visited are small and grouped in heads, as are those of the first four families listed.

Typically, the species of *Bembecinus* have the female foretarsus equipped with long sand-rakes, and excavate sloping nesting burrows in friable soil. The only known exceptions are two species of the *cinguliger* species group (*cinguliger* and *oxydorcus*) which lack sand-rakes and use water for excavating vertical burrows in non-friable soil (F. Gess and S. Gess 1975; F. Gess 1981; S. Gess and F. Gess 2014). Nesting has been documented for only four species of the *rhopalocerus* group: *hyperocrus*, *mutabilis*, *pakhuisae*, and *rhopalocerus*, but all species of this group have sand-rakes and therefore undoubtedly nest in sloping burrows excavated in friable soil.

Prey records are available for only the above four species of the *rhopalocerus* group. These are all Homoptera of the families Cicadellidae, Issidae, Nogodinidae and Flatidae.

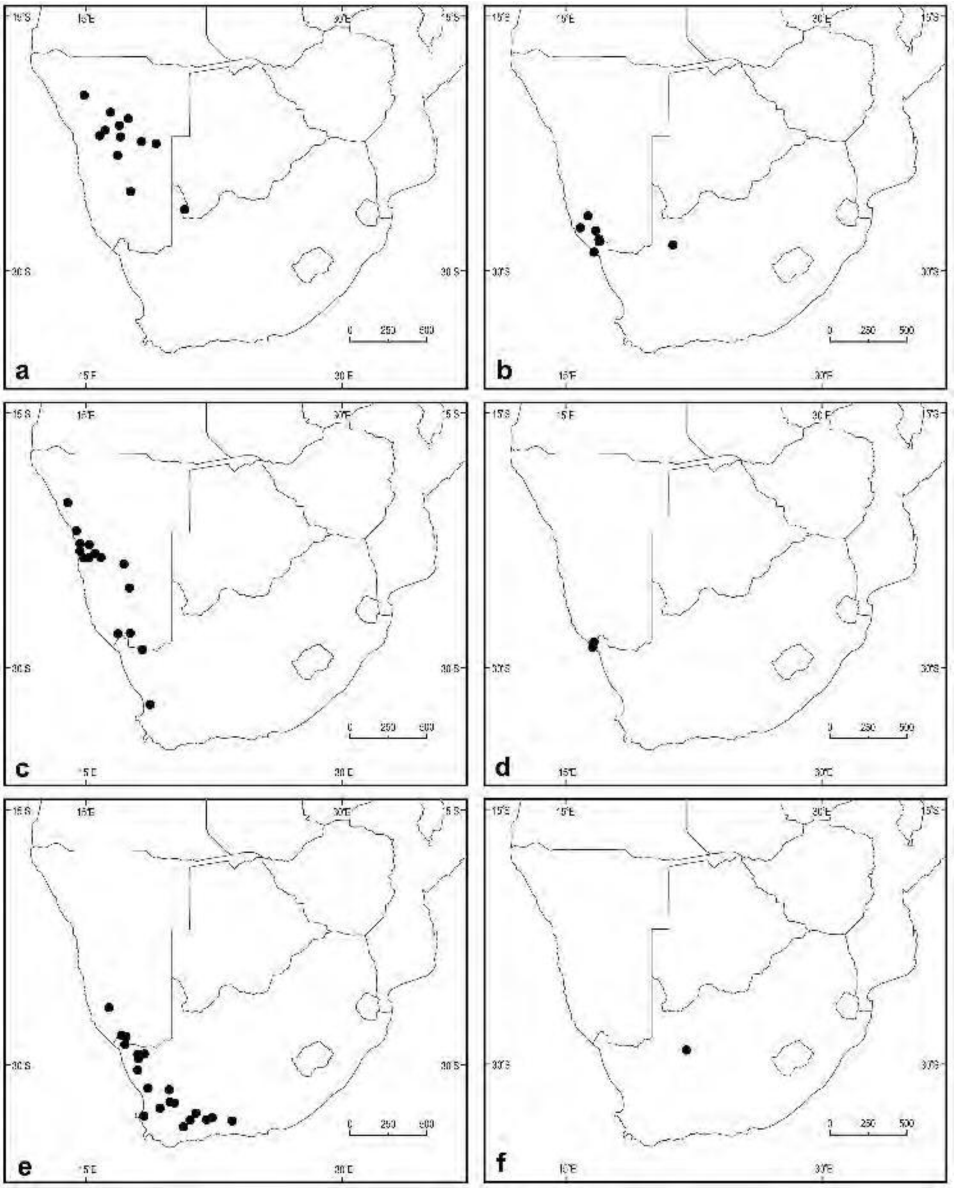

FIGURE 24. Collecting records of *Bembecinus* spp.: a – *damarensis*, b – *gariepensis*, c – *gilvus*, d – *helicicola*, e – *hyperocrus*, f – *inexpectatus*.

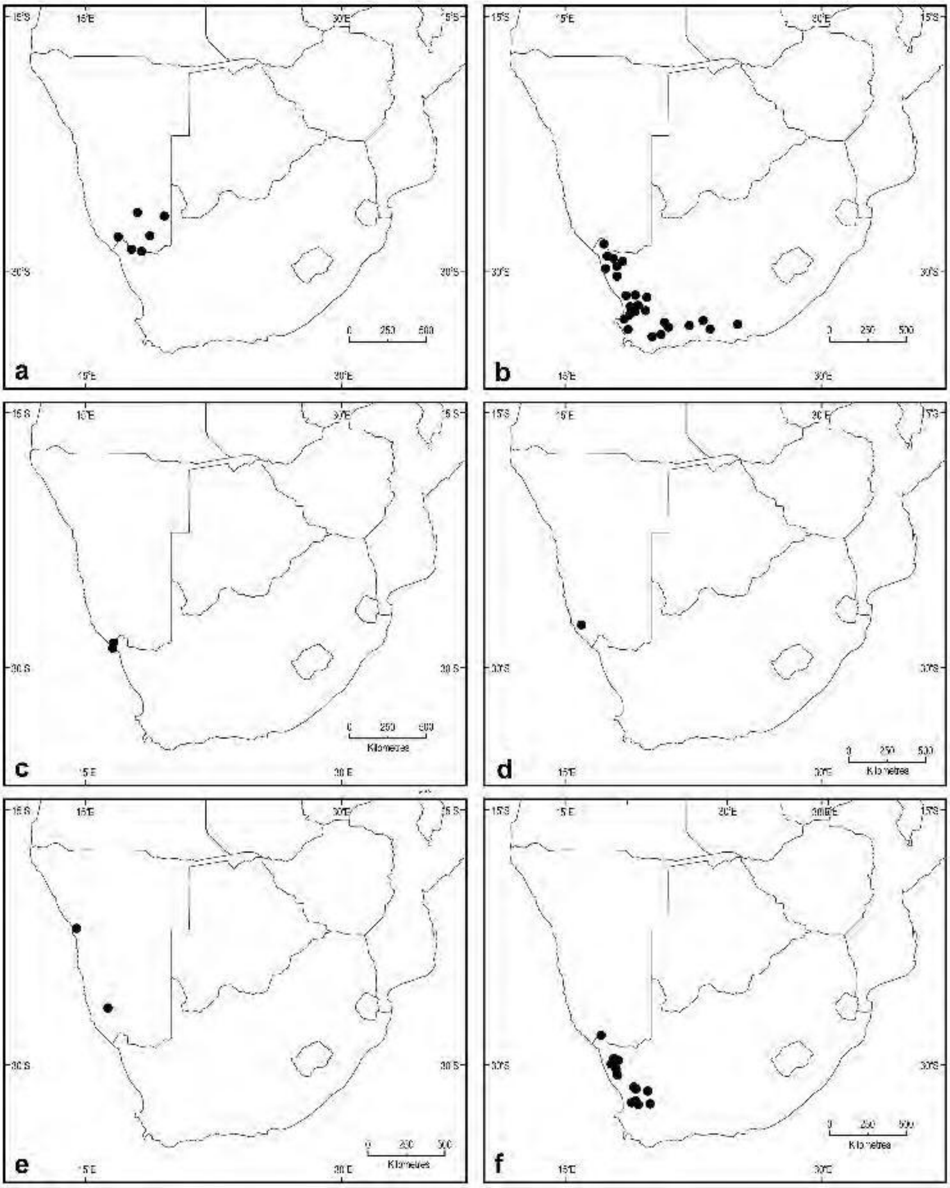

FIGURE 25. Collecting records of *Bembecinus* spp.: a – *karasanus*, b – *mutabilis*, c – *namaquensis,* d – *namibius*, e – *omaruru*, f – *pakhuisae*.

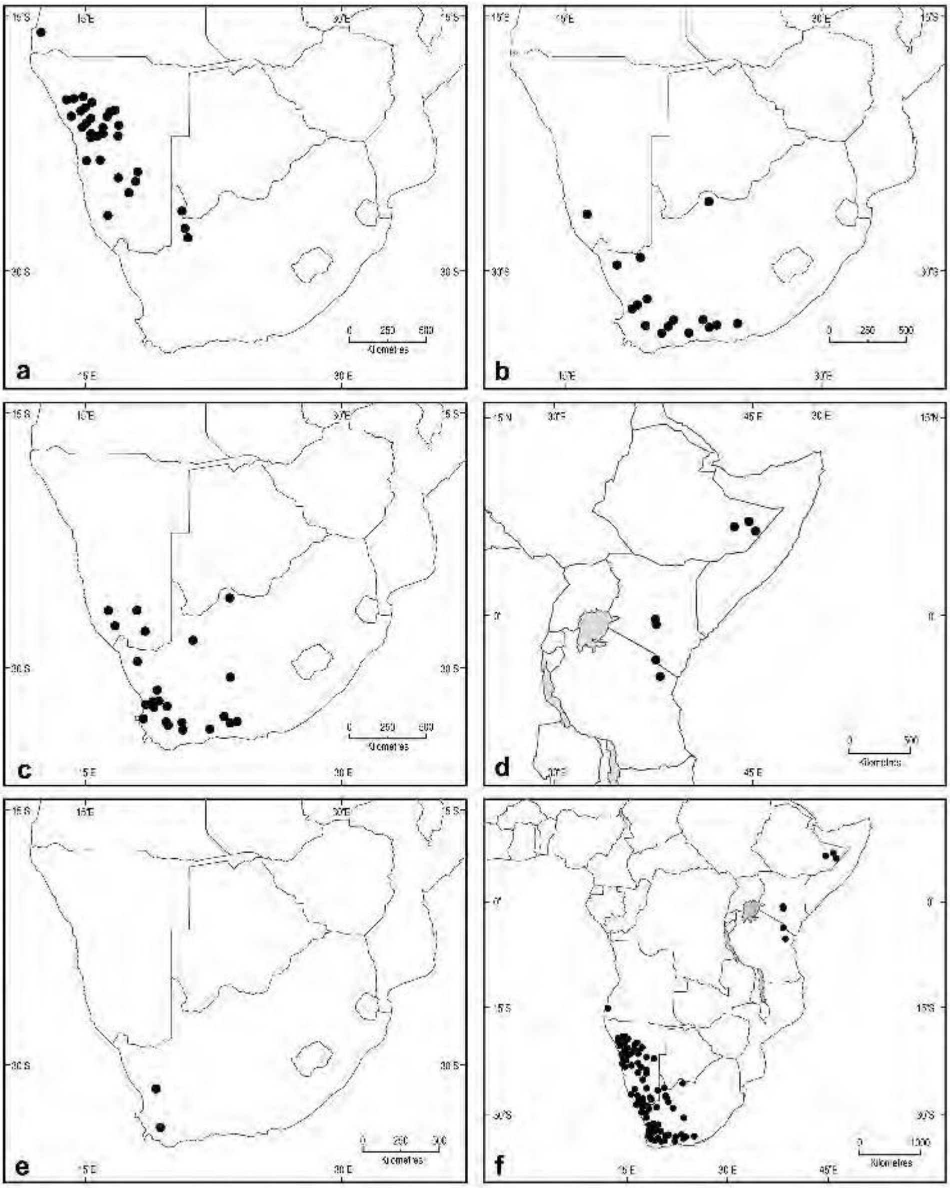

FIGURE 26. Collecting records of *Bembecinus* spp.: a – *quadristrigatus*, b – *rhopaloceroides*, c – *rhopalocerus*, d – *somalicus,* e – *zebratus,* f – all species combined.

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## REFERENCES

ARNOLD, G. 1929. The Sphegidae of South Africa. Part 12. *Annals of the Transvaal Museum* 13:217–319.

ARNOLD, G. 1930. *A Check-list of the Sphegidae of the Ethiopian Region.* University Press, Cambridge, England, UK. 21 pp.

ARNOLD, G. 1940. New species of African Hymenoptera. No 4. *Annals of the Transvaal Museum* 20:101–143.

BOHART, R. M. 1997. Notes on *Bembecinus* of southern Africa, Madagascar, and Australia with descriptions of new species (Hymenoptera, Sphecidae, Nyssoninae, Stizini). *Journal of Hymenoptera Research* 6:163–177.

BOHART, R. M., AND A. S. MENKE. 1976. *Sphecid Wasps of the World*. University of California Press, Berkley, California, USA. ix + 695 pp.

BRAUNS, H. 1911. Biologisches über südafrikanische Hymenopteran. *Zeitschrift für Wissenschaftliche Insektenbiologie* 7:16–19.

COWLING, R. M., D. M. RICHARDSON, AND S. M. PIERCE, EDS. 1997. *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, UK. xxxiv + 615 pp.

DALLA TORRE, K. W. 1897. *Catalogus Hymenopterorum hucusque descriptorum systematiciatis et synonymicus, Volumen VIII: Fossores (Sphegidae)*. Guilelmi Engelmann, Lipsiae [= Leipzig]. 749 pp.

EVANS, H. E. 1966. *The comparative ethology and evolution of the sand wasps*. Harvard University Press, Cambridge, Massachusetts, USA. xvi + 526 pp.

EVENHUIS, N. L. 2014. Abbreviations for insect and spider collections of the world. Available at: *http://hbs.bishopmuseum.org/codens/codens-inst.html* (last accessed February 2014)

GESS, F. W. 1981. Some aspects of an ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown, South Africa. *Annals of the Cape Provincial Museums* (*natural History*) 14(1):1–80.

Gess, F. W., and S. K. Gess. 1975. Ethological studies of *Bembecinus cinguliger* (Smith) and *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae), two southern African turret-building wasps. *Annals of the Cape Provincial Museums* (*natural History*) 11(2):21–46.

Gess, F. W., and S. K. Gess. 1999. The use by wasps, bees and spiders of shells of *Trigonephrus* Pilsb. (Mollusca: Gasteropoda: Dorcasiidae) in the desertic winter rainfall areas of southern Africa. *Journal of Arid Environments* 43:143–153.

Gess, S. K. 1996. *The pollen wasps: ecology and natural history of the Masarinae*. Harvard University Press, Cambridge, Massachusetts, USA. x + 340 pp.

Gess, S.K., and F. W. Gess. 2003. *A Catalogue of Flower Visiting Records for Aculeate Wasps and Bees in the Semi-arid to Arid Areas of Southern Africa.* Albany Museum, Grahamstown, South Africa. iii + 529 pp.

Gess, S. K., and F. W. Gess. 2006. Survey of flower visiting by aculeate wasps and bees in the semi-arid to arid areas of Southern Africa. *Annals of the Eastern Cape Museums* 5:1–51.

Gess, S. K., and F. W. Gess. 2008. Patterns of usage of snail shells for nesting by wasps (Vespidae: Masarinae and Eumeninae) and bees (Megachilidae: Megachilinae) in southern Africa. *Journal of Hymenoptera Research* 17:86–109.

Gess, S. K., and F. W. Gess. 2014. *Wasps and Bees in southern Africa*. SANBI Biodiversity Series 24. South African National Biodiversity Institute Pretoria, South Africa. 320 pp.

Guiglia, D. 1941. (27 Apr.). Su due specie di *Stizus* dell'Etiopia meridionale (Hymen. Sphecidae). *Annali del Museo Civico di Storia Naturale Giacomo Doria* 61:75–82.

Handlirsch, A. 1892. Monographie der mit *Nysson* und *Bembex* verwandten Grabwespen, Part VI. *Sitzungsberichten derAkademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Classe.* Abteilung I. 101:25–205.

Handlirsch, A. 1895. Nachträge und Schlusswort zur Monographie der mit *Nysson* und *Bembex* verwandten Grabwespen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe.* Abteilung I. 104:801–1079.

Krombein, K. V. 1984. Biosystematic studies of Celonese wasps, XIII: a monograph of the Stizinae (Hymenoptera: Sphecoidea, Nyssonidae). *Smithsonian Contributions to Zoology* 388:1–37.

Leistner, O. A., and J. W. Morris. 1976. Southern African Place Names. *Annals of the Cape Provincial Museums* 12: 4 unnumbered pages, 1–565.

Pulawski, W. J. 2014. Catalog of Sphecidae *sensu lato* (= Apoidea excluding Apidae). Available at: <*http://research.calacademy.org/ent/catalog_sphecidae*>. Last accessed February 2014.

Rutherford, M. C. 1997. Categorization of Biomes. Pages 91–97 *in* R. M. Cowling and S. M. Pierce, eds., *Vegetation of Southern Africa.* Cambridge University Press, Cambridge, England, UK.

Smith, F. 1856. *Catalogue of the Hymenopterous Insects in the Collection of the British Museum. IV. London. Sphegidae, Larridae and Crabronidae.* Taylor and Francis, London, England, UK. 497 pp.

# Appendix
## Gazetteer

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| ETHIOPIA | | |
| El Rago | 6°38′N 45°47′E | 6.6333°N 45.7833°E |
| Kebri Dahar | 6°44′N 44°16′E | 6.7333°N 44.2667°E |
| Wederer | 6°58′N 45°21′E | 6.9667°N 45.3500°E |
| KENYA | | |
| Archer's Post at Ewaso Ngiro River | 0°38′S 37°40′E | 0.6333°S 37.6667°E |
| Isiolo, 5 km NNE | 0°24′S 37°36′E | 0.4000°S 37.6000°E |
| Taveta | 3°24′S 37°41′E | 3.4000°S 37.6833°E |
| TANZANIA | | |
| Mkomazi, 2 km NE of | 4°38′S 38°06′E | 4.6333°S 38.0100°E |
| ANGOLA | | |
| Pedive ca 36 mi. E Porto Alexandre | ca 15°48′S 12°22′E | ca 15.8000°S 12.3667°E |
| NAMIBIA | | |
| Ai-Ais | 27°56′S 17°29′E | 27.9286°S 17.4833°E |
| Aroab | 26°48′S 19°39′E | 26.8000°S 19.6500°E |
| Aus | 26°40′S 16°16′E | 26.6667°S 16.2667°E |
| Aus (Pad C13) | 26°40′S 16°15′E | 26.6667°S 16.2500°E |
| Aus, 80 km south of on road 727 | 27°33′S 16°40′E | 27.5500°S 16.6667°E |
| Gaub Pass | 23°30′S 15°46′E | 23.5000°S 14.7667°E |
| Gibeon, SW of | 25°20′S 17°29′E | 25.3333°S 17.4833°E |
| Gibeon, SW of, 41 km on 1089 | 25°20′S 17°29′E | 25.3333°S 17.4833°E |
| Gobabeb, see Namib Desert Research Station | | |
| Gobabeb, 5 km N of | ca 23°27′S 15°00′E | ca 23.45°S 15.0000°E |
| Gobabeb, 8 km S of | ca 23°49′S 17°14′E | ca 23.8198°S 17.2261°E |
| Gobabis | 22°26′S 18°58′E | 22.4333°S 18.9667°E |
| Grootberg Pass, western end | 19°47′S 14°17′E | 19.7833°S 14.2833°E |
| Hentiesbaai, 20 km NE | 21°58′S 14°22′E | 21.9667°S 14.3667°E |
| Kalkveld, 3 km NE of | 20°51′S 16°12′E | 20.8500°S 16.2000°E |
| Kalkveld, 25 km NE of | 20°41′S 16°18′E | 20.6833°S 16.3000°E |
| Kamanjab | 19°38′S 14°50′E | 19.6333°S 14.8333°E |
| Karasburg | 28°00′S 18°45′E | 28.0000°S 18.7500°E |

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| Karibib, 26 km N of | 21°42′S 15°58′E | 21.7000°S 15.9667°E |
| Karibib, 23 km N of | 21°44′S 15°58′E | 21.7333°S 15.9667°E |
| Karibib, 15 km W of | 21°57′S 15°43′E | 21.9500°S 15.7167°E |
| Karibib to Omaruru | 21°51′S 15°55′E | 21.8500°S 15.9167°E |
| Keetmanshoop | 26°35′S 18°08′E | 26.5833°S 18.0133°E |
| Keetmanshoop, 48.28 km SE of | 27°50′S 18°32′E | 27.8333°S 18.4444°E |
| Khorixas, 38 km W of | 20°27′S 14°45′E | 20.45°S 14.75°E |
| Khorixas, 120 km on rd to Palm | 20°17′S 14°05′E | 20.2833°S 14.0833°E |
| Khorixas Rest Camp, 5 km N of | 20°20′S 14°55′E | 20.3333°S 14.9167°E |
| Khorixas, 15 km on rd to Palm | 20°26′S 14°54′E | 20.4333°S 14.9000°E |
| Klinghardtberge | 27°20′S 15°45′E | 27.3333°S 15.7500°E |
| Kuiseb/Gaub Passes | 23°27′S 15°46′E | 23.4500°S 15.7667°E |
| Kuiseb/Gaub Passes | 23°24′S 15°50′E | 23.4000°S 15.8333°E |
| Mariental, 5 km S of | 24°40′S 17°57′E | 24.6667°S 17.9500°E |
| Namib Desert Research Station, Gobabeb | 23°34′S 15°03′E | 23.5500°S 15.0333°E |
| Naribis | 20°16′S 16°23′E | 20.6667°S 16.3833°E |
| Nomtsas Farm | 24°25′S 16°51′E | 24.4167°S 16.8500°E |
| Okahandja | 21°59′S 16°55′E | 21.9833°S 16.9167°E |
| Okahandja, 70 km N of | 21°22′S 16°50′E | 21.3667°S 16.8333°E |
| Okahandja, 9 km W of, Leeu R. | 21°58′S 16°50′E | 21.9667°S 16.8333°E |
| Omaruru, 6 km N of | 21°27′S 15°59′E | 21.4500°S 15.9833°E |
| Omaruru/Usakos | 21°41′S 15°59′E | 21.6833°S 15.9833°E |
| Omaruru, 30km S of on road to Karibib | 21°41′S 15°59′E | 21.6833°S 15.9833°E |
| Omatjete, WNW on D2344 | 20°57′S 15°14′E | 20.9500°S 15.2333°E |
| Onze Rust | 24°09′S 18°02′E | 24.1500°S 18.0333°E |
| Osire | 21°01′S 17°22′E | 21.0167°S 17.3667°E |
| Otjiwarongo | 20°28′S 16°39′E | 20.4642°S 16.6528°E |
| Otjiwarongo, 44 km SW | 20°37′S 16°22′E | 20.6167°S 16.3667°E |
| Palmwag, 7 km N of | 19°51′S 13°54′E | 19.8500°S 13.9000°E |
| Rehoboth/Gamsberg | 23°10′S 16°42′E | 23.1666°S 16.7000°E |
| Rooibank, Kuiseb River bed | 23°11′S 14°39′E | 23.1833°S 14.6700°E |

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| Rooibank Desert Park | 23°11′S 14°38′E | 23.1833°S 14.6333°E |
| Rosh Pinah, 16 km S of | 28°04′S 16°51′E | 28.0667°S 16.8500°E |
| Skeleton Coast Park, east of on 3245 | 20°14′S 13°53′E | 20.2333°S 13.8833°E |
| Springbokwater, 12 km E of | 20°15′S 13°44′E | 20.2500°S 13.7333°E |
| Swakopmund, 5 km E of | 22°40′S 14°34′E | 22.6667°S 14.5631°E |
| Swakopmund, 63 km E of | 22°45′S 15°02′E | 22.7500°S 15.0333°E |
| Swakopmund, 117 km on rd to Usakos | 22°02′S 15°17′E | 22.0333°S 15.2833°E |
| Uis to Omaruru | 21°14′S 15°00′E | 21.2333°S 15.0000°E |
| Uis to Henties Bay | 21°27′S 14°45′E | 21.4500°S 14.7500°E |
| Uniab River, near Two Palms | 19°53′S 13°54′E | 19.8833°S 13.9000°E |
| Usakos, 17–19 km E of | 21°59′S 15°42′E | 21.9833°S 15.7000°E |
| Usakos, 8 km W of | 21°59′S 15°31′E | 21.9833°S 15.5167°E |
| Usakos, 34 km SW of | 22°02′S 15°17′E | 22.0333°S 15.2833°E |
| Usakos, 1–5 km E of | 21°58′S 15°36′E | 21.9667°S 15.6000°E |
| Usakos, 25 km NEE of | 21°52′S 15°19′E | 21.8667°S 15.3167°E |
| Walvis Bay | 22°57′S 14°30′E | 22.95°S 14.5000°E |
| Walvis Bay, 11 km E of | 22°25′S 14°37′E | 22.9833°S 14.6167°E |
| Walvis Bay, 147 E of | ca 23°15′S 15°24′E | ca 23.25°S 15.4000°E |
| Witvlei, 40 km W of | ca 22°22′S 18°08′E | ca 22.3667°S 18.1333°E |
| Junction 1237 and C26, 18 km W of | 23°09′S 16°42′E | 23.1500°S 16.7000°E |
| SOUTH AFRICA | | |
| Alexander Bay, 23 km S of | 28°46′S 16°37′E | 28.7667°S 16.6167°E |
| Anenous | 29°38′S 18°00′E | 29.6333°S 18.0000°E |
| Bloukrans [Pass] near Calvinia | 31°40′S 19°45′E | 31.6667°S 19.7500°E |
| Brandkaros, west of | 28°29′S 16°40′E | 28.4833°S 16.6667°E |
| Britstown | 30°35′S 23°30′E | 30.5833°S 23.5000°E |
| Bulshoek Dam | 32°03′S 18°49′E | 32.0367°S 18.8203°E |
| Cape Town, 60 km N of | ca 33°24′S 18°40′E | ca 33.4000°S 18.6667°E |
| Calvinia | 31°29′S 19°46′E | 31.4750°S 19.7728°E |
| Ceres, 43 km ENE of on road to Sutherland | 33°14′S 19°42′E | 33.2333°S 19.7000°E |
| Ceres, upper sources of Olifants River | ca 33°05′S 19°14′E | ca 33.0833°S 19.2333°E |
| Citrusdal | 32°35′S 19°01′E | 32.2500°S 19.0000°E |
| Citrusdal, 8 miles (12.88 km) north of | 32°28′S 18°54′E | 32.4600°S 18.9000°E |
| Citrusdal, 20 km N of | ca 32°26′S 18°54′E | ca 32.4333°S 18.9000°E |

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| Clanwilliam | 32°11′S 18°53′E | 32.1786°S 18.8911°E |
| Clanwilliam Dam | 32°12′S 18°54′E | 32.1917°S 18.8950°E |
| Clanwilliam Dam, Caleta Cove | 32°14′S 18°56′E | 32.2389°S 18.9292°E |
| Clanwilliam, 5 km west of on road to Graafwater | 32°10′S 18°15′E | 32.1667°S 18.8333°E |
| Clanwilliam, 11 km west of on road to Graafwater | 32°10′S 18°47′E | 32.1667°S 18.7833°E |
| Clanwilliam, 12 miles (19.3 km) north of | 32°03′S 18°49′E | 32.0367°S 18.8203°E |
| Clanwilliam, 4 miles (6.44 km) south of on old road to Citrusdal | 32°14′S 18°54′E | 32.2333°S 18.9000°E |
| Clanwilliam, 10 km S of | 32°15′S 18°51′E | 32.2500°S 18.9333°E |
| Clanwilliam, 15 km south of on old road to Citrusdal | 32°19′S 18°56′E | 32.3167°S 18.9333°E |
| Clanwilliam, 16.5 km south of on old road to Citrusdal | 32°20′S 18°57′E | 32.3333°S 18.9500°E |
| Clanwilliam, 19 km south of on old road to Citrusdal | 32°21′S 18°57′E | 32.3500°S 18.9417°E |
| Clanwilliam, 20 km south of on old road to Citrusdal | 32°22′S 18°57′E | 32.3667°S 18.9500°E |
| Clanwilliam, 17.5 km north of on road (R363) to Klaver | 32°01′S 18°49′E | 32.0500°S 18.8333°E |
| Clanwilliam, 24km NE of | ca 32°6′S 19°3′E | ca 32.2°S 19.05°E |
| Clanwilliam, 38 kn NE of | ca 32°2′S 19°12′E | ca 32.0333°S 19.2°E |
| Concordia | 29°33′S 18°00′E | 29.5500°S 18.0000°E |
| Concordia, 14 km N of | 29°26′S 17°57′E | 29.4333°S 17.9500°E |
| Constable | 25°49′S 23°26′E | 25.8567°S 23.4333°E |
| Die Koei | 28°17′S 16°59′E | 28.2833°S 16.9833°E |
| Doorn River Falls [north of Nieuwoudtville] | 31°19′S 19°07′E | 31.3167°S 19.1167°E |
| Doringbos, NE of Clanwilliam | 31°58′S 19°14′E | 31.9667°S 19.2333°E |
| Eksteenfontein, Namaqualand | 28°50′S 17°15′E | 28.3333°S 17.2500°E |
| Eksteenfontein, 42 km S of | 29°06′S 17°26′E | 29.1000°S 17.4333°E |
| Garies | 30°33′S 17°59′E | 30.5500°S 17.8833°E |
| Goegap | 29°38′S 17°59′E | 29.6333°S 17.9833°E |
| Goodhouse | 28°54′S 18°15′E | 28.9000°S 18.2500°E |
| Groenkloof, between Clanwilliam and Algeria | 32°19′S 19°02′E | 32.3167°S 19.0333°E |
| Fullarton | 33°11′S 23°50′E | 33.1833°S 23.8333°E |
| Hester Malan Nature Reserve = Goegap | | |
| Het Kruis | 32°36′S 18°45′E | 32.6000°S 18.7500°E |

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| Hex River | 33°24′S 19°46′E | 33.4000°S 19.7667°E |
| Kamieskroon | 30°12′S 17°56′E | 30.2000°S 17.9333°E |
| Kamieskroon, Bakleikraal | 30°13′S.18°03′E | 30.2167°S 18.0500°E |
| Kamieskroon, Bowesdorp | 30°20′S 17°56′E | 30.3333°S 17.9333°E |
| Kamieskroon, 6 km N of, Farm Arkoep | 30°19′S 17°56′E | 30.3167°S 17.9333°E |
| Kamieskroon, Farm Dassiefontein | 30°09′S 17°59′E | 30.1500°S 17.9833°E |
| Khubus/Ochta, near Vyfsusters Mt. | 28°12′S 16°55′E | 28.2000°S 16.9167°E |
| Klaver/Clanwilliam, Bulshoek | 32°01′S 18°47′E | 32.0167°S 18.7833°E |
| Koeroegabvlakte, Richtersveld National Park | 28°11′S 17°03′E | 28.1833°S 17.0500°E |
| Koup | 33°07′S 21°17′E | 33.1167°S 21.2833 °E |
| Laingsburg | 33°12′S 20°51′E | 33.2500°S 21.0000°E |
| Lamerfontein, Moordenaars Karoo | ca 32°22′S 19°54′E | ca 32.2167°S 19.9000°E |
| Lammerkraal, Prince Albert District | ca 33°13′S 22°02′E | 33.2253°S 22.0300°E |
| Leipoldtville | 32°13′S 18°29′E | 32.222°S 18.481°E |
| Matjiesfontein | 32°58′S 18°16′E | 32.9667°S 18.2667°E |
| Merweville, Dikbome, Koup | 32°54′S 21°22′E | 32.9000°S 21.3667°E |
| Mesklip | 29°50′S 17°51′E | 29.83°S 17.85°E |
| Montague | 33°47′S 20°07′E | 33.7833°S 20.1167°E |
| Moordenaars Karoo | ca 32°58′S 20°49′E | ca 32.9667°S 20.8167°E |
| Moedverloren Nature Reserve | 31°24′S 18°34′E | 31.3942°S 18.5610°E |
| Murraysburg | 32°33′S 19°16′E | 32.5500°S 19.2667°E |
| Nababeep, Namaqualand | 29°36′S 17°48′E | 29.6000°S 17.8000°E |
| Naib | 29°21′S 18°20′E | 29.3500°S 18.3333°E |
| Nieuwoudtville | 31°23′S 19.06′E | 31.3667°S 19.1000°E |
| Niewoudville Flower Reserve | 31°22′S 19.09′E | 31.3667°S 19.1500°E |
| Nieuwoudtville, 15 km north on road to Loriesfontein | 31°16′S 19.00′E | 31.2667°S 19.0000°E |
| Oudtshoorn, Onverwacht | 33°38′S 22°15′E | 33.6264°S 22.2382°E |
| Pakhuis Pass | 32°04′S 19°05′E | 32.0667°S 19.0833°E |
| PakhuisPass, east of | ca 32°16′S 19°13′E | ca 32.2742°S 19.2092°E |
| Paleisheuwel | 32°28′S 18°43′E | 32.4794°S 18.7208°E |
| Pofadder, Bushmanland | 29°08′S 19°24′E | 29.1286°S 19.3947 °E |
| Port Nolloth, 60 km N of | 28°47′S 16°38′E | 28.7833°S 16.6333°E |
| Port Nolloth, 67 km east of | ca 29°38′S 18°00′E | ca 29.6333°S 18.0000°E |

| | Degrees and minutes | Decimal degrees |
|---|---|---|
| Port Nolloth, 70 km east of | ca 29°38′S 18°00′E | ca 29.6333°S 18.0000°E |
| Putsonderwater | 29°14′S 21°53′E | 29.2333°S 21.8833°E |
| Rietbron | 32°54′S 23°09′E | 32.9000°S 23.1500°E |
| Springbok, Bloukrans Farm | 29°43′S17°55′E | 29.7167°S 17.9167°E |
| Skouerfontein | 28°47′S 17°10′E | 28.78333°S 17.1667°E |
| Steinkopf, 10 km west of = Anenous | | |
| Tankwa Karoo | ca 32°15′S 19°45′E | ca 32.2500°S 19.7500°E |
| Tankwa Karoo, Renoster River | ca 32°16′S 20°05′E | ca 32.2667°S 20.0833°E |
| Tierberg, Prince Albert District | 33°08′S 22°16′E | 33.1283°S 22.2733°E |
| Touws River/Hondewater | ca 33°39′S 20°46′E | 33.6500°S 20.6667°E |
| Touws River, 18 miles (28.97 km] east of to Hondewater | ca 33°39′S 20°46′E | 33.6500°S 20.6667°E |
| Touws River, 18 miles (28.97 km) SE of | ca 33°39′S 20°46′E | 33.6500°S 20.6667°E |
| Twee Rivieren | 26°28′S 20°37′E | 26.4667°S 20.6167°E |
| Twee Rivieren, 11 km on road to Nossob, river bed | 26°24′S 20°41′E | 26.4000°S 20.6833°E |
| Upington | 28°24′S 21°16′E | 28.40111°S 21.25972°E |
| Upington, 123 km N on road 360 to Kgalagadi | 27°30′S 20°48′E | 27.5000°S 20.8000°E |
| Upington, 61 km N on road 360 to Kgalagadi | 27°58′S 20°59′E | 27.9667°S 20.9833°E |
| Van Rhyn’s Pass | 31°23′S 19°01′E | 31.3833°S 19.0167°E |
| Veldrif, 25 km east of | ca 32°47′S 18°24′E | ca 32.7833°S 18.4000°E |
| Voelklip, south of Springbok | 29°45′S 17°22′E | 29.7500°S 17.3667°E |
| Vioolsdrif | 28°46′S 17°39′E | 28.7750°S 17.6250°E |
| Vioollsdrif, 53 km S of | 29°10′S 17°50′E | 29.1667°S 17.8333°E |
| Waterford, 4 miles (6.44 km) east of | 33°04′S 25°07′E | 33.0667°S 25.1167°E |
| Whitehill [railway station south east of Matjiesfontein] | 33°14′S 20°38′E | 33.2333°S 20.6333°E |
| Wildeperdehoek Pass, west end | 29°56′S 17.38′E | 29.9392°S 17.6250°E |
| Willowmore | 33°18′S 23°30′E | 33.3000°S 23.4833°E |
| Willowmore, 9 km E of | 33°15′S 23°34′E | 33.2500°S 23.5667°E |
| Worcester | 33°39′S 19°26′E | 33.6500°S 19.3333°E |

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# A Review of the Pennatulacean Genus *Stylatula*, with the Description of a New Species from Japan (Cnidaria: Octocorallia)

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**Until relatively recently, the pennatulacean genus *Stylatula* was known only from North and South America and the eastern Atlantic Ocean. In 2007, a new species was described from New Zealand. This paper describes an additional species, also from the western part of the Pacific Rim. In addition, historical and taxonomic reviews of the genus are included.**

KEYWORDS: Pennatulacea, Virgulariidae, sea pens, *Stylatula*, new species, Japan, key to the Pacific Ocean species of the genus

**HISTORICAL PERSPECTIVE.**— Verrill (1868:382) established the pennatulacean family Virgulariidae (spelled as Virgularidae by him), which included the two genera *Virgularia* Lamarck, 1816, and *Stylatula*, Verrill, 1864. Kőlliker (1880:33–34) distinguished two families – (1) Virgularidae for *Virgularia*, *Scytalium* Herklots, 1858, and the species *Pavonaria finmarchica* (Sars, 1851); and (2) the family Stylatulidae for *Stylatula*, *Dübenia* Koren & Danielssen, 1877, and *Acanthoptilum* Kolliker, 1870. Subsequently, *Dübenia* was considered a junior synonym of *Stylatula* by Kükenthal (1915:67), and *Pavonaria* Kőlliker, 1869 was synonymized with *Halipteris* Kőlliker, 1869, by Williams (1995:120) since the name *Pavonaria* was previously used by Schweigger, 1820 for a different pennatulacean in the family Funiculinidae. One valid family, Virgulariidae, is currently recognized to incorporate the five genera *Virgularia, Scytalium, Stylatula, Acanthoptilum,* and *Scytaliopsis* Gravier, 1906, while *Halipteris* is viewed as the sole genus of the family Halipteridae (Williams 1995:120–125).

## MATERIALS AND METHODS

**MATERIAL EXAMINED OF OTHER SPECIES OF *STYLATULA*.**— ***Stylatula elongata*** (CAS 173213) U.S.A., Washington, Squamish Harbor (aka Shine Cove) near Shine, WA; 47°51.582′N 122°39.130′W; 1 August 2010; 13–18 m depth; collector James Murray; two colonies fixed in 90% ethanol, preserved in 95% ethanol. ***Stylatula austropacifica*** Holotype (CAS 173209); Sta. No. NIWA (NZOI) C306; New Zealand; 36°41.00′S 173°58.00′E, 190 m depth; 24 October 1959; one partial colony preserved in 75% ethanol.

**ABBREVIATIONS USED IN THE TEXT.**— **AKM** (Asako K. Matsumoto Collection, Japan), **CASIZG** (Invertebrate Zoology and Geology Collections, California Academy of Sciences, San Francisco, California, USA). **SEM** Scanning electron micrographs.

## SYSTEMATIC ACCOUNT

### Subclass Octocorallia
### Order Pennatulacea
### Family Virgulariidae Verrill, 1868

### Genus *Stylatula* Verrill, 1864

**GENERIC DIAGNOSIS.**— Virgulariid pennatulaceans with slender, bilateral, often vermiform colony shape. Axis present throughout colony length, most often round in transverse section. Polyp leaves subtended by fanlike armatures of spindle-like to needle-like sclerites, which may or may not be three-flanged. Sclerites from other parts of colony inconspicuous to absent.

**TYPE SPECIES.**— *Virgularia elongata* (Gabb, 1862); subsequent designation by Verrill, 1864; type locality California.

**ETYMOLOGY.**— The generic name is derived from the Greek *Stylos*: a style, stake, or pillar.

**SYSTEMATICS AND PHYLOGENETIC ASSESSMENT.**— The genus *Stylatula* contains thirteen described species from the Atlantic and Pacific Oceans (Japan to Norway), between approximately 65° north and 50° south latitude (Fig. 9). With the addition of the new species described here, thirteen species are considered valid; known geographic range Atlantic and Pacific Oceans (Japan to North & South America to Norway and Namibia), 0–1020 m in depth (Williams 1995:122; Williams 2011:6; Williams 2014). The genus *Stylatula* differs from other genera in the family Virgulariidae by the presence of a conspicuous fan-shaped armature subtending each polyp leaf, comprised of relatively robust sclerites. Of the five described genera in the family, only *Stylatula, Acanthoptilum*, and *Scytalium* have sclerites in the rachis and polyp leafs, while *Virgularia* and *Scytaliopsis* do not.

### *Stylatula diminutiva* Williams and Matsumoto, sp. nov.

Figures 1–9.

**SPECIES DIAGNOSIS.**— Virgulariid pennatulaceans; mature colonies < 65 mm long; number of polyps per polyp leaf 2–4; number of large sclerites comprising fan-shaped polyp leaf armature < 7; sclerites three-flanged throughout.

**MATERIAL EXAMINED.**— HOLOTYPE: **CASIZ 198016**; Japan, Iwate Prefecture, Sanriku, Otsuchi Bay; 39°20,710′N x 141°56,923′E; 44 m depth; 28 April 2009; collection number AKM 1414; collector Asako K. Matsumoto on board *R/V Yayoi* with 1 m biological dredge; remarks – mud bottom inside bay, water temperature 9.6° C: one whole specimen preserved in 95% EtOH. PARATYPES: **CASIZ 198017**; same data as holotype. **CASIZ 203514**; Japan, Iwate Prefecture, Sanriku, east Otsuchi Bay; approximate coordinates 39°24′ – 39°34′N, ca. 142°10′–142°41′E; 118–120 m depth; 12 November 1993; collection number AKM 1627 (= 1618b); collector S. Ohta on board R/V Tansei-maru KT 93–15 cruise, St. 01 with 1 m biological dredge; remarks – separated from AKM 1618a; one whole specimen fixed in formalin and preserved in 95% EtOH. OTHER MATERIAL (non-type): **CASIZ 203513**; same data as holotype.

**DESCRIPTION.**— The wet-preserve holotype measures 36 mm in length and 2.5 mm at it widest point (across the second polyp pair from the terminal apex. The internal axis is thin and extends the length of the colony. It is cylindrical, round in cross section, and contains numerous surface pores, which are often narrow and elongated. The composition of the axis is that of radially-arranged, wedge-shaped columns of calcareous matter, as in other pennatulaceans (Figs. 2–4), which is similar to the axial structure of ellisellid gorgonians (Bayer, 1956: 224). Of the approxi-

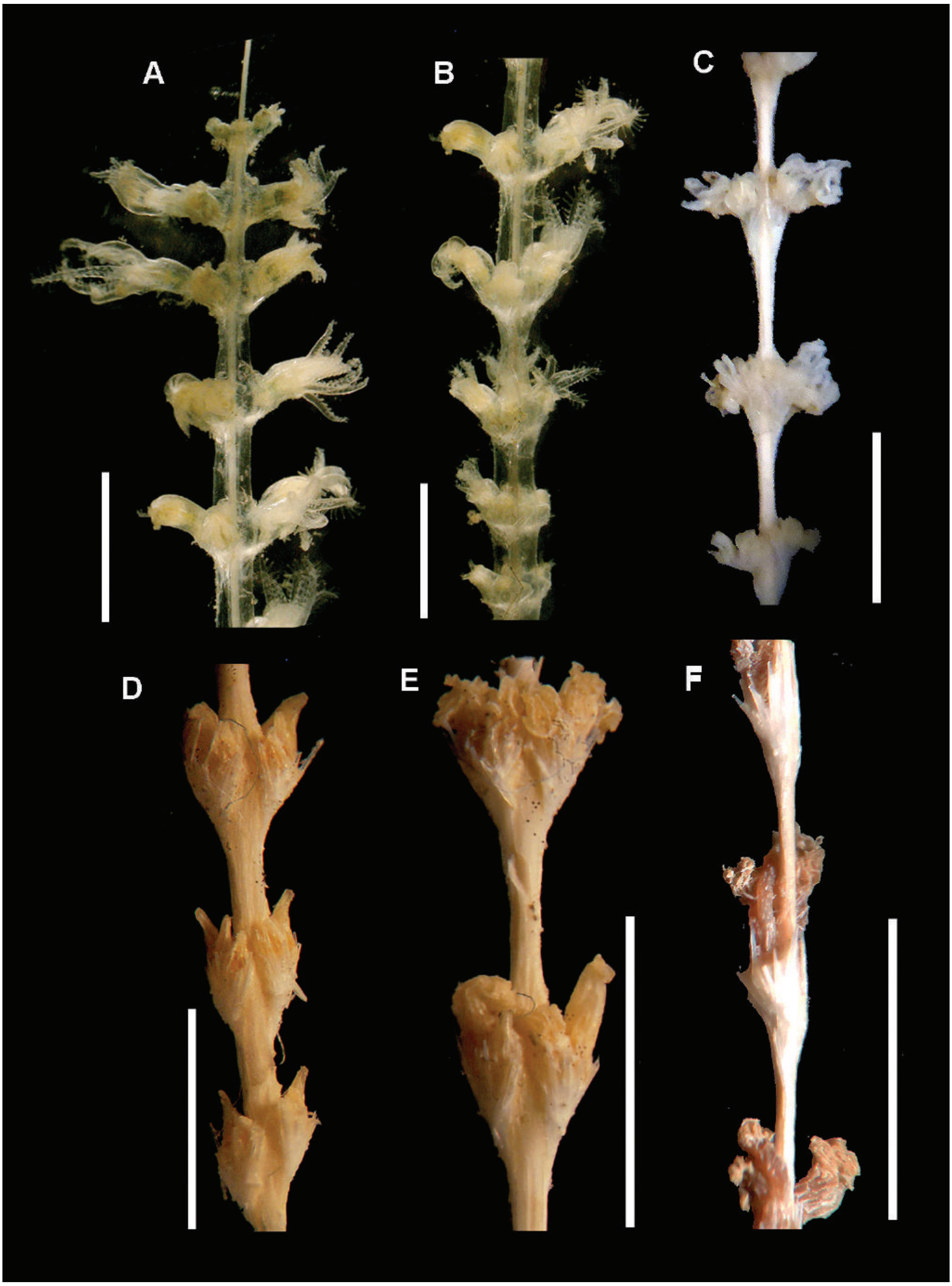

FIGURE 1. *Stylatula diminutiva* sp. nov. A-B. Living colony. C. Wet preserved holotype (CAS 198016). D-F. Wet preserved paratype (CAS 203514). Scale bars = 2.5 mm.

mately thirty-five pairs of polyp leaves that are distinguishable, nine of these at the upper end of the rachis are fully developed, have mature polyps and conspicuous fan-shaped basal armature. The other twenty-six polyp leaf pairs are incipient, or not fully mature, and are not separated from

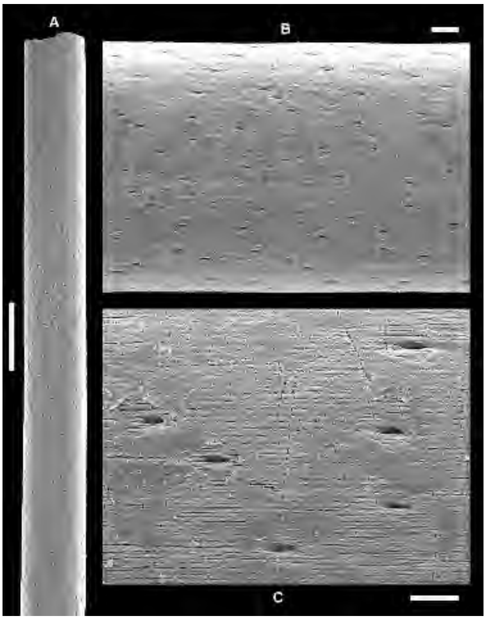

FIGURE 2. *Stylatula diminutiva* sp. nov. SEM of surface of axis (CAS 203513), showing surface pores. A. Portion of axis; scale bar = 0.2 mm. B. Detail of axial surface; scale bar = 0.02 mm. C. Ultrastructural detail of axial surface; scale bar = 0.01 mm.

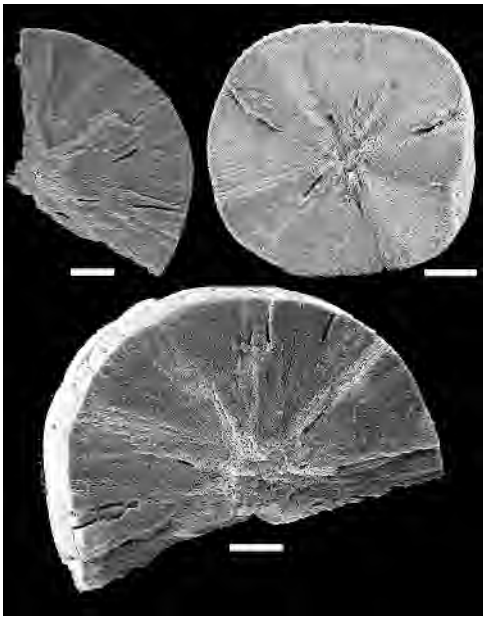

FIGURE 4. *Stylatula diminutiva* sp. nov. SEM of internal morphology of the axis (CAS 203514), showing radial arrangement of calcareous material. Transverse sections of axis; scale bars = 0.02 mm.

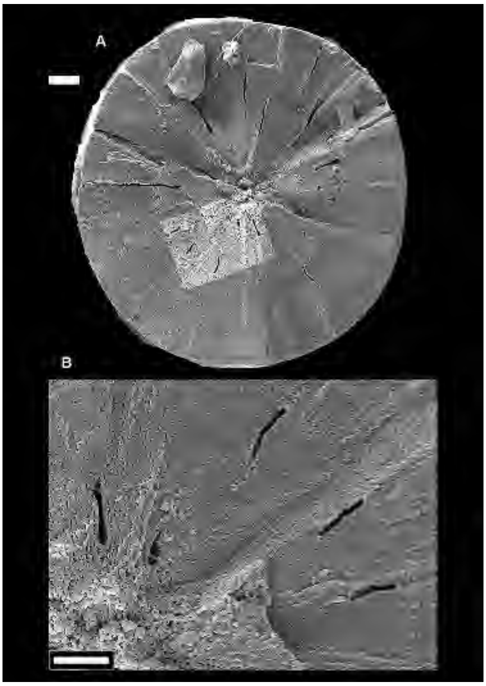

FIGURE 3. *Stylatula diminutiva* sp. nov. SEM of internal morphology of the axis (CAS 203513). A. Transverse section of axis, 0.23 mm in diameter, showing elongated pores; scale bar = 0.02 mm; lightened rectangle is shown enlarged in B below. B. Internal structural detail of axis; scale bar = 0.01 mm.

adjacent pairs in the proximal region of the rachis, or are separated by < 2 mm of bare rachis in the middle portion of the rachis. The uppermost polyp leaf pairs on the distal part of the rachis are separated from adjacent pairs of polyp leaves by approximately 2 mm of bare rachis (Fig. 1C). In the largest polyp leaves of the upper rachis, there are 2–4 polyps comprising each leaf. The peduncle is approximately 7 mm in length (Fig 7E).

The sclerites are predominantly three-flanged spindles and rods (0.04–0.85 mm in length). Each polyp leaf is subtended by a conspicuous V-shaped or fan-shaped polyp leaf armature of relatively large sclerites (Fig 1). The fan-shaped armature is narrowly V-shaped and gradually tapers proximally. The ends of each sclerite may be acute and pointed or truncated and blunt. Some sclerites are minutely toothed on a portion of the margins or on one terminal

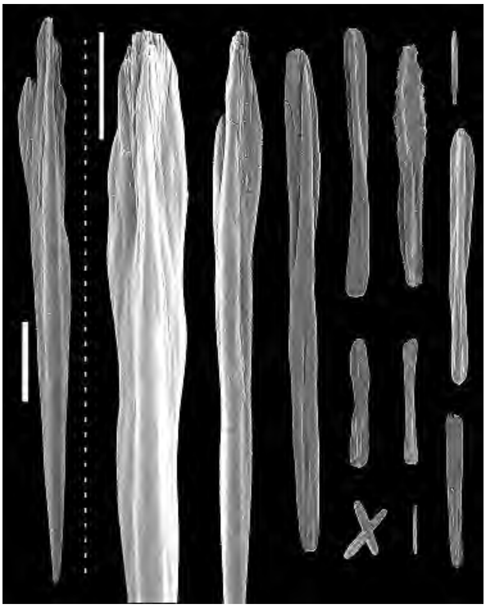

FIGURE 5. *Stylatula diminutiva* sp. nov. SEM of sclerites from region of the polyp leaf armature (Non-type CAS 203513); scale bars = 0.10 mm.

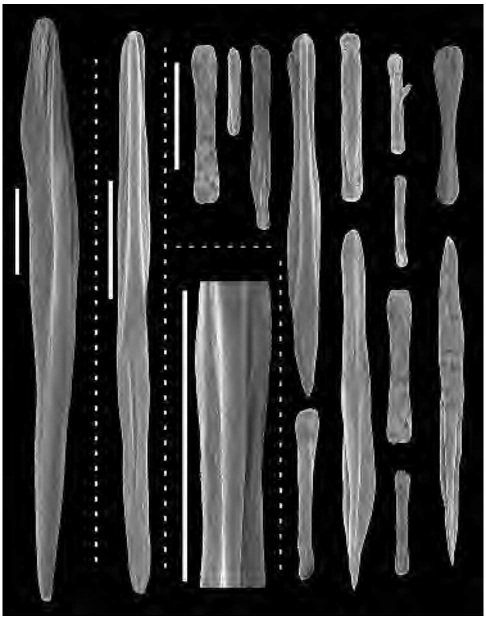

FIGURE 6. *Stylatula diminutiva* sp. nov. SEM of sclerites from region of the polyp leaf armature (Paratype CAS 203514); scale bars = 0.10 mm.

apex. Small, cross-like sclerites may also be present. Some sclerites may also have a short side branch (Figs. 5–6).

**ETYMOLOGY**.— The specific epithet is derived from the Late Latin, *deminutivum* (indicating small size); in reference to the miniature size of the colonies relative to those of other species in the genus.

**DISTRIBUTION**.— Otsuchi Bay, Iwate Prefecture, Japan; 44–120 m depth range.

**VARIATION**.— The polyp leaves that comprise a single pair can be arranged oppositely (as in the holotype CAS 198016) or sub-alternately (as in CAS 203513). The four entire specimens examined ranged in length from 36–60 mm.

## DISCUSSION AND CONCLUSIONS

A new species of the pennatulacean genus *Stylatula* is here described from Japan, and represents the most diminutive species in the genus (< 60 mm in length). With the addition of this new species, the genus is comprised of thirteen species that are currently considered valid (Table 1). The known distribution of the *Stylatula* is currently recognized as being restricted to the margins of the Pacific and Atlantic Oceans (Fig. 9). The recent descriptions of *Stylatula austropacifica* from New Zealand and the new species described below from Japan, have extended the range of the genus from the North American west coast to the margins of the western Pacific. Unlike other species of the genus, the sclerites comprising the polyp leaf armature of *Stylatula austropacifica* are not three-flanged (Fig. 8).

The first two species of the genus that were described, *Stylatula elongata* (Gabb, 1862) and *S. gracilis* (Gabb, 1864), were both first described from California. Gabb (1864:120) distinguishes *Stylatula gracilis* from *S. elongata* (both species were originally described by him in the genus *Vir-*

Figure 7. Wet-preserved colonies of Pacific Ocean species of *Stylatula*. A-C. *Stylatula elongata* (CAS 173213); scale bars: A = 40 mm, B & C = 15 mm. D-F. *Stylatula diminutiva* sp. nov.; scale bar = 10 mm. D. (CAS 203513). E. Holotype (CAS 198016). F. Paratype (CAS 198017). G. *Stylatula austropacifica* Paratype (CAS 173209); scale bar = 30 mm.

*gularia*) by its more slender form, proportionally large polypiferous lobes, cylindrical stem without grooves and comparatively small portion of the stem bearing the lobes. No mention is made of sclerites. Both species have been recorded from Monterey Bay, central California.

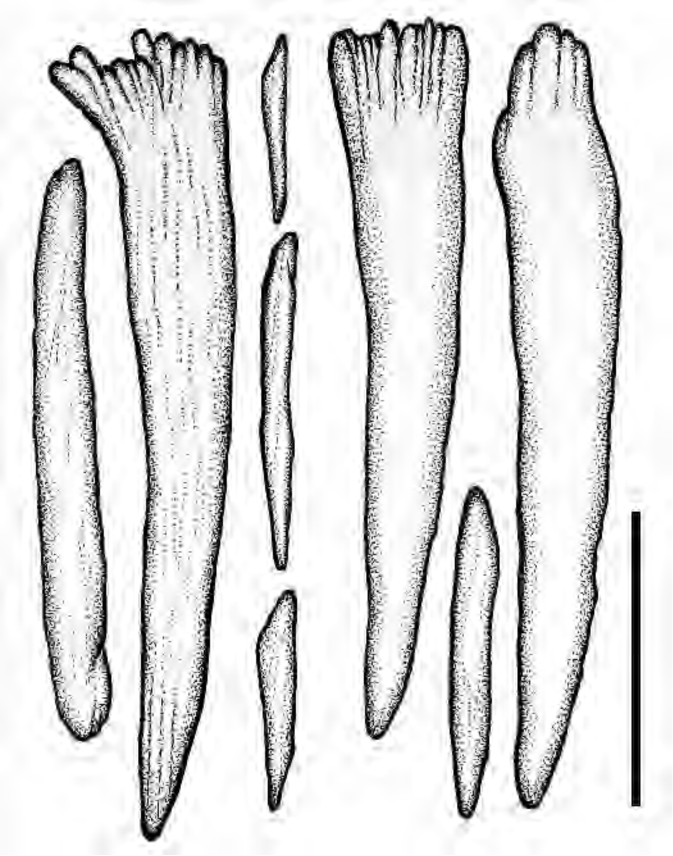

FIGURE 8. *Stylatula austropacifica,* sclerites from the holotype (CAS 173209), showing that they are not three-flanged; scale bar = 0.50 mm.

Kükenthal (1915: 68) distinguishes the species as follows: *S. elongata* with polyp calyces separate to the base and $\leq 24$ polyps per polyp leaf, and *S. gracilis* with polyp calyces fused at the base and 13–18 polyps per leaf. It is uncertain as to Kükenthal's exact meaning regarding the degree of fusion of the polyp cup or calyx as the large sclerites that form the fan-like armature subtending the polyp leaves never fuse, but rather may be in very close proximity or may overlap slightly. In addition, it is difficult to use the number of polyps in a given polyp leaf as diagnostic for species, since variation in colony age and size cannot be assessed by examining a small number of preserved specimens.

Nutting (1909:700) records *Stylatula elongata* from San Diego in the south to as far north as Sausalito in San Francisco Bay. Furthermore, he states that Verrill's specimens (presumably referring to *S. gracilis* Verrill, 1864) were from Panama and Cabo San Lucas, Mexico. He ends with a somewhat confusing statement, "Verrill regards this species of Gabb's as identical with his own *Stylatula elongata*; the priority, however, belongs to the species named by Gabb."

In consideration of the foregoing arguments, it is possible that the two species are synonymous or alternatively that *Stylatula elongata* is a more northern species (at least as far north as British Columbia to San Diego in the south), while *S. gracilis* (if valid) has a more southern distribution (southern tip of Baja California to the Pacific coast of Panama). However, a comparative examination of type material is necessary to make an adequate taxonomic assessment. One additional note: the California Academy of Sciences Invertebrate Zoology collection data base has a total of 68 records for these two species. Of these, 66 are allocated as *Stylatula elongata* and only two are identified as *S. gracilis*. One of the latter is from Panama.

TABLE. 1. The thirteen species of *Stylatula* currently considered valid (Williams 2014; Williams and Matsumoto, present paper).

| Species | Distribution |
|---|---|
| *S. antillarum* Kölliker, 1872 | Caribbean Sea and Gulf of Mexico |
| *S. austropacifica* Williams, 2007 | New Zealand |
| *S. brasiliensis* (Gray, 1870) | Brazil |
| *S. darwini* Kölliker, 1870 | Brazil to Argentinian Patagonia |
| *S. diadema* Bayer, 1959 | Surinam |
| ***S. diminutiva* Williams & Matsumoto sp. nov.** | Japan |
| *S. elegans* (Danielssen, 1860) | North Atlantic Ocean |
| *S. elongata* (Gabb, 1862) | British Columbia to California; Panama? |
| *S. gracilis* (Gabb, 1864) | Central to southern California; Panama? |
| *S. kinbergi* Kölliker, 1870 | Locality unknown |
| *S. lacazi* Kölliker, 1870 | Locality unknown |
| *S. macphersoni* López-González, Gili & Williams, 2001 | Namibia |
| *S. polyzoidea* Zamponi & Pérez, 1997 | Argentina |

FIGURE 9. Map of the Pacific and Indian Oceans showing the known geographic distribution of the genus *Stylatula*. Arrows point to type localities of 11 of the species. Localities of *S. lacazi* and *S. kinsbergi* are not known.

## Key to the Pacific Ocean Species of *Stylatula*

1a. Sclerites of the polyp leaf fans are not three-flanged. Polyps per polyp leaf 4–6 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. austropacifica*

1b. Sclerites of the polyp leaf fans are conspicuously three-flanged . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Mature colonies < 65 mm in length. Polyps per polyp leaf 2–4. Large needle-like sclerites of the polyp leaf fans less than 7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. diminutiva*

2b. Mature colonies > 65 mm in length. Polyps per polyp leaf more than 5. Large needle-like sclerites of the polyp leaf fans 9–12 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Number of polyps per polyp leaf up to 18 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. gracilis*

3b. Number of polyps per polyp leaf up to 24 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *S. elongata*

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## LITERATURE CITED

BALSS, H. 1910. Japanische Pennatuliden. In: Doflein, F. ed. *Beiträge zur Naturgeschichte Ostasiens. Abhandlungen der Mathematisch-Physischen Classe der Königlisch Sächsischen Gesellschaft der Wissenschaften* 1 (10, suppl.):1–106.

BAYER, F. M. 1956. Octocorallia. Pages 163–231 *in* R. C. Moore, ed., *Treatise on Invertebrate Paleontology Part F. Coelenterata.* The University of Kansas Press and the Geological Society of America and University of Kansas Press, Lawrence, Kansas, USA. 498 pp.

GABB, W. M. 1862. Description of Two New Species of Pennatulidae from the Pacific Coast of the United States. *Proceedings of the California Academy of Natural Sciences,* ser. 1, 2:166–167.

GABB, W. M. 1864. Description of new a species of *Virgularia* from the coast of California. *Proceedings of the California Academy of Natural Sciences,* ser. 1, 3(2):120.

GRAY, J. E. 1860. Revision of the family Pennatulidae, with some descriptions of some new species in the British Museum. *Annals and Magazine of Natural History*, ser. 3, 5:20–25.

GRAY, J. E. 1870. *Catalogue of Sea-pens or Pennatulariidae in the Collection of the British Museum*. British Museum, London, England, UK. 40 pp.

HICKSON, S. J. 1916. The Pennatulacea of the Siboga Expedition, with a general survey of the order. *Siboga Expeditie Monographs* 14 Livr 77:1–265.

JUNGERSEN, H. F. E. 1904. Pennatulida. *Danish Ingolf-Expedition* 5(1):1–95.

Kölliker, R. A. von. 1869–1872. Anatomisch-Systematische Beschreibung der Alcyonarien. I. Die Pennatuliden. *Abhandlungen von der Senckenbergischen naturforschenden Gesellschaft* 7:111–255 (1869); 487–602 (1870); 8:85–275 (1872).

Kölliker, R. A. von. 1880. Report on the Pennatulida dredged by H.M.S. *Challenger* during the years 1873–1876. *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876. Zoology* 1(2) 1–41.

Kűkenthal, W. 1915. Pennatularia. *Das Tierreich* 43:1–132. Verlag von R. Friedländer, Berlin, Germany.

Kűkenthal, W. and H. Broch.1911. Pennatulacea. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 13(1) Zweites Heft. pp 113–576.

Nutting, C. C. 1909. Alcyonaria of the California Coast. *Proceedings of the United State National Museum* 35(1658):681–727.

Verrill, A. E. 1868. Review of the corals and polyps of the west coast of America. *Transactions of the Connecticut Academy of Arts and Sciences* 1:377–422.

Williams, G. C. 1990. The Pennatulacea of southern Africa (Coelenterata, Anthozoa). *Annals of the South African Museum* 99(4):31–119.

Williams, G. C. 1995. Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. *Zoological Journal of the Linnean Society* 113:93–140.

Williams, G. C. 2007. New species of the pennatulacean genera *Acanthoptilum* and *Stylatula* (Octocorallia: Virgulariidae) from New Zealand and the Campbell Plateau: both genera previously considered endemic to the west coast of the American and Atlantic Ocean. *Proceedings of the California Academy of Sciences*, ser. 4, 58(15):339–348.

Williams, G. C. 2011. The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). *PLoS One* 6(7):1–11.

Williams, G. C. 2014. *Stylatula* Verrill, 1864. Accessed through: World Register of Marine Species at <*http://www.marinespecies.org/aphia.php?p=taxdetails&id=128502*> on 2015-02-13. Cited 12 February 2015.

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# A Review of the Genus *Cyclosomus* Latreille (Coleoptera: Carabidae: Cyclosomini) in the Afrotropical Region

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**A comparative morphological study of nearly 300 specimens of *Cyclosomus* Latreille accumulated through loans has permitted recognition of six species in the Afrotropical Region and a seventh species, *C. flexuosus*, probably introduced into northeastern Africa from the Oriental Region. A key is provided for the identification of adults to species and the known geographical distribution of each species is summarized. Also included is discussion of geographical range patterns, sympatry, and syntopy in the fauna. Lectotypes are designated for nine species-group names (*C. basalis* Kolbe, *C. buquetii* Dejean, *C. destitutus* Dupuis, *C. equestris* Boheman, *C. madecassus* Fairmaire, *C. rousseaui* Dupuis, *C. rugifrons* Jeannel, *C. seineri* Kuntzen and *C. somalicus* Alluaud) and two new synonymies are proposed (*Cyclosomus buqueti somalicus* Alluaud as a junior synonym of *C. collarti* Burgeon and *C. rugifrons* Jeannel as a junior synonym of *C. equestris* Boheman). No new species are described.**

KEYWORDS: Coleoptera, Carabidae, Cyclosomini, *Cyclosomus*, Afrotropical Region, distribution, key to species

*Cyclosomus* Latreille (1829) is a modestly diverse genus in the carabid beetle tribe Cyclosomini of subfamily Lebiinae, with only 13 described species at present (Lorenz 2005). The cumulative geographical range of included species is restricted to the Oriental and Afrotropical Regions. Members of all species in the genus share a common overall body form (as in Fig. 1) and all are basically pale in dorsal body color, with or without a variously developed pattern of dark areas on the pronotum and elytra. All observations of these beetles alive, as well as some detailed collection records, confirm that they live on the exposed sandy banks of mid- to large-size rivers or on sandy lake shores. Active on the surface mainly at night and hidden in the sand during the day, they can be driven to the surface by splashing water on the sand or by compressing the sand with one's feet (Jeannel 1949). If so disturbed, they can dig themselves back into the sand with surprising speed (Nietner 1857), aided no doubt by uniquely modified front tarsi and tibiae. Examination of gut contents has shown that they are general predators on other arthropods in their habitat, and numerous records of their collection at lights indicate that they can and do fly, at least at night. In their basic body form and coloration, in their habitat preferences and behavior, and also in their geographical range, they are very similar to members of the genus *Omophron* (tribe Omophronini), although the two groups are not closely related.

Recently, while obtaining material on loan from museums in North America and Europe in support of a study on the cyclosomines of an area in western Yunnan Province, China, I received a few specimens of *Cyclosomus* from the Afrotropical Region, mixed in with specimens from the

Oriental Region. This piqued my interest in learning more about the Afrotropical members of the genus, and I decided to solicit as much material from that region as possible for a taxonomic review. Individuals in charge of several collections (see below) generously made specimens in their care available on loan, including type specimens for virtually all the nominal species and subspecies names.

The history of taxonomic work on *Cyclosomus* in the Afrotropical region is mainly one of a few isolated descriptions of new species (Dejean 1831; Kolbe 1897; Fairmaire 1898; Jeannel 1949) or subspecies (Dupuis 1912; Kuntzen 1919), with minimal associated comparative information in most cases. Dupuis (1912) provided a detailed description of *Cyclosomus rousseaui* Dupuis and a key to African species of the genus, in which he distinguished four species, plus one additional subspecies. No synthetic study of the fauna has been published since then.

A study of the material accumulated through loans has permitted me to recognize six and perhaps seven species represented in the Afrotropical fauna, to recognize features of form and structure that distinguish them, to create a key for identification of their respective adults, and to summarize their known geographical distributions. To promote nomenclatural stability, lectotypes are designated where appropriate; two new synonymies are also proposed. No new species are described here.

## MATERIALS AND METHODS

**MATERIALS.**— A total of 286 cyclosomine specimens from the Afrotropical Region were examined during this study, including the primary type specimens for all species names and their synonyms except for those of *Cyclosomus madecassus* Fairmaire. More than 200 additional specimens, including type specimens, other identified specimens and undetermined specimens from the Oriental Region, were also examined. Codens used throughout this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

| | |
|---|---|
| AMNH | American Museum of Natural History, New York, New York, U.S.A. |
| BMNH | British Museum (Natural History), London, United Kingdom. |
| CAS | California Academy of Sciences, San Francisco, California, U.S.A. |
| IRSNB | Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France. |
| MRAC | Musée Royal de l'Afrique Centrale, Tervuren, Belgium. |
| NMNH | U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. |
| NHRS | Naturhistoriska Riksmuseet, Stockholm, Sweden. |
| ZMHB | Museum für Naturkunde der Humboldt-Universität, Berlin, Germany. |

**EXAMINATION OF SPECIMENS.**— Specimens were examined using a Leica MZ9.5 stereoscopic microscope with a Proline 80 LED Ring Illuminator.

**MEASUREMENTS.**— Several measurements (Fig. 1) were recorded for specimens examined: head length (LH), measured from the apex of the labrum to the occipital ridge of the head; pronotal length (LP), measured along midline from anterior margin to posterior margin (i.e., length of anterior angles not included in LP); pronotal width at widest point (WP); and elytral length (LE), measured from the basal groove of the scutellum (i.e., the point at which base of the pronotum contacts the scutellum, which is exposed in specimens where the forebody is bent downward relative to the elytra) to the apex of longer elytron. Body length (BL) was calculated as the sum of LH + LP + LE. The ratio of width to length of pronotum (WP/LP) was calculated based on those measurements. All measurements were taken with the aid of the Leica MZ9.5 stereoscopic microscope fitted with ocular grid and calibrated scale reticules.

**Color and color patterns.**— The predominant features used to describe and distinguish *Cyclosomus* species throughout the taxonomic history of this taxon have been those dealing with color and/or color pattern. To illustrate this point, I need only to cite Dupuis' (1912) key to the African *Cyclosomus*, which is the most comprehensive key for that fauna to date. With it, he distinguished four species and an additional subspecies on the basis of color (including presence or absence of metallic reflection) and color pattern only. The problem with such reliance on these features is that, in several if not all species, they are highly varied, both within and between populations, and undoubtedly subject to intense selection for concealment from predators in the open beach environment in which these beetles live. These color patterns and variations among them are very similar to those seen among *Omophron* species (Carabidae, tribe Omophronini), which share the same habitats.

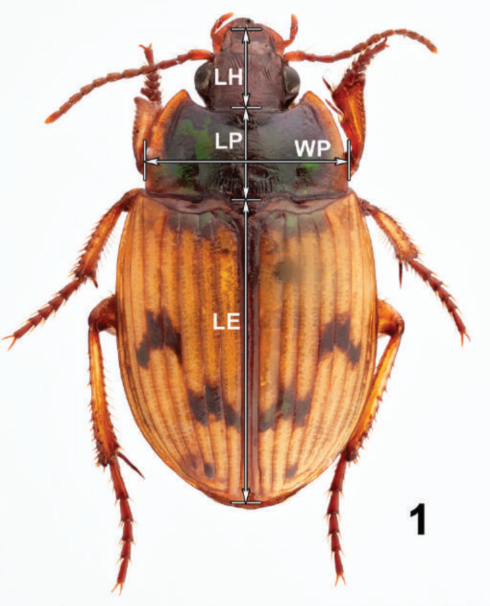


Figure 1. Digital photograph showing locations and limits of measurements; LE = length of elytra, LH = length of head, LP = length of pronotum, WP = width of pronotum.

Members of all species of *Cyclosomus* are basically pale (testaceous to a pale reddish brown) in ground color with variously developed contrasting dark patterns. Up to four dark elements, which appear to vary independently, are involved in the *Cyclosomus* color pattern, each of which may be dark and well developed, absent, or present at a state somewhere between these extremes. (1) The pronotum may be completely pale (Fig. 13–14) or have the disk darker, ranging from reddish brown (Fig. 11) to piceous (Fig. 4) or even black in different species, with variation in the tone even within populations and/or species. (2) The basal eighth of the elytra (from the midline to the lateral edge of interval 5), together with the length of interval 1, may be entirely pale (Fig. 13) or some darker tone (Figs. 6–12) up to and including black in some individuals. (3) The elytral middle transverse dark band may be present as a broad, continuous band extending from the midline to the lateral edge of interval 9 and extended anteriorly or posteriorly on that interval (Fig. 11) or variously narrowed, laterally limited, discontinuous (Figs. 1–3, 6–14) or even completely absent (Fig. 4). Again, at least some variation in the development of this band or its fragmented homologs is found both within and between populations of most of the species. (4) A subapical dark spot may also be present and well developed (Fig. 11) on each elytron, smaller or less distinctly developed (Figs. 1, 9, 10 and 13) or absent (Figs. 2–8, 12 and 14). Of course all of these dark areas may be indistinct or even invisible in newly-emerged adults that are still teneral and have not yet developed their full pigmentation pattern. Such individuals are difficult if not impossible to properly identify with color characters alone. Another feature that is useful in distinguishing members of some species, metallic reflection, requires presence of a dark background to be seen distinctly. Consequently, teneral specimens may not exhibit metallic reflection that would be visible if they were fully pigmented. All the above comments are provided as a caution against reliance on the most obvious features of the beetles, their colors and color patterns, in attempts to identify them.

**Illustrations.**— Digital images of whole specimens and particular structures were taken using a Visionary Digital BK Lab System with a Canon EOS 5D Mark II digital camera.

**Distributional data.**— Because locality names and geopolitical units throughout Africa have changed so dramatically and repeatedly over the last few centuries, type localities are cited using the current country, regional and locality names for them, not necessarily as in the original citations. Locality records for other specimens have also been converted to their current names where this could be done unambiguously. Maps illustrating the distributions of localities for specimens examined were modified from the "Whole world – land and oceans 12000.jpg" map available from Wikipedia Commons online at <*http://en.wikipedia.org/wiki/File:Whole_world_land_and_oceans_12000.jpg.*>

## Taxonomy

### Tribe Cyclosomini LaPorte de Castelnau, 1834

### Genus *Cyclosomus* Latreille

*Scolytus* Fabricius, 1790:221, in part [junior homonym of *Scolytus* Geoffroy, 1762] (type species *Carabus limbatus* Fabricius, 1801, designated by Latreille (1810:426). Fabricius (1792:180); Bousquet (2012:89).
*Cyclosomus* Latreille, 1829:394 (type species *Carabus flexuosus* Fabricius, 1775, by monotypy).

### Key for Identification of Adults of *Cyclosomus* species of the Afrotropical Region

Both male and female adults of *Cyclosomus* species from the Afrotropical Region can be identified using the key below. I have tried to avoid gender-specific features as much as possible in creating the key, and where features unique to males are used, they are presented only as secondary in importance. However, these features can be very helpful in confirming the identification of males. Male specimens of all species included in the key have small pads of adhesive setae on the ventral surfaces of front tarsomeres 1 to 3. Females have no such pads. Although in most carabid beetle species these front tarsomeres are also distinctly broader in males than in females, in the Afrotropical *Cyclosomus* species these differences are very slight and therefore difficult to assess. Contributing to this difficulty is the fact that both males and females have the basal three tarsomeres asymmetrically expanded laterally as flat plates that undoubtedly aid in digging into the sandy substrate they inhabit. I also recommend that users of the key review the cautions given in the section entitled "Color and color patterns" under Materials and Methods above.

1a. Elytra (Figs. 2a, 3) distinctly broader basally than base of pronotum, with humeri slightly projected anteriorly and broadly rounded, not angulate; pronotum (Fig. 15) with three to six lateral setae anterior to middle on each side, anterior angles narrow, sharply pointed, lateral margins distinctly sinuate subapically . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus basalis* Kolbe
1b. Elytra (Figs. 1, 4–14) not or only slightly broader at base than base of pronotum, with humeri sharply angulate; pronotum (Figs. 15–23) with one lateral setae at or anterior to middle on each side (very few specimens with a second such seta unilaterally), anterior angles broadly rounded to sharply pointed, lateral margins not or only faintly sinuate subapically . . . . . . . . . . . 2

2a. Elytral color pattern as in Fig. 11, with middle dark transverse band broad and complete across elytra, confluent with dark interval 1, and expanded across middle half of interval 9, subapical dark spot distinct on intervals 4 and 5; prosternal intercoxal process (Fig. 28) long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus flexuosus* (Fabricius)
2b. Elytral color pattern (Figs. 1–3, 4–10, 12–14) not as above, middle dark transverse band absent or interrupted, not extended to or expanded on interval 9, subapical dark spot absent, present

only on interval 4, or present on intervals 4 to 6; prosternal intercoxal process (Figs. 24–26, 29–30) short to long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3a. Pronotum (Figs. 17–18) with two or more setae inserted on anterior margin at and medial to anterior angles, anterior angles broadly or moderately rounded; size large (body length 9.0 to 10.7 mm); dorsum without metallic reflection; forebody dark reddish-brown, broadly and slightly paler laterally, elytral middle transverse band piceous or black; male with middle tarsomeres 1 to 3 laterally expanded and with ventral pads of adhesive setae (Fig. 32) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus collarti* Burgeon

3b. Pronotum (Figs. 16, 19–20, 22–23) without setae on anterior margin, anterior angles more narrowly rounded to pointed; size smaller (body length varied, 6.3 to 10.3 mm); forebody color varied from piceous to pale reddish-brown, width of lateral pronotal pale areas and elytral color pattern also varied; male with middle tarsomeres 1 to 3 not laterally expanded and without pads of adhesive setae on ventral surfaces (Fig. 31) . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4a. Pronotum pale yellow-tan to reddish brown, broadly and only slightly paler laterally, without metallic reflection; elytral color pattern (Figs. 13–14) with interval 1 not or only slightly darker than pale sections of other intervals, lateral portion of interrupted middle transverse band present on full width of interval 8 . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus rousseaui* Dupuis

4b. Pronotum dark reddish-brown or piceous, with contrasting paler areas laterally, dark areas with distinct to faint metallic green (bronze in a few specimens) reflection; elytral color pattern varied (Figs. 4–5, 10, 12), with interval 1 distinctly darker (dark brown to black) than pale sections of other intervals, lateral portion of interrupted middle transverse band not present on interval 8 or present only on the medial edge of interval 8. . . . . . . . . . . . . . . . . . . . . . . . . . 5

5a. Pronotum (Figs. 19–20) with lateral pale band narrow anteriorly, widened basally, anterior angles narrow, sharply pointed or narrowly rounded apically; pronotum relatively narrow, ratio WP/WPB less than 2.25 (mean = 2.15, n = 59); male with median lobe of aedeagus with shaft thick and abruptly tapered subapically, ventral margin of shaft slightly recurved subapically (Fig. 36), slightly deflected right at apical third in dorsal view (Fig. 43); apical lamella short, with sides evenly convergent to broadly rounded apex (Fig. 43) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus equestris* Boheman

5b. Pronotum (Figs. 16, 22) with lateral pale band broad anteriorly and distinctly widened basally, anterior angles broader, narrowly to broadly rounded apically; pronotum relatively broader, ratio WP/WPB greater than 2.30; male genitalia with different form. . . . . . . . . . . . . . . . . . 6

6a. Prosternal intercoxal process (Fig. 25) long; body length 7.8 mm or less; dark areas on pronotum and elytra with vivid metallic green reflection; male with median lobe of aedeagus with shaft broadly tapered apically, ventral margin of shaft straight or nearly so in apical third (Fig. 34), distinctly offset right at apical third in dorsal view (Fig. 41); apical lamella very short, with sides evenly convergent to broadly rounded apex (Fig. 41); specimens from mainland Africa . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus buquetii* Dejean

6b. Prosternal intercoxal process (Fig. 29) short; body length more than 8.0 mm; dark areas on pronotum and elytra with faint metallic green reflection; male with median lobe of aedeagus with shaft thick and abruptly tapered subapically, ventral margin of shaft nearly straight in apical half (Fig. 38), very slightly offset right at apical third in dorsal view (Fig. 45); apical lamella short, slightly deflected ventrally (Fig. 38), with sides evenly convergent to broadly and roundly pointed apex (Fig. 45); specimen from Madagascar . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyclosomus madecassus* Fairmaire

### *Cyclosomus basalis* Kolbe

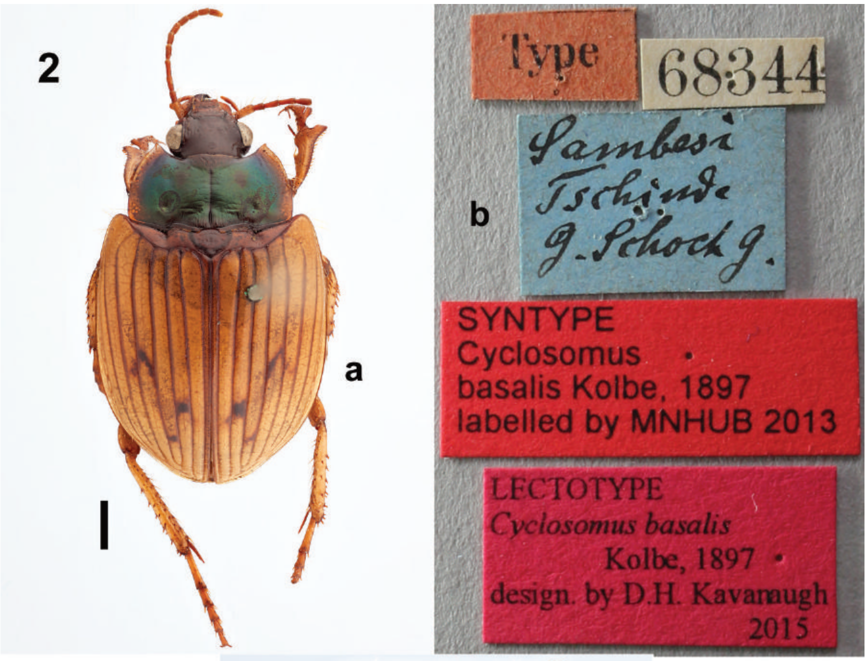
*Cyclosomus basalis* Kolbe, 1897:349. LECTOTYPE (Fig. 2), here designated, a female, in ZMHB, labeled: “Type” [faded red label]/ “68344”/ “Sambesi Tschinde, G. Schoch G.” [handwritten blue label]/ “Syntype *Cyclosomus basalis* Kolbe, 1897 labelled by MNHUB 2013” [redlabel]/ “LECTOTYPE *Cyclosomus basalis* Kolbe, 1897, design. by D.H. Kavanaugh 2015” [red label].Type locality: Mozambique, Zambezia Province, Chinde. Dupuis (1912:284); Csiki (1932:1294); Lorenz (2005:452).

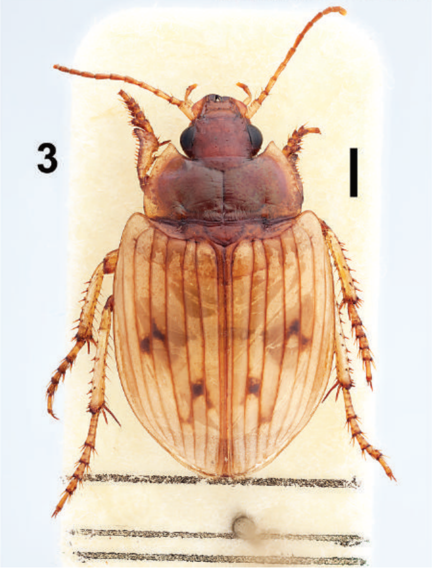
**Diagnosis.**— Adults of *C. basalis* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Figs. 2a and 3. Size moderate for genus, BL = 9.2–9.6 mm. Head dark brown to piceous or pale reddish-brown; pronotum dark brown to piceous or reddish-brown, with lateral pale areas narrow, only slightly broader basally; elytra mainly pale yellow-tan, darker color pattern (Figs. 2a, 3) with area anterior to basal margin and interval 1 light reddish brown, middle transverse dark band reddish-brown to piceous, W-shaped, extended laterally only to interval 5 or 6, very thin or discontinuous, subapical dark spot absent; dark areas of pronotum with distinct to faint metallic green reflection, dark areas of elytra without metallic reflection. Pronotum (Fig. 15) with anterior angles narrow, sharply pointed, lateral margins distinctly sinuate subapically, with three to six lateral setae anterior to middle on each side, without setae on anterior margin,. Prosternal intercoxal process (Fig. 24) medium-length. Elytra (Figs. 2a, 3) distinctly broader basally than base of pronotum, with humeri slightly projected anteriorly and broadly rounded, not angulate. Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (see Fig. 31). Male with median lobe of aedeagus as in Figs. 33 and 40, with shaft gradually tapered apically and ventral margin smoothly arcuate (Fig. 33); apical lamella short and broadly rounded apically (Fig. 40).

Adults of *C. basalis* are easily distinguished from members of all other *Cyclosomus* species by their broadly rounded elytral humeri and pronotum much narrower basally than the base of the elytra. They are also unique in having three or more lateral setae in the apical half along the pronotal margin. Members of all other species have a single seta on each side at or anterior to the middle of the pronotum [although a very few specimens have a second anterolateral seta unilaterally]. Specimens examined from Mozambique have darker heads and pronota than those from Tanzania and Malawi. It will be interesting to see if this apparent pattern of geographical variation is confirmed by additional specimens collected in the future from these areas or from areas between them.

**Geographical distribution.**— (Fig. 47.) At present, known only from a narrow zone in East Africa, extending from central Tanzania, through Malawi, and south to the Zambezi River Delta in Mozambique. I examined a total of 5 specimens (1 male and 4 females) from the following localities: **Malawi:** Northern Region (5 km S of Chintheche on shore of Lake Malawi [ZMHB]). **Mozambique:** Sofala Province (Caia [BMNH]); Zambesia Province (Chinde [ZMHB]). **Tanzania:** Iringa Region (50–70 km W of Iringa [ZMHB]). **Other records:** “E. Africa” ([BMNH]).

**Habitat distribution.**— Label data associated with the specimen from Lake Malawi (see above) indicate that it was collected on the sandy shore of the lake. These beetles probably occur on the open, sandy banks of lakes and rivers within their range in eastern Africa.They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian or lacustrine habitats.





FIGURES 2–3. *Cyclosomus basalis* Kolbe. Fig. 2. Lectotype female; a, digital photograph of dorsal habitus; b, specimen labels. Fig. 3. Digital photograph of male, dorsal habitus (5 km S of Chintheche on shore of Lake Malawi, Northern Region, Malawi). Scale lines = 1.0 mm.

### *Cyclosomus buquetii* Dejean

*Cyclosomus buquetii* Dejean, 1831:812. LECTOTYPE (Fig. 4), here designated, a female, in MNHN, labeled: "C[?, pin hole through a second, illegible, letter]" [handwritten on small blue square]/ "Buquetii sp. n., Seneg.Super" [handwritten on blue label/ "LePrieur." [handwritten on blue label]/ "Ex Musaeo Chaudoir" [red lettering on white label]/ "TYPE Buqueti" [red label]/ "LECTOTYPE *Cyclosomus buquetii* Dejean, 1831, design. by D.H. Kavanaugh 2015" [red label]. Type locality: northern Senegal. Lorenz (2005:452).

*Cyclosomus buqueti seineri* Kuntzen. 1919:121. LECTOTYPE (Fig. 5), here designated, a male, in ZMHB, labeled: "D. Sambesi Insel 15.10.06. Seiner S.G." [blue label with "Insel" handwritten]/ "TYPE" [faded red label/ "SYNTYPE Cyclosomus buqueti ssp. seineri Kuntzen, 1919 labelled by MNHUB 2013" [red label]/ "LECTOTYPE *Cyclosomus seineri* Kuntzen, 1919, design. by D.H. Kavanaugh 2015" [red label]. Paralectotypes examined: 1 female, also in ZMHB, labeled as lectotype except last label replaced with "PARALECTOTYPE *Cyclosomus seineri* Kuntzen, 1919, design. by D.H. Kavanaugh 2015" [yellow label]; and 1 female, also in ZMHB, labeled: "D.Sambesi Gebt. ~~10.06.~~ F. Seiner S.G." [blue label]/ "TYPE" [faded red label/ "C. buqueti sbsp. seineri m.[plus one additional illegible word]" [handwritten label]/ "SYNTYPE Cyclosomus buqueti ssp. seineri Kuntzen, 1919 labelled by MNHUB 2013" [red label]/ "PARALECTOTYPE *Cyclosomus seineri* Kuntzen, 1919, design. by D.H. Kavanaugh 2015" [yellow label]. Type locality: Namibia, Caprivi Strip, Impalila. Csiki (1932:1295).

*Cyclosomus buqueti* Dejean.Chaudoir (1876:32); Boheman (1848:189); Kolbe (1897:350); Dupuis (1912:284); Kuntzen (1919:121); Burgeon (1931:309); Csiki (1932:1295); Jeannel (1949:876).

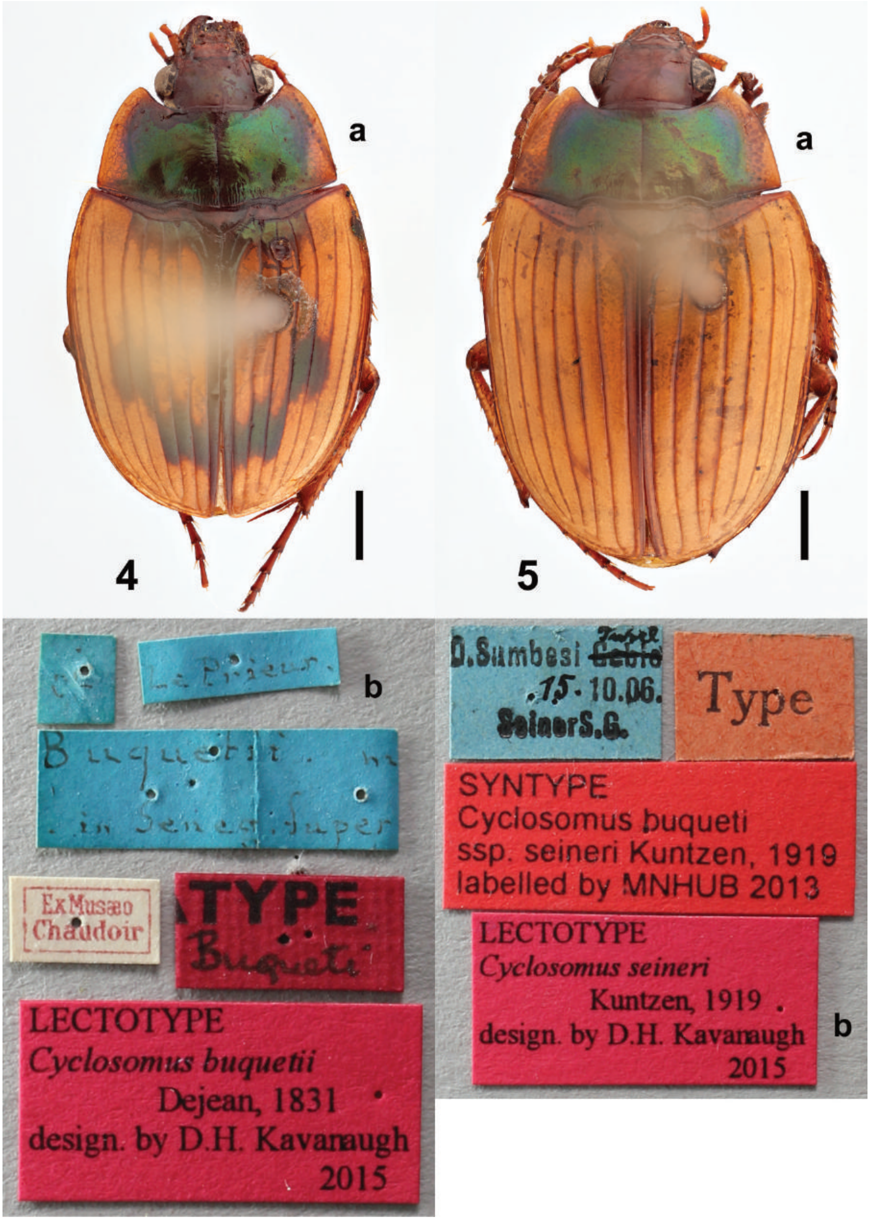
*Cyclosomus equestris,* Chaudoir (1876:32); Dupuis (1912:284), as a synonym.

*Cyclosomus buquetii seineri* Kuntzen.Lorenz (2005:452).

**NOTES ON TYPES AND NOMENCLATURE**.— The name *C. buquetii seineri* was proposed for specimens with the elytral middle transverse dark band absent or represented only by a small dark spot at the apical one-fourth on interval 4. This form (Fig. 5) has been found virtually throughout the range of this species, together at several localities with specimens having more extensively developed middle transverse dark bands (Fig. 4), so maintaining this name as a subspecific epithet seems unjustified.

**DIAGNOSIS**.— Adults of *C. buquetii* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Figs. 4–5. Size small for genus, BL = 6.3–7.8 mm. Head reddish-brown to piceous; pronotum dark brown to piceous with lateral pale areas broad anteriorly and further broadened basally; elytra mainly pale yellow-tan, darker color pattern (Figs. 4–5) with medial basal area and interval 1 light reddish-brown to piceous, middle transverse dark band absent or reddish-brown to piceous, W-shaped, extended laterally only to interval 5 or 6, very thin or discontinuous, subapical dark spot absent; dark area of pronotum with distinct metallic green or bronze reflection. Pronotum (Fig. 16) relatively broad, ratio WPB/LP = 2.28–2.88 (mean = 2.38; n = 34), anterior angles moderately to narrowly rounded or bluntly pointed, lateral margins evenly rounded, not sinuate subapically, with one lateral seta at or anterior to middle on each side (very few specimens with a second such seta unilaterally), without setae on anterior margin. Prosternal intercoxal process (Fig. 25) long. Elytra (Figs. 4–5) not or only slightly broader at base than base of pronotum, with humeri sharply angulate. Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (see Fig. 31). Male with median lobe of aedeagus as in Figs. 34 and 41, with shaft broadly tapered apically, its ventral margin straight or nearly so in apical third (Fig. 34), distinctly offset right at apical third in dorsal view (Fig. 41); apical lamella very short,with sides evenly convergent to broadly rounded apex (Fig. 41).

Adults of *C. buquetii* are most similar in habitus to those of *C. equestris* and *C. madecassus.*



FIGURES 4–5. Type specimens of *Cyclosomus* species; a, digital photograph of dorsal habitus; b, specimen labels. Fig. 4. *C.buquetii* Dejean, lectotype female. Fig. 5. *C. seineri* Kuntzen, lectotype male.

However, they are typically smaller in size (although the smallest adults of *C. equestris* are within the size range of *C. buquetii*) and have a distinctly longer prosternal intercoxal process than members of either species. They also differ from *C. equestris* members in having a relatively broader pronotum with more broadly rounded anterior angles and a lateral pronotal pale band that is distinctly broader anteriorly. From members of *C. madecassus*, they also differ in having more vividly metallic reflection on dark areas of the pronotum and elytra. Males of these three species are also easily distinguished by the form of the median lobe of their genitalia.

GEOGRAPHICAL DISTRIBUTION.— (Fig. 48.) Widespread across Sub-Saharan Africa, from Senegal to Sudan and Somalia, south to South Africa. I examined a total of 37 specimens (9 males and 28 females) from the following localities: **Burundi:** Bujumbura Rural Province (Rusizi River Delta [ZMHB]). **Cameroon:** (no locality [ZMHB]). **Democratic Republic of the Congo:** Bas Congo Province (Banana [IRSNB]); Kasai Oriental (Sankuru "Beni Bendi" [ZMHB]); Katanga Province (Kalemie [IRSNB]). **Malawi:** Northern Region (5 km S of Chintheche on shore of Lake Malawi [ZMHB]). **Mozambique:** Cabo Delgado Province (Porto Amelia [BMNH]); Manica Province (Amatongas [BMNH]); Sofala Province (Beira [BMNH]). **Namibia:** Caprivi Strip (Impalila [ZMHB]). **Senegal:** northern part ([MNHN]). **Somalia:** Awdal Province (Borama [NHRS]). **South Africa:** KwaZulu-Natal Province (Durban [BMNH]; Ithala Game Reserve [ZMHB]). **Sudan:** Khartoum State (Bahr-el-Abiad [NHRS]); West Darfur State (El Geneina [ZMHB]). **Tanzania:** Mbeya Region (Tukuyu [ZMHB]). **Other records:** "E. Africa" ([BMNH]); "Cape" ([BMNH]); "O. Sambesi Gebt." ([ZMHB]); "Wahrsih.: Sambesi" ([ZMHB]).

HABITAT DISTRIBUTION.— Label data associated with the specimens from of Lake Malawi (see above) indicate that they were collected on the sandy shore of the lake. These beetles probably occur on the open, sandy banks of lakes and rivers throughout Sub-Saharan Africa. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian or lacustrine habitats.

### *Cyclosomus collarti* Burgeon

*Cyclosomus collarti* Burgeon, 1931:307. HOLOTYPE (Fig. 6), a male, in MRAC, labeled: "MUSÉE DU CONGO, Ituri: Forêt de Kawa, 20-4–1929 (A. Collart)" [mostly handwritten]/ "Cyclosomus Collarti Type n. sp." [handwritten]/ "HOLOTYPE *Cyclosomus collarti* Burgeon, 1931" [red label] Paratypes examined: 1 female, in IRNSB, labeled: "Ituri: Forêt de Kawa, 20-4-1929 (A. Collart)" [mostly handwritten]/ "Cyclosomus collarti Burg. Paratype" [handwritten]; 3 males and 1 female, in MRAC, labeled: "PARATYPE" [orange label]/ "MUSÉE DU CONGO, Ituri: Forêt de Kawa, 20-4-1929 (A. Collart)" [mostly handwritten]; 1 female, in MNHN labeled: "PARATYPE" [orange label]/ "MUSÉE DU CONGO, Ituri: Forêt de Kawa, 20-4-1929 (A. Collart)" [mostly handwritten]/ "Museum Paris, Coll. Ch. Alluaud" [pale blue label]/ "Cyclosomus collarti Déterm. L. Burgeon" [partly handwritten]; 5 males and 5 females, in MRAC, labeled: "PARATYPE" [orange label]/ "MUSÉE DU CONGO, Ituri: Forêt de Kawa, 30-4-1929 (A. Collart)" [partly handwritten]/ "Forêt de Kawa 30-IV-29 A. Collart" [partly handwritten]; 1 males and 2 females, in MRAC labeled: "PARATYPE" [orange label]/ "MUSÉE DU CONGO, Lac Albert: Forêt de Kawa, 30-4-1929 (A. Collart)" [partly handwritten]/ "Forêt de Kawa 30-IV-29 A. Collart" [partly handwritten]; 5 males and 1 female, in IRNSB, labeled: "Forêt de Kawa, (Lac Albert) 10-IV-29 A. Collart" / "L. Burgeon det. 1930, CYCLOSOMUS collarti Burg."/ "Para-type" [orange label]/ "cf. Rev. Zool. Bot. afr., 20, pp. 307–308"/ "P. Basilewsky vid., 1947, CYCLOSOMUS Collarti Burg."; 2 males and 2 females, in MRAC, labeled: "PARATYPE" [orange label]/ "Forêt de Kawa, (Lac Albert) 10-IV-29 A. Collart" / "COL. MUS, CONGO, Col. P. Basilewsky"; 2 males, in MRAC, labeled: "PARATYPE" [orange label]/ "FORÊT DE KAWA, LAC ALBERT, A. COLLART" / "COL. MUS, CONGO, Col. P. Basilewsky"; 5 males and 2 females, in IRSNB, labeled: "Forêt de Kawa 19-IV-29 A. Collart" [partly handwritten]/ "L. Burgeon det. 1930, CYCLOSOMUS collarti Burg."/ "Para-type" [orange label]/ "cf. Rev. Zool. Bot. afr., 20, pp. 307–308"/ "P. Basilewsky vid., 1947, CYCLOSOMUS Collarti Burg."; 3 males and 4 females, in IRSNB, labeled: "Forêt de Kawa 20-IV-29 A. Collart" [partly handwritten]/ "L. Burgeon det. 1930, CYCLOSOMUS collarti Burg."/ "Para-type" [orange label]/ "cf. Rev. Zool. Bot. afr., 20, pp. 307–308"/ "P. Basilewsky vid., 1947, CYCLOSOMUS Collarti Burg."; 4 males and 5 females, in IRSNB, labeled: "Forêt de Kawa 30-IV-29 A. Collart" [partly handwritten]/ "L. Burgeon det. 1930, CYCLOSOMUS collarti Burg."/ "Para-type" [orange label]/ "cf. Rev. Zool. Bot. afr., 20, pp. 307–308"/ "P. Basilewsky vid., 1947, CYCLOSOMUS Collarti Burg.". Type locality: Democratic Republic of the Congo, Orientale Province, shore of Lake Albert. Alluaud (1935:11); Lorenz (2005:452).

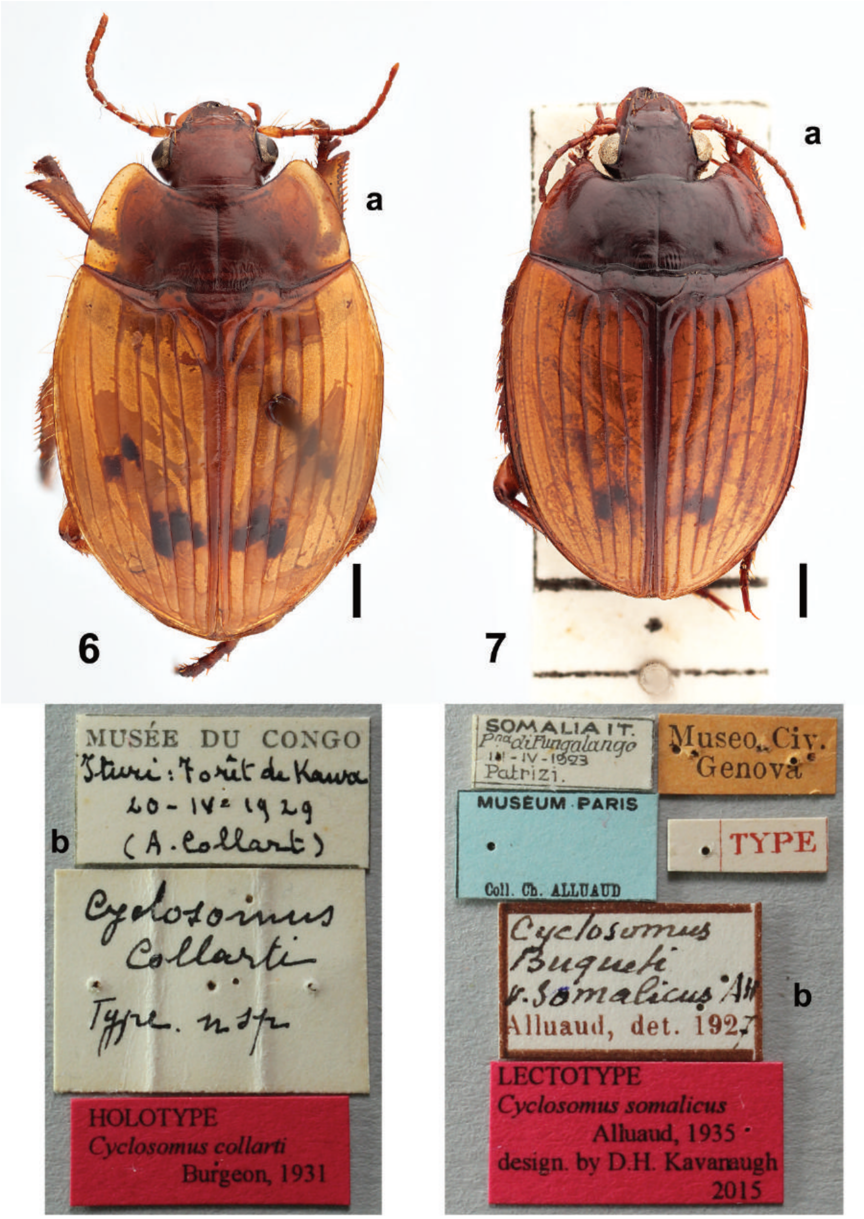
*Cyclosomus buqueti somalicus* Alluaud, 1935:11. LECTOTYPE (Fig. 7), here designated, a female, in MNHN, labeled: "SOMALIA IT., P$^{\text{na.}}$ di Fungalango, III-IV 1923, Patrizi"/ "Museo Civ. Genova" [orange label, facing downward]/ "Museum Paris, Coll. Ch. Alluaud" [pale blue label]/ "TYPE" [red ink on white label]/ "Cyclosomus buqueti v. somalicus Alluaud All., Alluaud, det. 1927"/ "LECTOTYPE *Cyclosomus somalicus* Alluaud, 1935, design. by D.H. Kavanaugh 2015" [red label]. Type locality: Somalia, Jubba River at Fungalango. **NEW SYNONYMY**.

**NOTES ON TYPES AND NOMENCLATURE.**— Although Alluaud described *C. somalicus* as a subspecies of *C. buquetii*, the presence of setae laterally on the anterior margin of the pronotum of the type is a feature unique to *C. collarti* members among all *Cyclosomus* species. Other features of the lectotype of *C. somalicus* are all within the known range of variation seen among *C. collarti* specimens.

**DIAGNOSIS.**— Adults of *C. collarti* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Figs. 6–7. Size moderate to large for genus, BL = 9.0–10.7 mm. Head reddish-brown to dark brown; pronotum reddish-brown to dark brown with lateral pale areas broad and broadened basally; elytra mainly pale yellow-tan, darker color pattern (Figs. 6–7) with area anterior to basal margin (also medial area just posterior to basal margin in some specimens) and interval 1 light reddish brown, middle transverse dark band reddish-brown to piceous, W-shaped, extended laterally only to interval 5 or 6, thick to very thin or discontinuous, subapical dark spot absent; dorsum without metallic reflection. Pronotum (Figs. 17–18) with anterior angles broadly rounded, lateral margins evenly rounded, not sinuate subapically, with one lateral seta at or anterior to middle on each side (very few specimens with a second such seta unilaterally) and with two or more setae inserted on anterior margin at and medial to anterior angles. Prosternal intercoxal process (Fig. 26) very short. Elytra (Figs. 6–7) not or only slightly broader at base than base of pronotum, with humeri sharply angulate. Male with middle tarsomeres 1 to 3 laterally expanded and with ventral pads of adhesive setae (Fig. 32). Male with median lobe of aedeagus as in Figs. 35 and 42, with shaft gradually tapered apically, its ventral margin smoothly arcuate (Fig. 33), slightly offset right at apical third in dorsal view (Fig. 42); apical lamella long, slightly recurved dorsally at apex (Fig. 35), parallel-sided and broadly rounded apically (Fig. 42).

Adults of *C. collarti* can be distinguished from those of all other *Cyclosomus* species by the presence of a fringe of two or more setae on the anterior margin of the pronotum on each side at and/or just medial to the apex of the apical angles. Males of this species are also unique in having the three basal tarsomeres of the middle tarsi laterally expanded and with large pads of adhesive setae ventrally.

**GEOGRAPHICAL DISTRIBUTION.**— (Fig. 49.) Widespread across Sub-Saharan Africa north of the Equator, from Nigeria to Sudan, Ethiopia and Somalia, and south to Cameroon and northern Democratic Republic of the Congo. I examined a total of 168 specimens (75 males and 93 females) from the following localities: **Cameroon:** Central Region (Loko [ZMHB]); North Region (Garoua [ZMHB]). **Democratic Republic of the Congo:** Ituri Province (Lac Albert at Kawa Forest [CAS;



Figures 6–7. Type specimens of *Cyclosomus* species; a, digital photograph of dorsal habitus; b, specimen labels. Fig. 6. *C. collarti* Burgeon, holotype male. Fig. 7. *C. somalicus* Alluaud, lectotype female. Scale lines = 1.0 mm.

IRNSB; MRAC, MNHN]). **Ethiopia:** Gambela Province (Gambela [MRAC]; 2 km N of Gambela [MRAC]). **Nigeria:** Kaduna State (Samaru [BMNH]); Kogi State (Amageda [ZMHB]; Lokoja [BMNH]). **Somalia**: Lower Juba Region (Jubba River at Fungalango [MNHN]). **Sudan:** Khartoum State (Bahr-el-Abiad [NHRS]); North Darfur State (Kutum [ZMHB]); River Nile State (Shendi [BMNH]); West Darfur State (El Geneina [ZMHB]). **Other records:** "Blue Nile" ([BMNH]); "Kamerun, [plus more illegible text]" [handwritten] ([ZMHB]).

**Habitat distribution**.— According to Burgeon (1931), specimens of the type series were collected on the shore of Lake Albert. Label data associated with specimens from localities in Ethiopia (Gambela), Nigeria (Samaru), and Sudan (El Geneina and Shendi) indicate that they were collected at white or mercury vapor lights at night, so members of this species apparently are excellent fliers. These beetles probably occur on the open, sandy banks of lakes and rivers throughout the Sub-Saharan region described above. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian or lacustrine habitats.

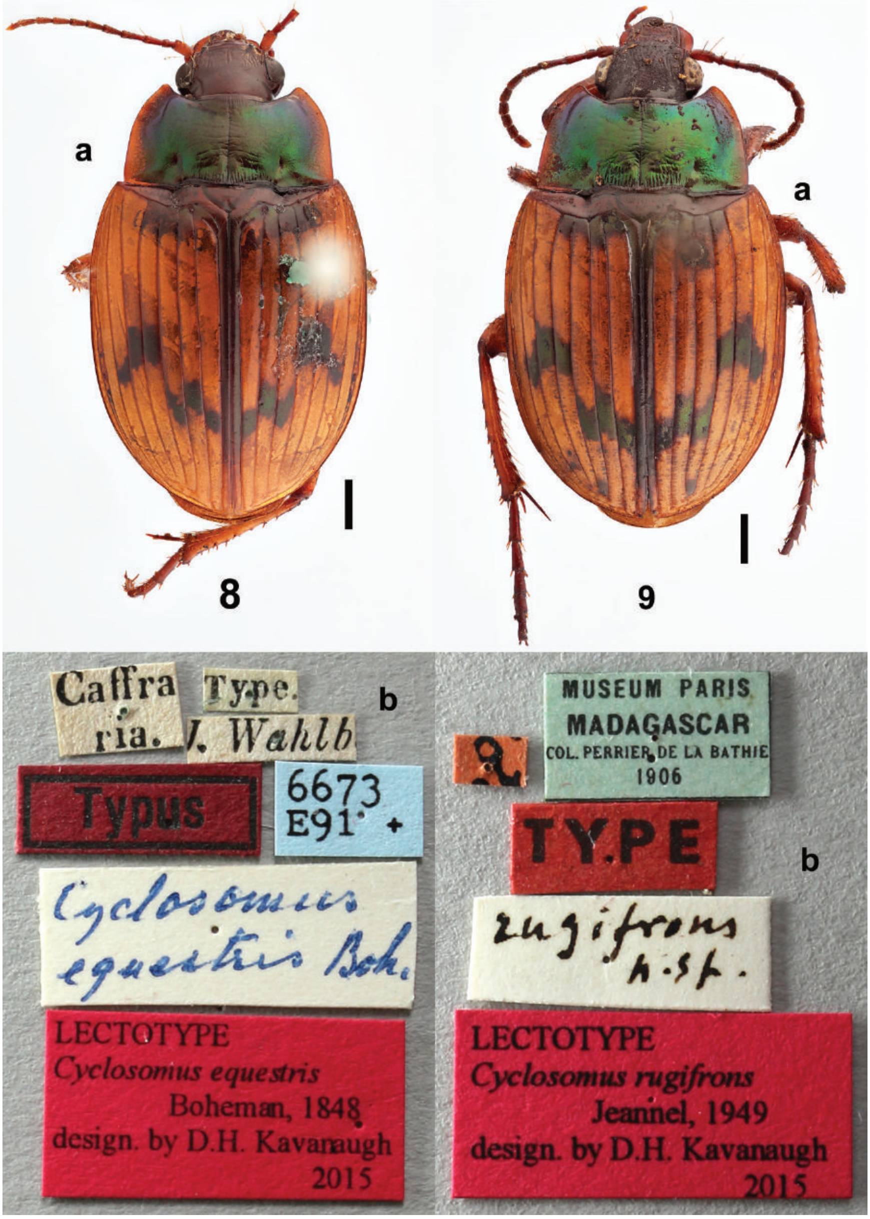
### *Cyclosomus equestris* Boheman

*Cyclosomus equestris* Boheman, 1848:189. LECTOTYPE (Fig. 8), here designated, a male, in NHRS, labeled: "Caffraria."/ "J. Wahlb"/ "Typus" [red label]/ "6673 E91" [pale blue label]/ "Cyclosomus equestris Boh." [handwritten]/ "LECTOTYPE *Cyclosomus equestris* Boheman, 1848, design. by D.H. Kavanaugh 2015" [red label]. Type locality: South Africa, Eastern Cape Province. Fairmaire (1989:222); Kolbe (1987:350); Kuntzen (1919:121); Burgeon (1931:309); Lorenz (2005:452).

*Cyclosomus rugifrons* Jeannel, 1949:876. LECTOTYPE (Fig. 9), here designated, a male, in MNHN, labeled: [small red square with male symbol]/ "MUSEUM PARIS, MADAGASCAR, COL. PERRIER DE LA BATHIE, 1906," [pale blue-green label]/ "TYPE" [red label]/ "rugifrons n.sp." [handwritten]/ "LECTOTYPE *Cyclosomus rugifrons* Jeannel, 1949, design. by D.H. Kavanaugh 2015" [red label]. Type locality: Madagascar, Mahajanga Province, Maevatanana. Lorenz (2005:452). **NEW SYNONYMY**.

**Notes on types and nomenclature**.— In his treatment of the Malagasy species of *Cyclosomus*, Jeannel (1949) compared *C. madecassus* with *C. flexuosus* and *C. buquetii*, but not with *C. equestris*, and *C. rugifrons* only with *C. madecassus*. It is possible that *C. equestris* was unknown to him. The lectotype of *C. rugifrons* is indistinguishable in features of external form and structure and form of the median lobe of male genitalia from specimens of *C. equestris*, which is why I consider *C. equestris* and *C. rugifrons* as synonmys.

**Diagnosis**.— Adults of *C. equestris* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Figs. 8–10. Size exceptionally varied for genus, BL = 7.0–10.3 mm. Head dark reddish-brown to piceous; pronotum reddish-brown to piceous with lateral pale areas narrow anteriorly and broadened basally; elytra mainly pale yellow-tan, darker color pattern (Figs. 8–10) with medial basal area and interval 1 light reddish-brown to piceous, middle transverse dark band absent or reddish-brown to piceous, W-shaped, extended laterally only to interval 6 or 7, thick to very thin or discontinuous, subapical dark spot present or absent; dark area of pronotum with distinct metallic green or bronze reflection, dark areas of elytra without or with only faint metallic green or bronze reflection. Pronotum (Figs. 19–20) relatively narrow, ratio WPB/LP = 2.02–2.23 (mean = 2.15; n = 59), anterior angles moderately rounded to sharply pointed, lateral margins not or only faintly sinuate subapically and moderately (Fig. 19) to very slightly (Fig. 20) arcuate, with one lateral setae at or anterior to middle on each side (very few specimens with a second such seta unilaterally), without setae on anterior margin. Prosternal intercoxal process (Fig. 27) medium-length. Elytra (Figs. 8–10) not or only slightly broader at base than base of pronotum, with humeri sharply angulate.



Figures 8–9. Type specimens of *Cyclosomus* species; a, digital photograph of dorsal habitus; b, specimen labels. Fig. 8. *C.equestris* Boheman, lectotype male. Fig. 9. *C. somalicus* Alluaud, lectotype male. Scale lines = 1.0 mm.

Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (see Fig. 31). Male with median lobe of aedeagus as in Figs. 36 and 43, with shaft thick and abruptly tapered subapically, its ventral margin slightly recurved subapically (Fig. 36), slightly deflected right at apical third in dorsal view (Fig. 43); apical lamella short, with sides evenly convergent to broadly rounded apex (Fig. 43).

Adults of *C. equestris* are most similar in habitus to those of *C. buquetii* and *C. madecassus.* They have a narrower pronotum with narrower, less rounded or pointed anterior angles and a lateral pronotal pale band that is distinctly narrower anteriorly than members of either of the other species. They different from members of *C. buquetii* also in having a shorter prosternal intercoxal process. From members of *C. madecassus*, they also differ in having more vividly metallic reflection on dark areas of the pronotum and elytra and a slightly longer prosternal intercoxal process. Males of these three species are also easily distinguished by the form of the median lobe of their genitalia.

GEOGRAPHICAL DISTRIBUTION.— (Fig. 50). At present, known only from East Africa south of the Equator, from southern Kenya to eastern South Africa, west to southeastern Democratic Republic of the Congo and central Zimbabwe. I examined a total of 59 specimens (29 males and 30 females) from the following localities: **Democratic Republic of the Congo:** Katanga Province (Kalemie [ZMHB]; Kolwezi [BMNH]). **Kenya:** Kitui County (Ikutha [ZMHB]). **Madagascar:** Mahajanga Province (Maevatanana [MNHN]). **Malawi:** Northern Region (5 km S of Chintheche on shore of Lake Malawi [ZMHB]); Southern Region (Mangochi [BMNH]; Zomba [BMNH]); Region unspecified (Lake Malawi [BMNH; ZMHB]). **South Africa:** Eastern Cape Province ([NHRS]). **Tanzania:** Manyara Region (Tarangire National Park [Bawawa La Bata Pond, Mawa ya Mbiti, Fernande's Camp at Tarangire Pool, Mbweha Camp] [all in AMNH]); Rukwa Region (Kasanga [ZMHB]). **Zimbabwe:** Matabeleland South Province (Mbalabala [BMNH]). **Other records:** "Afr. Or. Luitpoldkette" ([BMNH; ZMHB]).

HABITAT DISTRIBUTION.— Label data associated with specimens from Lake Malawi (near Chintheche, see above) indicate that they were collected on the sandy shore of the lake. These beetles probably occur on the open, sandy banks of lakes and rivers in eastern Africa. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian or lacustrine habitats.

### *Cyclosomus flexuosus* (Fabricius)

*Carabus flexuosus* Fabricius, 1775:246. Type locality: eastern India. Dejean (1831:812); Dupuis (1912:284); Jeannel (1949:876).

*Scolytus flexuosus* (Fabricius), Fabricius (1790:221; 1792:180).

*Cyclosomus dytiscoides* Nietner, 1857:312. Type locality: Sri Lanka, Western Province, Negombo.

*Cyclosomus flexuosus* (Fabricius), Andrewes (1921:153 and 166, 1924:464, 1927:105, 1930:365); Heller (1923:302); Csiki (1932:1295); Lorenz (2005:452).

NOTES ON TYPES AND NOMENCLATURE.— Lectotypes designations for *Carabus flexuosus* and *Cyclosomus dytiscoides* will be provided in a forthcoming paper treating the *Cyclosomus* species of the Oriental Region.

DIAGNOSIS.— Adults of *C. flexuosus* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Fig. 11. Size moderate for genus, BL = 9.7 mm. Head and pronotum reddish-brown to dark brown with lateral paler areas broad and slightly broadened basally; elytra mainly pale yellow-tan, darker color pattern (Fig. 11) with middle dark transverse band broad and complete across elytra, con-

FIGURES 10–12. Digital photographs of specimens of *Cyclosomus* species. Fig. 10. *C. equestris* Boheman (Kasanga, Rukwa Region, Tanzania). Fig. 11. *C. flexuosus* (Fabricius) (“Nubia”). Fig. 12. *C. madecassus* Fairmaire (Madagascar). Scale lines = 1.0 mm.

fluent medially with dark interval 1, and expanded along middle half of interval 9, subapical dark spot distinct on intervals 4 and 5; dorsum without metallic reflection. Pronotum (Fig. 21) with anterior angles broadly rounded, lateral margins evenly rounded, not sinuate subapically, with one lateral seta at or anterior to middle on each side, without setae on anterior margin. Prosternal intercoxal process (Fig. 28) long. Elytra (Figs. 11) not or only slightly broader at base than base of pronotum, with humeri sharply angulate. Based on male specimens examined from the Oriental region, I add the following: Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (as in Fig. 31). Male with median lobe of aedeagus as in Figs. 37 and 44, with shaft thick and abruptly tapered subapically, its ventral margin nearly straight in basal two-thirds, bent ventrally at apically one-third (Fig. 37), exceptionally broad in dorsal view (Fig. 44); apical lamella of moderate length, distinctly recurved dorsally (Fig. 37), with sides evenly parallel basally and then abruptly convergent to narrow, bluntly pointed apex (Fig. 44).

Adults of *C. flexuosus* can be distinguished from those of the other Afrotropical *Cyclosomus* species by the middle transverse dark band of their elytra, which extends from the midline, where it is contiguous with the dark interval 1, to interval 9, where it extends anteriorly and posteriorly on that interval for a total distance equal to half of the elytral length. In the single specimen known from the Afrotropical Region, that band is broad, wavy and unbroken, although some specimens from the Oriental Region have the band thinner and/or discontinuous. The large subapical spot, occupying intervals 4 and 5, is larger than that seen in members of any other species treated here (except for some specimens of *C. rousseaui*, which otherwise, paradoxically, have greatly reduced elytral dark areas).

All external features of the single known Afrotropical specimen, a female, match or are within the range of variation seen among *C. flexuosus* specimens from the Indian Subcontinent. It is unfortunate that, at present, we have no male specimen from the “Nubia” region because the male genitalia in members of this species are easily distinguished from those of all other Afrotropical species, and the appropriateness of my identification could be tested. Of course, it is possible that the specimen examined represents an undescribed species, but in the absence evidence to the contrary, it seems most appropriate to identify it as *C. flexuosus* at this time.

**GEOGRAPHICAL DISTRIBUTION.**— (Fig. 51.) The geographical range of *C. flexuosus* covers most of the Indian Subcontinent, from the southern base of the Himalayan Mountains in the north to Sri Lanka in the south. Among specimens received on loan from NHRS was a single female specimen labeled “Nubia”/ “Dohrn”/ “6678 E91”. The name, “Nubia”, has been applied historically to an area including southern Egypt and northern Sudan as far south as just above Khatoum, centered on the Nile River valley. As such, the locality at which this specimen is labeled as having been collected is at least 4000 km west of the nearest other known locality for this species, in the State of Gujarat, India. I have no reason to believe that the specimen is mislabeled, so we need to considered the implications of this record. Although adults of *C. flexuosus* are evidently good fliers, based on several records of capture at lights in India and Sri Lanka, it is hard to imagine an individual covering such a distance on its own. It is also unlikely that this specimen represents a relictual, disjunct population of *C. flexuosus* dating to a period when the range of this species might have included the intervening areas of the Middle East. It is more likely that the “Nubia” specimen either was itself transported by human means directly from the Indian Subcontinent or it represents an adventive population of this species possibly established in that part of northeastern Africa as a result of some prior introduction. Of course if this specimen represents a distinct species, none of the above scenarios would apply. Future collecting, directed at suitable habitats in the region, could establish if such a population exists there currently and whether or not it is conspecific with *C. flexuosus*.

**HABITAT DISTRIBUTION.**— In the Oriental Region, these beetles occur on the open, sandy banks of rivers and, at least at some localities in Sri Lanka, on sandy upper sea beaches as well. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian habitats.

### ***Cyclosomus madecassus*** **Fairmaire**

*Cyclosomus madecassus* Fairmaire, 1898:222. LECTOTYPE, here designated, a male, in MNHN, labeled: "Madag$^{r}$. Superb$^{lle}$ H. Perrier" [white label with black outlining box]/ "TYPE' [red label/ "Cyclosomus madecassus Fairmaire" [handwritten]/ "LECTOTYPE *Cyclosomus madecassus* Fairmaire, 1898, design. by D.H. Kavanaugh 2015" [red label]. Type locality: Madagascar, Mahajanga Province, Maevatanana. Dupuis (1912:284); Csiki (1932:1295); Jeannel (1949:875); Lorenz (2005:452).

**NOTES ON TYPES AND NOMENCLATURE.**— Although I have not seen the lectotype specimen, label data from it cited above were provided by A. Taghavian (MNHN), and my lectotype label has been added to that specimen.

**DIAGNOSIS.**— Adults of *C. madecassus* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Fig. 12. Size moderate for genus, BL = 8.4–9.3 mm. Head dark reddish-brown to piceous; pronotum reddish-brown to piceous with lateral pale areas broad anteriorlyand slightly broadened basally; elytra mainly pale yellow-tan, darker color pattern (Fig. 12) with medial basal area and interval 1 dark brown to piceous, middle transverse dark band dark brown to piceous, W-shaped, extended laterally only to interval 5 or 6, thin or discontinuous, subapical dark spot absent; dark areas of pronotum and elytra with very faint metallic green reflection. Pronotum (Fig. 22) relatively broad, ratio WPB/LP = 2.35–2.41 (mean = 2.37; n = 3), anterior angles moderately rounded, lateral margins evenly rounded, not or only faintly sinuate subapically, with one lateral seta at or anterior to middle on each side, without setae on anterior margin. Prosternal intercoxal process (Fig. 29) short. Elytra (Fig. 11) not or only slightly broader at base than base of pronotum, with humeri sharply angulate. Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (see Fig. 31). Male with median lobe of aedeagus as in Figs. 38 and 45, with shaft thick and abruptly tapered subapically, its ventral margin nearly straight in apical half (Fig. 38), very slightly offset right at apical third in dorsal view (Fig. 45); apical lamella short, slightly deflected ventrally (Fig. 38), with sides evenly convergent to broadly and roundly pointed apex (Fig. 45).

Adults of *C. madecassus* are most similar in habitus to those of *C. buquetii* and *C. equestris.* They have much less vivid metallic reflection on dark areas of the pronotum and elytra than members of either of the other species. They different from members of *C. buquetii* also in being larger and having a much shorter prosternal intercoxal process. From members of *C. equestris*, they also differ in having a relatively broader pronotum with more broadly rounded anterior angles and a lateral pronotal pale band that is distinctly broader anteriorly. Males of these three species are also easily distinguished by the form of the median lobe of their genitalia.

**GEOGRAPHICAL DISTRIBUTION.**— (Fig. 52.) Known only from a few localities in Madagascar. Jeannel (1949) recorded specimens from the Atsimo-Andrefana (Onilany River at Betroka) and Mahajanga (shore of Ikopa River near Maevatanana) Regions. I examined a total of 3 specimens (1 male and 2 females) from the following localities: Mahajanga Region (25 km SW of Ambalanjanakomby [NMNH]); "Madag." ([BMNH]); "Madagascar" ([BMNH]), both without specific locality.

**HABITAT DISTRIBUTION.**— Specimens of this species have been collected on the open sandy shores of rivers at up to 800 m elevation (Betroka), and they are likely to occur in such habitats over much of Madagascar. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian habitats.

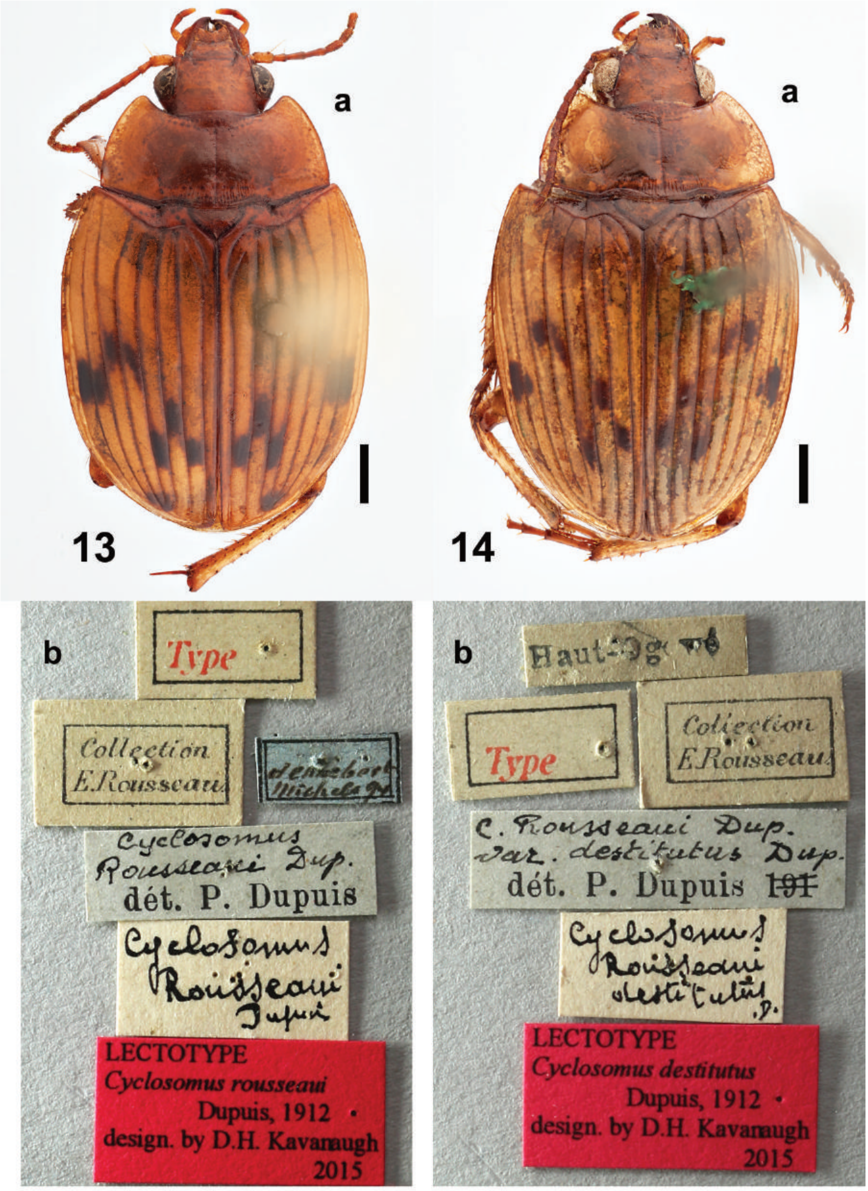
### ***Cyclosomus rousseaui* Dupuis**

*Cyclosomus rousseaui* Dupuis, 1912:385. LECTOTYPE (Fig. 13), here designated, a male, in IRSNB, labeled: “Type” [red ink on white paper with black outlining box]/ “Hennebert, Michela 94” [handwritten on blue paper with black outlining box]/ “Collection E. Rousseau”/ “Cyclosomus Rousseaui Dup. det. P. Dupuis” [pale grey label]/ “Cyclosomus Rousseaui Dupuis” [handwritten]/ “LECTOTYPE *Cyclosomus rousseaui* Dupuis, 1912, design. by D.H. Kavanaugh 2015” [red label]. Paralectotypes examined: 1 female, also in IRSNB, labeled: “Type” [handwritten]/ “Congo Belge” [handwritten]/ “Hennebert, M. 94” [handwritten on blue paper with black outlining box]/ “Cyclosomus Rousseaui Dup. det. P. Dupuis” [pale grey label]/ “Cyclosomus Rousseaui Dupuis” [handwritten]/ “PARALECTOTYPE *Cyclosomus rousseaui* Dupuis, 1912, design. by D.H. Kavanaugh 2015” [yellow label]. Type locality: Democratic Republic of the Congo (without specific locality). Burgeon (1931:308); Csiki (1932:1295); Alluaud (1935:11); Lorenz (2005:452).

*Cyclosomus rousseaui destitutus* Dupuis, 1912:388. LECTOTYPE (Fig. 14), here designated, a male, in IRSNB, labeled: “Haut-Ogowé”/ “Collection E. Rousseau”/ “Type” [red ink on white paper with black outlining box]/ “Cyclosomus Rousseaui Dup. var. destitutus Dup. det. P. Dupuis ~~191~~” [pale grey label]/ “LECTOTYPE *Cyclosomus destitutus* Dupuis, 1912, design. by D.H. Kavanaugh 2015” [red label]. Paralectotypes examined: 1 female, in IRSNB, labeled: “Type” [handwritten in red ink on white paper]/ “Haut-Ogowé”/ “Cyclosomus Rousseaui Dup. det. P. Dupuis” [pale grey label]/ “Cyclosomus Rousseaui D. var. destitutus D.” [handwritten]; 1 female, also in IRSNB, labeled: “Louloua Congo” [handwritten]/ “Collection E. Rousseau”/ “Type” [red ink on white paper with black outlining box]/ “Cyclosomus Rousseaui Dup. var. destitutus Dup. det. P. Dupuis ~~191~~” [pale grey label]/. Each paralectotype also bears the following label: “PARALECTOTYPE *Cyclosomus destitutus* Dupuis, 1912, design. by D.H. Kavanaugh 2015” [yellow label]. Type locality: Gabon, Haut-Ogooué Province. Burgeon (1931:308); Lorenz (2005:452).

NOTES ON TYPES AND NOMENCLATURE.— Dupuis (1912) distinguished members of his “variety” *C. rousseaui destitutus* from those of the nominate form based the absence (Fig. 14) of the subapical dark spot from each elytron seen in *C. rousseaui* s. str. (Fig. 13). For some of the species in which the subapical dark spot occurs at all, it is inconsistent, present or absent in different individuals in the same population and/or from different localities, depending on the species. The precise locality within “Congo Belge” (now the Democratic Republic of the Congo) at which the type series of *C. rousseaui* was collected is unknown, whereas specimens exhibiting the *destitutus* morph occur through the range of the species, including in the Democratic Republic of the Congo. Because the male lectotypes for both names have similar genitalia and there is no apparent allopatry between the two forms, I see no reason to retain *C. rousseaui destitutus* as a separate subspecies and therefore consider them synonyms.

DIAGNOSIS.— Adults of *C. rousseaui* can be distinguished from those of other *Cyclosomus* species in the Afrotropical Region by the following combination of character states: Habitus as in Figs. 13–14. Size small to moderate for genus, BL = 7.6–8.4 mm. Head and pronotum pale yellow-tan to pale reddish brown, lateral paler areas slightly to moderately broad and slightly broadened basally; elytra mainly pale yellow-tan, darker color pattern (Figs. 13–14) with interval 1 not or only slightly darker than pale sections of other intervals, base pale reddish-brown medially, middle transverse dark band reddish-brown to piceous, W-shaped, extended laterally to full-width of interval 8, thin or discontinuous and present only as isolated spots (including interval 8 in all specimens), subapical dark spot present or absent; dorsum without metallic reflection. Pronotum (Fig. 23) with anterior angles broadly to moderately rounded or broadly pointed, lateral margins not sin-



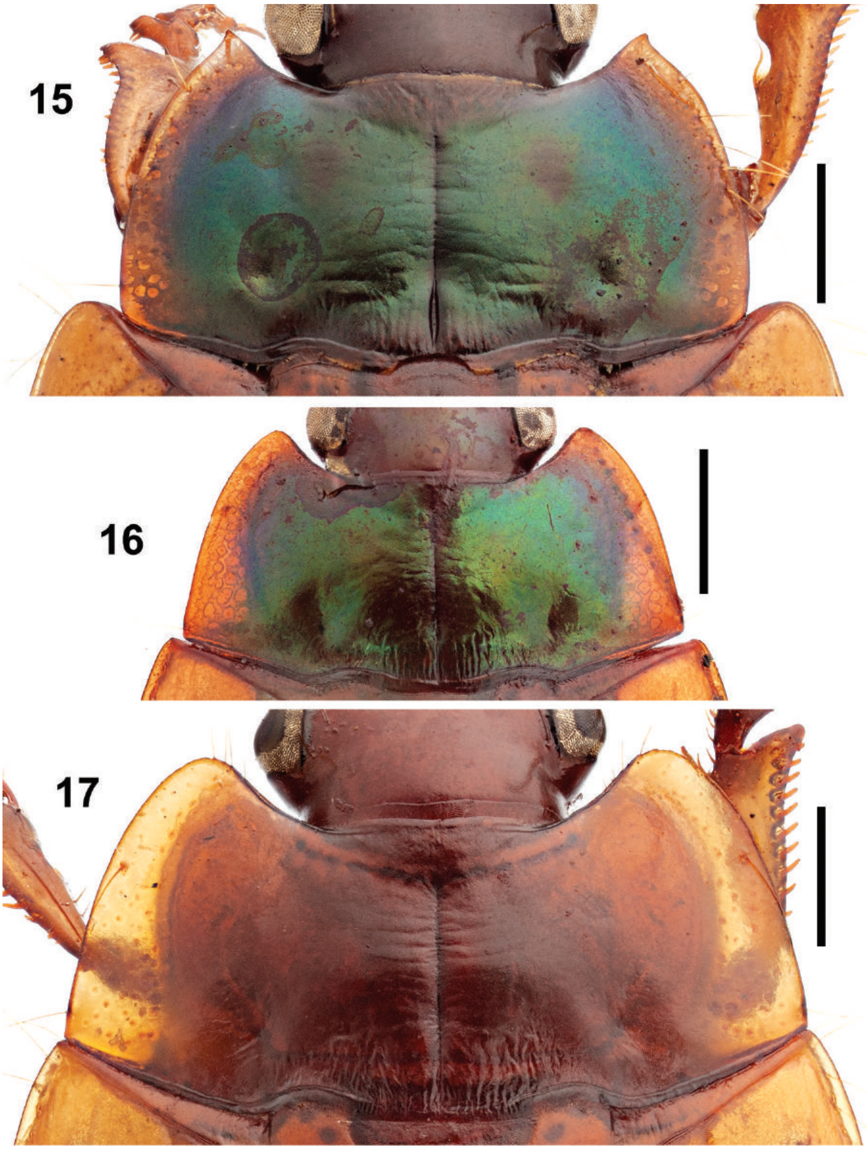
FIGURES 13–14. Type specimens of *Cyclosomus* species; a, digital photograph of dorsal habitus; b, specimen labels. Fig. 13. *C. rousseaui* Dupuis, lectotype male. Fig. 14. *C. destitutus* Dupuis, lectotype male. Scale lines = 1.0 mm.

uate subapically, with one lateral seta at or anterior to middle on each side, without setae on anterior margin. Prosternal intercoxal process (Fig. 30) medium-length or long. Elytra (Figs. 13–14) not or only slightly broader at base than base of pronotum, with humeri sharply angulate. Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae (see Fig. 31). Male with median lobe of aedeagus as in Figs. 39 and 46, with shaft gradually tapered apically, its ventral margin arcuate basally, nearly straight in medial third and ventrally deflected apically (Fig. 39), slightly offset right at apical third in dorsal view (Fig. 46); apical lamella very long, straight, slightly constricted basally and broadly rounded apically (Fig. 46).

Adults of *C. rousseaui* can be distinguished from those of all other *Cyclosomus* species in the Afrotropical Region in having the middle transverse dark band of their elytra fragmented into several small, unconnected patches or spots, varied in their darkness, but including, in all specimens examined, a darker spot occupying the full width of interval 8 and part or all of interval 7. Members of no other species have a spot or band that extends to the lateral edge of interval 8 except those of *C. flexuosus*, in which the band is broad and continuous onto interval 9. The pronotum is pale, even paler than in *C. collarti* or *C. flexuosus* members, and, as with them, the dorsum is without a trace of metallic reflection.

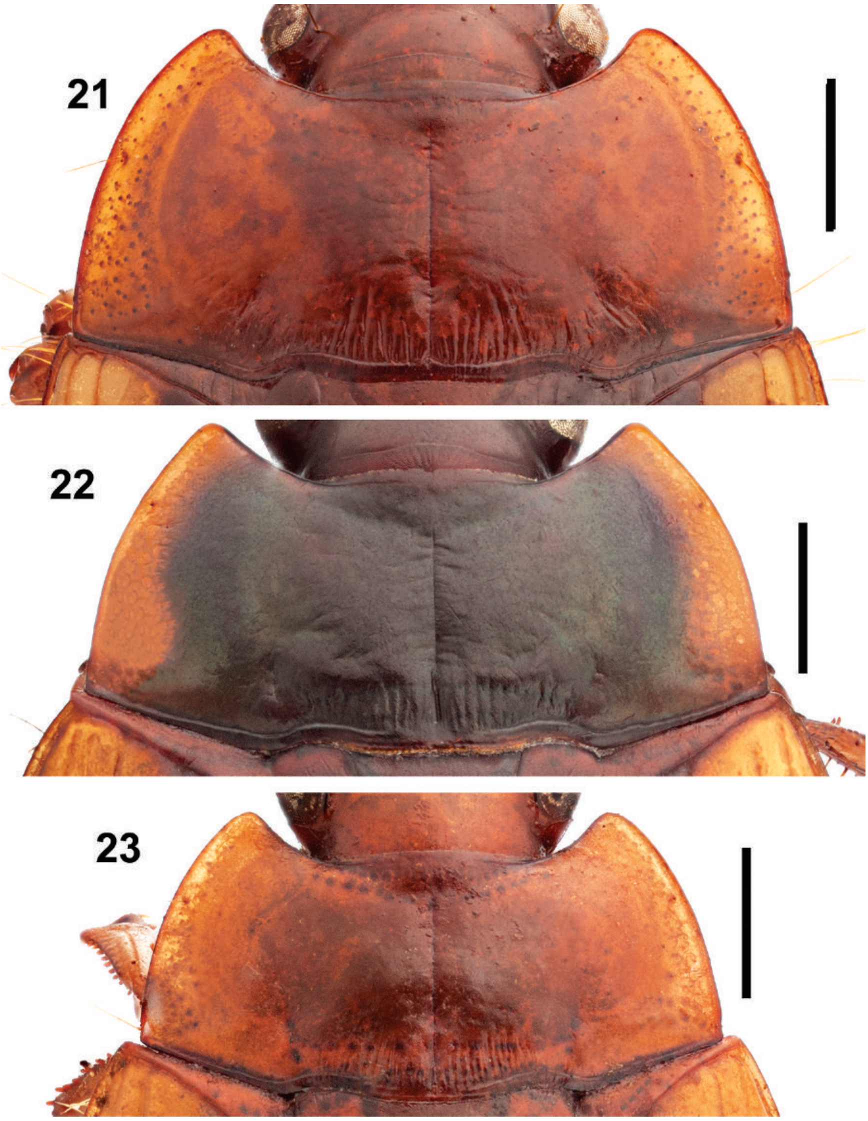
**GEOGRAPHICAL DISTRIBUTION**.— (Fig. 53.) Widespread across Sub-Saharan Africa. Known from scattered localities in the north from Sierra Leone to southern Sudan, in the south from Gabon and Democratic Republic of the Congo, not yet recorded from East Africa or southern Africa. I examined a total of 13 specimens (5 males and 8 females) from the following localities: **Democratic Republic of the Congo:** Kasai Oriental Province (Sankuru [ZMHB]); Katanga Province (Lodja [IRSNB]; Lualaba [IRSNB]). **Gabon:** Haut-Ogooué Province ([IRSNB]). **Sierra Leone:** Southern Province (Njala [BMNH]). **Sudan:** Sennar State (Abu Tiga [BMNH]). **Other records**: “W. Africa” ([BMNH]).

**HABITAT DISTRIBUTION**.— None of the specimens examined had associated habitat data. However, it most likely that members of this species, like those of all other species in the genus, occur on open sandy shores of rivers in the geographical region noted above. They are best collected at night when they are active on the dry sand surface of river banks or at lights in the vicinity of such riparian habitats.

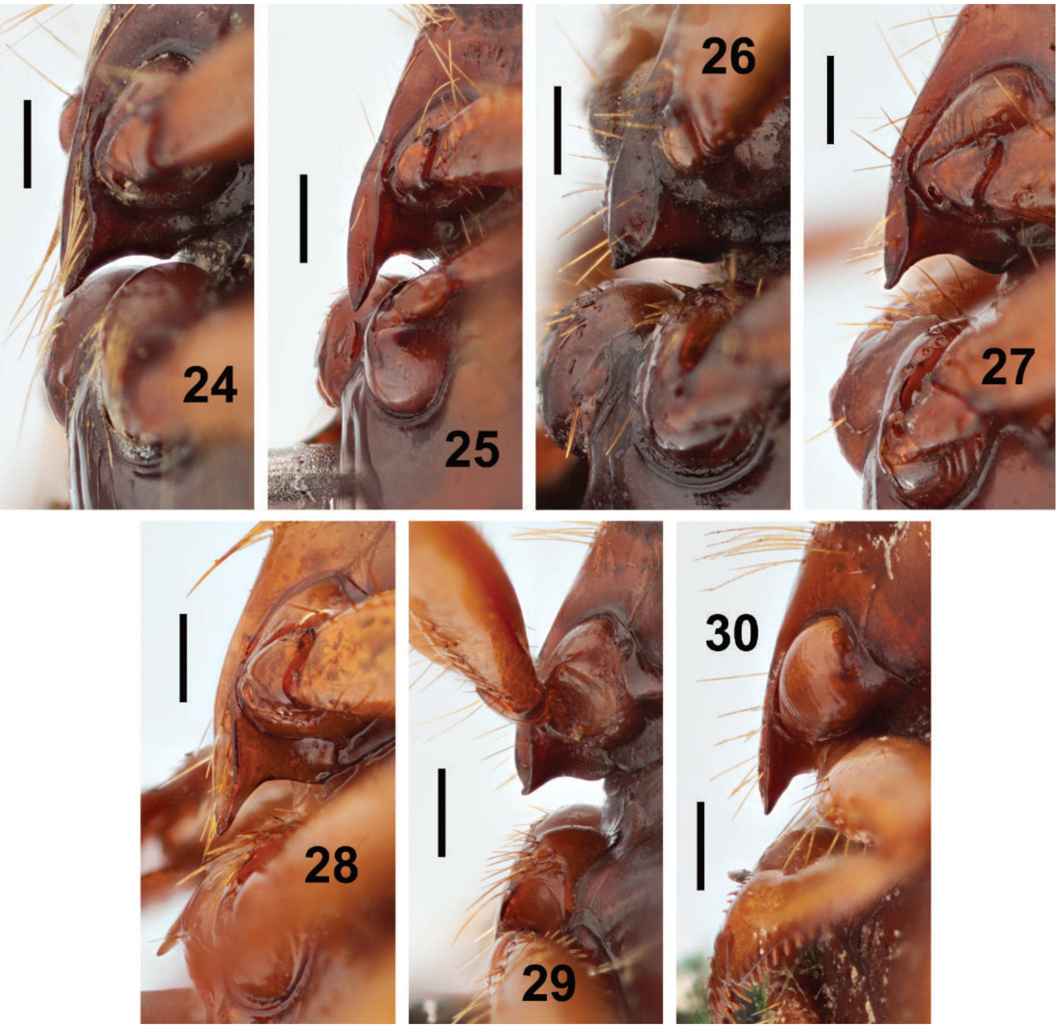


FIGURES 15–17. Digital photographs of prothoraces of *Cyclosomus* species, dorsal aspect. Fig. 15. *C. basalis* Kolbe (lectotype). Fig. 16. *C. buquetii* Dejean (lectotype). Fig. 17.*C. collarti* Burgeon (holotype). Scale lines = 1.0 mm.

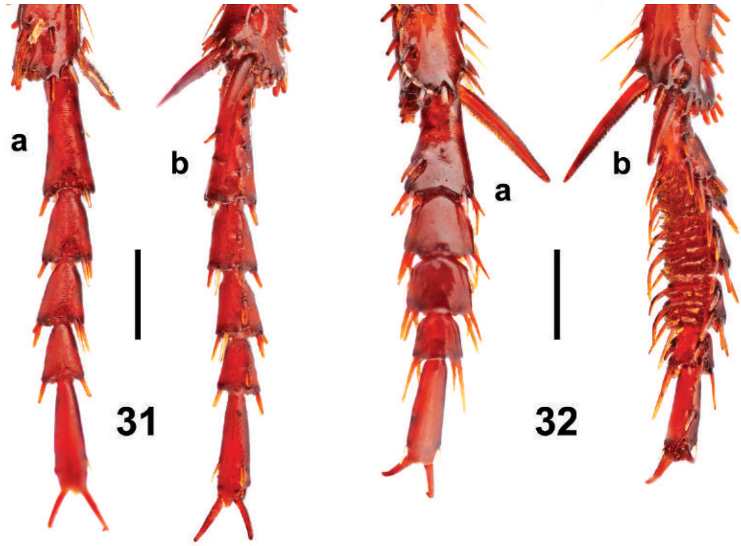
FIGURES 18–20. Digital photographs of prothoraces of *Cyclosomus* species, dorsal aspect. Fig. 18. *C. somalicus* Alluaud (lectotype). Fig. 19. *C. equestris* Boheman (lectotype). Fig. 20. *C. equestris* Boheman (Kasanga, Rukwa Region, Tanzania). Scale lines = 1.0 mm.



Figures 21–23. Digital photographs of prothoraces of *Cyclosomus* species, dorsal aspect. Fig. 21. *C. flexuosus* (Fabricius) ("Nubia"). Fig. 22. *C. madecassus* Fairmaire (Madagascar). Fig. 30. *C. rousseaui* Dupuis (lectotype). Scale line = 1.0 mm.

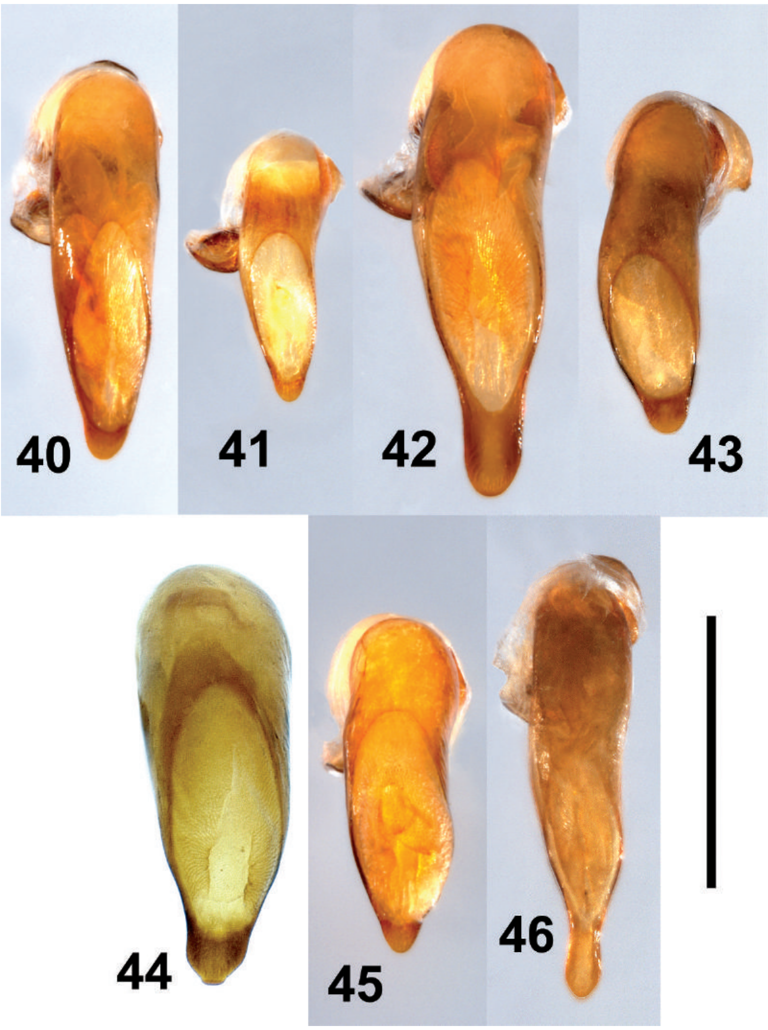


FIGURES 24–30. Digital photographs of thoracic venters showing relative length of prosternal intercoxal process of *Cyclosomus* species, left lateral oblique view. Fig. 24. *C. basalis* Kolbe (5 km S of Chintheche on shore of Lake Malawi, Northern Region, Malawi). Fig. 25. *C. buquetii* Dejean (Beira, Sofala Province, Mozambique). Fig. 26. *C. collarti* Burgeon (Lac Albert, Ituri Province, Democratic Republic of the Congo**)**. Fig. 27. *C. equestris* Boheman (5 km S of Chintheche on shore of Lake Malawi, Northern Region, Malawi). Fig. 28. *C. flexuosus* (Fabricius) ("Nubia"). Fig. 29. *C. madecassus* Fairmaire (25 km SW of Ambalanjanakomby, Mahajanga Region, Madagascar). Fig. 30. *Cyclosomus rousseaui* Dupuis (Njala, Northern Province, Sierra Leone). Scale line = 0.5 mm.



FIGURES 31–33. Digital photographs of male middle tarsi of *Cyclosomus* species; a, dorsal view; b, ventral view. Fig. 31. *C. equestris* Boheman (Ikutha, Kitui County, Kenya). Fig. 32. *C. collarti* Burgeon (Lac Albert, Ituri Province, Democratic Republic of the Congo). Scale line = 0.5 mm.

FIGURES 33–39. Digital photographs of male median lobe of aedeagus of *Cyclosomus* species, left lateral view. Fig. 33. *C. basalis* Kolbe (50–70 km W of Iringa, Tanzania). Fig. 34. *C. buquetii* Dejean (Beira, Sofala Province, Mozambique). Fig. 35. *C. collarti* Burgeon (Lac Albert, Ituri Province, Democratic Republic of the Congo). Fig. 36. *C. equestris* Boheman (5 km S of Chintheche on shore of Lake Malawi, Northern Region, Malawi). Fig. 37. *C. flexuosus* (Fabricius) (“eastern India”). Fig. 38. *C. madecassus* Fairmaire (Madagascar). Fig. 39. *C. rousseaui* Dupuis (Abu Tiga, Sennar State, Sudan). Scale line = 1.0 mm.



FIGURES 40–46. Digital photographs of male median lobe of aedeagus of *Cyclosomus* species, dorsal view in plane of apical orifice. Fig. 40. *C. basalis* Kolbe (50–70 km W of Iringa, Tanzania). Fig. 41. *C. buquetii* Dejean (Beira, Sofala Province, Mozambique). Fig. 42. *C. collarti* Burgeon (Lac Albert, Ituri Province, Democratic Republic of the Congo). Fig. 43. *C. equestris* Boheman (5 km S of Chintheche on shore of Lake Malawi, Northern Region, Malawi). Fig. 44. *C. flexuosus* (Fabricius) ("eastern India"). Fig. 45. *C. madecassus* Fairmaire (Madagascar). Fig. 46. *C. rousseaui* Dupuis (Abu Tiga, Sennar State, Sudan). Scale line = 1.0 mm.

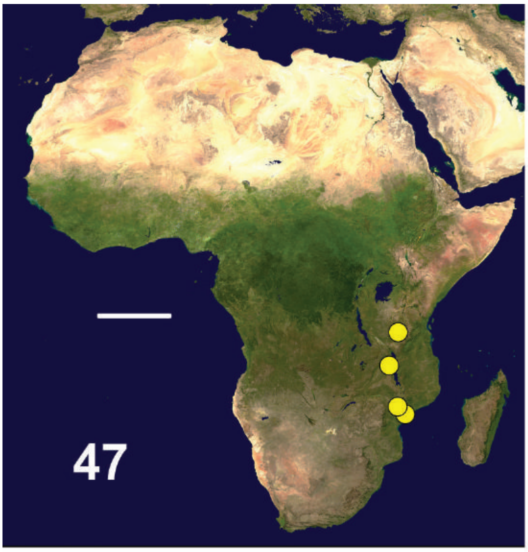
## DISCUSSION

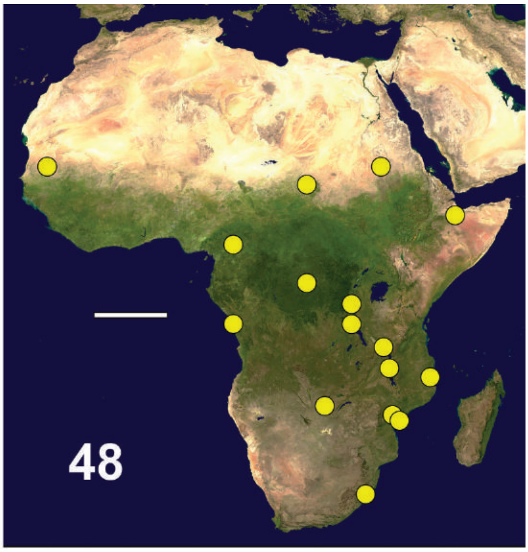
**GEOGRAPHICAL DISTRIBUTION PATTERNS.**— Even a quick glance at the maps illustrating the distributions of samples of the *Cyclosomus* species treated here (Fig. 47–53) reveals how little really is known about the distributions of species in the vast expanse of the Afrotropical Region. Some of these species, such as *C. buquetii* and *C. rousseaui*, range west to east across most of the continent and north to south across the Equator, but with huge gaps between recorded localities. Two species, *C. collarti* and *C. equestris*, have large geographical ranges but apparently only northward and southward from the Equator, respectively. *Cyclosomus basalis* and *C. equestris* appear to be restricted to eastern Africa south of the Equator, the former to a narrow zone extending from central Tanzania to coastal Mozambique near the mouth of the Zambesi River, the latter more broadly ranging, south to South Africa and east to Madagascar. One species, *C. madecassus* is known only from Madagascar. Three species, *C. buquetii*, *C. collarti* and *C. rousseaui*, have ranges that penetrate the southern edge of the Saharan zone along major rivers. The record for *C. flexuosus* from "Nubia", farther north than any record for another species in the Afrotropical Region, is discussed above in the treatment of that species. Much additional collecting will be required to better understand the geographical ranges of these species and set a baseline against which potential changes in those distributions as a result of climate change can be tracked.

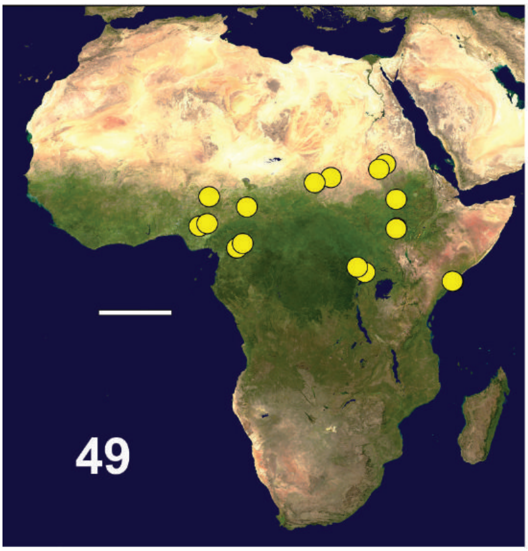
**SYMPATRY AND SYNTOPY AMONG SPECIES.**— Available evidence suggests that all *Cyclosomus* species prefer similar habitats, namely the open and exposed sandy margins of mid- to large-size streams and of large lakes. Given their shared habitat preferences, the extensive known geographical ranges of some of the species and the broad overlap of the their ranges, both sympatry (i.e., co-occurrence in the same region) and syntopy (i.e., co-occurrence at the same site in the same habitat ) should be expected. In general, distributional sampling of *Cyclosomus* species to date has been so sparse within their ranges, that sympatry and syntopy have not been well documented. However, a few instances of co-occurrence are documented with the specimens available.

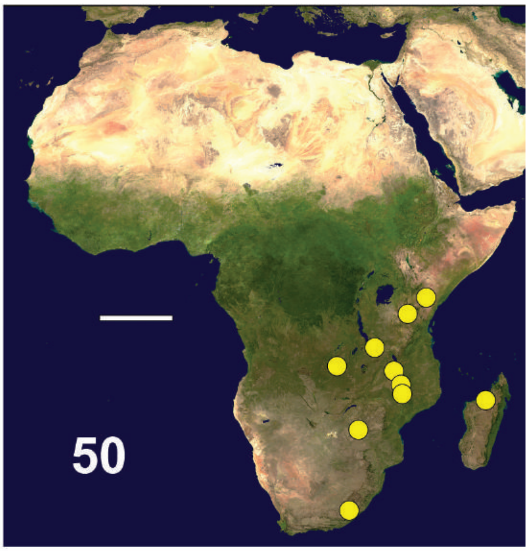
Adults of *C. buquetii* and *C. collarti* have been collected together at two localities in Sudan: at Bahr el Abiad (Khartoum State) and at El Geneina (West Darfur State); and adults of *C. basalis*, *C. buquetii* and *C. equestris* were found together on a sandy beach on the western shore of Lake Malawi, 5 km south of Chintheche (Northern Region), Malawi. These are the only documented instances of syntopy of which I am aware, but additional sampling is likely to demonstrate far greater co-occurrence of *Cyclosomus* species.The geographical range of C. *buquetii* overlaps all or part of the range of each of the other Afrotropical species except *C. flexuosus*, so it is likely sympatric with each of those other species in at least part of its range. *Cyclosomus basalis* is sympatric with *C. buquetii* and *C. equestris* in Malawi and probably in other parts of its range. *Cyclosomus collarti* is sympatric with *C. buquetii* in Sudan and probably throughout central Africa north of the Equator, and perhaps with *C. rousseaui* in these same general areas. *Cyclosomus equestris* is sympatric with *C. basalis* and *C. buquetii* in Malawi and with *C. madecassus* at least in northwestern Madagascar. Although it has not yet been found co-occurring with any other *Cyclosomus* species, the range of *C. rousseaui* overlaps broadly with those of *C. buquetii* and *C. collarti* and very slightly with that of *C. equestris* in the southern part of the Democratic Republic of the Congo. Otherwise, the ranges of *C. rousseaui* and *C. equestris* are allopatric or perhaps parapatric.

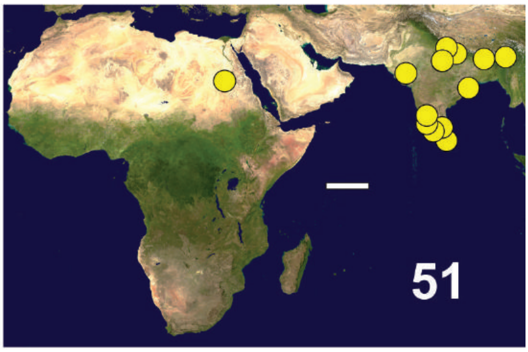
It is my hope that the information provided in this report, and particularly the key for identification of species, will both stimulate and facilitate future work with *Cyclosomus* species in Africa.



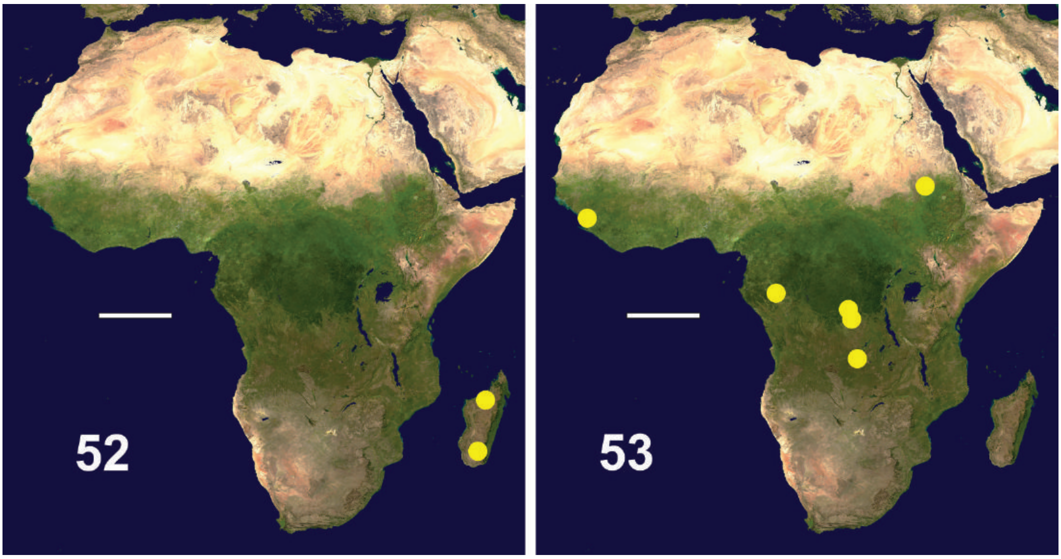








FIGURES 47–51. Maps showing distributions of records (yellow dots) for *Cyclosomus* specimens examined. Fig. 47. *C. basalis* Kolbe. Fig. 48. *C. buquetii* Dejean. Fig. 49. *C. collarti* Burgeon. Fig. 50. *C. equestris* Boheman. Fig. 51. *C. flexuosus* (Fabricius) ("eastern India"). Scale line = 1000 km.



Figures 52–53. Maps showing distributions of records for *Cyclosomus* specimens examined. Fig. 52. *C. madecassus* Fairmaire. Fig. 52. *C. rousseaui* Dupuis. Scale line = 1000 km.

## Acknowledgements

This project would not have been possible without the generous assistance of the curators and collection managers of the collections in which *Cyclosmus* specimens are deposited. I offer my sincere thanks to Lee Herman (AMNH), Beulah Garner and Max Barclay (BMNH), Alain Drumont (IRSNB), Azedah Taghavian (MNHN), Didier Van den Spiegel (MRAC), Terry Erwin (NMNH), Johannes Bergsten (NHRS), and Bernd Jaeger (ZMHB) for loans of specimens in their care and for data from the collections associated with those specimens. I also thank Victor Smith (CAS, Entomology) for his valuable advice about digital imaging on the BK Lab System, and David Maddison and Wojciech Pulawski for critical reviews of the draft manuscript.

## References

Alluaud, C. 1935. II. Carabiques d'Afrique. Descriptions isolées. *Afra* 9:11–16.

Boheman. C. H. 1848. *Insecta Caffaria, annis 1838–1845 a J. A. Wahlberg collecta. Pars I. Fascic. Coleoptera.* (*Carabici, Hydrocanthari, Gyrinii et Staphylinii*). Holmiae: Ex Officina Norstedtiana. viii + 297 pp., 2 pls.

Bousquet, Y. 2012. Catalogue of Geadephaga (Coleoptera, Adephaga) of America, North of Mexico. *Zookeys* 245:1–1722.

Burgeon, L. 1931. Une nouvelle espèce Congolaise de *Cyclosomus* (Col. Carabidae). *Revue Zoologique & Botanique Africaines* 20:307–309.

Chaudoir, M. 1876. Etude monographique des Masoréides, des Tetragonodérides et du genre *Nemotarsus*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 51:1–84.

Csiki, E. 1932. *Coleopterorum catalogus. Pars 124. Carabidae: Harpalinae VII*. W. Junk, Berlin, Germany. 1279–1598 pp.

Dejean, P. F. M. A. 1831. *Spécies général des coléoptères de la collection de M. le Comte Dejean. Tome cinquième.* Méquignon-Marvis, Paris, France. viii + 883 pp.

FABRICIUS, J. C. 1775. *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus.* Libraria Kortii, Flensburgi et Lipsiae. xxxii + 832 pp.

FABRICIUS, J. C. 1790. Nova insectorum genera. *Skrivter af Naturhistorie-Selskabet* 1:213–228.

FABRICIUS, J. C. (1792) *Entomologia systematica emendata et aucta, secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Tome I.* Pars I. Proft, Hafniae. xx + 330 pp.

FAIRMAIRE, M. L. 1898. Matériaux pour la faune Coléoptérique de la région Malagache. 5$^{e}$ note. *Annales de la Société Entomologique de Belgique* 42:222–260.

GEOFFROY, E. L. 1762. *Histoire abrégée des insectes qui se trouvent aux environs de Paris; dans laquelle ces animaux sont rangés suivant un ordre méthodique. Tome premier.* Durand, Paris, France. xxviii + 523 pp., 10 pls.

JEANNEL, R. 1949. *Faune de l'Empire Français XI. Coléoptères Carabiques de la région Malagache* (*Troisième partie*). Librairie Larose, Paris, France. Pages 767–1146.

KOLBE, H. 1897. Afrikanische Coleoptera des Königlichen Museums für Naturkunde zu Berlin. *Entomologische Nachrichten* 23:348–355.

KUNTZEN, H. 1919. Die Carabidenfauna Deutsch-Südwestafrikas. *Mitteilungen aus dem Zoologischen Museum in Berlin* 9:91–156.

LAPORTE DE CASTELNAU, F. L. 1834. *Etudes entomologiques, ou descriptions d'insectes nouveaux: et observations sur leur synonymie.* Méquignon-Marvis Père et Fils, Paris, France. 94 pp., 2 pls.

LATREILLE, P. A. 1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposés en familles.* F. Schoell, Paris, France. 444 pp.

LATREILLE, P. A. 1829. *Les crustacés, les arachnides et les insectes, distribués en familles naturelles, ouvrage formant les tomes 4 et 5 de celui de M. le Baron Cuvier sur le règne animal (deuxième édition). Tome premier.* Déterville, Paris, France.. xxvii + 584 pp.

LORENZ, W. 2005. *Systematic List of Extant Ground Beetles of the World* (*Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae*). *Second edition.* W. Lorenz, Tutzing. 530 pp.

NIETNER, J. 1857. Entomological papers, being chiefly descriptions of new Ceylon Coleoptera with such observations on their habits etc., as appear in any way interesting. *Journal of the Asiatic Society of Bengal* 26:132–153.

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