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Number 18		
235 (12)	3	"CASIZ 53465" to read "SIO-BIC P1368"
236 (1)	1	"CASIZ 35961" to read "SBMNH 345543"
Number 19		
280 (3)	9	"*walkeriana*" to read "*walkerina*"
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Rostanga byga Er. Marcus, 1958 from Argentina: Redescription and Comparison to *Rostanga pulchra* MacFarland, 1905 (Mollusca, Nudibranchia, Doridina)

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Rostanga byga **Marcus, 1958 is redescribed based on the examination of the type material and newly collected specimens from Golfo San José, Chubut, Argentina. The external coloration, radular morphology and reproductive system differ significantly from specimens of *Rostanga pulchra* MacFarland, 1905 collected from Monterey Bay, California (type locality), and examined for comparison. This latter species was probably recorded from Argentina (Camarones Bay, Chubut) as well. The geographic range of *R. byga* is extended from northern Brazil to Patagonia. *Rostanga pulchra* appears to have a disjunct geographic range in North and South America.**

RESUMEN

Se redescribe la especie *Rostanga byga* Marcus, 1958 a partir del estudio del material tipo y de varios especímenes recolectados por primera vez en el Golfo San José, Chubut, Argentina. La coloración del cuerpo, morfología radular y sistema reproductivo difieren significativamente de especímenes de *Rostanga pulchra* MacFarland, 1905 recolectados en la localidad tipo, la Bahía de Monterey, California y examinados para su comparación. Probablemente, esta última especie ha sido también citada para Argentina (Bahía Camarones, Chubut). La distribución de *R. byga* se extiende desde el norte de Brasil hasta la Patagonia. *Rostanga pulchra* parece tener dos áreas de distribución disjuntas, en Norte y Sur América.

The genus *Rostanga* Bergh, 1879 comprises species of caryophyllidia-bearing dorids characterized by having short rhinophores with few lamellae, inner radular teeth folded inwards and outer teeth elongate and denticulate.

So far, two species of *Rostanga* have been reported from South America. Ernest Marcus (1958) described *Rostanga byga* based on a single, preserved specimen collected from the intertidal zone of Ilhabela, São Sebastião Island, Brazil. Later, Eveline Marcus (1970) extended the geographical range of this species to northern Brazil. Rudman and Avern (1989) revised the genus *Rostanga* from the Indo-West Pacific, and discussed other species of this genus described from all over the world. These authors recognized *R. byga* as a valid species, even though there was very little available information about it.

Ernest Marcus (1959) reported *Rostanga pulchra* MacFarland, 1905 from Chile, the first record of this species (originally described from California), from South America. Years later, Marcus and Marcus (1969) extended the geographic range of this species to Argentina, based on a single specimen collected at 102 m depth from Camarones Bay (Chubut). More recent records of *R. pulchra* from Chile (Schrödl 1996, 1997) confirmed the presence of this species in the southern Hemisphere. According to the published information, *R. pulchra* is known to have a disjunct geographic range in North and South America, with a large gap between the populations.

The present paper includes a complete anatomical study of several specimens of *Rostanga* collected from Argentina, and a comparison with material of *R. pulchra* from the type locality. In addition, the type material of *R. byga* is re-examined and compared to the original description.

The material examined is deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ), and the American Museum of Natural History (AMNH).

SPECIES DESCRIPTIONS

Family Rostangidae Pruvot-Fol, 1951
Genus *Rostanga* Bergh, 1879

Rostanga pulchra MacFarland, 1905

Figs. 1, 2, 3A

Rostanga pulchra MacFarland, 1905:40–41; 1906:119–122, pl. 24, fig. 8, pl. 18, figs. 18–21, pl. 21, fig. 109; 1966:165–169, pl. 25, fig. 7, pl. 29, figs. 7–10, pl. 35, figs. 1–16; Er. Marcus, 1959:35–37, 106, figs. 65–68; Er. Marcus, 1961:15, pl. 3, figs. 46–49; Marcus and Marcus, 1969:20–21; Marcus and Marcus, 1970:202–203; Thompson, 1975:489; Rudman and Avern, 1989:330; Schrödl, 1996:22; Schrödl, 1997:38–42.

MATERIAL EXAMINED. — Monterey Bay, California, 17 August 1978, three specimens 11, 12 and 16 mm preserved length, collected by G. McDonald (CASIZ 069163); 24 August 1978, three specimens 14, 15 and 18 mm preserved length, collected by G. McDonald (CASIZ 070734).

EXTERNAL MORPHOLOGY. — The body shape is oval, somewhat elevated. The dorsum is covered with cup-shaped caryophyllidia, about 150 μm long. The rhinophoral and branchial sheaths are also surrounded by caryophyllidia. Each caryophyllidium consists of an extremely small, rounded, ciliated tubercle with small marginal cilia and 4–5, taller, thin spicules surrounding the tubercle. The living animals (Fig. 1) vary from orange-yellow to bright red in color. Some specimens may have small, brown spots scattered on the dorsum. The mantle margin is surrounded by small, white spots. The perfoliate rhinophores have the same color as the dorsum and are composed of 9 vertical, transverse lamellae. The gill has the same color as the rest of the body, and is composed of 6–10 bipinnate branchial leaves. The anal papilla lies within the circlet of the branchial plume.

Ventrally, the anterior border of the foot is bilabiate and notched. The foot is wide relative to the mantle margin. The oral tentacles are well formed, and appear conical in shape.

INTERNAL ANATOMY. — The radular formula is 50 × 48.0.48 in a 16 mm preserved length specimen (CASIZ 069163) and 53 × 51.0.51 in an 18 mm preserved length specimen (CASIZ 070734). The innermost lateral teeth are the shortest of the row. They are thin, folded inwards, and have 6–8 denticles on the inner side of the short cusp (Fig. 2A). The lateral teeth change gradually in size from the inner to mid-lateral. The mid-lateral teeth are wide, having a long, pointed, primary cusp and a large secondary cusp situated near the base (Fig. 2B). The outer lateral teeth are very thin and elongate, with a fine brush of 9–10 denticles at the end (Fig. 2C, D). The jaws are solid, with few rodlets of varying length (Fig. 2E).

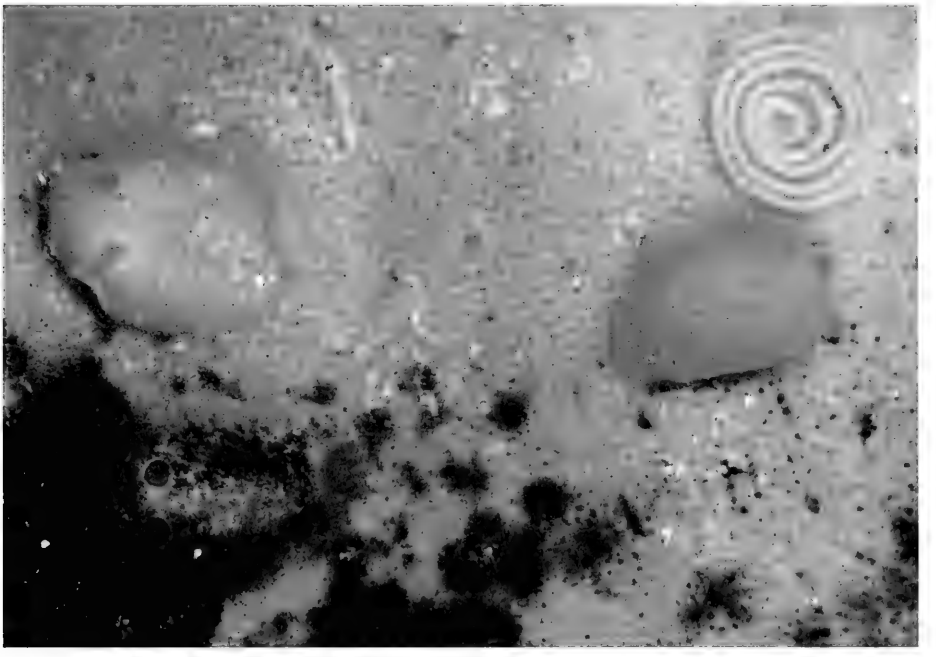

FIGURE 1. *Rostanga pulchra* MacFarland, 1905, living animals from Monterey Bay, showing color variation and an egg mass. Photograph by Robert Ames (CASIZ photo collection).

In the reproductive system the ampulla is wide and short. It narrows before branching into the oviduct, which enters the female gland, and the large prostate (Fig. 3A). The prostate is flat and massive, and has two well-differentiated portions. The prostate narrows and forms the proximal end of the deferent duct. The distal end of the deferent duct is very long. The penis has no armature. The deferent duct and vaginal duct meet at a common atrium. The vaginal duct is very long and narrows before opening into the large, oval bursa copulatrix. At some distance from the vaginal duct insertion, another long duct leads from the bursa copulatrix and connects to the seminal receptacle and the uterine duct. The seminal receptacle is small and oval, with a slightly pointed end opposite its short stalk.

GEOGRAPHIC RANGE. — This species is known from Alaska (Lee and Foster 1985) to Mexico (Marcus and Marcus 1970) in the Northern Hemisphere, and from Chile (Ernest Marcus 1959; Schrödl 1996, 1997) to Argentina (Marcus and Marcus 1969) in the Southern Hemisphere.

Rostanga byga Er. Marcus, 1958
Figs. 3B, 4–6

Rostanga byga Er. Marcus, 1958:22–25, figs. 34–36; Ev. Marcus, 1970:943; Rudman and Avern, 1989:329.
Rostanga cf. *pulchra* (MacFarland): Muniain, 1997:21

MATERIAL EXAMINED. — HOLOTYPE: Ilhabela, São Sebastião Island, Brazil, June 1956, one specimen 11 mm preserved length, collected under a stone in the intertidal zone (AMNH 3507). Golfo San José, Chubut, Argentina, November, 1991, one specimen 12 mm preserved length (CASIZ 118014) and one specimen 14 mm preserved length (MACN 34174) collected by C. Muniain; April 1998, one specimen 20 mm long, collected by C. Muniain.

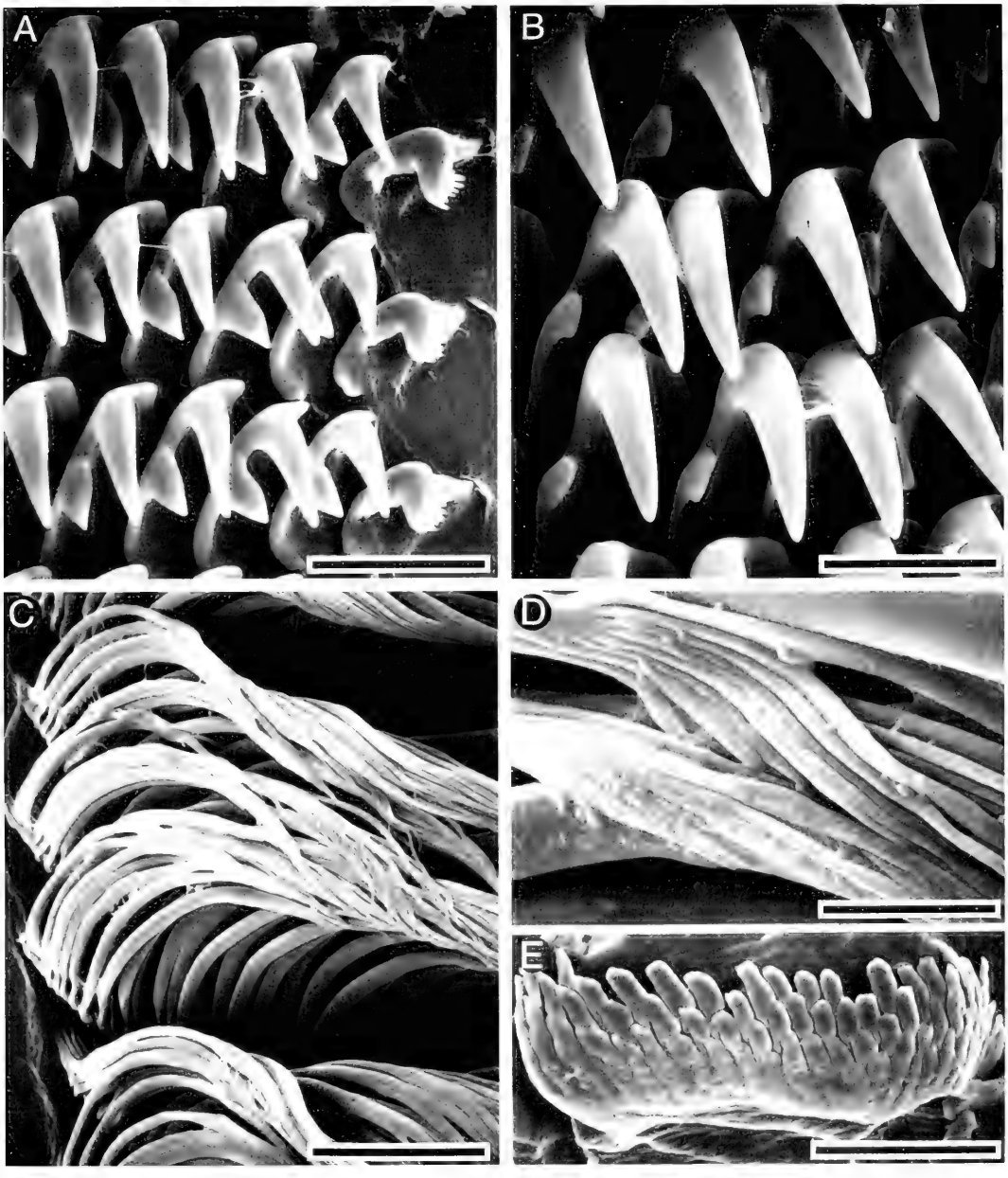

FIGURE 2. *Rostanga pulchra* MacFarland, 1905, scanning electron micrographs (CASIZ 070734). A. Inner lateral teeth, scale = 25 µm; B. Mid-lateral teeth, scale = 30 µm; C. Outer lateral teeth, scale = 60 µm; D. Detail of the outermost teeth denticulation, scale = 7.5 µm; E. Jaw, scale = 60 µm.

EXTERNAL MORPHOLOGY. — The body shape is oval and somewhat elevated (Figs. 4A, 5). The surface of the mantle is densely covered with caryophyllidia about 100 µm long. The rhinophoral and branchial sheaths are also surrounded by caryophyllidia. Each caryophyllidium consists of a large, rounded ciliated tubercle, with small marginal cilia and 6 spicules surrounding the tubercle. The ground color of the mantle is orange in the living animals, lightly spotted with white dots in the middle

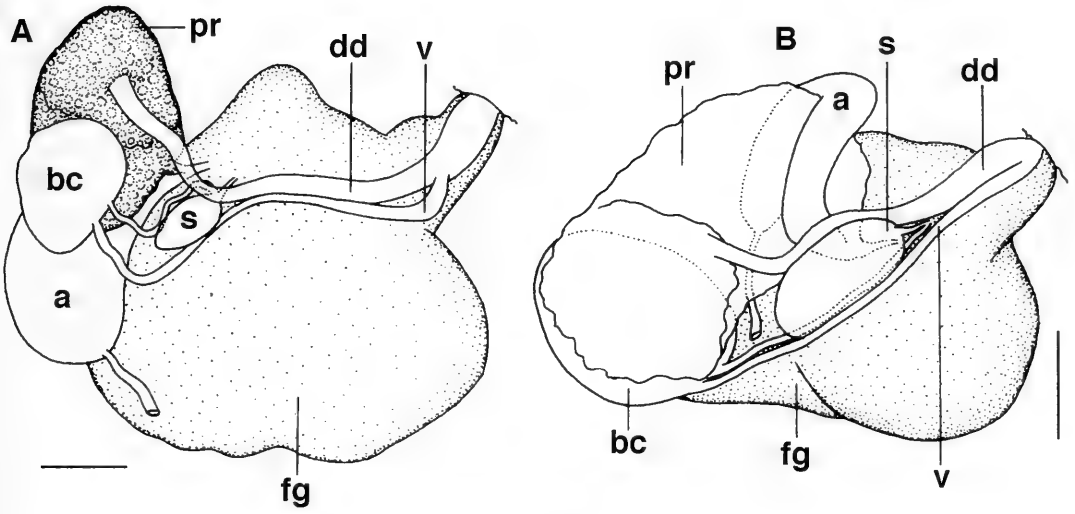

FIGURE 3. Reproductive systems. A. *Rostanga pulchra* MacFarland, 1905 (CASIZ 070734); B. *Rostanga byga* Er. Marcus, 1958 (CASIZ 118014). Abbreviations: a, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland; pr, prostate; s, seminal receptacle; v, vagina.

of the dorsum and between tubercles. The perfoliate rhinophores are pale orange with translucent tips, and are composed of 14–16 vertical, transverse lamellae (Fig. 4B). The gill has the same color as the dorsum, and is composed of 10 short, simply pinnate, branchial leaves. The anal papilla lies within the circlet of the branchial plume. Ventrally, the anterior border of the foot is notched and grooved (Fig. 4C). The foot is completely orange, and narrow relative to the mantle margin. The oral tentacles are digitiform.

INTERNAL ANATOMY. — The radular formula is 45 × 53.0.53 in a 12 mm preserved length specimen (CASIZ 118014) and 58 × 55.0.55 in a 14 mm preserved length specimen (MACN 34174). The innermost lateral teeth are the shortest of the row. They have a rounded, long cusp with 7–10 short denticles on the inner edge (Fig. 6A). The lateral teeth change gradually in size from the inner to mid-lateral. The mid-lateral teeth have a broad triangular base and a pointed primary cusp (Fig. 6B). These teeth lack a secondary cusp, but have a small lateral wing near the base. The outermost lateral teeth are very thin and elongate, having a fine brush of 6–10 denticles at the end (Fig. 6C, D). The jaws are very small, having few irregular rodlets of varying shape and length (Fig. 6E).

In the reproductive system the ampulla is thin and long. It narrows before branching into the oviduct, which enters the female gland, and the prostate (Fig. 3B). The prostate is flat and very large. It has two well-differentiated portions. In one of them the deferent duct leaves as a narrow long duct. The penis has no armature. The deferent duct and vaginal duct meet at a common atrium. The vaginal duct opens into the large, oval, bursa coopulatrix. Next to the opening of the vaginal duct leads another duct, which connects to the seminal receptacle and the uterine duct. The seminal receptacle is oval and conspicuous.

GEOGRAPHIC RANGE. — This species is known from the southwest Atlantic, from the North of Brazil to Argentina (Chubut).

DISCUSSION

The Argentinean specimens of *Rostanga* examined in this paper clearly belong to *R. byga*. The holotype of *R. byga* was dissected when it was originally examined, and the radula and reproductive system were missing. However, there is enough information in the original description (Ernest

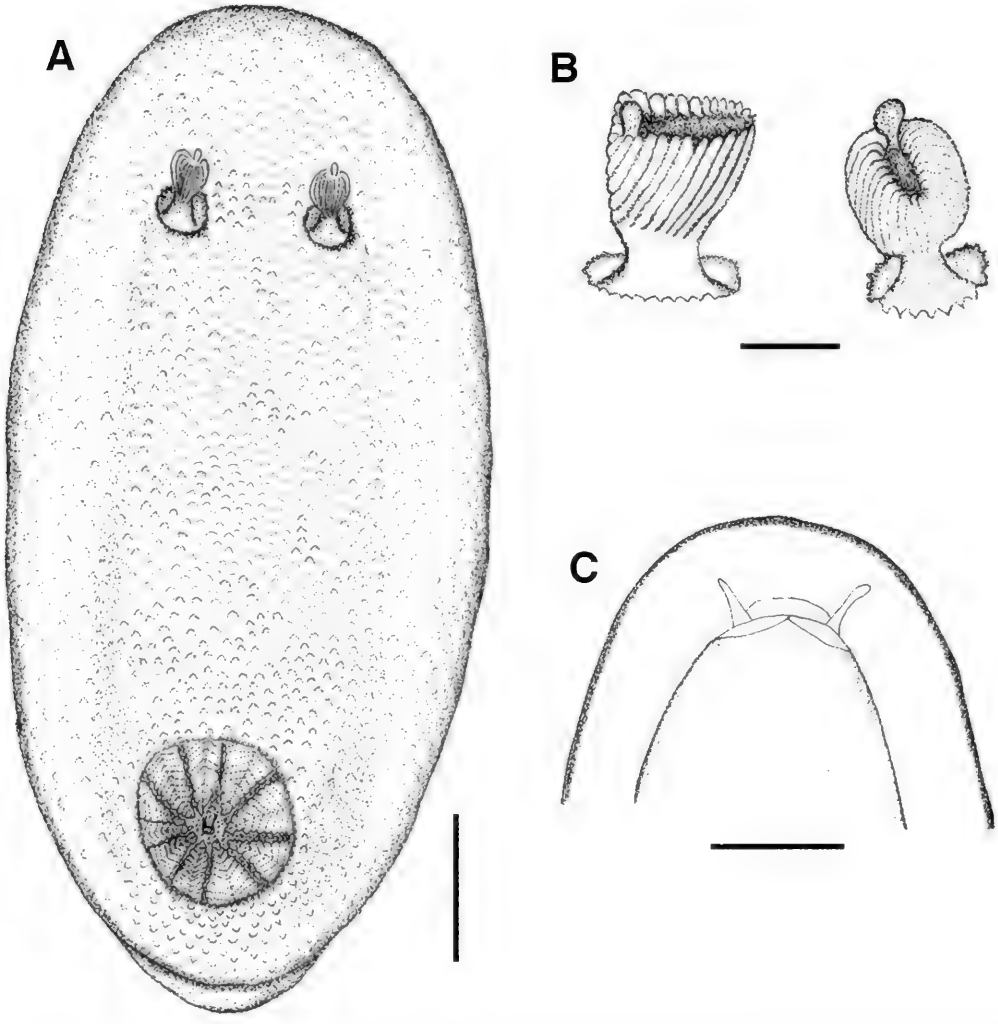

FIGURE 4. *Rostanga byga* Er. Marcus, 1958 (MACN 34174). A. Living animal, scale = 3 mm; B. Lateral and overview of the rhinophores, scale = 2.5 mm; C. Ventral view of the anterior border of foot, scale = 4.5 mm.

Marcus 1958), to compare our specimens with *R. byga*. According to Ernest Marcus (1958), *R. byga* is a bright, brick red species with dorsal white spots. Our specimens from Argentina have a similar coloration, with very distinctive white dots on the dorsum. Anatomically, in *R. byga* the innermost lateral teeth have a long cusp, longer than the base, and the lateral teeth lack a secondary cusp. Also, in the reproductive system drawn by Ernest Marcus (1958) for *R. byga*, the ducts leading from the bursa copulatrix are next to each other, the prostate is large and the ampulla is elongated. All of these characteristics, which are diagnostic of *R. byga*, are present in our specimens.

Based on the examination of several specimens of *R. pulchra* from California and *R. byga* from Argentina, it is clear that they constitute two distinct species (see Table 1). Externally, *R. byga* is an orange species with white spots on the dorsum, whereas *R. pulchra* varies from orange to bright red, sometimes having black or brown dorsal spots. Also, *R. byga* has twice as many lamellae in the rhinophores as *R. pulchra*. In addition, the caryophyllidia of *R. pulchra* have a small ciliated tubercle, whereas it is very large in *R. byga*. Internally, the innermost lateral teeth of *R. pulchra* have a short

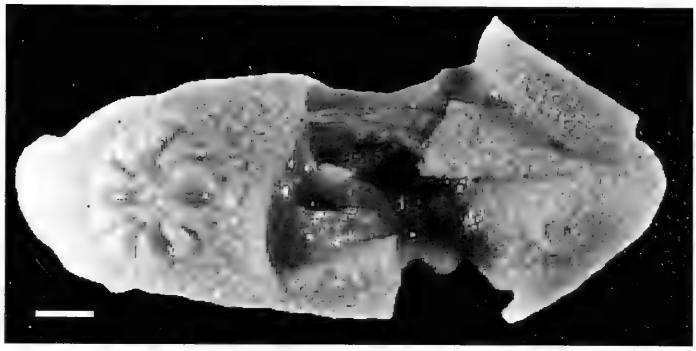

FIGURE 5. *Rostanga byga* Er. Marcus, 1958, holotype (AMNH 3507).

cusp, with long denticles, whereas in *R. byga* the cusp of the innermost teeth is longer, with shorter denticles. The mid-lateral teeth of *R. pulchra* have a large, secondary cusp situated under the main cusp, whereas this secondary cusp is very small in *R. byga*. The jaws of *R. pulchra* have several elements regularly arranged, whereas in *R. byga* the jaws are very reduced, with only a few, irregular elements. The ampulla of *R. pulchra* is comparatively shorter and wider than that of *R. byga*, and the prostate of *R. pulchra* appears to be smaller. In addition, the two ducts emerging from the bursa copulatrix of *R. pulchra* are separated, whereas they are next to each other in *R. byga*.

The other Atlantic species of *Rostanga* is *Rostanga rubra* (Risso, 1818) from the northeast Atlantic. This species is clearly distinguishable from *R. pulchra* and *R. rubra* by the presence of very wide inner lateral teeth, with strong denticles, and elongate outermost teeth with a single denticle (Thompson and Brown 1984). This is very different from both *R. pulchra* and *R. byga* that have narrower inner teeth and outer teeth with numerous denticles.

The present record of *R. byga* constitutes the first account of this species from the temperate waters of the Argentinean biogeographic Province, near the limit with the Magellanic Province. Records of the genus *Rostanga* from the Magellanic Province have been assigned to *R. pulchra* (Ernest Marcus 1959; Marcus and Marcus 1969; Schrödl 1996, 1997). The first of them (Ernest Marcus 1959), includes a complete anatomical description of the specimens collected from Chile. According to this description, there is no question that the specimens studied belong to *R. pulchra*. The morphology of the radula, with a short cusp on the innermost lateral teeth and a large secondary cusp on the mid-lateral teeth is characteristic of this species. The other records from Chile (Marcus and Marcus 1969; Schrödl 1996, 1997), include brief descriptions without anatomical information, and it is difficult to determine the identity of the animals studied. The record from Argentina (Marcus and Marcus 1969) is particularly problematic, not only because it is based on a single preserved specimen, but also because it was collected from a locality very close to the limit between the Magellanic and Argentinean Provinces. According to Marcus and Marcus (1969), the specimen was collected at 102 m depth, and had a very large radular formula (85 × 90.0.90), larger than that of either *R. pulchra* or *R. byga*. The animal was preserved, so there was no information available on the external coloration. However, Marcus and Marcus (1969) indicated that there were several dark spots on the dorsum of the preserved animal, which is characteristic of *R. pulchra*. With the available information we can not determine the identity of this specimen, but it is very likely that it belongs to *R. pulchra*.

The record of *Rostanga byga* from Northern Chubut is very close to the southern boundary of the Argentinean biogeographic Province with the cold waters of the Magellanic Province. According to Carcelles and Williamson (1951), this boundary is situated in Golfo Nuevo, about 42°30′S. However, it is not unusual to find warm-water species of opisthobranch mollusks in this transitional area. Other temperate or warm-water species with a similar distributional pattern to *R. byga* have been recently studied from Argentina (see Muniain 1997; Muniain and Ortea 1998; Muniain and Ortea, in press). On the other hand, Carcelles and Williamson (1951) and Muniain (1997), showed that the Magellanic

TABLE 1. Comparative morphology of *Rostanga pulchra* and *R. byga*.

Species	References	Radular formulae	Innermost tooth denticles	Length	Coloration	Locality
Rostanga pulchra MacFarland, 1905	MacFarland 1906	60 × 50–60.0.50–60	8–11	18 mm (alive)	Bright red, varying from light yellow-red to deep scarlet, with brown and black spots on the back.	Monterey Bay, CA
	MacFarland 1966	68–80 × 81.0.81	8–11	8–12 mm (alive)		Crescent City, CA
	Ev. Marcus and Er. Marcus 1969	85 × 90.0.90	3–5	9 mm (preserved)	?	Camarones Bay, Argentina
	Thompson 1975	69 × 53.0.53	?	15 mm (preserved)	?	Lopez Island, WA
	Present paper	50 × 48.0.48	6–8	16 mm (preserved)	Orange-yellow to bright red; brown spots scattered on the dorsum, white spots on the mantle margin.	Monterey Bay, CA
	Present paper	53 × 51.0.51	6–8	18 mm (preserved)		Monterey Bay, CA
Rostanga byga Er. Marcus, 1958	Er. Marcus 1958	60 × 60.0.60	5–8	11 mm (preserved)	Bright brick red, with white dots on some dorsal papillae.	Ilhabela, Brazil
	Present paper	45 × 53.0.53	7–10	12 mm (preserved)	Orange, lightly spotted with white dots on the middle of the dorsum.	Golfo San José, Argentina
	Present paper	58 × 55.0.55	7–10	14 mm (preserved)		Golfo San José, Argentina
	Present paper	62 × 62.0.62	7–10	20 mm (alive)		Golfo San José, Argentina

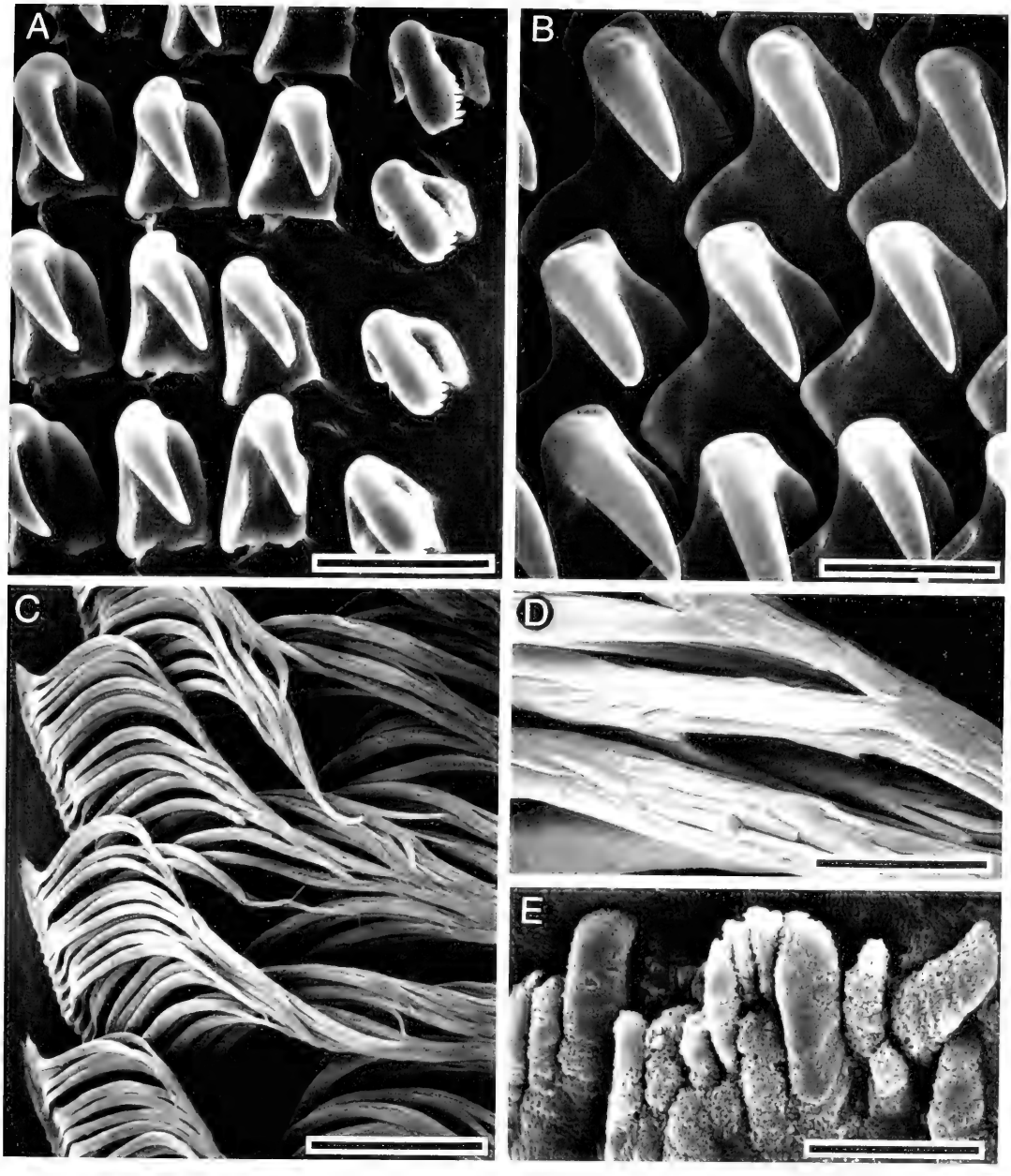

FIGURE 6. *Rostanga byga* Er. Marcus, 1958, scanning electron micrographs (CASIZ 118014). A. Inner lateral teeth, scale = 30 µm; B. Mid-lateral teeth, scale = 43 µm; C. Outer lateral teeth, scale = 75 µm; D. Detail of the outermost teeth denticulation, scale = 10 µm; E. Jaw, scale = 15 µm.

species collected from Northern Chubut to Río de la Plata (Argentinean Province) always occur in deeper and colder waters (100–200 m). This phenomenon is probably related to a northern extension of the Falklands Current in deeper waters (Carcelles and Williamson 1951; Muniain 1997). The fact that the specimen of *R. pulchra* reported by Marcus and Marcus (1969) from this area was collected from deep (102 m), and therefore colder waters, seems to support this hypothesis.

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LITERATURE CITED

CARCELLES, A. AND S. WILLIAMSON. 1951. Catálogo de los moluscos marinos de la Provincia Magallánica. Revista del Museo Argentino de Ciencias Naturales, Zoología 2:225–383.

LEE, R. AND N. FOSTER. 1985. A distributional list with range extensions of the opisthobranch gastropods of Alaska. Veliger 27:440–448.

MACFARLAND, F. M. 1905. A preliminary account of the Dorididae of Monterey Bay, California. Proceedings of the Biological Society of Washington 18:35–34.

———. 1906. Opisthobranchiate Mollusca from Monterey Bay, California, and vicinity. Bulletin of the United States Bureau of Fisheries 25:109–151, pls 18–31.

———. 1966. Studies of opisthobranch mollusks of the Pacific Coast of North America. Memoirs of the California Academy of Sciences 6:1–546, pls 1–72.

MARCUS, ERNEST. 1958. On Western Atlantic Opisthobranchiate gastropods. American Museum Novitates 1906:1–80.

———. 1959. Lamerallariacea und Opisthobranchia. Report of the Lund University Chile Expedition 1948–49, N° 36. Lunds Universitets Arsskrift (Ny. Foljd), Adv. 2, 55:1–133.

———. 1961. Opisthobranch mollusks from California. Veliger 3:1–85, pls. 1–10.

MARCUS, EVELINE. 1970. Opisthobranchs from Northern Brazil. Bulletin of Marine Science 20:922–951.

MARCUS, EVELINE AND ERNEST MARCUS. 1969. Opisthobranchian and lamellarian gastropods collected by "Vema." American Museum Novitates 2368:1–31.

———. 1970. Some gastropods from Madagascar and West Mexico. Malacologia 10:181–223.

MUNIAIN, C. 1997. Moluscos Opistobranquios de Argentina: revisión taxonómica y relación de ecología química en algunas especies patagónicas. Unpublished Ph. D. Thesis, Universidad de Oviedo, Spain.

MUNIAIN, C. AND J. ORTEA. 1998. The taxonomic status and redescription of *Polycera marplatensis* Franceschi, 1928 (Nudibranchia: Polyceratidae) from Argentina. Veliger 41:142–147.

———. In press. New records of the genus *Berghia* Trinchese, 1877 (Opisthobranchia: Aeolidiidae) from Argentina, with description of a new species. Avicennia.

RUDMAN, W. AND J. AVERN. 1989. The genus *Rostanga* Bergh, 1879 (Nudibranchia: Dorididae) in the Indo-West Pacific. Zoological Journal of the Linnean Society 96:281–338.

SCHRODL, M. 1996. Nudibranchia y Sacoglossa de Chile: morfología externa y distribución. Gayana Zoológica 60:17–62.

———. 1997. Range extensions of Magellanic nudibranchs (Opisthobranchia) into Peruvian Faunal Province. Veliger 40:38–42.

THOMPSON, T. E. 1975. Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). Journal of Zoology 176:477–517.

THOMPSON, T. E. AND G. H. BROWN. 1984. Biology of opisthobranch molluscs. Volume II. The Ray Society, London. 229 pp.

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Valve Ultrastructure of Some Eunotiaceae (Bacillariophyceae), with Comments on the Evolution of the Raphe System

by

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Ultrastructural observations on valve features of five diatom species from the family Eunotiaceae are presented, including four from the Amazon basin and one from California. Of the Amazonian taxa, *Peronia brasiliensis* Hustedt has a straight raphe system positioned on the valve face and a central sternum, *Eunotia synedraeformis* Hustedt and *E. curvula* Hustedt have raphe systems predominantly towards the valve mantle, as well as a central sternum. *Eunotia conversla* Hustedt has a raphe system positioned more on the valve face and a central sternum. Specimens of *Amphicampa eruca* Ehrenberg from California have a very short raphe on the mantle and lack a central sternum. These data, in addition to previously published observations, point to the diversity of raphe types in the Eunotiaceae. These data do not help to distinguish between differing hypotheses on the length and position of the raphe in the earliest raphe-bearing diatom.

The family Eunotiaceae was originally proposed by Kützing (1844:32) for those diatoms asymmetrical about the longitudinal axis, with convex dorsal and concave ventral margins, and striae extending across the entire face of the valve. Today, we understand the family to contain those raphid diatoms that also possess rimoportulae (Krammer and Lange-Bertalot 1991). The family is almost exclusively freshwater. Included in the group are *Eunotia* Ehrenberg (which, in a broad sense, also includes species formerly separated into the genera *Semiorbis* Patrick and *Desmogonium*), *Actinella* Lewis, *Peronia* Brébisson and Arnott, and *Amphicampa* Ehrenberg. *Peronia* has been reassigned to a new family in which it is the only member (Round et al. 1990), but it is clearly allied to the genera mentioned above. Species of the Eunotiaceae are most diverse in dystrophic or acid waters.

Members of the Eunotiaceae are thought to have a unique systematic position, because of their suite of characters, including both primitive (i.e., rimoportulae) and derived (i.e., raphe system) features. Because both primitive and derived features are found in all members of the group (except some highly derived forms that have secondarily lost a raphe system, see Kociolek and Rhode 1998), members of the Eunotiaceae have been thought to represent early archetypes in the development of the raphe system (Berg 1948). Some (e.g., Kolbe 1956; Geissler and Gerloff 1963) have speculated the raphe evolved through enlargement of the rimoportulae along the ventral margin, by way of small raphe-like slits (with taxa like *Amphicampa* proposed as intermediates between araphid and raphid diatoms). Hustedt (1952), in examining a wide range of eunotioid diatoms from the Amazon basin, believed the raphe evolved in a form similar to the genus *Peronia* (i.e., raphe elongated on the valve face but without a central nodule). In Hustedt's view, most of the Eunotiaceae represent a lineage off the main evolutionary track towards the Naviculaceae. Simonsen (1979) aligned the Eunotiaceae with one group of araphid diatoms, off the line in which the naviculacean raphe evolved. One implication of Simonsen's dendrogram is that the raphe in the Eunotiaceae is not homologous with the raphe system of the naviculoids.

In this report, I present light and scanning electron microscope observations on some Eunotiaceae species that have been suggested by Hustedt (1952) and Kolbe (1956) to represent important links in the evolution of the raphe system. Ultrastructural features are described and compared to other members of the family and to other raphid diatom groups.

Materials and Methods

Light and scanning electron microscope observations were conducted on several taxa within the Eunotiaceae thought critical to understanding the early evolution of the raphe system. The taxa examined and material on which the observations were made include *Eunotia curvula* Hustedt (samples AM 1027, AM 1028 from the Hustedt Collection), *E. synedraeformis* Hustedt (samples AM 1027, AM 1028 from the Hustedt Collection), *E. conversa* Hustedt (samples AM 1027, AM 1030, AM 2216 from the Hustedt Collection),

Amphicampa eruca Ehrenberg (sample 607663 of the Diatom Collection, CAS) and *Peronia brasiliensis* Hustedt (samples AM 1027, AM 1028, AM 2216 from the Hustedt Collection).

Hustedt material includes:
Sample AM 1027: "Brasilien. Lago Jurucui, an Pflanzen. 25.10.47. Braun, 252."
Sample AM 1028: "Brasilien. Lago Jurucui, Südufer, an Ast. 5.11.47. Braun, 253."
Sample AM 1030: "Brasilien. Lago Jurucui, überschwemmte Campos, an Gr sern. 25.6.48. Braun 2548."
Sample AM 2216: "Igarape do Tento. Uferschlick. 22.11.47. Braun 209.b."

CAS sample 607663: "USA, California, Mendocino Co., Lake Mendocino, drying inlet to lake. 28 Jun. 1995. coll. J. P. Kociolek."

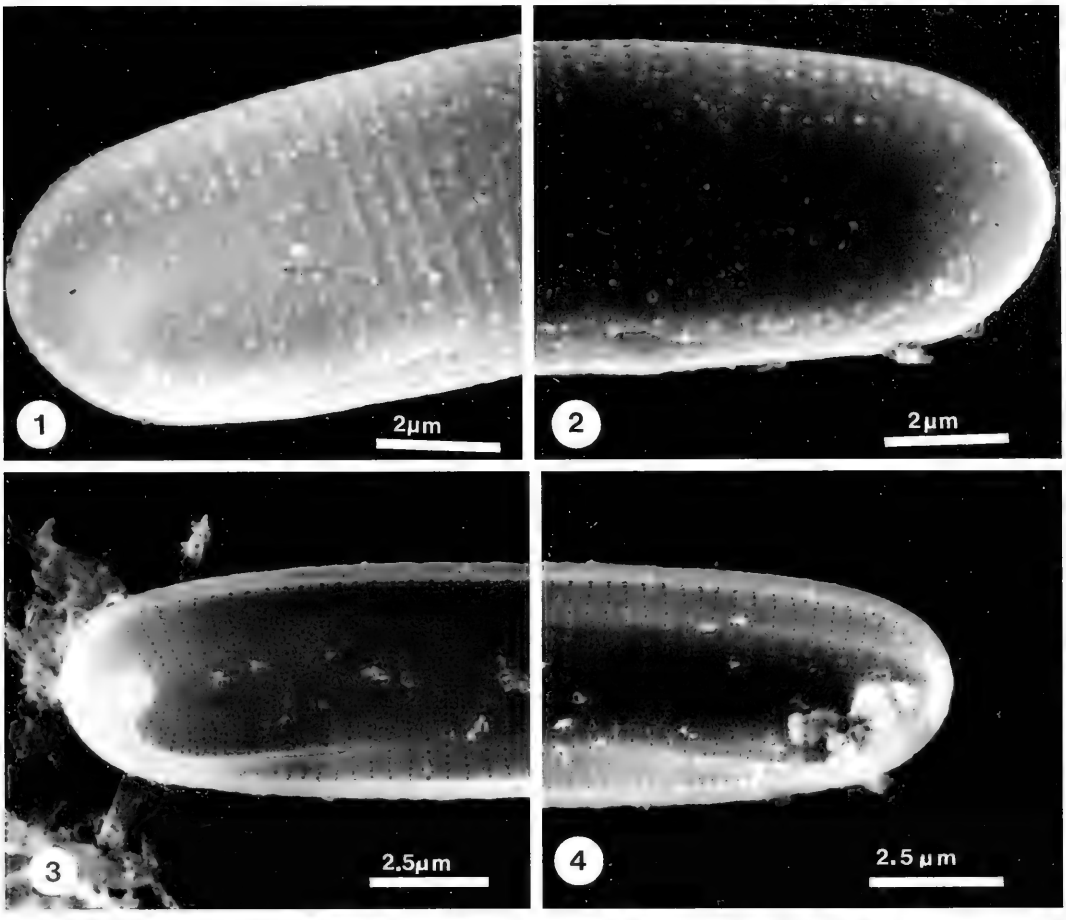
Material was cleaned in nitric acid, rinsed in distilled water, settled until neutral, and air-dried onto coverslips. Coverslips containing the dried material were attached to aluminum stubs and sputter-coated with approximately 20 nm of gold-palladium. The coated material was viewed on a Hitachi S-520 SEM at an operating voltage of 10 kV.

Results

Eunotia curvula Hustedt
Figures 1–4; Hustedt 1952, fig. 24; Simonsen 1987, pl. 568, figs. 1–5

Description. — Valves linear with margins nearly parallel, apices rounded, with convex dorsal margin and concave ventral margin, 150–500 µm long, 4.5–7.0 µm broad. Raphe short, j-shaped, curves from near the mantle onto the valve face, axial area distinct, striae 21/ 10 µm, punctate. Rimoportula present at each valve pole.

SEM Observations. — Round areolae are occluded externally. The raphe is hook- or j-shaped, and has a large dilated distal end and undistinguished proximal end. A single rimoportula opening is found at each valve terminus. The axial area extends the length of the valve. The valve is covered with small siliceous nodules. Internally the raphe slit is bordered on both sides by a small ridge of silica. The raphe runs from the proximal end, positioned on the valve face, towards the mantle, and recurves towards the face, terminating in a prominent helictoglossa. A rimoportula is positioned at the valve face-mantle junction.



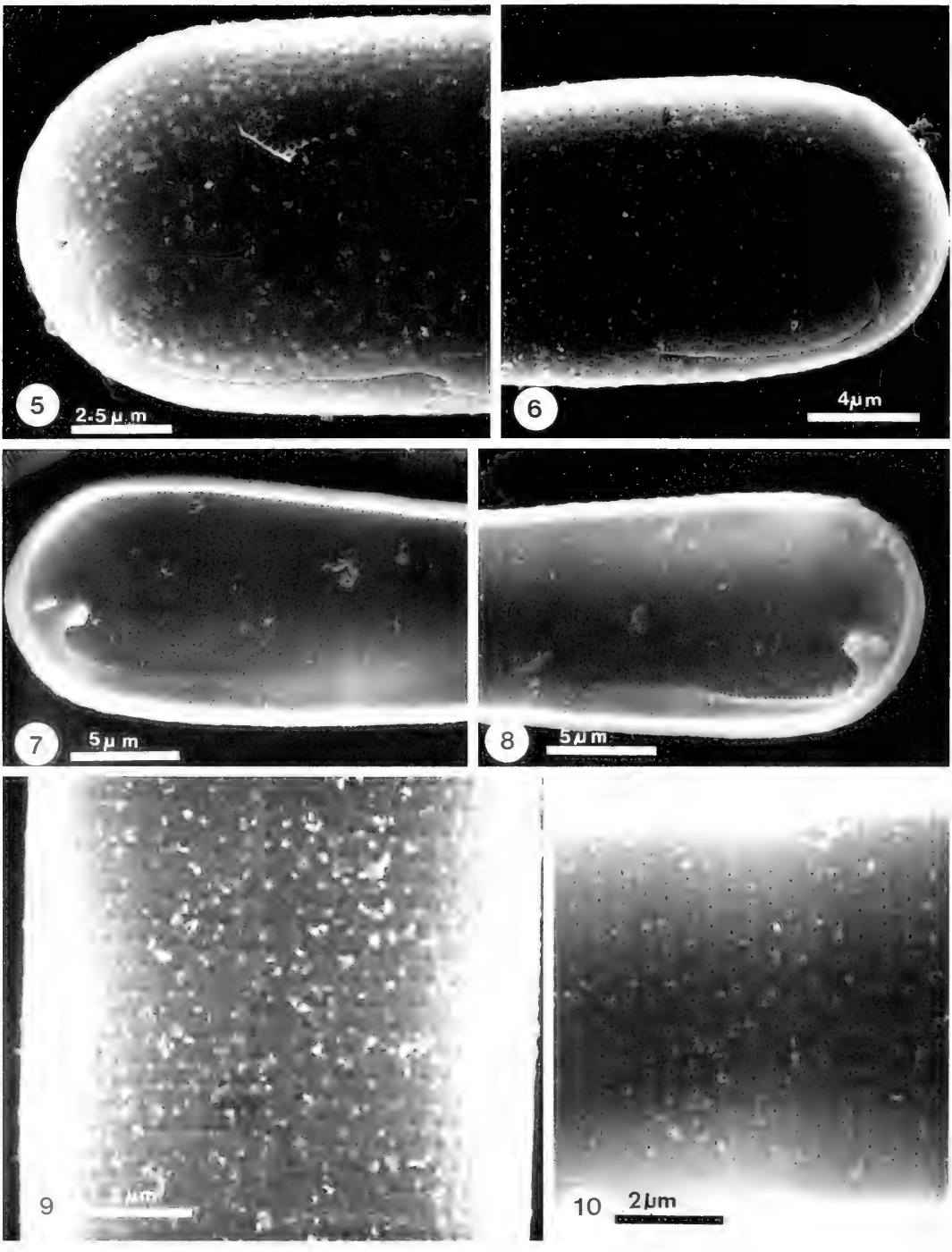
FIGURES 1–4. *Eunotia curvula*, SEM. (1–2) External views at the apices. J-shaped raphe has dilated distal ends terminating on valve face. Rimoportulae are positioned at the valve face-mantle junction. Valve face is covered with scattered siliceous nodules. (3–4) Internal views at the apices. Raphe branches are restricted to ventral margin, with a prominent helictoglossa at each pole. The raphe is bordered by a thin, elevated ridge. Rimoportulae are located near helictoglossa. Striae are interrupted near the center of the valve.

Eunotia synedraeformis Hustedt

Figures 5–10; Hustedt 1952, fig. 8; Simonsen 1987, pl. 566, figs. 1–8

DESCRIPTION. — Valves straight or nearly so, with parallel margins, apices appear slightly swollen and broadly rounded, obtuse, length 235–525 μm, breadth 9–10 μm. Raphe j- or hook-shaped, recurved on the valve face, axial area runs the length of the valve, striae punctate, with puncta near the axial area more coarse and irregularly arranged within the striae. Striae number 18–22/ 10 μm.

SEM OBSERVATIONS. — Rounded to nearly rectangular areolae are occluded externally. The hook-shaped raphe is dilated at both the proximal end (positioned close to the valve mantle) and distal end (positioned in the middle of the valve face). Striae are interrupted along the apical axis by a hyaline area running the length of the valve. A narrowly elliptical, prominent opening of the rimoportula is located at each pole and is positioned at the valve face-mantle junction. Internally, areolae become more distantly spaced as they approach the center of the valve. Occlusions are lacking internally. The raphe slit has a slight ridge bordering it as it runs from the proximal end on the valve



FIGURES 5–10. *Eunotia synedraeformis*, SEM. (5–6) External views at the apices. Prominent J-shaped raphe with dilated distal ends recurved towards center of valve. Rimoportula opening is visible. Occluded areolae appear sunken. (7–8) Internal views at the apices. Raphe opening is restricted to ventral margin, bordered by a thin, elevated ridge, and ends in large helictoglossae. Rimoportulae are found at both poles. (9) Center of the valve. External view showing interruption of striae forming central sternum. (10) Center of the valve. Internal view showing disruption of striae towards center.

face towards the mantle and recurves towards the valve center at the distal end. The raphe terminates in a prominent helictoglossa at its distal end. Located near the helictogossae at the valve-mantle junction are well-developed rimoportulae.

Eunotia conversa Hustedt
Figures 11–16; Hustedt 1952, fig. 25; Simonsen 1987, pl. 565, figs. 1–8

DESCRIPTION. — Valves narrow, straight for most of the length of the valve, bent about the apical axis, ends narrowly rounded. 50–120 μm long, 2.0–3.5 μm broad. Raphe j-shaped, but difficult to discern. Axial area present but indistinct. Striae about 28–30/10 μm.

SEM OBSERVATIONS. — Internally the raphe slit is located in a raised central rib and extends along the center of the valve. The raphe terminates in a helictoglossa. A rimoportula is found on the face at the valve terminus at only one end of each valve. An internally-raised ridge is found positioned towards the ventral margin of the valve. The ridge extends about 1/3 of the length of the raphe. Striae are interrupted by a wide unornamented axial area near the center of the valve . Externally, the relatively long raphe slit curves and continues back towards the center of the valve. The shorter portion of the raphe branch does not perforate the valve. A prominent opening of the single rimoportula is found at the junction of the valve face and mantle. Areolae appear as small, round openings internally.

Peronia brasiliensis Hustedt
Figures 17–20; Hustedt 1952, figs. 1, 2; Simonsen 1987, pl. 562, figs. 1–7

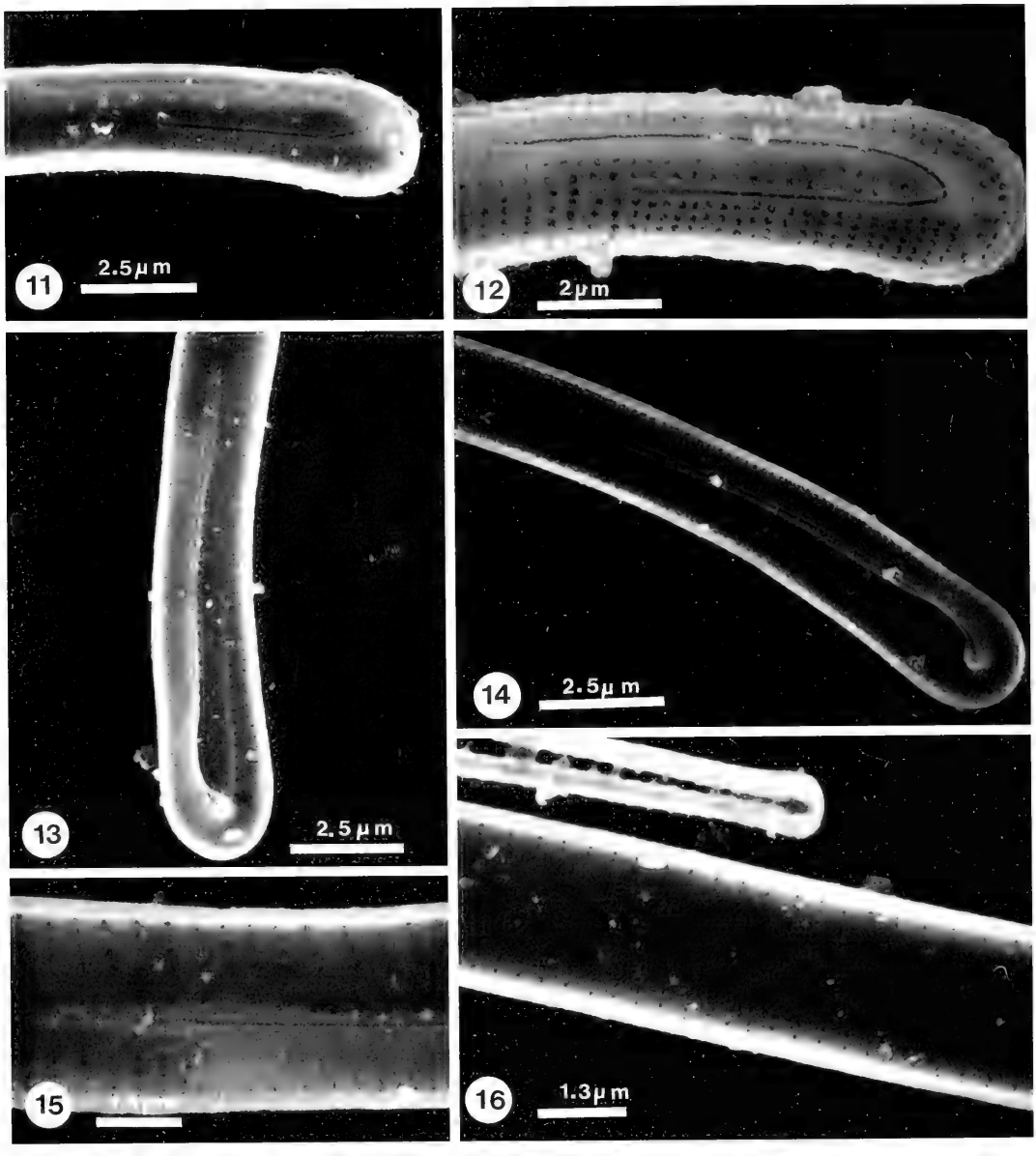
DESCRIPTION. — Valves narrow, asymmetrical about the transapical axis and have rounded poles. Length 15–30 μm, breadth 3–5 μm. The raphe branches are short, restricted to the apices, and positioned in the middle of the valve face. Striae are parallel, slightly radiate at the poles, 20–30/10 μm.

SEM OBSERVATIONS. — Internally, the centrally-positioned, short raphe slits extend from the proximal ends and terminate as prominent helictoglossae. A small, relatively inconspicuous rimoportula is located at one pole only, at the valve terminus. A central nodule is lacking. Between the proximal raphe ends is located an unornamented axial area. The round puncta appear to lack occlusions.

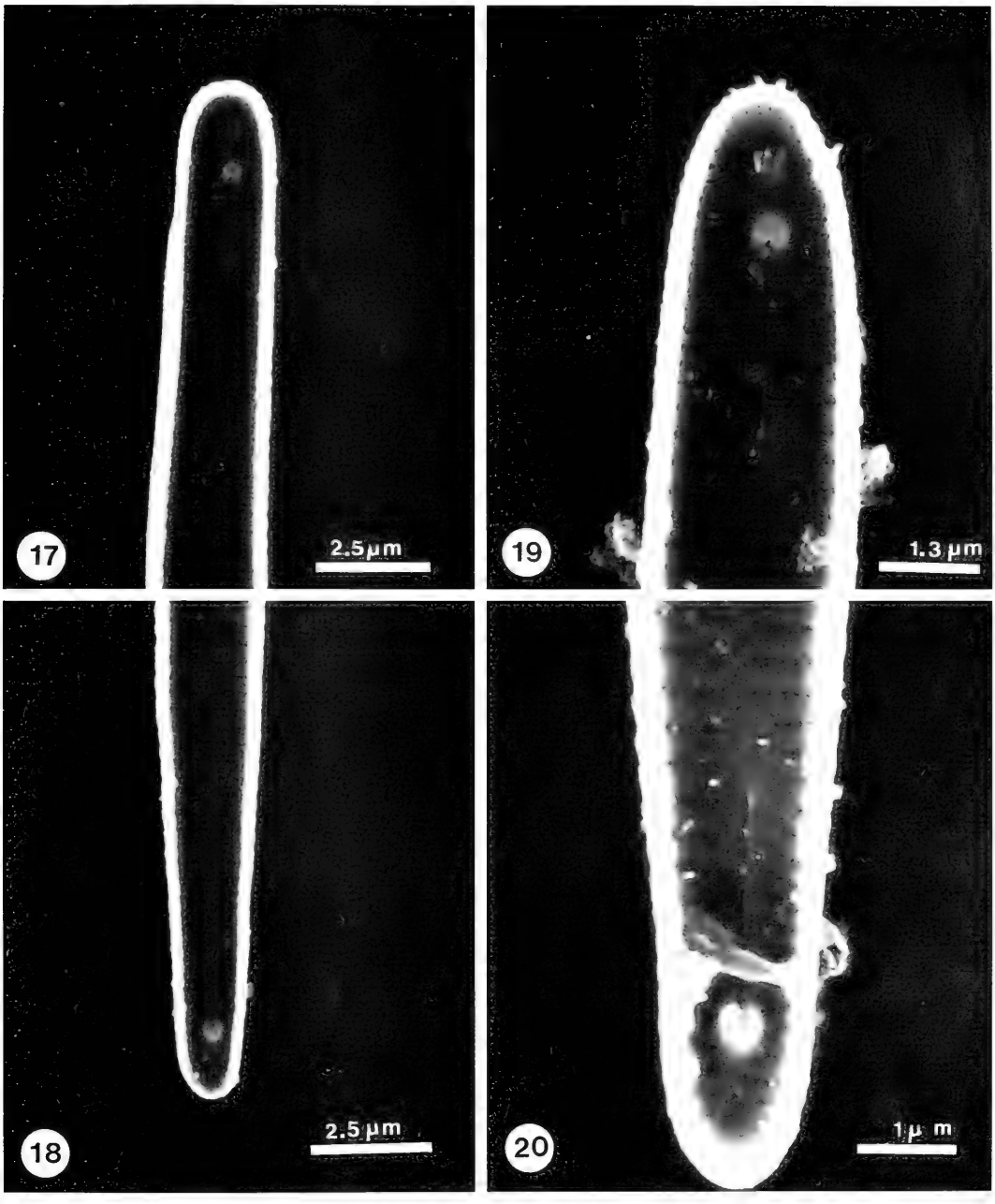
Amphicampa eruca Ehrenberg
Figures 21–35

DESCRIPTION. — Valves19–64 μm long, 9–11 μm broad. Both the dorsal and ventral margins are undulate; the dorsal margin has 3–7 undulations, whereas the ventral margin has 1–6 undulations. Striae are distinctly punctate, and the discontinuity across the striae is closer to the ventral margin. Small raphe slits are indistinct but visible near the valve terminus close to the ventral margin.

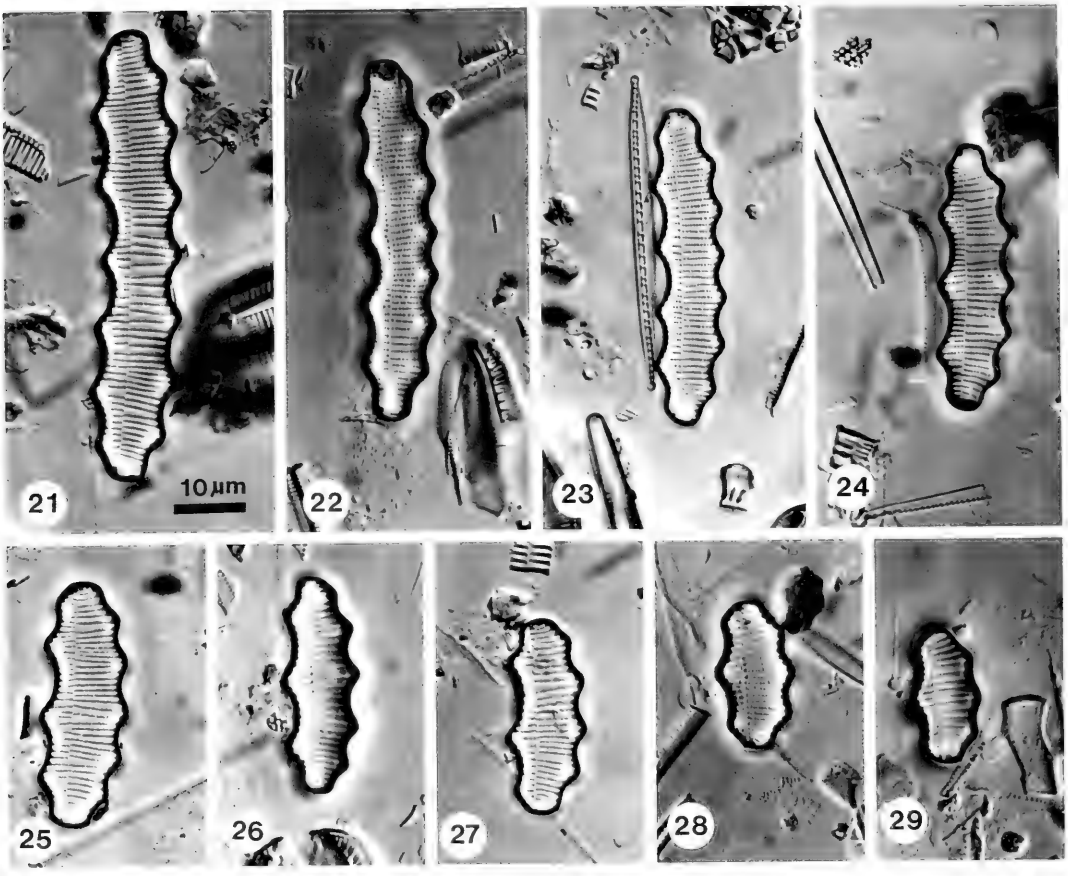
SEM OBSERVATIONS. — The external valve face is covered by striae composed of rounded areolae. Striae are interrupted towards the ventral margin on the valve face. Distinct breaks in the striae also occur around the margin of the valve. Long and short striae alternate on the valve mantle. Short raphe branches of variable shape are positoned close to the valve face-mantlejunction. Spines are lacking. Internally, raphe branch length and helictoglossa size are quite variable. A rimoportula is positoned at each end of the valve. The position of the rimoportulae is variable; they may be placed at the valve terminus, at the terminus/dorsal margin junction, or along the dorsal margin.



FIGURES 11–16. *Eunotia conversa*, SEM. (11) External view. Elongate raphe sharply recurved towards valve center. Single rimoportula opening is visible. (12) External view. Valve apex with prominent raphe branch and occluded areolae. FIGS. 13–16. Internal views. (13–14) Valve apices of same valve showing elongate raphe slit bordered by thin, elevated ridge. One end (Fig. 13) has a rimoportula. Linear swelling indicates where external groove of raphe is located. (15) Proximal raphe end undifferentiated, with lack of a central nodule. (16) Center of valve showing striae interrupted in middle of valve.



FIGURES 17–20. *Peronia brasiliensis*, SEM, internal views. (17–18) Headpole (Fig. 17) and footpole (Fig. 18) of the same valve. Small raphe branches are restricted to apices. Helictoglossae are prominent. Single rimoportule is located at headpole. (19–20) Headpole (Fig. 19) and footpole (Fig. 20) of the same valve. Headpole shows striae bordering raphe to be more dense. Striae are composed of round puncta. Rimoportule is located near helictoglossa at headpole. Central nodule is lacking.

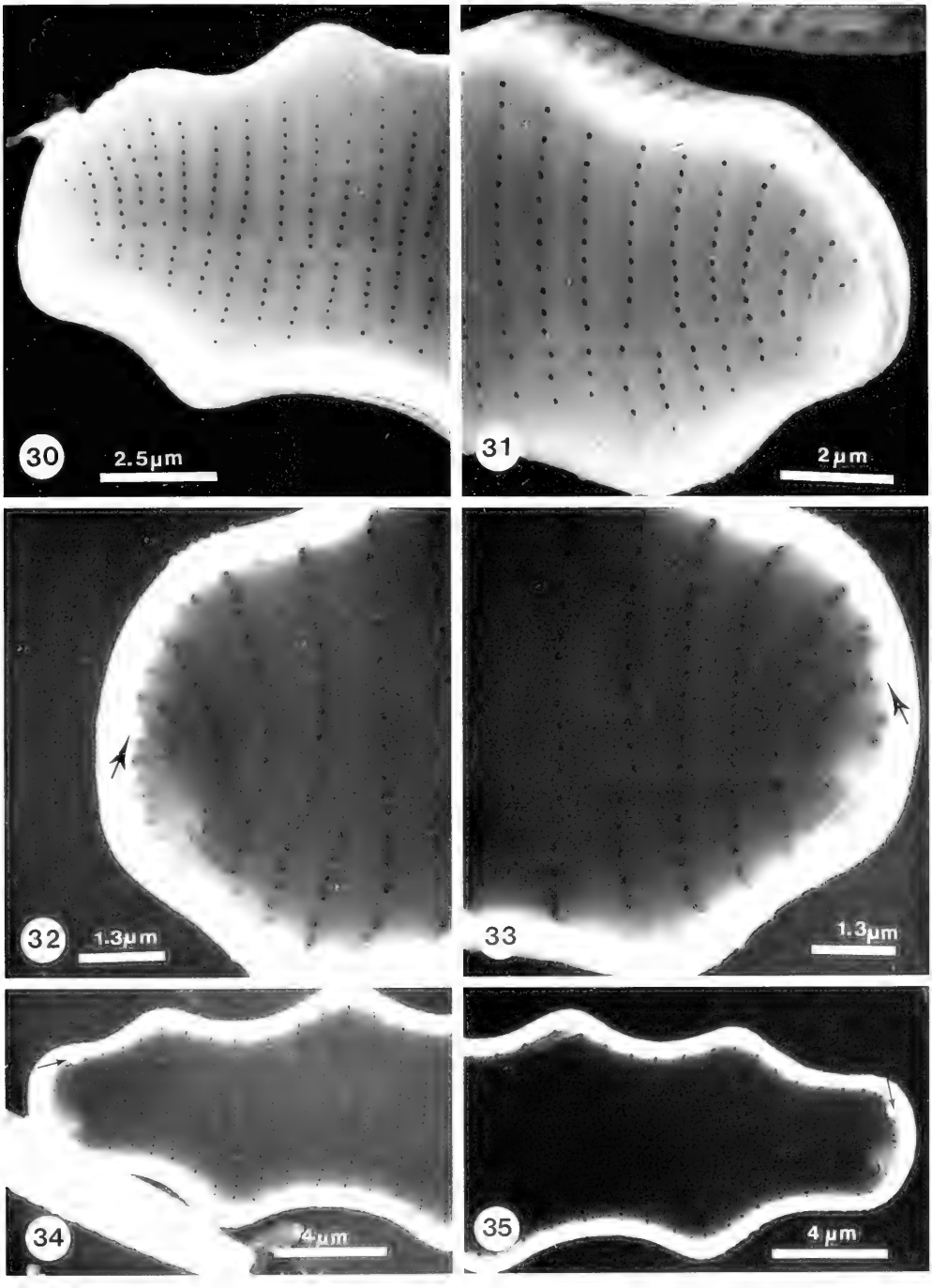


FIGURES 21–29. *Amphicampa eruca*, LM. Valve views showing variation in outline and size diminution. Scale bar is 10 µm for all figures.

DISCUSSION

Observations presented here provide additional evidence of considerable variation in raphe structure in the Eunotiaceae. This variation includes: (1) a short raphe system without a central sternum, restricted to the mantle (in *Amphicampa*); (2) a longer raphe system without a central sternum either restricted to or predominantly on the mantle (in *Eunotia* and *Actinella*; Round et al. 1990; Lange-Bertalot 1995; Kociolek et al. 1997); (3) an even longer, highly curved raphe mostly on the valve face with a central sternum (*E. conversa, E. curvula, E. synedraeformis*); and (4) a straight raphe centrally positioned on the valve face with a central sternum (*Peronia brasiliensis*).

The observations, which are based on raphe features, suggest there is variation within a genus, as well as within the family Eunotiaceae. For example, Round, Crawford, and Mann (1990:459, fig. m) illustrated what looks like a simple central nodule in a species of *Peronia*, and the lack of a central nodule in *P. brasiliensis* might suggest that *Peronia* is a non-monophyletic group. Clearly, with presence of rimoportulae being a primitive feature and presence of a raphe diagnosing the entire group of raphid diatoms, this suite of features cannot be used to diagnose the Eunotiaceae as has been done in the past (e.g., Krammer and Lange-Bertalot 1991). It is therefore possible that other rimoportula-bearing raphid diatoms do not necessarily belong to the Eunotiaceae (in either the strict or broad sense); an example of this is the genus *Eunophora*, which may be more closely aligned to *Amphora* and its relatives



FIGURES 30–35. *Amphicampa eruca*, SEM. (30–31) External views at the apices. Both figures show small raphe branches at ventral margin. Discontinuity in striae is located towards ventral margin. Striae are composed of round, unoccluded areolae. Spines are lacking. (32–33) Internal views at apices. Opposite ends of same valve showing presence of rimoportulae located on valve mantle (arrows). Raphe branches are small, with indistinct helictoglossae. (34–35) Internal views at apices. Apices of different cells showing variation in position of rimportulae (arrows). Raphe branches and helictoglossae are noticeable.

(Vyverman et al. 1998). Presence of a central nodule in some *Peronia* species would lend support to the creation of the Peroniaceae (Round et al. 1990), since a central nodule is absent in the members of the Eunotiaceae.

Eunotia sensu stricto appears to be composed of many disparate morphological subgroups, whose relationships within the Eunotiaceae require further research. Hustedt (1926), for example, suggested the earliest branch within *Eunotia* may be composed of the bilunaris group. Krammer and Lange-Bertalot (1991) have documented with SEM the ultrastructure of *E. bilunaris* and its allies, which have raphe and valve construction similar to *E. curvula* and *E. synedraeformis*. This similarity may suggest that the bilunaris group may have evolved separately from other *Eunotia* groups. L ange-Bertalot's (1995) *E. weisingii* may be a transitional form between *E. conversa* and the bilunaris group. Variation among other *Eunotia* taxa has been documented by Krammer and Lange-Bertalot (1991) and Lange-Bertalot (1995). An implication of these observations is that *Eunotia* may not necessarily be a monophyletic group. More work is necessary to resolve the finer relationships within the Eunotiaceae.

While we may now understand the variation in raphe expression to be greater than previously appreciated, our observations do not yet speak to the question of the evolution of the raphe system from araphid ancestors. Kolbe's (1956) hypothesis of the earliest raphid-bearing diatom being similar to *Amphicampa* (supported by the work of Mann 1984), then evolving through forms with progressively longer raphe systems until the naviculoid type is reached, is consistent with our observations. However, equally plausible is the idea that the earliest raphe system was fully developed (similar to that in *Peronia brasiliensis*, Hustedt 1952; see also Hustedt 1935), and that the rest of the eunotioid forms represent degeneration, with *Amphicampa* showing the greatest expression of raphe reduction. Kociolek and Rhode (1998) have suggested raphe reduction occurred elsewhere within the rhaphidiod line. In the *Actinella* lineage from Madagascar, a series of raphe types were observed, and suggested to represent reduction of a typical *Actinella* raphe system to a simple slit without a helictoglossa (Kociolek and Rhode 1998). Taxa such as *Falcula* Voigt, shown to have a slit positioned close to the ventral margin may reflect a degenerated (but derived) condition of the raphe, rather than a primitive raphe condition, as argued by Geissler and Gerloff (1963). Given the diversity within *Amphicampa* (Ehrenberg 1854) and the closely allied genera *Ophidocampa* and *Heterocampa* (Ehrenberg 1870), both of which have not been investigated since the taxa were described originally, the relationship of *Amphicampa* and its close allies within the Eunotiaceae needs further investigation. Also, examination of original Ehrenberg material to confirm the identity of *Amphicampa eruca* is crucial to confirming the present results.

Further observations on other naviculoid forms, including *Rouxia, Amphipleura* and *Frustulia* among others, as well as other raphe- and rimoportula-bearing taxa (such as *Eunophora*) will be critical in developing a formal phylogenetic hypothesis on the origin and early evolution of the raphe system.

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Sarah Spaulding, CAS, graciously provided technical assistance. Discussions with participants of the XIV North American Diatom Symposium (1997) about these findings were particularly helpful. Reviews of this manuscript by S. Spaulding, E. Fourtanier, R. Jahn, D. Williams and the research group in the laboratory of E. F. Stoermer were also helpful.

LITERATURE CITED

BERG, A. 1948. Observations on the development of the Eunotia-raphe. Arch. Botanik. 33A:1–10.

EHRENBERG, C. G. 1854. Mikrogeologie. Das Erden und Felsen schaffende Wirken des unsichtbar Kleinen selbstanigen Lebens auf der Erde. Leopold Voss, Leipzig. 374 pp.

———. 1870. Über mächtige Gebirgs-Schichten vorherrschend aus mikroskopischen Bacillarien unter und bei der Stadt Mexiko. Physik. Abhandl. könig. Akad. Wiss. Berlin. 1869:1–66.

GEISSLER, U. AND J. GERLOFF. 1963. Elektronenmikroskopische Beiträge zur Phylogenie der Diatomeenrhaphe. Nova Hedwigia 6:339–352.

HASLE, G. R. 1973. The "mucilage pore" of pennate diatoms. Beih. Nova Hedwigia 45:167–186.

HUSTEDT, F. 1926. Untersuchungen über den Bau der Diatomeen. I. Raphe und Gallertporen der Eunotioideae. Ber. Deutsche Bot. Gesell. 44:142–150.

———. 1935. Untersuchungen über den Bau der Diatomeen. XII. Ber. Deutsche Bot. Gesell. 53:246–264.

———. 1952. Neue und wenig bekannte Diatomeen III. Phylogenetische Variationen bei den rhaphidioiden Diatomeen. Ber. Deutsche Bot. Gesell. 65:133–144.

KOCIOLEK J. P. AND K. RHODE. 1998. Raphe vestiges in "*Asterionella*" species from Madagascar: evidence for a polyphyletic origin of the araphid diatoms? Crypto. Algol. 19:57–74.

KOCIOLEK J. P., K. RHODE, AND D. M. WILLIAMS. 1997. Taxonomy, ultrastructure and biogeography of the *Actinella punctata* species complex (Bacillariophyta: Eunotiaceae). Nova Hedwigia 65:177–193.

KOLBE, R. W. 1956. Zur Phylogenie des Raphe-Organs der Diatomeen: *Eunotia* (*Amphicampa*) *eruca* Ehr. Bot. Notiser. 109:91–97.

KRAMMER, K. AND H. LANGE-BERTALOT. 1991. Bacillariophyceae 2/3. Centrales, Fragilariaceae, Eunotiaceae. In Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fisher, Stuttgart. 576 pp.

KÜTZING, F. T. 1844. Die Kieselschaligen Bacillareen oder Diatomeen. Nordhausen. 152 pp.

LANGE-BERTALOT, H. 1995. 85 Neue Taxa und über 100 weitere neu definierte Taxa ergänzend zur Susswasserflora von Mitteleuropa Vol. 2/1–4. Bibl. Diatomol. 27:1–454.

MANN, D. G. 1984. An ontogenetic approach to diatom systematics. Pp. 113–144 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed.; 1982 August 22–27; Philadelphia, PA. O. Koeltz, Koenigstein. 541 pp.

ROUND F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The diatoms. Morphology and biology of the genera. Cambridge University Press, Cambridge, U. K. 747 pp.

SIMONSEN, R. 1979. The diatom system: ideas on phylogeny. Bacillaria 2:9–71.

———. 1987. Atlas and catalogue of the diatom types of Friedrich Hustedt. 3 Vols. J. Cramer, Berlin.

VYVERMAN, W., K. SABBE, D. G. MANN, C. KILROY, R. VYVERMAN, K. VANHOUTTE, AND D. HODGSON. 1998. *Eunophora* gen. nov. (Bacillariophyta) from Tasmania and New Zealand: description and comparison with *Eunotia* and amphoroid diatoms. European J. of Phycology 33:95–111.

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Silurian Polyplacophora and Rostroconchia (Mollusca) from Northern California

by

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Silicified polyplacophorans from the Gazelle Formation in California represent the second known Silurian (Ludlovian) occurrence of this class in North America. New taxa are *Paleochiton siskiyouensis* sp. nov. and *Thairoplax merriami* sp. nov. *Eusphairica distubula* gen. et sp. nov. is the first Silurian rostroconch identified in the United States and extends the range of the family Eopteriidae Miller, 1889, from the Middle Ordovician into the Upper Silurian.

The late C. W. Merriam (1972), U. S. Geological Survey, collected and processed samples of limestone cobbles with silicified fossils from a conglomeratic zone of the Silurian Gazelle Formation exposed in Siskiyou County, California, in 1951, and noted the presence of amphineuran plates. Some of the specimens obtained were placed in the collections of the California Academy of Sciences. Peter U. Rodda brought this polyplacophoran fauna to my attention.

Preservation of the silicified plates range from poor to excellent. Many are imcomplete and most have additional siliceous deposits adhering to them. All are intermediate plates with the exception of two tail plates. Head plates were not found among the more than 50 specimens.

A single specimen of a rostroconch is present with a portion of a chiton plate attached to it. The importance of this rostroconch occurrence necessitated the removal of as much of the plate and other adhering material as possible to allow better photographic representation of the specimen.

Based on the rugose coral fauna described by Merriam (1972), and the accompanying fauna of brachiopods, gastropods, and trilobites, the Gazelle Formation is mainly Late Silurian (Ludlovian) in age. Portions of the formation in this region may be slightly older or younger than this (Merriam 1972:23).

The collection locality in the Gazelle Formation, which represents the type locality for all of the new taxa herein, is 2 km southeast of Parker Ranch, East Fork of the Scott River, SW ¼ sec. 29, T41N, R7W, Siskiyou County, California, Etna quadrangle, USGS locality M1027.

Previous Studies

European Silurian polyplacophorans have been studied by Salter (in M'Coy 1846), de Koninck (1857; translated by Bailey 1860), Barrande (1867), Davidson and King (1874), Lindström (1884), Woodward (1885), Etheridge (1897), Couper Reed (1911), Bergenhayn (1943, 1955), and Cherns (1998a, 1998b, 1999).

Other than the noted presence by Merriam (1972:15), the only other account of North American Silurian polyplacophorans was by Kluessendorf (1987), from Wisconsin, Illinois, and Iowa. Collected from carbonate buildups, these specimens are preserved as impressions of the ventral surface.

Kluessendorf erected, *Chelodes raaschi* sp. nov. and *Hawthorneachiton lowenstami* gen. et. sp. nov. Other specimens were described as morphotypes. One of the latter, Morphotype H (Kluessendorf 1987, fig. 10), represents a turrileped plate.

SPECIES DESCRIPTIONS

Class Polyplacophora de Blainville, 1816
Subclass Paleoloricata Bergenhayn, 1955
Order Chelodida Bergenhayn, 1955
Suborder Chelodina Bergenhayn, 1955
Family Gotlandochitonidae Bergenhayn, 1955
Genus *Paleochiton* Smith *in* Smith and Toomey, 1964

***Paleochiton siskiyouensis* sp. nov.**
Fig. 1

TYPE MATERIAL. — HOLOTYPE: CAS 68395, PARATYPES: CAS 68396.01–68396.18.

DIAGNOSIS. — Intermediate plates strongly arched; shallow to deep jugal sinus; apical area short, bordering nearly straight to slightly produced posterior margin.

DESCRIPTION. — Intermediate plates strongly arched, subrectangular in dorsal view; jugal area rounded; side slopes flatly convex; posterior margin straight to slightly mucronate; lateral margins straight to slightly convex, nearly parallel; anterior margin with deep jugal sinus; jugal angle 83°–89°; apical area short, 1.4 mm in length, straight to flatly V-shaped; shell material thick medially, thinning laterally; surface smooth.

Tail plate wedge-shaped in dorsal view; posterior margin pointed, curved dorsally; anterior margin flatly convex; jugal area broadly rounded, side slopes flat.

MEASUREMENTS. — See Table 1.

DISCUSSIONS. — *Paleochiton siskiyouensis* differs from the Ordovician *P. kindbladensis* Smith *in* Smith and Toomey, 1964, by having a larger length:width ratio 1.26:1.14, a smaller jugal angle 86°–114°, and smaller valve size. Kluessendorf's Morphotype A (1987:439, fig. 4, Pl. 1, fig. 3) may be a *Paleochiton* but has a larger jugal angle, 100°–120°, and is a larger plate. The anterior margin is unknown.

ETYMOLOGY. — Named for Siskiyou County, California.

Genus *Thairoplax* Cherns, 1998b

***Thairoplax merriami* sp. nov.**
Figs. 2A–N

TYPE MATERIAL. — HOLOTYPE: CAS 68397, PARATYPES: CAS 68398.01–68398.10.

DIAGNOSIS. — Intermediate plates strongly mucronate, strongly arched; anterior margin with well-developed jugal sinus; apical area large, V-shaped.

DESCRIPTION. — Intermediate plates relatively thin, strongly mucronate with slightly convex posterolateral margins converging on apex; highly arched with narrow jugal area; jugal angle 95°–106°; side slopes flat, trapezoidal in outline; anterolateral margins often converging slightly anteriorly, curving narrowly into anterior margin; jugal sinus prominent, fairly deep; apical area large, 2.3 mm long, V-shaped, approximately one-third of total length at midline; shell material moderately thick medially, thinning laterally; surface smooth.

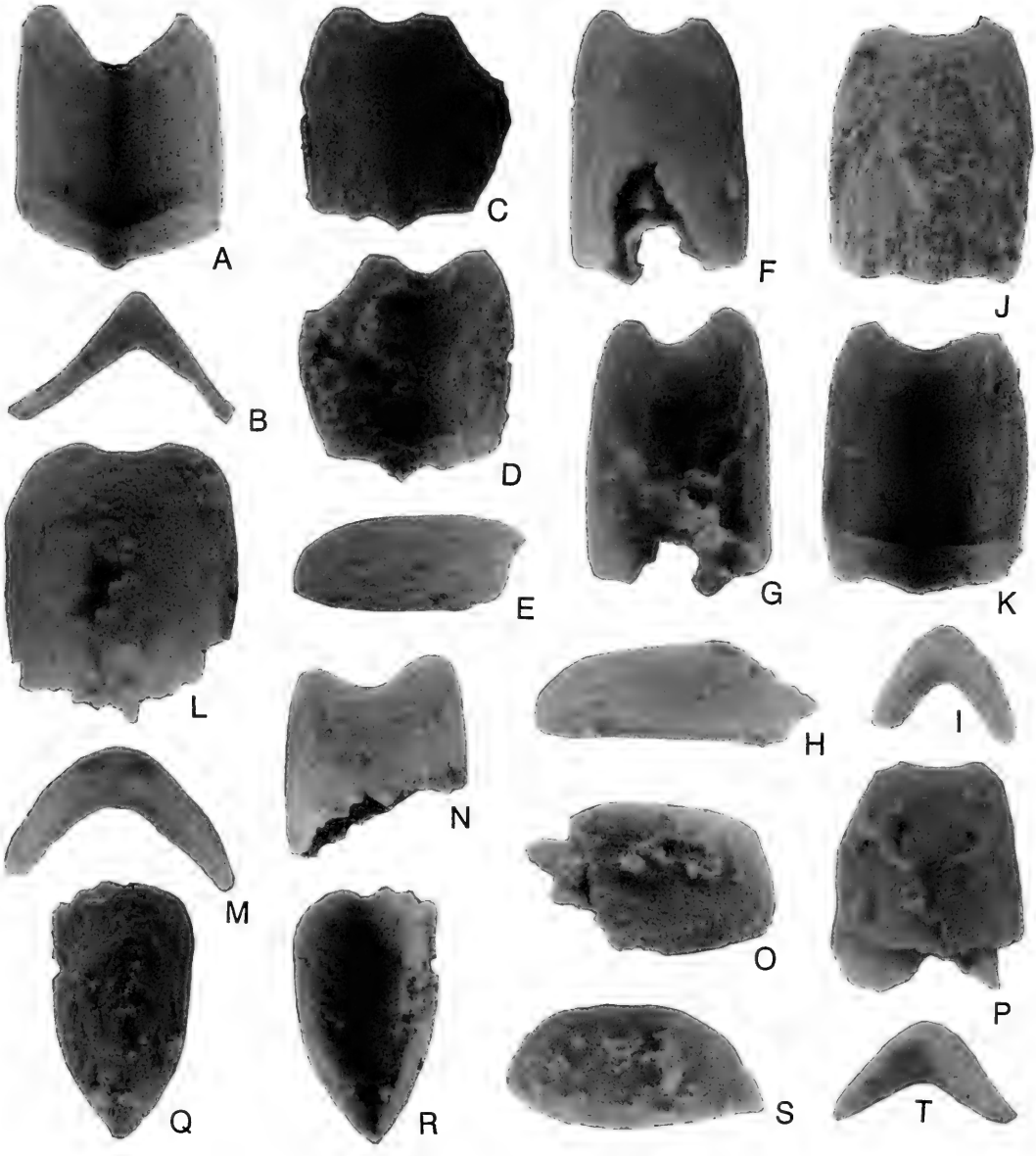

FIGURE 1. *Paleochiton siskiyouensis* sp. nov. A, B. Intermediate plate, ventral and posterior views (CAS 68396.01); C–E. Intermediate plate, dorsal, ventral, and left lateral views (CAS 68396.02); F–I. Intermediate plate, dorsal, ventral, left lateral, and anterior views (CAS 68396.03); J, K. Holotype, intermediate plate, dorsal and ventral views (CAS 68395); L, M. Intermediate plate, dorsal and anterior views (CAS 68396.04); N. Intermediate plate, dorsal view (CAS 68396.06); O, P. Intermediate plate with a second plate beneath it, right lateral and dorsal views (CAS 68396.08); Q–T. Tail plate, dorsal, ventral, left lateral, and anterior views (CAS 68396.05). All figures × 5.

TABLE 1. Measurements (in mm) of *Paleochiton siskiyouensis* sp. nov.

CAS Collection No.	Length	Width	Height	Apical area
68395*	7.3	5.6	3.0	1.2
68396.01	7.3	5.7	3.7	1.2
68396.02	6.0	5.8	1.6	1.2
68396.03	–	4.8	3.0	–
68396.04	–	6.4	3.8	1.0
68396.05	6.9	4.1	3.4	–
68396.06	–	5.0	1.5†	–
68396.07	5.4	5.0	3.0†	1.2
68396.08	5.2	5.0	3.5	1.6
68396.09	5.9	4.9	2.6	–
68396.10	5.3	5.4	3.4	1.3
68396.11	7.0	5.8	3.0	1.2
68396.12	5.8†	5.0	2.5	1.1
68396.13	6.5†	6.0	3.1	–
68396.14	6.0†	5.5†	3.1	–
68396.15	4.8	5.6	2.6	1.4
68396.16	5.5	5.0	2.8	0.7
68396.17	6.3	3.4	2.4	0.8
68396.18	5.8	5.0	2.3	–

* Holotype
† Estimated

Tail plate with well-developed jugal sinus; anterior lateral margins subparallel; posterolateral margins converging to posterior apex; not as strongly arched as intermediate plates; surface smooth. Head plate unknown.

MEASUREMENTS. — See Table 2.

DISCUSSION. — The genus *Thairoplax* was established by Cherns (1998b:946) for Silurian species from Gotland, Sweden, one of which had been previously placed in *Gotlandochiton* Bergenhayn, 1955. *Thairoplax* differs from the latter genus by its V-shaped apical area, more acute apex, and greater length:width ratio of intermediate plates. The primary difference between *T. merriami* and *T. pelta* Cherns, 1998b, the type species, is the larger, V-shaped apical area and converging anterordorsal margin in *T. merriami*. *Thairoplax* differs from *Chelodes* Davidson and King, 1874, by having thinner shell material, a sharp jugal flexure, and flat side slopes.

ETYMOLOGY. — Named for the late Charles W. Merriam, U. S. Geological Survey, who collected the specimens.

Family Mattheviidae Walcott, 1886

Genus and species A
Figs. 2O–T

MATERIAL. — CAS 68399.01, CAS 68399.02.

DESCRIPTION. — Intermediate plates subquadrate, thick, broadly arched; little to no distinction between jugum and side slopes; anterior margin with well-developed jugal sinus; posterior margin straight to slightly mucronate; posteror lateral margins converging posteriorly; apical area very short; surface smooth. Head and tail plates unknown.

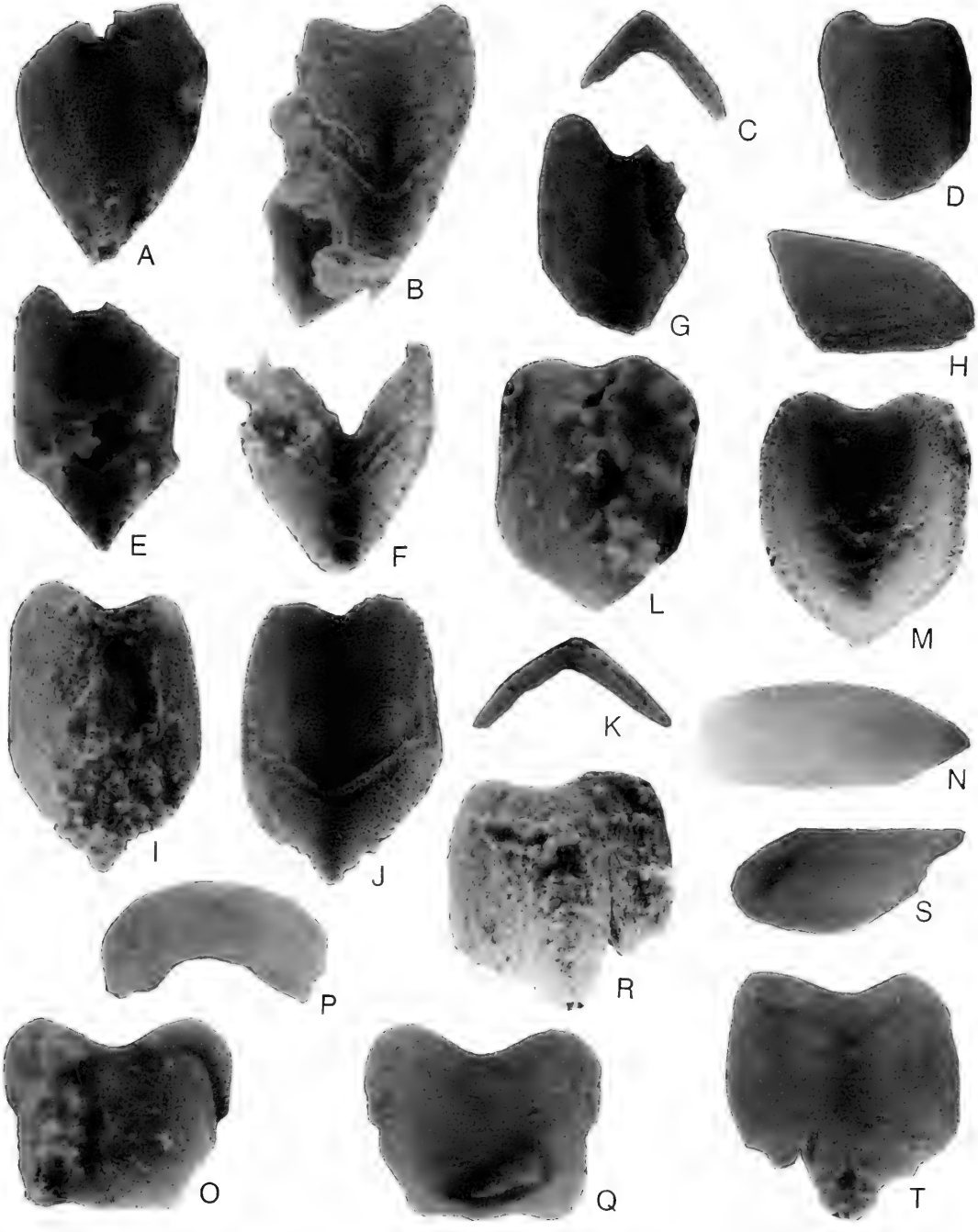

FIGURE 2. A–N. *Thairoplax merriami* sp. nov. A. Intermediate plate, dorsal view (CAS 68398.01); B. Intermediate plate, ventral view (CAS 68398.02); C, D. Intermediate plate, posterior and dorsal views (CAS 68398.03); E. Intermediate plate, ventral view (CAS 68398.04); F. Intermediate plate, ventral view (CAS 68398.05); G, H. Intermediate plate, ventral and right lateral views (CAS 68398.06); I–K. Holotype, intermediate plate, dorsal, ventral, and anterior views (CAS 68397); L–N. Intermediate plate, dorsal, ventral, and left lateral views (CAS 68398.07). O–T. Genus et sp. A. O–Q. Intermediate plate, dorsal, anterior, and ventral views (CAS 68399.01); R–T. Intermediate plate, dorsal, left lateral, and ventral views (CAS 68399.02). All figures × 5.

TABLE 2. Measurements (in mm) of *Thairoplax merriami* sp. nov.

CAS Collection No.	Length	Width	Height	Apical area
68397*	8.5	5.8	2.8	2.7
68398.01	7.6	5.6	3.1	3.0
68398.02	8.8	5.2	2.4	2.9
68398.03	5.5	4.4	2.2	2.0
68398.04	7.7	5.0†	2.5	2.4
68398.05	6.6	6.0†	3.0†	2.6
68398.06	6.4	5.0†	3.2	1.3
68398.07	7.2	4.5	2.5	2.0
68398.08	7.4	6.2	3.0	–
68398.09	6.3	5.0	3.2	2.0
68398.10	6.9	4.8	3.4	–

* Holotype
† Estimated

MEASUREMENTS. — Two plates range in length, 5.6–7.2 mm; in width, 6.9–6.8 mm; in height, 3.5–3.1 mm; in length of apical area, 0.5–0.6 mm.

DISCUSSION. — Two intermediate plates in the collection differ from both *Paleochiton siskiyouensis* and *Thairoplax merriami* in having a transversely thickened ridge on the ventral surface somewhat similar to that on *Alastega lira* Cherns, 1998b, from the Silurian of Sweden, but the latter taxon is more strongly arched and mucronate than the California specimens. The genus *Chelodes* Davidson and King, 1874, is similar in plate thickness and jugal sinus but is more mucronate, with a large apical area. *Kindbladochiton* Van Belle, 1975, and *Ivoechiton* Bergenhayn, 1955, do not have as great a shell thickness and are more strongly arched than the specimens described here, but they may represent a species of the latter genus.

Class Rostroconchia Pojeta, Runnegar, Morris, and Newell, 1972
Order Conocardioida Neumayr, 1891
Superfamily Eopteriacea Miller, 1889
Family Eopteriidae Miller, 1889

Genus *Eusphairica* gen. nov.

TYPE SPECIES. — *Eusphairica distubula* sp. nov.

DIAGNOSIS. — Body subcircular in cross section; snout short; rostrum lacking; gape extending from just ventral of rostral opening to anterior end; posterior clefts present.

DESCRIPTION. — See *Eusphairica distubula* sp. nov.

DISCUSSION. — *Eusphairica* is monotypic. It differs from the Ordovician genera *Eopteria* Billings, 1865, and *Euchasuna* Billings, 1865, by its more tumid body shape, lack of a rudimentary rostrum, and gape not extending to the rostral opening. Both *Wanwanella* and *Wanwanoidea*, both by Kobayashi, 1933, as illustrated by Pojeta and Runnegar (1970), are narrower forms with less distant snouts than *Eusphairica*.

ETYMOLOGY. — Greek *eu* meaning primitive, good; plus *sphairica*, globular.

***Eusphairica distubula* sp. nov.**
Fig. 3

TYPE MATERIAL. — HOLOTYPE: CAS68400.

DIAGNOSIS. — Same as genus.

DESCRIPTION. — Body small, subcircular in cross section; dorsal portion of posterior face extending posteriorly, slanted ventrally, curving sharply just below rostral opening and slanting anteriorly; rostrum not present; dorsal margin straight; beak slightly posterior to midlength; ventral margin of body straight, curving concavely into short snout; snout with keyhole gape anteriorly; ventral gape narrow, extending posteriorly to just ventral of rostral opening; body with marginal denticles in gape; area around rostral opening smooth or with nonpreserved ribs; central portion of face with five to six fine ribs; four coarser radial ribs at juncture of posterior face and body; 13 or more finer radial ribs on body; anterior portion of snout may lack radial ribs; comarginal growth lines present ventrally on body and snout; internal features not observed.

MEASUREMENTS. — Length 7.0 mm; width 5.2 mm; height 5.2 mm; width of anterior end 1.7 mm; length of ventral gape 6.2 mm; diameter of rostral opening 0.8 mm.

DISCUSSION. — The subspheroidal shape of the body, the slightly angular projection of the extended posterior face, and the gape ending ventral to the rostral opening are diagnostic of *Eusphairica distubula*. *Eopteria struszi* Pojeta, Gilbert-Tomlinson, and Shergold, 1977, described from the Lower Ordovician of Australia, is somewhat similar to *Eusphairica distubula* but differs in being narrower, having coarser radial ribs, a rudimentary rostrum, and a gape extending into the rostrum. Johnson and Chatterton (1983) described nine new species representing five genera of rostroconchs from the Middle Silurian of the Northwest Territories, Canada. None of these beautifully preserved, silicified spec-

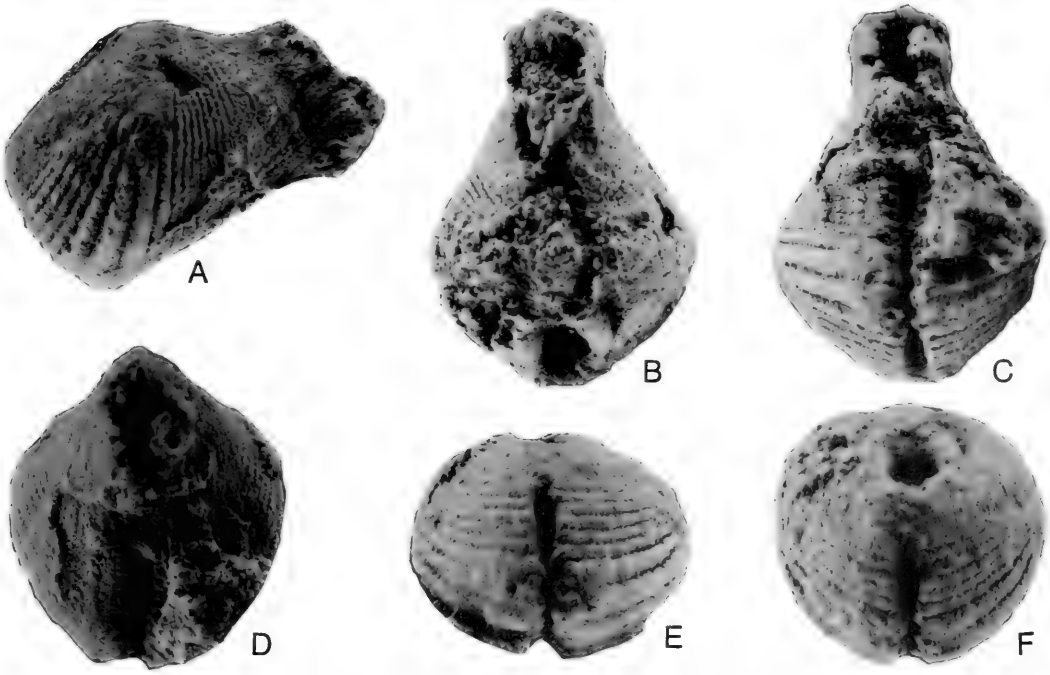

FIGURE 3. *Eusphairica distubula* gen. et sp. nov. (CAS 68400). A. Right lateral view; B. Dorsal view; C. Ventral view; D. Anterior view; E. Ventroposterior view; F. Posterior view. All figures × 7.

imens have the characters of the posterior face, ventral gape, and arrangement of ribs as are present on *E. distubula*.

ETYMOLOGY. — Latin *dis* meaning without; plus *tubulus*, tube (rostrum).

ACKNOWLEDGMENTS

I wish to thank P. U. Rodda, former Chairman of the Department of Geology, California Academy of Sciences, who notified me of the presence of the collection and J. DeMouthe, California Academy of Sciences, for making the specimens available for study. J. Thomas Dutro, Jr., U. S. Geological Survey, provided the source of information concerning the collection locality.

LITERATURE CITED

BAILEY, W. H. 1860. Observations on two new species of *Chiton* from the Upper Silurian "Wenlock Limestone" of Dudley. Annales and Magazine of Natural History 6(32):91–98. (An English translation of de Koninck, 1857).

BARRANDE, J. 1867. Système Silurien de centre de la Boheme. Première partie: recherches paléontologiques, tom. 3. Classe des Mollusques. Order des Ptéropodes. Prague and Paris. 179 pp.

BERGENHAYN, J. R. M. 1943. Preliminary notes on the fossil polyplacophoras from Sweden. Geologiska Föreningens, I, Stockholms, Förhandlingar 65(3):297–303.

———. 1955. Die Fossilien Schwedischen Loricaten nebst einer vorläufigen Revision des Systems der ganzen Klasse Loricata. Lund Universitet, Årsskrift. N.F. Avd. 2, 51(8); Kungliga Fysiografiska Sallskapets, Handlingar, N.F, Avd. 2, 66(8):1–41.

BILLINGS, E. 1865. Palaeozoic fossils, containing descriptions and figures of new or little known species of organic remains from the Silurian rocks, 1861–1865. Geological Survey of Canada, Volume 1, 426 pp.

BLAINVILLE, H. M. D. DE. 1816. Prodrome d'une nouvelle distribution systématique du règne animal. Bulletin Sciences Société Philomathigue de Paris 105–124.

CHERNS, L. 1998a. *Chelodes* and closely related Polyplacophora (Mollusca) from the Silurian of Gotland, Sweden. Palaeontology 41(3):545–573.

———. 1998b. Silurian polyplacophoran molluscs from Gotland, Sweden. Palaeontology 41(5):939–974.

———. 1999. Silurian chitons as indicators of rocky shores and lowstand on Gotland, Sweden. Palaios 14(2):172–179.

COUPER REED, F. R. 1911. A new fossil from Girvan. The Geological Magazine 8(8):337–339.

DAVIDSON, T. AND W. KING. 1874. On the Trimerellidae, a Paleozoic family of the palliobranchs or Brachiopoda. Quarterly Journal of the Geological Society of London 30(2):124–172.

ETHERIDGE, JR., R. 1897. On the occurrence of the genus *Chelodes* Davidson and King, in the Upper Silurian of New South Wales. Records of the Geological Survey of New South Wales 5(2):67–70.

JOHNSTON, D. I. AND B. D. E. CHATTERTON. 1983. Some silicified Middle Silurian rostroconchs (Mollusca) from the Mackenzie Mountarins, N. W. T., Canada. Canadian Journal of Earth Science 20(5):844–858.

KLUESSENDORF, J. 1987. First report of Polyplacophora (Mollusca) from the Silurian of North America. Canadian Journal of Earth Science 24:435–441.

KOBAYASHI, T. 1933. Faunal study of the Wanwanian (basal Ordovician) series with special notes on the Ribeiridae and the ellesmereiceroids. Tokyo Imperial University Faculty of Science Journal 3(7):249–328.

KONINCK, M. L. DE. 1857. Sur deux nouvelles espèces siluriennes appartenant au genre *Chiton*. Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique 11:190–199.

LINDSTRÖM, G. 1884. On the Silurian Gastropoda and Pteropoda of Gotland. Kongliga Svenska Vetenskaps-Akademiens Handlingar 19(6):48–52.

M'COY, F. 1846. A synopsis of the Silurian fossils of Ireland. Privately issued in 1846 by R. Griffiths, Dublin. 207 pp.

MERRIAM, C. W. 1972. Silurian rugose corals of the Klamath Mountains Region, California. U. S. Geological Survey Professional Paper 738, 50 pp.

MILLER, S. A. 1889. North American geology and paleontology for the use of amateurs, students and scientists. Western Methodist Book Concern, Cincinnati. 664 pp.

NEUMAYR, M. 1891. Beiträge zu einer morphologischen Eintheilung der Bivalven. K. Akademie der Wissenschaften zu Wien Denkschriften 58:701–801.

POJETA JR., J. AND B. RUNNEGAR. 1976. The paleontology of rostroconch mollusks and the early history of the Phylum Mollusca. U. S. Geological Survey Professional Paper 968, 88 pp.

POJETA JR., J., B. RUNNEGAR, N. J. MORRIS, AND N. D. NEWELL. 1972. Rostroconchia: a new class of bivalved mollusks. Science 177 (4045):264–267.

POJETA JR., J., J. GILBERT-TOMLINSON, AND J. H. SHERGOLD. 1977. Cambrian and Ordovician rostroconch molluscs from Northern Australia. Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin 171, 54 pp.

SALTER, J. W. 1847. Description of a fossil *Chiton* from the Silurian rocks, with remarks on the fossil species of the genus. Quarterly Journal of the Geological Society of London 3:48–52.

SMITH, A. G. AND D. F. TOOMEY. 1964. Chitons from the Kindblade Formation. Oklahoma Geological Survey Circular 66, 41 pp.

VAN BELLE, R. A. 1975. Sur la classification der Polyplacophora: I. Introduction at classification du Paleoloricata, avec la description de *Kindbladochiton* nom. nov. (pour *Eochiton* Smith, 1964). Informations de la Societe Belge de Malacologie 5:121–145.

WALCOTT, C. D. 1886. Studies on the Cambrian faunas of North America. U. S. Geological Survey Bulletin 30, 369 pp.

WOODWARD, H. 1885. On a new species of *Helminthochiton* from the Upper Bala (Silurian) of Girvan, Ayrshire. Geological Magazine 2:352–355.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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New Costa Rican and Panamanian Species of *Miconia* (Melastomataceae: Miconieae)

by

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Diagnoses, descriptions, and illustrations are presented for seven new Mesoamerican species of *Miconia* (*M. colliculosa* and *M. talamancensis* from Costa Rica and Panama, *M. vestita* from Costa Rica, and *M. correae*, *M. crocata*, *M. jefensis*, and *M. morii* from Panama). Distinguishing characters, distribution maps, citations of representative specimens, and comparisons with probable relatives are provided for each species.

RESUMEN

***Miconia*, con mas de 1,000 especies descritas, es el género más grande en la región de la Flora Mesoamericana. Se describen siete especies nuevas de *Miconia* (*M. colliculosa* y *M. talamancensis* de Costa Rica y Panama; *M. vestita* de Costa Rica; y *M. correae*, *M. crocata*, *M. jefensis* y *M. morii* de Panama). Se proveen descripciones, ilustraciones, notas sobre distribución y fenología para todas las especies. Además se presentan discusiones sobre las afinidades entre las especies nuevas y mapas de distribución.**

In the course of preparing a floristic treatment of the Melastomataceae for Flora Mesoamericana many new taxa have come to light. Several are from remote, little-collected regions while others are locally abundant at sites that have received repeated visits from collectors during the past two decades. Because work on this treatment has necessitated study of collections from well beyond the limits of the flora area, it has been possible to definitively identify new taxa and gain a better understanding of variation patterns in problematic species complexes over a broad geographic area. Of the 37 genera and approximately 500 species of melastomes presently recorded for the Mesoamerican region, 162 of the species are in the genus *Miconia*. Of this total, 126 species of *Miconia* occur in Costa Rica and Panama. It comes as no surprise, therefore, that the lion's share of novelties continues to come from these two countries, both of which are important centers of biodiversity in northern Latin America.

SPECIES DESCRIPTION

***Miconia colliculosa* Almeda, sp. nov.**
Fig. 1

TYPE. — COSTA RICA. Limón: Cantón de Talamanca Amubri. Camino entre Amubri y Soki. Siguiendo el Río Ñabri hacia Alto Soki, 9°29′50″N, 82°59′10″W, elev. 150 m, 3 Jul. 1989, *Herrera 3129* (holotype: CAS!; isotypes: CR!, INB!, MEXU! MO).

Section *Amblyarrhena*. Frutex vel arbuscula 2–6 m. Ramuli teretes sicut petioli foliorum subtus venae primariae inflorescentia hypanthiaque dense pilis penicillato-stellatis induti vel sicut petioli inflorescentia hypanthiaque pilis stipitato-dendroideus dense armati. Lamina 9.5–19 × 4.2–10.6 cm elliptico-ovata 5(–7)-plinervata, supra glabra, subtus in venis secundariis tertiariisque pilis stellatis modice puberuli. Panicula 4–8 cm longa multiflora; flores 5-meri; calycis tubus 0.5 mm altus, lobis interioribus 1–1.5 mm longis late ovatis, dentibus exterioribus 1.5–2 mm eminentibus. Stamina isomorphica glabra, thecis subulatis, poro dorsaliter inclinato; antherarum thecae 1 mm longae, connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et fere omnino inferum apice in collo 0.25 mm alto modice pilis glanduliferis.

Shrub or small tree 2–6 m tall. Old branches terete, glabrous, and somewhat striate. Uppermost cauline internodes, petioles, inflorescences, pedicels, and hypanthia densely covered with brown penicillate-stellate and/or coarse dendritic hairs. Leaves of a pair equal to somewhat unequal in size; petioles 0.7–1.5 cm long; blades chartaceous when dry, 9.5–19 × 4.2–10.6 cm, elliptic-ovate, apex acuminate, base obtuse to broadly rounded, oblique and then slightly decurrent on the petioles, margin undulate-denticulate varying to subentire, 5(–7)-plinerved, the innermost pair of elevated primaries diverging from the median vein in subopposite or alternate fashion 0.5–1.6 cm above the blade base, the transverse secondaries elevated and spaced 3–8 mm apart at the widest portion of the blade, adaxially glabrous at maturity, abaxially beset with a copious cover of penicillate-stellate hairs on the elevated primary veins and a moderate cover of stellate hairs on the prominulous network of transverse secondary and higher order veins. Inflorescence terminal, 4–8 cm long, sometimes appearing pseudolateral because of elongation of axillary shoots, paniculiform with ultimate branchlets terminating in simple dichasia; bracts of rachis nodes paired, linear-oblong, 2–4 mm long, 0.25–1 mm wide, essentially glabrous adaxially, copiously stellate-pubescent abaxially; bracteoles persistent, typically 3 per pedicel, sessile, linear-oblong, 1–3 mm long, 0.25–0.75 mm wide, margin entire, glabrous adaxially and moderately stellate-pubescent abaxially. Pedicels obsolete or up to ca. 0.25 mm long. Hypanthia (at anthesis) 2–2.5 mm long to the torus. Calyx tube 0.5 mm long, the calyx lobes ovate to suborbicular, often bluntly mucronate at the apex, stellulate-puberulent on both surfaces, 1–1.5 × 1.5–2 mm; exterior calyx teeth 5, subulate, 1.5–2 mm long and conspicuously exceeding the calyx lobes; torus glabrous on the adaxial face. Petals 5, glabrous, white, oblong-obovate, ± rounded apically, 3–4 mm long, 1.5–2 mm wide. Stamens 10, isomorphic, filaments glabrous, complanate, 1 mm long; anthers 1 mm long, 0.5 mm wide, yellow, laterally ± compressed, bluntly subulate in dorsal and ventral views, ± elliptic in profile view, ± truncate apically with a dorsally inclined pore; connective thickened dorsally but unappendaged. Ovary (at anthesis) completely inferior, 5-locular, globose, apex fluted but becoming ± rounded at maturity, apically crowned with an undulately lobed collar 0.25 mm high that is minutely glandular-puberulent along the rim. Style straight, glabrous, 3.25 mm long, stigma capitellate. Berry globose, 4–5 mm in diameter. Seeds ± triangular in outline, angulate varying to somewhat rounded on the convex face, 0.5 mm long, white to tan, the testa colliculose throughout, the lateral raphe extending the entire length of the seed.

PHENOLOGY. — The three known collections, made in January, February, and July, are in flower and fruit.

DISTRIBUTION. — A little-collected rain forest species known from the southeastern corner of Limón province in Costa Rica and the Nusagandí region of Comarca de San Blás province, Panama, at 150–350 m (Fig. 2).

PARATYPES. — PANAMA. Comarca de San Blás: Llano-Cartí road, kilometer 16 along trail to creek on the Caribbean drainage, 2 Feb. 1989, *Almeda et al. 6514* (CAS, MO, PMA, SCZ, US); headwaters of Río Nergala along continental divide, 11 Jan. 1985, *de Nevers & Herrera 4514* (CAS, MO).

DISCUSSION. — Among described species of *Miconia* section *Amblyarrhena*, *M. colliculosa* is most similar to a group of three allopatric species that includes *M. calocoma* Almeda of northeastern

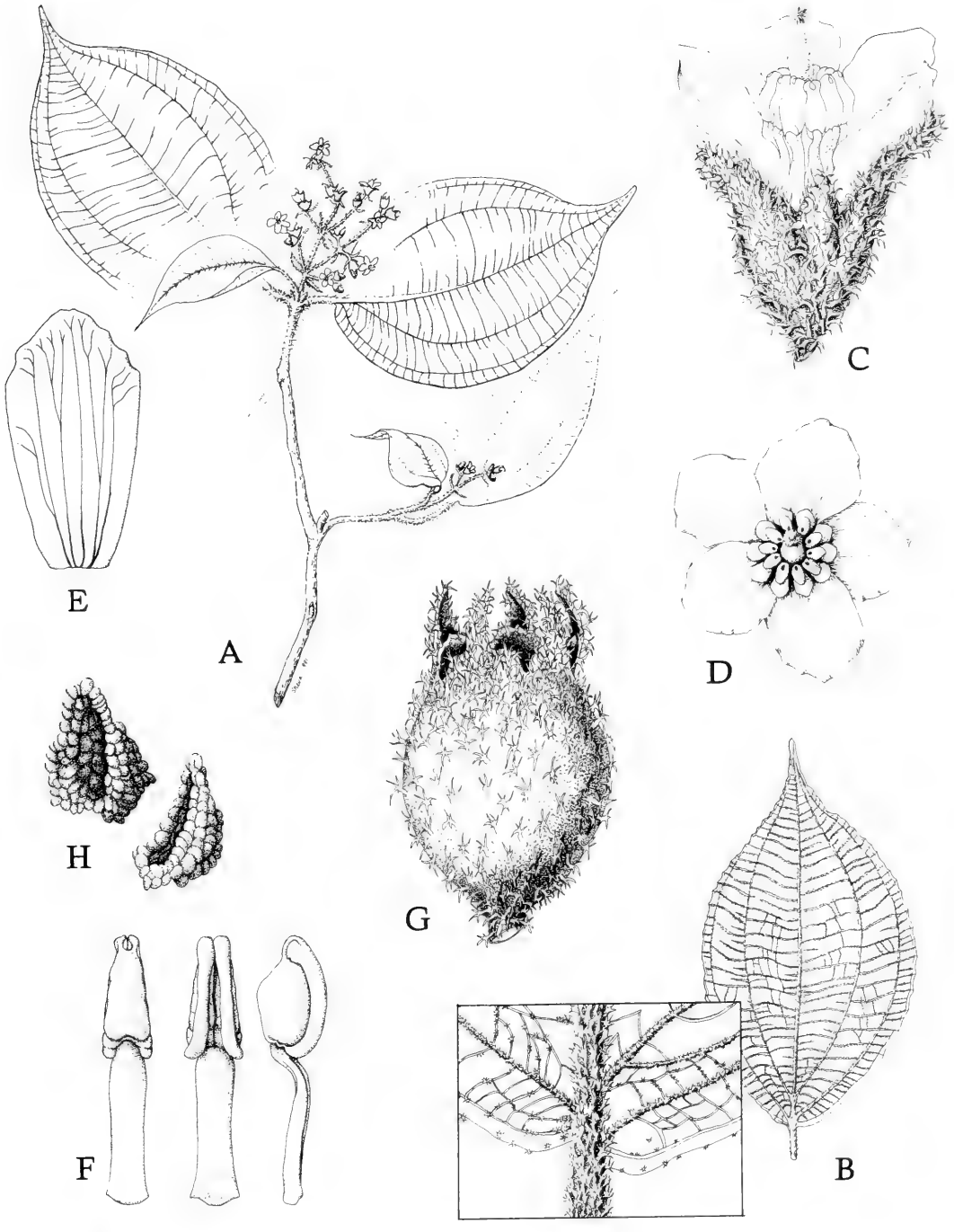

FIGURE 1. *Miconia colliculosa* Almeda. A, habit, × ½; B, representative leaf (abaxial surface), × ½, with enlargement of pubescence details at foliar base; C, flower (at anthesis) with one petal removed, × 10; D, flower as seen from above, × 5; E, petal (adaxial surface), × 10; F, stamens, dorsal view (left), ventral view (middle), and profile view (right), × 19; G, mature berry, × 7; H, seeds, × 40. (A–F from *Almeda et al. 6154*; G and H from the holotype.)

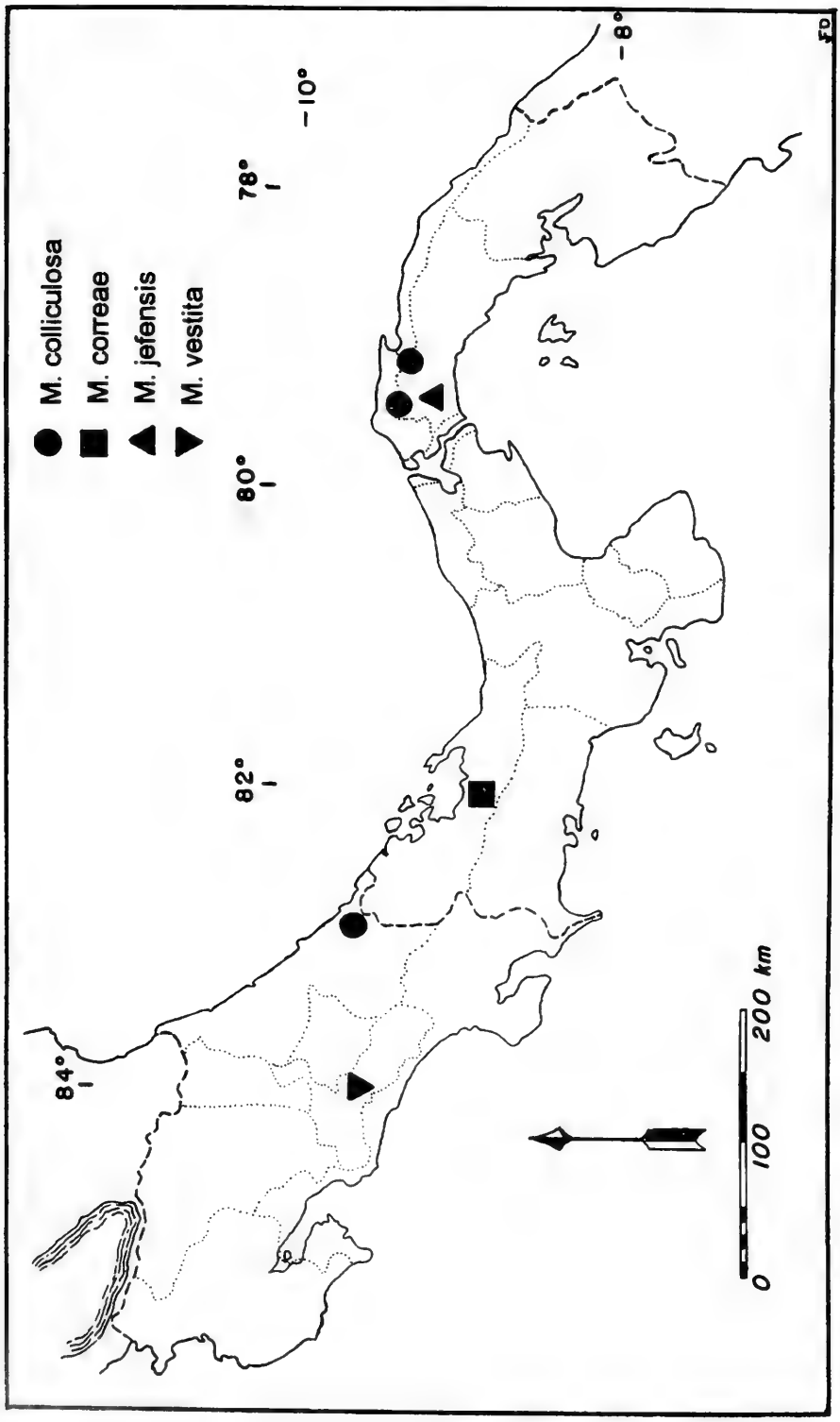

FIGURE 2. Distributions of *Miconia colliculosa*, *M. correae*, *M. jefensis*, and *M. vestita* in Costa Rica and Panama.

Costa Rica, *M. rupticalyx* Wurdack of Venezuela, and *M. wagneri* J. F. Macbr. of Peru, Bolivia, and northern Brazil (Almeda 1989a). All of these taxa differ from *M. colliculosa* in having 4-merous flowers, an irregularly rupturing apiculate calyx, and other diagnostic reproductive characters. *Miconia calocoma*, for example, has ventrally inclined anther pores and a 4-locular ovary. *Miconia rupticalyx* and *M. wagneri* share the character state of dorsally inclined anther pores with *M. colliculosa* but both have 2(–3)-locular ovaries. In addition, *M. rupticalyx* has reniform bracteoles whereas *M. wagneri* has anther connectives that are dilated at the filament insertion into dorso-basal spurs.

ETYMOLOGY. — The epithet for this species is diminutive of the Latin word *collinus*, of a hill, in reference to the little rounded or hillock-like elevations that make up the seed coat.

***Miconia correae* Almeda, sp. nov.**
Fig. 3

TYPE. — PANAMA. Bocas del Toro: Trocha 3 de noviembre, near Paso de la Zorra shelter, south and a bit west of Chiriquí Grande and ca. 2 km NE of the peak of Cerro Guayabo, 8°48′N, 82°14′–15′W,elev. ca. 1300 m, 5 Apr. 1978, *Dressler 5806* (holotype: CAS!; isotype: PMA).

Section *Jucunda*. Frutex 1 m. Ramuli teretes sicut inflorescentia primum sparsiuscule vel modice glandulis clavatis 1–1.75 mm longis induti demum glabrati. Folia in quoque pari disparilia; lamina 2.9–6.2 × 1.5–3.8 cm cordata vel ovata, 5–7-nervata, supra glabra, subtus pilis laevibus glanduliferis sparsiusculi puberuli. Panicula 4–4.5 cm longa pauciflora; flores 4-meri; calycis tubus 0.5–1 mm altus, lobis interioribus 1 × 1.5–2 mm triangularibus 1 mm altis, dentibus exterioribus subulatis 2.5–3 mm eminentibus. Stamina isomorphica glabra, thecis subulatis, poro dorsaliter inclinato; antherarum thecae 2.5 mm longae, connectivo dorsaliter ad basim tuberculo 0.5 mm elevato ornato. Ovarium 4-loculare et fere omnino inferum apice glabro.

Shrub to 1 m tall. The internodes terete, sparsely covered with spreading smooth glandular hairs 1 mm long when young like the inflorescence but becoming glabrous with age. Distal branchlet nodes copiously setose with spreading hairs (glandular in part) 1–1.75 mm long. Leaves of a pair unequal in size; petioles glabrous, 1–2.9 cm long; blades membranaceous, somewhat brittle when dry, 2.9–6.2 × 1.5–3.8 cm, cordate varying to ovate, apex caudate-acuminate, base cordate to broadly rounded, margin ciliate-serrulate, 5–7-nerved, adaxially glabrous, abaxially sparingly and irregularly covered with minute inconspicuous deciduous glandular hairs. Inflorescence terminal, 4–4.5 cm long, paniculiform, reportedly pendant with ultimate branchlets terminating in simple cymes or solitary flowers; bracts of rachis nodes paired, ensiform to ligulate, 2–3 × 0.5 mm (including apical hair) essentially glabrous on both surfaces; bracteoles narrowly lanceolate to subulate, 2 mm long (including apical hair) and less than 0.5 mm wide, glabrous on both surfaces. Pedicels 1–2 mm long at anthesis, sparsely beset with spreading glandular hairs. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus (vascular ring), glabrous throughout. Calyx lobes on flowering hypanthia 4, glabrous throughout, rounded-deltoid, 1 mm long and 1.5–2 mm wide basally; exterior calyx teeth subulate, 2.5–3 mm long, adnate to and exceeding the calyx lobes. Petals 4, glabrous, white, elliptic-ovate, rounded at the apex, 0.7–1 × 0.4–0.5 cm, the margin entire. Stamens 8, isomorphic; filaments glabrous, 2.5–3 mm long; anthers 2.5 mm long, yellow, subulate, rounded apically with a dorsally inclined pore; connective conspicuously thickened dorsally and prolonged basally into a caudiform appendage 0.5 mm long. Ovary (at anthesis) completely inferior, 4-locular, oblong, glabrous at the exposed apex. Style straight, glabrous, 7 mm long; stigma capitellate. Mature berry not seen.

PHENOLOGY. — The single known collection, which is in flower, was made in early April.

DISTRIBUTION. — The label on the type describes the habitat in western Panama as open rocky areas at 1300 m (Fig. 2).

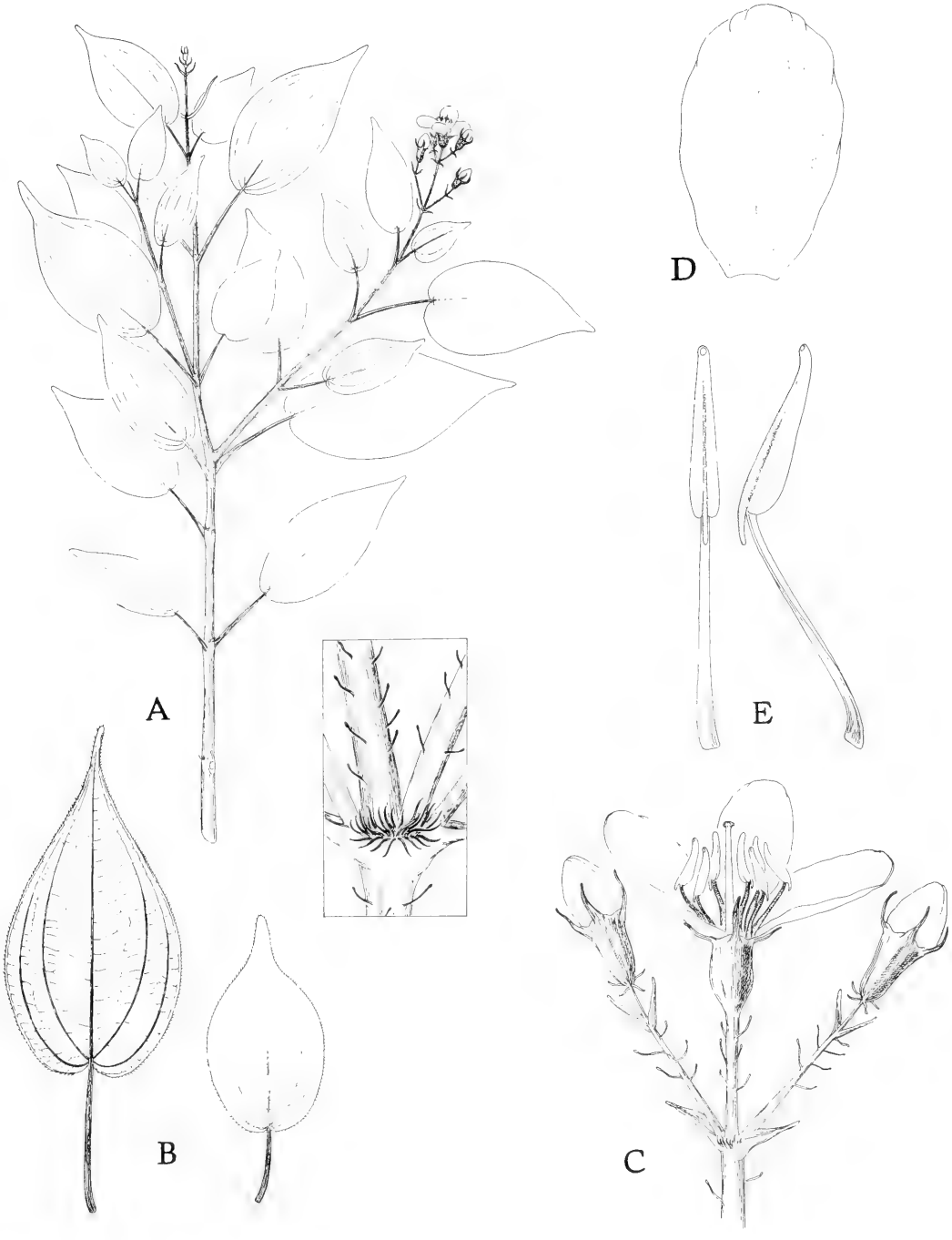

FIGURE 3. *Miconia correae* Almeda. A, habit, × ½, with enlargement (right) showing nodal pubescence details; B, representative leaves (abaxial surfaces) from a node, × ¾; C, portion of the inflorescence, × ca. 2; D, petal, × 4; E, stamens, dorsal view (left) and profile view (right), × ca. 11. (A–E from the holotype.)

DISCUSSION. — The subulate anther thecae, dorso-basal connective prolongation, and greatly developed calyx teeth that much exceed the calyx lobes dictate placement of *M. correae* in section *Jucunda* as defined by Cogniaux (1891) and elaborated upon by Gleason (1958). Among described species of *Miconia*, this new species most closely resembles *M. zemurrayana* Standl. & L. O. Williams of Mexico (Chiapas), Guatemala, El Salvador, and Honduras. They are similar in flower size, petal color, and the elongate projecting calyx teeth. *Miconia zemurrayana* differs most conspicuously in having glabrous internodes, narrower lanceolate leaves (0.5–1.7 cm) that are coarsely denticulate (at least distally), 5–merous flowers, unappendaged anther connectives, and ventrally inclined anther pores. Another distinctive feature of *M. zemurrayana* is the presence of tufts of stipitate-stellate hairs at the junction of the inner pair of elevated primaries with the median vein on the abaxial surface of each leaf blade. In the protologue of *M. zemurrayana*, Standley and Williams (1950) gave no sectional disposition for this species. Based on the characters enumerated above, it too can be assigned to section *Jucunda*.

ETYMOLOGY. — This species is named for Mireya D. Correa, Curator of the herbaria at the University of Panama and the Smithsonian Tropical Research Institute. Professor Correa first brought the only known collection of this species to my attention and has been a perennial source of assistance during my field work in Panama over many years.

***Miconia crocata* Almeda, sp. nov.**
Fig. 4

TYPE. — PANAMA. Coclé: Forested slopes above El Copé along abandoned road leading to the continental divide, elev. 700–850 m, 23 Feb. 1988, *Almeda et al. 5930* (holotype: CAS!; isotypes: DUKE!, MEXU!, MO!, NY!, PMA!, TEX!, US!).

Section *Cremanium*. Frutex vel arbor parva 2–5 m. Ramuli quadrangulati demum teretes sicut folia inflorescentia hypanthiaque plerumque glabri. Lamina 5–10 × 1.4–3.4 cm anguste elliptica trinervata. Panicula 1.5–2.5 cm longa multiflora; flores 5-meri; calycis tubus non evolutus, lobis interioribus 0.5 mm longis rotundatis, dentibus exterioribus crassis appressis inframarginalibus. Stamina isomorphica glabra poro ventraliter inclinato; antherarum thecae 0.5–0.25 m oblongo-cuneatae 4-porosae, connectivum vix (0.75 mm) prolongatum nec appendiculatum. Ovarium 3-loculare omnino inferum apice costato sparsissime glanduloso-puberulo vel sparse furfuraceo.

Shrub or small tree 2–5 m tall. Uppermost branchlet internodes glabrous, quadrate and conspicuously carinate, becoming rounded and somewhat ridged in age. Leaves of a pair equal or slightly unequal in size; petioles glabrous, 0.6–3.2 cm long, blades membranaceous, glabrous on both surfaces, 5–10 × 1.4–3.4 cm, narrowly elliptic, apex acuminate, base narrowly acuminate, margin mostly entire toward the blade base, otherwise obscurely crenulate, 3-nerved with an additional pair of inconspicuous inframarginal nerves evident above the blade base and becoming inconspicuous at the acuminate apex, the transverse secondaries prominulous and spaced 1–2 mm apart at the widest portion of the blade. Inflorescence a terminal corymbiform panicle 1.5–2.5 cm long, the rachis glabrous, quadrate and carinate; bracts and bracteoles evidently early deciduous and absent at anthesis but leaving well-developed scars at upper nodes and at the base of floral pedicels. Pedicels 0.25 mm long or not developed above the point of bracteole attachment, glabrous. Hypanthia (at anthesis) campanulate to cupulate, 1.5 mm long to the torus (vascular ring), glabrous. Calyx lobes 5, glabrous throughout, broadly rounded-undulate, 0.5 mm long and 0.5–0.75 mm wide basally, exterior teeth broadly deltoid or evident as a thickening mostly less than 0.25 mm long, adnate to and mostly shorter than the calyx lobes when dry. Petals 5, erect and concave, glabrous, yellow or yellow with a flush of red or maroon

apically, oblong-ovate, rounded at the apex, 1.5 × 1–1.25 mm, the margin entire. Stamens 10, isomorphic, incurved toward the central axis of the flower; filaments glabrous, complanate, tapered from base to apex, saffron yellow when dry, 2 mm long; anthers 4-celled, 0.5 mm long, 0.25 mm wide at the apex, yellow or yellow flushed with red apically, ± infundibuliform to obliquely cuneate in profile view, the pore ± quadrate and strongly inclined ventrally; connective thickened and prolonged 0.75 mm below the anther thecae but lacking appendages. Ovary (at anthesis) inferior, 3-locular, globose, apex fluted and sparsely glandular- or furfurate-puberulent but becoming rounded to truncate and glabrate in fruit. Style straight, glabrous, 2 mm long; stigma truncate to capitellate. Berry globose, blue-green becoming white with a faint flush of blue when mature, 4–5 mm in diameter. Seeds ± pyriform, 0.5 mm long, beige, tuberculate.

PHENOLOGY. — Flowering sporadically from January through September; fruiting specimens have been collected from January through May and in October.

DISTRIBUTION. — Low montane cloud forests along the continental divide in Coclé province from the El Copé region northeast to Los Volteaderos at 480–1000 m (Fig. 5).

PARATYPES. — PANAMA. Coclé: Slopes above El Copé along abandoned road leading to the continental divide, 8°38′N, 80°38′W, 24 Jan. 1989, *Almeda et al. 6388* (CAS, DUKE, MICH, MO, NY, PMA, US); about 7–10.5 km beyond El Copé in Omar Torrijos National Park along rocky trail to Río Blanco and Limón beyond Alto Calvario, 21 Feb. 1996, *Almeda et al. 7649* (CAS, MO, PMA, US); 12.4 km N of La Pintada on the road from Penonomé to Coclecito on trail through remnant forest on the continental divide at Los Volteaderos, 23 Feb. 1996, *Almeda et al. 7680* (CAS, PMA); El Copé, along gravel road to the right before the sawmill, 18 Oct. 1979, *Antonio 2204* (CAS, MO); región del Copé, 24 May 1981, *Correa et al. 4277* (CAS, PMA); Alto Calvario region, 4.5 miles N of El Copé, 8°38′N, 80°36′W, 12 Sep. 1987, *Croat 67517* (CAS, MO); Alto Calvario about 6 km N of El Copé, 8°39′N, 80°36′W, 23 June 1988, *Croat 68828* (CAS, MO); along Atlantic side of continental divide above El Copé, 8°40′N, 80°37′W, 25 Jul. 1983, *Miller et al. 835* (CAS, MO); Atlantic slope of the continental divide above El Copé, 8°40′N, 80° 36′W, 13 Feb. 1982, *Knapp & Dressler 3407* (CAS, MO); El Copé, División continental arriba de Barrigón y el aserradero viejo, 27 Apr. 1992, *Peña et al. 369* (CAS, PMA); above El Potroso sawmill N of El Copé, 13 May 1981, *Sytsma & Andersson 4561* (CAS, PMA); 4.5 miles N of El Copé near the old sawmill, 8° 38′N, 80°35′W, 8 Apr. 1988, *Thompson 4775* (CAS, CM).

DISCUSSION. — Among the species of section *Cremanium* characterized by a 3-locular ovary and obovoid, 4-celled anthers that open by a wide terminal pore, *M. crocata* appears to be most similar to *M. chiriquiensis* Almeda of Costa Rica and Panama and *M. rubens* (Sw.) Naudin of Jamaica, Colombia, and Venezuela. The latter differs from *M. crocata* by the somewhat swollen cauline nodes, ferrugineous pubescence on distal nodes and juvenile foliage, bracteoles with fimbriate margins, dioecious floral condition, and glabrous ovary apex. *Miconia crocata* seems closest to *M. chiriquiensis*. They share similarities in anther and stigma morphology, posture and orientation of petals and androecium at anthesis. In both species the petals are erect and concave and the filaments are geniculate in a way that closely juxtaposes the anther pores in a ring around the stigma. However, *M. chiriquiensis* has leaf blades that are ciliate-serrulate distally, caudate-acuminate apically, and furfurate-punctate abaxially. *Miconia chiriquiensis* also differs in a number of other diagnostic characters. It has an openly branched elongate paniculate inflorescence, suborbicular petals, a glabrous ovary apex, and seeds that superficially appear to have a smooth testa but are, in fact, minutely papillate. *Miconia crocata* and *M. chiriquiensis* are allopatric and have different elevational ranges. The latter ranges from the Cordillera de Talamanca in Costa Rica southeast to the Volcán Barú region of western Panama and consistently occurs at higher elevations (1600–2500 m).

All Panamanian and some Costa Rican populations of *M. chiriquiensis* also have white petals and anthers, but some recent Costa Rican collections (*Almeda & Anderson 5322*; *Grayum 10333*) have petals and stamens that are bright yellow like those of *M. crocata*.

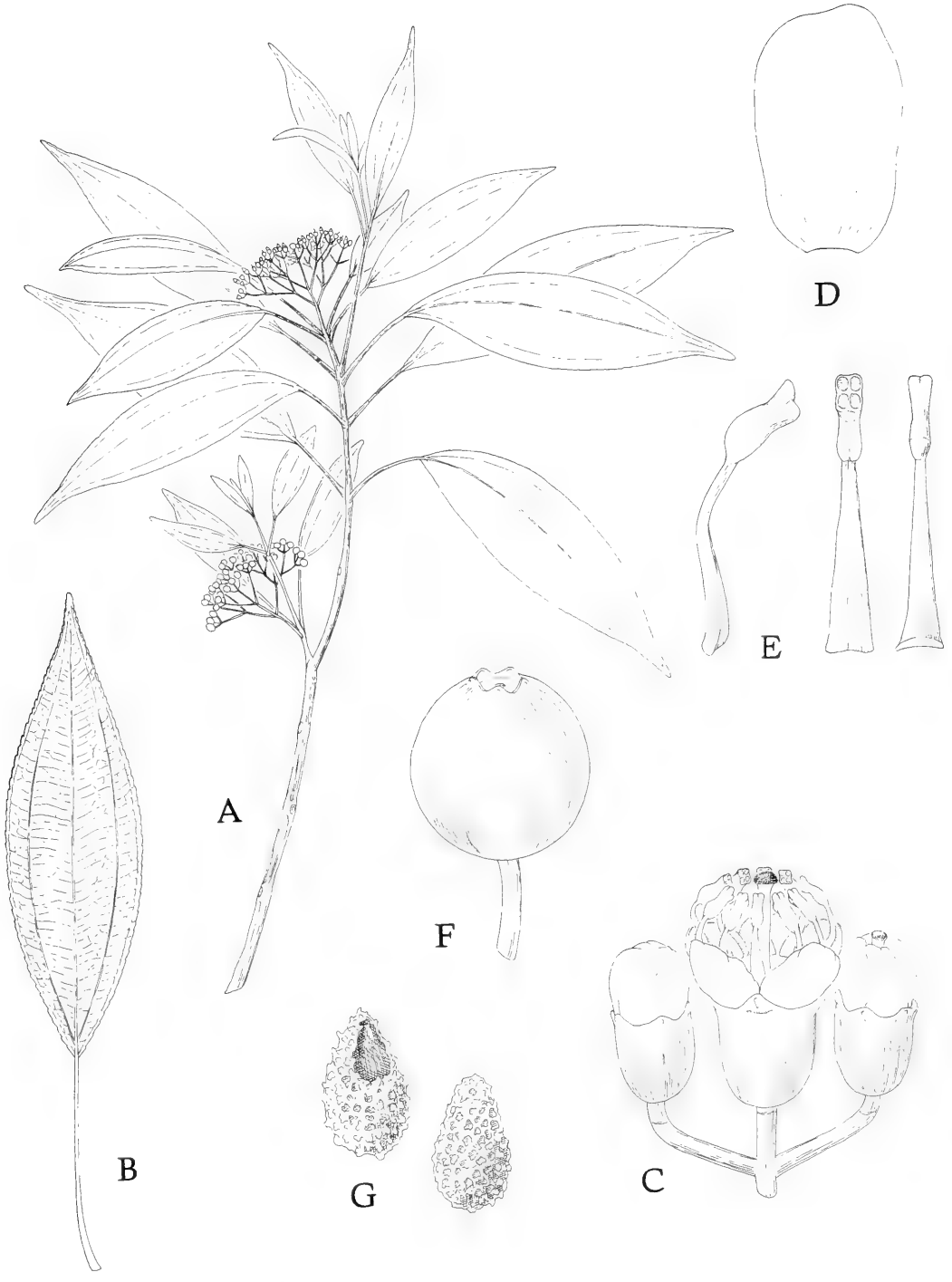

FIGURE 4. *Miconia crocata* Almeda. A, habit, × ½; B, representative leaf (abaxial surface), × ¾ ; C, portion of the inflorescence showing a fully opened flower, × ca. 8; D, petals (adaxial surface), × ca. 22; E, stamens, profile view (left), ventral view (center), and dorsal view (right), × 24; F, mature berry, × 6; G, seeds, × 40. (A–G from the holotype.)

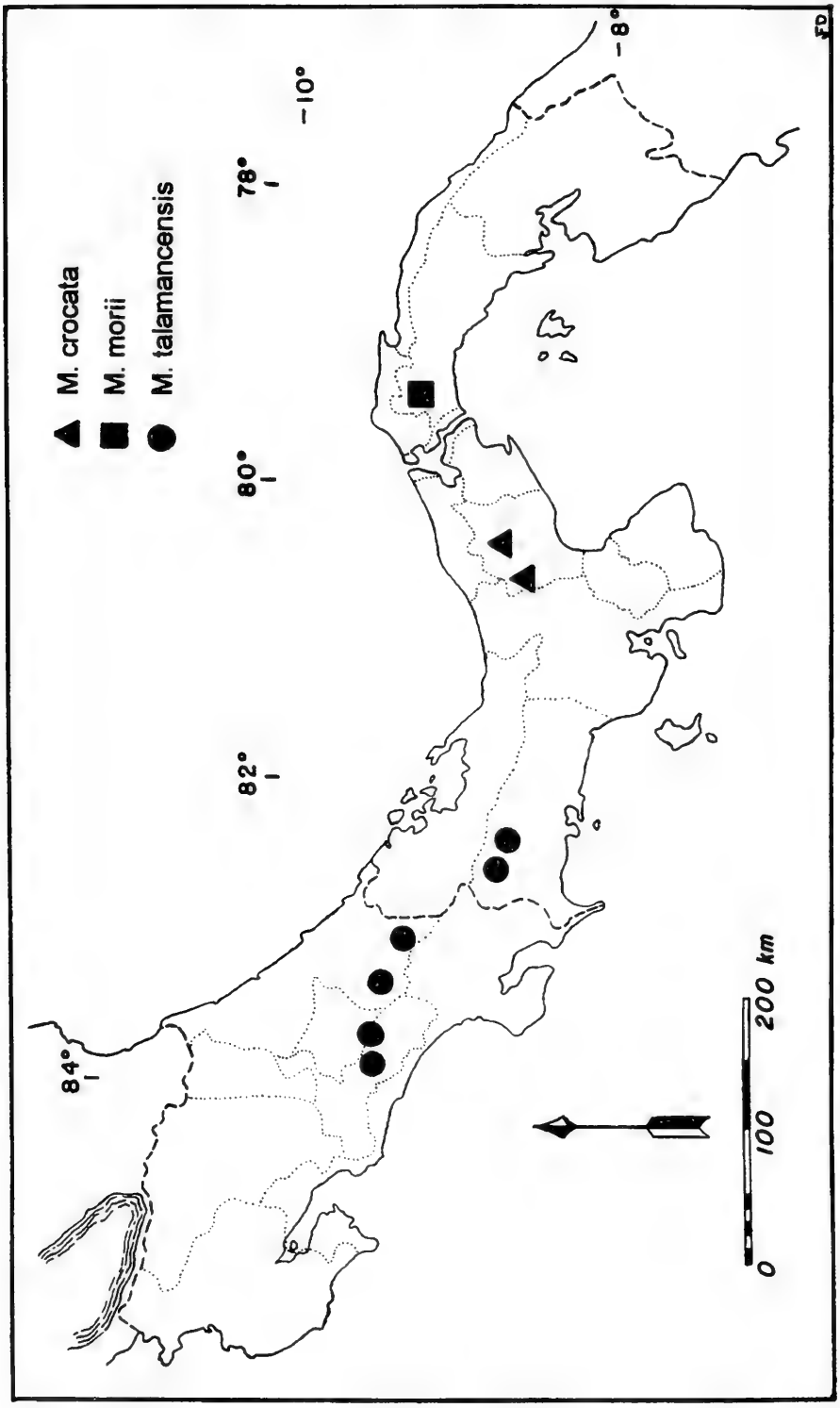

FIGURE 5. Distributions of *Miconia crocata*, *M. morii*, and *M. talamancensis* in Costa Rica and Panama.

ETYMOLOGY. — Because yellow is such an uncommon petal color in the tribe Miconieae, the name chosen for this new species emphasizes this feature. The epithet *crocata* is derived from the Greek word, *krokotos*, saffron-yellow, in reference to the striking color of the corolla and androecium, especially upon drying.

***Miconia jefensis* Almeda, sp. nov.**
Fig. 6

TYPE. — PANAMA. Panamá: Cerro Jefe, along summit road and along trail into the Chagres Valley, ca. 900 m, 19 Feb. 1988, *Almeda et al. 5826* (holotype: CAS!; isotypes: MO!, NY!, PMA!).

Section *Miconia*. Frutex 2–4 m. Ramuli primum paulo compressi demum sulcato-quadrangulati sicut petioli foliorum subtus venae primariae inflorescentiaque dense pilis penicillato-stellulatis induti. Lamina 13.5–41 × 7–14 cm elliptica vel elliptico-ovata 5–7-plinervata supra glabra, subtus in venis secundariis tertiariisque pilis stellulatis modice puberuli. Panicula 6–14 cm longa multiflora; flores 5-meri; calycis tubus 0.25 mm altus, lobis interioribus 0.25 longis late rotundatis, dentibus exterioribus crassis adhaerentibus lobos interiores aequantibus. Stamina isomorphica glabra, thecis subulatis, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et 4/5 inferum apice sparsicuscule glanduloso-puberulo.

Shrub 2–4 m tall. Uppermost branches compressed-rounded becoming bisulcate to rounded-quadrate with age, the young branchlets, petioles, elevated primaries of abaxial foliar surfaces, and inflorescence rachis and pedicels densely covered with a brown scurfy indument of penicillate-stellulate hairs. Leaves of a pair somewhat unequal in size; petioles 1–4(–7) cm long, blades subcoriaceous when dry, 13.5–41 × 7–14 cm, elliptic to elliptic-ovate, apex long acuminate to attenuate, base varying from subcordate to tapering and abruptly rounded at the petiole junction, margin entire, 5–7-plinerved, the innermost pair of elevated primaries diverging from the median vein in alternate fashion (2–)4.2–8.5 cm above the blade base, the transverse secondaries elevated and spaced 5–8 mm apart at the widest portion of the blade, adaxially glabrous at maturity, abaxially moderately covered with a brown scurfy-stellulate indument on the secondary and higher order veins. Inflorescence a terminal multiflowered panicle 6–14 cm long, divaricately branched at the node initiating the inflorescence; bracts of the rachis nodes persistent, 1.5–4.5 mm long, 0.25–1 mm wide, glabrous adaxially, glabrous or sparsely covered with scurfy puberulence abaxially; bracteoles sessile and persistent, paired, trimerous, or quaternate, sometimes fused basally to form a shallow nodal collar, subulate, 1–1.25 mm long, 0.5 mm wide basally, essentially glabrous adaxially and sparingly stelluate-furfuraceous to glabrous abaxially. Pedicels nearly obsolete or up to 1 mm long. Hypanthia (at anthesis) 1–1.5 mm long to the torus, copiously to moderately stellulate-furfuraceous. Calyx tube 0.25 mm long, the calyx lobes rounded-triangular, 0.25 mm long; exterior calyx teeth 5, bluntly subulate, up to 0.25 mm long, equaling or somewhat shorter than the calyx lobes but typically obscured by the dense indument; torus fimbrillate-puberulent or glandular-puberulent. Petals 5, glabrous, magenta, elliptic-ovate to oblong, rounded apically, 2–3 mm long, 0.75–1 mm wide. Stamens 10, isomorphic, filaments glabrous, complanate, constricted distally just below the anther thecae, 0.75–1 mm long; anthers 1 mm long, 0.25 mm wide, pale yellow, linear-oblong, rounded to truncate at the apex with a somewhat dorsally inclined terminal pore; connective thickened dorsally but unappendaged. Ovary (at anthesis) 4/5 inferior, 5-locular, globose, apex deeply fluted but becoming rounded at maturity, densely white-papillate with a few brown glandular hairs. Style typically declined to one side of the flower, glabrous, 2.5–3 mm long; stigma capitellate. Berry pink but turning blue-purple when mature, 3–4 mm long and 3–4 mm in diameter. Seeds angular-pyramidate, 0.5 mm long, brown or tan, smooth with finely verruculose angles on the convex face.

PHENOLOGY. — Flowering sporadically from February through July; fruiting specimens have been collected in February, July, and September.

DISTRIBUTION. — Uncommon in low montane cloud forests in the Cerro Jefe and Cerro Azul regions of Panama province at 700–1,000 m (Fig. 2).

PARATYPES. — PANAMA. Panamá: About 29–30 km beyond the Interamerican Highway off of a dirt road on Altos de Pacora, 26 Feb. 1996, *Almeda et al. 7696* (CAS, MO, PMA); Vicinity of Cerro Jefe, along road to summit, 9°14′N, 79°22′W, 8 Jul. 1987, *Croat 67079* (CAS); 3–3.5 miles NE of Altos de Pacora and 11.1–11.6 miles beyond Lago Cerro Azul, 19 June 1988, *Croat 68627* (CAS, MO); Sendero "El Cantar," borde de quebrada, Cerro Azul, Parque Nacional Chagres, 26 Jul. 1991, *Carrasquilla et al. 3267* (CAS, PMA); región de Cerro Jefe, area cercana la antena, 13 Jul. 1994, *Galdames & Montenegro 1389* (CAS, SCZ); región de Cerro Jefe, area cercana al límite con la Urbanización Altos de Cerro Azul, 13 Jul. 1994, *Galdames & Montenegro 1409* (CAS, SCZ); headwaters of the Río Utivé, Cerro Jefe, 2 km from last branch in road to summit, 13 Sep. 1981, *Knapp 1209* (CAS, MO).

DISCUSSION. — *Miconia jefensis* is related to a group of species that includes *M. iteophylla* Almeda, *M. ligulata* Almeda, and *M. peltata* Almeda. Like *M. jefensis*, two of these taxa are restricted to Panama; *M. ligulata* ranges from Nicaragua to Venezuela (Almeda 1989b). All of these species share a scurfy puberulent indument, linear or oblong petals, unappendaged anthers, a 5-locular ovary, a torus that is puberulent adaxially, and seeds that are nearly identical in size and shape. In overall aspect, *M. jefensis* is most like *M. ligulata*. These two species have angular-pyramidate seeds like the other members of this alliance but they alone share the fine verruculose ornamentation at the angles of the seed testa.

I was inclined to regard initial collections of *M. jefensis* as extraordinary variants of *M. ligulata*. Study of additional material, and the opportunity to examine more than one population of this entity in the field, revealed significant differences in a number of characters that are consistent with the kinds of characters that distinguish closely related species in other complexes within the genus. *Miconia jefensis* is a coarse, robust species with stout nodes that measure 6–10 mm on the widest face. Other diagnostic characters include its magenta petals, 5–7-plinerved leaves with a base varying from subcordate to abruptly rounded at the petiole junction, an inflorescence that is divaricately branched at the node initiating the inflorescence, and an ovary apex that is persistently white-papillate intermixed with a few brown glandular hairs at maturity. Plants of *M. ligulata*, in contrast, are slender in aspect with thinner cauline nodes that measure 3–5 mm at the widest face. This species has white petals, 5-plinerved leaves with a base that is gradually tapered and decurrent on the petiole, an inflorescence that typically branches 1.5–3.5 cm above the initiating node, and an ovary apex that is glabrous in fruit.

Miconia jefensis appears to be endemic to the low montane cloud forest that covers the volcanic region of Cerro Jefe and Cerro Azul, Panama. Hence, this narrowly endemic species joins a varied assemblage of flowering plants restricted to this region (Lewis 1971), including several recently described species of Melastomataceae such as *Adelobotrys jefensis* Almeda (Almeda 1981), *Miconia morii* Almeda (described herein), *Miconia peltata* Almeda (Almeda 1989b), *Tessmannianthus carinatus* Almeda (Almeda 1989c), and *Topobea hexandra* Almeda (Almeda 1990).

ETYMOLOGY. — The specific epithet is derived from the type locality, Cerro Jefe, where most of the collections of this species have been made.

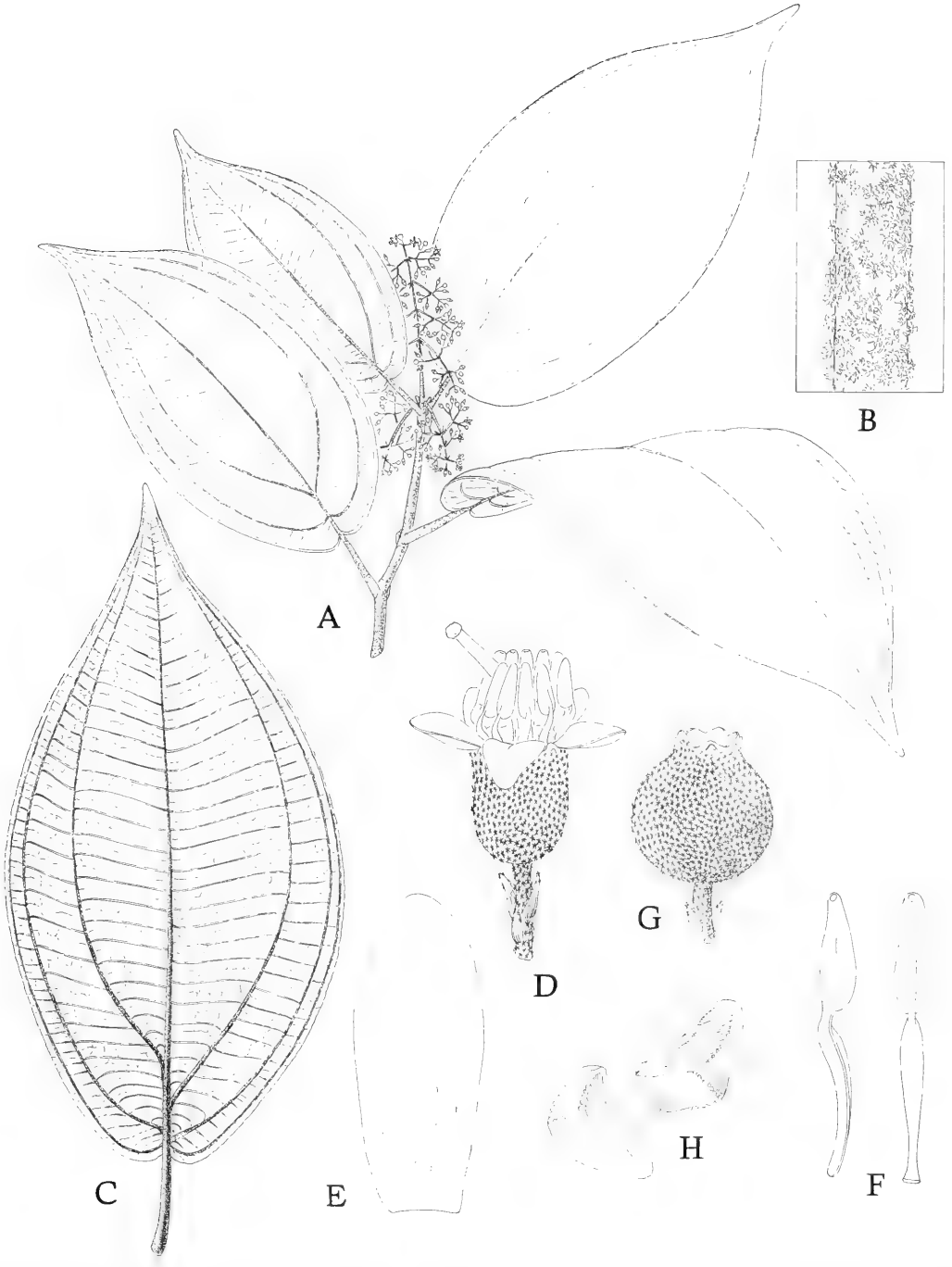

FIGURE 6. *Miconia jefensis* Almeda. A, habit, × 1/3; B, enlargement of detail on cauline internode; C, representative leaf (abaxial surface), × ½; D, fully opened flower, × ca. 13; E, petal (adaxial surface), × ca. 23; F, stamens, profile view (left) and dorsal view (right), × 18; G, mature berry, × 7; H, seeds, × 40. (A–F from the holotype; G and H from *Almeda et al. 7696*.)

***Miconia morii* Almeda, sp. nov.**
Fig. 7

TYPE.—PANAMA. Panamá: Cerro Jefe, along trail on ridge running NE from summit, cloud forest dominated by *Clusia* spp. and *Colpothrinax cookii*, ca. 1000 m, 18 Dec. 1974, *Mori et al. 3773* (holotype: CAS!; isotypes: MO, WIS!).

Section *Tamonea*. Frutex 1.2–3 m. Ramuli obtuse tetragoni demum teretes sicut petioli inflorescentia hypanthiaque modice vel dense pilis stellulatis induti. Lamina 6.5–10.5 × 2.5–5 cm elliptica vel elliptico-ovata trinervata, supra glabra, subtus in venulis superficieque sparsiuscule caduceque stellato-puberulo. Panicula 8–11 cm longa multiflora; flores 5-meri; petala extus pilis stellulatis modice induta; calyx 2–2.5 mm longus truncatus, dentibus exterioribus obscuris (0.25 mm) omnino adhaerentibus non eminentibus. Stamina isomorphica, thecis subulatis, poro ventraliter inclinato; antherarum thecae 4–4.25 mm longae, connectivum dorsaliter ad basim paulo elevatum ecalcaratum. Ovarium 5-loculare et ½ inferum apice in collo 0.25 mm alto sparsissime glanduloso puberulo.

Shrub 1.2–3 m tall. Uppermost cauline internodes compressed-rounded to obtusely quadrangular becoming terete with age, the uppermost branchlets, vegetative buds, young leaves and petioles, inflorescence branches, hypanthia, and pedicels moderately to densely appressed-puberulous with brown stellulate hairs 0.7–1 mm in diameter. Leaves of a pair equal to somewhat unequal in size, petioles 0.9–1.5 cm long, blades subcoriaceous when dry, 6.5–10.5 × 2.5–5 cm, elliptic to elliptic-ovate, apex acuminate, base obtuse to rounded, margin entire, adaxially glabrous or essentially so, abaxially moderately to sparsely stellulate-puberulous but sometimes becoming glabrate with age, 3-nerved, the transverse secondary veins elevated and spaced 4.5–8 mm apart at the widest portion of the blade. Inflorescence a terminal multiflowered panicle 8–11 cm long, branching at or 2–2.5 cm above the node initiating the inflorescence; bracts and bracteoles evidently early deciduous and not seen. Pedicels 0.5 mm long. Hypanthia (in fruit) 4–5 mm long to the torus, calyx tube 2–2.5 mm long, flangelike apically and sometimes splitting vertically down toward the torus at one or more points, the calyx lobes essentially obsolete, only evident as a truncate rim; exterior calyx teeth 5, barely evident as blunt callosities ca. 0.25 mm long; torus essentially glabrous adaxially. Petals 5, adaxially glabrous, abaxially densely stellulate-puberulous, oblong-obovate, cucullate distally and rounded at the apex, 5.5–7 mm long, 4–5 mm wide distally. Stamens 10, isomorphic, filaments glandular-puberulent basally, 3 mm long; anthers 4–4.25 mm long, ca. 0.75 mm wide at the base, linear-oblong to subulate, rounded at the apex and opening by a ventrally inclined pore; connective elevated dorso-basally into an elongate padlike thickening 1 mm long. Ovary (in fruit) ½-inferior, 5-locular, subglobose, apex conical, inconspicuously glandular-puberulent, terminating in a shallowly undulate collar 0.25 mm high that is typically glabrate but sometimes adorned with a few minute glandular hairs on the rim. Style straight, glandular-puberulent along the basal third of its length, 6 mm long, stigma capitate. Berry subglobose, 4–6 mm long, 5–7 mm in diameter. Seeds ± triangular in outline, rounded to angulate on the convex face, 0.5–1 mm long, brown, smooth with a dull luster, the lateral raphe extending the entire length of the seed.

PHENOLOGY. — The only flowering collection was made in March; fruiting specimens have been collected from December through May.

DISTRIBUTION. — Known only from the summit and vicinity of Cerro Jefe just east of the Canal Area in Central Panama at 900–1,000 m (Fig. 5).

PARATYPES. — PANAMA. Panamá: Vicinity of Cerro Jefe, near tower, 23 May 1980, *Antonio 4725* (CAS, MO); Cerro Jefe, 28 Sep. 1986, *Aranda 154* (PMA, US); road from summit of Cerro Jefe, 9°14′N, 79°23′W, 20 Jan. 1984, *Churchill 4298* (CAS, MO); Cerro Jefe, by radio tower, 15 Mar.

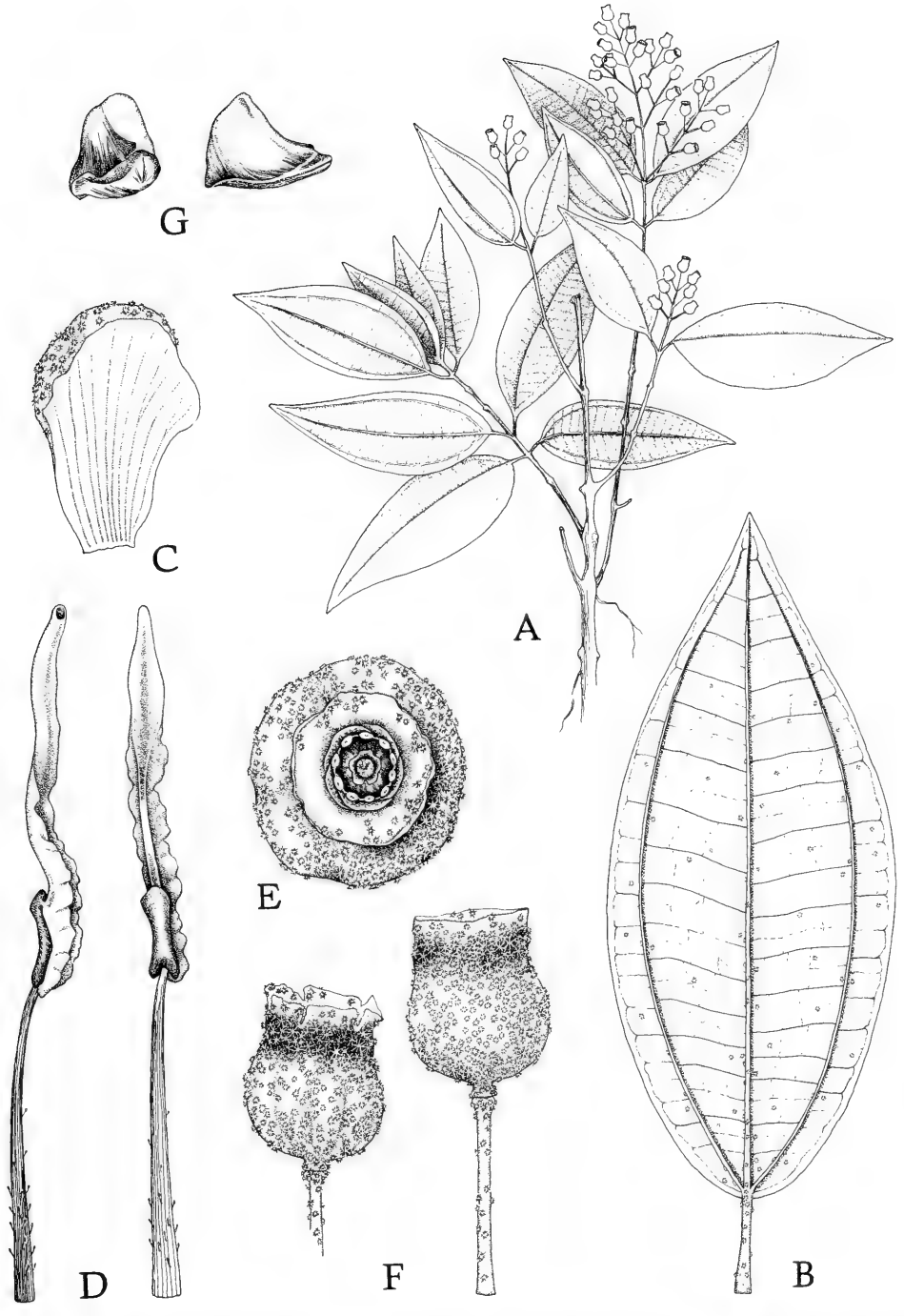

FIGURE 7. *Miconia morii* Almeda. A, habit, × 1/3; B, representative leaf (abaxial surface), × 1; C, petal (adaxial surface), × 6; D, stamens, profile view (left) and dorsal view (right), × 14; E, mature berry as seen from above, × 5; F, mature berries in profile view showing flangelike calyx (right) that sometimes splits in an irregular vertical fashion (left), × 4; G, seeds, × 20. (A from the holotype and *Churchill 4298*; B from the holotype; C and D from *Folsom et al. 2525*; E and F from *Churchill 4298*; G from *D'Arcy and McPherson 16060*.)

1985, *D'Arcy & McPherson 16060* (CAS, MO); top of Cerro Jefe, 23 km N of Pan-American Hwy., 11 Apr. 1977, *Folsom et al. 2325* (CAS, MO).

DISCUSSION. — Among the species of section *Tamonea*, *M. morii* is morphologically most similar to *M. acuminifera* Triana of western Colombia (Depts. of Caldas south to Nariño). These two species have similar leaf shape, hypanthial and petal indument, calyx details, and seed morphology. They are also similar in having isomerous flowers (ovary 5-locular and petals 5 in number). In *M. acuminifera*, however, the flowers are pleiostemonous (vs. diplostemonous in *M. morii*) and the stamens are dimorphic in size (vs. isomorphic in *M. morii*). Other differences that distinguish these two species involve floral or fruit characters. In *M. acuminifera* the style and filaments are glabrous, the toral vascular ring to which stamens and petals are attached is glandular-puberulent adaxially, and the connective lacks the elevated padlike thickening so typical of *M. morii* (Fig. 5D). The ovary summit in both *M. morii* and *M. acuminifera* is glandular-puberulent, although inconspicuously so at times, but the latter lacks the well-developed collar that surrounds the style base of the former.

There are other modal, but more subtle, differences that can be used to separate these two species. In *M. acuminifera* the leaf blades are typically larger (14–28 × 5–12.5 cm), the fruiting hypanthia are strongly constricted distally, and the stellate indument on flowering hypanthia is so dense that it conceals the actual surface. The leaf blades of *M. morii* are 6.5–10.5 × 2.5–5 cm, the fruiting hypanthia are tapered from the base to the apex (Fig. 5F), and the hypanthial indument does not conceal the actual surface. In addition to being allopatric, *M. acuminifera* appears to grow at higher elevations. Only one of the collections examined was gathered at 950 m; all others were collected at 1,550–2,100 m.

ETYMOLOGY. — This species is named for Scott A. Mori (1941–) collector of the type of this species and other interesting Melastomataceae during his early years of botanical field work in Panama.

***Miconia talamancensis* Almeda, sp. nov.**
Fig. 8

TYPE. — COSTA RICA. Cartago/San José border: Cordillera de Talamanca, Villa Mills in the vicinity of La Georgina, ca. 9750 ft (2972 m), 6 Mar. 1981, *Almeda & Nakai 4777* (holotype: CAS!; isotypes: CR!, INB!, MO!).

Section *Cremanium*. Arbor 6–15 m. Ramuli primum obtuse sulcato-quadrangulati demum teretes sicut petioli folia novella inflorescentia hypanthiaque pilis asperis dense vel modice induti demum glabrati. Lamina 4.5–12 × 1.9–3.8 cm oblongo-ovata 5-nervata, supra glabra, subtus in venarum primariarum axillis (et supra axillis) modice setosa pilis simplicibus 1–3 mm longis persistentibus. Panicula 6–9.5 cm multiflora; flores 5-meri; calycis tubus 0.25 mm altus, lobis interioribus 0.5 longis, dentibus exterioribus crassis inframarginalibus. Stamina in dimensionibus subisomorphica glabra, antherarum thecae 1.5–1.75 mm oblongae latae 4-porosae, connectivo prolongato dorsaliter inconspicue hebeti-dentato. Ovarium 3-loculare et ½ inferum apice glabro.

Tree 6–15 m tall. Uppermost cauline internodes quadrate becoming rounded-quadrate with age, the uppermost branchlets, vegetative buds, young leaves and petioles, inflorescence branches, and bracteoles densely covered with a rusty brown indument of asperous-headed, dendritic hairs. Leaves of a pair equal or slightly unequal in size, petioles 1.1–4.1 cm long, blades coriaceous when dry, 4.5–12 × 1.9–3.8 cm, oblong-ovate, apex caudate-acuminate to attenuate, base rounded, margin callose-serrulate, adaxially glabrous and somewhat bullate-reticulate, abaxially scattered asperous-lepidote on the actual surface but copiously covered with rusty brown dendritic or asperous-headed hairs on the elevated primary veins and moderately covered with simple spreading hairs (1–3 mm long) where the primary veins diverge at the blade base and commonly extending for

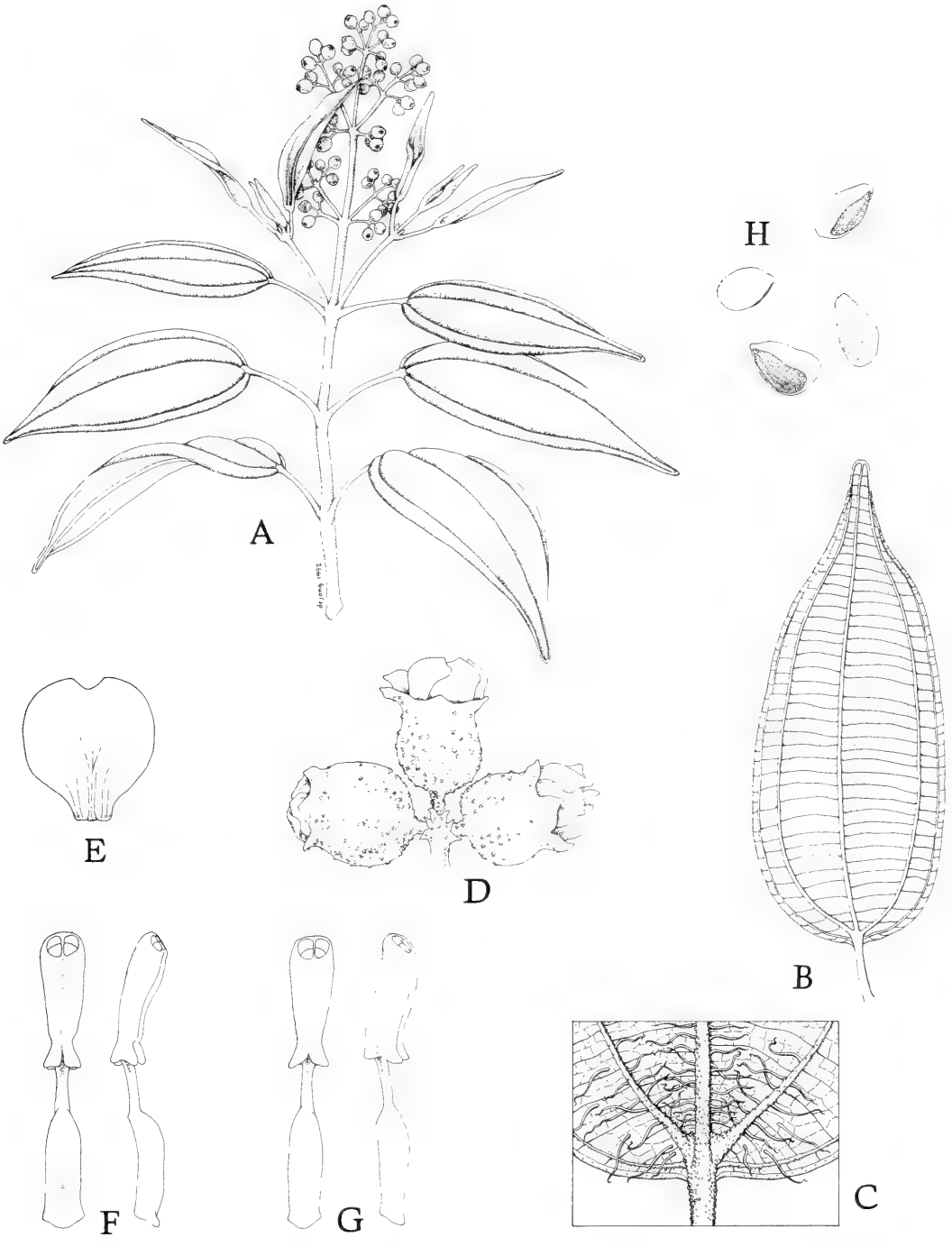

FIGURE 8. *Miconia talamancensis* Almeda. A, habit, × 1; B, representative leaf (abaxial surface), × 1; C, enlargement showing pubescence detail at a leaf base (abaxial surface); D, ultimate dichasial inflorescence unit showing flower buds, × 6; E, petal (adaxial surface), × 9; F, antepetalous stamen, ventral view (left) and profile view (right), × ca. 11; G, antesepalous stamen, ventral view (left) and profile view (right), × ca. 11; H, seeds, × ca. 18. (A–H from the holotype.)

some distance up the blade along the primaries (especially the median vein), 5-nerved (the outermost pair often inconspicuous), the transverse secondary veins elevated and spaced 1.5–4 mm apart at the widest portion of the blade. Inflorescence a terminal multiflowered panicle 6–9.5 cm long, branching 1.5–2.5 cm above the node initiating the inflorescence; bracts of the rachis nodes early deciduous and not seen; bracteoles also early deciduous and rarely seen at anthesis, paired, elliptic-oblong to oblong-obovate, 0.75–1.5 mm long, 0.25–0.5 mm wide (at the widest point). Pedicels 0.5–1.25 mm long. Hypanthia (at anthesis) 2–2.5 mm long to the torus, moderately covered with rusty brown dendritic or asperous-headed hairs that typically do not completely conceal the actual surface. Calyx tube 0.25 mm long, the calyx lobes deltoid to broadly rounded-deltoid, hyaline, 0.5 mm long; exterior calyx teeth 5, bluntly triangular, 0.25 mm long, shorter than and not obscuring the calyx lobes; torus glabrous adaxially. Petals 5, glabrous, white, obovate to ± suborbicular, rounded and often retuse or emarginate apically, 1.5–2 mm long, 1–1.5 mm wide. Stamens 10, subisomorphic, filaments glabrous, geniculate above the middle, constricted distally about 2/3 of the way up from the base, 2–2.5 mm long; anthers 1.5–1.75 mm long, 0.75 mm wide, white, oblong-obovate, widest above the middle, 4-celled, rounded to subtruncate at the apex and opening by a wide ventrally inclined opening; connective lobulate-thickened dorso-basally and prolonged ventrally below the thecae into two lateral lobes 0.24 mm long. Ovary (at anthesis) ½-inferior, 3-locular, globose, apex ± rounded and glabrous at maturity. Style straight, glabrous, 3–3.5 mm long; stigma capitellate. Berry globose, greenish-white becoming blue-black when mature, 5–6 mm in diameter. Seeds ovoid to ellipsoid, 0.5–0.75 mm long, tan, smooth with a dull luster, the lateral raphe extending for much of the seed length.

PHENOLOGY. — Collected in flower from February through July; in fruit during the months of March, June, and September.

DISTRIBUTION. — Locally common in high montane cloud forests and in rocky areas bordering páramo from near Villa Mills to Cerro Kámuk on the Cordillera de Talamanca of Costa Rica southeast to the Volcán Barú region of western Panama at 2900–3350 m (Fig. 5).

PARATYPES. — COSTA RICA. Cartago/San José border: About 3 km W of Villa Mills, 10 Mar. 1981, *Almeda & Nakai 4832* (CAS, CR); Cordillera de Talamanca, La Georgina, 27 Jul. 1972, *Kesel & Sauer 5307* (CAS); Limón: Cordillera de Talamanca, SW foot of Cerro Kámuk, 9°16′N, 83°02′30″W, 24 Mar. 1984, *Davidse et al. 25970* (CAS); Chirripó National Park, N end of Loma Larga, 15 Feb. 1983, *Garwood et al. 1262* (BM, MO). Puntarenas: Cordillera de Talamanca, across the Panamerican Hwy. from La Georgina, 23 Feb. 1991, *Almeda et al. 6785* (CAS, CR, MEXU, MO). San José: Along Interamerican Hwy. ca. 25 km SW of road to La Cima and 4.1 km NW of Cerro Asunción, 9°36′N, 83°46′W, 11 Sep. 1979, *Stevens 14269* (CAS). PANAMA. Chiriquí: 12 miles above Boquete on road to Volcán Barú, 18 May 1976, *Croat 34886* (CAS); La Nivera, below summit of El Barú, 14 Mar. 1979, *D'Arcy & Hammel 12467* (CAS); top of high ridge N of summit of Volcán Cerro Pavón, 15 Mar. 1979, *Hammel & D'Arcy 6436* (CAS); Volcán Barú, along road to summit, 8°45′N, 82°30′W, 10 June 1986, *McPherson 9487* (CAS).

DISCUSSION. — *Miconia talamancensis* has white, obovate to suborbicular petals; white, 4-celled anther thecae; ovoid to ellipsoid seeds with a dull luster; and oblong-ovate leaves with a concentration of simple spreading hairs where the primary veins diverge from one another at the abaxial base of the blade. In all of these characters, *M. talamancensis* is very similar to *M. schnellii* Wurdack, and there is no doubt that they are closely related. These two species differ in features of the indument, exterior calyx teeth, and anther details. In *M. talamancensis* the uppermost internodes, young leaves, petioles, and inflorescences are densely covered with a rusty brown indument of asperous-headed or dendritic hairs that are most reminiscent of the dendritic hairs with short arms illustrated by Wurdack (1986:64). *Miconia talamancensis* also has exterior calyx teeth that do not exceed or obscure the calyx lobes, and the septum separating the four anther cells does not conspicuously protrude beyond the anther apex. In *M. schnellii* the upper internodes and inflorescence branches are completely glabrous,

the calyx teeth exceed and obscure the calyx lobes, and the septum of the anther thecae protrudes beyond the anther apex.

In most collections of *M. talamancensis* the simple hairs at the abaxial leaf base commonly extend for some distance up the blade along the median vein. I have never observed this kind of pubescence distribution in any population or herbarium collection of *M. schnellii*. I have found both of these species growing side by side on the Cordillera de Talamanca in Costa Rica with no breakdown or intermediacy in the character differences noted above.

Although *M. talamancensis* and *M. schnellii* have overlapping geographic and elevational ranges, there are some modal differences worthy of note. The latter grows on Costa Rica's Cordillera de Talamanca and on the slopes of Volcán Irazú and Volcán Turrialba at elevations of 1,980–3,200 m. In Costa Rica, *M. talamancensis* occurs only on the Cordillera de Talamanca with populations extending southeast to the Volcán Barú region of Panama. All collections of this species have been made at 2,900–3,350 m.

ETYMOLOGY. — The specific epithet is derived from Cordillera de Talamanca, a plutonic uplift dominating the mountainous backbone of Costa Rica, where many of the collections of this species have been made.

***Miconia vestita* Almeda, sp. nov.**
Fig. 9

TYPE.—COSTA RICA. San José: Ridgetop due E of Finca Chacón near San Gerardo de Dota, elev. 2500 m, 9 Mar. 1995, *Almeda 7399* (holotype: CAS!; isotype: CR!).

Section *Cremanium*. Arbor parva 2–5 m. Ramuli teretes sicut petioli foliorum venae primariae subtus inflorescentiaque pilis stipitato-stellatis erectis dense vel modice armati et pilis laevibus glanduliferis sparse intermixtis. Lamina 8.7–14.4 × 4–6.9 cm elliptico-ovata 5–7-nervata, supra glabra, subtus in venis secundariis tertiariisque pilis stipitato-stellatis modice puberuli. Panicula 9–12 cm longa multiflora; flores 5-meri; calycis tubus 0.25 mm latus, lobis interioribus 0.5–1 mm longis oblongo-ovatis, dentibus exterioribus minutis inconspicuis inframarginalibus. Stamina isomorphica glabra, antherarum thecae 1–1.5 × 0.25 mm oblongae poro ventraliter inclinato, connectivo dorsaliter ca. 0.25 mm bilobulato. Ovarium 3-loculare et 2/3 inferum apicem versus sparsiuscule glandulis vel paullulo stellatis armatum.

Small openly branched tree 2–5 m tall. Uppermost cauline internodes and inflorescence rachis copiously covered with a rusty brown indument of dendritic and penicillate-stellate hairs (0.5 mm long) intermixed with smooth spreading glandular hairs (mostly 1.5 mm long). Leaves of a pair mostly equal in size; petioles 2.5–3.3 cm long; blades subcoriaceous when dry, 8.7–14.4 × 4–6.9 cm, elliptic to elliptic-ovate, apex acuminate to cuspidate, base obtuse to rounded, margin inconspicuously serrulate, 5–7-nerved, the transverse secondaries elevated and spaced 2–4 mm apart at the widest portion of the blade, adaxially glabrous or sparsely and irregularly beset with dendritic or stipitate-stellate hairs in the channels created by the impressed primary veins, abaxially beset with a dense to moderate cover of rusty colored dendritic and penicillate-stellate hairs on the elevated primary veins and on the prominulous network of transverse secondary and higher order veins. Inflorescence terminal, 9–12 cm long, paniculiform with ultimate branchlets terminating in simple dichasia; bracts of rachis nodes paired judging from nodal scars but evidently early deciduous and not seen, bracteoles early- or tardily-deciduous, oblong to narrowly oblanceolate, 2–2.5–3 mm long, 0.5 mm wide, glabrous adaxially, moderately to copiously stipitate-stellulate abaxially. Pedicels 0.25–0.5 mm long. Hypanthia (at anthesis) 2.5–3 mm long to the torus, moderately to sparsely covered with stellate and stipitate-stellate hairs that are sometimes intermixed with a few spreading glan-

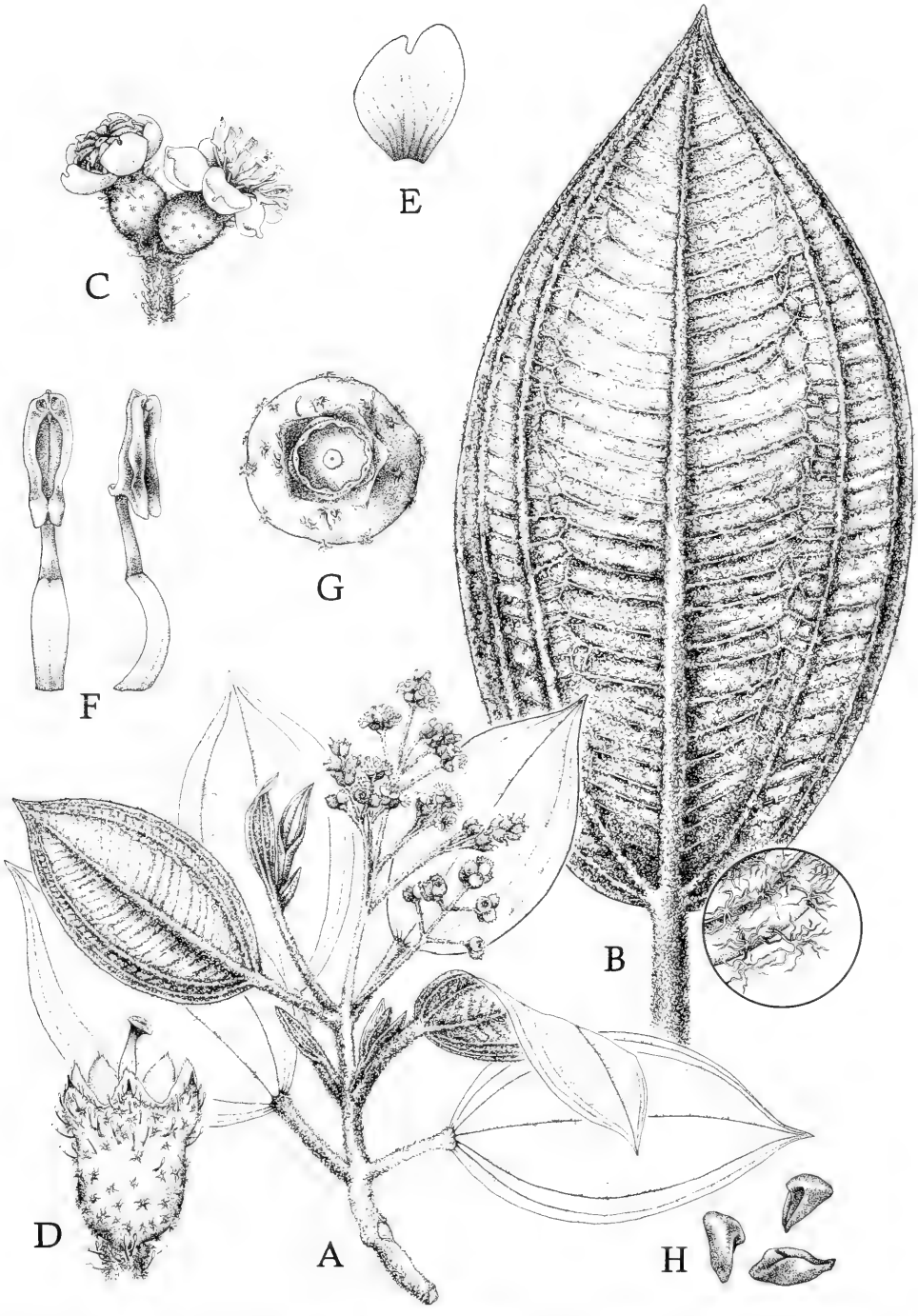

FIGURE 9. *Miconia vestita* Almeda. A, habit, × ca. ½; B, representative leaf (abaxial surface), with enlargement of pubescence detail, × 1; C, open flowers showing posture of petals and stamens, × ca. 4; D, hypanthium in profile view with petals and androecium removed, × ca. 7; E, petal, × 10; F, stamens, ventral view (left) and partial profile view (right), × ca. 17; G, berry as seen from above, × ca. 6; H, seeds, × ca. 10. (A–H from the holotype.)

dular hairs. Calyx tube 0.25 mm long, the calyx lobes oblong-ovate, rounded at the apex, abaxially glabrous, adaxially glabrate or sparingly stellate-pubescent at the base and adjacent to the calyx teeth, 0.5–1 × 0.5–0.75 mm; exterior teeth 5, subulate to triangular, 0.5 mm long, typically shorter than the calyx lobes but often obscured by an indument of stipitate-stellate and glandular hairs; torus glabrous on the adaxial face. Petals 5, glabrous, white, reflexed, obovate, rounded and emarginate apically, 2–2.5 mm long, 2 mm wide. Stamens 10, isomorphic, reflexed, forming a wide circle around the style and lying close to the expanded petals, filaments geniculate, glabrous, complanate, 2 mm long; anthers 1–1.5 mm long, 0.25 mm wide, white, linear-oblong, ± truncate apically with a ± ventrally inclined pore; connective thickened and elevated dorso-basally into a bilobed appendage mostly less than 0.25 mm long and prolonged ventro-basally into a caudiform lobe 0.25 mm long at the base of each anther sac. Ovary (in fruit) 2/3 inferior, 3-locular, globose, apex ± rounded and sparingly beset with a few stellate and/or glandular hairs. Style straight, glandular-puberulent, 3.5 mm long, stigma capitate. Berry globose, 3.5–4 mm in diameter. Seeds irregularly angulate-pyramidate, 1 mm long, the testa smooth and ± vernicose, the lateral raphe extending the entire length of the seed.

PHENOLOGY. — The type, which was collected in early March, is in flower and young fruit.

DISTRIBUTION. — Known only from the type locality on a ridgetop dominated by *Quercus bumelioides* Liebm. [*Q. copeyensis* C. H. Muller] near San Gerardo de Dota on the Cordillera de Talamanca, Costa Rica at 2500 m (Fig. 2).

DISCUSSION. — Although *M. vestita* is a typical member of section *Cremanium* in having oblong 2-celled anthers and permanently geniculate filaments above the middle, it does not appear to be particularly close to any of the 209 species currently placed in this section. In foliar size and shape there is a superficial resemblance to *M. acanthocoryne* Wurdack of Colombia, but that species has a rubiginose-furfuraceous indument on upper branches, petioles, and inflorescences, 4-celled anthers with broad pores and 2-locular ovaries.

The most striking feature of *M. vestita* is the indument on the abaxial foliar surface which consists of rusty brown dendritic or penicillate-stellate hairs reminiscent of a miniature forest of trees. The anthers are also noteworthy because the thecae appear thin-walled, somewhat collapsed but not malformed, and largely devoid of pollen. It is possible that all the flowers on the two individuals that I encountered in the field had been relieved of their pollen by buzzing bees, but it is also possible that I collected functionally pistillate individuals of a dioecious species. Non-functional stamens are produced on the pistillate flowers of other dioecious species of *Miconia*, all of which belong to section *Cremanium* and occur at high elevations. This will require further study when additional populations of *M. vestita* are located.

The berry measurements given in the species description are based on fruits that are not yet fully mature. They are sure to increase somewhat when ripened fruits are collected.

ETYMOLOGY. — The specific epithet is derived from the Latin word *vestitus*, meaning clothed or covered, alluding to the conspicuous hair covering on the abaxial foliar surface.

ACKNOWLEDGMENTS

I thank Robert L. Dressler for augmenting locality information for *Miconia correae* and Mireya D. Correa for bringing several important collections to my attention. Logistical support was provided by the Smithsonian Tropical Research Institute in Panama and the Museo Nacional de Costa Rica and the Instituto Nacional de Biodiversidad in Costa Rica. I am also grateful to the herbaria cited for gifts and/or loans of critical specimens and to the following individuals for preparing the line drawings: Sheva Myers (Figure 1), Ellen del Valle (Figures 2–4), Jenny Speckels (Figures 5 and 7), and Margaret de Jong (Figure 6).

LITERATURE CITED

ALMEDA, F. 1981. The Mexican and Central American species of *Adelobotrys* (Melastomataceae). Ann. Missouri Bot. Gard. 68:204–212.

———. 1989a. Five new berry-fruited species of Tropical American Melastomataceae. Proc. Calif. Acad. Sci. 46(5):137–150.

———. 1989b. New species and taxonomic notes on Mexican and Central American Melastomataceae. Proc. Calif. Acad. Sci. 46(9):209–220.

———. 1989c. *Tessmannianthus*, an arborescent genus of Melastomataceae new to Panama. Ann. Missouri Bot. Gard. 76:1–6.

———. 1990. New species and new combinations in *Blakea* and *Topobea* (Melastomataceae), with an historical perspective on generic limits in the tribe Blakeeae. Proc. Calif. Acad. Sci. 46(14):299–326.

COGNIAUX, C. A. 1891. Mélastomacées. *In* Monographiae phanerogamarum. Vol. 7. A. de Candolle and C. de Candolle, eds. G. Masson, Paris. 1256 pp.

GLEASON, H. A. 1958. Melastomataceae. *In* Flora of Panama, R. E. Woodson, Jr. and R. W. Schery, eds. Ann. Missouri Bot. Gard. 45:203–304.

LEWIS, W. H. 1971. High floristic endemism in low cloud forests of Panama. Biotropica 3:78–80.

STANDLEY, P. C. AND L. O. WILLIAMS 1950. New plants from Honduras. Ceiba 1:38–49.

WURDACK, J. J. 1986. Atlas of hairs for neotropical Melastomataceae. Smithsonian Contr. Bot. 63:1–80

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A New Species of Giant, Montane *Phrynobatrachus* (Anura: Ranidae) from the Central Mountains of Kenya

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A new species of large forest-dwelling frog of the genus *Phrynobatrachus* Günther (Ranidae) is described, based on material collected in two different montane localities in central Kenya. The new species differs in at least 10 characters from *Phrynobatrachus krefftii* Boulenger, an endemic to the Eastern Arc Mountains of Tanzania, and the only other large species of the genus in East Africa. A comparison of selected internal morphological character states among *P. krefftii*, the new species and several other species of the genus *Phrynobatrachus* suggests that the new species and *P. krefftii* are not closely related.

The ranid genus *Phrynobatrachus* Günther, 1862 is a poorly understood group. Individuals collected in the field are often difficult to identify to species, and past workers have frequently confused members of this group with cryptic, leaf-litter species of other genera including *Arthroleptis*, *Schoutedenella*, *Phrynodon* and *Dimorphognathus*. The few external characters that distinguish *Phrynobatrachus* from other genera include presence of a tarsal tubercle, absence of mandibular odontoids (present in *Dimorphognathus* and *Phrynodon*) and absence of a median dorsal skin raphe (present in *Arthroleptis* and *Schoutedenella*).

Of the 65 species of *Phrynobatrachus* listed in Frost (1985), many are based on scanty descriptions. Because of their cryptic nature, few species exhibit obvious, easily recognizable field characteristics upon which descriptions or identifications can be based; an exception is *P. cricogaster* (Perret 1957). Many species also exhibit a high degree of polymorphism (Stewart 1974). To date, few advertisement calls of *Phrynobatrachus* species have been analyzed or published.

Herein, we describe a new species which is apparently endemic to the central mountain massif of Kenya. This description is based on material collected at two separate localities between 20 and 30 years ago and deposited in four different institutions where it has remained unnoticed until recently. Institutional abbreviations follow Leviton et al. (1985).

SPECIES DESCRIPTION

***Phrynobatrachus irangi*, n. sp.**
Plate 1 and Fig. 1

HOLOTYPE. — MHNG 2230.76 male; KENYA: Meru District: Irangi Forest, above Irangi Forest Station, springs of Ena Stream. 0°24′S, 37°28′E, elevation 2100 m. Collected by J.-L. Perret and V. Mahnert, 12 October 1977.

PARATYPES. — MHNG 2230.74–75 males, MHNG 2230.77 sub-adult, MHNG 2230.78 female; CAS 158967 male, CAS 158966 (male, cleared and stained); AMNH 68808, 68810-11, AMNH 72854-56 males; AMNH 68790, 68809, 72853 females: vicinity of type locality, collected by R. Keith, 4 March, 28 April, 8 May, 1962 at 1965 m and 2286 m.

DIAGNOSIS. — A new montane species of *Phrynobatrachus* from the Kenya Massif and the Aberdare Range differing from all East African congeners in the large size of the females (to 51.0 mm), and from the large Tanzanian Highlands species *P. krefftii* in the following external (1-6) and internal (7-11) characters: (1) reduced webbing of the foot, (2) smaller inner metatarsal tubercle, (3) longer fifth toe, (4) central plantar surface of foot in breeding males with spiny asperities, (5) snout in breeding males rounded, not sharply projecting; (6) breeding males without dark outlining of lower jaw and without chrome yellow gular coloration, (7) nasals widely separated, not greatly dilated medially, not overlapped posteriorly by sphenethmoids, (8) neural spines of vertebrae not strongly imbricate, (9) base of omosternum not bifurcate, (10) base of thyrohyal originating well posterior to base of posterolateral process of hyoid, and (11) sternal style semi-rectangular, not strongly tapered medially.

ETYMOLOGY. — The specific epithet, a noun in apposition, refers to the type locality, Irangi Forest, Meru District, Kenya.

DESCRIPTION OF HOLOTYPE. — Male, 46.0 mm snout-vent length; habitus stout, robust; snout protruding but rounded, not sharply angled (Fig. 2); diameter of eye 4.5 mm, slightly more than half the distance to tip of snout, nearly equal to interorbital space; tympanum an oblique oval, its diameter approximately three-fourths that of eye and situated beneath a dermal fold that originates from mid-point of posterior margin of eye, curves ventrally around tympanum and terminates midway between angle of jaw and origin of forelimb; tip of fingers and toes rounded, only slightly dilated; tip of each toe in males with one or two lateral spines; webbing between fingers absent, webbing between toes reduced (Fig. 3) webbing formula I2-2+II1-2+III3-3IV3+-2+V (Savage and Heyer 1997); subarticular tubercles of both hands and feet single, palmar surfaces smooth, plantar surfaces beset with numerous, small, pale-colored spinose asperities, especially conspicuous along axes of fourth and fifth metatarsals (Fig. 3); large, thick greyish, granular nuptial pad extending from origin of thumb to just beyond proximal subarticular tubercle; tarsal tubercle a pale-colored eminence capped by white spine; fore- and hindlimbs stout, muscular; hindlimb length 2.5 times greater than snout-vent length; inner metatarsal tubercle white, small, about one-third diameter of eye.

Dorsum generally smooth in appearance but beset with widely spaced, very small, white-pointed tubercles that extend laterally to mid-lateral surface of body; thin, glandular ridge extends from the posterior margin of each eye, angling medially to level above posterior extent of tympanum but not converging with its fellow; a second, more posterior pair of slightly shorter, thin glandular ridges diverges obliquely in reverse direction to position above mid-point of forelimb insertion, forming following configuration:

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dorsal skin of forelimbs smooth, hindlimbs smooth in femoral region but becoming increasingly tuberculate from midpoint of tibio-fibula to foot; posterior surface of thighs generally smooth with

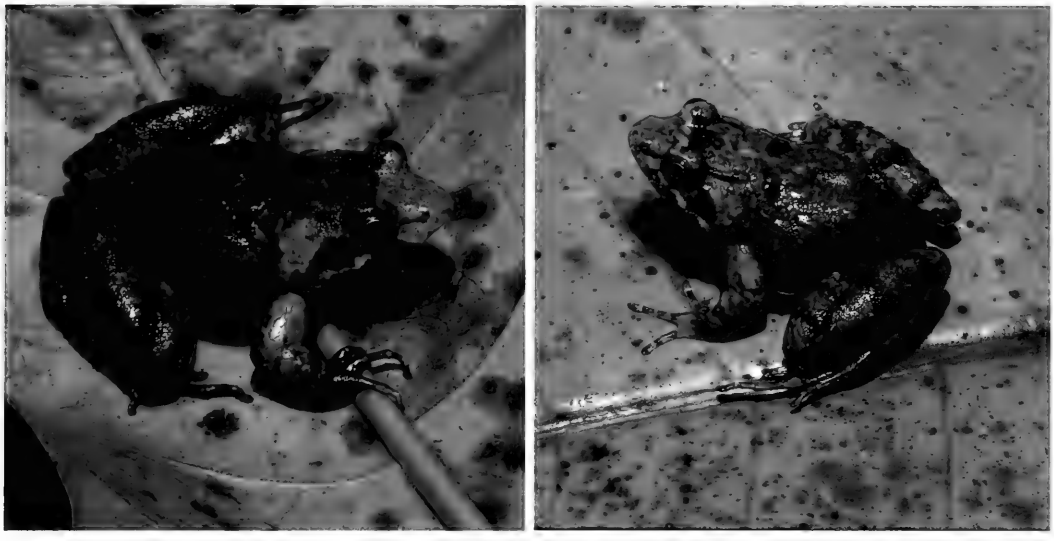

PLATE 1. A. (left) Holotype of *Phrynobatrachus irangi* (MHNG 2230.76). B. (right) Paratype (MHNG 2230.75). Photos by JLP in type locality, Irangi Forest, Kenya.

white-tipped, small spinous tubercles interspersed with larger flattened warts; ventral surface of body smooth, except for gular region, which consists of series of longitudinal, unpigmented, distensible folds comprising the vocal pouch.

Color in preservative. Ground color a medium, muddy brown; pale areas darkish beige; ventrum pale beige. Entire snout pale-colored, separated from darker dorsal coloration by sharply demarcated line across interorbital space including anterior one-third of each eyelid; pale area extending ventro-laterally and obliquely onto upper lip from anterior margin of eye; upper lip dark from posterior margin of pale patch and below eye to anterior margin of tympanum; tympanum dark; rounded pale patches extend antero-dorsally from anterior margin of origin of forelimbs to lateral margins of anterior pair of glandular ridges, and distally onto anterior surfaces of forearms to point near wrists; dorsal aspects of hands dark with darker band near each wrist; hindlimbs with nine, roughly equally-spaced, dark bands extending from thighs to feet; ventrum immaculate.

Color in life (Plate 1A). Dorsum dark brown; entire snout light orange-brown, sharply demarcated by transverse line running between eyelids; large patch of same contrasting color on shoulder, upper arm and elbow; hind limbs pale brown with dark, thick transverse bands; ventrum yellowish tan; gular region somewhat grayish.

VARIATION IN PARATYPES. — Morphological features in the paratype series are generally consistent with those described in the holotype. All female and a few male (AMNH 72854–72856) specimens lack small, pale dorsal and lateral spines; these are present in all remaining male specimens. Some variation exists in the plantar spines: plantar spines in the fourth metatarsal area are absent in the largest females (AMNH 72853 and AMNH 68790), present but reduced in females AMNH 68809 and MHNG 2230.78; present but reduced in males AMNH 72854, 72855 and 72856. Males AMNH 72854–72856 are soft and rather poorly preserved in comparison with the rest of the type series including males AMNH 68808, AMNH 68810–68811; these specimens are adults (snout-vent length 36.6–45.7 mm) so absence of dorsal and lateral spines in males is probably an artifact of preservation. Tarsal tubercles also vary; some individuals have a row of small tarsal spines, the largest and most posterior of which also occupies the position typical of tarsal tubercles in other species in the genus.

All specimens in the type series are consistent in dorsal color pattern with minor variations in intensity of ground color; all specimens exhibit the sharply-defined, pale-colored snout except one male

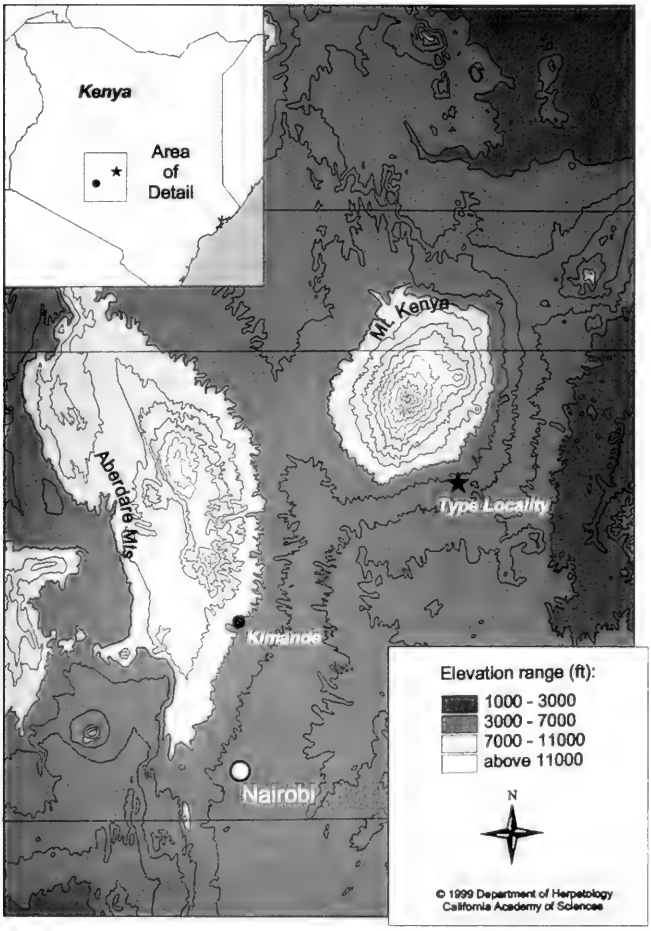

FIGURE 1. Type locality of *Phrynobatrachus irangi* sp. nov.: Irangi Forest, Mount Kenya, and location of Aberdare Range population (NMK specimens): former farm of Edna Oxtoby at Kimande, Kenya.

paratype (MHNG 2230.75) in which the snout is darker brown, but still demarcated by a pale orange-brown transverse bar (Plate 1B). One male specimen (AMNH 68808) has a thin, mid-dorsal pale stripe extending from the posterior margin of the pale snout patch to the tip of the urostyle; one female (MHNG 2230.74) is darker and more mottled in dorsal aspect than the remaining specimens. Supratympanic, rounded pale patches are discernable in six males (CAS 158967, MHNG 2230.74, AMNH 68808, 72854, 72855); these are less obvious in females and the remaining male specimens.

Ventral surfaces of three males (MHNG 2230.78, AMNH 68780, AMNH 68809) have diffuse greyish mottling that extends posteriorly from the gular region to the underside of the thighs; the underside in AMNH 72853 is immaculate; the venters of three males (AMNH 68811, 72855 and MHNG 2230.77) are also mottled but less so than in females; the ventral surface of the hindlimbs in male AMNH 72854 is moderately mottled in pale brown.

Measurements of the type series, and meristic comparisons with *Phrynobatrachus krefftii* are summarized in Tables 1 and 2.

VOICE. — The advertisement call of *Phrynobatrachus irangi* has been recorded (Perret) from a chorus of many males; evidently no single voice was close enough for sonographic analysis. The call is rather loud and evidently emitted during the day only. It was described by R. Keith (in her field notes, AMNH Archives) as "raugh-araugh-aaaaraugh-arararaugh-raraugh."

COMPARISONS

External Morphology

The only other species of large *Phrynobatrachus* in East Africa, *P. krefftii* Boulenger, 1909, is endemic to the Eastern Arc Mountain system (Howell 1993). In Table 1, we have summarized meristic data taken from the type series of *P. irangi* and 16 males and females of *P. krefftii* from Amani, East Usambara Mountains, Tanzania (see Additional Material Examined). Whereas adult males of both species are comparable in size, adult *P. irangi* females attain much larger snout-vent lengths; in fact, female *P. irangi* may be the largest member of the genus *Phrynobatrachus*.

Both male and female *P. irangi* have longer hindlimbs than *P. krefftii*, but smaller inner metatarsal tubercles. The tarsal tubercle of *P. irangi* is larger and more conspicuous than that of *P. krefftii*, which tends to be a single, small, spinous eminence at the terminus of a curved skin fold that originates near the posterior margin of the inner metatarsal tubercle. However, in some specimens of both species a series of small tubercles are present, with the largest occupying the posterior-most position. The plantar surfaces of the fourth metatarsal are spinose in male *P. irangi*, and smooth in *P. krefftii*. The presence of these small asperities on the ventral surfaces of the toes and feet, while differently distributed in these two species, appears to be a unique character within the genus *Phrynobatrachus*. Specimens of *P. krefftii* have more extensive webbing between the toes than do *P. irangi* (Fig. 3; webbing formula for *P. krefftii*: I1-1II0-0III1-2IV2+-1V [Savage and Heyer 1997]).

FIGURE 2. Right lateral aspects of *Phrynobatrachus irangi* male holotype (MHNG 2230.76) (above); *Phrynobatrachus krefftii* male CAS (186541) (below).

Breeding male *P. krefftii* have a pointed, projecting, shallow snout in lateral profile (Fig. 2); the lower jaw is sharply defined by dark pigment which, in turn, is outlined medially by starkly contrasting white pigment. The gular region is bright chrome yellow in life (Barbour and Loveridge 1928). In preservative, the yellow gular region of male *P. krefftii* fades to the same color as the venter, but the strongly marked coloration of the lower jaw persists. Male *P. irangi* have rounded, less-projecting snouts, the lower jaw is mottled, not evenly outlined, and the bright chrome yellow gular coloration of *P. krefftii* males is absent.

TABLE 1. Measurements of type series of *Phrynobatrachus irangi*. Mean (in mm) followed by range (in parentheses).

	n	SVL	Tibia	T/SVL (%)	Foot	F/SVL (%)	T/F (%)
P. irangi (male)	14	41.7 (36–46)	25.8 (21–27)	58.7 (54.7–62.3)	26.2 (21–29)	63.2 (53.4–64.0)	105.7 (93.1–108.6)
P. irangi (female)	4	45.7 (45–51)	24 (22–26)	53.1 (48.9–58.25)	25.7 (24–28)	55.6 (47.05–63.4)	95.1 (88.5–108.3)

TABLE 2. Comparison of mean measurements (in mm) of *Phrynobatrachus irangi* and *P. krefftii*.

	SVL	Tibia	T/SVL (%)	Foot	F/SVL (%)	T/F (%)	MT
P. irangi (male)	41.7	25.8	56.7	26.2	63.2	105.7	1.7
P. krefftii (male)	41.0	21.8	53.4	24.2	59.4	89.9	2.4
P. irangi (female)	45.7	24.0	53.1	25.7	55.6	95.1	1.6
P. krefftii (female)	38.4	18.2	47.6	19.6	51.0	93.3	2.05

FIGURE 3. (left) Right foot in plantar view of male *P. krefftii* (NMK A/883.11); (right) *P. irangi* male paratype (MHNG 2230.75).

Internal Morphology

Examination of cleared and double-stained specimens reveals notable differences between the two species. In dorsal view, the nasals of *P. irangi* are widely spaced, not greatly dilated medially and are not overlapped posteriorly by the sphenethmoids; *P. krefftii* nasals are more broadly dilated medially, less widely spaced, and overlapped by anterior projection of the sphenethmoids (Plate 2A, B).

The presacral vertebrae in *P. krefftii* are strongly imbricate; those of *P. irangi* are non-overlapping (Plate 2A, B).

Viewed ventrally, the base of the omosternum in *P. irangi* is slightly notched; that of *P. krefftii* is moderately forked (see states 16.1 and 16.2, in Drewes 1984). The sternal style of *P. irangi* is near-rectangular, only slightly compressed medially, with a medial width greater than half the width of the anterior margin; that of *P. krefftii* is compressed medially, so that the medial width is half the width of the proximal margin of the structure. (Plate 2C, D)

In *P. irangi*, the bases of the thyrohyals originate posterior to a line drawn through the bases of the posterolateral processes; in *P. krefftii*, the thyrohyals are deeply invasive into the corpus of the hyoid plate and extend anterior to the bases of the posterolateral processes (Plate 2C, D)

In an attempt to ascertain the degree of relatedness between *P. irangi* and *P. krefftii*, the internal characters that serve to separate the two were examined in cleared and stained specimens of eight additional species of *Phrynobatrachus* (see Additional Specimens Examined). A phenogram, a UPGMA tree generated by PAUP 4.0b1 (Fig. 4) was based on the character matrix in Table 3. An additional state of character 1, degree of separation of nasals, was found in the added species, and coded "M". The phenogram, indicates that in spite of large size and gross similarity between *P. irangi* and *P. krefftii*, they probably are not closely related. *Phrynobatrachus irangi* shares more of its diagnostic character states with *P. parvulus* and *P. parkeri* than with the rest of the group; based on the same characters, *P. krefftii* clusters with *P. dendrobates*.

The states of four characters (neural arch, omosternum, sternal style and separation of nasals) were polarized using works by Clarke (1981), Drewes (1984), Lynch (1973) and a data set on petropedetine ranid genera (Drewes, unpublished). PAUP was employed in an attempt to assess the phylogenetic positions of *P. krefftii* and *P. irangi* with respect to each other and the relatively small sample of additional species in the genus (15%, see Frost 1985). The resulting analysis yielded 311 most parsimonius trees and was not resolvable; however, it indicated that with respect to a presumptive ancestor, *Phrynobatrachus irangi*, *P. kinangopensis, P. natalensis, P. parvulus, P. versicolor, P. parkeri, P. perpalmatus, and P. plicatus* form an unresolved polytomy, but are more closely related to each other than any is to *P. krefftii* and *P. dendrobates*. The latter form a basal clade with respect to the former. Interestingly, calling males of *P. dendrobates* share the characteristic bright, chrome yellow gular region of *P. krefftii* males.

Both *P. irangi* and *P. krefftii* share spinous asperities in the subdigital areas of the feet, as well as on the terminal discs, although the distribution of these asperities on plantar surfaces is consistently different between the two species. To our knowledge, possession of this character state is unique to these two species within the genus *Phrynobatrachus*; we posit that the appearance of this character

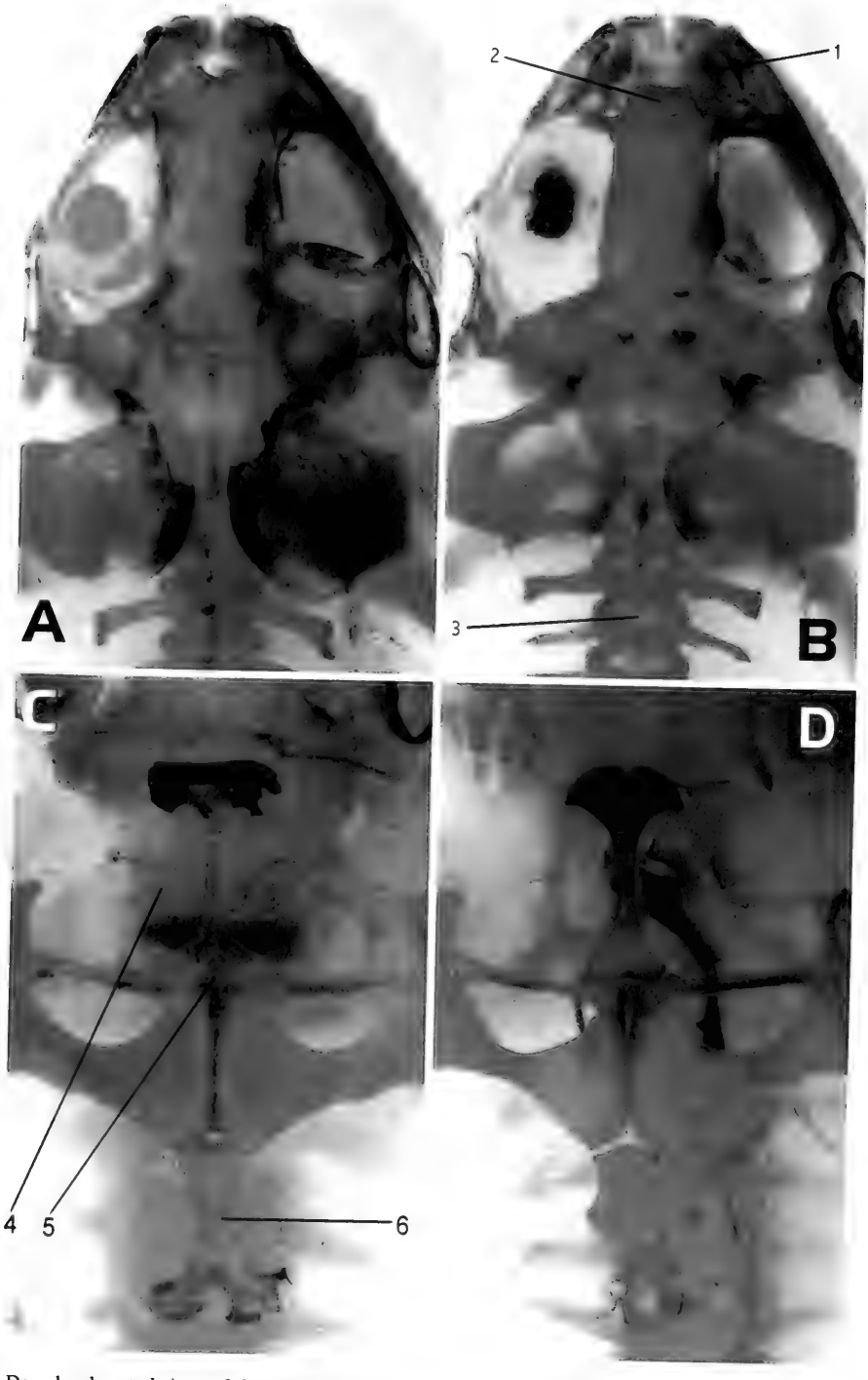

PLATE 2. Dorsal and ventral views of cleared and double-stained specimens of *Phrynobatrachus krefftii* (A, C, BM 1974.80) and male paratype *Phrynobatrachus irangi* (B, D, CAS 158966). Key: 1. nasal, 2. sphenethmoid, 3. non-imbricate neural arch, 4. base of thyrohyal, 5. base of omosternum, 6. sternal style.

TABLE 3. Distribution of internal character states differentiating *P. irangi* from *P. krefftii* among other *Phrynobatrachus* species.

	1	2	3	4	5	6	7
P. dendrobates	M	K	K	K	K	K	K
P. kinangopensis	I	I	I	I	K	I	K
P. natalensis (2)	M	K	I	I	I	I	I
P. parvulus	I	I	I	I	I	I	I
P. versicolor	I	K	I	I	K	K	I
P. parkeri	I	I	I	I	I	K	I
P. perpalmatus	I	K	K	I	K	I	I
P. plicatus (2)	M	K	K	I	K	K	I
P. irangi	I	I	I	I	I	I	I
P. krefftii	K	K	K	K	K	K	K

Character states: 1. nasal separation at midline
2. medial nasal dilation
3. posterior nasal overlap by sphenethmoid
4. neural arch imbrication (at least presacral vertebrae #1–3)
5. omosternum bifurcation
6. sternal style shape
7. thyrohyal condition

K = state found in *P. krefftii*
I = state found in *P. irangi*
M = state found in some additional species, i.e., nasals narrowly separated or meet at midline

may be the result of convergence, possibly related to their large size or derived from living in montane habitats.

Natural history

Based on the field experience of Perret and R. Keith's field notes, *Phrynobatrachus irangi* is active by day. Males were found calling on banks of small streams in the forest, from under roots or logs, and from holes in the mud. They were difficult to locate and capture. No amplexus has been observed, and although tadpoles were seen in nearby clear water, their identity was not ascertained.

DISCUSSION

The history of the material upon which this description is based is interesting and also necessary to document because of an error in the field data associated with the material from the National Museums of Kenya ([NMK], Additional Materials Examined). The specimens originally collected by E. Oxtoby at Kimande were first brought to the attention of Drewes in the early 1970s by the then Head of Herpetology at NMK. At that time, no attempt had been made on the part of NMK staff to collect further material, in spite of urging on the part of Oxtoby. Following Oxtoby's death, Drewes and an NMK staff member, Peter Nyamenya, made a day trip to the former Oxtoby property in October 1979 and found it severely modified by local subsistence farming. No *Phrynobatrachus* were seen or collected. For the next several years, attempts on the part of Drewes to borrow the Oxtoby material from the National Museums of Kenya for purposes of description were fruitless, and it was assumed that the Oxtoby material had been misplaced or lost.

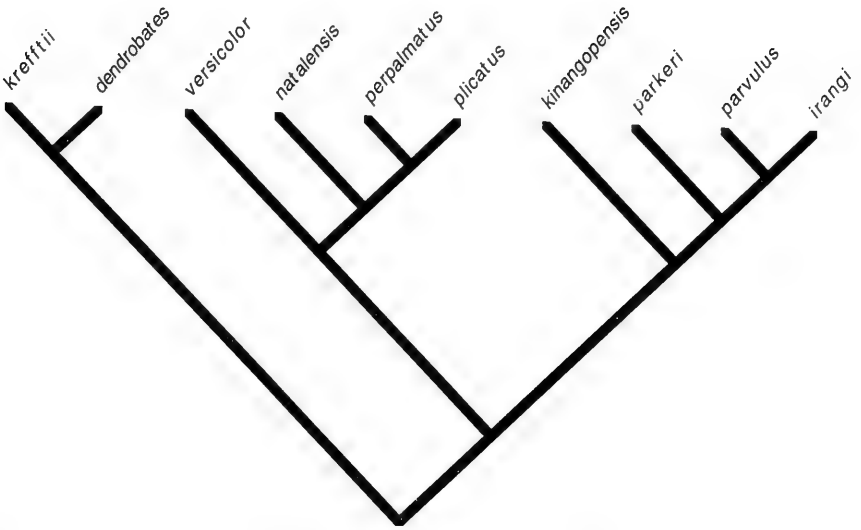

FIGURE 4. UPGMA Phenogram generated by PAUP, based on character states in Table 3.

During a visit to the MHNG in Geneva in 1985, Perret showed Drewes a series of large *Phrynobatrachus* that he and V. Mahnert had collected in the Irangi Forest in 1979. Irangi is on the eastern slope of Mt. Kenya, while Kimande, the former Oxtoby property is on the south-southeastern slope of the Aberdares, a range of mountains some 90 km., as the crow flies (see Fig. 1), from the Irangi site. It became obvious to Drewes that if the two samples did not represent the same undescribed species, they were almost certainly, closely related species. It seemed unwise to describe the MHNG material without including the NMK material; attempts by both authors to borrow the NMK material continued to be unsuccessful. In 1993, Drewes queried Dr. Linda Ford of the American Museum of Natural History as to whether or not Ronalda Keith, a field worker who made extensive collections in East Africa in the early sixties, had ever collected in the Irangi Forest. The response was positive and more than half of the type series described below is in the American Museum of Natural History.

In 1993, during a visit to the NMK, Drewes learned that the original Oxtoby Aberdares material had been found in a locked cabinet, and it has been included under Additional Material Examined. With respect to the NMK material, it is clear that the cataloged collection date of "1979" is in error; the specimens had to have been collected earlier, most likely in the early 1970s, inasmuch as the date of the day trip undertaken by Drewes and Nyamenya in 1979 is documented in photographs of the property taken at the time. The NMK specimens were not included as paratypes because the locality from which they were taken has evidently been destroyed, the population may be extinct, and we know of no field worker who has seen members of this population in life.

ADDITIONAL MATERIAL EXAMINED

Phrynobatrachus irangi: NMK A/1203/1-2, A/1203/4.Kenya: Murang'a Dist: Kimande. 0°49′S, 36°48′E; males, collected by E. Oxtoby, 30 April 1979(?); Kenya: Meru Dist: type locality: AMNH 68791-68793, AMNH 68795-68796, AMNH 135816. juveniles, collected by R. Keith, 1962.

Phrynobatrachus krefftii: CAS 168511–168557. Tanzania: Tanga Region: Muheza Dist: East Usambara Mtns, vic. of Amani.; BMNH 1974.79–91. Tanzania: West Usambara Mtns. Mazumbai

Forest Reserve, 4°48′S, 39°29′E; NMK A/883/7, A/883.11 males; A/883/16-17, females. Tanzania: East Usambara: Amani collected by B. Watulege, July 1969.

Cleared and Stained: *Phrynobatrachus dendrobates*, CAS 145294: Zaire: Ituri Prov: Manguerete Hipa; *P. kinangopensis*, CAS 152381: Kenya: Murang'a Dist: Kimande; *P. krefftii,* BM 1974.80: Tanzania: West Usambara Mtns: Mazumbai Forest Reserve; *P. natalensis*, CAS 141564: Kenya: Kakamega Dist: Kakamega Forest Station; CAS 141666: Kenya: Kakamega Dist: Lubao; *P. parvulus*, CAS 145258: Zaire: Kivu Prov: Fizi Terr: Mokanga; *P. versicolor*, CAS-SU 13008: Zaire: Kivu Prov: Albert N.P.: Kundhuru-ya-Tshuwe; *P. parkeri*, CAS 98168: Zaire: Uele: Monga; *P. perpalmatus*, CAS 98156: Zaire: Uele: Albert N. P.: Buta; *P. plicatus*, CAS 136294, 136298: Ghana: Eastern Reg.: Kade Agricultural Station.

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LITERATURE CITED

BARBOUR, T. AND A. LOVERIDGE. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. Mem. Mus. Comp. Zool., Harvard Univ. 50:86–265, 4 pls.

CLARKE, B. T. 1981. Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). Monit. zool. ital. (N. S.) Suppl. 15:285–331.

DREWES, R. C. 1984. A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar and the Seychelles Islands. Occ. Pap. Calif. Acad. Sci. 139:1–70.

FROST, D. R., ed. 1985. Amphibian species of the world: a taxonomic and geographical reference. Assoc. Syst. Collections and Allen Press, Lawrence, Kansas. v + 732 p.

HOWELL, K. M. 1993. Herpetofauna of the eastern African forests. Pp. 173–201 *in* Biogeography and ecology of the rain forests of Eastern Africa. J. C. Lovett and S. K. Wasser, eds. Cambridge University Press, United Kingdom.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1, Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 1985:802–832.

LYNCH, J. D. 1973. 3. The transition from archaic to advanced frogs. Pp.133-182 *in* Evolutionary biology of the anurans. J. L. Vial, ed. University of Missouri Press, Columbia, Missouri.

PERRET, J.-L. 1957. Un nouveau *Phrynobatrachus* du Cameroun. Rev. suisse Zool. 46:527–531.

SAVAGE, J. M. AND W. R. HEYER. 1997. Digital webbing formulae for anurans: a refinement. Herpetol. Rev. 28:131.

STEWART, M. M. 1974. Parallel pattern polymorphism in the genus *Phrynobatrachus* (Amphibia, Ranidae) Copeia 1974:823–832.

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Two New Genera of Soft Corals (Anthozoa: Alcyoniidae) from South Africa, with a Discussion of Diversity and Endemism in the Southern African Octocorallian Fauna

by

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Two previously described taxa of soft corals, each apparently endemic to southern Africa, are each given new generic names. The two species were originally described in the genus *Alcyonium* Linnaeus, 1758, but are shown here to belong to distinct genera. Several southern African soft coral taxa share a similar growth form, i.e., unbranched, digitiform to capitate, with a conspicuously elongated stalk, and polyps restricted to a distal polyparium. A comparison of superficially similar taxa is provided, along with a revised faunistic analysis regarding diversity and endemism in the Octocorallia of southern Africa.

Since 1985, a resurgence of interest in the systematics of southern African octocorals has produced a variety of publications describing various taxa comprising the fauna. Included here are: Alderslade (1985), Benayahu (1993), Benayahu and Schleyer (1995, 1996), Branch, Griffiths, Branch and Beckley (1994), Grasshoff (1988, 1991, 1992), Lopez-Gonzalez, Gili, and Williams (2000), Ofwegen and Schleyer (1997), Richmond (1997), Verseveldt and Bayer (1988), Verseveldt and Ofwegen (1992), Verseveldt and Williams (1988), Williams (1986a, 1986b, 1986c, 1987a, 1987b, 1988, 1989a, 1989b, 1989c, 1989d, 1990a, 1990b, 1992a, 1992b, 1992c, 1992d, 1992e, 1993, in press), Williams and Lindo (1997), and Williams and Rogers (1989).

Two new genera of soft corals from the Cape Endemic Province of southern Africa (as defined by Williams, 1992d), are here described. Each genus includes a single species previously described in the genus *Alcyonium*. It is here argued that these taxa are better placed in genera other than *Alcyonium*.

METHODS

An examination of recently collected material was made for part of this study. The material was collected by SCUBA and preserved in 70% ethanol. Sclerites were isolated using sodium hypochlorite. Scanning electron micrographs were made on a Hitachi S-510 scanning electron microscope. Photographic plates for publication were made using Adobe Photoshop 4.0 software. Abbreviations used in the text are as follows: CAS (California Academy of Sciences, San Francisco), CRRF (Coral Reef Research Foundation, Palau), SAM (South African Museum, Cape Town).

SYSTEMATIC ACCOUNT

Family Alcyoniidae Lamouroux, 1812

Lampophyton gen. nov.

non *Alcyonium* Linnaeus, 1758:803; Williams, 1992a:271 (in part).

DIAGNOSIS. — Upright, unbranched soft corals, clavate or torch-shaped. Stalk prominent, expanding distally to form a flat-topped polyparium. Polyps monomorphic, retractile, restricted to the distal terminus of the coral. Polyp calyces absent. Sclerites colorless, densely set coarse spindles, more or less longitudinally arranged along the walls of the stalk and polyparium. Color alcohol soluble.

TYPE SPECIES. — *Alcyonium planiceps* Williams, 1986.

ETYMOLOGY. — The new generic name is derived from the Greek, *lampas* (a lamp or torch) and *phyton* (a creature, either plant or animal); in reference to the torchlike appearance of colonies of this species, with narrow stalk and expanded, flat-topped polyparium.

Lampophyton planiceps (Williams, 1986) new comb.

Figs. 1A–C, 2A–F, 3

Alcyonium planiceps Williams, 1986:53, figs. 1–7. 1992a:289, figs. 20 e–j, 21.

MATERIAL EXAMINED. CAS 118496 (Sta. No. SAFR 334), South Africa, Cape Province, off Port Elizabeth, Algoa Bay, Riy Banks, 15–24 m, 23 February 1999; collected by John Starmer with aid of SCUBA, two whole specimens. CAS 118497 (Sta. No. SAFR 365), South Africa, Cape Province, off Port Elizabeth, Algoa Bay, White Sands 6, 20 m depth, 26 February 1999, collected by John Starmer with aid of SCUBA, two whole specimens. Fig. 1B from SAM-H3280, Llandudno, Atlantic side of Cape Peninsula, Cape Province, South Africa, 21 m in depth, 24 January 1984, collected by G. C. Williams with aid of SCUBA. Fig. 1A, C from SAM-H3281, Llandudno, Atlantic side of Cape Peninsula, Cape Province, South Africa, 25–30 m in depth, 24 March 1984, collected by G. C.Williams with aid of SCUBA.

DESCRIPTION. — The specimens examined range in length from 18–32 mm. In each specimen, the distal polyparium arises from an upright and unbranched stalk, which in turn arises from the basal holdfast. The distal-most portion of the stalk expands gradually to form the polyparium at the distal terminus. This feature gives the body of the coral a club-shaped or torch-shaped appearance (Fig 1A–C). The polyps are restricted to the flat, disc-shaped distal terminus. The polyps are monomorphic, retractile, and without calyces. The sclerites are relatively large and robust spindles with varying amounts of surface ornamentation (Fig. 2A–F). The tubercles vary from simply rounded and relatively sparsely distributed knoblike structures to more densely-set crownlike arrangements (Fig. 2D–F). The sclerites are densely set and are mostly longitudinally arranged along the surface of the stalk (Fig. 1A). A few sclerites are scattered in the shallow subsurface of the stalk and polyparium, but are not present in the deep interior. The sclerites range in length from 0.82–1.80 mm. Sclerites are altogether absent from the polyps. The wet preserved specimens have stalks that are tan to yellowish brown in color (but apparently without zooxanthellae), with polyps and polyparies greenish gray or brown. Pigments are alcohol soluble. The vivid coloration of living material is recorded in Fig. 1A–C.

DISTRIBUTION. — Cape Province of South Africa; Atlantic side of the Cape Peninsula, Cape St. Francis, Algoa Bay, and East London; 21–90 m in depth (Fig. 3).

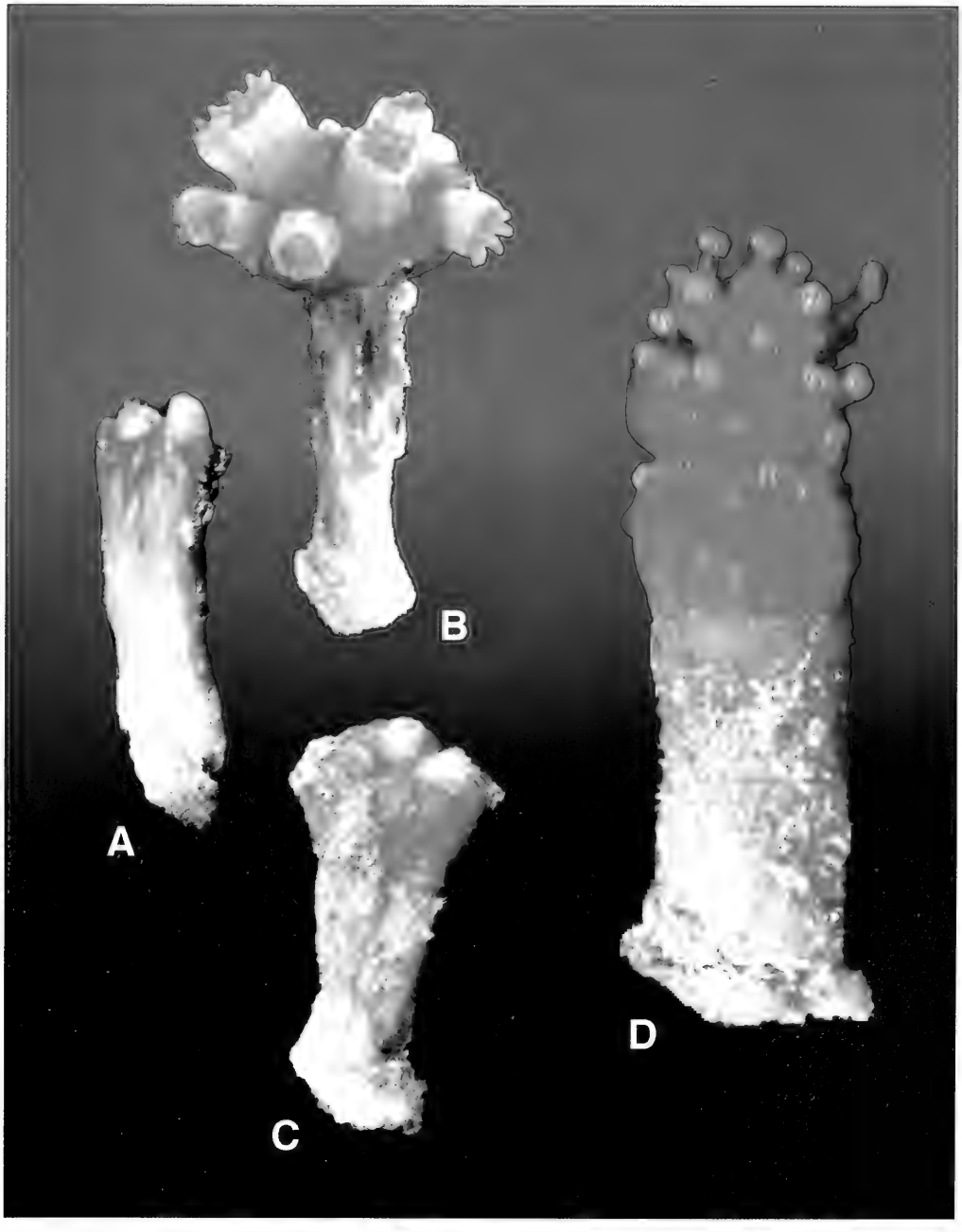

FIGURE 1. Living soft corals A-C. *Lampophyton planiceps*. A. Colony with polyps retracted, total length 18 mm (SAM-H3281). B. Colony with polyps partially expanded, total length 30 mm (SAM-H3280). C. Colony with polyps retracted, total length 17 mm (SAM-H3281). D. *Dimorphophyton mutabiliforme*; 25 mm in length (SAM-H3716).

REMARKS. — The surface of the stalk is often partly covered with a variety of epizoic organisms, including tubicolous amphipods, tubicolous terebellid polychaetes, sponges, foraminiferans, and diatoms (Fig 1B, C).

Turbellarian flatworms and an undescribed species of the arminacean nudibranch genus *Dermatobranchus* have also been found on colonies of *Lampophyton planiceps*. It is probable that the nudibranch feeds on the soft coral. Both predator and prey exemplify similar rose lavender colorations.

Dimorphophyton gen. nov.

non *Alcyonium* Linnaeus, 1758:803; Williams, 1992a:271 (in part).

DIAGNOSIS. — Upright, unbranched soft corals, with changing growth form: digitiform or cylindrical in shape when expanded, capitate during retraction. Stalk conspicuous, comprising half of total body length when expanded, more than half during retraction. Polyparium finger-shaped when expanded, subspherical during retraction. Polyps monomorphic, retractile into the capitulum. Polyp calyces absent. Sclerites thin, flattened, irregularly-shaped rods with smooth surface texture, tuberculation not evident. Sclerites colorless, few in number; sparsely scattered in anthocodiae and often in circles surrounding the bases of the polyps. Rust orange color, alcohol-soluble.

TYPE SPECIES. — *Alcyonium mutabiliforme* Williams, 1988.

ETYMOLOGY. — The new generic name is derived from the Greek, *di-* (a prefix meaning two or double), *morphe* (form or shape), and *phyton* (a creature, either plant or animal); in reference to the two colony shapes (digitiform when expanded and capitate when retracted) displayed by these soft corals.

Dimorphophyton mutabiliforme (Williams, 1988) new comb.

Figs. 1D; 2G, H; 3

Alcyonium mutabiliforme Williams, 1988:14, figs. 11–14; 1992a:286, figs. 19, 20 a–d.

MATERIAL EXAMINED. — SAM-H3716, Hottentot's Huisie, Atlantic side of Cape Peninsula, Cape Province, South Africa, 15–18 m in depth, 11 November 1984, four whole specimens, collected by G. C. Williams with aid of SCUBA.

DESCRIPTION. — Williams (1988:14–19 and 1992a:286–289) has previously described this species. A brief redescription is provided as follows: The seven known specimens are upright and unbranched, each less than 40 mm in length. The distal polyparium arises from a conspicuous stalk, which in turn arises from the basal holdfast. Expanded specimens are digitiform, with the cylindrical polyparium comprising 50–55% of the total length of the specimen (Fig. 1D). Retracted specimens are capitate, with the subspherical polypary comprising 35–45% of the total length of the specimen. The monomorphic polyps are retractile and are evenly distributed over the surface of the polyparium. They do not have calyces. Sclerites are very thin, relatively smooth, irregularly-shaped rods, with little to no surface ornamentation. They vary in length from 0.06–0.26 mm (Fig. 2G, H). The sclerites are very few in number and are sparingly distributed in the anthocodiae; as well as on the surface of the polyparium where they are arranged in rings surrounding the bases of most of the polyps. Sclerites are absent from other areas of the specimens. The specimens are deep orange to rust orange in life (apparently without zooxanthellae), fading to a dull reddish brown wet preserved. Pigments are alcohol-soluble. The vivid coloration of living material is recorded in Fig. 1D.

DISTRIBUTION. — Llandudno and Hottentot's Huisie, Atlantic side of the Cape Peninsula, Cape Province of South Africa; 15–21 m in depth (Fig. 3).

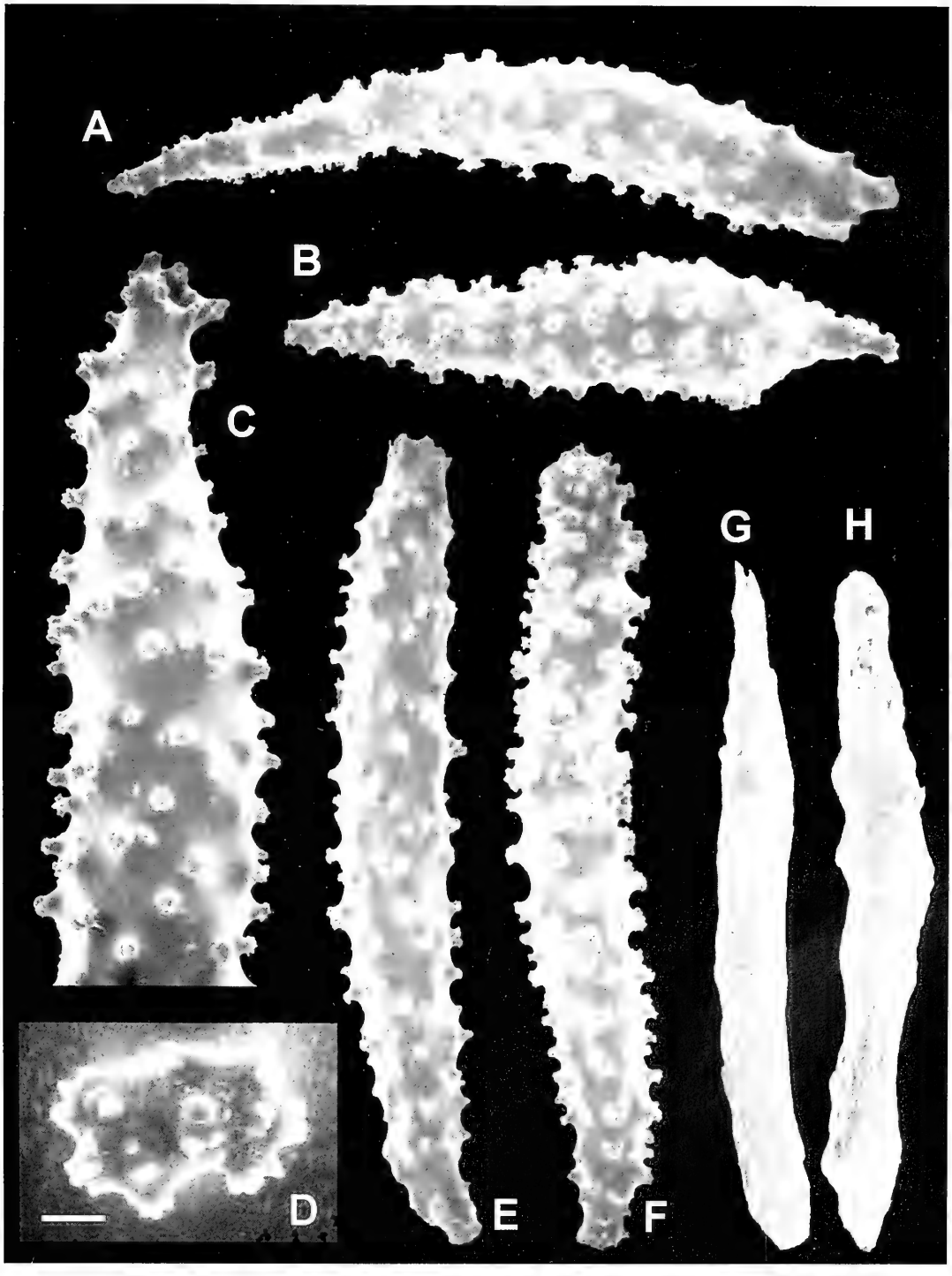

FIGURE 2. Scanning electron micrographs of sclerites. A-F. *Lampophyton planiceps*. A. 1.18 mm in length. B. 0.82 mm in length. C. Detail of one end of a sclerite; length of portion shown 0.64 mm. D. Detail of a single tubercle from sclerite shown in C; scale bar = 0.005 mm. E. 1.20 mm in length. F. 1.20 mm in length. G-H. *Dimorphophyton mutabiliforme*. G. 0.16 mm in length. H. 0.18 mm in length.

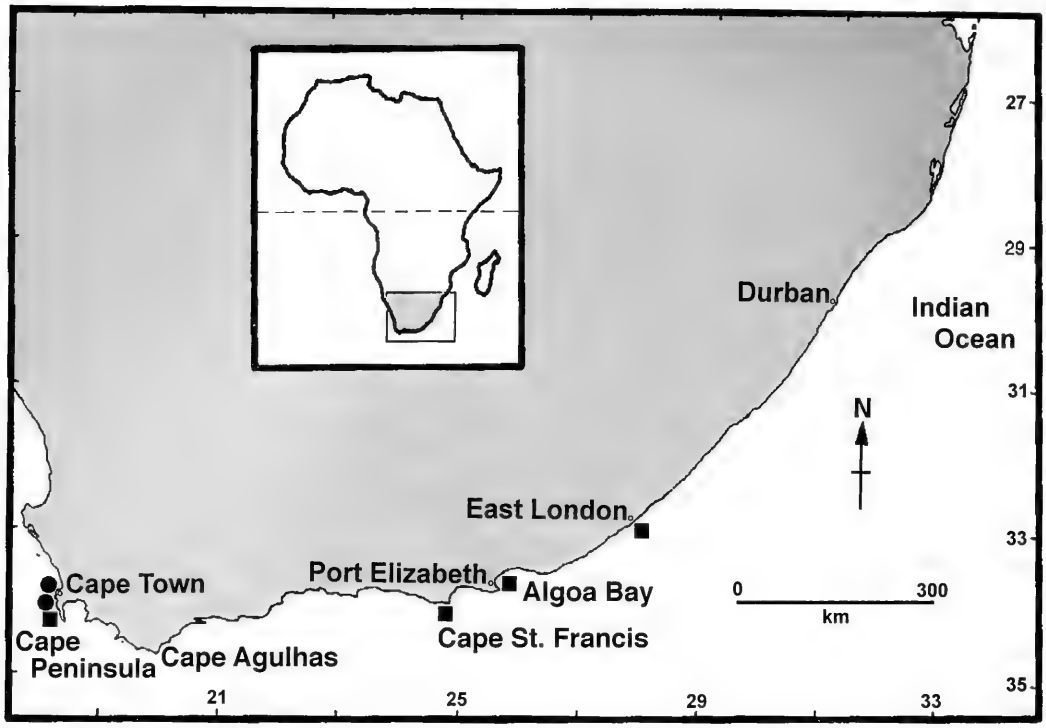

FIGURE 3. Map of southern Africa showing collecting stations for *Dimorphophyton mutabiliforme* (●) and *Lampophyton planiceps* (■).

REMARKS. — The surface of the stalk is often partly covered with a variety of epizoic organisms such as sponges, barnacles, and tunicates (Fig 1D).

DISCUSSION

SYSTEMATICS. — I have discussed and revised the definition of the genus *Alcyonium* Linnaeus, 1758, in earlier publications (1986a:262–264; 1986b:61–62; 1988:18–19; 1992a:271), and I also provided (1986:259–262) a synopsis of the history of taxonomy relating to this genus and related taxa. Since that period, it has been generally agreed by workers in soft coral systematics (P. Alderslade and L. P. van Ofwegen, pers. comm., and the present work) that it is more realistic to recognize a *sensu stricto* definition reflecting the lobate or digitate growth form of the type secies *Alcyonium digitatum* Linnaeus, 1758, rather than a broader *sensu lato* definition encompassing a variety of growth forms as I have listed previously (1988:19). It is proposed that as our knowledge of alcyoniid taxonomy increases, species previously included in the genus *Alcyonium* that do not suitably fit the original definition, should either be placed in other previously described genera such as *Eleutherobia* Pütter, 1900, or new genera should be named to accommodate them (such as *Lampophyton* gen. nov., and *Dimorphophyton* gen. nov.).

In addition, recent study has indicated that the genus *Alcyonium* as presently recognized may actually be comprised of two distinct clades: one representing cold-water to temperate, azooxanthellate, often brightly-colored species such as *Alcyonium fauri* J. S. Thomson, 1910; and the other represented mostly by coral reef taxa of tropical regions, such *as Alcyonium utinomii* Verseveldt, 1971, which are zooxanthellate and mostly white or light brown in color (pers. observ. and P. Alderslade,

pers. comm.). It remains to be determined whether or not the latter clade deserves separate generic designation. Alderslade (in press) addresses this issue.

Other taxa of southern African or Indian Ocean soft corals are superficially similar in growth form (unbranched: digitiform, clavate, or capitate) to *Lampophyton planiceps* and *Dimorphophyton mutabiliforme*, but differ as follows. *Malacanthus capensis* (Hickson, 1900), *Acrophytum claviger* Hickson, 1900, *Anthomastus* spp., *Paraminabea* spp., and *Verseveldtia* spp. are dimorphic. *Bellonella* spp. have spindles less than 0.15 mm in length, while *Eleutherobia* spp. have radiates. *Alcyonium* spp. are mostly lobate to digitate or membranous in growth form. *Pieterfaurea* spp. have a palisade-like arrangement of sclerites around the base of each polyp.

DIVERSITY AND ENDEMISM IN THE SOUTHERN AFRICAN OCTOCORALLIA. — I have previously (1992d) provided a detailed biogeographic analysis of the octocorallian fauna of southern Africa, describing diversity and levels of endemism in the Cape Endemic Province, as well as faunal contributions to the regional biota from neighboring zoogeographic provinces. Included here are the Indo-Pacific, Atlantic, and Southern Oceans (Antarctic and Subantarctic). Since 1992, new information has allowed for a refinement of analysis concerning diversity and endemism in the fauna. Figures 4 and 5 summarize the results of this revised assessment. The charts are based on data presented in Tables 1–3. A revised list of valid species of southern African octocorals will be published after the publication of several generic revisions and descriptions of new taxa.

Some definitions relevant to the reassessment are as follows: Soft corals are octocorals without an internal axis (families Alcyoniidae, Nephtheidae, Nidaliidae, and Xeniidae). Gorgonians refer to octocorals with an internal axis (families Anthothelidae, Melithaeidae, Keroeididae, Acanthogorgiidae, Plexauridae, Gorgoniidae, Ellisellidae, Chrysogorgiidae, Primnoidae, and Isididae). Widespread refers to scattered or cosmopolitan distributions as I have previously defined (1992d:356–357). This reference also defines the limits of other biogeographic regions such as Cape Endemic, Indo-Pacific, Atlantic, and Southern Oceans. I have previously elucidated the geographical limits of southern Africa (1992d:355). A particular genus is assigned a biogeographic affinity if the majority of species within the genus are endemic to that particular biogeographic region (Williams 1992d:368–369).

TABLE 1. Southern African Octocorallia - largest genera by number of species.

Genus	Number of species
Sinularia	15
Eleutherobia	7
Alcyonium	6
Sarcophyton	6
Leptogorgia	5
Lobophytum	5
Pieterfaurea	5
Simpsonella	5
Xenia	5
Drifa	4
Virgularia	4
Cavernularia	3
Eunicella	3
Ditypic genera	30
Monotypic genera	62
Total	165

TABLE 2. Southern African Octocorallia - biogeographic composition.

Biogeographic category	Number of genera	Number of species
Indo-Pacific	36	47
Widespread	30	9
Endemic	13	78
Atlantic	9	2
Antarctic	2	0
Unidentified	–	29
Total	90	165

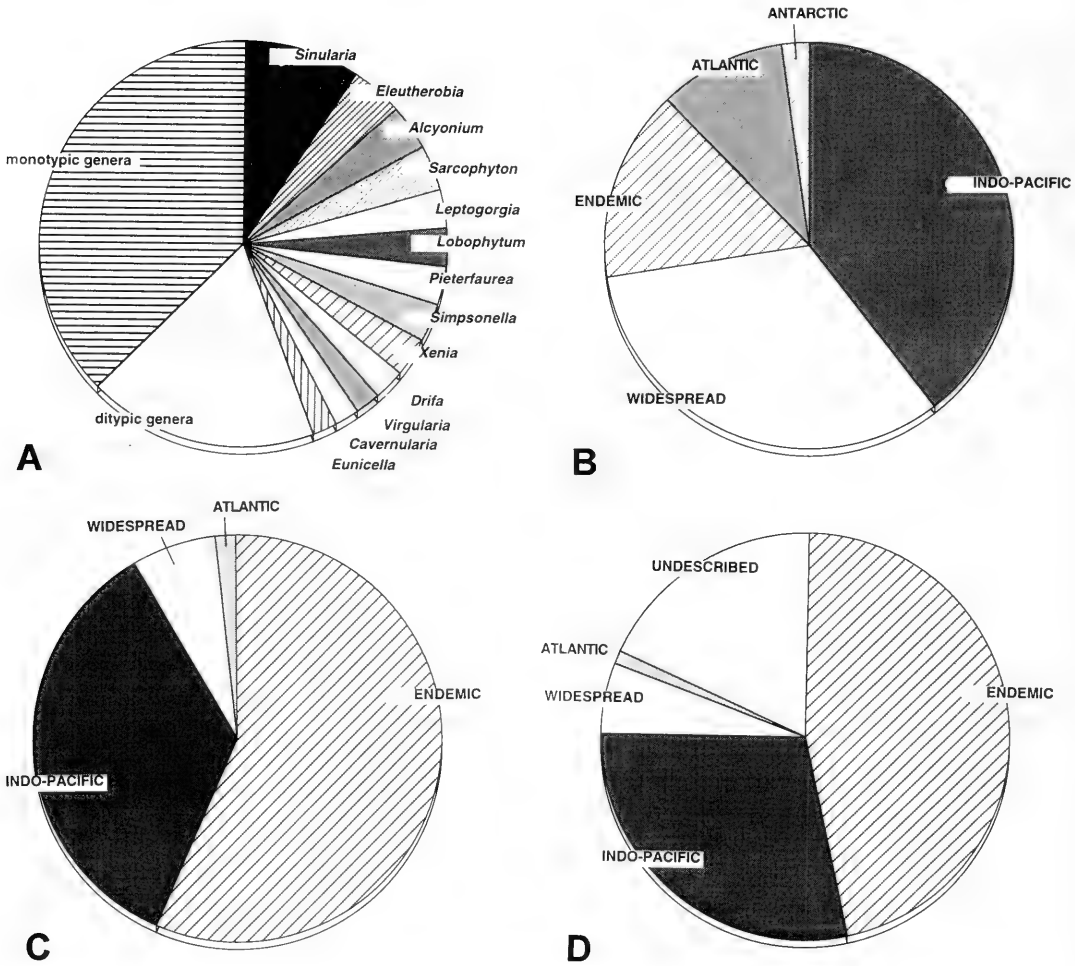

FIGURE 4. Faunistic analysis of southern African Octocorallia. A. Largest genera by number of species per genus, n = 165 (estimated number of species). B. Biogeographic affinities of the genera, n = 90 (number of genera). C. Biogeographic categories of species considered valid, n = 135 (number of valid described species). Biogeographic categories including undescribed species, n = 165 (estimated number of species).

Of the thirteen largest genera in the fauna, nine are soft corals, two are gorgonians (*Leptogorgia* and *Simpsonella*), and two are pennatulaceans (*Cavernularia* and *Virgularia*). The fauna also contains 15 ditypic genera and 62 monotypic genera. The largest genus is *Sinularia* (9.1% of the fauna), followed by *Eleutherobia* (4.3%), and *Alcyonium* and *Sarcophyton* (both 3.6%) (Table 1 and Fig. 4A).

An analysis of biogeographic affinities at the generic level shows that the Indo-Pacific represents the largest source contribution to the fauna with 40%, followed by those with widespread distributions (33%), and southern African endemic genera (15%). Atlantic (10%) and Antarctic or Southern Ocean (2%) contributions are relatively minor (Table 2 and Fig. 4B). The previous assessment (Williams 1992d:369, fig. 12A) showed similar percentages, except for the Indo-Pacific (45%) and the endemic component (10%). This change partly reflects the fact that four new endemic genera have been recognized since the last analysis was published.

Regarding identified species that are considered valid, the endemic component is by far the largest with 57%, followed by the Indo-Pacific with 35%, species with widespread distributions (7%), and

Atlantic species (1%) (Table 2 and Figure 4C). When the undescribed species that are considered valid (18%) are added to this, the endemic component shows a contribution of 46%, while the Indo-Pacific component represents 29%, with minor contributions from the widespread category (6%) and the Atlantic (1%) (Table 3 and Figure 4D).

It is presumed that if undescribed species were described and added to the data set, that the percentages shown in Figure 4C would probably reflect a relatively accurate and consistent quan-

TABLE 3. Southern African Octocorallia - comparative species richness.

Taxonomic group	Number of species
Heliporaceans	1
Stoloniferans	9
Soft corals	78
Gorgonians	43
Pennatulaceans	34
Total	165

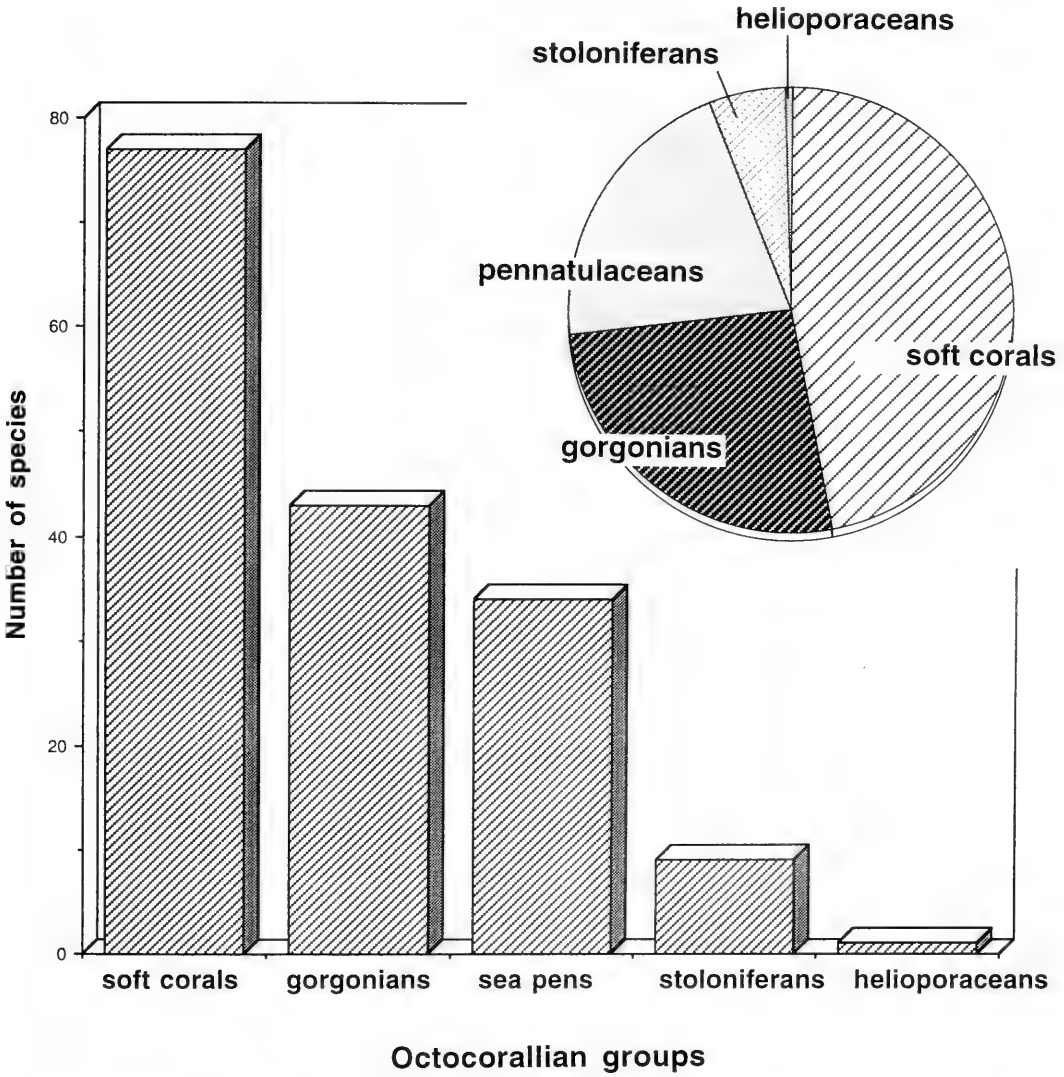

FIGURE 5. Species richness in southern African octocorals (n=165).

titative portrayal of the faunistic elements. Williams (1992d:632, fig. 6F) shows a 53.30% contribution for endemics based on estimated number of species of Octocorallia. The new assessment shows a 56.72% contribution. Therefore, a reasonable interpretation is that over one-half of the southern African octocorallian fauna is represented by endemic species.

Soft corals comprise the largest group regarding species richness (47%), followed by gorgonians (26%), pennatulaceans (21 %), stoloniferans (5%), and helioporaceans (1%) (Table 3 and Figure 5).

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LITERATURE CITED

ALDERSLADE, P. 1985. Redescription of *Acrophytum claviger* (Coelenterata: Octocorallia). The Beagle 2(1):105–113.

———. In press. Three new genera of soft corals (Coelenterata: Octocorallia) with notes on the classification of some established taxa. Zoologische Mededelingen.

BENAYAHU, Y. 1993. Corals of the South-west Indian Ocean I. Alcyonacea from Sodwana Bay, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report No. 67:1–16.

BENAYAHU, Y. AND M. H. SCHLEYER. 1995. Corals of the South-west Indian Ocean II. *Eleutherobia aurea* spec. nov. (Cnidaria, Alcyonacea) from deep reefs on the KwaZulu-Natal Coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report No. 68:1–12.

———. 1996. Corals of the South-west Indian Ocean III. Alcyonacea (Octocorallia) of Bazaruto Island, Mozambique, with a redescription of *Cladiella australis* (Macfadyen, 1936) and a description *of Cladiella kashmani* spec. nov. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report No. 69:1–22.

BRANCH, G., C. L. GRIFFITHS, M.L. BRANCH, AND L. E. BECKLEY. 1994. Two oceans, a guide to the marine life of southern Africa. David Philip, Cape Town. 360 pp.

GRASSHOFF, M. 1988. The genus *Leptogorgia* (Octocorallia: Gorgoniidae) in West Africa. Atlantide Reports 14:91–147.

———. 1991. Die von E. J. C. Esper 1788-1809 beschriebenen Anthozoa (Cnidaria). I. Die Sammlung Esper im Senckenberg-Museum. II. Octocorallia. III. Antipatharia. Senckenbergiana biol. 71(4/6):325–368.

———. 1992. Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). Courier Forschungsinstitut Senckenberg 149:1–135.

LOPEZ-GONZALEZ, P., J.-M. GILI, AND G. C. WILLIAMS. 2000. On some veretillid pennatulaceans from the eastern Atlantic and western Pacific Oceans (Anthozoa: Octocorallia), with a review of the genus *Cavernularia* Valenciennes, and descriptions of new taxa. Journal of Zoology 250(2):201–216.

OFWEGEN, L. P. VAN AND M. H. SCHLEYER. 1997. Corals of the South-west Indian Ocean V. *Leptophyton benayahui* gen. nov. and spec. nov. (Cnidaria, Alcyonacea) from deep reefs off Durban and on the KwaZulu-Natal south coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report No. 71:1–12.

RICHMOND, M. D., ed. 1997. A guide to the seashores of eastern African and the western Indian Ocean islands. Sida, Department for Research Cooperation, SAREC, Stockholm, Sweden. 448 pp.

VERSEVELDT, J. AND F. M. BAYER. 1988. Revision of the genera *Bellonella*, *Eleutherobia*, *Nidalia* and *Nidaliopsis* (Octocorallia: Alcyoniidae and Nidaliidae), with descriptions of two new genera. Zoologische Verhandelingen 245:1–131.

VERSEVELDT, J. AND L. P. VAN OFWEGEN. 1992. New and redescribed species of *Alcyonium* Linnaeus, 1758 (Anthozoa: Alcyonacea). Zoologische Mededelingen Leiden 66 (7):155–181.

VERSEVELDT, J. AND G. C. WILLIAMS. 1988. A redescription of the soft coral *Alcyonium valdiviae* Kukenthal, 1906, with the description of a new species of *Litophyton* Forsskål, 1775 from southern Africa (Octocorallia, Alcyonacea). Annals of the South African Museum 97(12):315–328.

WILLIAMS, G. C. 1986a. Morphology, systematics, and variability of the southern African soft coral *Alcyonium variabile* (J. Stuart Thomson, 1921) (Octocorallia, Alcyoniidae). Annals of the South African Museum 96(6):241–270.

———. 1986b. A new species of the octocorallian genus *Alcyonium* (Anthozoa: Alcyonacea) from southern Africa, with a revised definition of the genus. Journal of Natural History 20(1):53–63.

———. 1986c. What are corals? Sagittarius, Natural History Magazine of the South African Museum, Cape Town 1(2):11-15. [Reprinted in Underwater, Ihlane Publications (Pty) Ltd., Northway, Natal, South Africa 6:26–27].

———. 1987a. A new species of stoloniferous octocoral (Cnidaria: Alcyonacea) from the southwestern Indian Ocean. Journal of Natural History 21(1):207–218.

———. 1987b. The aberrant and monotypic soft coral genus *Malacacanthus* Thomson, 1910 (Octocorallia: Alcyoniidae), endemic to southern Africa. Journal of Natural History 21(6):1337–1346.

———. 1988. Four new species of southern African octocorals (Cnidaria: Alcyonacea) with a further diagnostic revision of the genus *Alcyonium* Linnaeus, 1758. Zoological Journal of the Linnean Society 92(1):1–26.

———. 1989a. A review of recent research on the sublittoral coral reefs of northern Natal with a provisional assessment of findings regarding the distribution of octocorals on Two-Mile Reef, Sodwana Bay. South African Journal of Science 85(3):140–141.

———. 1989b. A provisional annotated list of octocorallian coelenterates occurring on the sublittoral coral reefs at Sodwana Bay and Kosi Bay, northern Natal, with a key to the genera. South African Journal of Science 85(3):141–144.

———. 1989c. The pennatulacean genus *Cavernularia* Valenciennes (Octocorallia: Veretillidae). Zoological Journal of the Linnean Society 95(4):285–310.

———. 1989d. A comparison of the stoloniferous octocorallian genera *Bathytelesto*, *Stereotelesto*, *Rhodelinda*, and *Scyphopodium*, with the description of a new species from southeastern Africa (Anthozoa: Clavulariidae). Journal of Zoology 219(4):621–635.

———. 1990a. A new genus of dimorphic soft coral from the southwestern fringe of the Indo-Pacific (Octocorallia: Alcyoniidae). Journal of Zoology 221(1):21–35.

———. 1990b. The Pennatulacea of southern Africa (Coelenterata, Anthozoa). Annals of the South African Museum 99(4):31–119.

———. 1992a. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Annals of the South African Museum 100(3):249–358.

———. 1992b. The Alcyonacea of southern Africa. Gorgonian octocorals (Coelenterata, Anthozoa). Annals of the South African Museum 101(8):181–296.

———. 1992c. Revision of the Indo-Pacific soft coral genus *Minabea* Utinomi, 1957, with new taxa from the Indo-West Pacific. Proceedings of the California Academy of Sciences 48(1):1–26.

———. 1992d. Biogeography of the octocorallian coelenterate fauna of southern Africa. Biological Journal of the Linnean Society 46(4):351–401.

———. 1992e. Revision of the gorgonian genus *Simpsonella* (Octocorallia: Chrysogorgiidae) from the western margin of the Indo-Pacific, with the description of a new species from southeastern Africa. Zoological Journal of the Linnean Society 105:377–405.

———. 1993. Coral reef octocorals: an illustrated guide to the soft corals, sea fans, and sea pens inhabiting the coral reefs of northern Natal. Durban Natural Science Museum, Durban, South Africa. 64 pp.

———. In press. A review of the endemic southern African soft coral genus *Pieterfaurea* (Octocorallia: Nidaliidae), with descriptions of three new species. Zoologische Mededelingen, Leiden.

WILLIAMS, G. C. AND K. LINDO. 1997. A review of the octocorallian genus *Leptogorgia* (Anthozoa: Gorgoniidae) in the Indian Ocean and subantarctic, with description of a new species and comparisons with related taxa. Proceedings of the California Academy of Sciences 49(15):499–521.

WILLIAMS, G. C. AND J. ROGERS. 1989. Photographic evidence of bathyal octocorals from the Cape Basin. South African Journal of Science 85(3):191–192.

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Redescription and Reassessment of *Cadlina luarna* (Ev. Marcus and Er. Marcus, 1967), comb. nov. (Mollusca, Opisthobranchia, Doridina)

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***Inuda luarna* is the type species of the problematic genus *Inuda*, and the only species so far assigned to it. Several newly collected specimens from Baja California Sur, Mexico, allowed a redescription of this species. These specimens are clearly conspecific with the original type material of *Inuda luarna*, which was also re-examined, but show some anatomical differences. The external morphology of the living animals of this species, including the presence of mantle glands, is described for the first time.**

The anatomical features of *Inuda luarna* are very similar to those of the genus *Cadlina*, and *Inuda* is regarded as a junior synonym of *Cadlina*. *Cadlina luarna* appears to be a basal member of the *Cadlina* clade, and retains several plesiomorphies also present in *Actinocyclus*.

Resumen

***Inuda luarna* es la especie tipo del problemático género *Inuda*, y la única especie que le ha sido asignada hasta este momento. Varios ejemplares recolectados en Baja California Sur, México, han permitido redescribir esta especie. Estos especímenes son claramente conespecíficos con el material tipo de *Inuda luarna*, que también ha sido re-examinado, pero presentan algunas diferencias anatómicas. La morfología externa de los animales vivos, incluyendo la presencia de glándulas del manto, se describe por primera vez.**

Las características anatómicas de *Inuda luarna* son muy similares a las del género *Cadlina*, e *Inuda* es considerado como un sinónimo de este último. Aparentemente *Cadlina luarna* es un miembro basal de *Cadlina*, y mantiene varias características plesiomórficas que también están presentes en *Actinocyclus*.

The genus *Inuda* was originally described by Marcus and Marcus (1967) based on a single species, *Inuda luarna*, which is the type species by original designation. Since then, no additional species have been assigned to the genus *Inuda*, and the systematic position of this taxon remained uncertain.

The anatomy of *Inuda* was studied by Marcus and Marcus (1967), but the information provided was not adequate by modern standards. In addition, the external morphology and coloration of the living animals were unknown.

Most authors agreed to consider *Inuda* as a member of the Chromodorididae (Marcus and Marcus 1967; Skoglund 1991; Angulo Campillo 2000), except for Keen (1971), who placed this genus in its own family-level taxon. However, Rudman (1984), in his review of the genera of Chromodorididae, did not refer to *Inuda*.

This paper redescribes *Inuda luarna* based on newly collected material from Baja California Sur, Mexico, and attempts to determine the relationships of this taxon.

The material examined is deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ), the Museo de Historia Natural de la Universidad Autónoma de Baja California Sur (MHNUABCS) and the National Museum of Natural History, Washington D. C. (USNM).

Species Description

Genus *Cadlina* Bergh, 1879

Acanthochila Mörch, 1869, suppressed by Opinion 812 (ICZN, 1967). Type species: *Doris laevis* Linnaeus, 1767.
Echinochila Mörch, 1869, suppressed by Opinion 812 (ICZN, 1967). Type species: *Doris laevis* Linnaeus, 1767.
Cadlina Bergh, 1878 (*nomen nudum*).
Cadlina Bergh, 1879. Type species: *Doris repanda* Alder and Hancock, 1842 (= *Cadlina laevis* Linnaeus, 1767), by original designation.
Juanella Odhner, 1922. Type species: *Juanella sparsa* Odhner, 1922, by monotypy.
Inuda Ev. Marcus and Er. Marcus, 1967. Type species: *Inuda luarna* Ev. Marcus and Er. Marcus, 1967, by original designation (new synonym).

Cadlina luarna (Ev. Marcus and Er. Marcus, 1967)
Figs. 1–5

Inuda luarna Marcus and Marcus, 1967:182–184, figs 38–44; Keen, 1971:826; Abbott, 1974:356; Farmer, 1980:104; Skoglund, 1991:12; González, 1993:247; Angulo Campillo, 93–94, fig. 41.

Type Material. — Lectotype (here selected): Puerto Peñasco, Sonora, Mexico, 23 mm preserved length, contracted and dissected, leg. P. Pickens (USNM 678405).

Remarks on the Type Material. — There is a single specimen of *Inuda luarna* deposited at USNM. It was collected from Puerto Peñasco, Sonora, Mexico (type locality) by P. Pickens, and has several labels. One of the labels, handwritten by Eveline Marcus, only includes the name of the species. Another label, handwritten by a different person (probably the collector) contains the numbers "14.22." A more modern label, printed with USNM format indicates the name of the species, locality, collector and that this specimen is the holotype of *Inuda luarna*. The two remaining labels (also USNM format) just repeat the taxonomic status and the registration number of the specimen.

Marcus and Marcus (1967) mentioned that they examined two specimens for the description of this species, and did not select either of them to be the holotype. Thus, the specimen deposited at the USNM collection is not the holotype, but one of the two syntypes of *Inuda luarna*. Since the other specimen is untraceable, and its identity could not be confirmed, we designate the available syntype as the lectotype of this species.

Additional Material Examined. — Calerita, Bahía de La Paz, Baja California Sur, Mexico, 23 February 1997, 2 specimens 55–60 mm long, leg. O. Angulo Campillo (MHNUABCS-INV 1808). Calerita, Bahía de La Paz, Baja California Sur, Mexico, 10 April 1999, 3 specimens 20–44 mm preserved length, leg. O. Angulo Campillo (CASIZ 121103). Ensenada de los Muertos, southeast of La

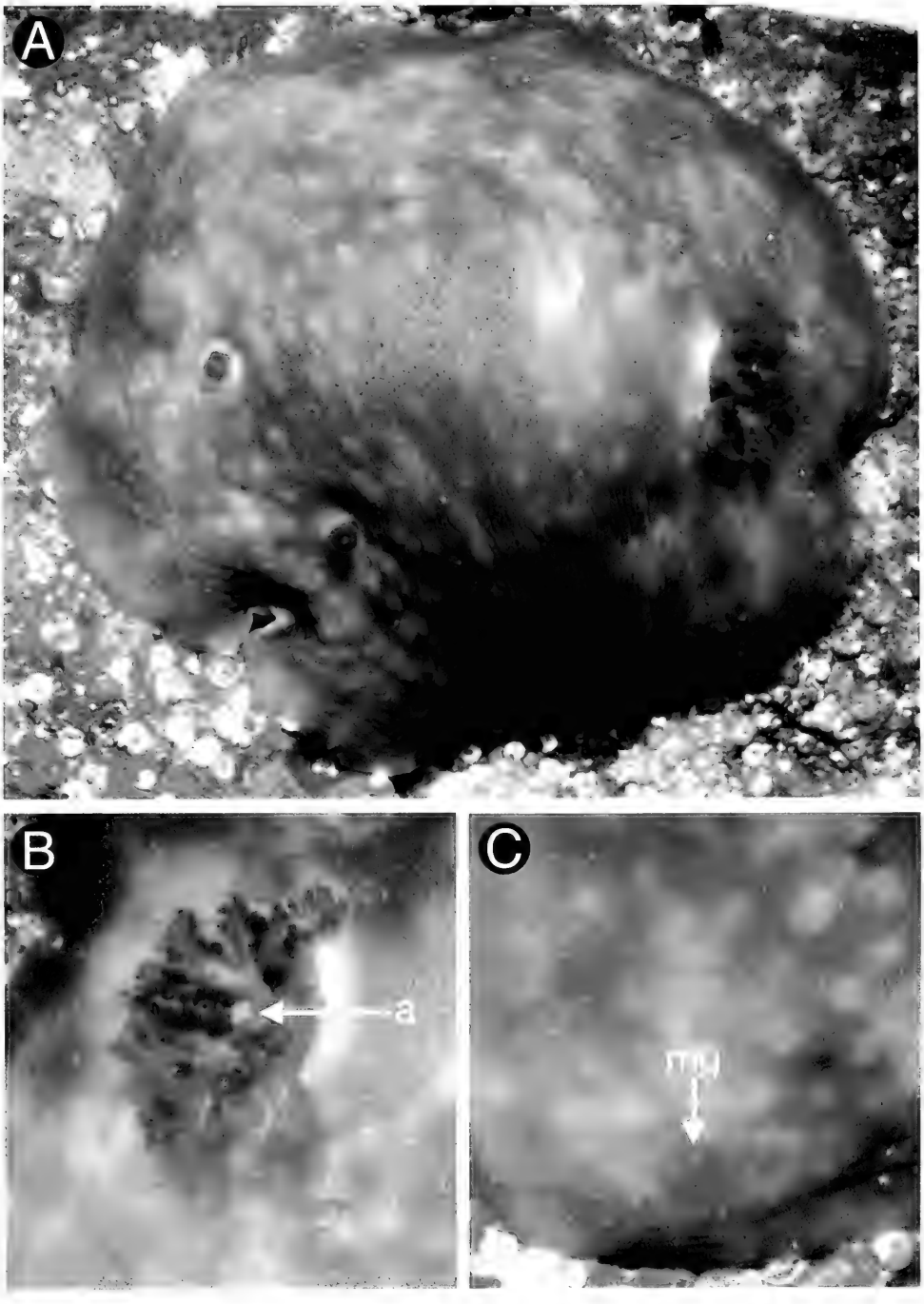

FIGURE 1. Living animal of *Cadlina luarna* from Baja California Sur, Mexico (CASIZ 121104). A. Dorsal view; B. Detail of the gill; C. Detail of the border of the mantle showing mantle glands. Abbreviations: a, anal papillae; mg, mantle gland.

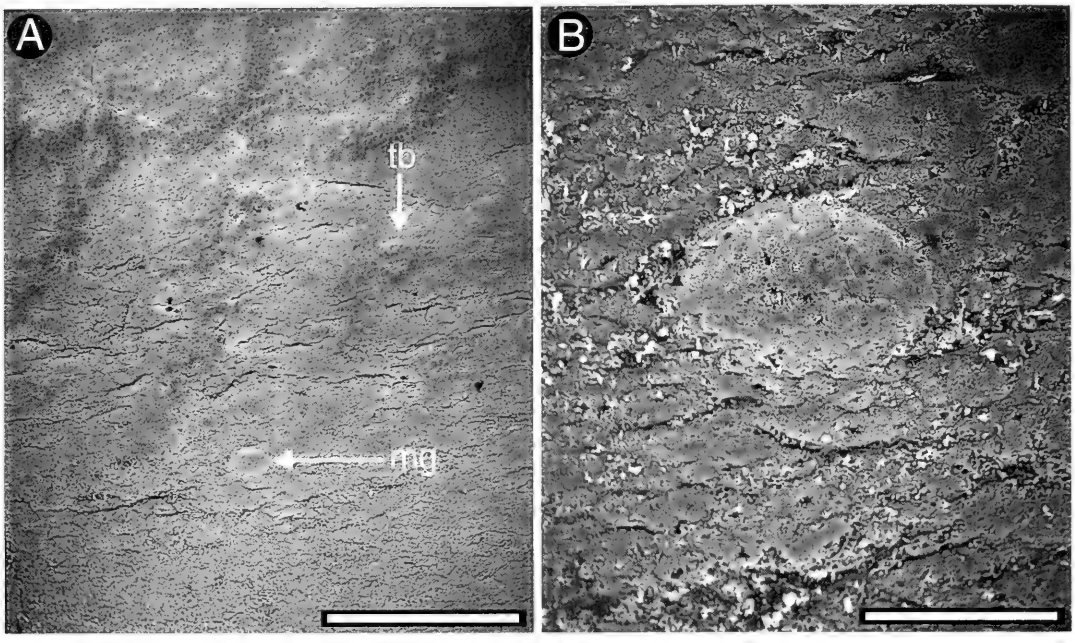

FIGURE 2. Scanning electron micrographs of *Cadlina luarna* (CASIZ 121104). A. Dorsal surface, scale bar = 600 μm. B. Detail of a mantle gland, scale bar = 100 μm. Abbreviations: mg, mantle gland; tb, tubercle.

Paz, Baja California Sur, Mexico, 11 March 2000, 1 specimen 42 mm preserved length, leg. O. Angulo Campillo (CASIZ 121104). Mazatlán, Sinaloa, Mexico, 8 December 1932, 1 specimen 36 mm preserved length, collector unknown (CASIZ 073360).

EXTERNAL MORPHOLOGY. — The body shape is oval to rounded (Fig. 1A). The center of the dorsum is elevated. There are numerous, low and rounded tubercles (Fig. 2A) that are more densely concentrated on the mantle margin. On the mantle margin there are several rows of small mantle glands (Figs 1C, 2B). They are conical in shape and irregularly arranged. The gill is composed of nine bipinnate branchial leaves (Fig. 1B). The perfoliate rhinophores have 12 lamellae. The anal papillae is situated in the center of the circlet of branchial leaves (Fig. 1B).

The foot sole is narrow, about half as wide as the mantle margin. The anterior border of the foot is grooved but not notched. The oral tentacles are short and wide, having a deep notch on their ventral side (Fig. 3G).

The background color of the body is pale brown. There are numerous pale creamy white, rounded blotches, that are more densely arranged on the mantle margin. These blotches may be fused together forming larger creamy white areas. The center of the dorsum is covered with minute dark brown spots. The branchial sheath is pale creamy white, and the rhinophoral sheaths translucent gray. The gill and rhinophores are dark brown, with the rachis translucent pale gray. The mantle glands are bright orange.

ANATOMY. — **Digestive system**. The oral tube has three strong muscles that attach to the body wall (Fig. 3D). The muscular buccal bulb is about four times shorter than the oral tube and has two additional muscles attached. The jaws are composed of a number of bifid elements, about 20 μm long (Fig. 4D). The radular formula is 135 × 65.1.65 in one specimen examined (CASIZ 121104). The rachidian teeth have a single central cusp, and one or two large denticles on each side (Fig. 4A). The mid-lateral teeth have a strong, short cusp, and one or two triangular denticles on the outer side (Fig. 4B). The outermost teeth are elongate, having one to three small denticles (Fig. 4C). The esophagus

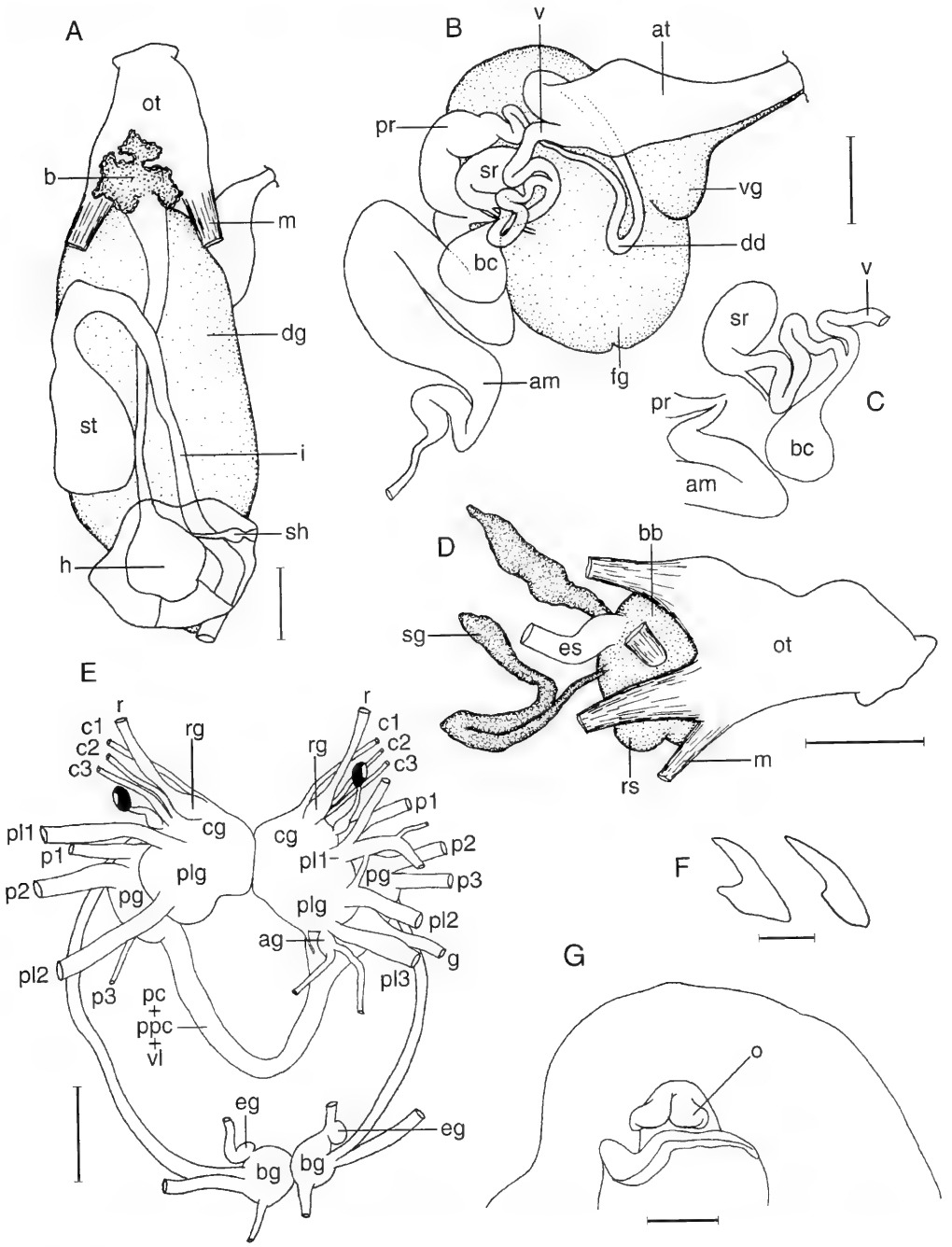

FIGURE 3. Anatomy of *Cadlina luarna*. A. Dorsal view of the internal organs (CASIZ 121104), scale bar = 2 mm; B. Reproductive system (CASIZ 121104), scale bar = 1 mm; C. Detail of several reproductive organs (CASIZ 121104), scale bar = 1 mm; D. Central nervous system (CASIZ 121104), scale bar = 1 mm; E. Lateral view of the anterior portion of the digestive system (CASIZ 121104), scale bar = 1 mm; F. Penial hooks (CASIZ 121104), scale bar = 10 μm. G. Ventral view of the mouth area (CASIZ 121103), scale bar = 5 mm. Abbreviations: ag, abdominal ganglion; am, ampulla; at, genital atrium; b, blood gland; bb, buccal bulb; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; dd, deferent duct; dg, digestive gland; eg, esophageal ganglion; es, esophagus; fg, female glands; h, heart; i, intestine; m, retractor muscle; o, oral tentacle; ot, oral tube; p, pedal nerve; pc, pedal commissure; ppc, parapedal commissure; pg, pedal ganglion; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; rg, rhinophoral ganglion; rs, radular sac; sg, salivary gland; sh, syrinx; sr, seminal receptacle; st, stomach; v, vagina; vg, vestibular gland; vl, visceral loop.

opens into the proximal end of the buccal bulb. Near this point two large salivary glands attach to the buccal bulb. The esophagus is short, connecting distally to the digestive gland. The stomach is oval and connects distally to the long intestine, which runs almost straight down to the anal opening (Fig. 3A).

Reproductive system. The ampulla is very long and convoluted (Fig. 3B). It branches into the short oviduct and the prostate. The prostate is short and tubular, but well differentiated. It narrows into the deferent duct, which expands again into the muscular ejaculatory portion. The penis is armed with several rows of hooks (Fig. 3F). These hooks have an elongate cusp about 20 μm long and a shorter base. There is an undifferentiated vestibular gland near the distal aperture of the female glands. The vagina is long and convoluted. At mid-length it branches into a duct that connects to the seminal receptacle and the uterine duct (Fig. 3C). The uterine duct is short and thin, and opens near the center of the female gland mass. The seminal receptacle is slightly oval, almost as large as the pyriform bursa copulatrix.

Central nervous system. The cerebral and pleural ganglia of each side are fused together and are distinct from the pedal ganglia (Fig. 3E). On the right side, there is a distinct abdominal ganglion, connected to the right pleural ganglion. Optical, rhinophoral, buccal, and esophageal ganglia are also present and well differentiated. The pedal and parapedeal commissures are enveloped together by connective tissue with the visceral loop. There are three cerebral nerves leading from each cerebral ganglion and three pedal nerves leading from each pedal ganglion. From the pleural ganglia lead two nerves on the right one and three nerves on the left one.

Circulatory and excretory systems. There is a large heart that connects to a single, ramified blood gland by the aorta. The blood gland is situated covering the central nervous system. The syrinx is small and pyriform.

GEOGRAPHIC RANGE. — This species was previously known from Puerto Peñasco, Sonora, Mexico, which is situated in the north part of the Mar de Cortés (Sea of Cortez). The present paper provides the second record of this species, from the La Paz area, Baja California Sur, and Mazatlán, Sinaloa, and constitutes a range extension of approximately 900 km (Fig. 5). So far this species appears to be endemic to the Gulf of California.

DISCUSSION

Inuda luarna was originally described from Puerto Peñasco, Sonora, Mexico, based on two preserved specimens collected by P. Pickens. The original description of this genus and species (Marcus and Marcus 1967), includes anatomical descriptions and information on the external coloration of the preserved specimens. According to these authors, *Inuda luarna* is a whitish species mottled with brown, due to numerous dots of dark brown pigment. The rhinophores are brown and the gill is darker than the notum. This coloration is very similar to our specimens from Baja California Sur, which are brown with creamy white areas and dark brown spots on the center for the dorsum. In addition, the gill and rhinophores of our specimens are dark brown. Anatomically, the radula described for the Sonora specimens is identical to that of the specimens from Baja California Sur. However, there are some anatomical differences in the reproductive system between the specimens examined by Marcus and Marcus (1967) and our own material. Our specimens have a smaller prostate and a larger ampulla than the animal illustrated by Marcus and Marcus (1967, fig. 43). These differences could be due to a different state of maturity in the specimens studied or to intraspecific variation. Despite these differences, there is no doubt that all the animals belong to the same species.

Marcus and Marcus (1967) considered that the genus *Inuda* resembled *Cadlina* Bergh, 1879, but according to these authors the well-developed prostate of *Inuda* "makes it impossible to allocate these genera in the same subfamily." Thus they erected the new subfamily Inudinae (family Chromodorididae) to accomodate *Inuda luarna*. The subsequent references to this genus and species

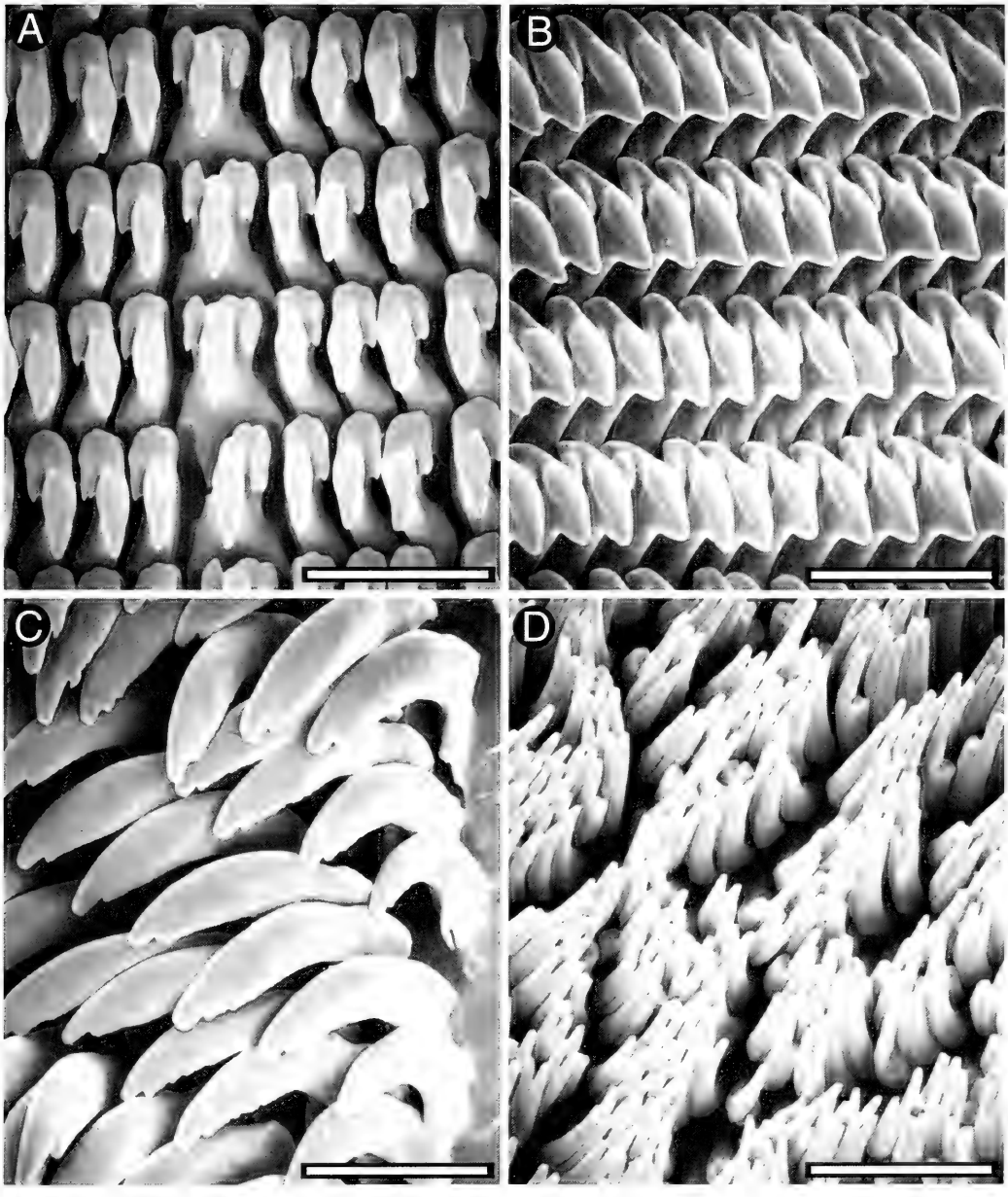

FIGURE 4. Scanning electron micrographs of *Cadlina luarna* (CASIZ 121104). A. Innermost radular teeth, scale bar = 43 μm; B. Mid-lateral radular teeth, scale bar = 38 μm; C. Outermost radular teeth, scale bar = 30 μm. D. Jaw elements, scale bar = 23.1 μm.

by Keen (1971), Abbott (1974), Skoglund (1991) and González (1993) are based on the paper by Marcus and Marcus (1967) and not on newly-collected animals. Farmer (1980) re-examined and illustrated the type material of this species but did not provide additional anatomical information. Angulo Campillo (2000) collected additional specimens of this species, which are also re-examined here, and provided the first data on the external coloration of the living animals. All these authors agreed to maintain the genus *Inuda* as valid.

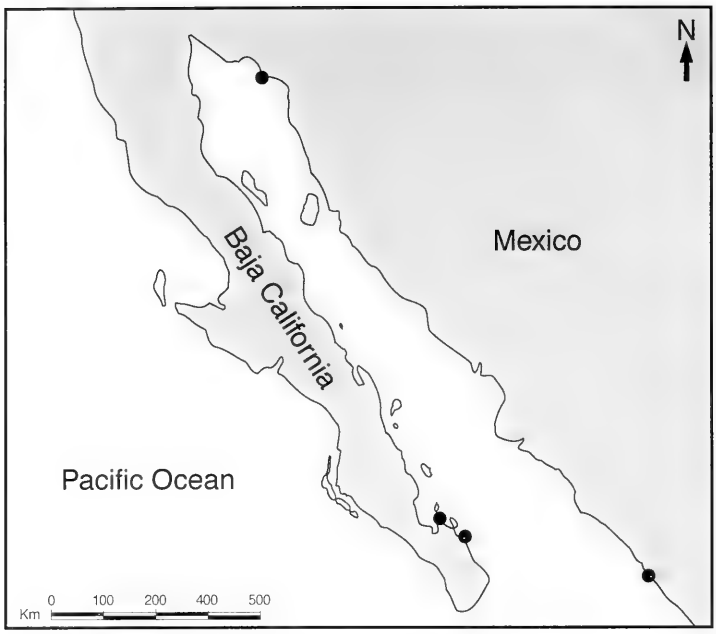

FIGURE 5. Geographic range of *Cadlina luarna* in Mexico.

The presence of mantle glands in *Inuda luarna* clearly places this species in the family Chromodorididae (see Rudman 1984; Gosliner and Johnson 1994; Gosliner and Johnson 1999). These glands were overlooked by Marcus and Marcus (1967), who worked with preserved material. Of all members of Chromodorididae, *Inuda* most resembles *Cadlina*. Rudman (1984) reviewed the genus *Cadlina*, which according to him is characterized by having a heavily spiculose mantle with small tubercles. The mantle glands are large, forming a submarginal row around the mantle. The branchial leaves are simple with a tendency to bipinnate and tripinnate branching. The radula is narrow with the number of teeth in the half-row being approximately equal to one-third the number of rows of teeth. The denticles on the teeth are normally few and large. There is a rachidian tooth with no central cusp, but on each side of the midline there are one or two large denticles. Most species have a penis armed with minute hooks. *Inuda luarna* fits this diagnosis, except for the presence of a large, central cusp in the rachidian teeth. In our opinion, this small difference does not justify the maintenance of a different genus, and therefore *Inuda* is here synonymized with *Cadlina*.

Cadlina luarna is clearly different from other species of the genus. The main diagnostic feature is the presence of a well-developed prostate, a character used by Marcus and Marcus (1967) to place this species in a different genus and subfamily. Other species of *Cadlina* present on the west coast of the Americas are *Cadlina flavomaculata* MacFarland, 1905, *Cadlina sparsa* (Odhner, 1921), *Cadlina limbaughorum* Lance, 1962, *Cadlina luteomarginata* MacFarland, 1966, and *Cadlina modesta* MacFarland, 1966. All these species clearly differ from *Cadlina luarna* in having a white or pale creamy white background body color (see Behrens 1991).

Gosliner and Johnson (1994) hypothesized that Actinocyclidae is the sister clade to the Chromodorididae. Rudman (1984) recognized *Cadlina* to be basal within the Chromodorididae, being the sister group to a clade containing the genera *Glossodoris* Ehrenberg, 1831, *Verconia* Pruvot-Fol, 1931 and *Ardeadoris* Rudman, 1984. Recently Gosliner and Johnson (1999) provided a parsimony-based phylogeny of the Chromodorididae and found *Cadlina* to be the most basal member of a clade containing *Tyrinna* Bergh, 1898 and *Cadlinella* Thiele, 1931, which is the sister group to the rest of the Chromodorididae. The genus *Cadlina* possesses several plesiomorphic features such as spiculose body, rachidian teeth, serial seminal receptacle (Gosliner and Johnson 1999). In addition, *C. luarna* retains plesiomorphies present in *Actinocyclus*, but absent in other members of *Cadlina*. These include a rounded body with an elevated dorsal hump and a well-developed prostate. The arrangement and size of the mantle glands of *C. luarna* also appear to be plesiomorphic. They are smaller than in most members of *Cadlina*, and disorganized, whereas in other species of *Cadlina* they are arranged in a single submarginal row. Another possible plesiomorphy of *C. luarna* is the presence of a large, cen-

tral cusp in the rachidian teeth. According to this particular external morphology and anatomy, *Cadlina luarna* appears to be a very basal member of *Cadlina*, which is also basal within the Chromodorididae. Therefore, this species is extremely important to the study of the phylogenetic relationships within the Chromodorididae and the basal clades of Cryptobranchia.

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LITERATURE CITED

ABBOTT, R. T. 1974. American Seashells. The marine Mollusca of the Atlantic and Pacific coasts of North America, 2nd ed. Van Nostrand Reinhold, New York. 663 pp. + 24 pls.

ANGULO CAMPILLO, O. J. 2000. Moluscos opistobranquios (Mollusca: Opisthobranchiata) de Baja California Sur, México. B.A. Dissertation, Universidad Autónoma de Baja California Sur, La Paz. 176 pp.

BEHRENS, D. W. 1991. Pacific coast nudibranchs. A guide to the opisthobranchs Alaska to Baja California. Sea Challengers, Monterey, California. 107 pp.

FARMER, W. M. 1980. Sea-slug gastropods. Farmer Enterprises, Tempe, Arizona. 177 pp.

GONZÁLEZ, N. E. 1993. Moluscos endémicos del Pacífico de México. Pp. 223–252 *in* Biodiversidad marina y costera de México, S. I. Salazar-Vallejo and N. E. González, eds. Comisión Nacional de Biodiversidad y CIQRO, México D. F. 865 pp.

GOSLINER, T. M. AND R. F. JOHNSON. 1999. Phylogeny of *Hypselodoris* (Nudibranchia: Chromodorididae) with a review of the monophyletic clade of Indo-Pacific species, including descriptions of twelve new species. Zoological Journal of the Linnean Society 125:1–114.

GOSLINER, T. M. AND S. JOHNSON. 1994. Review of the genus *Hallaxa* (Nudibranchia: Actinocyclidae) with descriptions of nine new species. The Veliger 37:155–191.

ICZN, 1967. Opinion 812. *Cadlina* Bergh, 1878 (Gastropoda): validate under the plenary powers. Bulletin of Zoological Nomenclature 24:91–92.

KEEN, A. M. 1971. Sea shells of tropical West America. Marine mollusks from Baja California to Peru, 2nd ed. Standford University Press, Stanford, California. 1064 pp. + 22 pls.

MARCUS, EVELINE AND ERNEST MARCUS. 1967. American opisthobranch mollusks. Studies in Tropical Oceanography 6:1–256, pl. 1.

RUDMAN, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zoological Journal of the Linnean Society 81:115–273.

SKOGLUND, C. 1991. Additions to the Panamic Province Opisthobranchia (Mollusca) literature 1971 to 1990. The Festivus 22 (Supplement 1):1–27.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Genus and Species of Soft Coral (Octocorallia: Alcyoniidae) from South Africa

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A new genus and species of recently discovered soft coral is described from the shallow-water temperate reefs of the eastern Cape Province of South Africa. The new taxon is somewhat similar to the southern African endemic soft coral *Malacacanthus capensis* (Hickson, 1900). However, the new species has sclerites and appears to be monomorphic, while *Malacacanthus capensis* does not have sclerites and has dimorphic polyps.

In the past twelve years, several new endemic genera of southern African octocorals have been described. Included here are the soft coral genera *Pieterfaurea* Verseveldt and Bayer (1988), *Verseveldtia* Williams (1990), *Leptophyton* Ofwegen and Schleyer (1997), *Lampophyton* Williams (2000), and *Dimorphophyton* Williams (2000); and the pennatulacean genus *Amphibelemnon* López-González, Gili, and Williams (2000).

This paper reports the discovery and description of an additional new genus and species of soft coral from the South Coast of South Africa.

METHODS

An examination of recently collected material was made for this study. The material was collected by SCUBA and preserved in 70% ethanol. Sclerites were isolated using sodium hypochlorite. Micrographs were made using a Kodak MDS100 digital video camera and a Wild M400 photomicroscope. Scanning electron micrographs were made on a Hitachi S-510 scanning electron microscope. Abbreviations used in the text are as follows: CAS (California Academy of Sciences, San Francisco), CRRF (Coral Reef Research Foundation, Palau).

A small specimen of *Malacacanthus capensis* (Hickson, 1900), collected from the same locality as the new taxon, was examined for comparative purposes. Collection data for this specimen is as follows: CAS 118498, (Sta. No. SAFR 365), Republic of South Africa, Cape Province, off Port Elizabeth, Algoa Bay, White Sands 6, 20 m depth, 26 February 1999, collected by John Starmer with aid of SCUBA, one whole specimen 15 mm in length.

SYSTEMATIC ACCOUNT

Family Alcyoniidae Lamouroux, 1812

Lanthanocephalus gen. nov.

TYPE SPECIES. — *Lanthanocephalus clandestinus* sp. nov. by original designation and monotypy.

DIAGNOSIS. — Growth form upright, unbranched, cylindrical to clavate. Polypary retractile into distal region of stalk. Polyps monomorphic and retractile, without calyces. Surface coenenchymal sclerites: small spindles and radiates.

ETYMOLOGY. — The new generic name is derived from the Greek, *lanthano* (to escape notice; unknown or unseen) and *kephale* (a head); in reference to the ability of the polypary to retract into the distal portion of the stalk.

Lanthanocephalus clandestinus sp. nov.
Figs. 1–6

TYPE MATERIAL. — Holotype: CAS 118500 (Sta. No. SAFR 365), Republic of South Africa, Cape Province, off Port Elizabeth, Algoa Bay, White Sands 6, on exposed rock, 20 m depth, 26 February 1999, collected by John Starmer with aid of SCUBA, one whole specimen 16 mm in length. Paratype: CAS 118499, same data as holotype, one 22 mm long specimen cut longitudinally into two halves.

DIAGNOSIS. — Alcyoniid soft corals with upright, unbranched, cylindrical to clavate growth form. Stalk rigid with rough surface texture. Polyps retractile, without calyces, presumably monomorphic, restricted to distal portion of the soft coral. Polypary retractile into distal portion of stalk. Retracted polypary conical to mammiform. Polypary sclerites: small spindles with pronounced conical tubercles 0.11–0.18 mm long. Stalk sclerites: radiates 0.04–0.09 mm in length. All sclerites colorless. Wet-preserved color dark brown.

DESCRIPTION OF THE HOLOTYPE. — **Growth form and size**. The holotype is 16 mm in length and 6 mm in width at its widest portion. The growth form is unbranched and cylindrical to clavate (Figs. 1B; 2C).

Stalk and Polypary. The stalk is relatively rigid and exhibits a tough, somewhat crenulated surface texture. The polypary is retractile into the distal region of the stalk, forming a conical or mammiform distal terminus (Figs. 1A, B; 2A–C). The retracted polypary comprises 5–12% of the total body length of the paratype and holotype (Fig. 1A, B).

Polyps. A detailed study of the polyps is not possible since the polypary is almost completely retracted into the distal region of the stalk. However, examination of the tip of the polypary of the holotype, as well as the interior of the longitudinally sectioned paratype, shows that the polyps are fully retractile (without calyces) and presumably monomorphic, since no siphonozooids are visible. Microscopic examination of the longitudinally sectioned paratype as well as a transverse section through the retracted polypary did not reveal any evidence for the presence of siphonozooids.

Sclerites. The surface coenenchyme of the distal tip of the polypary contains short robust spindles with pronounced, mostly conical tubercles (Fig. 3B). They vary in length from 0.11–0.18 mm. Also present are some radiates. The sclerites of the surface coenenchyme of the stalk are radiates: mostly eight-radiates, and irregularly-shaped forms that are presumably derived from radiates (Fig. 3A, 4, 5). They vary in length from 0.04–0.09 mm. The interior of the polypary and stalk appears not to contain sclerites or at most they are very sparse. All sclerites are colorless.

Color of wet-preserved material. Exterior dark chocolate brown throughout; interior uniform reddish brown.

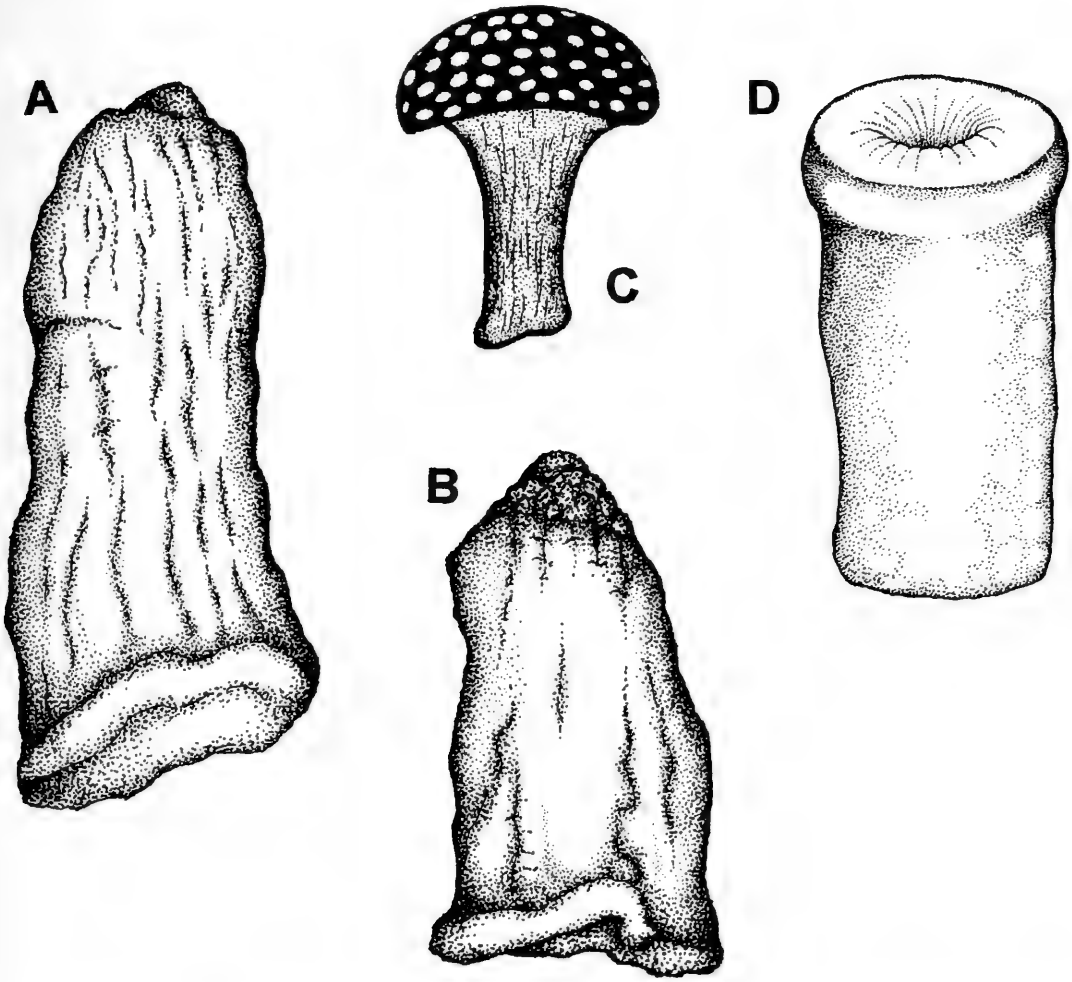

FIGURE 1. A–B. *Lanthanocephalus clandestinus* gen. and sp. nov. A. Paratype (CAS 118499); 22 mm in length. B. Holotype (CAS 118500); 16 mm in length. C–D. *Malacacanthus capensis* (Hickson, 1900). C. Specimen 80 mm long with retracted polyps, showing capitulate growth form. D. Specimen 75 mm long with retracted polypary. C and D after Williams (1987:1339, fig. 2).

DISTRIBUTION. — Algoa Bay, eastern Cape Province, South Africa (Fig. 6): 20 m in depth.

ETYMOLOGY. — The specific epithet of the new species is derived from the Latin, *clandestinus* (hidden or secret); in reference to the retractile polyps, and the ability of the polypary to withdraw into the distal portion of the stalk.

REMARKS. — The new taxon is at present known only from the holotype and paratype. Both of these specimens have the polypary tightly retracted into the distal region of the stalk. It is therefore not possible to provide detailed descriptions of the polypary or polyps.

DISCUSSION

Lanthanocephalus clandestinus gen. and sp. nov. is sympatric with, and most closely resembles, the southern African endemic soft coral *Malacacanthus capensis* (Hickson, 1900). The latter species has been illustrated or described, or at least mentioned, in several publications under various

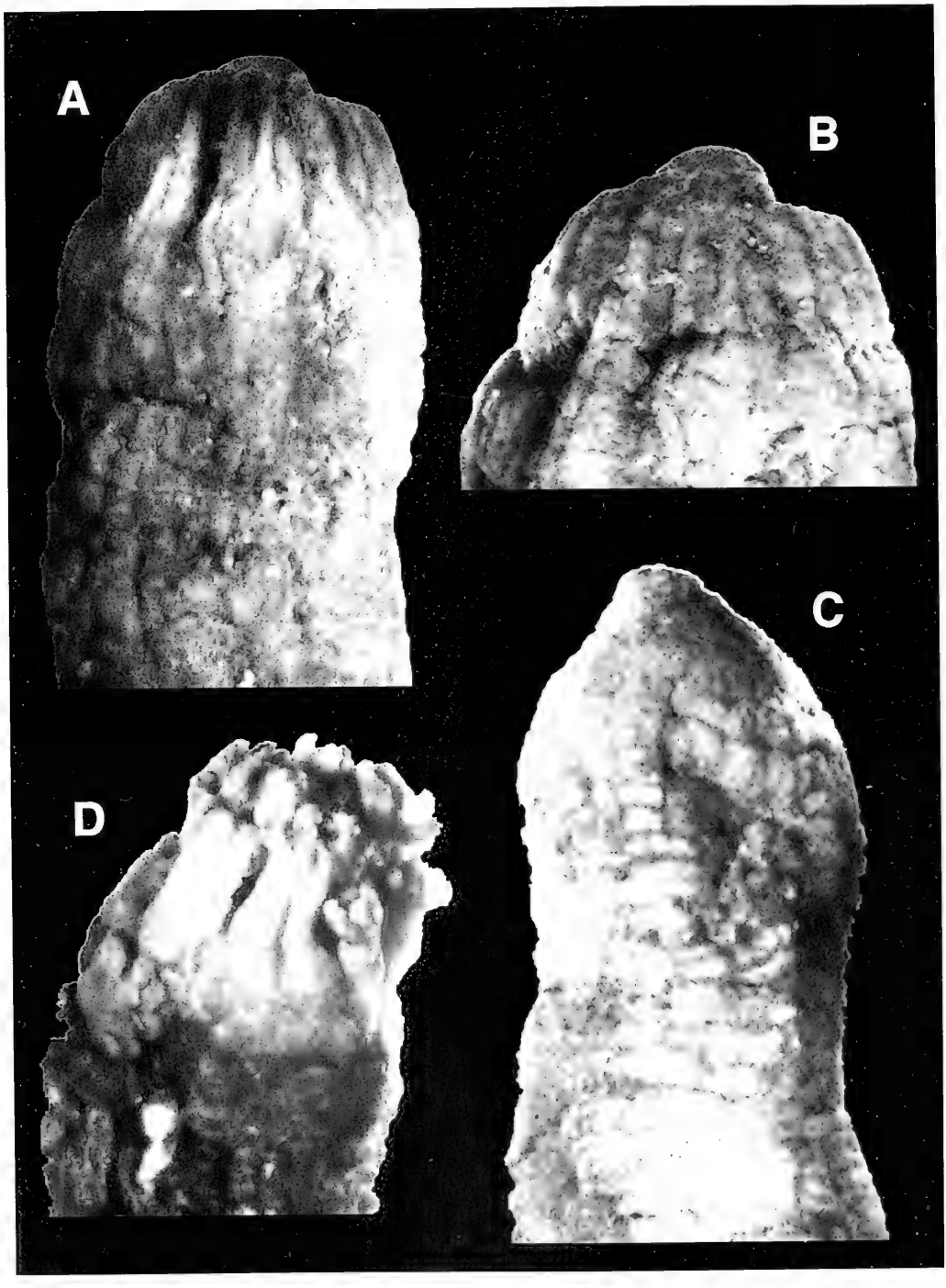

FIGURE 2. *Lanthanocephalus clandestinus* gen. and sp. nov. A. Micrograph of distal portion of wet-preserved paratype with retracted polypary; length of portion shown – 14 mm. B. Micrograph of distal tip of wet-preserved paratype; length of portion shown – 5 mm. C. Micrograph of distal portion of wet-preserved holotype with retracted polypary; length of portion shown – 14 mm. D. *Malacacanthus capensis* (Hickson, 1900). Micrograph of distal portion of wet-preserved specimen showing partly expanded polyps; length of portion shown – 10 mm.

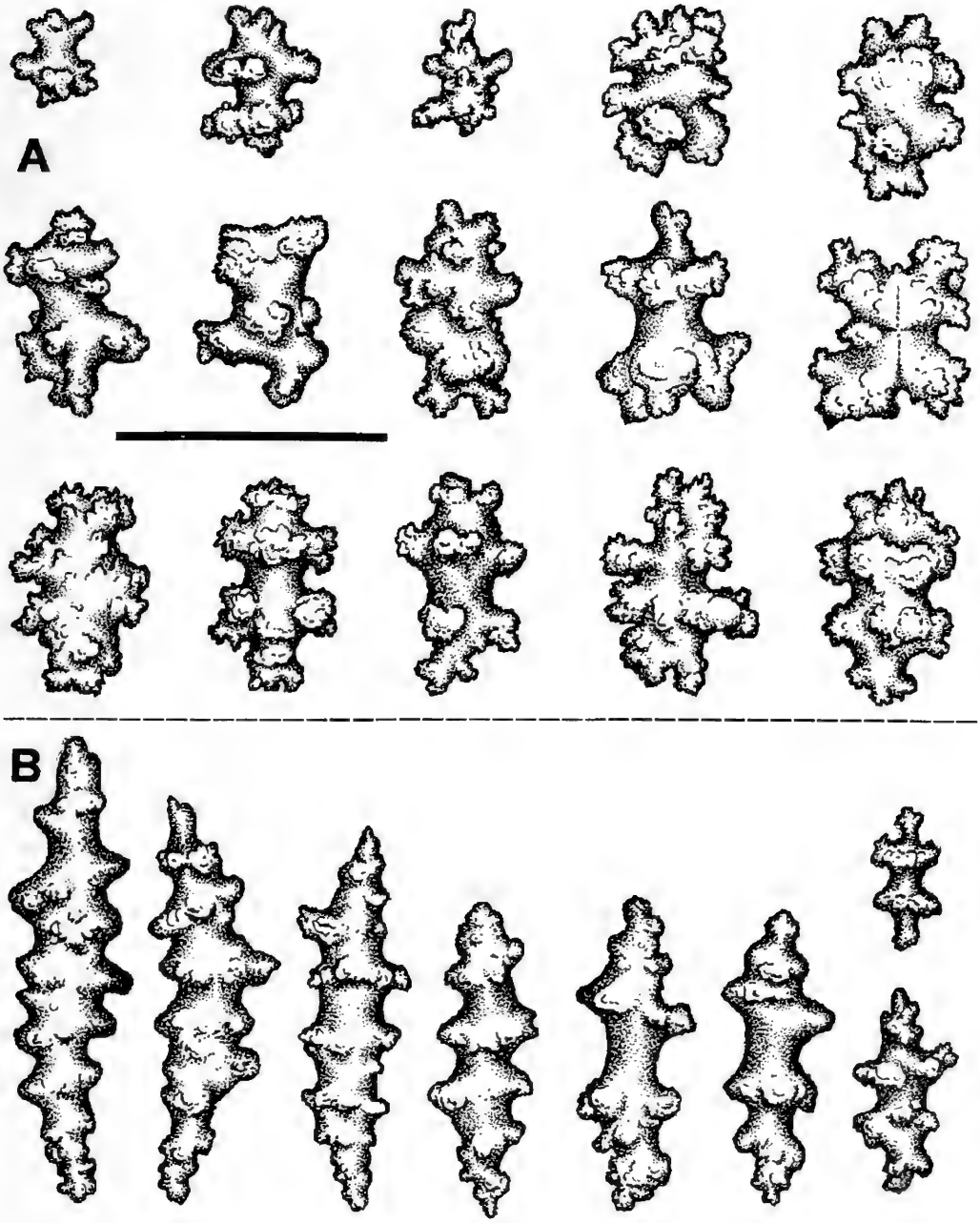

FIGURE 3. *Lanthanocephalus clandestinus* gen. and sp. nov. Variation in sclerites from the surface coenenchyme of the holotype. A. Sclerites from the stalk. B. Sclerites from the distal tip of the polypary. Scale bar for both A and B = 0.1 mm.

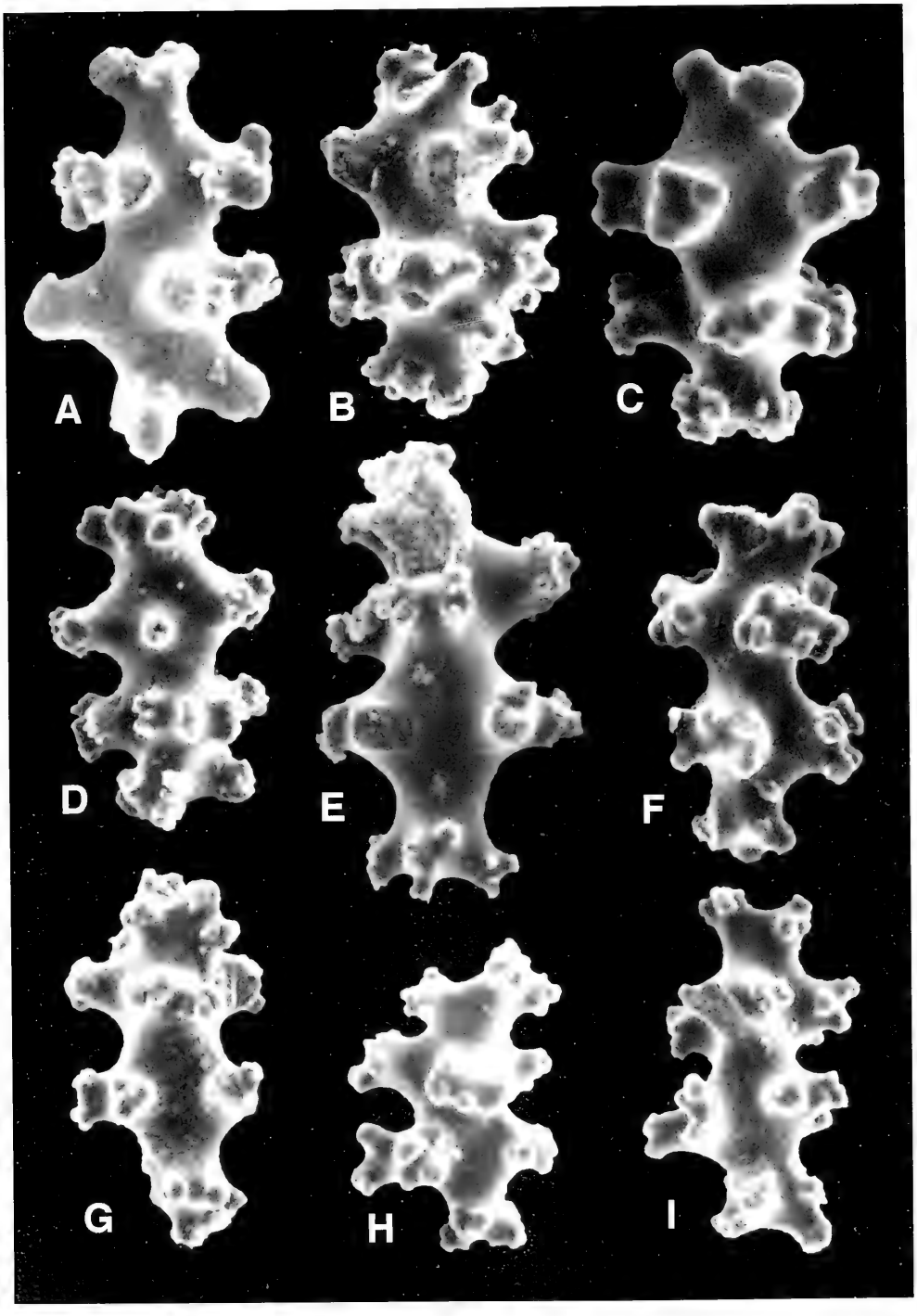

FIGURE 4. *Lanthanocephalus clandestinus* gen. and sp. nov. Scanning electron micrographs of sclerites from the surface coenenchyme of the holotype. Lengths: A. 0.07 mm. B. 0.09 mm. C. 0.07 mm. D. 0.08 mm. E. 0.09 mm. F. 0.08 mm G. 0.08 mm. H. 0.07 mm. I. 0.09 mm.

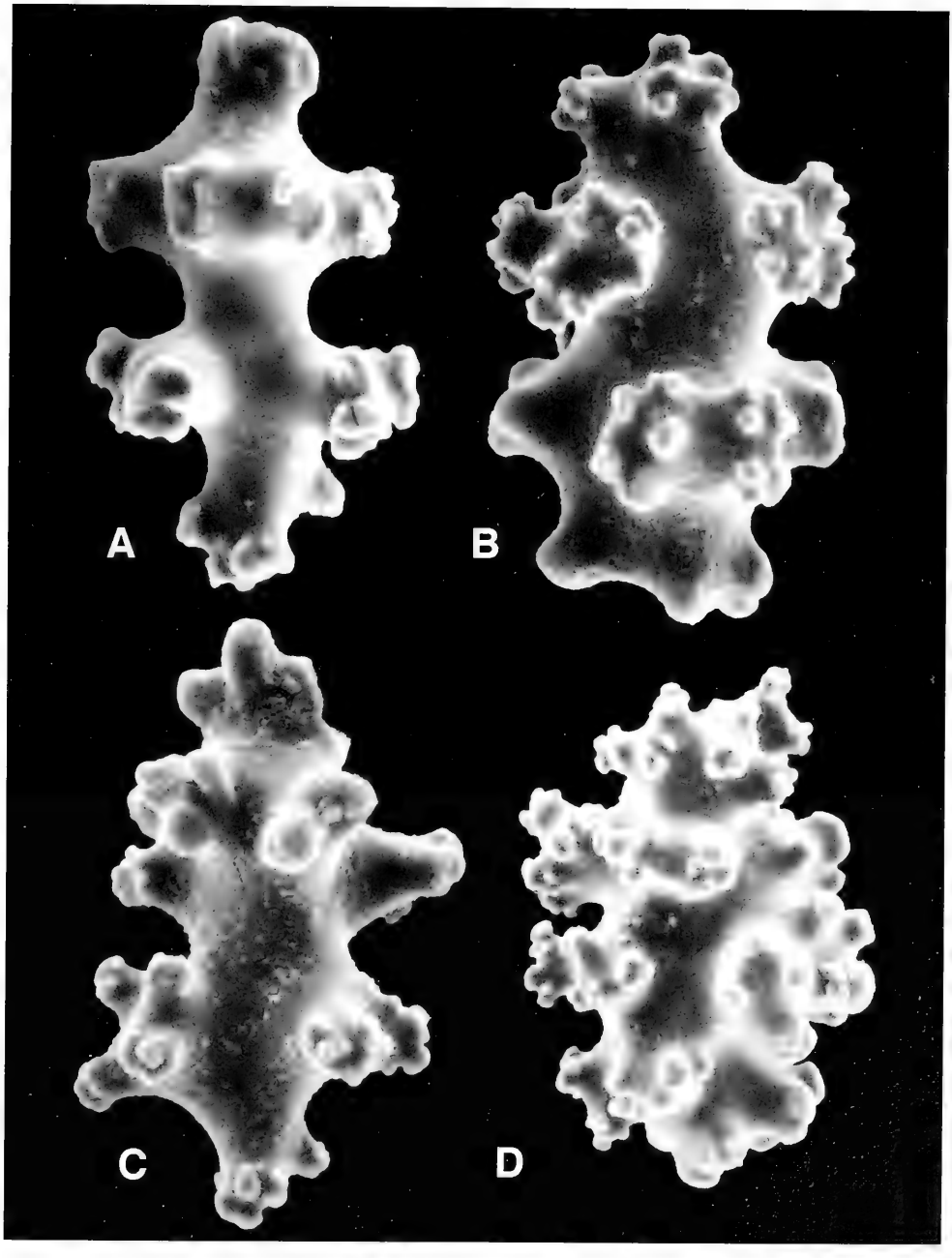

FIGURE 5. *Lanthanocephalus clandestinus* gen. and sp. nov. Scanning electron micrographs of sclerites from the surface coenenchyme of the holotype. Lengths: A. 0.06 mm. B. 0.08 mm. C. 0.08 mm. D. 0.09 mm.

binomens. These names include *Heteroxenia capensis*, *Xenia uniserta*, *Malacacanthus rufus*, *Heteroxenia uniserta*, and *Malacacanthus capensis*, as well as *Malacacanthus*, and the vernacular "sunburst soft coral." The relevant publications include Bayer (1981), Branch and Branch (1981), Branch et al. (1994), Broch (1939), Day et al. (1970), Hickson (1900, 1931), Kükenthal (1906), J. S.

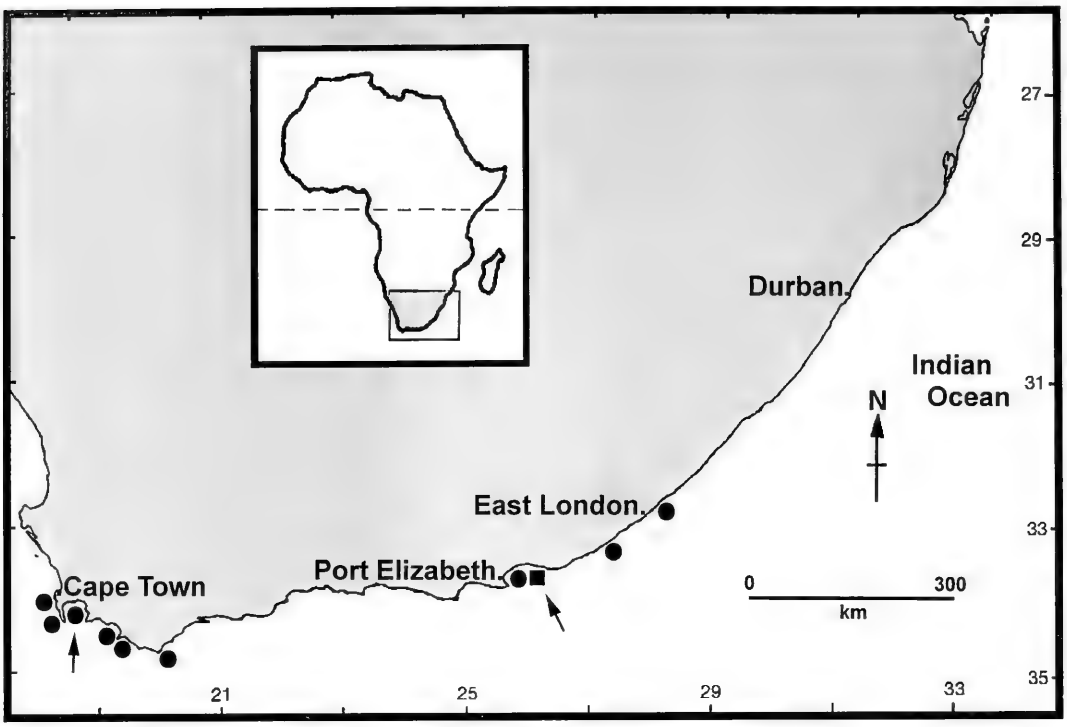

FIGURE 6. Map of southern Africa showing distributions of *Lanthanocephalus clandestinus* gen. and sp. nov. (■), and *Malacacanthus capensis* (Hickson, 1900) (●). Arrows represent type localities.

Thomson (1910, 1921, 1924), Tixier-Durivault (1954), Williams (1987, 1990, 1992a, 1992b), and Williams and Alderslade (1999).

Lanthanocephalus clandestinus and *Malacacanthus capensis* share one important morphological character besides having sympatric distributions (Fig. 6; Table 1). Both taxa have polyparies capable of retraction into the stalk (Figs. 1D, 2B). However, they differ in three significant characters. *Lanthanocephalus clandestinus* has sclerites, does not have a cuticle surrounding the stalk, and appears to be monomorphic since siphonozooids are not evident in the two retracted specimens. The capitate *Malacacanthus capensis* (Fig. 1C), on the other hand, does not have sclerites, a reddish orange cuticle covers the epidermis of the stalk, and it is conspicuously dimorphic. In light of these observations, it is therefore justified to differentiate the two taxa into separate genera. A 15-mm, wet-preserved specimen of *Malacacanthus capensis* (CAS 118498) was examined for comparison. The autozooids are partly expanded and measure 3–4 mm in length (Fig. 2D). Minute siphonozooids are apparent between the autozooids, each approximately 0.3 mm in diameter.

Ceratocaulon wandeli Jungersen, 1898, from subarctic waters, also has a distinct horny cuticle surrounding the stalk as in *Malacacanthus capensis*, but is monomorphic and cylindrical in shape as is *Lanthanocephalus clandestinus*. It differs from these two taxa however, in having sclerites that resemble minute ovals or rounded platelets.

Species of the paralcyoniid genus *Studeriotes* Thomson and Simpson, 1909, can also withdraw the polyparium into the stalk and are also monomorphic, but they differ in having sclerites that are predominantly large robust spindles, numerous fingerlike branches that compose the polyparium, and polyps with conspicuous calyces comprised of abundant sclerites. Pertaining to *Studeriotes mirabilis* (J. A. Thomson, 1908) from the Andaman Islands, J. A. Thomson and Simpson (1909:8, figs. 3–4)

TABLE 1. Comparison of *Lanthanocephalus clandestinus* and *Malacacanthus capensis*.

	Lanthanocephalus clandestinus	*Malacacanthus capensis*
Maximum length	22 mm	80 mm
Growth form	cylindrical to clavate	cylindrical to capitate
Sclerites	radiates ≤ 0.09 mm, colorless; spindles ≤ 0.18, colorless	absent
Distribution	Port Elizabeth	Cape Town to East London
Depth range	20 m	10–93 m
Polyps	presumably monomorphic	dimorphic
Stalk cuticle	absent	present
Polypary shape (wet preserved)	conical to mammiform	usually capitate
Polypary retraction into stalk	yes	yes
Wet-preserved color	dark brown	orange polyps, reddish brown stalk

clearly illustrate the fully retracted polyparium within the trunklike stalk, as well as the conspicuous calyces of the retracted polyps.

ACKNOWLEDGMENTS

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LITERATURE CITED

BAYER, F. M. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. Proceedings of the Biological Society of Washington 94:902–947.

BRANCH, G. AND BRANCH, M. 1981. Living Shores of Southern Africa. C. Struik (Pty) Ltd., Cape Town. 272 pp.

BRANCH, G. M., C. L. GRIFFITHS, M. L. BRANCH AND L. E. BECKLEY. 1994. Two oceans—A guide to the marine life of southern Africa. David Philip, Cape Town and Johannesburg. 360 pp.

BROCH, H. 1939. Some South African shallow water octactinians. Kungliga Fysiografiska sällskapets i Lund förhandlingar 9(6):1–32.

DAY, J. H., J. G. FIELD AND M. J. PENRITH. 1970. The benthic fauna and fishes of False Bay, South Africa. Transactions of the Royal Society of South Africa 39(1):1–108.

HICKSON, S. J. 1900. The Alcyonaria and Hydrocorallinae of the Cape of Good Hope. Marine Investigations in South Africa 1:67–96.

———. 1931. The alcyonarian family Xeniidae, with a revision of the genera and species. Great Barrier Reef Expedition 4(5):137–179.

JUNGERSEN, H. F. E. 1892. *Ceratocaulon Wandeli*, en ny nordisk Alcyonide. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 1891(1892):234–242.

KÜKENTHAL, W. 1906. Alcyonacea. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898–1899 13(1) Lieferung 1:1–111.

LÓPEZ-GONZÁLEZ, P. J., J.-M. GILI, AND G. C. WILLIAMS. 2000. On some veretillid pennatulaceans from the eastern Atlantic and western Pacific Oceans (Anthozoa: Octocorallia), with a review of the genus *Cavernularia*, and descriptions of new taxa. Journal of Zoology 250(2):201–216.

OFWEGEN, L. P. VAN AND M. H. SCHLEYER. 1997. Corals of the South-west Indian Ocean V. *Leptophyton benayahui* gen. nov. and spec. nov. (Cnidaria, Alcyonacea) from deep reefs off Durban and on the KwaZulu-Natal south coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report No. 71:1–12.

THOMSON, J. A. 1908. Note on a remarkable alcyonarian *Studeria mirabilis*, g. et sp. n. Journal of the Royal Microscopical Society 1908:675–681.

THOMSON, J. A. AND J. J. SIMPSON. 1909. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. II. The Alcyonarians of the littoral sea. Calcutta, The Indian Museum. 312 pp.

THOMSON, J. S. 1910. The Alcyonaria of the Cape of Good Hope and Natal. Alcyonacea. Transactions of the Royal Society of Edinburgh 47(3):549–589.

———. 1921. South African Alcyonacea. Transactions of the Royal Society of South Africa 9:149–175.

———. 1924. Charts and comparisons of the distribution of South African Alcyonaria. With a statement of some of the problems of their dispersal. Transactions of the Royal Society of South Africa 11:45–84.

TIXIER-DURIVAULT, A. 1954. Les octocoralliaires d'Afrique du sud (I. Alcyonacea). Bulletin du Muséum national d'Histoire naturelle (2)26(3):385–390.

VERSEVELDT, J. AND F.M. BAYER. 1988. Revision of the genera *Bellonella*, *Eleutherobia, Nidalia* and *Nidaliopsis* (Octocorallia: Alcyoniidae and Nidaliidae), with descriptions of two new genera. Zoologische Verhandelingen 245:1–131.

WILLIAMS, G. C. 1987. The aberrant and monotypic soft coral genus *Malacacanthus* Thomson, 1910 (Octocorallia: Alcyoniidae) endemic to southern Africa. Journal of Natural History 21:1337–1346.

———. 1990. A new genus of dimorphic soft coral from the south-western fringe of the Indo-Pacific (Octocorallia: Alcyoniidae). Journal of Zoology, London 221:21–35.

———. 1992a. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Annals of the South African Museum 100(3):249–358.

———. 1992b. Biogeography of the octocorallian coelenterate fauna of southern Africa. Biological Journal of the Linnean Society 46(4):351–401.

———. 2000. Two new genera of soft corals (Anthozoa: Alcyoniidae) from South Africa, with a discussion of diversity and endemism in the southern African octocorallian fauna. Proceedings of the California Academy of Sciences 52(6):65–75.

WILLIAMS, G. C. AND P. ALDERSLADE. 1999. Revisionary systematics of the western Pacific soft coral genus *Minabea* (Octocorallia: Alcyoniidae), with descriptions of a related new genus and species from the Indo-Pacific. Proceedings of the California Academy of Sciences 51(7):337–364.

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The Hexandrous Species of *Topobea* (Melastomataceae)

by

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A key and updated geographic and taxonomic notes are presented for the five known species comprising the hexandrous clade of *Topobea*. *Topobea arboricola*, a Panamanian endemic described and illustrated here, is distinguished by its six stamens per flower, 2-locular ovary, elliptic to ovate leaves with a caudate-acuminate to long-attenuate apex, and unappendaged anther connectives.The need for recording field data on taxonomically useful floral and fruit characters is emphasized.

RESUMEN

Se describe una especie nueva, *Topobea arboricola* de Panamá. Se proveen descripciones, notas sobre distribución y fenología, y discusiones referentes a las afinidades de las cinco especies de *Topobea* que tienen seis estambres. También se presenta una clave y mapas de la distribución para todas ellas. El color y tamaño de los pétalos y estambres, forma de los poros de las anteras, y el número de lóculos en el ovario son a menudo caracteres taxonómicos muy útiles en *Topobea*.

Topobea, with approximately 70 species, is a berry-fruited genus of mostly shrubby epiphytes and hemiepiphytes restricted to wet forests of tropical America. Over 55 species occur in the biodiversity hotspot extending from Costa Rica south to Colombia.

Traditionally, *Topobea* has been defined by its 6-merous isomerous flowers with 12 stamens, 6-locular ovary, and elongate anther thecae with broad confluent apical pores. Although this characterization applies to a majority of species in *Topobea*, discovery of new species in southern Central America in the past two decades has necessitated a broadened circumscription of the genus to accommodate the accumulation of new and unusual species and a reconsideration of generic limits between *Topobea* and its sister genus *Blakea* (Almeda 1990).

I here provide a review of the most specialized evolutionary line within the genus that I informally refer to as the hexandrous species. These species, which are largely centered in Panama, share several synapomorphic characters that include: (1) 6-merous flowers with six stamens, each of which is attached to the hypanthial torus opposite a calyx lobe; (2) subsessile or short-pedunculate flowers; and (3) 2-locular or 4-locular completely inferior ovaries. Until recently, most of the species treated here were known from few collections. A study of additional material generated by my recent field work and that of colleagues now makes it possible to emend and augment morphological and distributional information for described species, propose another new species in this alliance, and provide a preliminary assessment of interspecific relationships within this well-defined clade.

Understanding intraspecific variation in woody epiphytes has always been a challenge. Many epiphytic species of Melastomataceae are composed of widely dispersed, low density populations. This coupled with spotty sampling by collectors and the fragmentary preservation or loss of critical

floral characters on dried specimens has contributed to the paucity of adequate study material. Petal shape and color, stamen number, morphology of anther pores, and ovary locule number are essential characters for the delimitation of species in *Topobea*. Unfortunately, some of these characters are difficult to evaluate once specimens have been pressed and dried. Ideally, notes on these characters should be recorded in the field, if the preservation of flowers and fruits in a liquid medium is not possible.

Key to the Hexandrous Species of *Topobea*

1a. Leaves sessile and cordate-clasping; calyx lobes oblong-ovate; petals white, 8–13 mm long; anthers subulate, 5–7 mm long . . . . . *T. cordata*

1b. Leaves distinctly petioled, varying from elliptic-ovate to obovate or subrotund; calyx lobes lance-triangular; petals pink, 4.5–7 mm long; anthers bluntly oblong, 2–2.5 mm long.

2a. Ovary 4-locular, anther pores dorsally inclined at the truncate apex; anther connective elevated dorso-basally into a blunt spurlike appendage . . . . . *T. crassifolia*

2b. Ovary 2-locular, anther pores somewhat ventrally inclined at the truncate apex; anther connective unappendaged dorso-basally (if connective is appendaged then uppermost cauline nodes beset with spreading tufts of hairs).

3a. Leaves thick and leathery when dry, the apex obtuse to rounded, the abaxial surface glandular punctate.

4a. Hemiepiphytic shrub with adventitious roots on the cauline internodes; uppermost cauline nodes beset with caducous tufts of spreading hairs; leaves ovate-elliptic to subrotund; Cerro Jefe, Panama . . . *T. hexandra*

4b. Terrestrial shrub without adventitious roots on the cauline internodes; uppermost cauline nodes lacking tufts of spreading hairs; leaves obovate to oblanceolate; Cerro Tute, Panama . . . . . *T. caliginosa*

3b. Leaves not thick and leathery when dry, the apex caudate-acuminate, the abaxial surface not glandular punctate . . . . . *T. arboricola*

Species Description

1. *Topobea arboricola* Almeda, sp. nov.

Fig. 1

Type. — PANAMA. Bocas del Toro/Chiriquí border: windswept cloud forest on slopes and valleys of the Cerro Colorado region, elev. 1450 m, 27 Jan. 1989, *Almeda et al. 6456* (holotype: CAS!; isotypes: MO!, PMA!).

Frutex epiphyticus. Lamina 3.8–7.1 × 1.6–3.9 cm elliptica vel ovata apice caudato-acuminata vel attenuata basi acuta vel rotundata, 3–5-nervata papyracea et integra, nervis secundariis nervulisque invisis; petioli 0.9–2.8 cm longi. Flores 6-meri sessiles vel subsessiles in quoque nodo superiori singuli; bracteae omnino liberae; bracteae exteriores 2.5–4 × 1.5–4 mm, ellipticae vel ovato-ellipticae apice acuto vel obtuso; bracteae interiores 2–3 × 2–3 mm, ovatae vel suborbiculares apice rotundato. Calycis tubus 0.5 mm longus, lobis 2 mm longis. Petala 5 × 3.5 mm obovata vel obovato-elliptica apice obtuso. Antherae 6, ca. 2 × 0.5 mm oblongae inter se non cohaerentes; connectivum nec prolongatum nec appendiculatum. Ovarium 2-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Epiphytic shrub to 1.5 m tall. Uppermost branchlets glabrous, somewhat compressed and bluntly two-edged; older branches becoming ± rounded with nodular leaf scars. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 0.9–2.8 cm long; mature blades papyraceous, 3.8–7.1 cm long and 1.6–3.9 cm wide, elliptic to ovate, apex caudate-acuminate to attenuate, base acute varying to rounded, margin entire, 3–5-nerved, the outermost intramarginal pair often depressed and inconspicuous, the transverse secondary veins typically not elevated or conspicuous. Flowers erect, solitary in leaf axils of uppermost branches, sessile, subsessile, or with short (1–2 mm) ill-defined peduncles formed by the compressed bases of the outer floral bracts. Floral

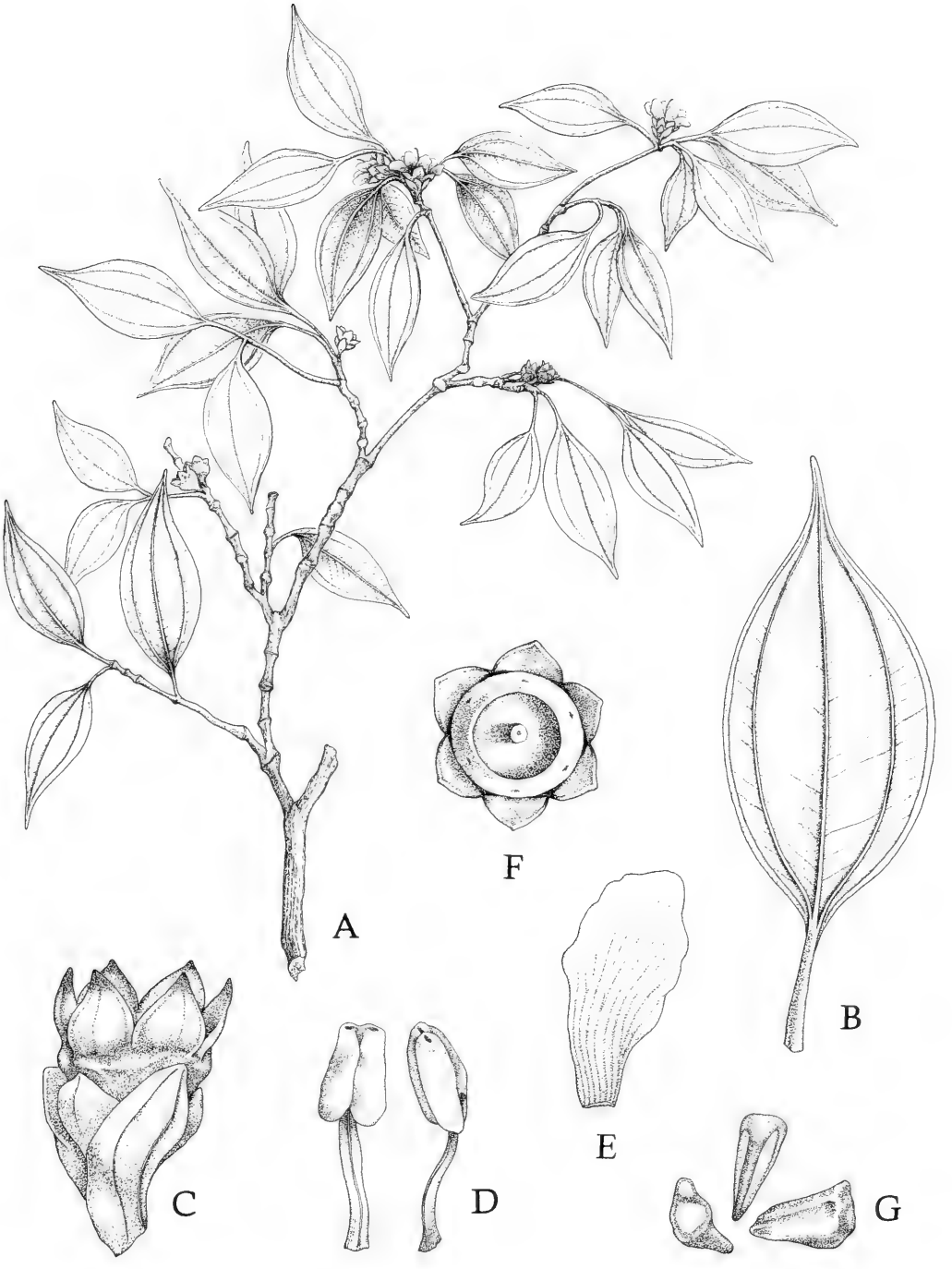

FIGURE 1. *Topobea arboricola* Almeda. A. habit, × ca. ½; B. representative leaf (abaxial surface), × 1; C. young fruiting hypanthium with decussate floral bracts, × 6; D. stamens, ventral view (left) and partial profile view (right), × 7; E. petal (adaxial surface), × 7; F. berry (top view) showing calyx lobes, ovary summit, and torus with staminal filament scars, × 4; G. seeds, × 15. (A, B from the holotype; C-E from *McPherson 12813*, MO; F, G from *McPherson 7739*, CAS.)

bracts free and entire, glabrate or sparingly beset abaxially (mostly toward the apex) with a lanate or stellulate-lepidote, coppery brown indument; outer bracts 2.5–4 × 1.5–4 mm, concave, elliptic to elliptic-ovate, apex acute to obtuse; inner bracts 2–3 × 2–3 mm, depressed-ovate to semicircular, apex rounded. Calyx tube 0.5 mm long; calyx (in fruit) erect, 2 mm long and 2 mm wide basally, deltoid to deltoid-ovate, entire but callose-thickened along the interlobe sinuses, sometimes sparingly beset at the abaxial apex with an indument like that of the floral bracts. Petals 6, sparingly beset with disc-shaped glands when dry, 5 × 3.5 mm, translucent pink, obovate to elliptic-obovate, apex obtuse, entire. Stamens 6, filaments complanate and glabrous, 2.5–3 mm long; anthers 2 mm long, 0.5 mm wide, pale yellow, oblong with two broad pores at the truncate apex; connective barely thickened and unappendaged. Ovary completely inferior, 2-locular, apex glabrous, stylar scar evident but not elevated into a prominent cone or stylar collar. Style somewhat declinate and sigmoid apically, glabrous, 5 mm long; stigma punctiform. Berry 4–6 × 4.5–6 mm, white at maturity. Seeds cuneate to narrowly deltoid, 1 mm long, tan with a smooth, glossy testa.

PHENOLOGY. — Flowering in February, May, July and August; fruiting specimens have been collected in July, December, and January.

DISTRIBUTION. — Known only from wet cloud forests of western Panama from Valle de la Sierpe (Chiriquí) east to Cerro Tute (Veraguas) at 1000–1500 m (Fig. 2).

PARATYPES. — PANAMA. Bocas del Toro/Chiriquí border: above Fortuna dam, along divide trail, ca. 8°45′N, 82°15′W, 4 Dec. 1985, *McPherson 7739* (CAS, MO). Chiriquí: Fortuna dam area, along Quebrada Bonita to E of road, 8°45′N, 82°13′W, 8 Feb. 1984, *Churchill et al. 4759* (MO); Valle de la Sierpe, en dirección SE a lo largo de Quebrada Bonita, 17 May 1987, *Correa et al. 5092* (MO, PMA); Fortuna dam area, N of reservoir, ridge along continental divide and southward from Quebrada de Arena, Aug. 1984 (no day given), *D'Arcy & Todzia 15959* (CAS, MO). Veraguas: trail to Reserva Biológica Serranía de Tute about 0.7 km beyond the Escuela Agricola Río Piedra just outside of Santa Fé, 18 Feb. 1996, *Almeda et al. 7622* (CAS, MO, PMA, US); Distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2676* (CAS, SCZ); Distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2657* (CAS, SCZ); vicinity of Cerro Arizona-Tute, above Santa Fé and Altos Piedra, along trail to summit, 8°30′N, 81°10′W, 28 Jul. 1988, *McPherson 12813* (MO).

DISCUSSION. — *Topobea arboricola* appears to be a true epiphytic shrub that never has root contact with the ground. It is distinguished by its 2-locular ovary, comparatively long petioles (0.9–2.8 cm), elliptic to ovate leaves with a caudate-acuminate to long-attenuate apex, and short oblong anthers with unappendaged connectives.

Of the three hexandrous species of *Topobea* with 2-locular ovaries, *T. arboricola* is most similar to *T. caliginosa*. The latter differs in being a terrestrial shrub and in having obovate leaves with an obtuse to rounded apex, shorter petioles (0.5–1 cm), longer floral peduncles (3–5 mm), and abaxial foliar surfaces that are inconspicuously glandular-punctate.

All collections of *T. arboricola* come from a scattering of localities along the Cordillera Central of Panama. For an epiphyte with a dispersed population structure, this species is remarkably uniform in vegetative and reproductive characters. An exception to this homogeneity is exhibited by the Cerro Tute population which has uniformly ovate leaves (vs. elliptic leaves).

ETYMOLOGY. — The epithet for this species, *arboricola*, is derived from the Latin word, arbor, meaning dwelling in a tree, in reference to its epiphytic habit in the forest canopy.

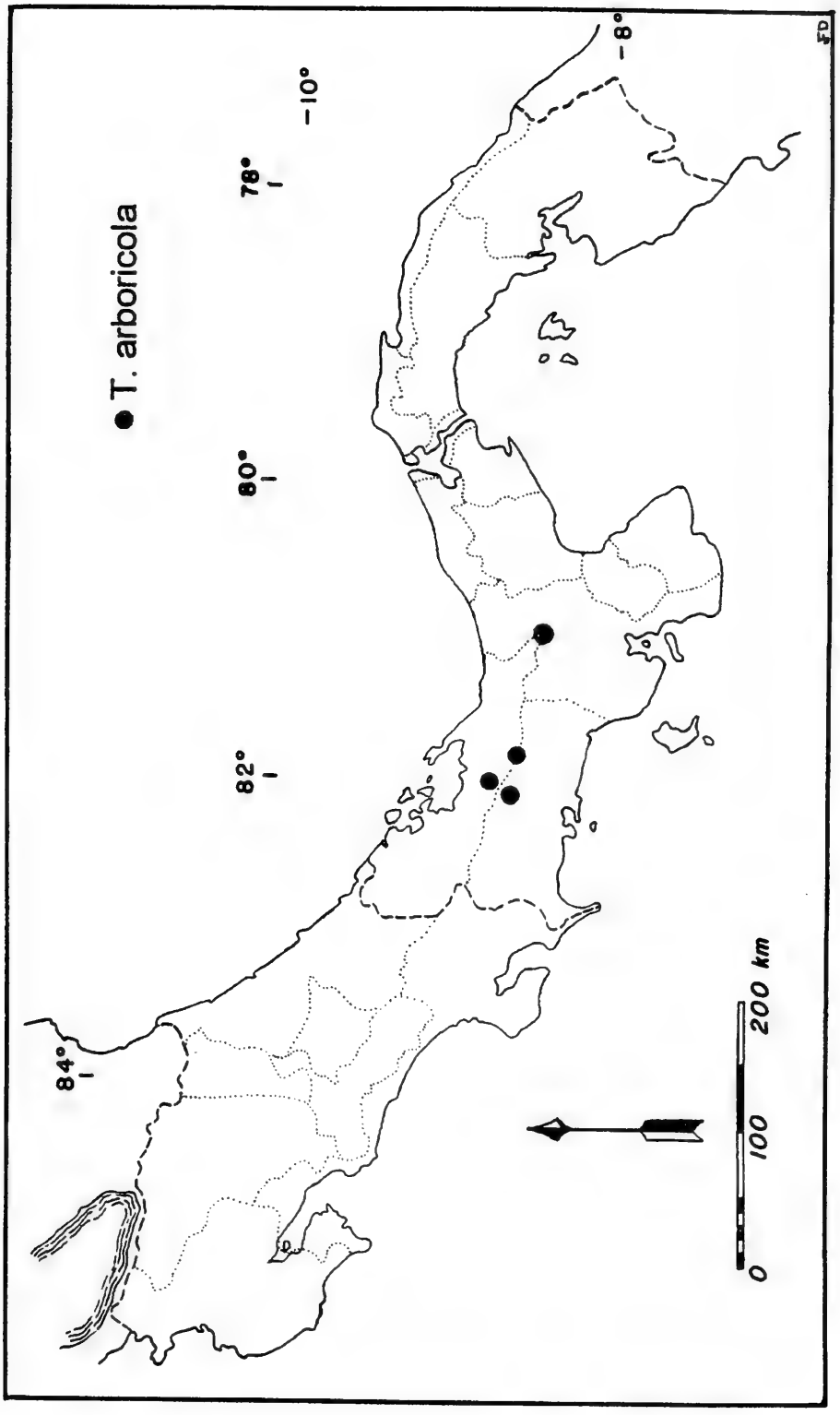

FIGURE 2. Distribution of *Topobea arboricola* in Panama.

2. *Topobea caliginosa* Almeda, Proc. Calif. Acad. Sci. 46(14):317. 1990.

Blakea micrantha Almeda, Rhodora 82:614. 1980.

TYPE. — PANAMA. Veraguas: Cerro Tute ca. 10 km NW of Santa Fé on ridgetop in cloud forest above 1000 m, 19 June 1975, *Mori 6765* (holotype: CAS!; isotype: MO!).

Rigidly branched terrestrial shrub to 1 m tall. Upper cauline internodes quadrangular to distinctly carinate. Young vegetative buds and juvenile foliage commonly beset with a sparse coppery brown furfuraceous indument, otherwise glabrous throughout. Leaves coriaceous and glabrous when dry but inconspicuously punctate abaxially, 1–4 × 0.4–1.6 cm, obovate to oblanceolate, apex obtuse to rounded, base acute to attenuate, the margin entire, often revolute when dry, 3-nerved; petioles 0.5–1 cm long. Flowers solitary in the axils of distal branches, sessile, subsessile or with outermost floral bracts compressed into an ill-defined peduncle 3–5 mm long. Floral bracts rounded at the apex, sparsely floccose to glabrous at maturity, margin entire; outer bracts 3–5 × 2–3 mm, fused at the base for 1–2 mm, elliptic-lanceolate; inner bracts 3–4 × 2–3 mm, free, elliptic-ovate. Calyx lobes bluntly deltoid, 1.5 mm long and 2 mm wide basally. Petals 6, glabrous but sparsely verrucose abaxially when dry, 4.5–6 × 2.5–3 mm, pink, ovate to elliptic-ovate, apex obtuse to rounded, entire. Stamens 6, filaments 2–3.5 × 0.5 mm, erect, glabrous; anthers free, 2 × 0.5–1 mm, linear-oblong and erect, each with two confluent pores at the truncate apex; connective not thickened or appendaged dorsally. Ovary completely inferior, 2-locular, glabrous at the apex which is elevated into a short cone. Style glabrous, 5–6 mm long; stigma punctiform. Berry 4–5 × 3–5 mm. Seeds mostly 1 mm long, cuneate to narrowly pyriform.

PHENOLOGY. — Flowering specimens were collected in February, April, and June; fruiting specimens collected in April, June, and July.

DISTRIBUTION. — Western Panama where it is known only from Cerro Tute (Veraguas) at 1400–1453 m (Fig. 3).

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Veraguas: windswept summit of Cerro Tute, 18 Feb. 1996, *Almeda et al. 7627* (CAS, MO, PMA); distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2724* (CAS, SCZ); summit of Cerro Tute above Escuela Agricola Alto de Piedra, just W of Santa Fé, 8°32′N, 81°07′W, 5 June 1982, *Knapp & Dressler 5394* (CAS, MO).

DISCUSSION. — This species was originally described as an epiphytic shrub based on information provided by the collector of the type and only known collection at the time (Almeda 1980). During recent field work I have found *T. caliginosa* growing only as a terrestrial shrub above tree line on the shrubby summit of Cerro Tute.

Three other congeners in this hexandrous group of species also occur on Cerro Tute—*T. arboricola*, *T. cordata*, and what may be an undescribed taxon most closely related to *T. hexandra*. The two former taxa appear to be true epiphytic shrubs that grow on trees within the cloud forest zone. The third entity, which grows in the upper zone just below tree line, is a vinelike secondary hemiepiphyte that germinates terrestrially, ascends nearby trees by adventitious roots, and later becomes epiphytic by losing root contact with the ground. This sympatry and parapatry suggest that strong isolating mechanisms are operating to maintain phenotypic distinctions among four closely related species. That this all occurs on a tropical mountain of 1453 m elevation makes it all the more remarkable.

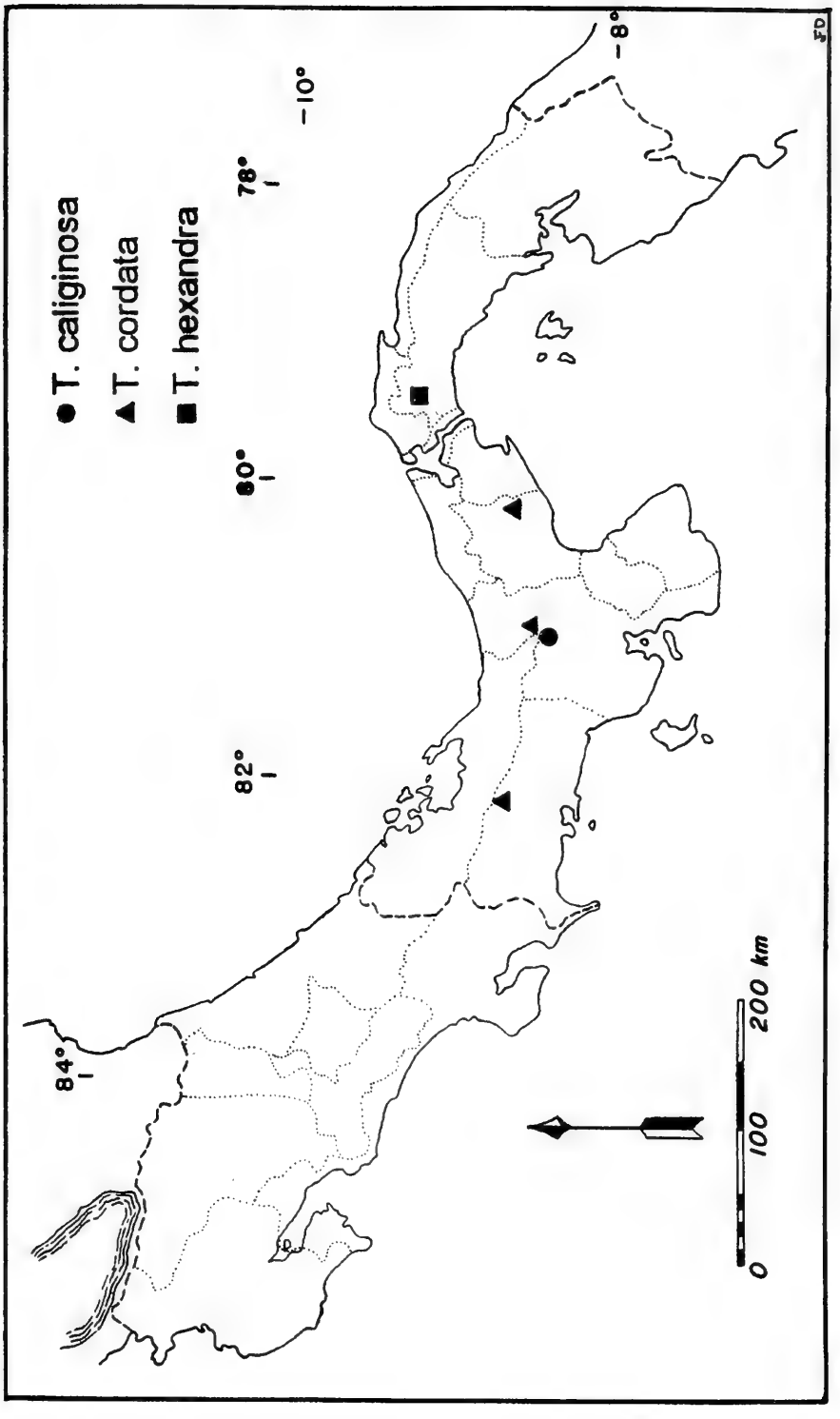

FIGURE 3. Distributions of *Topobea caliginosa*, *T. cordata*, and *T. hexandra* in Panama.

3. *Topobea cordata* Gleason, Phytologia 3:354. 1950.

TYPE. – PANAMA. Coclé: Cerro Pajita, north of El Valle de Antón, elev. 1000–1200 m, *Allen 4178* (holotype: NY!; isotype: MO!)

Epiphytic shrub to 1 m tall. Uppermost internodes ± compressed and quadrisulcate, the angles distinctly carinate sometimes varying to narrowly winged; older branches ± rounded to rounded-quadrate. Leaves of a pair sessile, equal to slightly unequal in size, the younger ones of a pair typically fused basally at the node into a narrow collar, glabrous throughout; mature blades coriaceous, 5.1–12.9 cm long and 3–5.8 cm wide, cordate-clasping to subcordate or ovate, apex acute, base rounded to cordate, margin entire, 5–7-nerved, the secondary veins typically not evident. Flowers erect, coconut-scented (fide *McPherson 8738*), solitary or paired in each upper leaf axil; peduncles 3–4 mm long, conspicuously compressed. Floral bracts entire, glabrate or sparingly beset abaxially (mostly toward the apex) with a coppery brown lanate indument; outer bracts 0.8–1.1 × 0.6–0.9 cm, fused at the base for 2 mm, elliptic, apex acute to obtuse; inner bracts 0.8–0.9 × 0.4–0.6 cm, free to the base, oblong-ovate, apex rounded. Calyx tube 1–1.5 mm long; calyx lobes (at anthesis) 4.5 mm long and 3 mm wide, oblong-ovate, ± entire, essentially glabrous but sometimes beset with a coppery brown lanate indument toward the apex on both surfaces. Petals 6, 0.8–1.3 × 0.4–0.7 cm, translucent-white, obovate, apex rounded, entire. Stamens 6, filaments complanate and glabrous, 6–7 mm long; anthers 5–7 mm long, 1–1.5 mm wide, yellow, subulate with two broad confluent ventrally inclined apical pores; connective not conspicuously thickened and unappendaged. Ovary completely inferior, 4-locular, apex glabrous and elevated into a blunt basally swollen cone 2 mm long. Style somewhat declinate and sigmoid apically, glabrous, 8–9 mm long; stigma truncate. Berry 1 × 1 cm, red at maturity. Seeds narrowly pyriform to cuneate, 1–1.5 mm long, beige, the testa smooth and glossy.

PHENOLOGY. — Flowering from February through May, September and probably during intervening months; the only fruiting specimen was collected in September.

DISTRIBUTION. — Wet cloud forests of western Panama from the Fortuna region (Chiriquí) east to Cerro Pajita (Coclé) at 1050–1250 m (Fig. 3).

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Chiriquí: Fortuna dam region, along Quebrada Arena near continental divide, 8°45′N, 82°15′W, 9 Mar. 1986, *McPherson 8738* (CAS, MO); Fortuna cauce de Quebrada Arena, 9 Apr. 1987, *Valdespino et al. 639* (CAS, PMA). Veraguas: Cerro Tute, trail past agricultural school near Santa Fé, 17 Sep. 1979, *Antonio 1875* (CAS, MO).

DISCUSSION. — The type specimen of this species lacks petals and stamens which accounts for the incomplete descriptions provided in the protologue (Gleason 1950) and subsequent treatment of this species in the Flora of Panama (Gleason 1958). The collection of flowering material with attached stamens facilitated a critical assessment of its generic placement and relationships to other species with six antesepalous stamens (Almeda 1990).

Topobea cordata is characterized by a distinctive suite of characters including sessile cordate-clasping leaves, oblong-ovate calyx lobes, comparatively large (8–13 mm) translucent white petals, and subulate anthers with ventrally inclined apical pores. *Topobea cordata* has a 4-locular ovary like *T. crassifolia*, but the latter has petiolate leaves, lance-triangular calyx lobes, smaller (5–7 mm) pink petals, and short (2–2.5 mm) apically truncate anthers.

One enigmatic collection (*McPherson 9864*, CAS) from the Fortuna region of western Panama resembles *T. cordata* in its overall vegetative morphology and white petals. In calyx shape and staminal details, however, it is a good match for *T. crassifolia*, the species to which *T. cordata* is most closely related. In the size of its floral bracts, hypanthia, and petals this collection also approaches *T. crassifolia*. This kind of character sorting is suggestive of hybridization or introgression between *T. cordata* and *T. crassifolia*. Typical *T. cordata* has also been collected at Fortuna. I have not seen au-

thentic material of *T. crassifolia* from Fortuna but it may well occur there since its range extends both east and west of that region.

4. *Topobea crassifolia* (Almeda) Almeda, Proc. Calif. Acad. Sci. 46(14):318. 1990.

Blakea crassifolia Almeda, Rhodora 82:612. 1980.

TYPE. — PANAMA. Coclé: La Mesa above El Valle in forest on both sides of junction with road to Cerro Pilón, ca. 800 m, 21 Jul. 1974, *Croat 25430* (holotype: CAS!; isotypes: MO!, US!).

Epiphytic shrub to 1 m tall. Uppermost branches quadrangular to rounded, glabrous throughout. Leaves thick, succulent or semisucculent, coriaceous or chartaceous when dry, 1.5–6.5(–12) × 1–4.3 cm, ovate to elliptic-ovate or elliptic-lanceolate, apex acute to attenuate varying to cuspidate or mucronate, base rounded to cordate, the margin entire, 3–5-nerved, often with only the median nerve elevated and conspicuous abaxially, essentially glabrous throughout; petioles 0.1–0.4 cm long. Flowers solitary, paired or in subfasciculate clusters of three to five in axils of distal branches, sessile, subsessile or with ill-defined peduncles 1–2 mm long. Floral bracts glabrous or sometimes beset with an inconspicuous lanate or floccose indument distally, margin entire; outer bracts 5–8 × 2.5–4 mm, fused at the base for about 1 mm, elliptic-lanceolate, apex acute to obtuse or rarely rounded; inner bracts 4–7 × 2.5–4 mm, free but closely subtending the hypanthium, elliptic-ovate, apex acute to rounded or broadly truncate. Calyx lobes lance-triangular, 3–4.5 mm long and 2–2.5 mm wide between sinuses. Petals 6, glabrous and coarsely verrucose, sometimes fringed with a scattering of minute matted hairs, 5–7 × 1.5–2.5 mm, reportedly white or pink, oblong-lanceolate to narrowly oblanceolate, apex acute, base somewhat clawed, entire. Stamens 6, filaments 3.5–4.5 × 0.5 mm, erect, glabrous; anthers free, 2–2.5 × 0.5 mm, linear-oblong and erect distally, each with two confluent dorsally inclined apical pores; connective thickened dorso-basally into a spurlike appendage. Ovary completely inferior, 4-locular and glabrous at the truncate apex. Style glabrous, 6 mm long; stigma punctiform. Berry 6 × 5 mm. Seeds mostly 1 mm long or less, ranging from ovoid or clavate to lunate or pyriform.

PHENOLOGY. — Flowering in February and May through August; fruiting collections have been made in May and August.

DISTRIBUTION. — Cloud forests in central Costa Rica from Braulio Carillo National Park (San José) and vicinity disjunct to Panama from Cerro Colorado (Bocas del Toro) and El Valle de Antón (Coclé) to El Llano-Cartí region (Comarca de San Blas) at 350–1750 m (Fig. 4).

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela/Heredia border: Colonia Virgen del Socorro along road from Costa Rica #9 to the Colonia, 2 Aug. 1976, *J. & K. Utley 5629* (CAS, DUKE, F). San José: Parque Nacional Braulio Carillo. La Montura, 25–30 Jul. 1982, *Todzia et al. 1964* (NY). PANAMA. Bocas del Toro/Chiriquí border: Cerro Colorado, road along top, 13 Aug. 1977, *Folsom et al. 4681* (CAS). Coclé: La Mesa, 4 km N of El Valle de Antón, 6 May 1981, *Sytsma et al. 4364* (CAS, MO); along trail to La Mesa about 4.5 miles beyond El Valle de Antón, 21 May 1970, *Wilbur & Luteyn 11697* (CAS, DUKE, F, MO, US). Comarca de San Blas: El Llano-Cartí road. Nusagandi, 19 km from Interamerican Hwy, 9°19′N, 78°55′W, 26 Aug. 1984, *de Nevers & de León 3767* (CAS, MO); El Llano-Cartí road, km 19.1, 9°19′N, 78°55′W, 1 Jul. 1985, *de Nevers 5943* (CAS, MO); entrada a Nergan Igar, km 15 de la carretera Llano-Cartí, 9°20′N, 78°58′W, 2 Jul. 1994, *Galdames et al. 1243* (CAS, SCZ).

DISCUSSION. — Among the hexandrous species, *T. crassifolia* is the most widely distributed and has the broadest elevational amplitude. Like many woody epiphytes, the fragmented but small population structure of this species has evidently promoted morphological divergence.

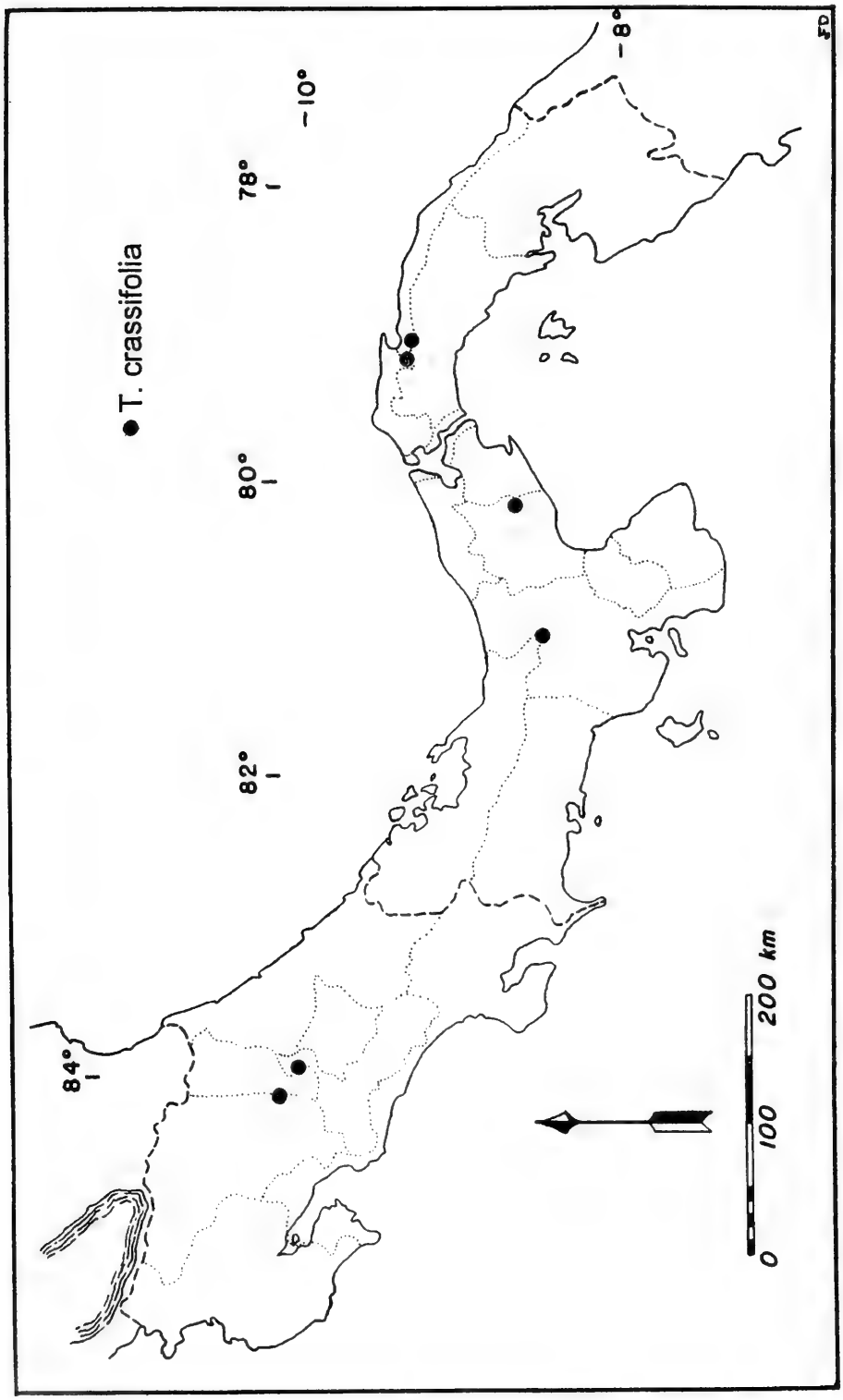

FIGURE 4. Distribution of *Topobea crassifolia* in Costa Rica and Panama.

Most of the known populations of *T. crassifolia* can be distinguished by leaf shape alone. Plants from the type locality near El Valle, Panama, have thick semisucculent leaves that are ovate to elliptic-ovate and bluntly apiculate to obtuse or rounded apically. The Cerro Colorado population in western Panama has smaller (4.5–5 × 1.7–2.5 cm) elliptic to elliptic-ovate leaves that are coriaceous. The northernmost population from central Costa Rica has longer elliptic-ovate to elliptic-lanceolate leaves (5.3–12 cm × 3–3.4 cm) that are thinner, flexuous, and acute to attenuate apically. All of these populations are otherwise identical in other vegetative and reproductive characters. Because of this, I here emphasize their unity and underlying similarities by recognizing a single variable species. Variation of this kind, while striking, is not unprecedented among other epiphytic Melastomataceae. *Leandra subulata* Gleason, for example, is another woody epiphytic melastome with many geographical variants and a comparable montane distribution in Costa Rica and Panama.

Another population from the El Copé region of west-central Panama may also prove to be a geographical variant of *T. crassifolia*. It has ovaries with 4-locules like *T. crassifolia* but its thick leathery leaves are narrowly elliptic, 2.3–3 cm wide, and uniformly long-acuminate basally and apically. This variant is known from two specimens, *Almeda et al. 7650* (CAS) and *Folsom & Robinson 2437* (CAS), both of which are only in bud. These specimens are tentatively excluded from my concept of *T. crassifolia*, pending study of additional material.

5. *Topobea hexandra* Almeda, Proc. Calif. Acad. Sci. 46(14):320. 1990.

TYPE. — PANAMA. Panamá: Cerro Jefe, along summit road and along trail into the Chagres Valley, elev. ca. 900 m, 19 Feb. 1988, *Almeda et al. 5837* (holotype: CAS!; isotypes: CR!, DUKE!, F!, MO!, NY!, PMA!, TEX!, US!).

Hemiepiphytic shrub to 1 m tall adhering to the bark of host trees by nodal and internodal adventitious roots. Upper cauline internodes quadrate to quadrisulcate, glabrous or sparsely covered with spreading, caducous, glandular hairs 1–2 mm long, as are the young petioles and both surfaces of juvenile leaves; older branches rounded, the leaf scars typically swollen. Uppermost nodes beset with brown spreading hairs. Vegetative buds copiously covered with a deciduous brown indument of stellate-lepidote hairs. Leaves coriaceous and glabrous throughout but inconspicuously punctate abaxially, 2–3.9 × 1.1–3 cm, suborbicular to elliptic-ovate, apex rounded varying to obtuse, base obtuse to rounded, margin entire, 3-nerved, often with an additional inconspicuous intramarginal pair; petioles 0.5–1.4 cm long. Flowers erect, solitary or paired in the leaf axils of distal branches, sessile or subsessile with short (to 1 mm) ill-defined peduncles formed by the compressed bases of the outer floral bracts. Floral bracts thick and semisucculent, free and entire, sparingly stellulate-furfuraceous abaxially; outer bracts 5–6.5 × 3–5 mm, concave, ovate to elliptic-ovate, apex obtuse to bluntly mucronate; inner bracts 4–5 × 4–6 mm, broadly ovate to suborbicular, apex rounded. Calyx tube 1 mm long; calyx lobes erect, 2 × 2–2.5 mm, ovate to deltoid-ovate, entire but irregularly roughened along interlobe sinuses, sparingly stellate-lepidote. Petals 6, liberally covered with hyaline disc-shaped glands when dry, 6.5–7 × 4 mm, pink, elliptic-obovate, apex obtuse. Stamens 6, filaments 3 mm long and somewhat declinate; anthers free, 2 × 1 mm, pale yellow turning brownish orange with age, oblong, each with two ventrally inclined pores at the broadly rounded apex, connective slightly thickened and dilated dorso-basally at the filament insertion into a blunt spur up to 0.25 mm long. Ovary completely inferior, 2-locular, glabrous at the apex and not modified into a cone or collar. Style glabrous, 5.5 mm long; stigma punctiform. Berry 5–6 × 4–7.5 mm. Seeds 1–1.5 mm long, beige, bluntly deltoid.

PHENOLOGY. — The only known flowering specimen was collected in February; fruiting specimens have been collected in February, September, October, and December.

DISTRIBUTION. — Known only from low cloud forests at the summit of Cerro Jefe east of the Canal Area in central Panama at 900–1025 m (Fig. 3). The Cerro Jefe region was an important island refugium from the middle Miocene until the land bridge between North America and South America was established ca. 3.5–2.4 million years ago (Graham 1985; Lewis 1971). This geologic history is reflected in the high incidence of vascular plant endemism on Cerro Jefe. Of the approximately 1230 species of plants thought to be endemic to Panama (Carrasquilla 1997), about 150 occur on Cerro Jefe including 6 locally endemic species of Melastomataceae.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Panamá: summit and S facing slopes of Cerro Jefe, 9 Feb. 1978, *Almeda & Nakai 3459* (CAS); Cerro Jefe along summit road beyond the Intel tower, 3 Feb. 1996, *Almeda et al. 7495* (CAS); Cerro Jefe, along trail on ridge running NE from summit, 18 Dec. 1974, *Mori & Kallunki 3755* (MO); Cerro Jefe, 29 Oct. 1980, *Sytsma 2007* (MO); Cerro Jefe, road leading N from summit, 26 Sep. 1975, *J. T. & F. Witherspoon 8552* (MO).

DISCUSSION. — As noted in the protologue, *T. hexandra* is a common hemiepiphyte in the summit forest of Cerro Jefe, but it appears to be overlooked by most collectors because it has small flowers that are rarely evident to the casual observer without the aid of binoculars (Almeda 1990). This species is variable in indument characters. The uppermost cauline internodes can either be glabrous or sparsely covered with spreading glandular hairs. These glandular hairs are also produced on petioles of juvenile foliage and on upper and lower surfaces of some young leaves, but they commonly fall away with age.

Topobea hexandra is readily distinguished from the other hexandrous species with 2-locular ovaries by its ovate-elliptic to subrotund leaves, dorso-basally appendiculate anther connectives, and dark brown tufts of hairs on the uppermost nodes.

What may be an extreme variant or perhaps an undescribed taxon is known from two collections (*Almeda et al. 7621*, CAS and *Aranda et al. 2733*, CAS) made on Cerro Tute, Panama, in 1996. This entity is also a hemiepiphyte but it has small leaves (0.9–1.4 × 0.4–1 cm) that are obovate with a rounded to emarginate apex. One of these collections is in bud and the other is in young fruit. In view of the small sample size and the lack of mature flowers and fruits, no taxonomic disposition of the Cerro Tute population is possible at this time.

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LITERATURE CITED

ALMEDA, F. 1980. Central American novelties in the genus *Blakea* (Melastomataceae). Rhodora 82(832):609–615.

———. 1990. New species and new combinations in *Blakea* and *Topobea* (Melastomataceae), with an historical perspective on generic limits in the tribe Blakeeae. Proc. California Acad. Sci. 46(14):299–326.

CARRASQUILLA, L. G. 1997. Cerro Azul-Cerro Jefe Region, Panama. Pp. 221–225 *in* Centres of plant diversity: A guide and strategy for their conservation (Volume 3. The Americas), S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, eds. WWF-World Wildlife Fund for Nature and IUCN-The World Conservation Union. IUCN Publications Unit, Cambridge, U. K.

GLEASON, H. A. 1950. Observations on tropical American melastomes. Phytologia 3:345–360.

———. 1958. Melastomataceae. *In* Flora of Panama, R. E. Woodson, Jr. and R. W. Schery, eds. Ann. Missouri Bot. Gard. 45:203–304.

GRAHAM, A. 1985. Vegetational paleohistory studies in Panama and adjacent Central America. *In* The botany and natural history of Panama, W. G. D'Arcy and M. D. Correa A., eds. Monogr. Syst. Bot. Missouri Bot. Gard. 10:161–176.

LEWIS, W. H. 1971. High floristic endemism in low cloud forests of Panama. Biotropica 3:78–80.

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Two New Species of Chromodorididae (Mollusca: Nudibranchia) from the Tropical Indo-Pacific, with a Redescription of *Hypselodoris dollfusi* (Pruvot-Fol, 1933)

by

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Two new species of the family Chromodorididae are described. *Chromodoris buchananae* is known from northern New South Wales, Australia. It is similar in appearance to several members of the *Chromodoris quadricolor* complex, but differs in its color pattern with a creamy white body with brown flecks, white longitudinal lines and an orange marginal band. *Hypselodoris dollfusi* (Pruvot-Fol, 1933) was originally described from the Gulf of Suez and is here documented for the first time since its original description. It is also known from the United Arab Emirates. It is readily distinguished from other members of the genus by its opaque white body with pink-purple rings and yellow-orange marginal band. It is similar in its anatomy to several species of the monophyletic clade containing *H. fucata*, *H. kaname*, *H. koumacensis* and *H. paulinae*. The color pattern, distribution of mantle glands and radular tooth morphology clearly separate *H. dollfusi* from other members of this clade. *Hypselodoris babai* is known from Okinawa. It can be distinguished by its red-brown body color with opaque white markings. It is similar in appearance to *H. bullocki* in having an elevated gill sheath, but differs in its coloration and by the presence of mantle glands.

At the end of the twentieth century, numerous papers described new species of Chromodorididae from the tropical Indo-Pacific (Rudman 1984, 1986, 1987, 1995; Baba 1995, 1996; Hamatani 1995; Gosliner and Behrens 1998; Johnson and Gosliner 1998; Gosliner and Johnson 1999; Schrödl 1999; Valdés et al. 1999). These papers added much to our knowledge of biodiversity of the region and also clarified higher systematic relationships within the family. Most of these papers have focused on species that have been found along the margins of the Pacific and Australasian plates and have added many new taxa from Japan, Philippines, Papua New Guinea, and Australia. Recently, we were provided with additional material of two undescribed, large chromodorids from Australia and Okinawa. This paper describes the anatomy and systematic relationships of these additional taxa and provides a redescription of *Hypselodoris dollfusi* from the United Arab Emirates.

Species Descriptons

Family Chromodorididae Bergh, 1891
Genus *Chromodoris* Alder and Hancock, 1855

***Chromodoris buchananae* sp. nov.**
Figs. 1A, 2A-D, 3A-D

Type Material. — Holotype: Australian Museum C. 383578, specimen dissected, South Solitary Island, Coffs Harbour, New South Wales, Australia, 15 m depth, February 1997, Carol Buchanan.

Etymology. — *Chromodoris buchananae* is named for friend and colleague Carol Buchanan who first discovered this species, and provided us with the holotype.

Distribution. — Thus far, this species is known only from the type locality, South Solitary Island, Coffs Harbour, New South Wales, Australia.

External Morphology. — The living animal (Fig. 1A) was approximately 48 mm in length. The body is a translucent cream color with small brown flecks dispersed over the notum. Around the margin of the notum there is a wide orange band. Within this band is a thin opaque white band. There are two opaque white lines running from just posterior of the rhinophores to the side of the gills pocket. There is also a short white line anterior to each rhinophore, and a line forming a posterior to the gills. The hyponotum and posterior end of the foot are cream colored with a broad orange marginal band, similar to that on the notum. The posterior end of the foot has a white line forming a "V", and there are several white lines of varying length along the side of the hyponotum. The rhinophores and gill are orange. There are 7 unipinnate branchial leaves forming the branchial plume. The perfoliate rhinophores bear about 20 lamellae.

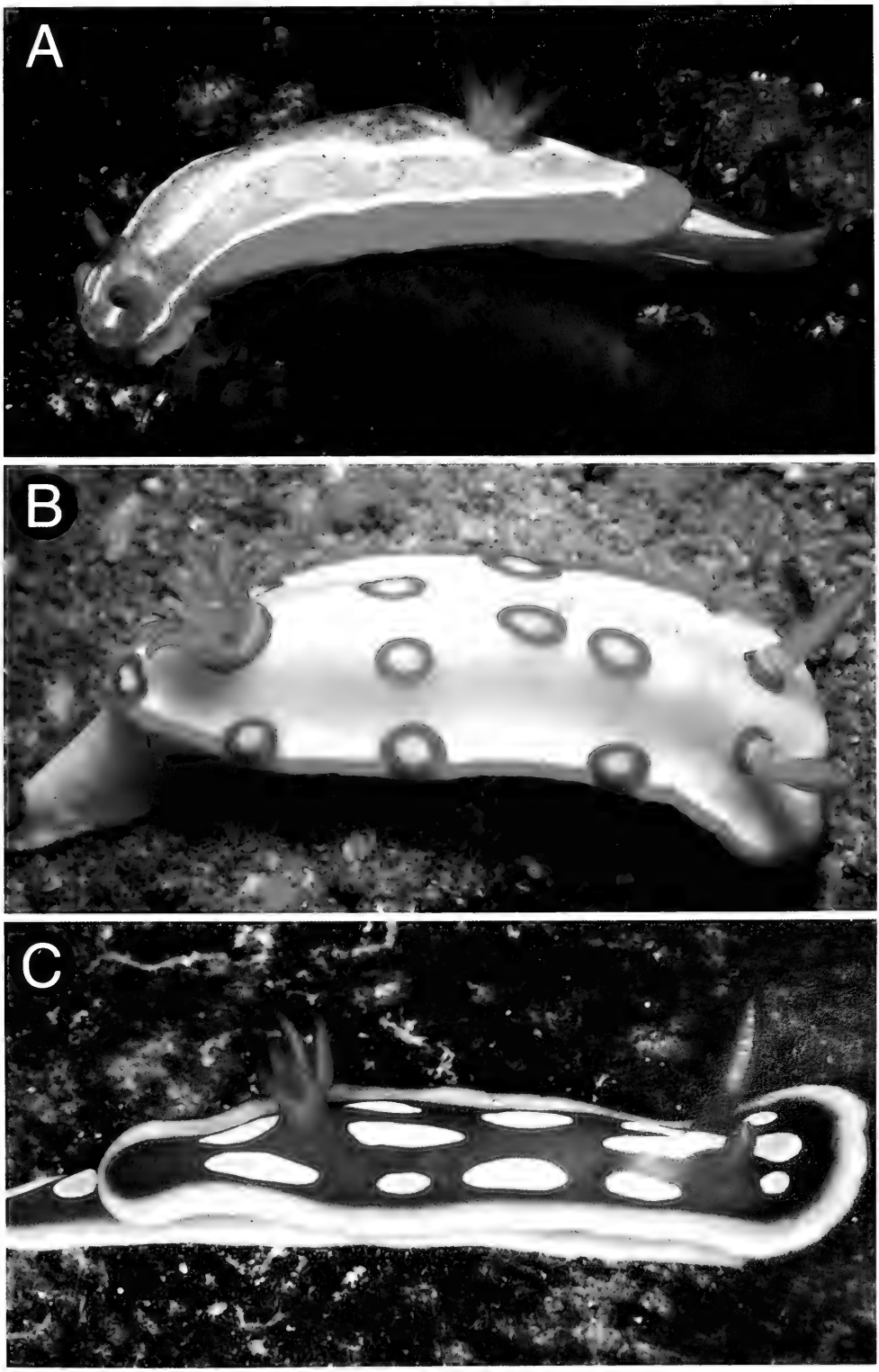
Mantle Glands. — The subcutaneous mantle glands (Fig. 2A) form a discontinuous submarginal band around the notum of the animal. They are absent from the anterior portion of the animal to just behind the rhinophores. These glands consist of highly ramified, spherical lobes that are clustered together, resembling bunches of grapes (Fig. 2B).

Buccal Armature. — The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end ot the muscular portion of the buccal mass is a chitinous labial cutical, which bears numerous jaw rodlets. These rodlets (Fig. 3A) are elongate with spreading, bifid apices. The radular formula is 81 × 63.0.63. There is no trace of a row of rachidian teeth. The innermost lateral teeth (Fig. 3B) are broad and quadrangular. There are three to four elongate denticles on the inner side of the elongate, triangular primary cusp and four to five denticles on the outer side of the cusp. The next successive inner lateral teeth lack denticles on the inner side of the cusp, but have three to four denticles on the outer side. The middle lateral teeth (Fig. 3C) are elongate with 7–9 denticles on the outer side of the broader cusp. The outermost teeth (Fig. 3D) are unevenly curved with an abbreviated portion containing 3–7 short, rounded denticles below the small primary cusp.

Reproductive System. — (Fig. 2C) The ampulla is thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The prostatic proximal portion of the vas deferens is folded over itself once before it narrows markedly into the relatively short, muscular, ejaculatory portion. The ejaculatory portion

→

Figure 1. Living animals. A. *Chromodoris buchananae* sp. nov., specimen from South Solitary Island, Coffs Harbour, New South Wales, Australia, photograph by C. Buchanan. B. *Hypselodoris dollfusi* (Pruvot-Fol, 1933), specimen from Khor Fakken, United Arab Emirates, photograph by C. Harris and L. Betts. C. *Hypselodoris babai* sp. nov., specimen from Seragaki, Okinawa, photograph by R. Bolland.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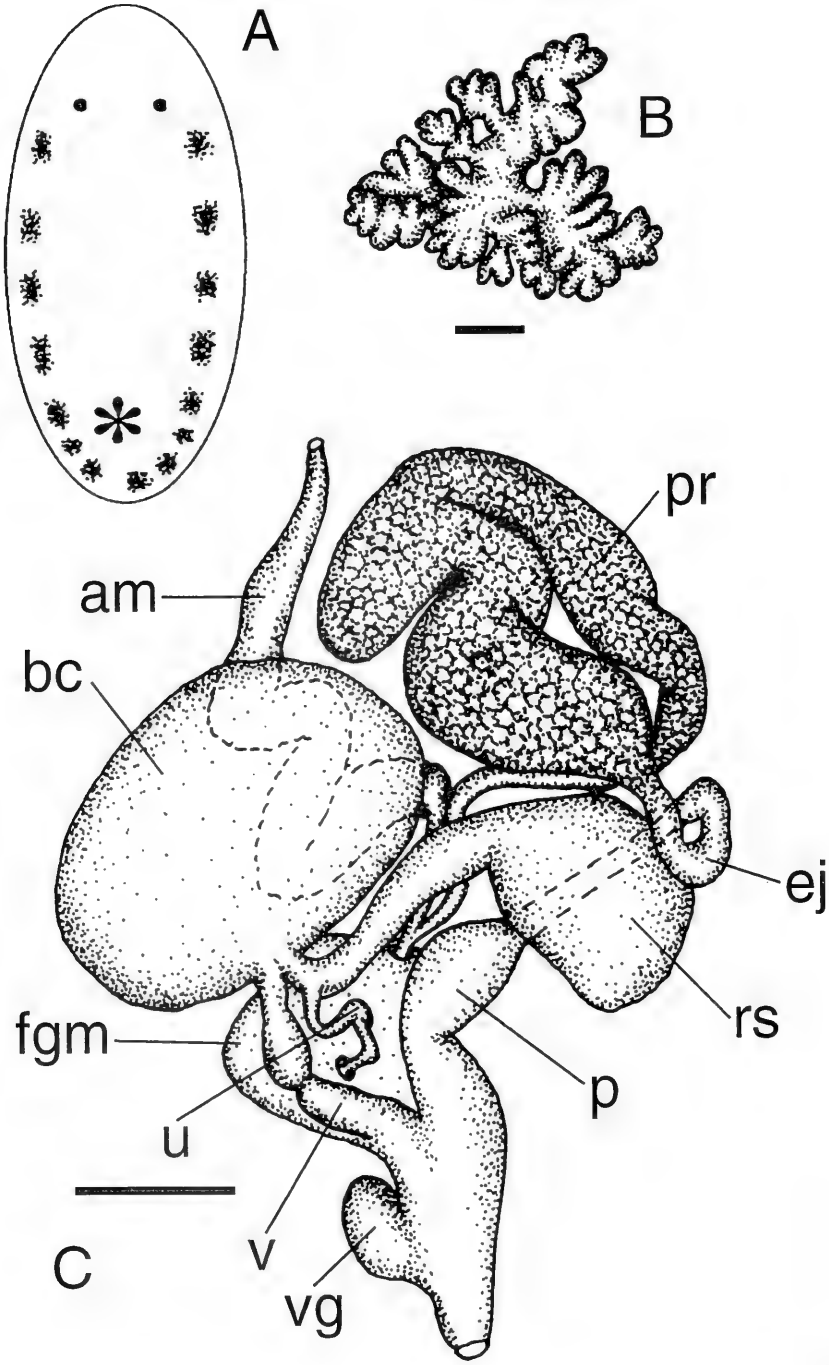

FIGURE 2. *Chromodoris buchananae* sp. nov. A. Subcutaneous glandular network. B. Mantle glands, enlarged, scale = 1.0 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

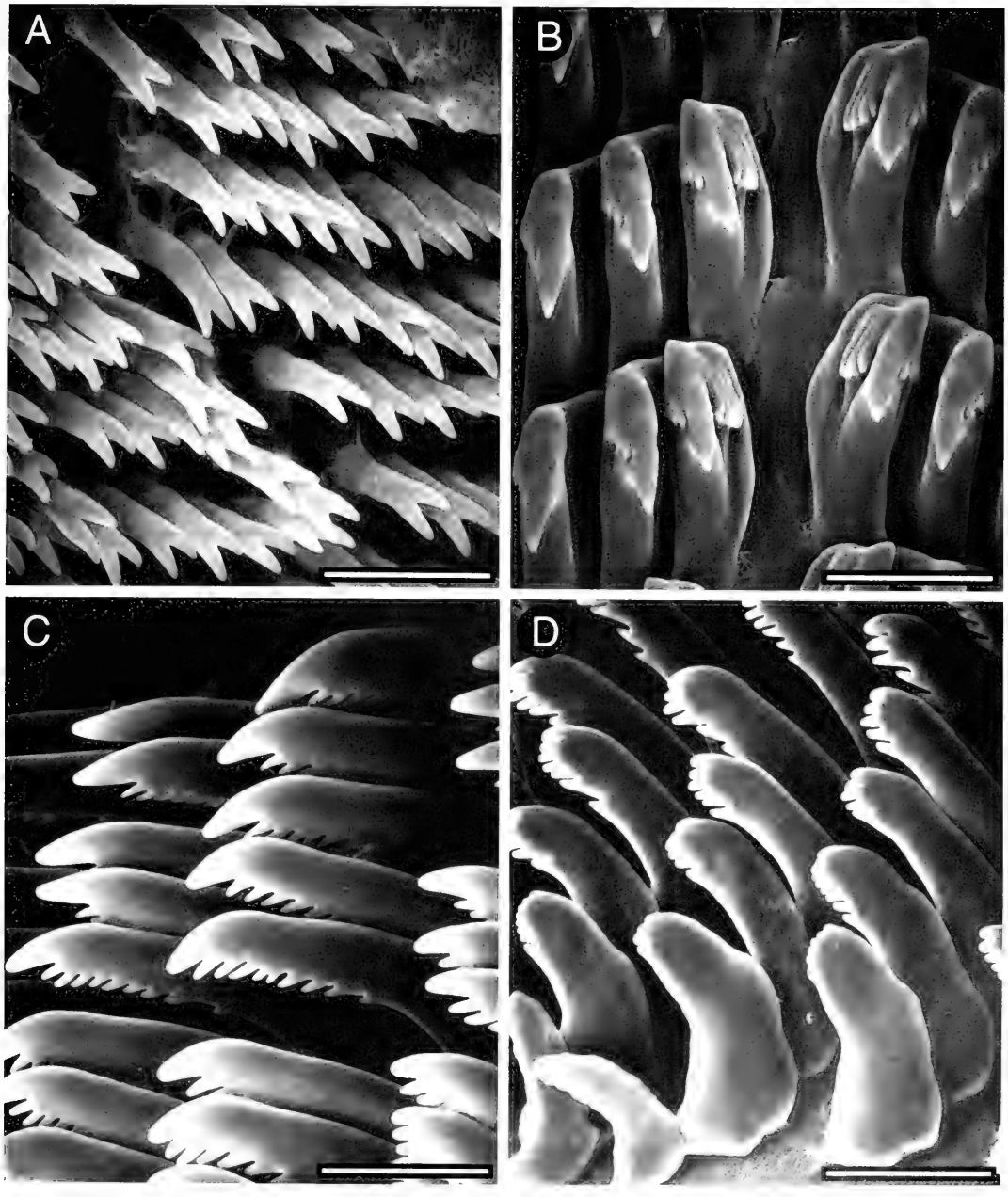

FIGURE 3. *Chromodoris buchananae* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 8.6 μm. B. Inner lateral teeth, scale = 27 μm. C. Lateral teeth from central portion of half-row, scale = 23.1 μm. D. Outer lateral teeth, scale = 25 μm.

narrows abruptly to a curved segment and then enters the short penial bulb, which is adjacent to the slender vaginal duct at the common gonopore. The distal end of the vas deferens is devoid of any penial hooks. The female gland mass consists of the large mucous gland and small membrane and albumen glands. Near the exit of the mucous gland there is a small, ovoid vestibular gland. A relatively short vagina leads to a spherical bursa copulatrix. Adjacent to the vagina, a short duct emerges and

connects to the pyriform receptaculum seminis. The uterine duct emerges a quarter of the length along the duct to the receptaculum seminis. The uterine duct is relatively short and enters the female gland mass near the albumen gland.

DISCUSSION. — The color pattern of this species is reminiscent of some members of the *Chromodoris quadricolor* complex (Rudman 1982; Gosliner and Behrens 1998). Members of this group have longitudinal lines, an orange marginal or submarginal band and orange gills and rhinophores. Of the numerous species in this complex, only *C. africana* Eliot, 1904 and *C. magnifica* (Quoy and Gaimard, 1832) have white lines on the body. The remaining species all have black lines or other markings. Both *C. magnifica* and *C. africana* differ from *C. buchananae* in having a black rather than a cream body color. The only other chromodorids with a body color similar to *C. buchananae* are *C. decora* (Pease, 1860) and *C. lekker* Gosliner, 1994. Both of these species have a creamy white body with an orange marginal band and opaque white markings on the notum. In *C. decora* there is a central white line that bifurcates anterior to the gills. In *C. lekker* there are scattered opaque white spots. Both species differ from *C. buchananae* in having opaque white spots and dark plum to black spots submarginally. They also have white gills and rhinophores whereas *C. buchananae* has orange gills and rhinophores and has small brown spots on the notum that are absent in the other two species.

The mantle glands of *Chromodoris buchananae* are highly ramified as have been described for members of the *C. quadricolor* complex (Gosliner and Behrens 1998). The radular teeth of *C. buchananae* are similar in configuration to many of the members of this complex, as well. The radular arrangement differs from that of *C. decora* and *C. lekker* in that these species have a well-developed rachidian row of teeth while in *C. buchananae* there is no trace of a rachidian row. The reproductive system of *C. buchananae* does not differ markedly from that of other members of *Chromodoris quadricolor* complex. Members of this group of species have a relatively short ejaculatory portion of the vas deferens and a simple ovoid vestibular gland.

Genus *Hypselodoris* Stimpson, 1855

***Hypselodoris dollfusi* (Pruvot-Fol, 1933)**
Figs. 1B, 4A–B, 5A–D

Glossodoris dollfusi Pruvot-Fol, 1933:126, pl, 1, figs. 7–8; pl. 3, fig. 40.
Hypselodoris dollfusi (Pruvot-Fol, 1933) comb. nov.

MATERIAL EXAMINED. — HOLOTYPE: Muséum National d'Histoire Naturelle, Paris, St. XXV, Dollfus Expedition, 12 January 1919, leg. R. Ph. Dollfus. CASIZ 127918, one specimen, 21 m depth, Anemone Gardens, Khor Fakken, Dubai, United Arab Emirates, Gulf of Oman, 24 December 1999, Carole Harris. CASIZ 127919, one specimen, dissected, 20 m depth, Coral Gardens, Khor Fakken, Dubai, United Arab Emirates, Gulf of Oman, 16 July 1999, Carole Harris and Leon Betts.

OTHER MATERIAL. — Photographs of additional material from Dubai were examined to determine variability in external morphology and coloration.

DISTRIBUTION. — Thus far, this species is known only from the type locality, the Gulf of Suez, and Khor Fakken, United Arab Emirates.

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1B) reach 45–50 mm in length. The body is opaque white overall, with a bright yellow-orange marginal band. The notum has a series of deep pink-purple rings of varying diameters, which surround a circle of lavender. In some specimens the circle within these rings have a bluish tinge. A similarly colored ring is found around the branchial plume pit and at the base of the rhinophores. The pink rings are situated along the notal margin, with one at both the anterior and posterior ends and midlaterally between the rhinophores and gill. The rings vary in number from 9 to 21. The hyponotum bears 4–6 pink rings and there is one at the tip of the

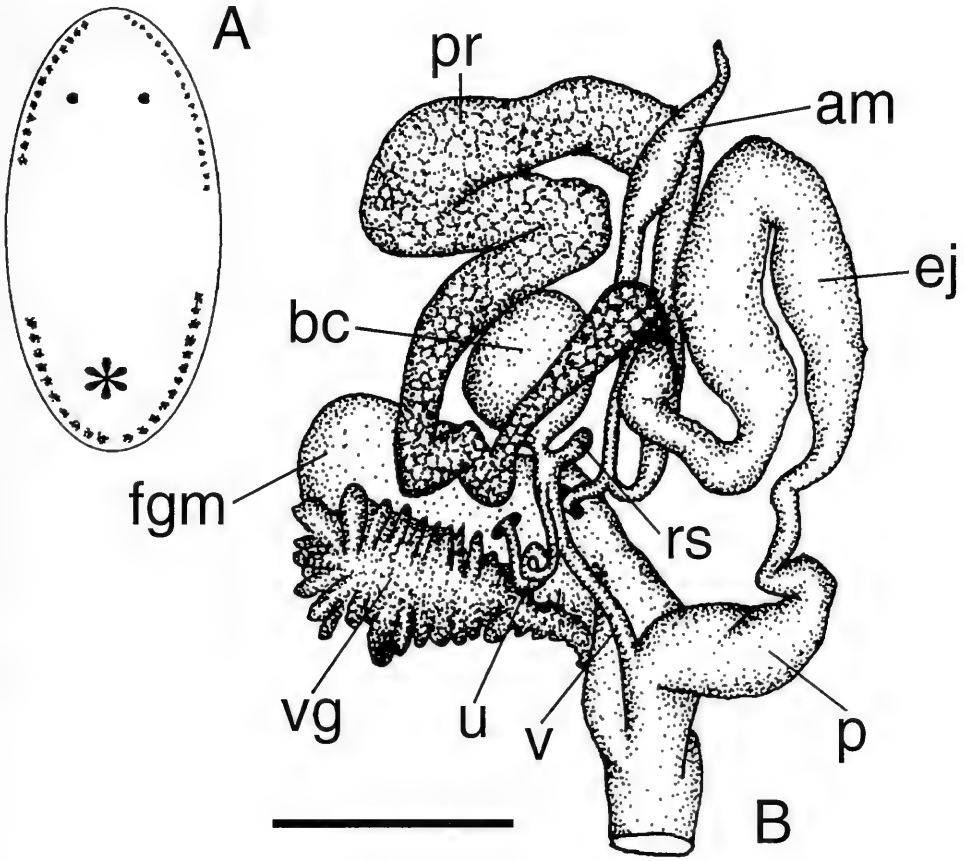

FIGURE 4. *Hypselodoris dollfusi* (Pruvot-Fol, 1933) A. Subcutaneous glandular network. B. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

posterior end of the foot. The rhinophores and gill are red. The rhinophores are perfoliate with 27 lamellae. The branchial plume is partially spreading, with 10 unipinnate gill leaflets.

MANTLE GLANDS. — (Fig. 4A) There are about 22 large posterior glands. A lateral series of glands is absent. There are 12–18 anterolateral glands on either side of the head. In the paratype, the 18 glands on the right side of the head were smaller (some indicating recent regeneration) than the 13 glands on the left side.

BUCCAL ARMATURE. — The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end of the muscular portion of the buccal mass there is a chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 5A) have a short base and a curved apex without lateral rodlets. The radular formula is 66 × 88.0.88. There is no trace of a rachidian row of teeth. The inner lateral teeth (Fig. 5B) have a short wide base with a bifid cusp. On the right side of the radula, inner and outer denticles are absent, while on the left side a single short inner denticle is present. The remainder of the inner and middle lateral teeth (Fig. 5C) are broad with a bifid cusp and no lateral denticles on either the inner or outer margins of the teeth. The outer 4–10 teeth (Fig. 5D) also have a bifid cusp and 4–6 denticles on the outer side.

REPRODUCTIVE SYSTEM. — (Fig. 4B) The arrangement of the organs is triaulic. The ampulla is elongate and curved. It divides into the short, thick, slightly convoluted prostate and short oviduct,

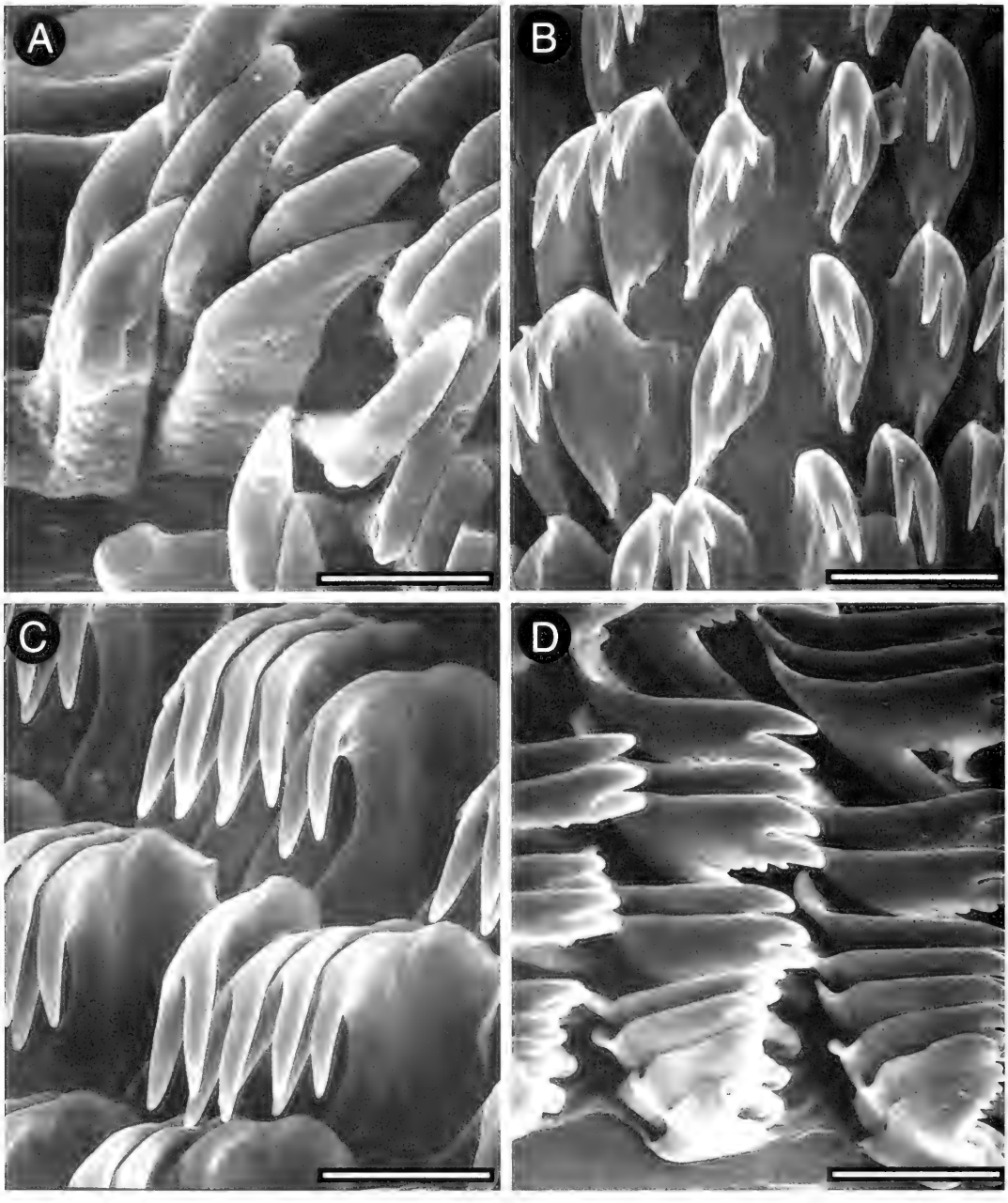

FIGURE 5. *Hypselodoris dollfusi* (Pruvot-Fol, 1933) Scanning electron micrographs. A. Jaw rodlets, scale = 10 μm. B. Inner lateral teeth, scale – 38 μm. C. Lateral teeth from central portion of half-row, scale – 30 μm. D. Outer lateral teeth, scale – 30 μm.

which enters the female gland mass. The prostate narrows into the moderately short ejaculatory portion, which terminates in a slightly enlarged penis. The vaginal duct is narrow and long. The minute, short, pyriform receptaculum seminis has a short duct which attaches to the vaginal duct at the base of the spherical bursa copulatrix. The uterine duct is long and narrow forming a loop before entering the

female gland mass below the entrance of the oviduct into the mass. It branches from the vagina just below the common insertion of the bursa and receptaculum seminis.The female gland mass is large and completely developed. A large, lobate vestibular gland is present.

DISCUSSION. — *Glossodoris dollfusi* was originally described from a single 30 mm preserved specimen collected from the Gulf of Suez, Egypt. This species has not been documented in other publications since its original description and its status has remained in question. Pruvot-Fol (1951) suggested that the color description of *G. dollfusi* was based on a preserved specimen. This statement led Rudman (1973:196–197) to suggest that the animal was a species of *Chromodoris* similar to *C. inornata* Pease, 1871. Later, Rudman (1983:169) noted the discrepancy between Pruvot-Fol's original description and subsequent comments regarding the coloration being from a living rather than preserved specimen. On the basis that the coloration was from a living specimen, Rudman concluded that the *G. dollfusi* was most likely a chromodorid, but that its was doubtful that it could be identified with any degree of certainty. The original description contains two color plates of the living animal and several figures of the radular teeth. The color plate clearly shows a whitish animal with red to violet rings on the notum and a yellowish marginal band. The radular teeth are described and depicted as being bifid, which is characteristic of members of the genus *Hypselodoris*. There are some minor differences in the external color pattern between Pruvot-Fol's original description and the present specimens. For example the marking on the notum are described by Pruvot-Fol as spots rather than circles and there are also some minor differences in the coloration of the rhinophores as to the distribution of reddish pigment. Nevertheless, the description of the radular teeth, with inner edenticulate teeth and outer denticulate ones closely matches the form of the radular teeth in the present material. The partially dissected holotype was re-examined. The buccal mass had been removed for preparation of the radula. No pigment remains. The external anatomy and arrangement of the mantle glands are entirely consistent with the specimens examined here from the Gulf of Oman. As no other species of *Hypselodoris* has a similar color pattern, there is little doubt that the present specimens are conspecific with Pruvot-Fol's species. Although, Pruvot-Fol's animal was from the Gulf of Suez and the present material is known from the Persian Gulf, there is sufficient geographical overlap in the biota as to make this a likelihood.

Hypselodoris dollfusi differs markedly from any described species of *Hypselodoris* (Gosliner and Johnson, 1999). It is the only member of the genus known to possess circular rings on the notum. The general whitish body color is similar to most Indo-Pacific members of the genus.

This species appears to be a member of the clade of *Hypselodoris* species that contains *H. fucata* Gosliner and Johnson, 1999; *H. kaname* Baba, 1994, *H. koumacensis* Rudman, 1995 and *H. paulinae* Gosliner and Johnson, 1999. All members of this clade share three important synapomorphies: erect rather than spreading branchial plume, a short jaw element shaft and a receptaculum seminis that inserts at the base of the bursa copulatrix rather than more distally along the vaginal duct. *Hypselodoris dollfusi* shares all of these features with the other members of this clade. In the above-mentioned species the mantle glands are small and arranged uniformly around the mantle margin. In *H. dollfusi* there are small glands that are interrupted in the mid-region of the body, on either side. The body color of *H. dollfusi* most closely resembles that of *H. paulinae*, but differs in having pink rings rather than red blotches. *Hypselodoris dollfusi* also lacks the purple submarginal line on the foot that is present in *H. paulinae*.

The inner lateral radular teeth of *H. dollfusi* closely resemble those of *H. fucata* and *H. paulinae* where a denticle is present on the inner side of the radular tooth, but is absent on the outer side. In *H. kaname* and *H. koumacensis* the outer side of the tooth also bears a denticle. The denticulation of the radular teeth of *H. dollfusi* is most similar to that of *H. fucata*. In this species only the outer 15 teeth possess denticles on the outer face of the teeth whereas in *H. dollfusi* the outer 4–10 teeth are denticulate. The other members of this clade have more denticulate teeth with the most extreme case being *H. kaname*, where all radular teeth are denticulate.

The reproductive system of *H. dollfusi* is similar to that of other members of the clade described above. All members of this clade have a receptaculum seminis that inserts at the base of the bursa copulatrix rather than more distally along the vaginal duct. In *H. dollfusi*, the vagina is narrower than in the other members of the clade. Also, the ejaculatory portion of the vas deferens appears shorter in *H. dollfusi* than in other members of the clade.

***Hypselodoris babai* sp. nov.**
Figs. 1C, 6A–E, 7A–E

TYPE MATERIAL. — HOLOTYPE: CASIZ 115758, one specimen, 55 m depth, Seragaki, Okinawa, 26 April 1996, Bob Bolland. PARATYPES: CASIZ 115804, one specimen, 44 m depth, Seragaki, Okinawa, 4 April 1997, Bob Bolland. CASIZ 127924, one specimen, 58 m depth, Seragaki, Okinawa, 16 May 2000, Bob Bolland.

ETYMOLOGY. — *Hypselodoris babai* is named for our friend and colleague Dr. Kikutaro Baba. He has been an inspiration to us throughout our careers in opisthobranch systematics. For more than almost 70 years, Baba has been carefully documenting the remarkable diversity of Japanese opisthobranchs. This is a truly remarkable achievement.

DISTRIBUTION. — Thus far, this species is known only from the type locality, Seragaki, Okinawa.

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1C) reach at least 25 mm in length. The body is opaque white with a rich red-brown central region. There are a series of long irregular oval white spots distributed over the mantle. The oval marking, beginning between the rhinophores varies in length and shape, and may extend mid-dorsally half the length of the mantle to the gill. A wide white band, similar to that on the mantle, edges the foot. A series of white ovals occur medially along the posterior end of the foot. The gill and rhinophores are bright red. The rhinophores are very long, bearing 25 lamellae. The branchial plume is also very tall and unipinnate, with 5 gill leaflets.

MANTLE GLANDS. — (Fig. 6A, B) The mantle glands are limited to the anterolateral and posterior ends of the dorsum. There are 3–4 large posterior glands and 4–6 smaller, anterolateral glands. The holotype has three small glands positioned just anterior to the gill plume, on the left side of the body.

DIGESTIVE SYSTEM AND BUCCAL ARMATURE. — The buccal mass (Fig. 6C) is very small relative to the size of the body. The oral tube is extremely narrow and elongate. The cerebral nerve ring is situated well behind the posterior end of the buccal mass. The muscular portion of the buccal mass is approximately equal in length to the oral tube (Fig. 6D). At its posterior end there are a pair of short salivary glands and more ventrally situated are the paired buccal ganglia. At the anterior end of the muscular portion of the buccal mass is a chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 7A) have an elongate base with unifid, bifid and trifid cusps. The radular formula of the paratype is 57 × 43–45.0.43–45. There is no trace of a rachidian row of teeth. The innermost lateral teeth (Fig. 7B) have a simple, bifid cusp with one or two denticles on the inner side of the primary cusp. There are no denticles on the outer side of the cusps. The subsequent inner lateral teeth lack denticles on either side of the cusp. At approximately the fifteenth row of teeth, a single denticle is present below the primary cusps. More external midlateral teeth have 4–5 denticles below the cusps (Fig. 7C). The outermost laterals (Fig. 7D) bear 7–10 rounded denticles below the primary cusps.

REPRODUCTIVE SYSTEM. — (Fig. 6E) The arrangement of the organs is triaulic. The ampulla is elongate and swollen. It divides into the short, thick, slightly convoluted prostate and short oviduct, which enters the female gland mass. The prostate narrows into the moderately short ejaculatory portion, which terminates in a much-enlarged penis. The vaginal duct is relatively straight and short. The small, short, pyriform receptaculum seminis has a short duct that attaches to the vaginal duct near the middle of its length. The uterine duct is long and narrow, forming several convoluted loops before en-

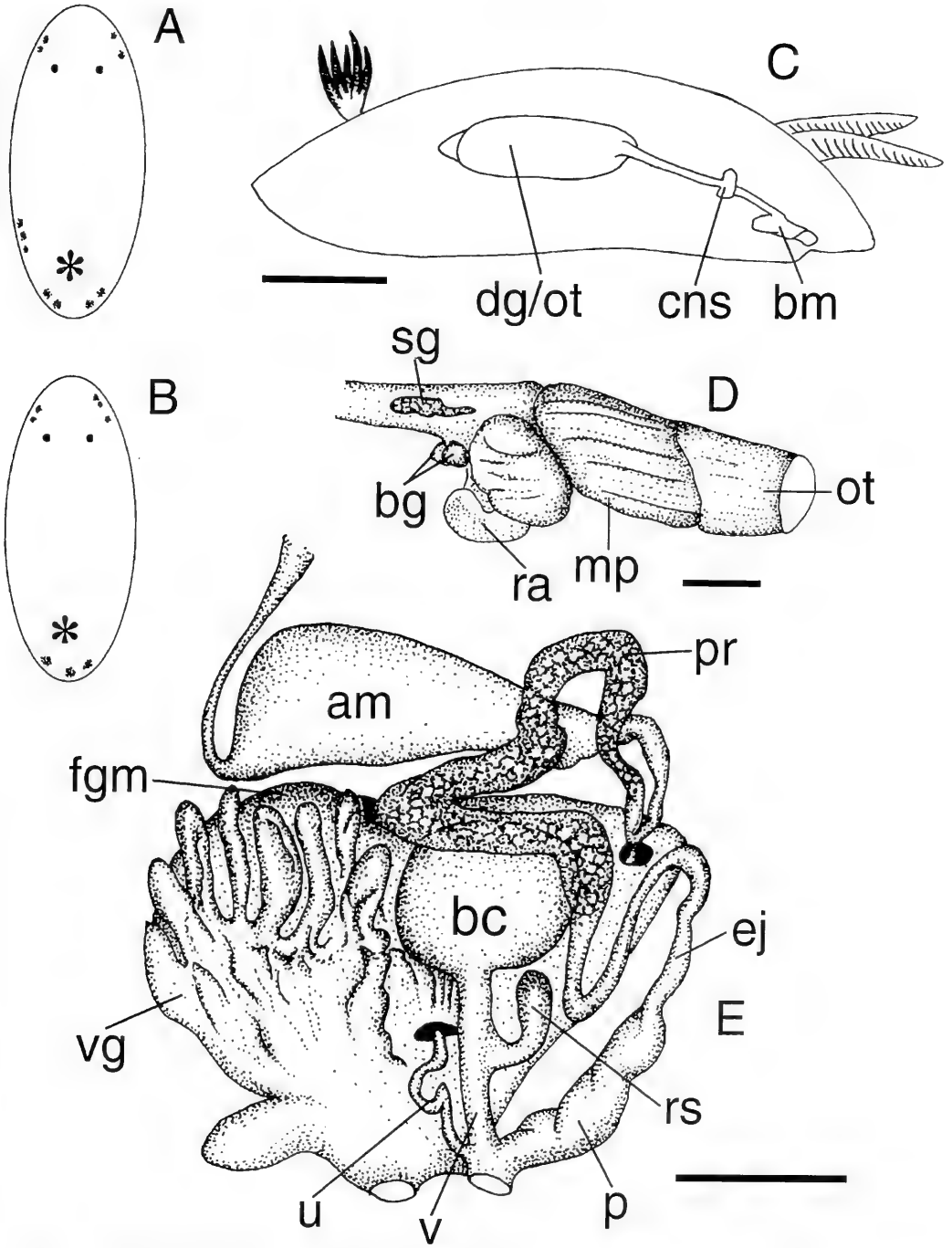

FIGURE 6. *Hypselodoris babai* sp. nov. A. Subcutaneous glandular network (CASIZ 115758). B. Subcutaneous glandular network (CASIZ 115804). C. Digestive system, bm = buccal mass; cns = central nervous system; dg/ot = digestive gland/ovotestis, scale = 5.0 mm. D. Buccal mass, bg = buccal ganglia; mp = muscular portion of buccal mass; ot = oral tube; ra = radular sac; sg = salivary gland, scale = 1.0 mm. E. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

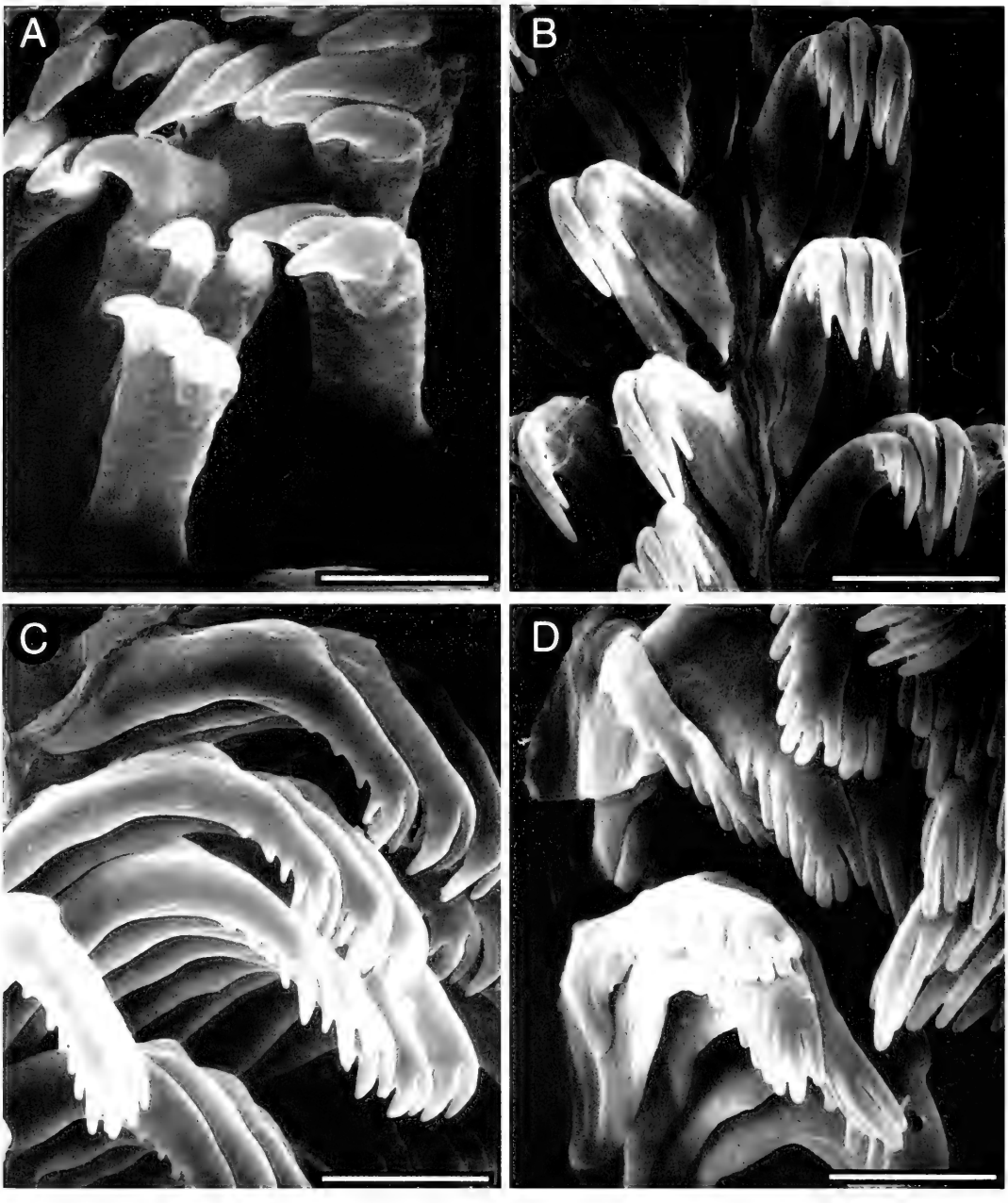

FIGURE 7. *Hypselodoris babai* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale – 5 μm. B. Inner lateral teeth, scale – 17.6 μm. C. Lateral teeth from central portion of half-row, scale – 13.6 μm. D. Outer lateral teeth, scale – 12 μm.

tering the female gland mass below the entrance of the oviduct into the mass. The uterine duct branches from the vagina near the base. The female gland mass is large and completely developed. A large, lobate vestibular gland is present.

DISCUSSION. This species is most similar in its external coloration to *Hypselodoris bullocki* (Collingwood, 1881). Both species have a reddish or pink to purple body color and red to orange gills

and rhinophores. *Hypselodoris babai* differs from *H. bullocki* in having a broader white marginal band and numerous white spots and blotches over the dorsal surface of the mantle and foot. While details of the anatomy of *H. bullocki* remain largely undescribed, the present species differs in several significant regards. *Hypselodoris bullocki* has a highly elevated gill sheath and lacks any mantle glands around the margin of the mantle (present study). *Hypselodoris babai* has a slightly elevated gill sheath and has three to four large posterior glands and smaller lateral and anterolateral glands. Details of the internal anatomy of *H. bullocki* need to be described to more fully compare these two species. The present species also bears some resemblance to *Durvilledoris pusilla* (Bergh, 1874). The latter species differs externally in having a yellow rather than white marginal band and also has fewer white spots than in *H. babai*.

Hypselodoris babai is unusual among described species of *Hypselodoris* in that the central nervous system and the buccal bulb are much smaller. It is unclear whether this is a also a characteristic of *H. bullocki* and related taxa and certainly warrants further study.

ACKNOWLEDGMENTS

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LITERATURE CITED

BABA, K. 1994. Descriptions of four new, rare, or unrecorded species of *Hypselodoris* (Nudibranchia: Chromodorididae) from Japan. Venus 53(3):175–187.

_____ 1995. Anatomical and taxonomical review of four blue patterned species of *Hypselodoris* (Nudibranchia: Chromodorididae) from Japan. Venus 54 (1):1–15.

GOSLINER, T. M. 1994. New species of *Chromodoris* and *Noumea* (Nudibranchia: Chromodorididae) from the western Indian Ocean and southern Africa. Proceedings of the California Academy of Sciences 48(12):239–252.

GOSLINER, T. M. AND D. W. BEHRENS. 1998. Five new species of *Chromodoris* (Mollusca: Nudibranchia: Chromodorididae) from the tropical Indo-Pacific Ocean. Proceedings of the California Academy of Sciences 50(5):139–165.

GOSLINER,T. M. AND R. F. JOHNSON. 1999. Phylogeny of *Hypselodoris* (Nudibranchia: Chromodorididae) with a review of the monophyletic clade of Indo-Pacific species, including descriptions of twelve new species. Zoological Journal of the Linnean Society 125:1–114.

HAMATANI, I. 1995. Two species of Chromodorididae (Nudibranchia), one newly recorded and one newly established, from middle Japan. Venus 54(2):101–107.

JOHNSON, R. F. AND T. M. GOSLINER. 1998. The genus *Pectenodoris* (Nudibranchia: Chromodorididae) from the Indo-Pacific, with the description of a new species. Proceedings of the California Academy of Sciences 50(12):295–306.

PRUVOT-FOL, A. 1933. Mission Robert Dollfus en Egypte. Opisthobranchiata. Memoires de l'Institute d'Egypte 21:89–159.

———. 1951. Revision du genre *Glossodoris* Ehrenberg. Journal de Conchyliologie 91:76–164.

RUDMAN, W. B. 1973. Chromodorid opisthobranch Mollusca from the Indo-West Pacific. Zoological Journal of the Linnean Society 52(3):175–199.

———. 1982. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris quadricolor*, *C. lineolata* and *Hypselodoris nigrolineata* colour groups. Zoological Journal of the Linnean Society 76(3):183–241.

———. 1983. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris splendida*, *C. aspersa* and *Hypselodoris placida* colour groups. Zoological Journal of the Linnean Society 78(2):105–173.

———. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zoological Journal of the Linnean Society 81(2 and 3):115–273.

———. 1986. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Noumea purpurea* and *Chromodoris decora* colour groups. Zoological Journal of the Linnean Society. 86:309–353.

———. 1987. The Chromodorididae (Opisthobranchia, Mollusca) of the Indo-West Pacific: *Chromodoris epicuria*, *C. aureopurpurea*, *C. annulata*, *C. coi* and *Risbecia tryoni* colour groups. Zoological Journal of the Linnean Society 90(4):305–407.

———. 1995. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: further species from New Caledonia and the *Noumea romeri* group. Molluscan Research 16:1–43.

SCHRÖDL, M 1999. *Glossodoris charlottae*, a new chromodorid nudibranch from the Red Sea (Gastropoda, Opisthobranchia). Vita Marina 46(3–4):89–94.

VALDÉS, Á., E. MOLLO, AND J. ORTEA, 1999. Two new species of *Chromodoris* (Mollusca, Nudibranchia, Chromodorididae) from southern India, with a redescription of *Chromodoris trimarginata* (Winkworth, 1946). Proceedings of the California Academy of Sciences 51(3):461–472.

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A Review of the Genus *Hemibagrus* in Southern Asia, with Descriptions of Two New Species

by

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The species of the southern Asian bagrid catfish genus *Hemibagrus* are reviewed in this study. Five previously-named species are recognized as valid: *Hemibagrus maydelli* (Rössel, 1964), *H. menoda* (Hamilton, 1822), *H. microphthalmus* (Day, 1877), *H. peguensis* (Boulenger, 1894) and *H. punctatus* (Jerdon, 1849). Two additional species, *H. imbrifer* and *H. variegatus*, from the Salween and Tenasserim River drainages, respectively, are described here as new. The status of controversial names *Pimelodus menoda* Hamilton, 1822, and *Bagrus corsula* Valenciennes, 1840, are stabilized with the designation of a single neotype for both names.

Bleeker (1862) established the genus *Hemibagrus* for a group of bagrid catfishes characterized by having a depressed head, rugose head shield not covered by skin, slender occipital process, and moderately long adipose fin. However, workers since Günther (1864) have placed species of this genus in either *Mystus* Scopoli, 1777, or *Macrones* Dumeril, 1856, and it was not until Mo's (1991) phylogenetic study of the Bagridae that the genus was considered distinct from *Mystus*.

In much of southern Asia (defined in this study as consisting of the Indian subcontinent and Myanmar west of the Tenasserim and Salween River drainages) and particularly in India, *Hemibagrus* species appear to be less common than in Southeast Asia, inasmuch as they are less frequently encountered in markets, certainly less so than other genera of large bagrid catfishes, such as *Sperata* and *Rita*. In this study, the taxonomy of the southern Asian species of *Hemibagrus* is reviewed and seven valid species, two of which are new and described herein, are recognised.

Materials and Methods

Measurements were made point to point with dial calipers and data recorded to tenths of a millimeter. Counts and measurements were made on the left side of specimens whenever possible. Subunits of the head are presented as percent of head length (HL). Head length and measurements of body parts are given as percent of standard length (SL). Measurements and counts were made following Ng and Ng (1995) with the following exceptions: head length is measured from the tip of the snout to the

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posteriormost extremity of fleshy opercular flap. Length of the adipose-fin base is measured from the anteriormost point of origin to the posteriormost point of the adipose-fin base. Post-adipose distance is measured from the posteriormost point of the adipose-fin base to the posterior margin of the hypural complex.

The following additional measurements were made: predorsal, preanal, prepelvic and prepectoral lengths are those measured from the tip of the snout to the anterior bases of the dorsal, anal, pelvic, and pectoral fins, respectively. Pelvic- and pectoral-fin lengths are measured from the origin to the tip of the longest ray. Dorsal and pectoral spine lengths are measured from the base to the tip. Dorsal to adipose distance is measured from the base of the last dorsal-fin ray to the origin of the adipose fin. Caudal-fin length is the length of the longest ray of the lower lobe measured from the posterior margin of the hypural complex. The length of the caudal peduncle is measured from base of the last anal-fin ray to the posterior margin of the hypural complex. Nasal-, maxillary-, and mandibular-barbel lengths are measured from the base to the tip.

Fin-ray counts were obtained under a binocular dissecting microscope using transmitted light. Vertebral counts were taken from radiographs. Following the method of Roberts (1994), the first vertebra bearing fully-developed ribs was counted as vertebra 6, and the first postanal vertebra is taken to be the anteriormost vertebra having its hemal spine posterior to the anteriormost anal-fin pterygiophore. The number in parentheses following a particular count indicates the number of examined specimens with that count. Drawings of the specimens were made with a Nikon SMZ-10 camera lucida. Institutional codes for the repositories of specimens follow Eschmeyer (1998).

Systematic Accounts

Hemibagrus imbrifer sp. nov.

Fig. 1

Type Material. — Holotype: ZRC 45406, 186.6 mm SL; Thailand, Tak Province, Salween basin, Mae Nam Moei at Ban Wa Le (16°17′24″N, 98°42′21″E); K. Kubota, Apr 1998. Paratype: CMK 13445 (1, 144.2 mm SL), Thailand, Tak Province, Salween basin, Mae Nam Moei at Na Rei (16°17′23″N, 98°42′20″E); K. Kubota, Mar 1997.

Diagnosis. — *Hemibagrus imbrifer* can be distinguished from its congeners in having relatively large sensory pores arranged in vertical columns along the sides of the body and the following unique combination of characters: length of caudal peduncle 18.8–19.5 %SL, interorbital distance 31.7–32.3 %HL, eye diameter 17.3–18.5 %HL, 48 vertebrae (with 24 postanal vertebrae) and 14 gill rakers on the first gill arch.

Description. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. Adipose fin with long base, spanning most of postdorsal distance. Sensory pores of lateral line system readily visible, arranged in nine vertical columns on sides of body. In %SL: head length 26.6–28.4, head width 18.8–20.0, head depth 13.0–13.1, predorsal distance 38.8–39.2, preanal length 68.4–70.6, prepelvic length 51.0–51.5, prepectoral length 23.7–24.5, body depth at anus 14.4–14.9, length of caudal peduncle 18.8–19.5, depth of caudal peduncle 9.8–11.1, pectoral-spine length 12.2–12.3, pectoral-fin length 16.6, dorsal-spine length 11.7–12.5, length of dorsal fin 22.6–23.5, length of dorsal-fin base 14.4–16.9, pelvic-fin length 14.6–15.5, length of anal-fin base 11.1–13.2, caudal-fin length 19.7–21.6, length of adipose-fin base 38.4–44.2, adipose-fin maximum height 4.2–5.5, post-adipose distance 8.1–10.1; in %HL: snout length 39.3–39.8, interorbital distance 31.7–32.3, eye diameter 17.3–18.5, nasal barbel length 41.3–41.7, maxillary barbel length 175.4–211.7, inner mandibular barbel length 48.8–52.0, outer mandibular barbel length 85.4–88.1.

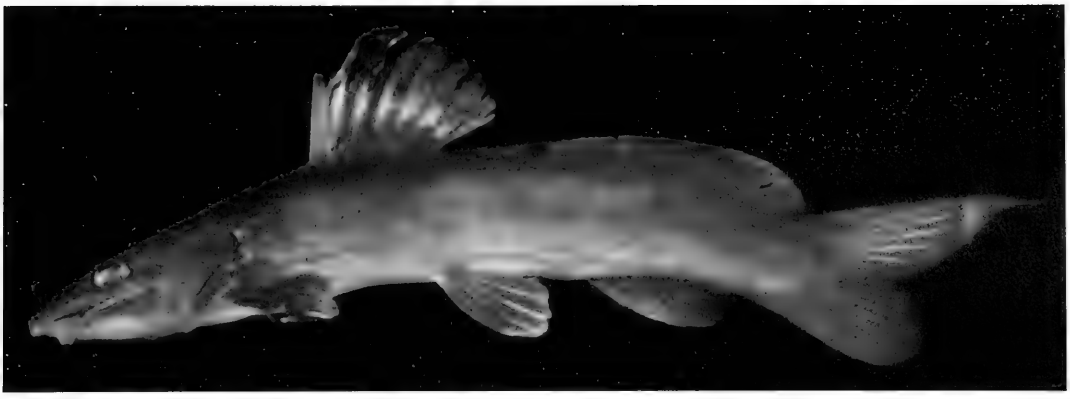

FIGURE 1. *Hemibagrus imbrifer*, ZRC 45406, holotype, 186.6 mm SL; Thailand: Mae Nam Moei.

Branchiostegal rays 10 (1) or 11 (1). Gill rakers 3 + 11 = 14 (1). Vertebrae 26 + 21 = 47 (1) or 26 + 22 = 48 (1).

Fin ray counts: dorsal II,7 (2); pectoral I,10 (1) or I,10,i (1); pelvic i,5 (2); anal iv,8 (1) or iv,8,i (1); caudal i,7,7,i (1) or i,7,8,i (1). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, without serrations on posterior edge. Pectoral spine stout, with 12–13 large serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Dorsal surface of head and body uniform gray; ventral surfaces of head and body dirty white; adipose fin gray, distal edge fading to light gray; caudal and anal fins gray, with melanophores more dense on the fin rays. Distal two-thirds of pectoral and pelvic fins gray, with melanophores more dense on fin rays and proximal third dirty white.

ETYMOLOGY. — From the Latin *imbrifer*, meaning rainy. In allusion to the pattern of the sensory pores being arranged in vertical columns on the sides of the body.

DISTRIBUTION. — Known only from the Salween River drainage (Fig. 2).

REMARKS. — *Hemibagrus imbrifer* can be differentiated from its congeners in having relatively large sensory pores of the lateral line system arranged in vertical columns along the sides of the body. No other species of *Hemibagrus* have the sensory pores of the lateral line system so obviously visible. Furthermore, *H. imbrifer* is one of the only two known species of southern Asian *Hemibagrus* (the other being *H. variegatus*) which has a long-based adipose fin spanning nearly all of the postdorsal distance. *Hemibagrus olyroides* from Borneo and all East Asian species allied with *H. guttatus* have similar long-based adipose fins, but can be differentiated from *H. imbrifer* in having more vertebrae (52–60 vs. 47–48). *Hemibagrus baramensis* and *H. sabanus* (both from Borneo) also have long-based adipose fins with a relatively low vertebral count (44–47), but can be differentiated from *H. imbrifer* in lacking the readily-visible sensory pores arranged in vertical columns. *Hemibagrus imbrifer* can be differentiated from *H. variegatus* in having a shorter caudal peduncle (18.8–19.5 %SL vs. 20.2%SL) with fewer postanal vertebrae (21–22 vs. 24), smaller eyes (17.3–18.5 %HL vs. 23.1%HL), a larger interorbital distance (31.7–32.3 %HL vs. 28.6%HL), fewer gill rakers (14 vs. 21), and a gray body with the sensory pores plainly visible (vs. a variegated brown body with the sensory pores not readily apparent).

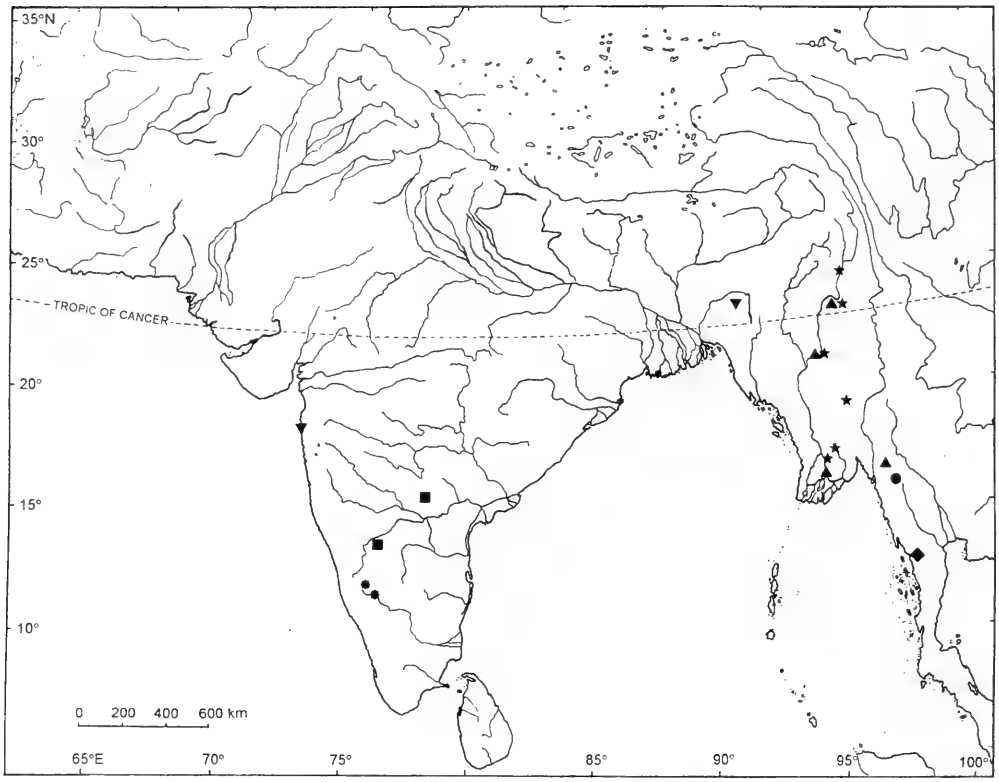

FIGURE 2. Map of southern Asia showing the distribution of *Hemibagrus* species: *H. imbrifer* (●); *H. maydelli* (■), *H. menoda* (▼); *H. microphthalmus* (▲); *H. peguensis* (★); *H. punctatus* (✱) and *H. variegatus* (◆).

Hemibagrus maydelli (Rössel, 1964)

Fig. 3

Mystus maydelli Rössel, 1964:149, fig. 1; Wilkens 1977:159.
Mystus sp. – Govind and Rajagopal, 1975:79.
Mystus malabaricus (in part) – Jayaram, 1977:32; Talwar and Jhingran, 1991:564.
Mystus krishnensis Ramakrishniah, 1988:139, figs. 1–2; Talwar and Jhingran, 1991:563; Jayaram, 1995:97, 105, 108.
Mystus punctatus (non Jerdon) – Barman, 1993:225, fig. 96.
Hemibagrus maydelli – Grant, 1999:172, fig. 2.

DIAGNOSIS. — *Hemibagrus maydelli* can be differentiated from its congeners by a unique combination of the following characters: head length 30.8–32.4 %SL, length of caudal peduncle 15.3–16.1 %SL, depth of caudal peduncle 7.8–8.5 %SL, dorsal to adipose distance 4.0–7.0 %SL, eye diameter 11.5–12.3 %HL, 52 vertebrae, and olive green body with orange fins.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. Head extremely depressed. In %SL: head length 30.8–32.4, head width 18.9–20.5, head depth 11.7–13.3, predorsal distance 42.0–46.7, preanal length 71.1–73.8, prepelvic length 54.8–58.8, prepectoral length 25.4–28.7, body depth at anus 13.0–15.6, length of caudal

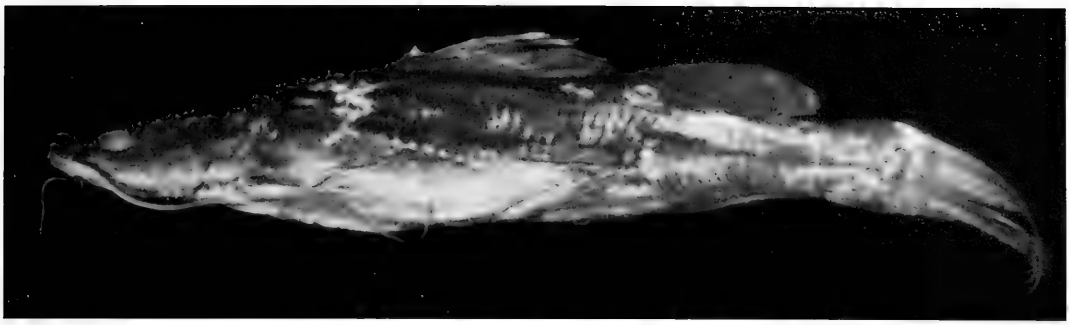

FIGURE 3. *Hemibagrus maydelli*, CAS 62087, 167.2 mm SL; India: Tungabahdra River.

peduncle 15.3–16.1, depth of caudal peduncle 7.8–8.5, pectoral-spine length 13.6–15.3, pectoral-fin length 17.1–19.1, dorsal-spine length 11.4–12.9, length of dorsal fin 24.4–27.3, length of dorsal-fin base 14.4–15.2, pelvic-fin length 13.9–15.5, length of anal-fin base 10.7–13.1, caudal-fin length 19.7–23.2, length of adipose-fin base 14.3–20.3, adipose-fin maximum height 4.0–5.1, post-adipose distance 14.1–14.6, dorsal to adipose distance 4.0–7.0; in %HL: snout length 31.1–35.2, interorbital distance 28.6–29.9, eye diameter 11.5–12.3, nasal barbel length 31.9–35.4, maxillary barbel length 237.6–298.9, inner mandibular barbel length 44.1–48.9, outer mandibular barbel length 78.2–93.9. Branchiostegal rays 9 (6). Gill rakers 3 + 9 = 12 (1). Vertebrae 27 + 25 = 52 (2).

Fin ray counts: dorsal II,7 (6); pectoral I,7 (1), I,8 (1) or I,9 (4); pelvic i,5 (6); anal iv,8 (3), v,8 (2) or iv,10 (1); caudal i,7,8,i (6). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, without distinct serrations on posterior edge. Pectoral spine stout, with 13–19 serrations on posterior edge. Caudal fin forked; first principal ray of upper lobe extending into a long filament; distal margin of upper and lower lobes rounded.

COLOR. — Preserved specimens have dorsal surface of head and body brown, gradually fading to dirty white on ventral surface. Pectoral, pelvic, anal and caudal fins brown with melanophores concentrated in interradial membranes. Dorsal fin brown with melanophores evenly distributed. Live specimens are olive green in color with orange-tipped fins (after Ramakrishniah 1988).

DISTRIBUTION. — Known only from the middle reaches of the Krishna River drainage in southern India (Fig. 2).

REMARKS. — *Hemibagrus maydelli* can be differentiated from all other species of *Hemibagrus* on the Indian subcontinent in having more vertebrae (52 vs. 44–46). In its general morphology, *H. maydelli* resembles both *H. microphthalmus* and *H. wyckioides* in having a strongly depressed head. It can be differentiated from both species in having a shorter distance between the dorsal and adipose fins (4.0–7.0 %SL vs. 8.6–14.2%SL), larger eyes (eye diameter 11.5–12.3 %HL vs. 8.4–11.6%HL), and an olive green body with orange fins (vs. gray body with red fins). *Hemibagrus maydelli* can be further differentiated from *H. microphthalmus* in having a shorter and deeper caudal peduncle (length of caudal peduncle 15.3–16.1 %SL vs. 16.4–18.1 %SL, depth of caudal peduncle 7.8–8.5 %SL vs. 6.8–7.7 %SL), a longer head (30.8–32.4 %SL vs. vs. 29.4–31.0 %SL).

Govind and Rajagopal (1975) reported the occurrence of *H. maydelli* from the Tungabahdra River as an unidentified the species of *Mystus*, stating that it resembled *H. punctatus* and further studies were needed to clarify its identity. Barman (1993) then erroneously considered *H. punctatus* to be present in the Krishna River drainage (*H. punctatus* is only known from the Cauvery River drainage further south), basing his record on that of Govind and Rajagopal (1975). *Hemibagrus maydelli* is a relatively large species that grows up to 1650 mm TL and 58.5 kg in weight (Govind and Rajagopal 1975; Jayaram 1995).

MATERIAL EXAMINED. — ZMH 2180 (1), holotype, 82.0 mm SL; India: Maharashtra state, Bhima River at Wadgaon; Maydell, 1955 (photograph and radiograph examined). ZSI FF2532, 271.8 mm SL; India: Andhra Pradesh State, Krishna River below Nagarjunasagar Reservoir; M. Ramakrishniah, 10 Feb 1982 (holotype of *Mystus krishnensis*). ZSI FF 2533 (1, 402.6 mm SL), locality as for ZSI FF2532; M. Ramakrishniah, 9 Mar 1983 (paratype of *Mystus krishnensis*). ZSI FF 2534 (1, 228.0 mm SL), locality as for ZSI FF2532; M. Ramakrishniah, 29 Jan 1985 (paratype of *Mystus krishnensis*). ZSI FF 2535 (1, 278.8 mm SL), locality as for ZSI FF2532; M. Ramakrishniah, 14 Dec 1980 (paratype of *Mystus krishnensis*). CAS 62087 (2, 167.2–214.7 mm SL), India, Karnataka State, Bellary District, Krishna River basin, Tungabahdra River and reservoir at Hospet, Hampi and Kampli; T. R. Roberts, 28 Jan–3 Feb 1985.

***Hemibagrus menoda* (Hamilton, 1822)**
Figs. 4, 5

Pimelodus menoda Hamilton, 1822:203, pl. 1 fig. 72 (figure erroneously labelled *Mugil corsula*; see below for explanation).
Bagrus trachacanthus Valenciennes, in Cuvier and Valenciennes, 1840:419; Bleeker, 1853:56.
Bagrus corsula Valenciennes, in Cuvier and Valenciennes, 1840:408; Bleeker, 1853:56.
Macrones menoda – Günther, 1864:74; Day, 1871b:706 (in part).
Macrones trachacanthus – Günther, 1864:75.
Macrones corsula – Day, 1869:307; 1877:446, pl. 100 fig. 5; 1889:153 (in part).
Mystus menoda – Shaw and Shebbeare, 1937:92, fig. 91; Jayaram and Singh, 1977:263; Menon, 1977:61; Ataur Rahman, 1974:7, 1989:199, fig. 119D; Shrestha. 1994:52, fig. 80.
Mystus (*Mystus*) *menoda* (in part) – Jayaram, 1954:546, fig. 9.
Mystus (*Mystus*) *menoda trachacanthus* – Jayaram, 1954:546.
Mystus (*Mystus*) *punctatus* (in part) – Jayaram, 1954:547.
Mystus (*Mystus*) *menoda* – Motwani et al., 1962:21; Srivastava, 1968:73, fig. 46.
Mystus corsula – Qureshi, 1965:42, fig. 103.
Mystus menoda menoda – Jayaram, 1977:33, fig. 25B (in part); Sen, 1985:137, fig. 75; 1992:183, fig. 60; Dutta et al., 1993:26.
Mystus menoda trachacanthus – Jayaram, 1977:33; Singh and Yazdani, 1993:21.
Mystus trachacanthus – Mo, 1991:130.
Hemibagrus menoda – Mo, 1991:132.

DIAGNOSIS. — *Hemibagrus menoda* can be differentiated from its congeners by the following unique combination of characters: head length 32.7–33.5 %SL, head depth 14.2–15.3 %SL, depth of caudal peduncle 7.5–8.8 %SL, eye diameter 11.9–12.3 %HL, a pattern of dark dots arranged in vertical columns on the sides of the body, a convex snout and a broad, shallowly incised humeral process.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. In %SL: head length 32.7–33.5, head width 19.3–21.7, head depth 14.2–15.3, predorsal distance 42.2–45.3, preanal length 71.2–77.5, prepelvic length 55.0–60.5, prepectoral length 28.6–30.3, body depth at anus 13.3–17.1, length of caudal peduncle 15.2–17.0, depth of caudal peduncle 7.5–8.8, pectoral-spine length 14.6–19.9, pectoral-fin length 18.6–24.0, dorsal-spine length 13.7–16.6, length of dorsal fin 24.3–27.4, length of dorsal-fin base 14.2–16.5, pelvic-fin length 14.7–16.1, length of anal-fin base 11.9–12.6, caudal-fin length 22.8–24.8, length of adipose-fin base 13.0–15.8, adipose-fin maximum height 3.8–4.5, post-adipose distance 15.0–17.4, dorsal to adipose distance 14.2–14.9; in %HL: snout length 36.2–38.8, interorbital distance 31.4–35.1, eye diameter 11.9–12.3, nasal barbel length 26.4–37.8, maxillary barbel length 191.4–213.3, inner mandibular bar-

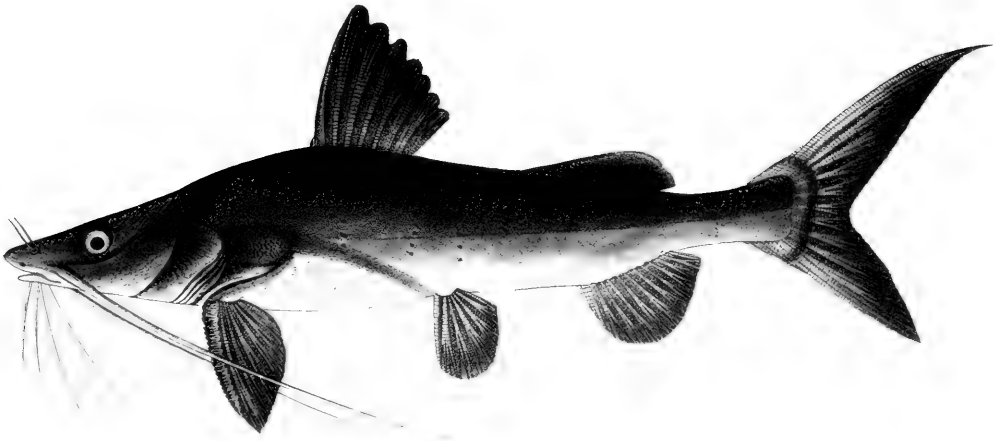

FIGURE 4. *Hemibagrus menoda*, illustration from Hamilton (1822), pl. 1, fig. 72.

bel length 36.8–48.1, outer mandibular barbel length 65.2–73.5. Branchiostegal rays 10 (2) or 11 (1). Gill rakers 3 + 9 = 12 (1) or 4 + 14 = 18 (1). Vertebrae 22 + 22 = 44 (1) or 24 + 21 = 45 (1).

Fin ray counts: dorsal II,7 (4); pectoral I,7 (2) or I,8 (2); pelvic i,5 (4); anal iv,8 (2), iii,9 (1) or iv,9 (1); caudal i,7,8,i (4). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, with 6–9 serrations on posterior edge. Pectoral spine stout, with 11–17 serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Preserved specimens have dorsal surface of head and body grayish-brown, gradually fading to dirty white on ventral surface. Lateral surface of body with about nine vertical columns of

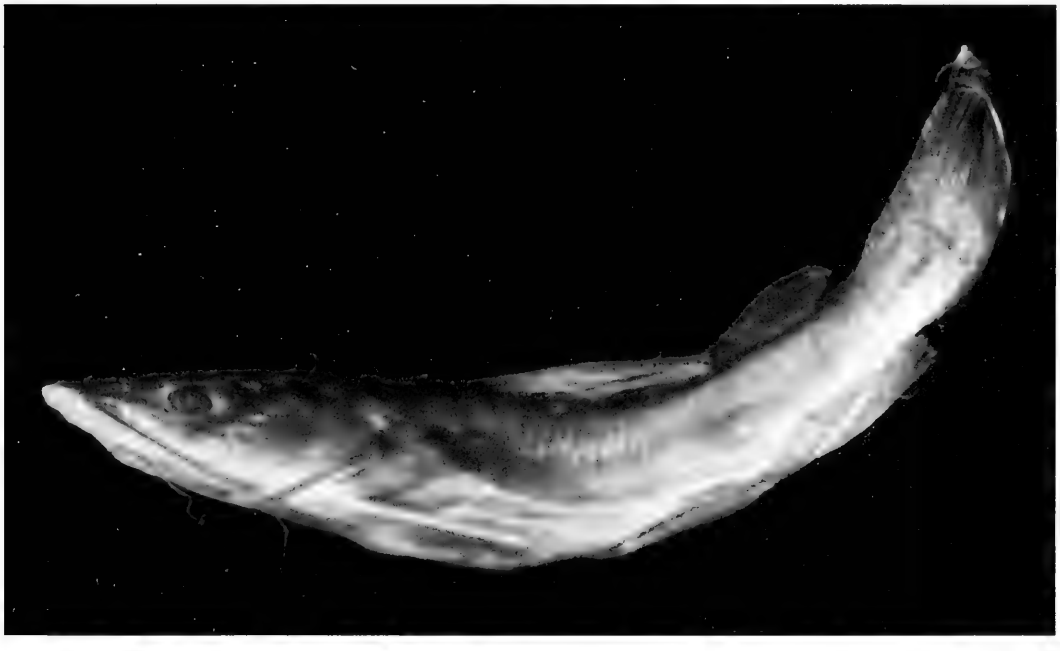

FIGURE 5. *Hemibagrus menoda*, neotype, UMMZ 208726, 202.6 mm SL; Bangladesh: Shari River.

black spots, largest spots being those in middle of columns along lateral line. Dorsal, pectoral, pelvic, and anal fins grayish brown, with scattered melanophores on fin rays and interradial membranes. Caudal fin grayish brown, with lighter hue along posterior margin, and on procurrent and outer principal caudal rays.

DISTRIBUTION. — Known from the Ganges, Brahmaputra, Mahanadi and Godavari river drainages in Bangladesh and northern India (Fig. 2).

REMARKS. — As indicated by the extensive synonymy of this species, the identity of *H. menoda* has been problematic. This is due, in large part, to the brief and vague original description in Hamilton (1822) and confusion over the significance of an illustration in that publication. The illustration in question, Plate 1 (Fig. 72), includes a lateral view of a catfish identified as "*Mugil corsula.*" A tipped-in corrigenda in one copy of Hamilton (1822) at the California Academy of Sciences includes the following statement: "For *Mugil Corsula* read *Pimelodus*, the *Mugil Corsula* being delineated Plate IX, Fig. 97." This sentence has been interpreted by several authors (e.g., Valenciennes, in Cuvier and Valenciennes, 1840 and Day, 1877) to mean that the name for the fish should be *Pimelodus corsula*, a name that is otherwise not mentioned in Hamilton's book. By examining the original drawings from which the plates of Hamilton (1822) were made, Day (1871a) found the names *Pimelodus menoda* and *P. telgagra* associated with the figure labeled as drawing no. 18, which was later published as Plate 1 (Fig. 72). On this basis, he later (Day 1877) placed the name *Pimelodus menoda* Hamilton in the synonymy of *Pimelodus corsula*. Somewhat later, Hora (1929) examined a duplicate set of drawings prepared for Hamilton and noted that the drawing that formed the basis of Plate 1 (Fig. 72) was identified as *Pimelodes telagra menoda*. On the basis of that drawing, Hora also concluded that the fish illustrated in Plate 1 (Fig. 72) was *Pimelodus menoda* Hamilton. Following Hora, most Indian ichthyologists have used the name *Macrones menoda*, or *Mystus menoda*, for the species that is represented in Hamilton's Plate 1 (Fig. 72). However, Valenciennes (in Cuvier and Valenciennes 1840) had previously attempted to match that illustration with one of the species described in Hamilton's text. Valenciennes concluded that the description of only one species, *Pimelodus carcio*, resembled the illustration to any degree. Even so, the description was considered sufficiently different such that Valenciennes chose not to associate the name with the figure and, instead, adopted the name *Bagrus corsula* for the illustrated species.

It is generally recognized that Hamilton did not retain specimens. Therefore, the identity of Hamilton's *Pimelodus menoda* and the relationship between that name and Plate 1 (Fig. 72) remains open to question. In order to stabilize the name *Hemibagrus menoda* (Hamilton), we believe it necessary to name a neotype for *Pimelodus menoda* and, in keeping with the current use of the name, we designate UMMZ 208726 as neotype. To further stabilize the nomenclature of this group, we choose the same specimen as the neotype of *Bagrus corsula* Valenciennes, a species name based only on Hamilton's Plate 1 (Fig. 72). By this action, *Bagrus corsula* becomes an objective junior synonym of *Pimelodus menoda*.

Hemibagrus menoda differs from all other species of *Hemibagrus* except *H. peguensis* in having a pattern of dark dots arranged in vertical columns on the sides of the body. *Hemibagrus menoda* differs from *H. peguensis* in having a longer head (32.7–33.5 %SL vs. 29.0–32.5 %SL), a more convex snout (Fig. 6) and a broader, less deeply incised humeral process (Fig. 7). *Hemibagrus menoda* is found only in the river drainages in Bangladesh and northern India. All records of *H. menoda* from Myanmar refer to *H. peguensis* instead.

MATERIAL EXAMINED. — NEOTYPE: UMMZ 208726, 202.6 mm SL; Bangladesh: Surma (Meghna) drainage, Sharighat bazaar, 22 miles NE of Sylhet on Sylhet-Shillong highway (said to be from Shari River); W. J. Rainboth and A. Rahman, 20 Feb 1978. Other material: ANSP 85796 (1, 115.0 mm SL), India, Bombay; Bombay Natural History Society, 1923. MNHN 1191 (1, 285.4 mm SL syntype of *Bagrus trachacanthus*), India, Bengal, A. Duvaucel, date unknown. ZSI 426 (1, 167.2 mm SL), India, Bombay: F. Day collection.

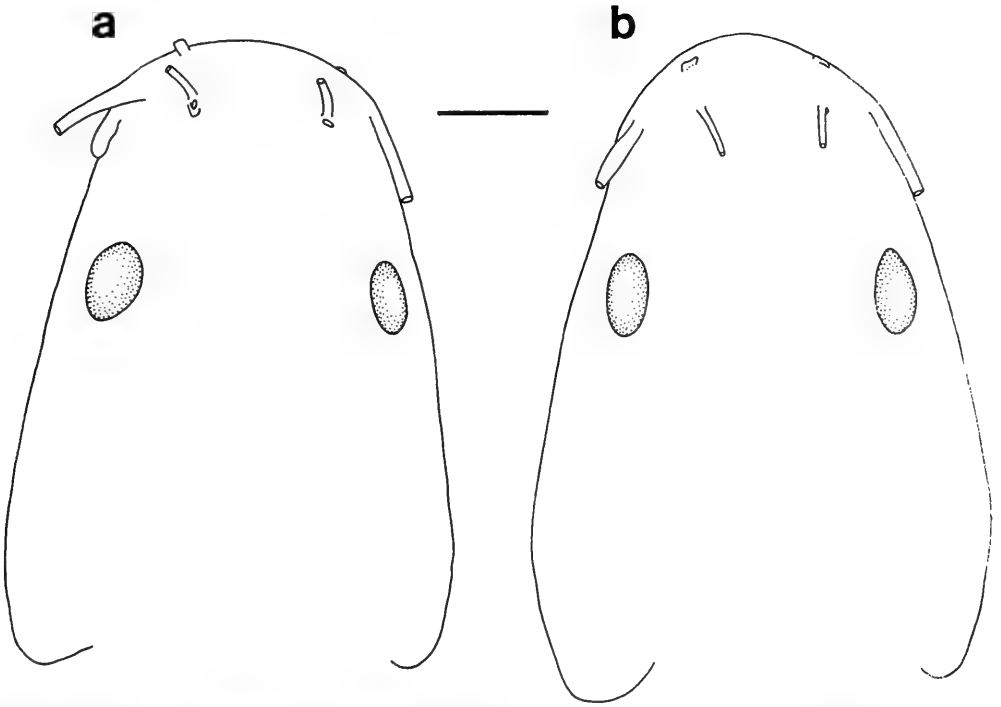

FIGURE 6. Dorsal views of heads of: a. *Hemibagrus peguensis*, CAS 133789, 212.7 mm SL; b. *H. menoda*, UMMZ 208726, 202.6 mm SL.

***Hemibagrus microphthalmus* (Day, 1877)**
Fig. 8

Macrones microphthalmus Day, 1877:446, pl. 100 fig. 4; 1889:154; Vinciguerra, 1890:225.
Mystus (Mystus) menoda microphthalmus – Jayaram, 1954:547.
Mystus microphthalmus – Tint Hlaing, 1971:513; Jayaram, 1977:34; Viswanath and Singh, 1986:197, fig. 1; Mo, 1991:130; Talwar and Jhingran, 1991:566.
Hemibagrus micropthalmus – Ukkatawewat and Vidthayanon, 1998:46.

DIAGNOSIS. — *Hemibagrus microphthalmus* can be differentiated from its congeners by a unique combination of the following characters: length of dorsal-fin base 13.7–16.7 %SL, dorsal to adipose distance 8.6–14.2 %SL, interorbital distance 28.4–31.8 %HL, eye diameter 9.2–11.3 %HL and a rounded snout.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. Head extremely depressed. In %SL: head length 29.4–31.0, head width 18.0–19.7, head depth 11.2–14.0, predorsal distance 40.6–44.1, preanal length 70.8–74.8, prepelvic length 53.2–55.9, prepectoral length 25.5–28.9, body depth at anus 10.2–14.5, length of caudal peduncle 16.4–18.1, depth of caudal peduncle 6.8–7.7, pectoral-spine length 11.0–14.1, pectoral-fin length 13.9–17.6, dorsal-spine length 9.2–10.8, length of dorsal fin 23.0–25.5, length of dorsal-fin base 13.7–16.7, pelvic-fin length 13.1–15.4, length of anal-fin base 11.2–13.3, caudal-fin length 19.8–23.5, length of adipose-fin base 18.4–25.9, adipose-fin maximum height 4.2–5.8, post-adipose distance 13.4–16.1, dorsal to adipose distance 8.6–14.2; in %HL: snout length 32.9–34.7, interorbital

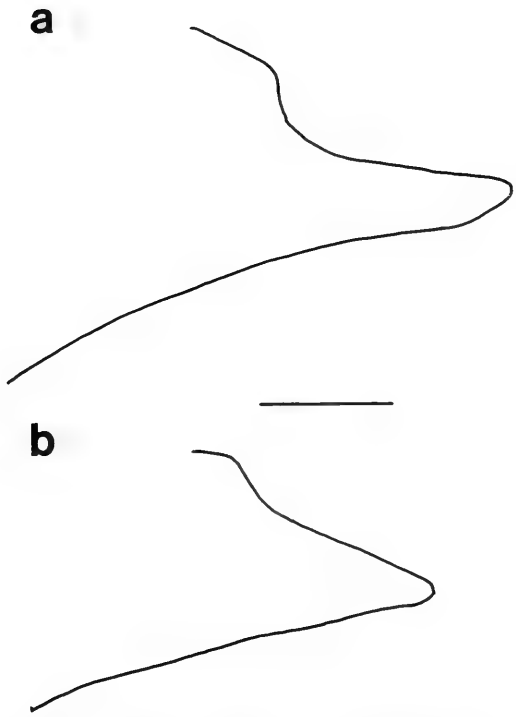

FIGURE 7. Humeral processes of: a. *Hemibagrus menoda*, UMMZ 208726, 202.6 mm SL; b. *H. peguensis*, CAS 89005, 261.9 mm SL.

distance 28.4–31.8, eye diameter 9.2–11.3, nasal barbel length 24.5–35.3, maxillary barbel length 256.4–300.6, inner mandibular barbel length 36.0–57.6, outer mandibular barbel length 65.8–97.2. Branchiostegal rays 9 (3) or 10 (8). Gill rakers 2 + 9 = 11 (1), 2 + 10 = 12 (2), 3 + 7 = 10 (1) or 3 + 9 = 12 (1). Vertebrae 26 + 25 = 51 (1), 28 + 23 = 51 (1), 28 + 24 = 52 (2), 28 + 25 = 53 (2), 29 + 25 = 54 (1) or 30 + 24 = 54 (1).

Fin ray counts: dorsal II,7 (11); pectoral I,7 (1), I,7,i (1), I,8 (1), I,8,i (1), I,9 (4) or I,9,i (3); pelvic i,5 (11); anal iv,8 (6), iii,9 (1) or iv,9 (4); caudal i,7,8,i (11). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, without distinct serrations on posterior edge. Pectoral spine stout, with 9–10 serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Preserved specimens with dorsal surface of head and body uniform gray (live or freshly-dead specimens generally darker, fading on preservation); ventral surfaces of head and body dirty white; adipose fin gray, distal edge orange in life but fading to light gray on preservation; caudal fin red in life, fading to gray with very light gray procurrent and outer principal caudal-rays on preservation; all other fins gray with distal portions of fin rays and inter-radial membranes red in life, fading to light gray on preservation. Maxillary barbel white.

DISTRIBUTION. — Known from the Salween River of Thailand, Irrawaddy and Sittang drainages in Myanmar and the Manipur drainage in India (Fig. 2).

REMARKS. — *Hemibagrus microphthalmus* is similar in form and coloration to *H. wyckioides*. In recent years, Roberts (1993) and Roberts and Warren (1994) have considered the latter species a junior synonym of *H. microphthalmus*. However, as discussed in Ng and Rainboth (1999), the two species differ in the shape of their snouts: *H. microphthalmus* has a rounded snout while *H. wyckioides* has a truncate snout (Fig. 11). *Hemibagrus microphthalmus* also has a narrower head (18.0–19.7 %SL vs. 19.5–23.9 %SL), shorter dorsal-fin base (13.7–16.7 %SL vs. 16.3–18.3 %SL) and more closely-set eyes (interorbital distance 28.4–31.8 %HL vs. 31.6–36.9 %HL) compared to *H. wyckioides*. Finally, the two species are geographically separate: *H. microphthalmus* is found only in the Salween, Irrawaddy, Sittang and Manipur drainages in Myanmar and India while *H. wyckioides* is only known from the Mekong and Chao Phraya drainages, and possibly the Mae Khlong drainage [reported by Roberts (1993) as *H. microphthalmus*, but we have not examined any specimen from the Mae Khlong to ascertain the exact identity of Roberts' record] in central Indochina.

MATERIAL EXAMINED. — AMS B.7918 (1, 164.0 mm SL syntype), and ZSI 2952 (1, 138.9 mm SL syntype), Burma: Irrawaddy River; F. Day, date unknown. BMNH 1893.2.16.7 (1, 133.5 mm SL). CAS 93192 (3, 132.0–151.5 mm SL), Myanmar: Irrawaddy River drainage, Mandalay markets; T. R. Roberts, Apr 1993. CMK 14706 (1, 204.6 mm SL), Thailand: Tak province, Mae Nam Moei at Mae Sarid (17°26′25″, 98°3′41″E); M. Kottelat and K. Kubota, 8 Apr 1998. NRM 13892 (1, 116.1 mm SL), Myanmar: Mandalay Division, Irrawaddy River drainage, Mandalay area; O. Hetzel, Apr 1935.

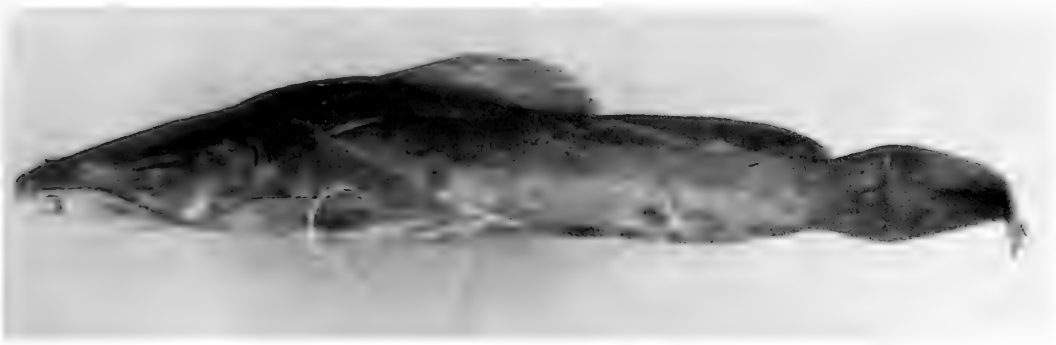

FIGURE 8. *Hemibagrus microphthalmus*, USNM 344670, 201.6 mm SL; Myanmar, Mandalay.

NRM 24979 (2, 144.6–165.1 mm SL), Myanmar: Sagaing Division, Irrawaddy River drainage, Shweli River; Maung Lu Daw, Feb 1935. NRM 31072 (1, 147.1 mm SL), Myanmar: Yangon Division, Yangon River at Yangon; R. Malaise, 30 Nov 1934. USNM 44754 (1, 158.7 mm SL), Myanmar: Irrawaddy River drainage, Mandalay; L. Fea, 1885–1889. USNM 344670 (2, 201.6–239.8 mm SL), Myanmar: Irrawaddy River drainage, Mandalay fish markets; C. J. Ferraris, D. Catania and U Myint Pe, 23 Apr 1996.

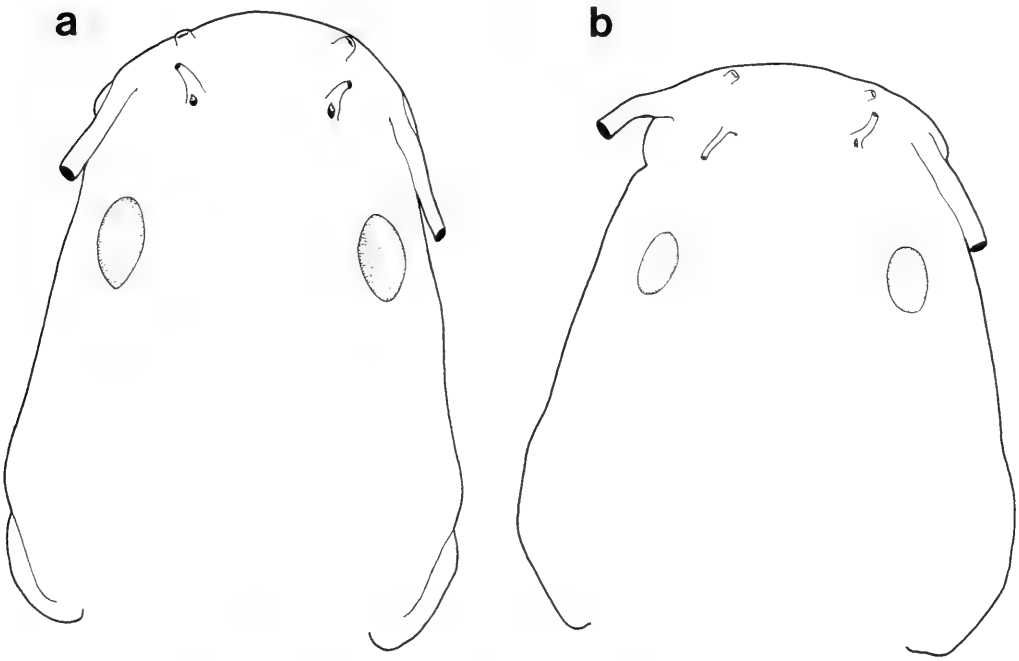

FIGURE 9. Dorsal views of heads of: a. *Hemibagrus microphthalmus*, NRM 13892, 116.1 mm SL; b. *H. wyckioides*, UMMZ 213974, 177.9 mm SL.

***Hemibagrus peguensis* (Boulenger, 1894)**
Fig. 10

Bagrus menoda (non Hamilton, 1822) – Blyth, 1860:285.
Macrones menoda (non Hamilton, 1822) – Day, 1871b:706 (in part); Vinciguerra, 1890:223.
Macrones corsula (non Hamilton, 1822) – Anderson, 1879:863; Kyaw Win, 1971:53, fig. 21.
Macrones peguensis Boulenger, 1894:196.
Mystus (*Mystus*) *menoda* (in part) – Jayaram, 1954:546.
Mystus (*Mystus*) *peguensis* – Jayaram, 1954:552.
Mystus menoda menoda (in part) – Jayaram, 1977:33.
Mystus peguensis – Jayaram, 1977:35; Talwar and Jhingran, 1991:569.
Hemibagrus peguensis – Mo, 1991:132.

DIAGNOSIS. — *Hemibagrus peguensis* can be differentiated from its congeners by a unique combination of the following characters: head length 29.0–32.5 %SL, a gently curving snout and a slender, deeply-incised humeral process, and nine vertical columns of black spots on the sides of the body.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. In %SL: head length 29.0–32.5, head width 18.8–21.7, head depth 12.9–15.2, predorsal distance 39.8–44.9, preanal length 70.6–74.0, prepelvic length 52.5–57.6, prepectoral length 25.4–30.8, body depth at anus 12.3–16.3, length of caudal peduncle 16.2–18.2, depth of caudal peduncle 7.6–8.8, pectoral-spine length 15.3–19.6, pectoral-fin length 18.2–20.9, dorsal-spine length 13.5–16.2, length of dorsal fin 23.8–27.8, length of dorsal-fin base 13.6–15.9, pelvic-fin length 13.3–15.5, length of anal-fin base 11.2–14.0, caudal-fin length 19.3–23.9, length of adipose-fin base 14.2–19.3, adipose-fin maximum height 3.7–4.9, post-adipose distance 15.4–17.4, dorsal to adipose distance 10.4–15.0; in %HL: snout length 36.3–39.9, interorbital distance 30.5–35.4, eye diameter 11.2–13.5, nasal barbel length 22.7–34.0, maxillary barbel length 160.6–212.6, inner mandibular barbel length 34.5–45.1, outer mandibular barbel length 57.4–70.2. Branchiostegal rays 9 (4) or 10 (13). Gill rakers 3 + 9 = 12 (2) or 4 + 8 = 12 (1). Vertebrae 23 + 21 = 44 (2), 24 + 20 = 44 (1), 23 + 22 = 45 (2) or 24 + 21 = 45 (4).

Fin ray counts: dorsal II,6 (1) or II,7 (16); pectoral I,8 (5), I,8,i (3), I,9 (5), I,9,i (3) or I,10 (1); pelvic i,5 (17); anal iv,6 (1), iv,7 (1), iii,8 (2), iv,8 (7), iii,9 (1), v,8 (2) or iv,9 (3); caudal i,7,8,i (17). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, with 6–11 serrations on posterior edge. Pectoral spine stout, with 15–19 serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Preserved specimens with dorsal surface of head and body grayish brown, gradually fading to dirty white on ventral surface. Lateral surfaces of body with about nine vertical columns of black spots, largest spots being those in middle of columns, along the lateral line. Dorsal, pectoral, pelvic and anal fins grayish brown, with scattered melanophores on fin rays and interradial membranes. Caudal fin grayish brown, with lighter hue along posterior margin, and on procurrent and outer principal caudal rays.

DISTRIBUTION. — Known from the Irrawaddy, Sittang and Pegu drainages in Myanmar (Fig. 2).

REMARKS. — *Hemibagrus peguensis* has long been misidentified as *H. menoda* (e.g., Day 1889; Jayaram 1954). Even in cases where it was considered a distinct species (e.g., Jayaram 1977; Talwar and Jhingran 1991), no clear distinguishing characters were used to separate the two species, nor was it recognised that *H. peguensis* superficially resembled *H. menoda*. As a result, these accounts often listed the presence of *H. menoda* in Myanmar when in fact the records actually refer to *H. peguensis*. *Hemibagrus peguensis* can be differentiated from *H. menoda* in having a shorter head (29.0–32.5

FIGURE 10. *Hemibagrus peguensis*, ZRC 43511, 243 mm SL; Myanmar, Yangon Division, Win Paw Hta River.

%SL vs. 32.7–33.5 %SL), a gently curving snout (Fig. 6) and a thinner, more deeply incised humeral process (Fig. 7).

Hemibagrus peguensis can be differentiated from *H. punctatus* in having a longer adipose-fin base (14.2–19.3 %SL vs. 10.1–13.2 %SL), a shorter distance between the dorsal and adipose fins (10.4–15.0 %SL vs. 16.3–19.4 %SL), a narrower caudal peduncle (7.6–8.8 %SL vs. 8.8–9.9 %SL) and a smaller eye (11.2–13.5 %HL vs. 13.8–15.7 %HL).

The original description of *H. peguensis* gives the total lengths of the syntypes as 20 mm. This is clearly a typographical error for 20 cm, which is the approximate total length of each of the syntypes.

MATERIAL EXAMINED. — BMNH 1894.5.21:25–26 (2, 168.8–185.1 mm SL syntypes), Myanmar, Taungoo; E. W. Oates, 1893. BMNH 1891.11.30:200–209 (16, 168.7–285.6 mm SL), Myanmar, Sittang River; E. W. Oates, 8 May 1891. CAS 89005 (1, 261.9 mm SL), Myanmar: Bago Division, Sittang River at Taungoo; C. J. Ferraris and D. Catania, 7 Apr 1996. CAS 93201 (1, 148.0 mm SL), Myanmar, Irrawaddy River drainage, Mandalay markets; T. R. Roberts, Apr 1993. CAS 133789 (1, 212.7 mm SL), Myanmar, Yangon Division, Pegu River drainage, 9 miles NW of Hlegu; A. W. Herre, 2 Apr 1937. NRM 15064 (2, 116.8–138.9 mm SL), Myanmar, Sagaing Division, Irrawaddy River drainage, Shweli River; Maung Lu Daw, Feb 1935. NRM 15105 (1, 166.8 mm SL), Myanmar, Mandalay Division, Mandalay; collector unknown, 1935. NRM 31068 (1, 186.1 mm SL), Myanmar, Kachin State, Irrawaddy River drainage, Myitkyina; R. Malaise, 10 Mar 1934. NRM 39397 (1, 290.6 mm SL), Myanmar, Bago Division, Bago; R. Malaise, 1934. ZSI 550 (1, 241.2 mm SL) and ZSI 551 (1, 265.6 mm SL), Myanmar: Tagoung; J. Anderson, date unknown.

Hemibagrus punctatus (Jerdon, 1849)

Fig. 11

Bagrus punctatus Jerdon, 1849:339.
Hemibagrus punctatus – Day, 1867:284.
Macrones punctatus – Day, 1877:445, pl. 100 fig. 3; 1889:153.
Mystus (*Mystus*) *punctatus* (in part) – Jayaram, 1954:547.
Mystus punctatus – Jayaram, 1977:36, fig. 25A; 1981:197, 201, fig. 95A; Mo, 1991:131; Talwar and Jhingran, 1991:570, fig. 188.
Mystus menoda menoda (non Day) – (?)Barman, 1993:223, fig. 94.

DIAGNOSIS. — *Hemibagrus punctatus* can be differentiated from its congeners by a unique combination of the following characters: head length 28.1–29.6 %SL, head depth 11.9–14.3 %SL, depth of caudal peduncle 8.8–9.9 %SL, eye diameter 13.8–15.7 %HL.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. In %SL: head length 28.1–29.6, head width 16.4–20.5, head depth 11.9–14.3, predorsal distance 39.8–42.0, preanal length 71.0–74.2, prepelvic length 53.3–54.2, prepectoral length 26.2–26.6, body depth at anus 11.9–14.3, length of caudal peduncle 16.1–18.6, depth of caudal peduncle 8.8–9.9, pectoral-spine length 15.6–18.1, pectoral-fin length 18.7–21.1, dorsal-spine length 13.9–15.9, length of dorsal fin 24.7–27.6, length of dorsal-fin base 14.7–17.4, pelvic-fin length 14.9–17.2, length of anal-fin base 11.8–14.3, caudal-fin length 21.4–23.9, length of adipose-fin base 10.1–13.2, adipose-fin maximum height 3.9–5.4, post-adipose distance 16.2, dorsal to adipose distance 16.3–19.4; in %HL: snout length 35.7–38.9, interorbital distance 31.3–32.5, eye diameter 13.8–15.7, nasal barbel length 27.5–40.3, maxillary barbel length 163.2–203.4, inner mandibular barbel length 31.7–45.6, outer mandibular barbel length 68.8–80.2. Branchiostegal rays 9 (2) or 10 (1). Gill rakers 4 + 8 = 12 (1) or 5 + 13 = 18 (1). Vertebrae 25 + 21 = 46 (1).

Fin ray counts: dorsal II,7 (3); pectoral I,9 (2) or I,10 (1); pelvic i,5 (3); anal iv,8 (1) or iv,9 (2); caudal i,7,8,i (3). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, with 5–7 serrations on posterior edge. Pectoral spine stout, with 12–19 serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Preserved specimens have dorsal surface of head and body grayish brown, fading to dirty white on ventral surface. Lateral surface of body with about 9–10 black spots arranged in horizontal row along lateral line. Dorsal, pectoral, pelvic and anal fins grayish brown, with scattered melanophores on fin rays and interradial membranes. Caudal fin grayish brown, with lighter hue along posterior margin, and on procurrent and outer principal caudal rays.

DISTRIBUTION. — Known only from the Cauvery River drainage in southern India (Fig. 2).

REMARKS. — *Hemibagrus punctatus* has generally been regarded as a species of *Mystus*, as recently as the work of Mo (1991). Our examination of specimens shows that the species has the depressed head characteristic of *Hemibagrus*, and should be placed within this genus instead.

Hemibagrus punctatus differs from *H. menoda* in having a shorter, flatter head (head length 28.1–29.6 %SL vs. 32.7–33.5%SL; head depth 11.9–14.3 %SL vs. 14.2–15.3%SL), deeper caudal peduncle (8.8–9.9 %SL vs. 7.5–8.8%SL) and larger eye (13.8–15.7 %HL vs. 11.9–12.3%HL). The color pattern of *H. punctatus* differs from that of *H. menoda* and *H. peguensis*. In the latter two species, the sides of the body are marked with a series of vertical columns of black spots, the largest of which is in the middle of the columns along the lateral line whereas in *H. punctatus*, there is only a single row of black spots located along the lateral line.

Babu Rao and Chattopadhyay (1969) record *H. punctatus* from west Bengal based on a specimen of 62.0 mm SL. According to their description, the specimen lacked the black spots on the sides of the body, a feature they attributed to the small size of the specimen. We have not examined enough material to ascertain if this is indeed the case, but the rest of their description does not seem to match that of *H. punctatus*. They stated that the maxillary barbels reached up to the middle of the pelvic fins, but the specimens of *H. punctatus* we examined do not have the maxillary barbels extending beyond the origin of the pelvic fins. Furthermore, they describe the snout of their specimen as being narrow (compared to *Mystus gulio*), but the snout of *H. punctatus* is actually broader than that of *M. gulio*. Therefore in the light of the available evidence, it seems very unlikely that their specimen was really *H. punctatus*. We have also examined specimens recorded as *H. punctatus* from Bombay, and have reidentified them as *H. menoda*. Barman (1993) recorded *H. menoda* (as *Mystus menoda menoda*) from the Krishna River drainage; although he had not examined any specimens, we feel that his record may refer to *H. punctatus* instead, given the proximity of the Cauvery and Krishna river drainages. Therefore, on the basis of the specimens we have examined and the literature, it appears that the distri-

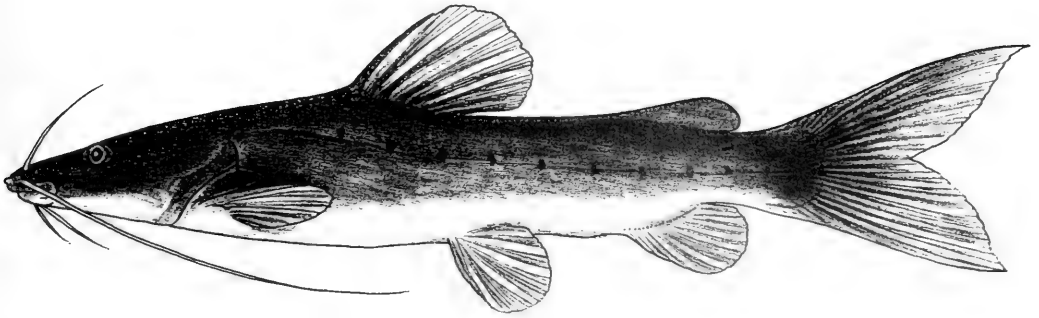

FIGURE 11. *Hemibagrus punctatus*, ZSI FF 1223, 1 ex., 193.1 mm SL; India: Hemavathy River at Huliva Laom.

bution of *H. punctatus* is restricted to the Cauvery River drainage (although it may occur in the Krishna River drainage) in southern India.

MATERIAL EXAMINED. — BMNH 1868.5.14:8 (1, 154.6 mm SL), India; F. Day collection. - ZSI F12403 (1, 120.2 mm SL), India, Karnataka State, Cauvery River at Coorg; C. R. Narayan Rao. ZSI FF 1223 (1, 193.1 mm SL), India, Karnataka State, Hemavathy River at Huliva Laom; K. C. Jayaram, 7 May 1977.

***Hemibagrus variegatus* sp. nov.**
Fig. 12

TYPE MATERIAL. — HOLOTYPE: BMNH 1992.11.16:11, 121.2 mm SL; Myanmar: Tenasserim River; T. R. Roberts, 3–8 Mar 1992.

DIAGNOSIS. — *Hemibagrus variegatus* can be differentiated from its congeners by a unique combination of the following characters: length of caudal peduncle 20.2 %SL, length of adipose-fin base 30.8 %SL, eye diameter 23.1 %HL, interorbital distance 28.6 %HL, 21 gill rakers, 50 vertebrae (24 postanal) and a variegated brown body with the sensory pores not readily visible.

DESCRIPTION. — Head depressed and broad, body moderately compressed. Dorsal profile rising evenly but not steeply from tip of snout to origin of dorsal fin, then sloping gently ventrally from there to end of caudal peduncle. Ventral profile horizontal to origin of anal fin, then sloping dorsally to end of caudal peduncle. Adipose fin with long base, spanning most of postdorsal distance. In %SL: head length 26.8, head width 18.2, head depth 13.6, predorsal distance 38.3, preanal length 69.6, prepelvic length 28.2, prepectoral length 23.8, body depth at anus 15.3, length of caudal peduncle 20.2, depth of caudal peduncle 9.1, pectoral-spine length 11.0, pectoral-fin length 16.5, dorsal-spine length 15.9, length of dorsal fin 24.3, length of dorsal-fin base 15.8, pelvic-fin length 7.9, length of anal-fin base 10.7, caudal-fin length 21.4, length of adipose-fin base 30.8, adipose-fin maximum height 4.9, post-adipose distance 13.8, dorsal to adipose distance 5.0; in %HL: snout length 40.6, interorbital distance 28.6, eye diameter 23.1, nasal barbel length 36.3, maxillary barbel length 243.1, inner mandibular barbel length 49.8, outer mandibular barbel length 78.2. Branchiostegal rays 11 (1). Gill rakers 5 + 16 = 21 (1). Vertebrae 26 + 24 = 50 (1).

Fin ray counts: dorsal II,7 (1); pectoral I,10 (1); pelvic i,5 (1); anal iv,7 (1); caudal i,7,8,i (1). Dorsal-fin origin nearer to tip of snout than to caudal flexure. Dorsal spine stout, without serrations on posterior edge. Pectoral spine stout, with 11 large serrations on posterior edge. Caudal fin forked; distal margins of upper and lower lobes rounded.

COLOR. — Preserved specimen has the dorsal surfaces of the head and body brown with irregular dark brown markings forming a variegated pattern; this color fades to a dirty white on the ventral sur-

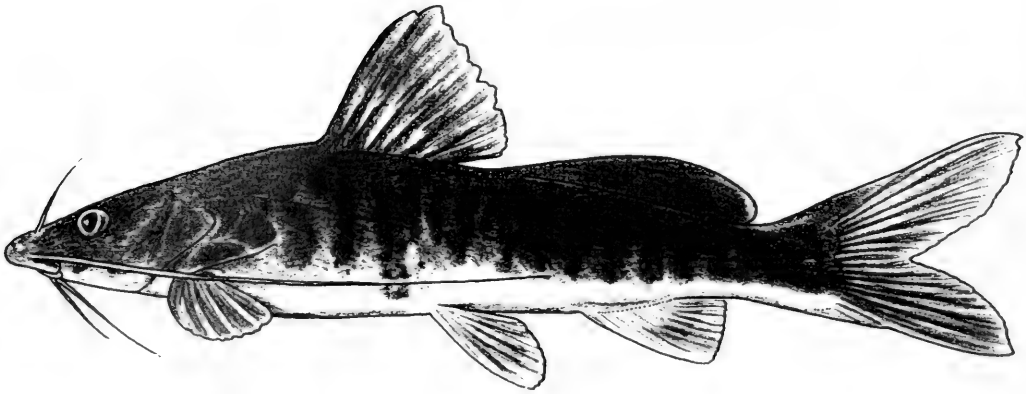

FIGURE 12. *Hemibagrus variegatus*, holotype, BMNH 1992.11.16.11; Myanmar: Tenasserim River.

faces. All fins brown, with melanophores on fin rays and interradial membranes; melanophores are more concentrated in the interradial membranes of the dorsal, pectoral, pelvic and anal fins.

ETYMOLOGY. — From the Latin *variegatus*, meaning of different colors. In reference to the irregular dark brown markings on the sides of the body.

DISTRIBUTION. — Known only from the Tenasserim River drainage in southern Myanmar (Fig. 2).

REMARKS. — As mentioned above, *H. variegatus* is one of the only two known species of southern Asian *Hemibagrus* (the other being *H. imbrifer*) which has a long-based adipose fin spanning nearly all of the postdorsal distance. When compared with other species of *Hemibagrus* with long adipose-fin bases, *H. variegatus* has fewer vertebrae (50 vs. 52–60) than *H. olyroides* and East Asian species allied with *H. guttatus*, and more vertebrae (50 vs. 44–47) than *H. baramensis* and *H. sabanus*.

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LITERATURE CITED

ANDERSON, J. 1879. Anatomical and zoological researches; comprising an account of the zoological results of the two expeditions to western Yunnan in 1868 and 1875. Bernard Quaritch, London.

ATAUR RAHMAN, A. K. 1974. Aid to the identification of the mystid catfishes of Bangladesh. Bangladesh Journal of Zoology 2:1–112.

———. 1989. Freshwater fishes of Bangladesh. Zoological Society of Bangladesh, Dhaka. xvii + 364 pp.

BABU RAO, M. AND S. K. CHATTOPADHYAY. 1969. Systematic studies on *Mystus* spp. (Pisces: Bagridae) of west Bengal. Journal of the Bengal Natural History Society 35:86–104.

BARMAN, R. P. 1993. Pisces: Freshwater Fishes. Pp. 89–334 *in* State Fauna Series 5: Fauna of Andhra Pradesh. Part 1. A. K. Ghosh, ed. Zoological Survey of India, Calcutta.

BAILEY, R. M. 1951. The authorship of names proposed in Cuvier and Valenciennes' "Histoire Naturelle des Poissons." Copeia 1951(3):249–251.

BLEEKER, P. 1853. Nalezingen op de ichthyologische fauna van Bengalen en Hindostan. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 25:1–164.

———. 1862. Atlas ichthyologique des Indes Orientales Néêrlandaises, publié sous les auspices du Gouvernement colonial néêrlandais. Tome II. Siluroïdes, Chacoïdes et Hétérobranchoïdes. Lange and Co., Amsterdam, 1–112, pls. 49–101.

BLYTH, E. 1860. Report on some fishes received chiefly from the Sitang River and its tributary streams. Journal of the Asiatic Society (Calcutta) 29:138–174.

BOULENGER, G. A. 1894. Description of a new siluroid fish from Burma. Annals and Magazine of Natural History, Series 6 14:196.

CUVIER, G. AND A. VALENCIENNES. 1840. Histoire naturelle des poissons. Tome 14. Pitois-Levrault, Paris. xxiv + 464 pp. [Date of publication corrected from 1839, based on Bailey (1951).]

DAY, F. 1867. On the fishes of the Neilgherry Hills and rivers around their bases. Proceedings of the Zoological Society of London 1867:281–302.

———. 1869. On the fishes of Orissa – Part I. Proceedings of the Zoological Society of London 1869:296–310.

———. 1871a. On Hamilton Buchanan's original drawings of fish in the library of the Asiatic Society of Bengal. Proceedings of the Asiatic Society of Bengal 1871:195–209.

———. 1871b. On the freshwater siluroids of India and Burmah. Proceedings of the Zoological Society of London 1871:703–721.

———. 1877. The fishes of India, being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Bernard Quaritch, London. Part 3:369–552, pls. 79–138.

———. 1889. The fauna of British India, including Ceylon and Burma. Fishes. Vol. 2. Taylor and Francis, London. xiv + 509 pp.

DUTTA, A. K., D. K. KUNDU, AND A. K. KARMAKAR. 1993. Freshwater Fishes. Pp. 1–37 *in* State Fauna Series 1: Fauna of Orissa. Part 4. A. K. Ghosh, ed. Zoological Survey of India, Calcutta.

ESCHMEYER, W. E., ed. 1998. Catalog of Fishes. California Academy of Sciences, San Francisco. 2905 pp.

GOVIND, B. V. AND K. V. RAJAGOPAL. 1975. Occurrence of a giant *Mystus* species in Krishna river system. Matsya 1:79–80.

GRANT, S. A. 1999. A replacement name (*nomen nudum*) and neotype designation for *Hara malabarica* Day, 1865, with notes on related species (Siluriformes). Aqua 3:169–174.

GÜNTHER, A. 1864. Catalogue of the fishes in the British Museum, volume 5. Catalogue of the Physostomi, containing the families Siluridae, Characinidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae in the collection of the British Museum. British Museum (Natural History), London. xxii + 455 pp.

HAMILTON, F. 1822. An account of the fishes found in the river Ganges and its branches. Privately published, Edinburgh and London. vii + 405, atlas with 39 pls.

HORA, S. L. 1929. An aid to the study of Hamilton Buchanan's "Gangetic Fishes." Memoirs of the Indian Museum 9:169–192.

JAYARAM, K. C. 1954. Siluroid fishes of India, Burma and Ceylon XIV. Fishes of the genus *Mystus* Scopoli. Records of the Indian Museum 51:527–558.

———. 1977. Aid to the identification of the siluroid fishes of India, Burma, Sri Lanka, Pakistan and Bangladesh 1. Bagridae. Records of the Zoological Survey of India, Miscellaneous Publication, Occasional Paper No. 8. 41 pp.

———. 1981. The freshwater fishes of India, Pakistan, Bangladesh, Burma and Sri Lanka—a handbook. Zoological Survey of India, Calcutta. viii + 475 pp.

———. 1995. The Krishna River System Bioresources Study. Records of the Zoological Survey of India, Occasional Paper No. 160. 167 pp.

JAYARAM, K. C. AND K. P. SINGH. 1977. On a collection of fish from North Bengal. Records of the Zoological Survey of India 72:243–275.

JERDON, T. C. 1849. On the fresh-water fishes of southern India. (Continued from p. 149.). Madras Journal of Literature and Science 15:302–346.

KYAW WIN. 1971. A taxonomy of fishes of Taung-tha-man 'inn', upper Burma. Union of Burma Journal of Life Sciences 4:39–63.

MENON, A. G. K. 1977. A check-list of fishes of the Himalayan and Indo-Gangetic plains. Inland Fisheries Society of India, Special Publication No. 1. vii + 136 pp.

MO, T. 1991. Anatomy and systematics of Bagridae (Teleostei) and siluroid phylogeny. Koeltz Scientific Books, Koenigstein, Germany. vii + 216 pp, 63 pages of figures.

MOTWANI, M. P., K. C. JAYARAM, AND K. L. SEGHAL. 1962. Fish and fisheries of Brahmaputra river system, Assam. 1. Fish fauna with observations on their zoogeographical significance. Tropical Ecology 3:17–43.

NG, P. K. L. AND H. H. NG. 1995. *Hemibagrus gracilis*, a new species of large riverine catfish (Teleostei: Bagridae) from Peninsular Malaysia. Raffles Bulletin of Zoology 43:133–142.

NG, H. H. AND W. J. RAINBOTH. 1999. The bagrid catfish genus *Hemibagrus* (Teleostei: Siluriformes) in central Indochina with a new species from the Mekong River. Raffles Bulletin of Zoology 47(2):555–576.

QURESHI, M. R. 1965. Common freshwater fishes of Pakistan. Government Press, Karachi. viii + 61 pp.

RAMAKRISHNIAH, M. 1988. A new bagrid fish of the genus *Mystus* (Scopoli) from Krishna river system. Matsya 12–13:139–143.

ROBERTS, T. R. 1993. Artisanal fisheries and fish ecology below the great waterfalls of the Mekong River in southern Laos. Natural History Bulletin of the Siam Society 41:31–62.

———. 1994. Systematic revision of Asian bagrid catfishes of the genus *Mystus* sensu stricto, with a new species from Thailand and Cambodia. Ichthyological Explorations of Freshwaters 5(3):241–256.

ROBERTS, T. R. AND T. J. WARREN. 1994. Observations on fishes and fisheries in southern Laos and northeastern Cambodia, October 1993–February 1994. Natural History Bulletin of the Siam Society 42:87–115.

RÖSSEL, F. 1964. Welse (Siluroidea), gesammelt von de deutschen Indien-Expedition 1955/58. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 61:145–158.

SEN, T. K. 1985. The Fish Fauna of Assam and the Neighbouring North-eastern States of India. Occasional Paper of the Zoological Survey of India No. 64. 216 pp.

———. 1992. Freshwater fish. Pp. 101–242 *in* State Fauna Series 3: Fauna of West Bengal. Part 2. Reptilia, Amphibia, Fishes, Hemichordata and Archaeozoology. A. K. Ghosh, ed. Zoological Survey of India, Calcutta.

SHAW, G. E. AND E. O. SHEBBEARE. 1937. The fishes of northern Bengal. Journal of the Royal Asiatic Society, Science 3:1–137, 6 pls.

SHRESTHA, J. 1994. Fishes, fishing implements and methods of Nepal. Smt. M. D. Gupta, Lashkar. Iv + 150 pp.

SINGH, D. F. AND G. M. YAZDANI. 1993. Ichthyofauna of Konkan region of Maharashtra (India). Records of the Zoological Survey of India, Occasional Paper No. 145. 46 pp.

SRIVASTAVA, G. J. 1968. Fishes of eastern Uttar Pradesh. Vishwavidyalaya Prakashan, Varanasi. xxii + 163 pp.

TALWAR, P. K. AND A. G. JHINGRAN. 1991. Inland fishes of India and adjacent countries. Oxford and IBH Publishing Company, New Delhi, 2 vols., 1158 pp.

TINT HLIANG. 1971. A classified list of fishes of Burma. Union of Burma Journal of Life Sciences 4:507–526.

UKKATAWEWAT, S. AND C. VIDTHAYANON. 1998. Fishes of the Salween River basin, Thailand. Aquatic Natural Resources Museum Technical Paper 2:1–89.

VINCIGUERRA, D. 1890. Viaggo di Leonardo Fea in Birmania e regioni vicini. XXIV. Pesci. Annali del Museo Civico de Storia Naturale de Genova (serie 2a) 9:129–362, pls. 7–11.

VISHWANATH, W. AND H. T. SINGH. 1986. First record of the bagrid catfish *Mystus microphthalmus* from India. Japanese Journal of Ichthyology 33:197–199.

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Chromosome Numbers of South African Acanthaceae

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Original meiotic chromosome counts are presented for 19 species in 14 genera of Acanthaceae from South Africa. These counts represent the initial reports of chromosome numbers from southern African Acanthaceae. Chromosome numbers of 13 species representing 11 genera are reported for the first time. The counts in *Aulojusticia*, *Duvernoia*, and *Metarungia* are the first for these genera. Counts for five species confirm numbers previously reported for them based on plants from other regions. A new chromosome number is reported in *Justicia* (n = 26 in *J. petiolaris*). Systematic implications of these chromosome counts are addressed.

The Acanthaceae are a large (ca. 4000 species in some 230 genera) pantropical family with major concentrations of species in southeastern mainland Asia, insular Malesia, the Indian subcontinent, Madagascar, tropical Africa, Brazil, Andean South America, and Mexico-Central America. Knowledge of chromosome numbers among Acanthaceae has proven useful in resolving generic positions of problematic species, reassessing phylogenetic relationships among subfamilial taxa, and understanding morphological variation (e.g., Ensermu Kelbessa 1990; Daniel and Chuang 1993; McDade et al. in press). A major problem with using chromosome number data in the study of systematic and evolutionary relationships among Acanthaceae is that numbers remain unknown for the vast majority of both genera and species. Daniel (2000) noted that chromosome numbers had been reported for only 29% of the genera and less than 12% of the species of Acanthaceae. Similarly, chromosome numbers remain undetermined for five of the 12 tribes recognized by Bremekamp (1965) in the family: Haselhoffieae, Louteridieae, Rhombochlamydeae, Stenandriopsideae, and Whitfieldieae. Another problem is the lack of, or poor sampling of, species from regions rich in Acanthaceae but underrepresented by chromosome counts of them. One such region, as identified by Daniel (2000), is southern Africa. This region, comprising Namibia, Botswana, South Africa, Lesotho, and Swaziland, has an acanthaceous flora of some 341 species (Welman 1993). Chromosome numbers have been reported previously for 28 of these (see Appendix), but none of these reports was based on collections from southern Africa. This study of chromosome numbers in selected Acanthaceae from South Africa is our first attempt to provide this systematically useful information for taxa from this region.

METHODS

In February and March of 1999, floral buds and herbarium vouchers of South African Acanthaceae were collected from their native habitats and from plants cultivated in gardens. Buds were fixed in absolute ethanol:glacial acetic acid (3:1) for 24 hours and subsequently washed and stored in ethanol (70%) until analyzed. Anthers were macerated in ferric acetocarmine (1%) on a microscope slide, squashed under a coverslip by hand, and studied under oil immersion on a phase contrast microscope at a magnification of 1000×. Counts were made from microsporocytes in various stages of meiosis. Preparations from which counts were obtained were recorded with camera lucida drawings. Voucher specimens are deposited at CAS and J. The camera lucida drawings are attached to the vouchers at CAS.

In the following discussion, all previously published chromosome counts are listed as n (gametic, haploid, meiotic) numbers irrespective of whether they were originally reported as gametophytic or sporophytic numbers. Voucher specimens, if they exist, documenting previous counts by other workers have not been examined.

RESULTS

Chromosome numbers determined for 19 species representing 14 genera of Acanthaceae from South Africa are summarized in Table 1 and illustrated in Figures 1–3. Chromosome numbers of 13 of these taxa are reported for the first time. The counts for *Aulojusticia*, *Duvernoia*, and *Metarungia* represent the first reports for these genera. Counts for five species (*Asystasia gangetica*, *Hypoestes aristata*, *H. forskaolii*, *Justicia betonica*, and *Rhinacanthus gracilis*) agree with some or all numbers previously reported for them from different sources. The chromosome number reported here for *Justicia odora* is the first non-approximate number reported for the species. The count of $n = 26$ for *J. petiolaris* is the first report of this number in the genus.

DISCUSSION

Asystasia Blume. Fifty or more species are recognized in this genus, which is native to the Old World. Eight species are known from southern Africa (Welman 1993). Daniel (2000) summarized previous reports of chromosome numbers in both *A. gangetica* and in the genus. Although a diversity of meiotic numbers, including 14, 22, 24 and 25, has been reported for *A. gangetica*, counts of $n = 13$ and $n = 26$ are much more common. A meiotic number of 13 is also the most frequently reported chromosome number among other species in the genus.

Asystasia gangetica has a broad distribution, occurring indigenously in southern and tropical Africa and in the Indian subcontinent. It has become naturalized in several other tropical regions (e.g., Hawaii, Java). Previous counts (including those reported for *A. coromandeliana* Nees; see summary of counts in Daniel 2000) have come from plants in cultivation (without provenance data; e.g., Grant 1955), from the Indian subcontinent (e.g., Valsala Devi and Mathew 1982), from tropical west Africa (e.g., Gadella 1977), and from plants naturalized outside of the native range of the species (e.g., Daniel 2000). Our count of $n = 13$ for a southern African representative of the species reveals a continuity of chromosome number with plants from other portions of the species' range. Plants from which our count was determined would appear to be diploid within the species. As indicated by Daniel (2000), a basic number of $x = 13$ appears likely for the genus.

Aulojusticia Lindau. Our count of $n = 40$ for *A. linifolia* is the first chromosome count for this genus. *Aulojusticia* has been variably treated by students of Acanthaceae: Dyer (1975) recognized it as a unispecific genus endemic to northeastern South Africa; Graham (1988) included it within her broad

TABLE 1. Meiotic chromosome counts of South African Acanthaceae. Note: Counts for *Duvernoia aconitiflora*, *Justicia petiolaris*, *Metarungia longistrobus*, *Pseuderanthemum hildebrandtii*, and *Ruspolia hypocrateriformis* were obtained from plants in cultivation; * indicates first counts for taxa.

Taxon	Chromosome number (n)	Locality (province)	Collection number (Daniel et al.)
Asystasia gangetica (L.) T. Anderson	13	KwaZulu-Natal	9348
Aulojusticia linifolia Lindau	40*	Mpumalanga	9388
Barleria senensis Klotzsch	16*	Mpumalanga	9375
Crabbea angustifolia Nees	21*	Mpumalanga	9370
Dicliptera heterostegia Presl. ex Nees	15*	KwaZulu-Natal	9329
Dicliptera magaliesbergensis K. Balkwill	13*	Gauteng	9357
Duvernoia aconitiflora A. Meeuse	17*	Gauteng	9361
Hypoestes aristata (Vahl) Sol. ex R. & S.	30	KwaZulu-Natal	9351
Hypoestes forskaolii (Vahl) R.Br.	15	Gauteng	9358
Isoglossa hypoestiflora Lindau	17*	KwaZulu-Natal	9341
Isoglossa ovata (Nees) Lindau	17*	KwaZulu-Natal	9336
Justicia betonica L.	17	KwaZulu-Natal	9330
Justicia betonica L.	17	KwaZulu-Natal	9334
Justicia odora (Forssk.) Lam.	14	North-West	9364
Justicia petiolaris (Nees) T. Anderson	26*	Mpumalanga	9387
Metarungia longistrobus (C. B. Cl.) Baden	14*	Gauteng	9355
Pseuderanthemum hildebrandtii Lindau	21*	Mpumalanga	9394
Rhinacanthus gracilis Klotzsch	15	KwaZulu-Natal	9340
Rhinacanthus gracilis Klotzsch	15	KwaZulu-Natal	9328
Ruspolia hypocrateriformis (Vahl) Milne-Redh.	21*	Gauteng	9359
Ruttya ovata Harv.	21*	KwaZulu-Natal	9338

circumscription of *Justicia*; and Immelman (1995a) treated it as *Siphonoglossa linifolia* (Lindau) C. B. Clarke. *Siphonoglossa*, which is based on an American type, is conspecific with *Justicia* (Graham 1988, Daniel 1995). Molecular studies that seek to improve our understanding of *Justicia* and allied genera in Africa are currently underway. *Aulojusticia* undoubtedly falls within the morphological circumscription of *Justicia* as delimited by Graham. If treated in that genus, the chromosome number here reported for *A. linifolia* would be the highest number so far known in *Justicia*; the highest number previously reported is $n = 34$ (Daniel 2000). Also, if treated in *Justicia*, which appears to have a basic number of $x = 7$ (see below), then this species likely would have been derived from a hexaploid ancestor.

Barleria L. *Barleria* is a pantropical genus of perennial herbs and shrubs comprising some 300 species. The majority of species are African and 69 occur in southern Africa (Balkwill and Balkwill 1997). Daniel and Chuang (1989, 1998) summarized previously reported chromosome numbers in *Barleria*. They noted the prevalence of $n = 20$ among species of the genus and the likelihood of $x = 20$ as a basic number in the genus.

Our count of $n = 16$ for *Barleria senensis* is the first count for this species, which is native to southern and tropical Africa. Previously, this number has been reported in the genus once for *B. cristata* L. (Datta and Maiti 1970, as "*B. cristata* var. *dichotoma*"). There are many counts for this species and most of them are $n = 20$ (Daniel and Chuang 1989). Because these two species are treated in

different subgenera of *Barleria* (Balkwill and Balkwill 1997), a common chromosome number between them is doubtfully due to common ancestry.

Barleria was treated in tribe Barlerieae by Lindau (1895) and in tribe Ruellieae, subtribe Barleriinae by Bremekamp (1965) and Balkwill and Getliffe Norris (1988). Based on DNA sequence data (Hedrén et al. 1995; Scotland et al. 1995; McDade and Moody 1999), *Crabbea* and *Lepidagathis* would appear to be closely related to *Barleria*. A chromosome number of $n = 21$ has been reported in species from each of these three genera (Chuang et al. 1963; Grant 1964; De 1966; Daniel in press, see below) suggesting a possible symplesiomorphic number among them. Additional counts of species in *Barleria* are needed in order to ascertain whether knowledge of chromosome numbers will help to resolve infrageneric relationships.

Crabbea Harv. Two previous chromosome counts have been reported for this African genus of about 12 species, seven of which occur in southern Africa (Welman 1993). Our count of $n = 21$ for the South African endemic, *C. angustifolia*, is the first report of a chromosome number in the species. It agrees with a previous count for *C. velutina* S. Moore (Grant 1964, as *C. reticulata* C. B. Clarke). Renard et al. (1983) reported n = ca. 14 for *C. velutina*.

Based on the few counts for species of *Crabbea*, a basic number of $x = 21$ is tentatively proposed for the genus. Lindau (1895) included *Crabbea* in his tribe Barlerieae and the genus would be included in Bremekamp's (1965) tribe Ruellieae, subtribe Barleriinae. As noted above under *Barleria*, this number is known in the related genera *Barleria* and *Lepidagathis*. Balkwill and Getliffe Norris (1988) advocated the placement of *Crabbea* in the Ruellieae, Ruelliinae. Among genera of Ruelliinae for which chromosome numbers are known, $n = 21$ has been reported in several species of *Eranthemum* L. (e.g., Kaur 1970; Govindarajan and Subramanian 1985; Mangenot and Mangenot 1958, 1962).

Dicliptera Juss. Chromosome numbers have been reported for 22 of the more than 100 species of perennial herbs and shrubs in this pantropical genus. Fifteen of these species are from the New World and seven are native to the Old World. Counts for all New World species are $n = 40$ (or n = ca. 40; Daniel 2000, Daniel and Chuang 1993, Piovano and Bernardello 1991) whereas previous counts of species from the Old World comprise $n = 10, 13, 15, 24$, and 26 (with $n = 13$ being most frequently reported; Daniel and Chuang 1993). The species of *Dicliptera* from the Old World that were studied are all indigenous to Asia and comprise: *D. bupleuroides* Nees, *D. cuneata* Nees, *D. elegans* W. W. Smith [Kaur (1970) identified this taxon as "*Dicliptera elegans* Dalz.," and neither the source of the plant nor a voucher was cited; Dalziel did not publish a species with this name and whether the plant studied by Kaur is actually the Chinese species described by Smith or an Indian taxon is not known], *D. leonotis* Dalziel ex C. B. Clarke, *D. parvibracteata* Nees, *D. roxburghiana* Nees, and *D. verticillata* (Forsk.) C. Chr. Although two of these species (i.e., *D. leonotis* and *D. verticillata*) also occur in tropical Africa, chromosome numbers for all of the Old World species of *Dicliptera* were apparently determined from Asian populations. Our counts would therefore appear to be the first from African plants, and the first for species of *Dicliptera* native to southern Africa. Twelve species of *Dicliptera* are known to occur in southern Africa (Balkwill et al. 1996). The count of $n = 13$ for *D. magaliesbergensis* agrees with the majority of previous counts for Old World species. The count of $n = 15$ for *D. heterostegia* agrees with a count by Kaur (1970) for the widespread Paleotropical species *D. verticillata*.

Daniel et al. (1990) noted that the difference in ploidal level between species of *Dicliptera* in the Old and New Worlds suggests a major geographical division in the genus. Recent phylogenetic studies of the Justicieae that included Paleotropical and Neotropical species of *Dicliptera* indicate that the genus is monophyletic and is related to *Hypoestes* and *Peristrophe* in subtribe Diclipterinae (McDade et al. in press).

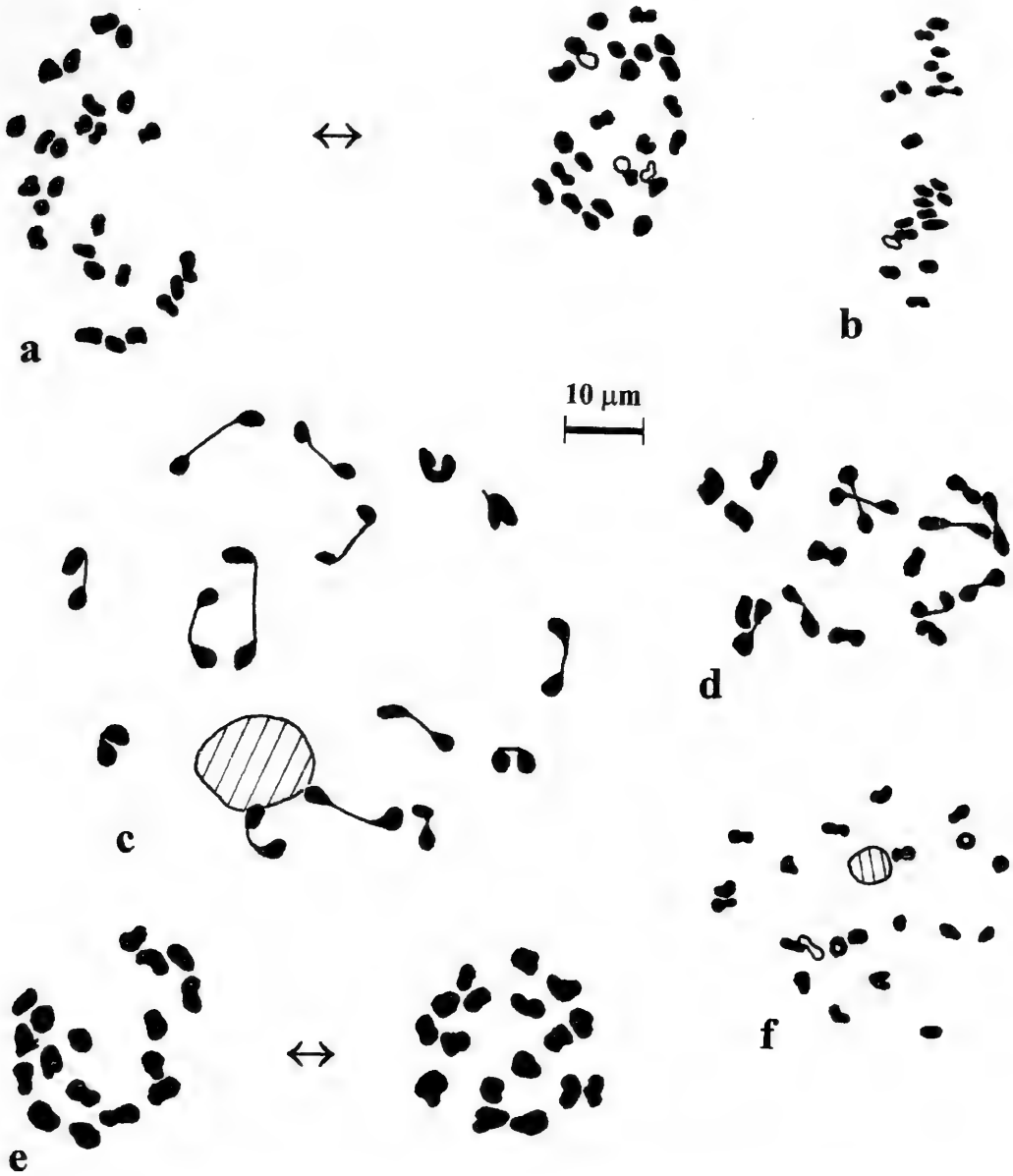

FIGURE 1. Camera-lucida drawings of meiotic chromosome preparations. a. *Justicia petiolaris* (*Daniel et al. 9387*), $n = 26$ (telophase I). b. *Ruttya ovata* (*Daniel et al. 9338*), $n = 21$ (metaphase I). c. *Dicliptera heterostegia* (*Daniel et al. 9329*), $n = 15$ (diakinesis I). d. *Duvernoia aconitiflora* (*Daniel et al. 9361*), $n = 17$ (metaphase I). e. *Isoglossa ovata* (*Daniel et al. 9336*), $n = 17$ (telophase I). f. *Pseuderanthemum hildebrandtii* (*Daniel et al. 9394*), $n = 21$ (diakenesis I).

Piovano and Bernardello (1991) noted that, based on chromosome numbers so far reported in *Dicliptera*, $x = 10$ is likely the basic number of the genus. The occurrence of $n = 15$ in species of all genera of Diclipterinae, however, suggests that $x = 15$ is symplesiomorphic for both the subtribe and *Dicliptera* (Daniel and Chuang 1993, McDade et al. in press).

Duvernoia E. Mey. ex Nees. This genus of two species that are endemic to eastern South Africa and Mozambique is sometimes treated within *Justicia* (Graham 1988; Brummitt 1992). Bremekamp (1939) argued for the recognition of *Duvernoia*, primarily on the basis of its pollen, and treated at least one species from the New World in it. Our count of $n = 17$ for *D. aconitiflora* is the first report of a chromosome number for both the genus and the species. Manning and Getliffe Norris (1995) treated the genus as distinct from others in the tribe Justicieae, subtribe Justiciinae on the basis of its pedunculate inflorescences with small bracts and campanulate calyces. It remains to be determined whether these characteristics are sufficient to delimit the two species sometimes treated in *Duvernoia* from other Justiciinae on a global basis. A meiotic complement of 17 is known, but infrequently reported, in *Justicia*; it has been noted in four species, *J. adhatoda* L. (e.g., Daniel and Chuang 1998), *J. betonica* L. (e.g., Daniel and Chuang 1998 and see below), *J. carnea* Lindl. (Daniel and Chuang 1989), and *J. trinervia* Vahl (e.g., Krishnappa and Ranganath 1982), representing three sections of the genus (Graham 1988). It is perhaps revealing that *J. adhatoda* is the type of one of these, section *Vasiaca* Lindau, in which Graham (1988) placed the other species of *Duvernoia*, *D. adhatodoides* E. Mey ex Nees.

Hypoestes Sol. ex R.Br. *Hypoestes* consists of about 70 species of herbs and shrubs from Africa, eastern Asia, Malesia, and Australia. Three species occur in southern Africa (Balkwill and Getliffe Norris 1985). Our count of $n = 15$ for *H. forskaolii*, a species occurring in Africa and the Arabian peninsula, agrees with a previously reported chromosome number for this species (Podlech 1986) and with most numbers reported for other species in the genus (Daniel and Chuang 1998). Our count of $n = 30$ for *H. aristata*, a species native to tropical and southern Africa, agrees with a previous count for this species based on cultivated plants (Daniel and Chuang 1998). This is the only known species of *Hypoestes* with a chromosome number other than $n = 15$. If a basic number of $x = 15$ is accepted for *Hypoestes* then *H. aristata* would represent a tetraploid species in the genus. A haploid chromosome number of 15 is also known in *Dicliptera*, *Peristrophe*, and *Rhinacanthus* (see below), all southern African relatives of *Hypoestes* in tribe Justicieae, subtribe Diclipterinae. Our collection of *H. aristata* is referable to var. *alba* K. Balkwill.

Isoglossa Oerst. *Isoglossa* consists of about 60 species native to the Old World. Welman (1993) listed 15 species as occurring in southern Africa. Our counts of $n = 17$ for two of these, *I. hypoestiflora* (southern and tropical Africa) and *I. ovata* (southern Africa), agree with the sole previous report of a chromosome number in the genus. Daniel and Chuang (1998) reported $n = 17$ for the tropical eastern African species *I. grandiflora* C. B. Clarke.

Isoglossa was treated by Bremekamp in tribe Justicieae, subtribe Rhytiglossinae (= Isoglossinae). McDade et al. (in press) demonstrated that *Isoglossa* is part of a "core" Isoglossinae that is strongly supported as monophyletic. Chromosome numbers have been determined for only two other genera in this subtribe; Daniel (1999) reported $n = 18$ for both *Stenostephanus* Nees (including *Habracanthus* Nees and *Hansteinia* Oerst.) and *Razisea* Oerst. Although a basic number of $x = 17$ appears likely for *Isoglossa*, and may represent dysploid evolution from an ancestor with $x = 18$, a well-substantiated basic number for the subtribe remains to be determined.

Justicia L. *Justicia* is the largest genus of Acanthaceae with estimates of about 700 species occurring worldwide (McDade et al. in press). Twenty-two species were recognized by Immelman (1995b) in the treatment of Acanthaceae: Justicieae for the *Flora of Southern Africa*. Several other genera from the region that are recognized in the *Flora of Southern Africa* (i.e., *Adhatoda* Mill., *Aulojusticia*, *Duvernoia*, *Siphonoglossa* Oerst.) are sometimes included in *Justicia* (Graham 1988, Brummitt 1992) as well. Daniel (2000) noted the presence, frequency, and distribution of 21 chromosome numbers reported for 93 species in the genus. He noted the prevalence of $n = 14$ throughout *Justicia* and a

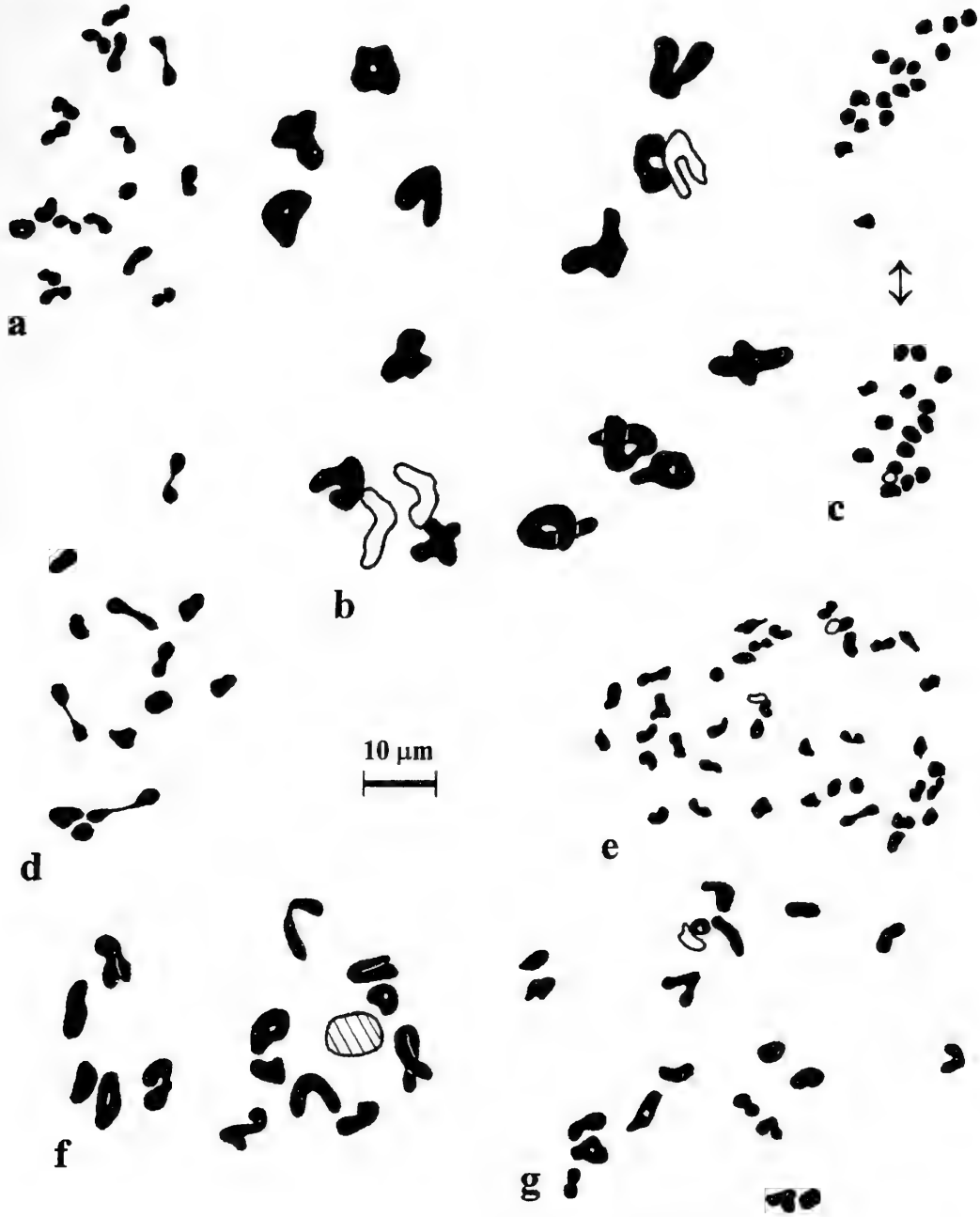

FIGURE 2. Camera-lucida drawings of meiotic chromosome preparations. a. *Justicia betonica* (*Daniel et al. 9334*), $n = 17$ (metaphase I). b. *Isoglossa hypoestiflora* (*Daniel et al. 9341*), $n = 17$ (diakenesis I). c. *Barleria senensis* (*Daniel et al. 9375*), $n = 16$ (telophase I). d. *Asystasia gangetica* (*Daniel et al. 9348*), $n = 13$ (metaphase I). e. *Aulojusticia linifolia* (*Daniel et al. 9388*), $n = 40$ (metaphase I). f. *Justicia odora* (*Daniel et al. 9364*), $n = 14$ (diakenesis I). g. *Crabbea angustifolia* (*Daniel et al. 9370*), $n = 21$ (early metaphase I).

probable basic number of $x = 7$ for the genus. Within *Justicia* several sections are characterized by a diversity of chromosome numbers whereas others are homogeneous in the counts reported (Daniel 2000).

Our counts for three species of southern African *Justicia* illustrate the diversity of numbers reported in the genus. The counts of $n = 17$ for two collections of *J. betonica* agree with the majority of previous counts for this native of Africa and the Indian subcontinent (Daniel 2000, Daniel and Chuang 1998). Hedrén (1989) reported n = ca. 13 from a Tanzanian collection of the African and Arabian species, *J. odora*. Our count for this species, based on a collection from South Africa, is $n = 14$. This number has been reported previously in 10 of the 13 sections of *Justicia* recognized by Graham (1988) in which at least one chromosome number has been reported. This is the first report of $n = 14$ in section *Harnieria* (Solms) Benth., however. Our count of $n = 26$ in *J. petiolaris*, a species occurring in eastern South Africa and Swaziland, represents the first report of a chromosome number for the species. It is also the first report of this chromosome number in the genus. Graham (1988) treated *J. petiolaris* in sect. *Tyloglossa* (Hochst.) Lindau. The only other chromosome number known among the species included in this section by Graham is $n = 13$, which has been reported several times (e.g., Mangenot and Mangenot 1962, Podlech 1986) in *J. flava* (Vahl) Vahl. Our collection of *J. petiolaris* pertains to subspecies *petiolaris*. Chromosome numbers reported here for South African species of *Justicia* reflect the putative polyploid and dysploid evolution seen for the genus in other regions (Daniel 2000). Given the large number of species of *Justicia*, its worldwide distribution, and the diversity of chromosome numbers already reported within it, additional cytological studies of the genus are highly desirable.

Metarungia Baden. This genus comprises three species occurring in eastern and southern Africa (Baden 1981, 1984). Our count of $n = 14$ for *M. longistrobus*, a species native to South Africa, Swaziland, and Mozambique, is the first report of a chromosome number in the genus. *Metarungia* is closely related to *Rungia* Nees in the tribe Justicieae and these genera are sister to a clade that includes *Justicia* (McDade et al. in press). Numerous counts have been reported for each of four species of *Rungia*. Counts for three of these (i.e., *R. laeta* C. B. Clarke, *R. parviflora* Nees, and *R. pectinata* (L.) Nees) are mostly $n = 13$ or $n = 26$. Most counts for *Rungia repens* Nees are $n = 10$. Although $n = 14$ is not known in *Rungia*, this is the most commonly reported number in *Justicia* (Daniel 2000).

Pseuderanthemum Radlk. *Pseuderanthemum* consists of about 60 species of perennial herbs and shrubs occurring in both the Old and New Worlds. Two species are known from southern Africa, *P. subviscosum* (C. B. Clarke) Stapf and *P. hildebrandtii* (Welman 1993; Edwards and Harrison 1998). Our count of $n = 21$ for *P. hildebrandtii*, which is native to southern Africa and tropical east Africa, is the first report of a chromosome number for this species and for an African species of the genus. Chromosome numbers have been reported for seven other species of *Pseuderanthemum* native to America, southern Asia, and the Pacific Islands (Daniel and Chuang 1989, 1998; Daniel 2000). Six of these have meiotic complements of 21. Kaur (1969) reported $n = 30$ for the Fijian species, *P. laxiflorum* (A. Gray) F. T. Hubb. As noted by Daniel and Chuang (1998), a basic number of $x = 21$ appears likely for this genus as well as for several of its relatives in the Justicieae. McDade et al. (in press) identified a lineage of Justicieae, including *Pseuderanthemum*, characterized by an androecium of two stamens and two staminodes and by $x = 21$. New World relatives include *Chileranthemum* Oerst., *Odontonema* Nees, and *Oplonia* Raf. Old World relatives include *Ruspolia* and *Ruttya*.

Rhinacanthus Nees. *Rhinacanthus* comprises about 20 species occurring in Africa, Madagascar, and Asia. Three species are known in southern Africa (Balkwill 1995). One of these, *R. gracilis*, is sometimes cultivated. Daniel and Chuang (1998) reported a count of $n = 15$ from cultivated materials of this species. Our count of $n = 15$ from two wild-collected plants of the same species confirms the previous count. All other counts reported for species of *Rhinacanthus* are likewise $n = 15$ (Daniel and

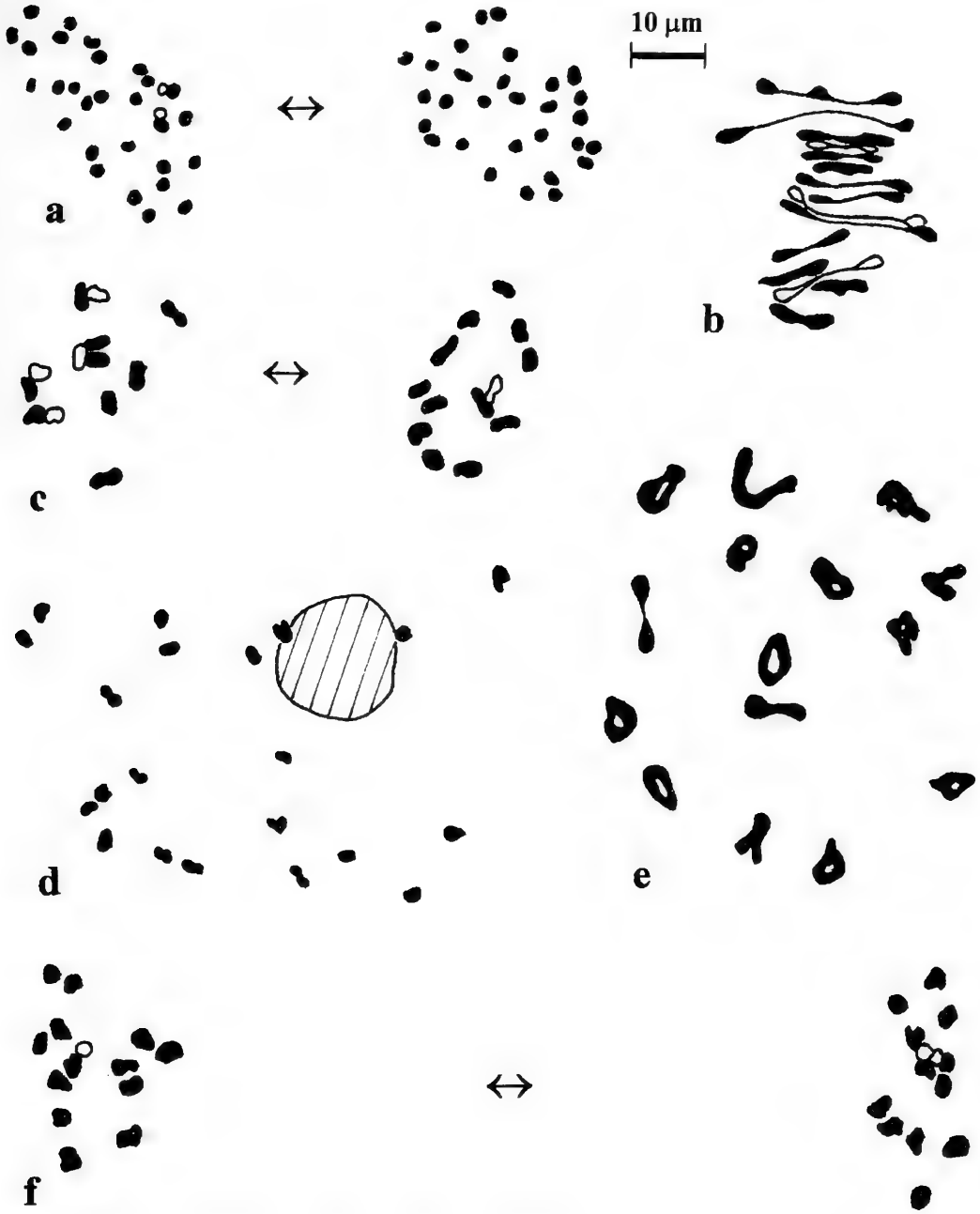

FIGURE 3. Camera-lucida drawings of meiotic chromosome preparations. a. *Hypoestes aristata* (*Daniel et al. 9351*), $n = 30$ (telophase II, only half of cell shown). b. *Rhinacanthus gracilis* (*Daniel 9340*), $n = 15$ (metaphase I). c. *Dicliptera magaliesbergensis* (*Daniel et al. 9357*), $n = 13$ (telophase I). d. *Ruspolia hypocrateriformis* (*Daniel et al. 9359*), $n = 21$ (diakenesis I). e. *Hypoestes forskaolii* (*Daniel et al. 9358*), $n = 15$ (diakenesis I). f. *Metarungia longistrobus* (*Daniel et al. 9355*), $n = 14$ (telophase I).

Chuang 1998). Thus, a basic number of $x = 15$ can be advanced for the genus. Based on morphological characteristics *Rhinacanthus* would appear to be best treated in tribe Justicieae, subtribe Justiciinae (Balkwill and Getliffe Norris 1988), but molecular sequence data (McDade et al. in press) place it in subtribe Diclipterinae with strong support. Cytological data corroborate this latter placement. Other Diclipterinae (i.e., *Dicliptera*, *Hypoestes*, and *Peristrophe*) also have probable basic chromosome numbers of 15 (see above).

Nomenclatural and taxonomic confusion surrounding *R. gracilis* was discussed by Balkwill (1995), who recognized two varieties of the species in southern Africa. Plants used for our counts pertain to *R. gracilis* var. *latilabris* K. Balkwill. The voucher specimen of Daniel and Chuang's (1998) count pertains to *R. gracilis* var. *gracilis*.

Ruspolia Lindau. Six species of *Ruspolia* have been described from Africa and Madagascar and three of them occur in southern Africa (Welman 1993). Our count of $n = 21$ for *R. hypocrateriformis*, a species native to western tropical Africa and South Africa, is the first report of a chromosome number for the species. It agrees with previous counts of $n = 21$ for *R. seticalyx* (C. B. Clarke) Milne-Redh. (Daniel and Chuang 1998). This same chromosome number has been reported in several relatives of *Ruspolia* in the Justicieae (see above under *Pseuderanthemum*). Plants from South Africa are commonly treated as *R. hypocrateriformis* var. *australis* Milne-Redh. (e.g., Heine 1963).

Ruttya Harv. *Ruttya* comprises three species native to Africa. Only one of these, *R. ovata*, occurs in southern Africa where it is found in South Africa and Swaziland. Our count of $n = 21$ for the species agrees with the only previous report of a chromosome number in the genus. Daniel and Chuang (1998) reported this number for *R. fruticosa* Lindau, a native of eastern tropical Africa, based on cultivated plants. The affinities of *Ruttya* are with *Ruspolia* and other genera of tribe Justicieae with an androecium of two stamens and two staminodes and $x = 21$ (see above under *Pseuderanthemum*). Morphological distinctions among *Ruttya*, *Ruspolia*, and *Pseuderanthemum* were noted by Daniel and Chuang (1998).

CONCLUSIONS

As shown by McDade et al. (in press), knowledge of chromosome numbers can be useful for suggesting or corroborating phylogenetic relationships among Acanthaceae. Even in this small sampling of taxa from South Africa, the importance of knowledge of chromosome numbers among Acanthaceae is evident. A continuity of chromosome numbers between southern African endemics and congeners from other regions provides additional evidence for several previously proposed suprageneric relationships based on morphology and molecular markers (e.g., *Hypoestes-Dicliptera-Peristrophe* and *Pseuderanthemum-Ruttya-Ruspolia*). However, the chromosome numbers reported for *Rhinacanthus* support molecular rather than morphological data in placing this genus in the Diclipterinae rather than in the Justiciinae. Based on the treatment of Justiciinae in the *Flora of Southern Africa* (Baden et al. 1995), *Aulojusticia* and *Duvernoia* are recognized here. Using morphological characteristics, both might be readily accommodated in a broadly interpreted *Justicia*. However, their respective chromosome numbers are either unknown or uncommon in that genus and their systematic affinities based on molecular markers are currently being studied.

It will be useful to obtain additional chromosome numbers among Acanthaceae from southern Africa by sampling more taxa from South Africa as well as from other countries in the region. For example, chromosome numbers remain unknown for the following acanthaceous genera that occur in southern Africa: *Acanthopsis* Harv., *Anisotes* Nees, *Chaetacanthus* Nees, *Chorisochora* Vollesen, *Duosperma* Dayton, *Glossochilus* Nees, *Megalochlamys* Lindau, *Neuracanthus* Nees, and *Ruelliopsis* C. B. Clarke. Also, no chromosome counts have been determined for Acanthaceae from

any southern African country except South Africa. An increase in the number of taxa for which chromosome numbers are known would help to identify basic numbers for additional genera and assist efforts to understand phylogenetic relationships within the family.

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LITERATURE CITED

BADEN, C. 1981. The genus *Macrorungia* (Acanthaceae), a taxonomic revision. Nordic J. Bot. 1:143–153.

———. 1984. *Metarungia*, a valid name for *Macrorungia* auctt. (Acanthaceae). Kew Bull. 39:638.

BADEN, C., K. BALKWILL, F. M. GETLIFFE NORRIS, K. L. IMMELMAN, J. C. MANNING, AND J. MUNDAY. 1995. Acanthaceae, Fascicle 1: Justiciinae. *In* Flora of southern Africa, O. A. Leistner, ed. 30(3, 1):1–71.

BALKWILL, K. 1995. 3. *Rhinacanthus*. *In* Flora of southern Africa, O. A. Leistner, ed. 30(3, 1):11–14.

BALKWILL, M.-J. AND K. BALKWILL. 1997. Delimitation and infra-generic classification of *Barleria* (Acanthaceae). Kew Bull. 52:535–573.

BALKWILL, K. AND F. GETLIFFE NORRIS. 1985. Taxonomic studies in the Acanthaceae; the genus Hypoestes Soland. ex R. Br. in southern Africa. S. Afr. J. Bot. 51:133–144.

———. 1988. Classification of the Acanthaceae: a southern African perspective. Monogr. Syst. Bot. Missouri Bot. Gard. 25:503–516.

BALKWILL, K., F. GETLIFFE NORRIS, AND M.-J. BALKWILL. 1996. Systematic studies in the Acanthaceae; Dicliptera in southern Africa. Kew Bull. 51:1–61.

BREMEKAMP, C. E. B. 1939. Acanthaceae. *In* LIX—Contributions to the Flora of Tropical America: XLIII, N. Y. Sandwith et al., eds. Kew Bull. 1939:545–563.

———. 1965. Delimitation and subdivision of the Acanthaceae. Bull. Bot. Surv. India 7:21–30.

BRUMMITT, R. K. 1992. Vascular plant families and genera. Royal Botanic Gardens, Kew.

CHUANG, T. I., C. Y. CHAO, W. W. L. HU, AND S. C. KWAN. 1963. Chromosome numbers of the vascular plants of Taiwan. I. Taiwania 8:51–66.

DANIEL, T. F. 1995. Acanthaceae. *In* Flora of Chiapas, Part 4, D. E. Breedlove, ed. California Academy of Sciences, San Francisco. 158 pp.

———. 1999. Revision of *Stenostephanus* (Acanthaceae) in Mexico. Contr. Univ. Michigan Herb. 22:47–93.

———. 2000. Additional chromosome numbers of American Acanthaceae. Syst. Bot. 25:15–25.

———. In press. Chromosome numbers of some Acanthaceae from Papua New Guinea. Austrobaileya.

DANIEL, T. F. AND T. I. CHUANG. 1989. Chromosome numbers of some cultivated Acanthaceae. Baileya 23:86–93.

———. 1993. Chromosome numbers of New World Acanthaceae. Syst. Bot. 18:283–289.

———. 1998. Chromosome numbers of cultivated Acanthaceae and systematic implications. Pp. 309–330 *in* Diversity and taxonomy of tropical flowering plants, P. Mathew and M. Sivadasan, eds. Mentor Books, Calicut.

DANIEL, T. F., T. I. CHUANG, AND M. A. BAKER. 1990. Chromosome numbers of American Acanthaceae. Syst. Bot. 15:13–25.

DATTA, P. C. AND R. K. MATAI. 1970. Relationships of Justicieae (Acanthaceae) based on cytology. Genetica 41:437–450.

DE, A. 1966. Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. I. Cytological Studies. Trans. Bose Res. Inst. 29:139–175.

DYER, R. A. 1975. The genera of the southern African flowering plants, vol. 1. Department of Agricultural Technical Services, Pretoria.

EDWARDS, T. J. AND E. HARRISON. 1998. New records from KwaZulu-Natal, South Africa. Bothalia 28:187–190.

ENSERMU KELBESSA. 1990. *Justicia* sect. *Ansellia* (Acanthaceae). Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 29(2):1–96.

GADELLA, T. W. J. 1977. *In* IOPB chromosome number reports LVI. Taxon 26:259–261.

GOVINDARAJAN, T. AND D. SUBRAMANIAN. 1985. Karyomorphological studies in South Indian Acanthaceae. Cytologia 50:473–482.

GRAHAM, V. A. W. 1988. Delimitation and infra-generic classification of *Justicia* (Acanthaceae). Kew Bull. 43:551–624.

GRANT, W. F. 1955. A cytogenetic study in the Acanthaceae. Brittonia 8:121–149.

———. 1964. *In* IOPB chromosome number reports. I. Taxon 13:108.

HEDRÉN, M. 1989. *Justicia* sect. *Harnieria* (Acanthaceae) in tropical Africa. Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 29(1):1–141.

HEDRÉN, M., M. W. CHASE, AND R. G. OLMSTEAD. 1995. Relationships in the Acanthaceae and related families as suggested by cladistic analysis of *rbc*L nucleotide sequences. Pl. Syst. Evol. 194:93–109.

HEINE, H. 1963. Acanthaceae. Pp. 391–432 *in* Flora of west tropical Africa 2(ed. 2), F. N. Hepper, ed.

IMMELMAN, K. L. 1995a. 2. *Siphonoglossa*. *In* Flora of southern Africa, O. A. Leistner, ed. 30(3, 1):6–10.

———. 1995b. 5. *Justicia*. *In* Flora of southern Africa, O. A. Leistner, ed. 30(3, 1):18–46.

KAUR, J. 1969. Chromosome numbers in Acanthaceae—IV. Sci. and Cult. 35:61–63.

———. 1970. Chromosome numbers in Acanthaceae—V. Sci. and Cult. 36:103–106.

KRISHNAPPA, D. G. AND R. M. RANGANATH. 1982. *In* IOPB Chromosome number reports LXXV. Taxon 31:364–365.

LINDAU, G. 1895. Acanthaceae. *In* Die natürlichen Pflazenfamilien, A. Engler and K. Prantl, eds. 4(3b):274–354.

MANGENOT, S. AND G. MANGENOT. 1958. Deuxième liste de nombres chromosomiques nouveaux chez diverses Dicotylédones et Monocotylédones d'Afrique occidentale. Bull. Jard. Bot. (Bruxelles) 28:315–329.

———. 1962. Enquête sur les nombres chromosomiques dans une collection d'espèces tropicales. Rev. Cytol. Biol. Vég. 25:411–447.

MANNING, J. C. AND F. M. GETLIFFE NORRIS. 1995. 4. *Duvernoia*. *In* Flora of southern Africa, O. A. Leistner, ed., 30(3, 1):15–17.

MCDADE, L. A. AND M. L. MOODY. 1999. Phylogenetic relationships among Acanthaceae: evidence from noncoding *trn*L-*trn*F chloroplast DNA sequences. Amer. J. Bot. 86:70–80.

MCDADE, L. A., T. F. DANIEL, S. E. MASTA, AND K. M. RILEY. In press. Phylogenetic relationships within the tribe Justicieae (Acanthaceae): evidence from molecular sequences, morphology, and cytology. Ann. Missouri Bot. Gard.

PIOVANO, M. A. AND L. M. BERNARDELLO. 1991. Chromosome numbers in Argentinean Acanthaceae. Syst. Bot. 16:89–97.

PODLECH, D. 1986. Chromosomenstudien an Pflanzen des Saharo-sindischen Trockengebietes. Mitt. Bot. Staatssamml. München 22:5–20.

RENARD, R., J. LAMBINON, M. REEKMANS, P. VAN DER VEKEN, AND M. GOVAERT. 1983. Nombres chromosomiques de quelques angiospermes du Rwanda, du Burundi et du Kenya. Bull. Jard. Bot. Belg. 53:343–371.

SCOTLAND, R. W., J. A. SWEERE, P. A. REEVES, AND R. G. OLMSTEAD. 1995. Higher-level systematics of Acanthaceae determined by chloroplast DNA sequences. Amer. J. Bot. 82:266–275.

VALSALA DEVI, G. AND P. M. MATHEW. 1982. *In* IOPB chromosome number reports LXXVII. Taxon 31:773.

WELMAN, W. G. (compiler). 1993. Acanthaceae. *In* Plants of southern Africa: names and distribution, T. H. Arnold and B. C. de Wet, eds. Memoirs of the Botanical Survey of South Africa 62:652–665.

APPENDIX

Species occurring in southern Africa for which chromosome numbers have been published previously. The taxon name is followed by the author of the name, the chromosome number(s) reported (listed as *n* numbers), literature citation(s), and the country from which the plants studied came. The provenance of the plants is based on information provided in the original publications. Two references with chromosome numbers (both Ph.D. theses) have not been seen and the probable provenance is indicated with a question mark and "not seen" follows. In other publications, where the source of materials studied is unclear or not provided, a question mark is indicated. The provenance of cultivated plants noted below is unknown.

Acanthus pubescens (Oliv.) Engl., $n = 28$, Renard et al. 1983 (Burundi).

Asystasia gangetica (L.) T. Anderson (including *A. coromandeliana* Nees), $n = 13$: Mangenot and Mangenot 1957 (western Africa), Mangenot and Mangenot 1962 (western Africa), Gadella 1977 (Cameroun), Ugborogho and Adetula 1988 (Nigeria); 14: Subramanian and Govindarajan 1980 (India), Govindarajan and Subramanian 1983 (India); 22: Narayanan 1951a (India?); 24: Narayanan 1951a (India?); 25: De 1966 (India?), Sarkar et al. 1978 (India, cultivated); 26: Narayanan 1951b (India), Grant 1955 (U.S. A., cultivated), Ellis 1962 (India), Kaur 1965 (India, cultivated), Valsala Devi and Mathew 1982 (India), Saggoo and Bir 1983 (India), Saggoo and Bir 1986 (India), Daniel 2000 (U.S. A., naturalized).

Barleria repens Nees, $n = 20$: Daniel and Chuang 1998 (cultivated).

Blepharis integrifolia (L.f.) E. Mey. (including *B. molluginifolia* Pers. and *B. repens* (Vahl) Roth), $n = 17$: Kaur 1966 (India, probably cultivated), Sareen and Sanjogta 1976 (India), Ranganath 1981 (India? not seen), Krishnappa and Ranganath 1982 (India), Ranganath and Krishnappa 1982 (India); $n = 18$: Govindarajan and Subramanian 1983 (India), Subramanian and Govindarajan 1980 (India).

B. maderaspatensis (L.f.) Heyne ex Roth (including *B. boerhaaviaefolia* Pers.), $n = 8$: Valsala Devi and Mathew 1982 (India), Saggoo 1983 (India?, not seen), Saggoo and Bir 1982a (India), 1983 (India), 1986 (India), Govindarajan and Subramanian 1983 (India); $n = 11$: Ranganath 1981 (India? not seen), Krishnappa and Ranganath 1982 (India), Ranganath and Krishnappa 1982 (India); $n = 12$: Ranganath and Krishnappa 1982 (India); $n = 13$: Kaur 1966 (India), Sareen and Sanjogta 1976 (India); $n = 14$: Vasudevan 1976 (India), Subramanian and Govindarajan 1980 (India); $n = 15$: Miège 1962 (Senegal), Bir and Saggoo 1979 (India), Saggoo 1983 (India? not seen), Bir and Saggoo 1981 (India), Saggoo and Bir 1982b (India), 1983 (India); $2n = 23$: Ranganath and Krishnappa 1982 (India).

Crabbea velutina S. Moore (including *C. reticulata* C. B. Clarke), n = ca. 14: Renard et al. 1983 (Rwanda); $n = 21$, Grant 1964 (cultivated).

Dyschoriste depressa Nees, $n = 15$: Govindarajan and Subramanian 1985 (India); $n = 30$: Bir and Saggoo 1979 (India), 1981 (India), Saggoo 1983 (India? not seen), Saggoo and Bir 1982b (India).

Elytraria acaulis (L.f.) Lindau, $n = 17$: Kaur 1969 (India?); $n = 22$: Govindarajan and Subramanian 1983 (India); $n = 23$: Subramanian and Govindarajan 1980 (India).

Hygrophila auriculata (Schum.) Heine (including *Asteracantha longifolia*), $n = 16$, De 1966 (India?), Trivedi and Trivedi 1992 (India), Subramanyam and Kamble 1971 (India), Saggoo 1983 (India? not seen), Bir and Saggoo 1981 (India), Saggoo and Bir 1982b (India), 1986 (India).

Hypoestes aristata R.Br., $n = 30$, Daniel and Chuang 1998 (cultivated).

H. forskaollii Vahl, $n = 15$, Podlech 1986 (Yemen).

H. triflora Roem. and Schult., *n* = 15: Saggoo 1983 (India? not seen), Sagoo and Bir 1982a (India), 1983 (India).

Justicia anagalloides (Nees) T. Anderson, *n* = 9: Ensermu Kelbessa 1990 (Ethiopia); *n* = 18: Ensermu Kelbessa 1990 (Ethiopia).

J. betonica L., *n* = 14: Subramanian and Govindarajan 1980 (India), Narayanan 1951b (India?); *n* = 17: Ellis 1962 (India), Ranganath 1981 (India?, not seen), Bir and Saggoo 1979 (India), Krishnappa and Ranganath 1982 (India), Saggoo 1983 (India?, not seen), Valsala Devi and Mathew 1982 (India), Govindarajan and Subramanian 1983 (India), Bir and Saggoo 1981 (India), Saggoo and Bir 1982b (India), 1986 (India), Daniel and Chuang 1998 (cultivated), Daniel 2000 (U.S. A., naturalized).

J. exigua S. Moore, *n* = 7: Renard et al. 1983 (Rwanda), Ensermu Kelbessa 1990 (Ethiopia, Tanzania).

J. flava (Forssk.) Vahl, *n* = 13: Mangenot and Mangenot 1957 (western Africa), 1962 (western Africa), Podlech 1986 (Yemen).

J. glabra Koenig ex Roxb., *n* = 27: Ranganath 1981 (India? not seen), Krishnappa and Ranganath 1982 (India).

J. matammensis (Schweinf.) Oliv., *n* = 7: Ensermu Kelbessa 1990 (Ethiopia).

J. odora (Forssk.) Lam., *n* = ca. 13: Hedrén 1989 (Tanzania).

Mackaya bella Harv., *n* = 42: Daniel and Chuang 1989 (cultivated).

Nelsonia canescens (Lam.) Spreng., *n* = 17: Saggoo 1983 (India? not seen), Saggoo and Bir 1983 (India); *n* = 18: Daniel and Chuang 1993 (Panama).

Peristrophe paniculata (Forssk.) Brummitt (including *P. bicalyculata* (Retz.) Nees), *n* = 10: Narayanan 1951b (India); *n* = 15: Ahuja 1955 (India), Miège and Josserand 1972 (Senegal), Vasudevan 1976 (India), Saggoo and Bir 1983 (India), 1986 (India), Verma and Dhillon 1967 (India).

Phaulopsis imbricata (Forssk.) Sweet, *n* = 16: Manktelow 1996 (Ethiopia, Tanzania, Madagascar); *n* = 17: Daniel and Chuang 1998 (cultivated); *n* = ca. 32: Manktelow 1996 (Madagascar); 2n = 65: Manktelow 1996 (Malawi).

Rhinacanthus gracilis Klotz., *n* = 15: Daniel and Chuang 1998 (cultivated).

Ruellia cordata Thunb., *n* = 16, Rao and Mwasumbi 1981 (Tanzania, probably cultivated).

R. patula Jacq., *n* = 16: Baquar et al. 1966 (Pakistan), Rao and Mwasumbi 1981 (Tanzania, probably cultivated), Govindarajan and Subramanian 1983 (India), Subramanian and Govindarajan 1980 (India).

Ruspolia seticalyx (C. B. Clarke) Milne-Redh., *n* = 21: Daniel and Chuang 1998 (cultivated).

Thunbergia alata Boj., *n* = 9: Grant 1955 (cultivated), Takizawa 1957 (cultivated), Shibata 1962 (Colombia, naturalized), Saggoo 1983 (India?, not seen), Bir and Saggoo 1981 (India), Saggoo and Bir 1982b (India), 1986 (India), Daniel and Chuang 1989 (cultivated), Sugiura 1931 (cultivated?), Tijo 1948 (Indonesia), Narayanan 1951b (India), Kaur 1970 (India?); *n* = 16: Snoad 1952 (cultivated).

REFERENCES FOR APPENDIX

AHUJA, M. R. 1955. Chromosome numbers of some plants. Indian J. Genet. Pl. Breed. 15:142–143.

BAQUAR, S. R., A HUSAIN, AND S. AKHTAR. 1966. Meiotic chromosome numbers in some vascular plants of Indus Delta II. Bot. Notis. 119:24–32.

BIR, S. S. AND M. I. S. SAGGOO. 1979. *In* IOPB chromosome number reports LXV. Taxon 28:630–631.

———. 1981. Cytopalynology of certain Acanthaceae and Labiatae. J. Palynol. 17:93–102.

DANIEL, T. F. 2000. Additional chromosome numbers of American Acanthaceae. Syst. Bot. 25:15–25.

DANIEL, T. F. AND T. I. CHUANG. 1989. Chromosome numbers of some cultivated Acanthaceae. Baileya 23:86–93.

———. 1993. Chromosome numbers of New World Acanthaceae. Syst. Bot. 18:283–289.

———. 1998. Chromosome numbers of cultivated Acanthaceae and systematic implications. Pp. 309–330 *in* P. Mathew and M. Sivadasan (eds.), Diversity and taxonomy of tropical flowering plants. Mentor Books, Calicut.

DE, A. 1966. Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. I. Cytological Studies. Trans. Bose Res. Inst. 29:139–175.

ELLIS, J. L. 1962. Chromosome numbers in some members of Acanthaceae. Sci. and Cult. 28:191–192.

ENSERMU KELBESSA. 1990. *Justicia* sect. *Ansellia*_(Acanthaceae). Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 29(2):1–96.

GADELLA, T. W. J. 1977. *In* IOPB chromosome number reports LVI. Taxon 26:259–261.

GOVINDARAJAN, T. AND D. SUBRAMANIAN. 1983. Karyomorphological studies in South Indian Acanthaceae. Cytologia 48:491–504.

———. 1985. Karyomorphological studies in South Indian Acanthaceae. Cytologia 50:473–482.

GRANT, W. F. 1955. A cytogenetic study in the Acanthaceae. Brittonia 8:121–149.

———. 1964. *In* IOPB chromosome number reports. I. Taxon 13:108.

HEDRÉN, M. 1989. *Justicia* sect. *Harnieria* (Acanthaceae) in tropical Africa. Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 29(1):1–141.

KAUR, J. 1965. Chromosome numbers in Acanthaceae—II. Sci. and Cult. 31:531–532.

———. 1966. Chromosome numbers in Acanthaceae 111 [sic]. Sci. and Cult. 32:142–143.

———. 1969. Chromosome numbers in Acanthaceae—IV. Sci. and Cult. 35:61–63.

———. 1970. Chromosome numbers in Acanthaceae—V. Sci. and Cult. 36:103–106.

KRISHNAPPA, D.G. AND R. M. RANGANATH. 1982. *In* IOPB Chromosome number reports LXXV. Taxon 31:364–365.

MANGENOT, S. AND G. MANGENOT. 1957. Nombres chromosomiques nouveaux chez diverses dicotylédones et monocotylédones d'Afrique occidentale. Bull. Jard. Bot. (Bruxelles) 27:639–654.

———. 1962. Enquête sur les nombres chromosomiques dans une collection d'espèces tropicales. Rev. Cytol. Biol. Vég. 25:411–447.

MANKTELOW, M. 1996. *Phaulopsis* (Acanthaceae)—a monograph. Symb. Bot. Upsal. 31(2):1–184.

MIÈGE, J. 1962. Quatrième liste de nombres chromosomiques d'espèces d'Afrique occidentale. Rev. Cytol. Biol. Vég. 24:149–164.

MIÈGE, J. AND N. JOSSERAND. 1972. Nombres chromosomiques d'espèces africaines et malgaches. Candollea 27:283–292.

NARAYANAN, C. R. 1951a. Nucleolar behaviour and chromosomal aberrations in mitosis of *Acanthus ilicifolius* and *Asystasia coromandeliana*. Indian J. Genetics Pl. Breed. 11:205–210.

———. 1951b. Somatic chromosomes in the Acanthaceae. J. Madras Univ. Bot. 21:220–231.

PODLECH, D. 1986. Chromosomenstudien an Pflanzen des Saharo-sindischen Trockengebietes. Mitt. Bot. Staatssamml. München 22:5–20.

RANGANATH, R. M. 1981. Morphological and cytological studies in Acanthaceae. Ph.D. Thesis, Bangalore, 1981. [not seen]

RANGANATH, R. M. AND D.G KRISHNAPPA. 1982. Telocentric chromosomes and karyotypes in the genus *Blepharis*. Caryologia 35:237–246.

RAO, P.N. AND L.B. MWASUMBI. 1981. *In* IOPB chromosome number reports LXX. Taxon 30:79–80.

RENARD, R., J. LAMBINON, M. REEKMANS, P. VAN DER VEKEN, AND M. GOVAERT. 1983. Nombres chromosomiques de quelques angiospermes du Rwanda, du Burundi et du Kenya. Bull. Jard. Bot. Belg. 53:343–371.

SAGGOO, M. I. S. 1983. Cytomorphological studies on plants of economic importance of Bicarpellatae from India. Ph.D. Thesis, Punjabi Univ., Patiala. [not seen]

SAGGOO, M. I. S. AND S. S. BIR. 1982a. *In* IOPB chromosome number reports LXXVI. Taxon 31:574–598.

———. 1982b. Cytological studies on certain Acanthaceae from central India. Proc. Indian Acad. Sci. (Pl. Sci.) 91:479–486.

———. 1983. Cytopalynological studies on Indian members of Acanthaceae and Labiatae. J. Palyn. 19:243–277.

———. 1986. Meiotic studies in certain members of family Acanthaceae from South India. J. Indian Bot. Soc. 65:310–315.

SAREEN, T. S. AND K. SANJOGTA. 1976. Chromosome numbers in some species of Acanthaceae. Cytologia 41:283–290.

SARKAR, A.K., M. CHAKRAVERTY, N.C. SAHA, S. K. DAS, AND D. HAZRA. 1978. *In* IOPB chromosome number reports LXII. Taxon 27:519–535.

SHIBATA, K. 1962. Estudios citológicos de plantas colombianas silvestres y cultivadas. J. Agricul. Sci. 8:49–62.

SNOAD, B. 1952. Chromosome counts of species and varieties of garden plants. Annual Report, John Innes Horticultural Institution 42:47–50.

SUBRAMANIAN, D. AND T. GOVINDARAJAN. 1980. Cytotaxonomy of some species of Acanthaceae. J. Cytol. Genet. 15:90–92.

SUBRAMANYAM, K. AND N.P. KAMBLE. 1971. *In* IOPB chromosome number reports XXXI. Taxon 20:160.

SUGIURA, T. 1931. A list of chromosome numbers in angiospermous plants. Bot. Mag. (Tokyo) 45:353–355.

TAKIZAWA, Y. 1957. Die Struktur der Pachytänchromosomen einiger Acanthaceen, sowie eine Reihe neu bestimmter Chromosomenzahlen. Cytologia 22:118–126.

TIJO, J. H. 1948. The somatic chromosomes of some tropical plants. Hereditas 34:135–146.

TRIVEDI, M. P. AND R. N. TRIVEDI. 1992. Chromosomal behaviour in weeds. Proc. Conf. Cytol. and Genet. 3:188–198.

UGBOROGHO, R. E. AND O. A. ADETULA. 1988. The biology of the *Asystasia gangetica* complex (Acanthaceae) in Lagos State, Nigeria. Feddes Rep. 99:507–517.

VALSALA DEVI, G. AND P.M. MATHEW. 1982. *In* IOPB chromosome number reports LXXVII. Taxon 31:773.

VASUDEVAN, K. N. 1976. Contribution to the cytotaxonomy and cytogeography of the flora of the western Himalayas (with an attempt to compare it with the flora of the Alps). Part III. Ber. Schweiz. Bot. Ges. 86:152–203.

VERMA, S. C. AND S. S. DHILLON. 1967. *In* IOPB chromosome number reports XI. Taxon 16:221–222.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of the Soft Coral Genus *Eleutherobia* Pütter, 1900 (Coelenterata: Alcyoniidae) from the Tonga Islands

by

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The soft coral genus *Eleutherobia* (family Alcyoniidae) was previously known to contain fifteen valid species, and is distributed from eastern and southern Africa to the western Pacific. A new species is here described from Tonga, thereby making a total of sixteen species, and extending the known range of the genus approximately 3000 km to the southeast into the central South Pacific. The new taxon is superficially similar to *Eleutherobia grayi* (J. A. Thomson and Dean, 1931), from the Indonesian and Ryukyuan archipelagos, but is distinguished from it and all other species by a unique complement of sclerite types.

The Indo-Pacific and southern African soft coral genus *Eleutherobia* is noteworthy for recently discovered, bioactive, natural products that have been isolated from two Indian Ocean species. These compounds include novel diterpenes (Hooper et al. 1997) and the cytotoxic agent eleutherobin (Long et al. 1998). The latter compound has recently been found to have anticancer properties and has recently been synthesized (Xiao et al. 1999). The diterpenes are produced by *Eleutherobia lutea* Benayahu and Schleyer, 1995, from the east coast of South Africa, and eleutherobin comes from an undescribed species off the west coast of Australia.

Of the fifteen described species that are considered valid for the genus *Eleutherobia*, twelve inhabit the Indo-West Pacific from East Africa to Japan and Indonesia, and three are considered endemic to southern Africa [Verseveldt and Bayer (1988) and the present paper]. Verseveldt and Bayer (1988) provided a taxonomic revision of the genus *Eleutherobia*, Williams (1992a) reviewed the southern African species, and Benayahu and Schleyer (1995) described a new species from South Africa. Color photographs of living soft corals in the genus are provided by Williams (1996:34) and Benayahu and Schleyer (1995:2).

A recently discovered species from Tonga is here described. It differs from other members of the genus by having a sclerite complement that includes very slender capstans with thin radiating whorls of tubercles, a relatively large number of crosses > 0.10 mm in length (many of which have elongated tapering points), and a scarcity of triradiate forms or needle-like spindles. The addition of the new species makes a total of sixteen species of *Eleutherobia* recognized as valid—three from southern Africa and thirteen from the Indo-West Pacific.

METHODS

Material was collected by SCUBA and preserved in 70% ethanol. Sclerites were isolated using sodium hypochlorite. Micrographs were made using a Kodak MDS100 digital video camera and a

Wild M400 photomicroscope. Scanning electron micrographs were made on Hitachi S-510 and Leo 1400 Series scanning electron microscopes. Abbreviations used in the text are as follows: CAS (California Academy of Sciences, San Francisco), CRRF (Coral Reef Research Foundation, Palau).

SYSTEMATIC ACCOUNT

Family Alcyoniidae Lamouroux, 1812

Eleutherobia Pütter, 1900

Eleutherobia Pütter, 1900:449. Verseveldt and Bayer, 1988:27. Williams, 1992:306.
Nidalia (in part): *non* Gray, 1835.
Bellonella (in part): *non* Gray, 1862.
Metalcyonium (in part): *non* Pfeffer, 1889.

DIAGNOSIS. — Alcyoniid soft corals with colonies digitiform, finger-shaped, often conical and tapering, rarely multilobate. Polyps monomorphic. Calyces absent, although retracted polyps often form low rounded to conspicuous protuberances. Sclerites mostly derived from radiates, although spindles, crosses, barrels, or tuberculate spheroids may also be present.

TYPE SPECIES. — *Eleutherobia japonica* Pütter, 1900, by monotypy.

DIVERSITY AND DISTRIBUTION. — Sixteen species of the Indo-West Pacific (southern and eastern Africa to Japan and Tonga).

Eleutherobia zanahoria sp. nov.

Figs. 1–8

MATERIAL EXAMINED. — HOLOTYPE: CAS 118501, station number CRRF #OCDN 5464-X, Tonga, southwest of Vavau, south side of Kitu channel, a small channel between Kitu Island and north side of Nuapapu Island (18° 41.25′S, 174° 04.05′W), 25–30 m depth, 12 November 1997, collected by Coral Reef Research Foundation, one whole specimen, 64 mm in length. PARATYPES: CAS 118502, same data as holotype, one whole specimen, 63 mm in length. CAS 118503, same data as holotype, one specimen cut in half longitudinally, 53 mm in length.

DIAGNOSIS. — Alcyoniid soft corals with digitiform to lobate colony shape. Several finger-like lobes may be united by a common basal holdfast. Stalk very short, polyps distributed over approximately 95% of each colony. Sclerites are radiates, crosses, and irregular forms presumably derived from radiates; some crosses with finely attenuated tips. Polypary sclerites relatively gracile, 0.04–0.12 mm long; holdfast and stalk sclerites more robust, 0.07–0.16 mm long. Polyp sclerites absent. External coenenchymal color carrot orange throughout. Sclerites pale yellow-orange.

DESCRIPTION. — Growth form and size: The wet-preserved holotype is unbranched and finger-shaped, elongate conical, gradually tapering from proximal base to distal end. The apex is gently rounded. The basal holdfast has the largest width (20 mm), while the apex region has the smallest width (5 mm). The polypary comprises over 95% of the total colony length, as the polyps begin to appear immediately above the holdfast (Fig. 1). Wet-preserved paratype CAS 118702 is 63 mm in length, and lobate with four terminal lobes arising from two trunks that are unified into a single trunk and holdfast at the base (Fig. 2). The widest portion of the specimen is in the holdfast region (31 mm), while the narrowest lobe is 4 mm in width just below its apex. The lobes vary from 8 to 28 mm in length. They are mostly cylindrical in shape and slightly curved with gently rounded ends. Wet-preserved paratype CAS 118503 is 53 mm in length and similar in shape to the holotype. The widest portion at the base measures 9 mm, while the narrowest portion near the apex is 3 mm in width

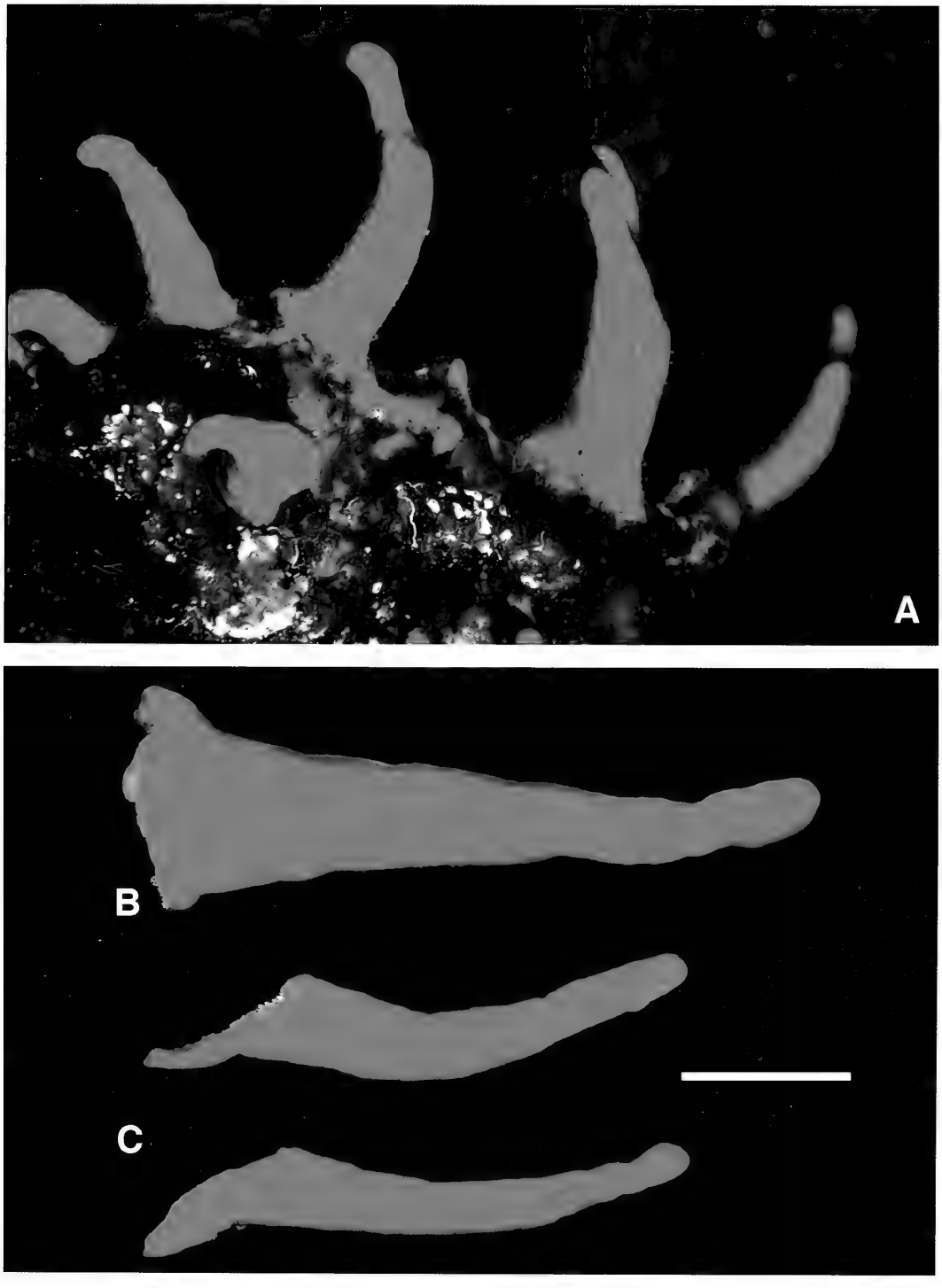

FIGURE 1. *Eleutherobia zanahoria* sp. nov. A. Underwater photograph of living soft corals at the type locality. Photograph by Pat Colin, courtesy of the Coral Reef Research Foundation, Palau. B. Wet-preserved holotype (CAS 118501), 64 mm in length. C. Wet-preserved paratype (CAS 118503), 53 mm in length; cut longitudinally into two halves; scale bar = 16 mm.

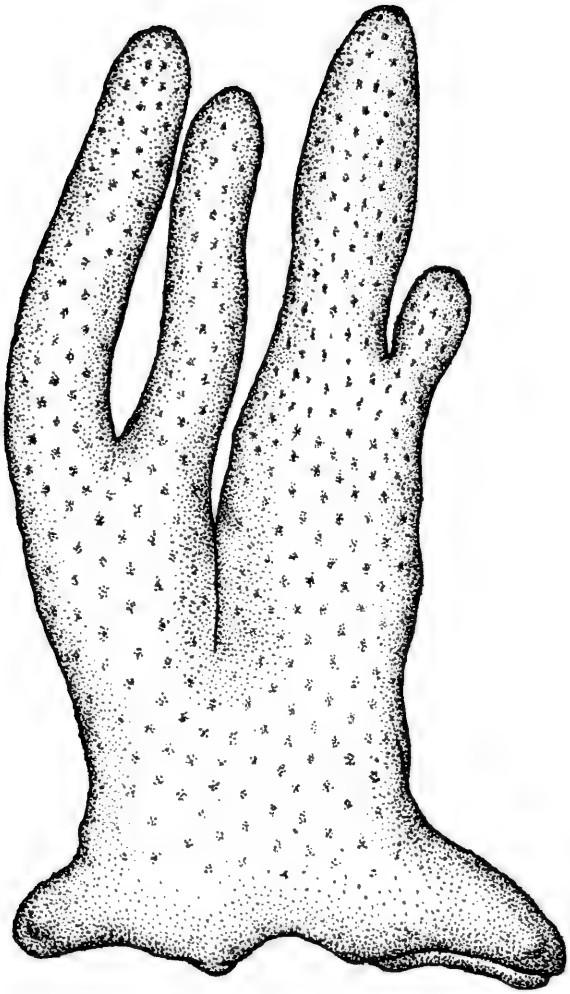

FIGURE 2. *Eleutherobia zanahoria* sp. nov. Paratype (CAS 118502); maximum length 63 mm.

(Fig. 1C). In both paratypes, as in the holotype, polyps appear immediately above the holdfast region, so that it is difficult to distinguish a conspicuous stalk region.

Polyps. The polyps are retracted into the colonies in all specimens and are thus not observable. A piece of surface coenenchyme was removed in paratype CAS 118503 to show the arrangement of several retracted polyps (Fig. 3). A single polyp that was isolated from paratype CAS 118503 and dissolved in sodium hypochlorite, revealed no sclerites in the anthocodial region or polyp walls. Calyces are absent, the retracted polyps form recessed slits or depressions on the surface of the polypary, or they are flush with the surrounding polypary surface.

Sclerites. The sclerites are densely set in the surface and subsurface coenenchyme of the polypary and holdfast region, as well as in the deep interior of the holdfast region. Sclerites are absent from the polyps and walls of the gastric cavities. The sclerites are radiates, crosses, and irregularly-shaped forms that are presumably derived from radiates, 0.04–0.17 mm in length. The sclerites of the polypary are more gracile and, for the most part, somewhat smaller than sclerites of the stalk and holdfast region. Sclerites from the polypary surface are mostly slender radiates, 0.05–0.09 mm in length (Figs. 4A, 5). Sclerites from the subsurface of the polypary are similar radiates, including some crosses and irregular forms, 0.04–0.12 mm in length (Figs. 5, 6B). Sclerites from the surface of the holdfast region are relatively robust radiates, crosses, and irregular forms, 0.07–0.17 mm long (Figs. 4B, 7). Sclerites from the deep interior of the holdfast region are robust, mostly irregular forms derived from and similar to radiates, with some radiates and crosses, 0.08–0.16 mm long (Figs. 6A, 7).

Color. The coenenchyme is vivid orange throughout (Fig. 1); polyps are creamy white. Sclerites are pale orange or yellowish, some are colorless.

ETYMOLOGY. — The specific epithet is derived from the Spanish, *zanahoria* (a carrot); in reference to the carrot-like appearance and color of this soft coral.

DISTRIBUTION. — Known from the type locality—the Tonga Islands in the central, South Pacific Ocean (Fig. 8). This species is also reported to occur on the Great Barrier Reef, Queensland, Australia (P. Alderslade, pers. comm.).

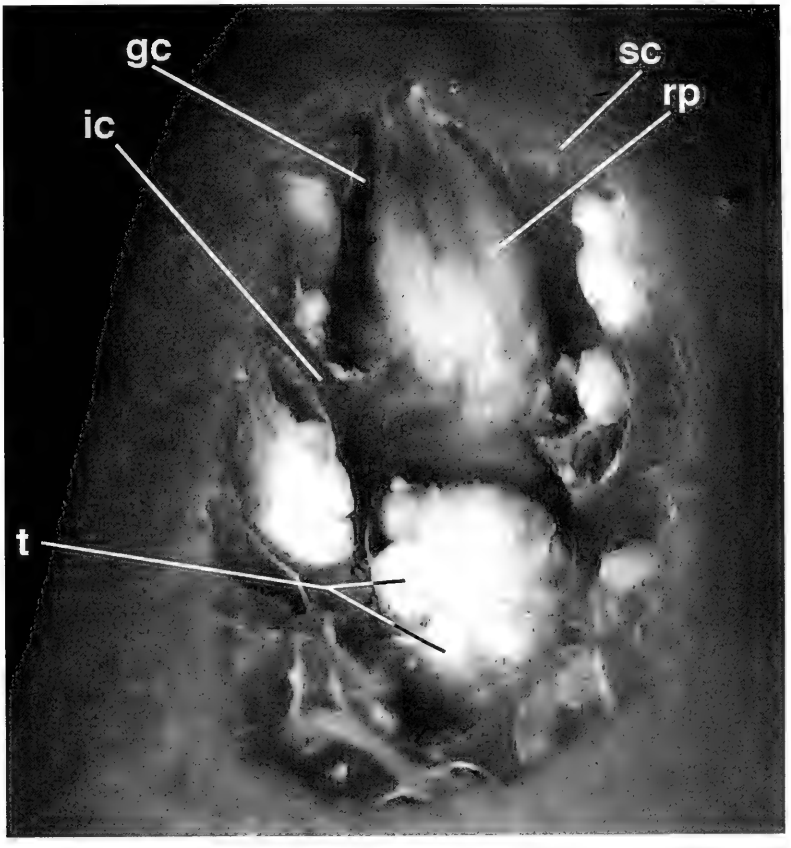

FIGURE 3. *Eleutherobia zanahoria* sp. nov. Micrograph of paratype (CAS 118503) with portion of surface coenenchyme removed, showing interior of colony and several retracted polyps. Abbreviations: gc - gastric cavity; ic - interior coenenchyme; rp - retracted polyp; sc - surface coenenchyme; t - tentacle. Scale bar = 1.3 mm.

DISCUSSION

Species of the genus *Eleutherobia* closely resemble those of another Indo-West Pacific genus, *Paraminabea* Williams and Alderslade, 1999. The two taxa differ however, in that species of *Eleutherobia* are monomorphic, while those of *Paraminabea* have dimorphic polyps (Williams 1992b:5, fig. 2C; Williams and Alderslade 1999:347, fig. 6B). Unfortunately, siphonozooids are often very difficult to observe in preserved material. This circumstance has been at least partly responsible for the misidentification of soft coral material in the past, and will no doubt result in similar mistakes being made in the future. Thin sectioning of the surface and subsurface coenenchyme of the polypary of the soft coral in question, together with the microscopic examination of these sections, is often necessary to detect siphonozooids in tightly contracted and retracted preserved material.

Of the twenty valid species of the genus *Eleutherobia*, *E. zanahoria* sp. nov. is superficially most similar to *Eleutherobia grayi* (J. A. Thomson and Dean 1931), redescribed by Verseveldt and Bayer (1988:33), from Indonesia and the Ryukyu Islands. The two species can be differentiated as follows. In wet-preserved specimens of *E. grayi*, the retracted polyps often form low rounded, to more pronounced and mammiform, to conical protuberances on the surface of the polypary. In *E. zanahoria* sp. nov., on the other hand, retracted polyps in preserved specimens or retracted living animals, appear as shallow slits or pits, or are flush with the surface of the polypary (Fig. 1). Although sclerite size is simi-

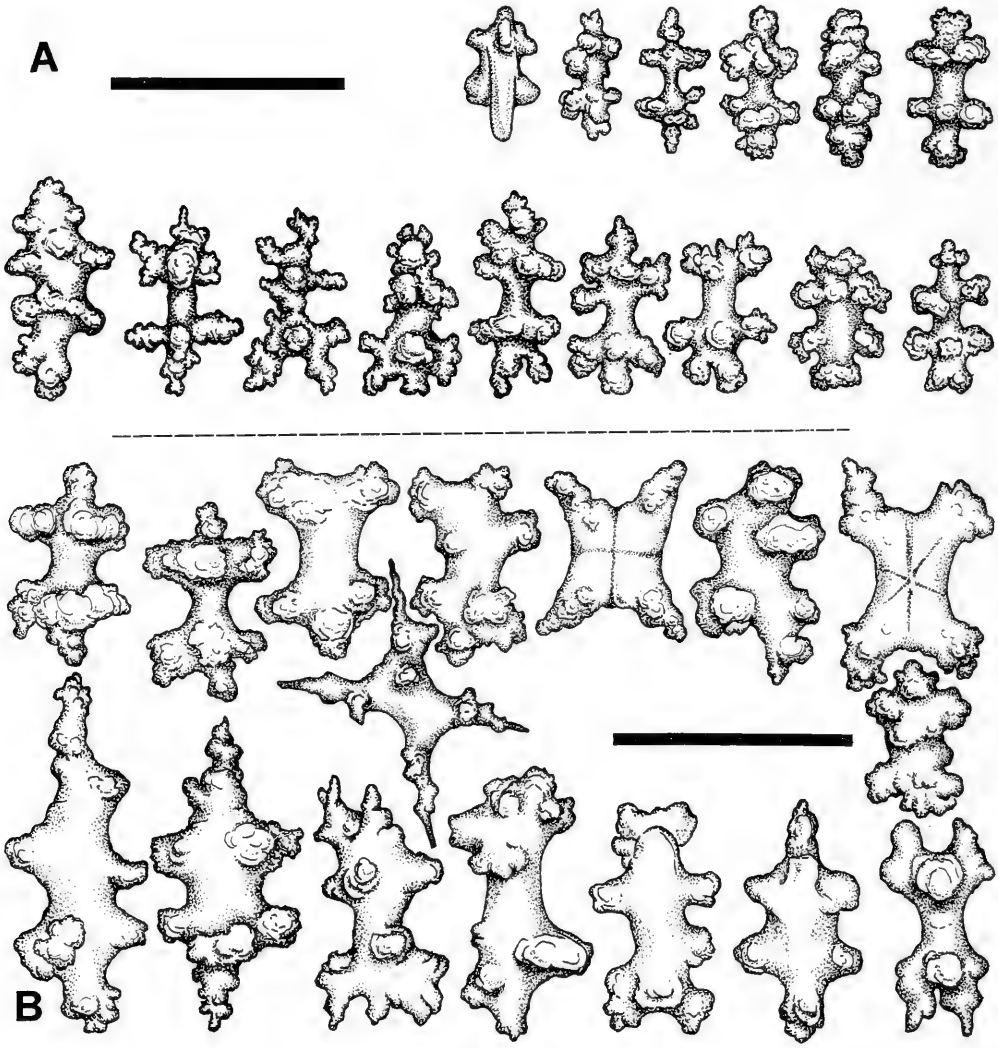

FIGURE 4. *Eleutherobia zanahoria* sp. nov. A. Sclerites from the surface of the polypary. B. Sclerites from the surface of the holdfast region of the stalk. Scale bars = 0.1 mm.

lar in both species, the complement of sclerites differs. In *E. grayi*, triradiates are relatively common and the crosses (quadriradiates) that are found, are relatively small (< 0.06 mm long), and have short and knobby or truncated rays (Verseveldt and Bayer 1988:93, fig. 24). By comparison, in *E. zanahoria* sp. nov., triradiates are rare or absent, and many crosses are relatively large (up to 0.14 mm in length), and have finely tapered and acute-tipped rays (Figs. 4B, 5A, 6A, 7A–B, 7F). Finally, in regards to coloration, the two species differ in that *E. grayi* is bicolored (red or red-orange with yellow retracted polyp mounds, while *E. zanahoria* sp. nov. is uniform bright orange throughout (Fig. 1).

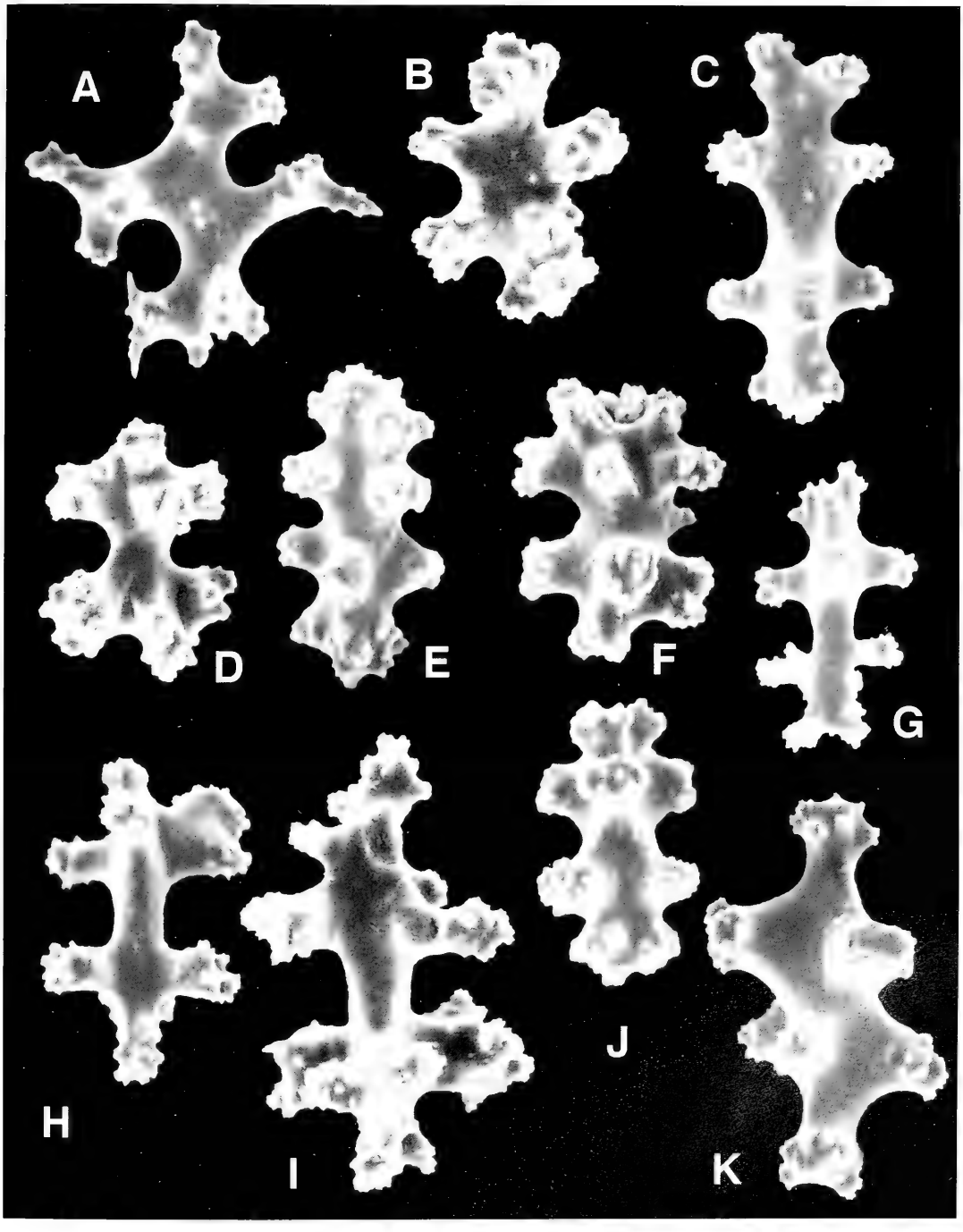

FIGURE 5. *Eleutherobia zanahoria* sp. nov. Scanning electron micrographs of sclerites from the polyparium. A. 0.09 mm; B. 0.05 mm; C. 0.07 mm; D. 0.05 mm; E. 0.07 mm; F. 0.06 mm; G. 0.06 mm; H. 0.06 mm; I. 0.06 mm; J. 0.06 mm; K. 0.09 mm.

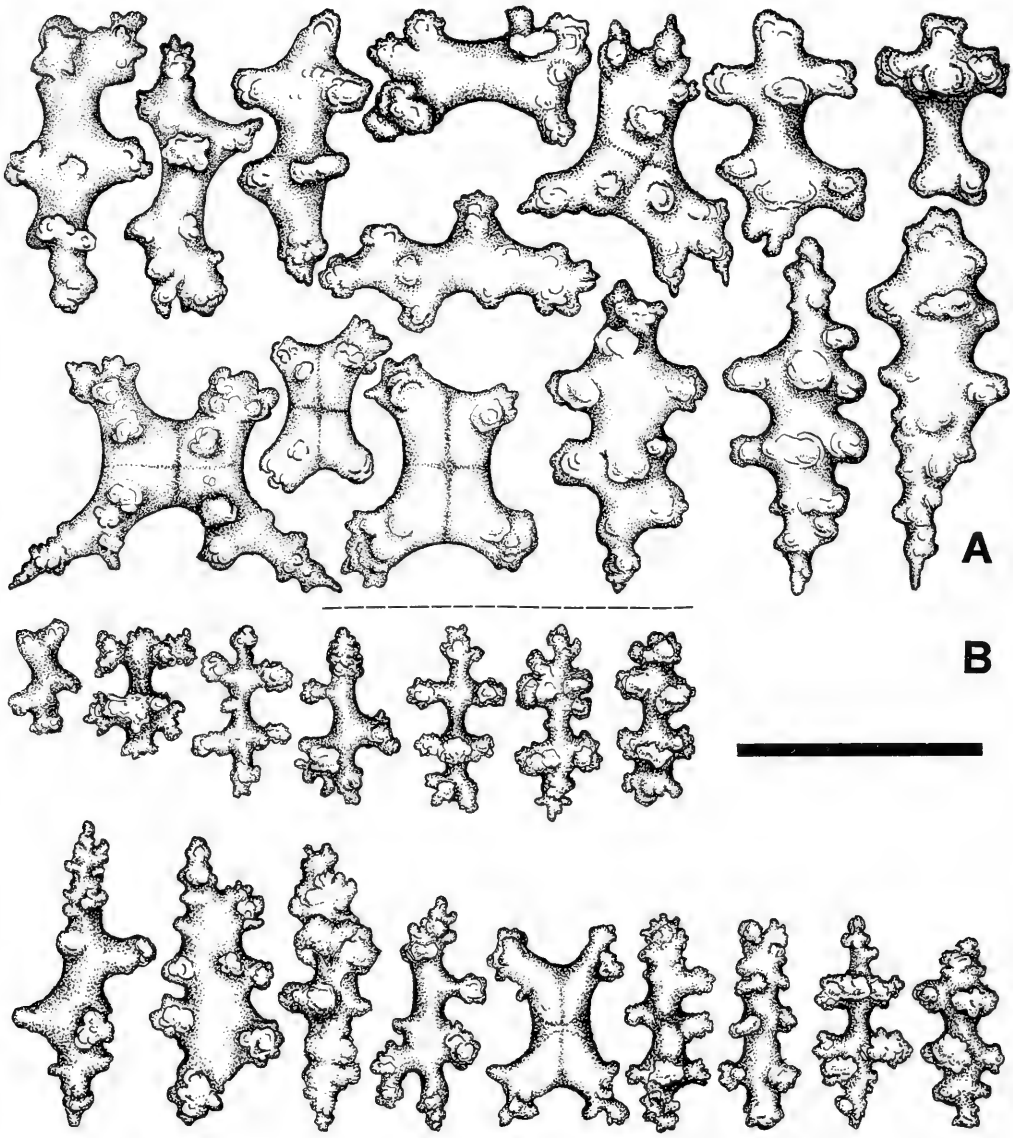

FIGURE 6. *Eleutherobia zanahoria* sp. nov. A. Sclerites from the interior of the holdfast. B. Sclerites from the interior of the polypary. Scale bar for A and B = 0.1 mm.

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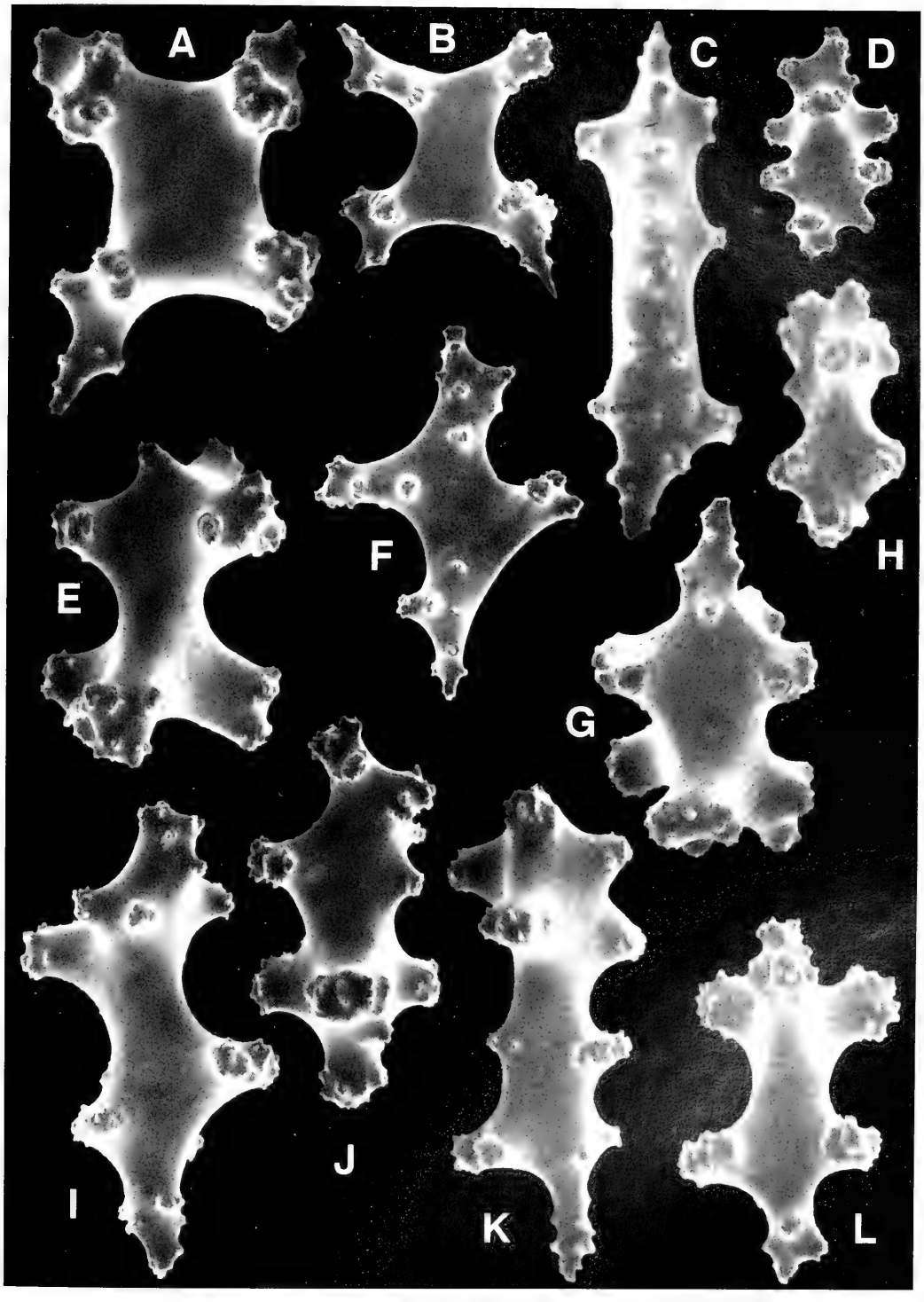

FIGURE 7. *Eleutherobia zanahoria* sp. nov. Scanning electron micrographs of sclerites from the holdfast region of the stalk. A. 0.14 mm; B. 0.10 mm; C. 0.09 mm; D. 0.08 mm; E. 0.08 mm; F. 0.10 mm; G. 0.08 mm; H. 0.08 mm; I. 0.10 mm; J. 0.08 mm; K. 0.10 mm; L. 0.09 mm.

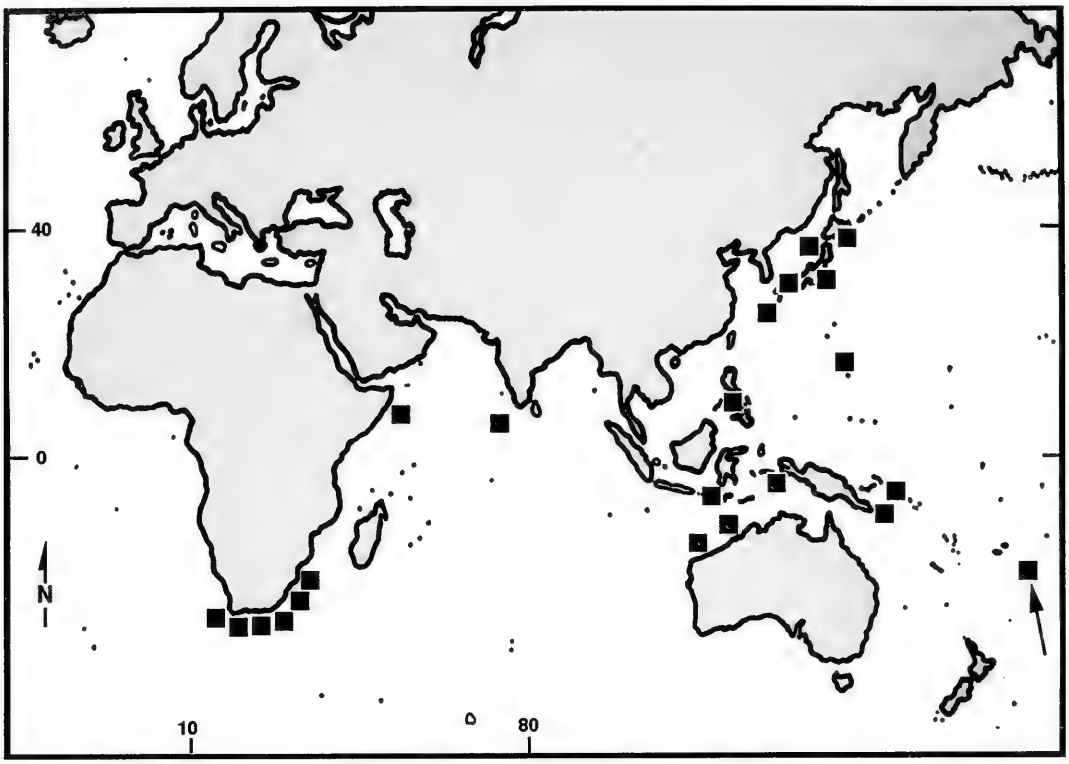

FIGURE 8. Map of the Indo-West Pacific showing geographic distribution of the genus *Eleutherobia*. Arrow shows type locality of *Eleutherobia zanahoria* sp. nov.

LITERATURE CITED

BENAYAHU, Y. AND M. H. SCHLEYER. 1995. Corals of the south-west Indian Ocean II. *Eleutherobia aurea* spec. nov. (Cnidaria, Alcyonaria) from deep reefs on the KwaZulu-Natal Coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report 68:1–12.

GRAY, J. E. 1835. Characters of a new genus of corals (*Nidalia*). Proceedings of the Zoological Society of London 3:59–60.

———. 1862. Description of two new genera of zoophytes (*Solenocaulon* and *Bellonella*) discovered on the north coast of Australia by Mr. Rayner. Proceedings of the Zoological Society of London 1862:34–37.

HOOPER, G. J., M. T. DAVIES-COLEMAN, AND M. SCHLEYER. 1997. New diterpenes from the South African soft coral *Eleutherobia aurea*. Journal of Natural Products 60:889–893.

LONG, B. H., J. M. CARBONI, A. J. WASSERMAN, L. A. CORNELL, A. M. CASAZZA, P. R. JENSEN, T. LINDEL, W. FENICAL, AND C. R. FAIRCHILD. 1998. Eleutherobin, a novel cytotoxic agent that induces tubulin polymerization, is similar to paclitaxel (Taxol). Cancer Research 58:1111–1115.

PFEFFER, G. 1889. Zur Fauna von Sud-Georgien. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 6(2):49–55.

PÜTTER, A. 1900. Alcyonaceen des Breslauer Museum. Zoologische Jahrbücher (Systematik)13(5):443–462.

THOMSON, J. A. AND L. M. I. DEAN. 1931. The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga Expedition Monographs 13d:1–227.

VERSEVELDT, J. AND F.M. BAYER. 1988. Revision of the genera *Bellonella*, *Eleutherobia*, *Nidalia* and *Nidaliopsis* (Octocorallia: Alcyoniidae and Nidalliidae), with descriptions of two new genera. Zoologische Verhandelingen 245:1–131.

WILLIAMS, G. C. 1992a. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Annals of the South African Museum 100(3):249–358.

———. 1992b. Revision of the soft coral genus *Minabea* (Octocorallia: Alcyoniidae) with new taxa from the Indo-West Pacific. Proceedings of the California Academy of Sciences 48(1):1–26.

———. 1996. Octocorallia—Octocorals. Pp. 32–60 *in* Coral reef animals of the Indo-Pacific—animal life from Africa to Hawai'i exclusive of the vertebrates. T. M.Gosliner, D. W. Behrens, and G. C. Williams. Sea Challengers, Monterey. 314 pp .

WILLIAMS, G. C. AND P. ALDERSLADE. 1999. Revisionary systematics of the western Pacific soft coral genus *Minabea* (Octocorallia: Alcyoniidae), with descriptions of a related new genus and species from the Indo-Pacific. Proceedings of the California Academy of Sciences 51(7):337–364.

XIAO, T. C., S. K. BHATTACHARYA, B. ZHOU, C. E. GUTTERIDGE, T. R. R. PETTUS, AND S. J. DANISHEFSKY. 1999. The total synthesis of eleutherobin. Journal of the American Chemical Society 121(28):6563–6579.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Two New Species of *Aldisa* Bergh, 1878 (Mollusca, Nudibranchia) from the Tropical Indo-Pacific

by

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This paper provides descriptions of two new species of the genus *Aldisa* from the tropical Indo-Pacific. *Aldisa albatrossae* sp. nov. from Japan, the Philippines, and Indonesia, is characterized by having a blue-green dorsum with distinctive black markings and blotches of yellow-orange color. *Aldisa williamsi* sp. nov. from Papua New Guinea and Indonesia, has a bluish dorsum with a circular black mark. The two species are distinguishable based on differences in body coloration, arrangement of tubercles and characters of the reproductive system. Other species that have similar color patterns and also appear to be mimics of phylllidid nudibranchs are discussed. The new species appear to have two plesiomorphic traits that were previously undescribed for the genus *Aldisa*, unipinnate gills (only in *A. williamsi*), and presence of two large hamate radular teeth (in both species).

The genus *Aldisa* is characterized by having elongate denticulate teeth, penial spines, conical tubercles and absence of oral tentacles. The genus *Aldisa* presently contains twelve valid species, mainly found in the cold-temperate waters of the Atlantic Ocean. Eleven species were identified as valid during the revision of this genus by Millen and Gosliner (1985) and one species has been described since, *Aldisa barlettai* Ortea and Ballesteros, 1988 from the Cape Verde Islands. Only one of these twelve previously described species is from the tropical Indo-Pacific, *Aldisa pikokai* Bertsch and Johnson, 1967, from Hawaii.

The objective of this paper is to describe two new species from the tropical Indo-Pacific. The descriptions are based on specimens deposited in the Department of Invertebrate Zoology of the California Academy of Sciences (CASIZ).

Species Descriptions

Aldisa albatrossae sp. nov.
Figs. 1A–B, 2, 3

Doris sp. 1 Ono, 1999:138, fig. 178.
Chromodoris sp. Masuda, 1999:195, bottom photo.

Material Examined. — Holotype: Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan (26°30.4′N, 127°52.6′E), 3 April 1993, 19 mm long, collected by Robert Bolland (CASIZ 89034). Paratypes: Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan (26°30.4′N, 127°52.6′E), 11 April 1993, 1 specimen, 21 mm long, collected by Robert Bolland (CASIZ 88884); Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa,

Ryukyu Islands, Japan (26°30.0′N, 127°50.9′E), 9 May 1998, 1specimen, 17 mm long, collected by Robert Bolland (CASIZ 115720); Seragaki Tombs, Okinawa, Ryukyu Islands, Japan (26°30.4′N, 127°52.6′E), 29 April 1995, 2 specimens, 22 mm long and 19 mm long, collected by Robert Bolland (CASIZ 105287); Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan (26°30.0′N, 127°50.9′E), 26 March 1994, 1 specimen, 11 mm long, collected by Robert Bolland (CASIZ 99086).

ETYMOLOGY. — *Aldisa albatrossae* gets its name from the Albatross expedition of 1907–10 to the Philippines in which a specimen of this species was collected and illustrated (Fig. 1A).

GEOGRAPHIC RANGE. — So far this species is known from the Kerama and Ryukyu Islands of Japan, the Albatross specimen collected in the Philippines, and from a photograph of a species from Komodo Island, Indonesia taken by Jim Black.

EXTERNAL MORPHOLOGY. — The living animals are 11–21 mm in length. The dorsum of the living animal is a bluish color (Fig. 1B). This color is darker at the edges and lighter towards the middle of the dorsum. It is interrupted by the presence of numerous white tubercles. The dorsum also contains a distinctive black pattern, which is virtually identical in all specimens examined. The black pattern begins as a T-shape crossing in front of and between the rhinophores. Behind the rhinophores, the T-shape connects with a black rectangular mark that spans the dorsum to the branchial pocket. Two black lines extend from the rectangular mark around the sides of the branchial pocket. In one specimen the black marks form a continuous band around the posterior margin of the branchial sheath. These characteristic black markings on the dorsum can also be seen in the preserved specimens. Yellow-orange splotches are present on the dorsum of the living animal. These marks of yellow-orange lie at the front edges of the T of the black mark and along the anterior edge of the rectangular portion of the black mark. Yellow-orange lines also extend from the sides of the branchial pocket to the posterior edges of the dorsum.

The rhinophores are dark, uniformly off-white and lamellate, containing 18 lamellae in a 21 mm long specimen. The branchial leaves are a darker gray than the rhinophores and range from 6–9 in number. They are bipinnate and relatively sparsely branched.

There are numerous rounded tubercles over the surface of the body. Four to five rows of tubercles are found outside of the broad black ring on all sides of the body. An additional four to five rows are found within the black band. The tubercles of the body are smaller towards the edges of the dorsum (Fig. 2D) with a row of small tubercles around the entire margin. Around the branchial pocket, there are two rows of tubercles. The tubercles nearest the gill are equally spaced and of alternating large then small size. The other row also consists of tubercles of alternating sizes. Each rhinophore is surrounded by four tubercles. These tubercles also alternate large and small with the larger tubercles on the left and right sides of each rhinophore. All tubercles are opaque white and conical (Fig. 2D).

The anterior portion of the foot is grooved but not notched. The head has short oral protrusions (Fig. 3C) with a short grove along their outer edge.

RADULA. — The radular formula is undeterminable owing to the elongate, overlapping teeth. The radular teeth are narrow and elongate with broad triangular bases (Fig. 2A). The top third or fourth of each tooth bears 20–24 sharp denticles, which extend along the side of each tooth. The denticles near the apex of the teeth are much longer than those on the sides (Fig. 2B). There are also two large, hamate teeth, each one situated on one half-row, which lack denticles (Fig. 2C).

REPRODUCTIVE SYSTEM. — The ampulla is tubular and thick, winding back on itself before narrowing into a thin tube that connects with the oviduct and the prostate (Fig. 3A). The oviduct connects to the female gland underneath the prostate. The prostate is granular, tubular and slightly larger than the ampulla. Its end joins with the thin deferent duct. The deferent duct loops before meeting the vaginal duct at the genital atrium. The genital atrium is no wider than the width of the ducts and extends only slightly beyond their meeting. The penial bulb is armed with 13 rows of six hooks each. The hooks have a wide base tapering off to a thin cusp (Fig. 3B). The vaginal duct is about the same length

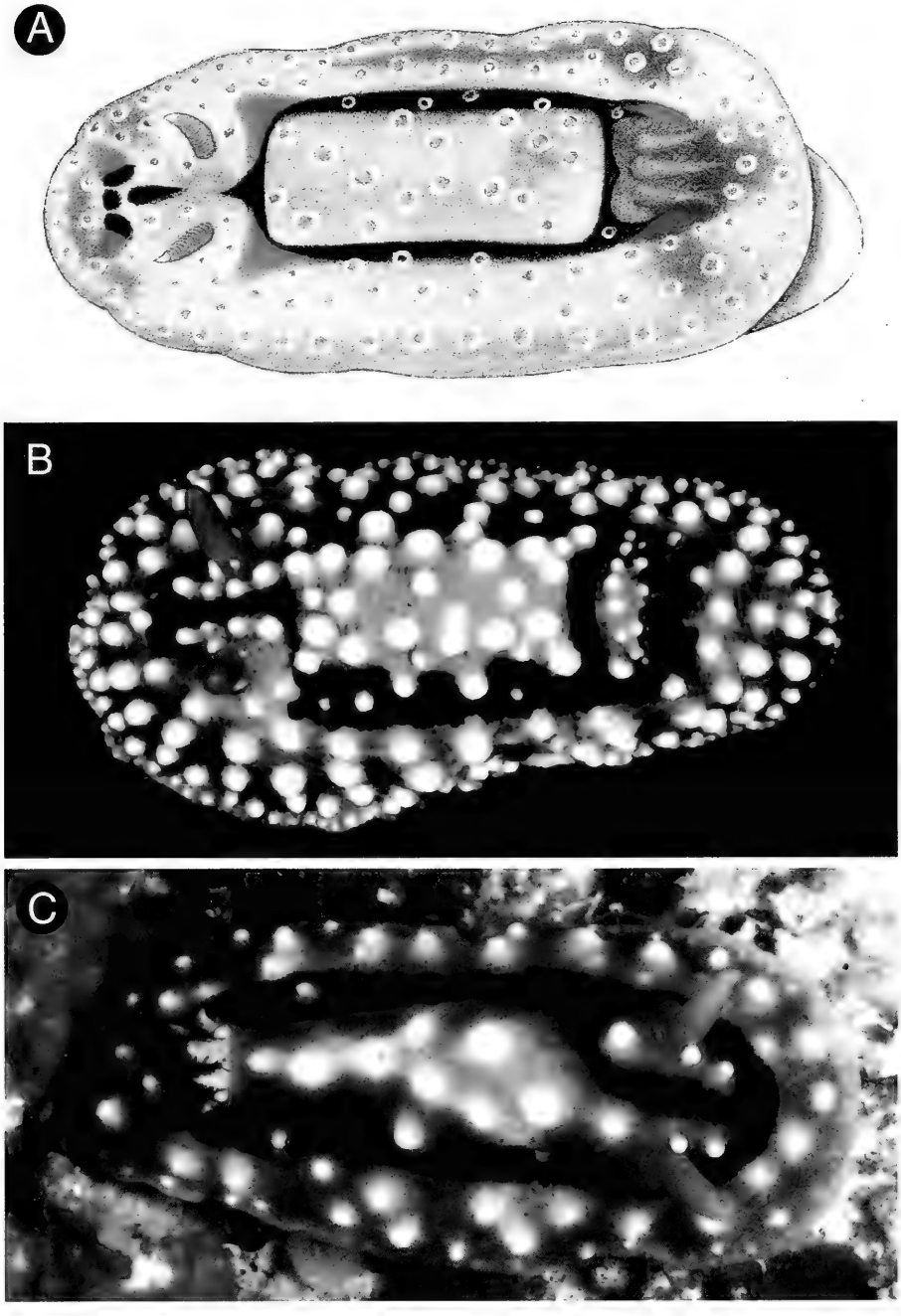

FIGURE 1. Color illustrations of the living animals. A. Unpublished painting of *Aldisa albatrossae* from the Albatross Expedition; B. Living paratype of *A. albatrossae* sp. nov. from the Ryukyu Islands, Japan (CASIZ 88884); C. Living paratype of *A. williamsi* sp. nov. from Barracuda Point, Papua New Guinea (CASIZ 109791).

and width as the deferent duct. The vaginal duct runs underneath the seminal receptacle to connect to the round bursa copulatrix. Another duct connects the bursa copulatrix to the smaller, stalked seminal receptacle. The short uterine duct connects to the middle of this duct and leads into the female gland.

***Aldisa williamsi* sp. nov.**
Figs. 1C, 4, 5

Doris? sp. 10 Rudman, 2000.

MATERIAL EXAMINED. — HOLOTYPE: Barracuda Point, E side of Tab Island, near Madang, N coast of Papua New Guinea, 14 November 1990, 11 mm preserved length, collected by Terry Gosliner (CASIZ 075936). PARATYPE: Bomber Reef, Madang, Papua New Guinea, 2 November 1996, 1 specimen 14 mm preserved length, collected by Gary Williams (CASIZ 109791).

ETYMOLOGY. — This species is named after our good friend and colleague, Gary Williams (CASIZ). He collected one of the specimens of this new species and a number of other nudibranchs during several expeditions to the tropical Indo-Pacific.

GEOGRAPHIC RANGE. — This species has only been collected at Madang, Papua New Guinea, but there are records from two photographs of specimens from Sulawesi, Indonesia taken by Lindsay Warren (Rudman, 2000).

EXTERNAL MORPHOLOGY. — The dorsum of the living animal is a uniform bluish gray color with opaque white tubercles (Fig. 1C). There is a distinctive black pattern on the dorsum of the living animal that can also be seen in preserved specimens. This pattern consists of an oval line that stretches from in front of the rhinophores to behind the branchial pocket. In the two specimens examined there is also a short line that runs between the two rhinophores and connects posteriorly to the oval line behind the left rhinophore.

The rhinophores are a pale brown color with a bluish base. They have 13 lamellae in a 14 mm long preserved specimen. The gill consists of six unipinnate branchial leaves. The two posteriormost leaves are bifurcated at the base. They are a light yellow hue with splotches of opaque white.

The tubercles of the dorsum are opaque white and are of roughly equal size. Smaller tubercles are present at the edges of the dorsum. There are two to three rows of tubercles outside of the broad black band that encircles the notum with an additional two to three rows inside the band. Around each rhinophore, there are two tubercles. In the paratype specimen the outer tubercle is the same pale brown color as the rhinophore. The inner tubercle is opaque white. In the holotype, both tubercles are opaque white. Around the branchial pocket, there is a single row of 8 white tubercles of alternating large and small size. These tubercles are evenly spaced between the branchial leaves and are different from those of the dorsum.

The anterior portion of the foot is not notched. The head contains short oral protrusions (Fig. 5C) and these protrusions have a groove along the outer edge.

RADULA. — The radular formula is undeterminable. The radular teeth are narrow and elongate with broad triangular bases (Fig. 4A). The top third or fourth of each tooth bear 15–20 sharp denticles, which extend along the side of each tooth. The denticles near the apex of the teeth are much longer than those on the sides (Fig. 4B). There are also two large, hamate teeth, each one situated on one half-row (Fig. 4C), which lack denticles.

REPRODUCTIVE SYSTEM. — The ampulla is tubular and convoluted (Fig. 5A). It narrows into a thin tube and connects to the oviduct and prostate. The prostate is longer and slightly thinner than the ampulla. It loops a few times before connecting to the thin deferent duct. The deferent duct and vaginal duct connect at the genital atrium. The two ducts are of roughly equal width and length. The penial bulb is armed with 11 rows of 8 penial hooks each. The hooks have a wide base and a relatively short cusp (Fig. 5B). The vaginal duct connects to the large round bursa copulatrix. A separate duct con-

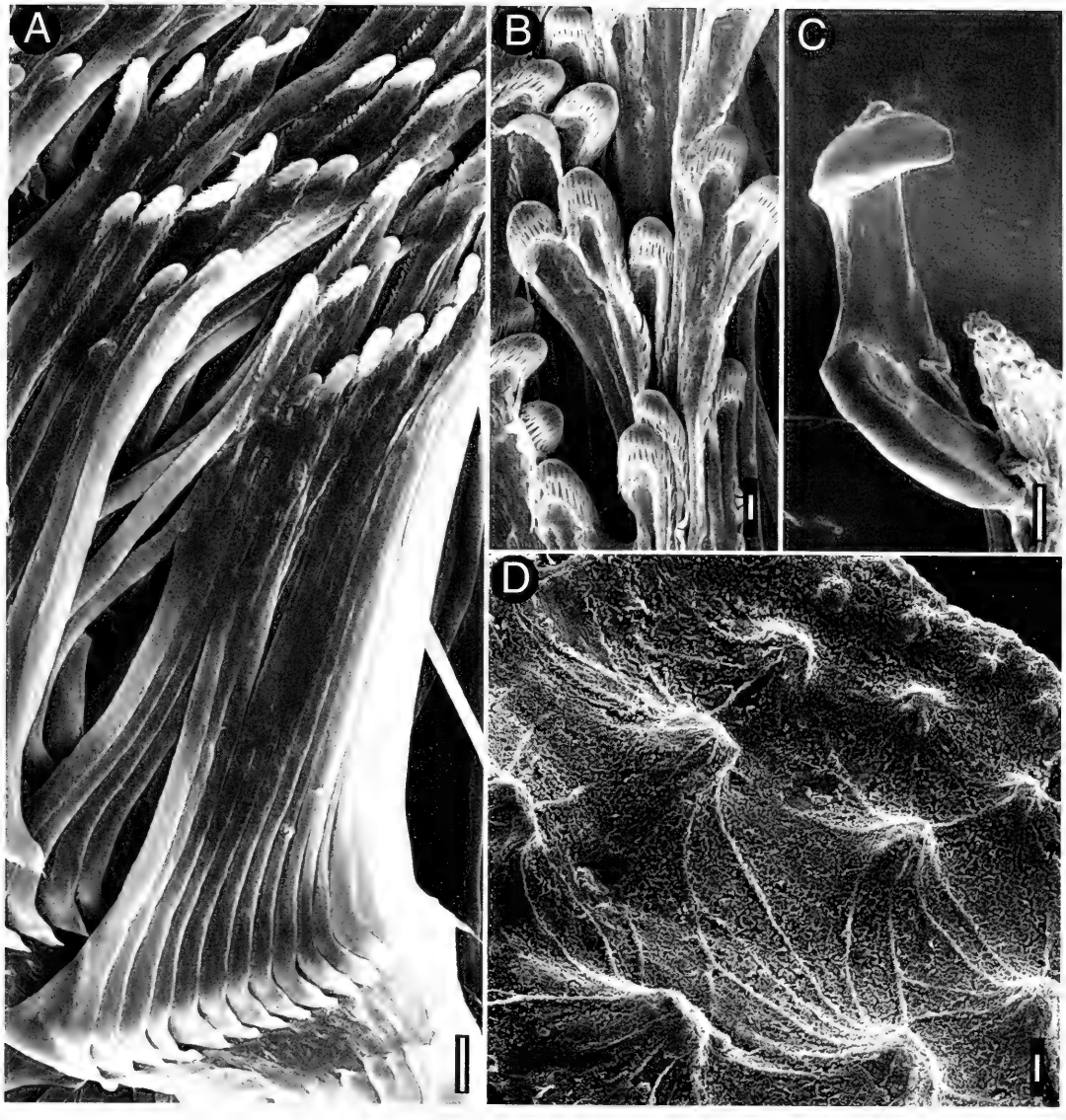

FIGURE 2. *Aldisa albatrossae* sp. nov. (CASIZ 88884) scanning electron micrographs. A. Elongate radular teeth, scale bar = 10 μm; B. Heads of elongate radular teeth, scale bar = 2 μm; C. Hamate tooth, scale bar = 20 μm; D. Tubercles of dorsum, scale bar = 200 μm.

nects to the short stalk of the seminal receptacle. The very thin uterine tube connects to this duct and then connects to the female gland near the genital atrium.

DISCUSSION

The revision of the genus *Aldisa* by Millen and Gosliner (1985) produced a diagnosis of the genus with the following characteristics: elongate radular teeth with multiple denticulations, a dorsum with low conical tubercles (except for *A. pikokai*, which lacks dorsal tubercles), a ring of tubercles around branchial and rhinophoral pockets, bipinnate or tripinnate branchial leaves, penial spines in almost all

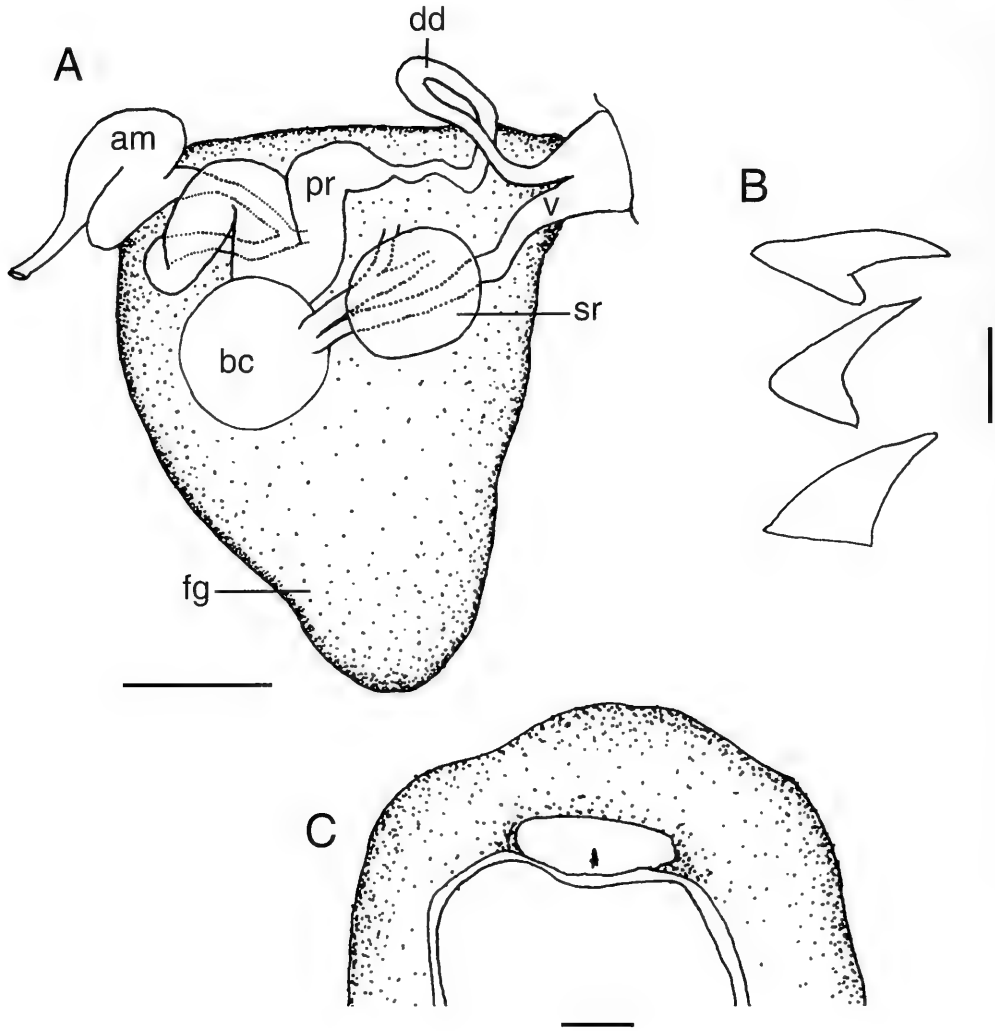

FIGURE 3. *Aldisa albatrossae* sp. nov. (CASIZ 88884). A. Reproductive system, scale bar = 0.5 mm; B. Penial hooks, scale bar = 5 μm; C. Ventral view of the anterior border of the foot, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; v, vagina.

species, absence of oral tentacles and an anterior portion of the foot that is not notched. The two species described in this paper exhibit almost all the characteristics of the genus *Aldisa* noted above and are identified as such.

They join the 12 previously described species of *Aldisa*. The species previously described include the 11 species identified as valid during revision of *Aldisa* by Millen and Gosliner (1985) and one species that has been described since, *Aldisa barlettai* Ortea and Ballesteros, 1988, from the Cape Verde Islands. While the species described in this paper are clearly placed within the genus *Aldisa*, they differ markedly from the species previously described.

Aldisa albatrossae and *A. williamsi* both exhibit a character that, before now, has not been described for the genus *Aldisa*: the presence of a pair of unique teeth in their radula. As mentioned before, these two teeth are short, wide, smooth and hamate, differing from the numerous thin, elongate teeth, characteristic of *Aldisa*, that make up the rest of the radula. The presence of these two broad

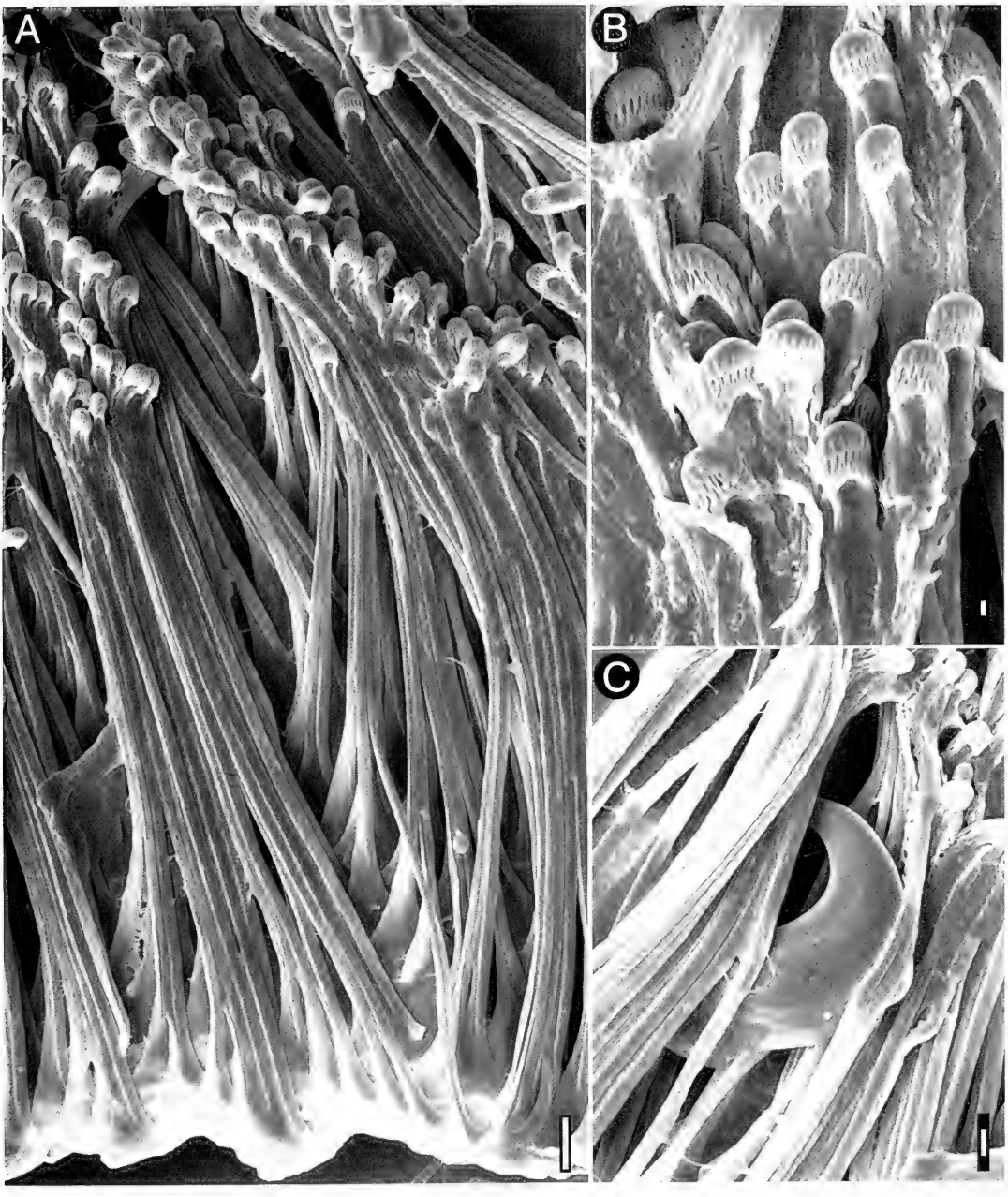

FIGURE 4. *Aldisa williamsi*, sp. nov. (CASIZ 109791) scanning electron micrographs. A. Elongate radular teeth, scale bar = 10 μm; B. Heads of elongate radular teeth, scale bar = 1 μm; C. Hamate tooth, scale bar = 10 μm.

teeth in these species is believed to be a plesiomorphic state due to the resemblance of these teeth to the hamate teeth of the other cryptobranch dorids. Also the unipinnate branchial leaves of *A. williamsi*, which occur in some basal dorids, may well be a plesiomorphy within *Aldisa*.

The coloration of *A. albatrossae* and *A. williamsi* also distinguishes them from the 12 species of *Aldisa* previously described. None of the 11 species that Millen and Gosliner (1985) identify as valid

exhibit any of the bright colors or black markings found on the notum of the new species. *Aldisa barlettai* from the Cape Verde Islands is the only other species to exhibit a bright and multi-colored body. However, the coloration of *A. barlettai*, which has a dorsum of blue-violet with white and orange tubercles (Ortea and Ballesteros 1988), is quite different from the new species which have a blue-green dorsum, white tubercles, black markings, and, in the case of *A. albatrossae*, yellow-orange splotches. Both species were collected in the warm waters of the Indo-Pacific, *A. albatrossae* from around the Kerama and Ryukyu Islands of Japan, the Philippines and Indonesia and *A. williamsi* from Papua New Guinea and Indonesia. *Aldisa pikokai*, from Hawaii, is the only other species found in the tropical Indo-Pacific. The orange-red coloration and absence of tubercles on the dorsum of *A. pikokai* (Bertsch and Johnson 1982), readily distinguishes it from the new species.

Aldisa albatrossae and *A. williamsi* share some characteristics of the radula, reproductive system and coloration, but there is little doubt that they are indeed distinct species.

Aldisa albatrossae is known from the six specimens examined in this study from Okinawa. Photographs of an additional three specimens from Okinawa were provided by Bob Bolland. Two additional photographs of specimens from the Kerama Islands appear in two Japanese books (Ono 1999; Masuda 1999). A single specimen was depicted in the drawing of the Albatross specimen from the Philippines (Fig. 1A). An additional specimen was photographed by Jim Black from Komodo Island, Indonesia. In all of these 13 specimens there are consistent elements of the external morphology. A black T-shaped marking is present on the anterior end of the notum and continues posteriorly between the rhinophores. This band then bifurcates and continues posteriorly as two bands that reconnect in front of the branchial sheath. In one specimen a second black band encircles the posterior portion of the branchial sheath. In all specimens, anterior and posterior patches of yellow-orange are present. In all of these specimens there are four tubercles surrounding each rhinophore sheath. In all specimens there are two bands of tubercles surrounding along the margin and immediately ventral to the branchial sheath. All specimens of *A. albatrossae* have bipinnate gill branches.

Aldisa williamsi is described here from two specimens from Papua New Guinea. Two additional specimens from Sulawesi, Indonesia, depicted by Rudman (2000) as *Doris*? sp. 10, also appear to be the conspecific with *A. williamsi*. These two specimens differ from the Papua New Guinea specimens in two minor details. In the specimens from New Guinea only one black band encircles the left rhinophore. In the specimens from Indonesia the black band runs between the rhinophores and bifurcates and reconnects with the primary black band that encircles most of the notum. In the Indonesian specimens an additional black band connects the primary oval of black anterior to the branchial plume. All four specimens have unipinnate branchial leaves, a single row of tubercles around the branchial sheath and a pair of tubercles around the rhinophore sheath. One of the Papuan specimens has one rhinophoral tubercle that is the same color as the rhinophore while the other tubercles is opaque white. In the remaining three specimens, both rhinophoral tubercles are opaque white. It is evident that all four specimens discussed here, likely represent a single species, *A. williamsi*.

Despite some variability in the external anatomy of both *A. albatrossae* and *A. williamsi*, there are consistent differences that clearly separate them. In *A. albatrossae*, there is always a T- shaped mark in front and between the rhinophores and then bifurcates to form a black oval that terminates at the anterior end of the branchial sheath, while in *A. williamsi* there is a continuous black oval band that extends from the anterior end of the notum and encircles the posterior end of the branchial sheath. Yellow-orange pigment is present in all specimens of *A. albatrossae*, while in *A. williamsi*, none of this pigment is present. In *A. albatrossae*, there is a double row of tubercles around the branchial sheath while in *A. williamsi* there is only a single row. In *A. albatrossae*, there are four tubercles around the rhinophoral sheath while in *A. williamsi* there are only two tubercles. *Aldisa albatrossae* consistently has more tubercles (4–5 rows outside of the oval band and 4–5 additional rows inside the band) than does *A. williamsi* (2–3 rows outside of the oval band and 2–3 additional rows inside the band). The gill

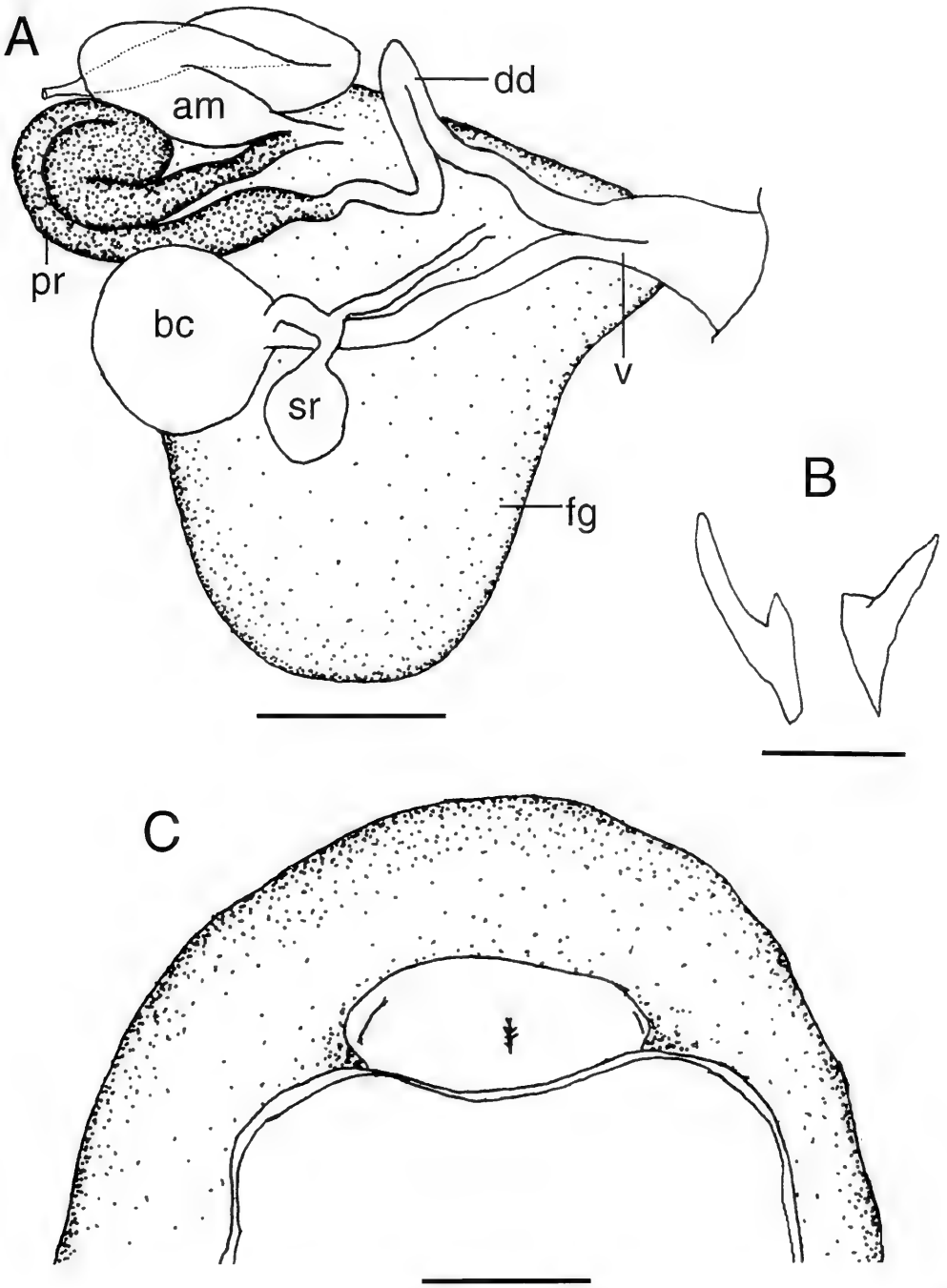

FIGURE 5. *Aldisa williamsi*, sp. nov. (CASIZ 109791). A. Reproductive system, scale bar = 0.5 mm; B. Penial hooks, scale bar = 5 μm; C. Ventral view of the anterior border of the foot, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; v, vagina.

branches of *A. albatrossae* appear to be more numerous (6–8) than those of *A. williamsi* (6) and more highly pinnate.

The radular teeth of both species are similar in that there is a pair of hamate teeth in addition to the elongate pectinate teeth. In *A. albatrossae* there are 20–24 denticles along the pectinate teeth while in *A. williamsi* there appear to be fewer (15–20).

A few differences are seen between the reproductive systems of the two species. In one specimen of *A. williamsi* the seminal receptacle is about a quarter the size of the bursa copulatrix, while the seminal receptacle in one specimen of *A. albatrossae* almost equals the size of its bursa copulatrix. The uterine tube of *A. williamsi* connects to the female gland at a point much closer to the genital atrium than does the uterine tube of *A. albatrossae*. These reproductive and radular differences should be reconfirmed when additional material of *A. williamsi* becomes available.

There are consistent differences in the external morphology of these two species that warrant their description as distinct taxa. The fact that these differences are consistent within overlapping geographical ranges in Indonesia is supportive of the fact that they do not simply represent geographical variants of a single species.

Discodoris liturata Bergh, 1905, is another dorid with a similar color pattern. It has a gray-green body with opaque white pustules and black markings. The radular morphology of this species has typically hamate teeth and lacks any of the pectinate teeth of *Aldisa* (Rudman 1998c). Both *D. liturata* and *A. williamsi* bear a strong resemblance to another dorid, *Phyllidiella pustulosa* (Cuvier, 1804), and are probably mimics of this species (Rudman 1998b; 2000). In *P. pustulosa* a dorsal gill and a radula are absent. *Phyllidiella pustulosa* and *D. liturata* also differ from *A. williamsi* and *A. albatrossae* in having black rather than off-white to pale brown rhinophores.

Two undescribed species, referred to as *Doris?* sp. 2 (Rudman 1998a) and *Chromodoris* sp. (Debelius 1996:213, bottom photo) are similar in their appearance to this group of *Phyllidia* mimics. *Doris?* sp. 2, from Thailand, is quite similarly colored to *A. albatrossae*, but it has consistent differences in its color pattern. It has black rather than off white to pale brown rhinophores and has yellow pigment on the tubercles rather than between them. It also has a complete oval of black pigment anteriorly rather than a T-shaped mark. Also the black oval terminates posterior to the branchial sheath rather than anteriorly. *Chromodoris* sp. of Debelius is blue in color with irregular black markings and yellow pustules on the notum that are similar in appearance to *Phyllidia varicosa* Lamarck, 1801. We were unable to obtain specimens to examine radular or reproductive systems characters. Therefore it is not possible, at present, to state anything further about their systematic placement.

Acknowledgments

The material studied has been collected by Gary Williams and Robert Bolland. Jim Black kindly provided a photo of *Aldisa albotrossae* from Indonesia. This paper was supported by the National Science Foundation through the PEET Grant DEB - 9978155 (Phylogenetic systematics of dorid nudibranchs) and the REU Grant DBI - 9820251 (Summer Systematics Institute).

Literature Cited

Bertsch, H. and S. Johnson. 1982. Three new species of dorid nudibranchs from the Hawaiian Islands. The Veliger 24:208–218.

Debelius, H. 1996. Nudibranchs and sea snails, Indo-Pacific field guide. IKAN-Unterwasserarchiv, Frankfurt, 321 pp.

Masuda, H. 1999. Guide Book to Marine Life. Tokai University Press, Tokyo, 404 pp.

Millen, S. V. and T. M. Gosliner. 1985. Four new species of dorid nudibranchs belonging to the genus *Aldisa*, with a revision of the genus. Zoological Journal of the Linnean Society 84:195–233.

Ono, A. 1999. Opisthobranchs of Kerama Islands. TBS-Britannica, Tokyo, 110 pp.

ORTEA, J. AND M. BALLESTEROS. 1988. Descripción de una espectacular especie del género *Aldisa* Bergh, 1878. Bollettino Malacologico 24:155–160.

RUDMAN, W. B. 1998a. *Doris*? sp. 2 available via http://www.seaslugforum.net/dorisp2.htm.

———. 1998b. Mimicry—*Phyllidiella*, flatworms, *Chromodoris* available via http://www.seaslugforum.net/mimicry.htm.

———. 1998c. *Discodoris*? *liturata* Bergh, 1905 available via http://www.seaslugforum.net/disclitu.htm

———. 2000. *Doris*? sp. 10 available via http://www.seaslugforum.net/dorisp10.htm.

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The Identity of *Doris* (*s.l.*) Species MacFarland, 1966 (Mollusca, Nudibranchia, Discodorididae): A Persistent Mystery from California Solved

by

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The Californian dorid nudibranch species, previously referred to by several authors as *Doris* (*s.l.*) species, based upon its original reference in MacFarland (1966), is a synonym of *Diaulula sandiegensis* (Cooper, 1863). The single specimen examined by MacFarland, and other animals collected from southern California, matching the external coloration of *Doris* (*s.l.*) species, have been examined and their internal anatomy is identical to that of *Diaulula sandiegensis*. Some variation has been observed in the shape of the outermost radular teeth of this species. The obscure and poorly described species *Doris odonoghuei* Steinberg, 1963 (= *Doris echinata* O'Donoghue, 1922) is probably a synonym of *Diaulula sandiegensis* as well.

The monographic work "Studies of the Opisthobranchiate Mollusks of the Pacific Coast of North America" by F. M. MacFarland was published posthumously in 1966. This work is composed of a series of unpublished notes that MacFarland had been preparing at the time of his death. One of several of the undescribed species included was referred to as *Doris* (*s.l.*) species. MacFarland frequently used Latin abbreviations in his notes and manuscripts, and in this instance "s.l." referred to the Latin, *sensu lato*, in the broader sense. MacFarland (1966) did not provide a specific name for this animal, which has similar external morphology and coloration to *Diaulula sandiegensis* (Cooper, 1863). He examined only one specimen of *Doris* (*s.l.*) species (Fig. 1), collected from Arch Rock Pool, Newport Bay, California, but he never studied it anatomically. The name *Doris* (*s.l.*) has been carried in the literature in numerous publications (Sphon and Lance 1968; Behrens 1980; McDonald and Nybakken 1981; McDonald 1983), and it is normally used for dorid nudibranchs similar to *Diaulula sandiegensis* but having pale dorsal spots. Other authors referred to this animal as *Doris* sp. (McDonald and Nybakken 1981; McDonald 1983) or *Diaulula* sp. 1 (Behrens 1991, 1992). All these references are based on MacFarland's descriptions and newly collected specimens as well. However, the question of whether this animal constitutes a different species from *Diaulula sandiegensis* remains unresolved.

Prior to the publication of MacFarland's (1966) memoir, a species with similar external characteristics was described as *Doris echinata* by O'Donoghue (1922). Later, Iredale and O'Donoghue (1923) reassigned this species to *Doridigitata* d'Orbigny, 1839 and changed the name (without explanation) to *Doridigitata maculata*. Steinberg (1963) noted that both O'Donoghue's names were preoccupied by *Doris echinata* Lovén 1846 and *Doris maculata* Garstang 1896, respectively, and proposed a new name, *Doris odonoghuei* for this species. Additionally, Steinberg (1963) questioned whether

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the placement of this species in the genus *Doris* is accurate and suggested that further study was necessary.

In this paper we attempt to determine the identity of *Doris* (*s.l.*) species based on the study of MacFarland's original material and additional specimens deposited at the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ). In addition, the status of *Doris odonoghuei* is discussed.

MATERIAL AND METHODS

For this paper several species matching the external coloration described for *Diaulula sandiegensis* and *Doris* (*s.l.*) species were examined. Table 1 summarizes the material sources and collection localities. Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a dissecting microscope using a camera lucida. Parts of the dorsum have been critical point dried for scanning electron microscopy (SEM) of the caryophyllidia. Special attention was paid to the morphology of the reproductive system and digestive system, including the radulae, which have been prepared for examination on SEM. Features of living animals were recorded from photographs or notes of collectors.

DESCRIPTIONS

EXTERNAL MORPHOLOGY.—The living animals measured up to 53 mm in length. The background color varies from translucent white to tan (Figs. 1; 2A, B). The notal surface is covered with brown specks and bears numerous irregular oval brown spots. In most specimens the center of the brown spots is lighter in color, surrounded by a dark ring. A white band, composed of minute white specks occurs along the notal margin. The body is oval, highest along its midline, sloping gradually to the margins. The notal surface is densely covered with various sized caryophyllidia (Fig. 3D). The gill is completely retractile into a branchial pit. The six tripinnate branchial leaves are upstanding and do not spread to the edges of the notum. The branchial leaves are white to cream in color and are densely sprinkled with brown specks. The anal papilla is located at the center of the branchial plume. The rhinophores are perfoliate with 12–18 lamellae and are retractile into short upright sheaths. The color of the rhinophores is similar to that of the branchial plume. Ventrally, the foot is grooved and notched, wide, tapering posteriorly into a round end. The posterior end of the foot extends only slightly beyond the posterior margin of the notum. The oral tentacles are slender and pointed distally (Fig. 5C).

ANATOMY.—The labial cuticle is smooth. The radular formula is 14 × 16.0.16 in a 10-mm-long specimen (CASIZ 060977), 15 × 23.0.23 in an 18-mm-long specimen (CASIZ 025880) and 22 × 27.0.27 in a 46-mm-long specimen (CASIZ 068277). There is no trace of rachidian teeth. The lateral teeth (Figs. 3A, B; 4A, B) are simple hamate increasing in size from the center of the radular ribbon to the ninth and tenth tooth, then decreasing to the margin. The outermost two lateral teeth are very elongate and are smooth (Fig. 3C), or have one to three small denticles (Fig. 4C, D), depending on the specimen.

The reproductive system is triaulic (Fig. 5A, B). The ampulla is tubular and convoluted. It narrows into a short thin tube and connects to the oviduct and prostatic portion of the vas deferens. Immediately after branching, the oviduct enters the massive female gland mass. The vas deferens is long and slightly thinner than the ampulla, until it expands into two wide and large, contiguous prostatic portions. A long, thin duct emerges from the prostatic portion and becomes highly convoluted in the ejaculatory segment, prior to entering a common genital atrium with the vagina. The vaginal duct is thick, normally straight and connects to the large, round bursa copulatrix. A separate duct from the bursa copulatrix connects to the smaller, spherical seminal receptacle. A short, thin uterine tube

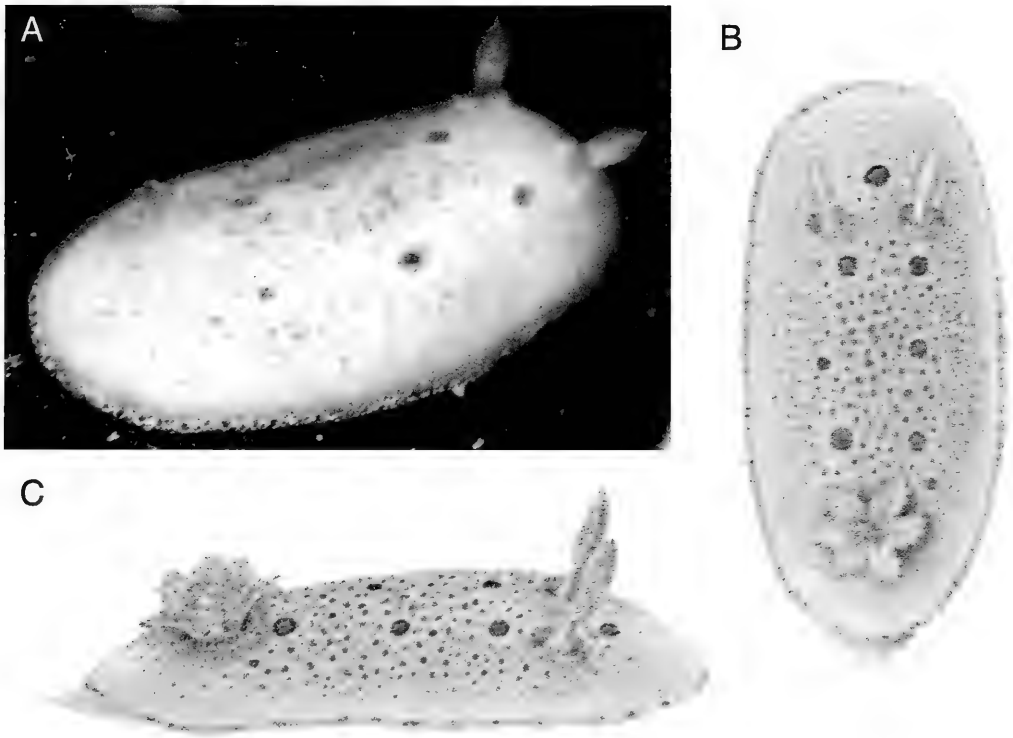

FIGURE 1. Specimen identified by MacFarland (1966) as *Doris* (*s.l.*) species (CASIZ 025880). A. Photograph of the living animal taken by G. E. MacGinitie. B, C. Drawings published by MacFarland (1966, pl. 25, figs. 1, 2).

emerges near the connection of this duct and then connects the seminal receptacle to the female gland near the genital atrium.

DISCUSSION

After the anatomical study of the material of *Doris* (*s.l.*) species examined by MacFarland (CASIZ 025880), of additional specimens with a similar external coloration from southern California (CASIZ 060976), and of specimens matching the original description of *Diaulula sandiegensis* (CASIZ 068277; CASIZ 071641), we were unable to find any consistent differences. It is clear that *Doris* (*s.l.*) species constitutes a color variation of *Diaulula sandiegensis*. The external coloration of this species is extremely variable. It ranges from white or cream to yellow, with brown rings or solid spots, sometimes surrounded by an opaque white ring (Fig. 2). Specimens from Canada, Alaska, and the Russian far east generally have the dorsum covered with numerous very dark spots (Fig. 2E, F), whereas in southern California and Mexico the spots are lighter and less common. Specimens from central and northern California, Oregon, and Washington match the original description by Cooper (1863).

The reproductive system of all the specimens examined has two large and distinct prostatic regions in the vas deferens. There is a long, thick, straight vaginal duct. The oviduct, vas deferens and uterine duct all enter the female gland mass in the same proximity, near the genital atrium (Figs. 5A, B; 6A, B).

TABLE 1. Sources of material examined. Specimens originally identified as *Doris* (*s.l.*) species are marked with an asterisk *.

Locality	Date	Specimens	Length	Collector	Catalog No.
Mexico					
Roca Ben, Pacific coast of Baja California	20 August 1987	7	16–36 mm	T. M. Gosliner	CASIZ 071641
California					
San Onofre State Beach, San Diego Co.	9 December 2000	3	4–10 mm	J. Goddard	CASIZ 060977*
Bird Rock, La Jolla, San Diego Co.	10 December 2000	1	14 mm	J. Goddard	CASIZ 060976*
Paradise Cove, Malibu, Los Angeles Co.	14 September 1971	1	12 mm	S. Anderson	CASIZ 070753*
Corona del Mar Way, Orange Co.	8 May 1946	1	18 mm	F. MacFarland	CASIZ 025880*
Santa Barbara, Santa Barbara Co.	August 1966	1	15 mm	J. Steinberg	CASIZ 025785*
Virg's Landing, Morro Bay, San Luis Obispo Co.	22 November 1971	1	10 mm	G. McDonald	CASIZ 070822*
Asilomar, Monterey Co.	5 May 1973	1	7 mm	G. McDonald	CASIZ 070825
West side of Tomales Bay, Marin Co.	12 March 1961	3	21–46 mm	A. G. Smith	CASIZ 068277
Canada					
Round Island, British Columbia	30 May 1946	1	22 mm	E. Ricketts	CASIZ 068265

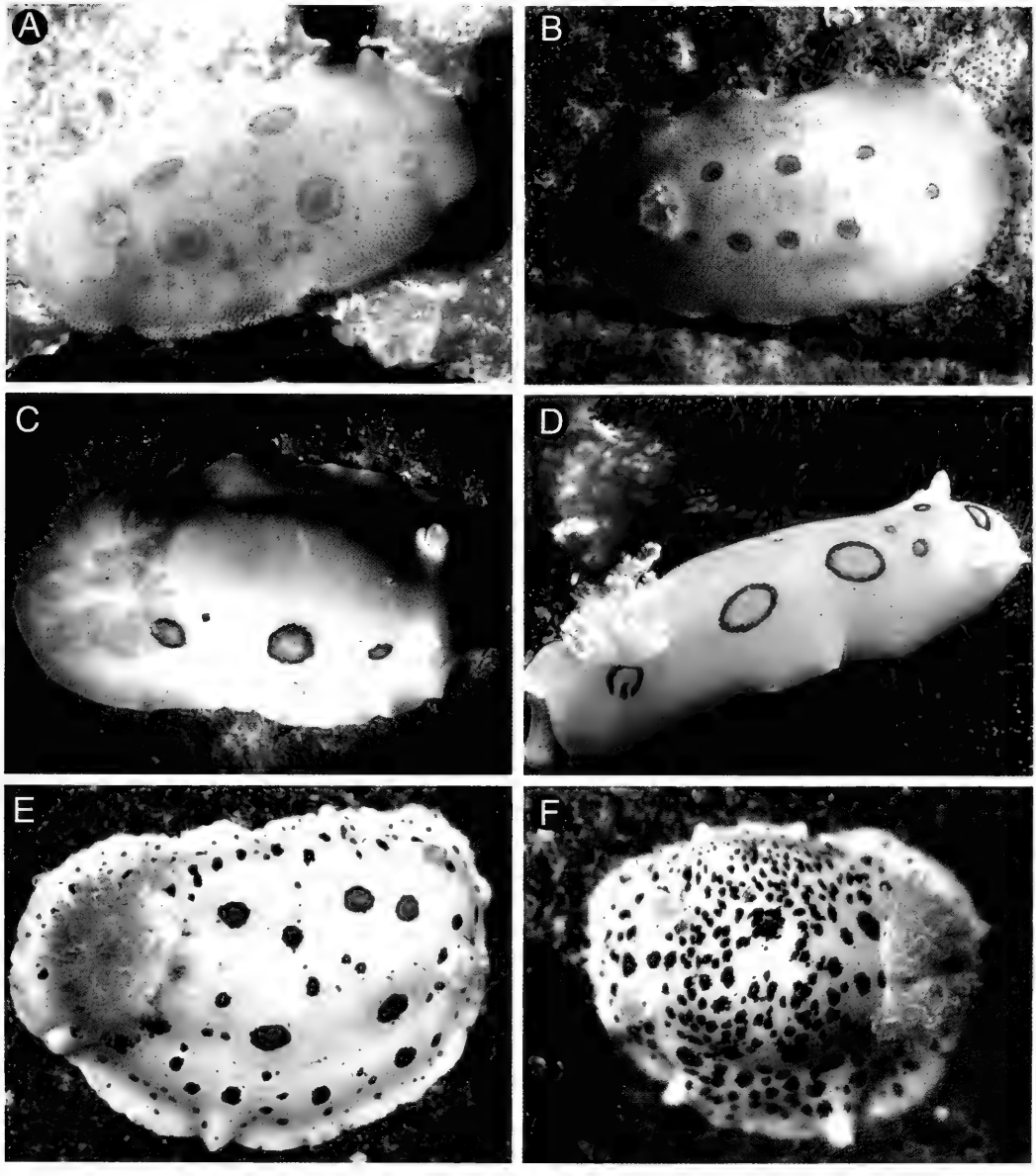

FIGURE 2. Living animals of *Diaulula sandiegensis* (Cooper, 1863). A. Specimen from San Diego, California, originally identified as *Doris* (*s.l.*) species; B. Specimen from Orange County, California, originally identified as *Doris* (*s.l.*) species; C. Specimen from San Luis Obispo, California; D. Specimen from the Channel Islands, California; E. Specimen from Vancouver Island, British Columbia, Canada; F. Specimen from Vancouver Island, British Columbia, Canada. Photograph 1A by J. Hamann, others by D. Behrens.

Camera lucida drawings based on light microscopy of the radula of *Doris* (*s.l.*) species (MacFarland 1966; McDonald 1983, 1997; Behrens 1992) suggests that the species has smooth, hamate, outer lateral teeth. Scanning electron microscopy of the specimen seen by MacFarland (Fig. 4C, D) shows the presence of denticles on the outer two lateral teeth. This character is not present in other examined specimens with the same color pattern collected from southern California (Fig.

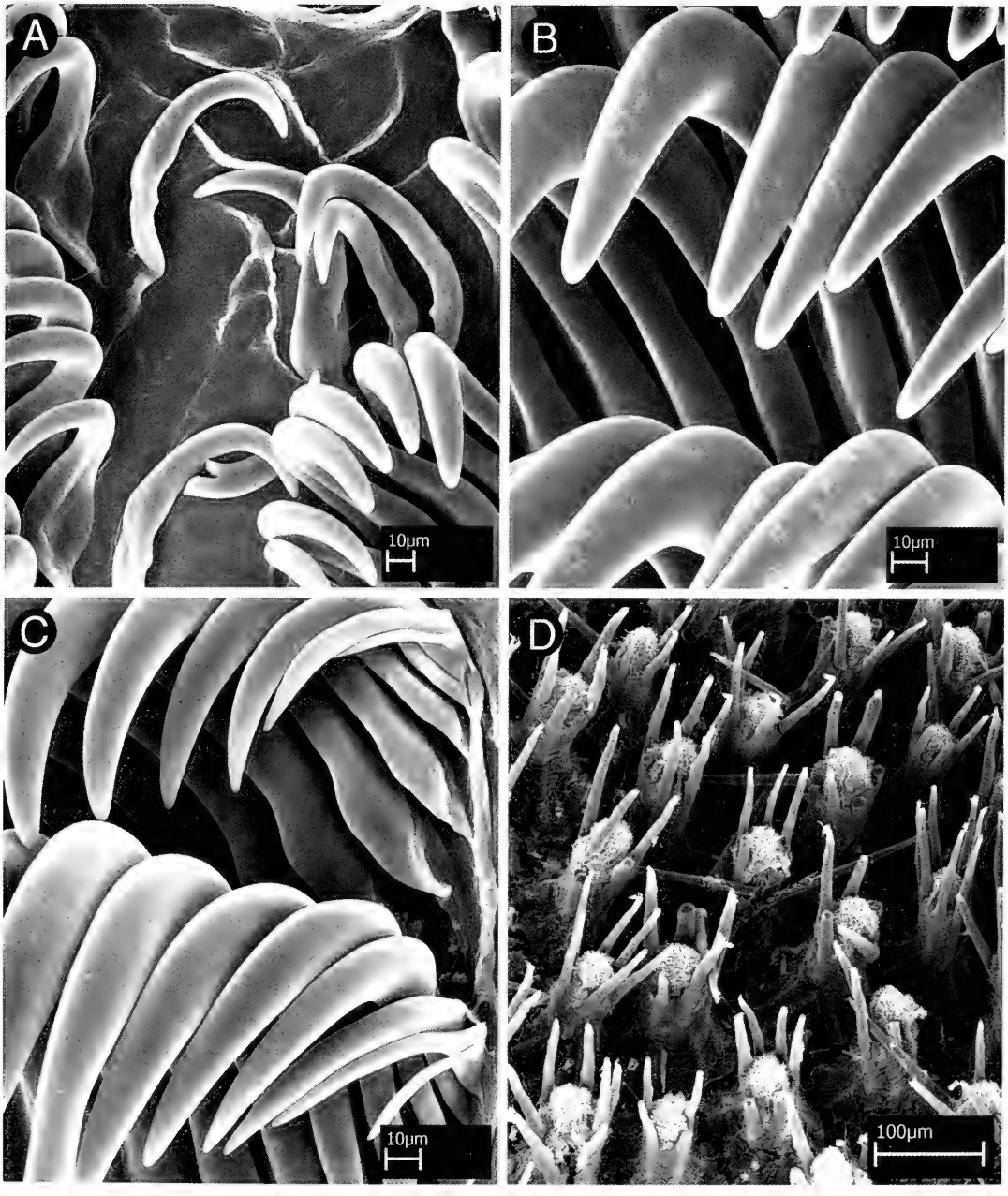

FIGURE 3. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs of a specimen originally identified as *Doris* (*s.l.*) species (CASIZ 060977). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Caryophyllidia.

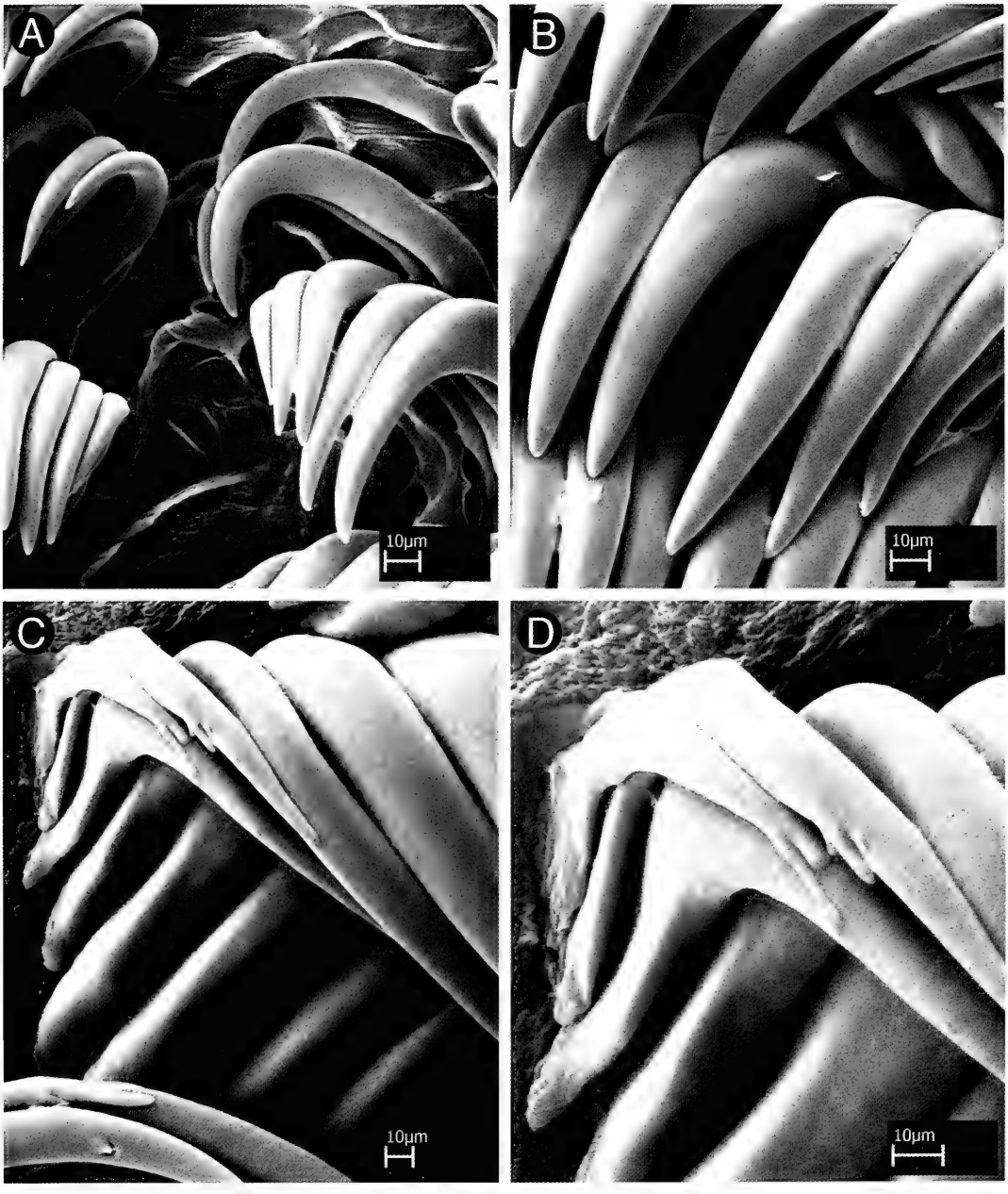

FIGURE 4. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs of a specimen identified by MacFarland (1966) as *Doris* (*s.l.*) species (CASIZ 025880). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Detail of the denticles on the outer lateral teeth.

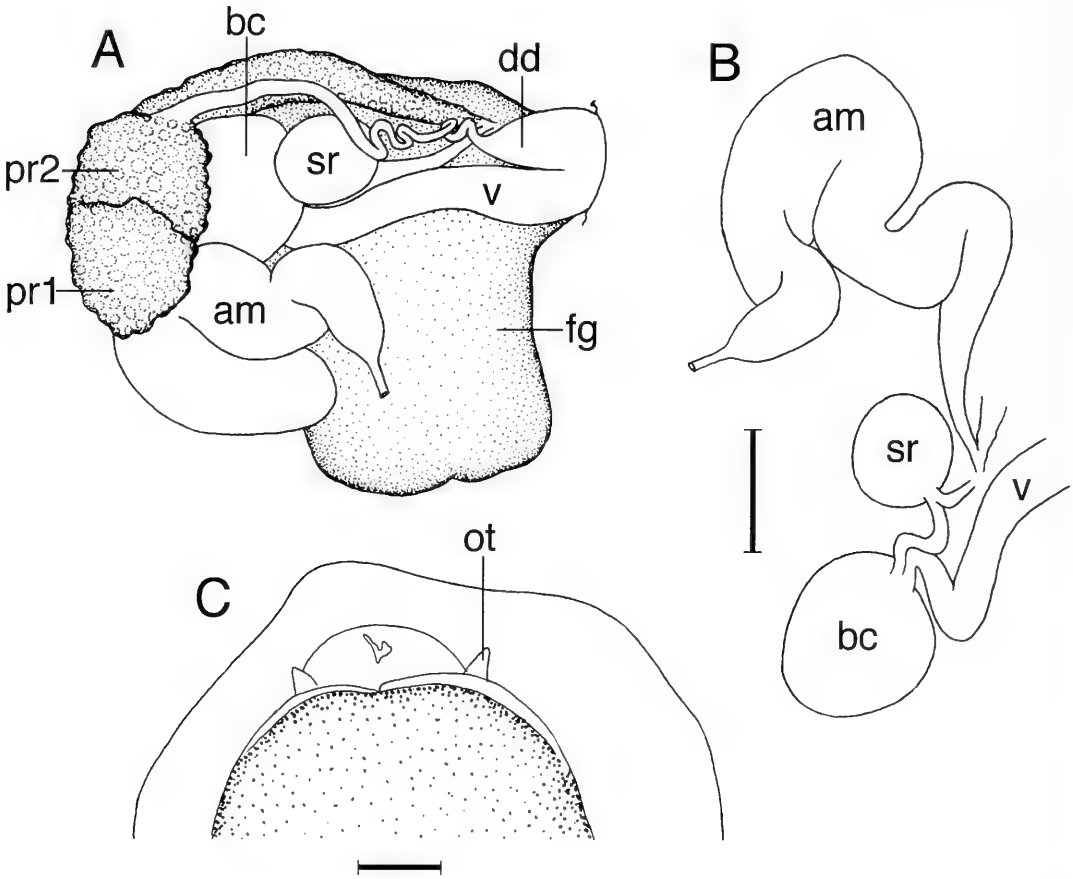

FIGURE 5. *Diaulula sandiegensis* (Cooper, 1863), anatomy of a specimen originally identified as *Doris* (*s.l.*) species (CASIZ 060977). A. Reproductive system, scale bar = 1 mm; B. Detail of several organs, scale bar = 1 mm; C. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr1, proximal prostatic region; pr2, distal prostatic region; sr, seminal receptacle; v, vagina.

3A–C), so it is clearly due to intraspecific variation. Other specimens of *Diaulula sandiegensis* have smooth, sharply-pointed, hamate-shaped teeth across the entire row (Fig. 7A–C), identical to those of *Doris* (*s.l.*) species.

Scanning electron microscopy of *Diaulula sandiegensis* clearly indicates the presence of caryophyllidia (Fig. 7D), which are identical in size and density to those present in *Doris* (*s.l.*) species (Fig. 3D).

O'Donoghue's (1922) description of *Doris echinata* was brief, stating simply that the dorsum is covered with spiculate papillae and the color is opaque white with from a dozen to forty small brown spots scattered irregularly over the surface. The radula was described as simply hamate, 16–18 rows of 13–15 lateral teeth per half-row. A description of the reproductive system is lacking, except for mention that the penis is unarmed. O'Donoghue (1922) stated that though he felt that the classification of the family was unsatisfactory, *Doris echinata* falls within its definition.

In proposing the name *Doris odonoghuei* to rectify the preoccupancy issue discussed earlier, Steinberg (1963) examined two specimens from the collection of the Friday Harbor Marine Laboratories. Questioning the assignment of the species to *Doris*, she dissected the smaller of the two, but came to no satisfactory conclusion. Recent review of her personal notes (J. Steinberg, pers. commun., Jan. 2001) revealed no further evidence to assist in its placement.

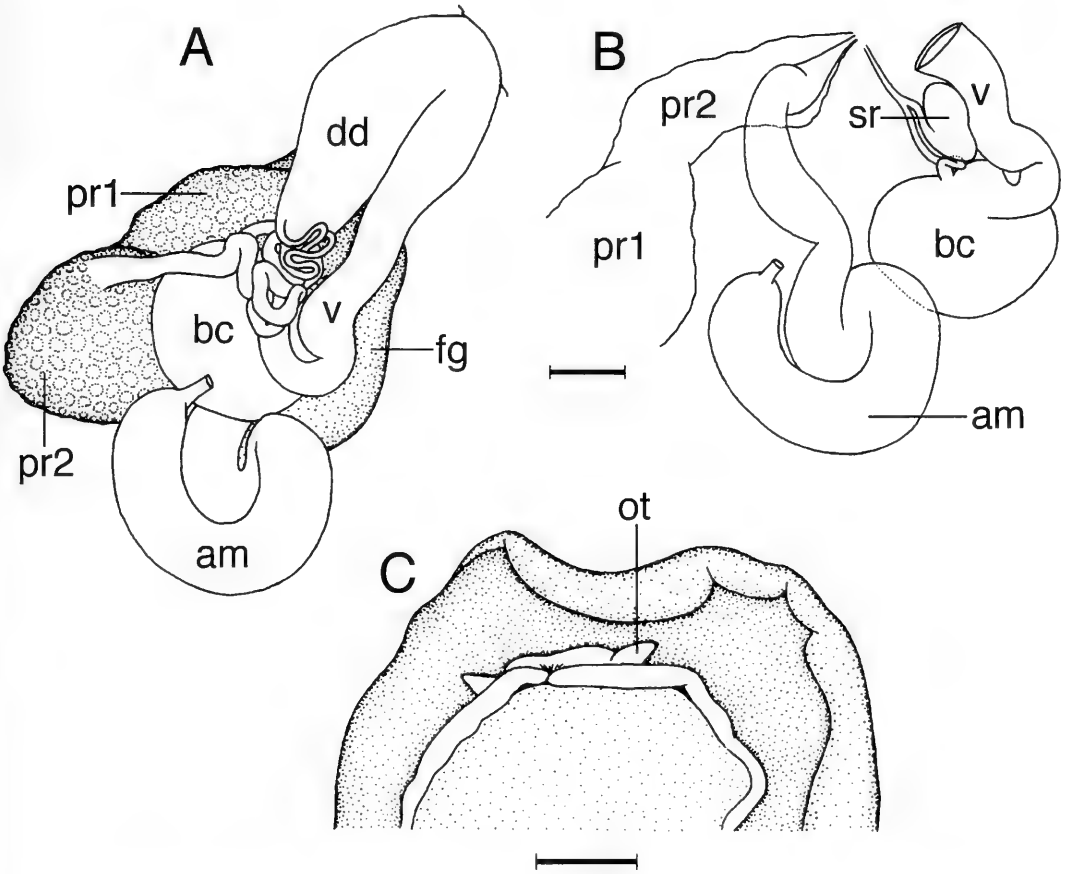

FIGURE 6. *Diaulula sandiegensis* (Cooper, 1863), anatomy (CASIZ 068277). A. Reproductive system, scale bar – 1 mm; B. Detail of several organs, scale bar = 1 mm; C. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr1, proximal prostatic region; pr2, disstal prostatic region; sr, seminal receptacle; v, vagina.

Since that time no published accounts or casual observations have been made of this species. Sandra Millen (pers. commun., April 1982) indicated that she had never collected specimens in the Vancouver area, British Columbia, that she could clearly identify as *Doris odonoghuei*. According to Millen it is impossible to distinguish *Doris odonoghuei* from small *Diaulula sandiegensis*.

Whereas this species has not been definitely confirmed since O'Donoghue's (1922) original description and no type material is available for examination, and whereas this description cannot be differentiated from *Diaulula sandiegensis*, we propose that this species be regarded as a synonym of *Diaulula sandiegensis*.

ACKNOWLEDGMENTS

We thank Jeff Goddard for collection of material, Jeff Hamann for use of his photograph and Joan Steinberg and Sandra Millen for sharing their field and laboratory notes. Joan Steinberg made constructive comments on the manuscript. This paper has been supported by the National Science Foundation, through the PEET grant (DEB-9978155, "Phylogenetic systematics of dorid nudibranchs") to Terrence M. Gosliner.

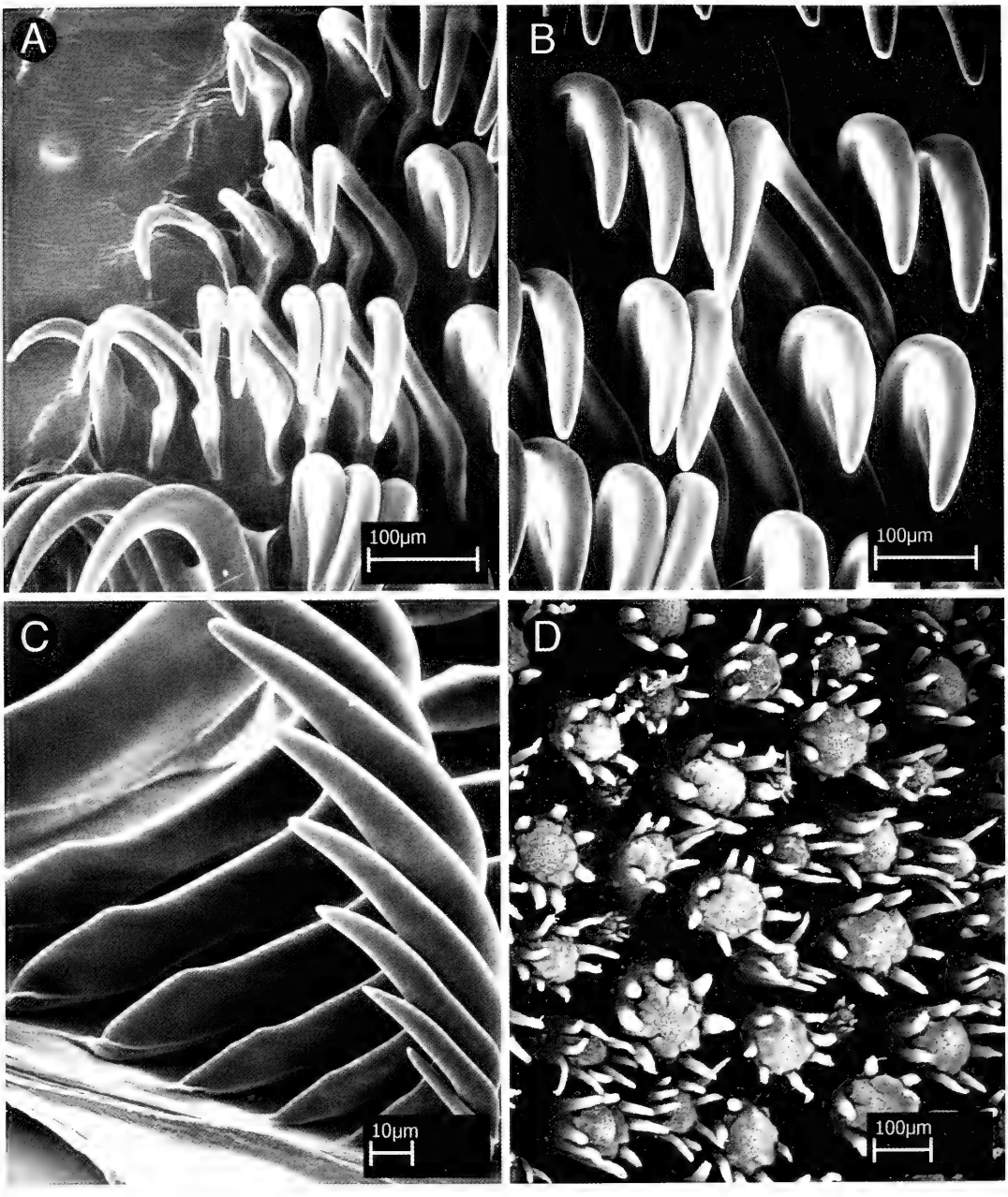

FIGURE 7. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs (CASIZ 068277). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Caryophyllidia.

LITERATURE CITED

BEHRENS, D. W. 1980. Pacific coast nudibranchs: A guide to the opisthobranchs of the northeastern Pacific. Sea Challengers, Los Osos, California. 112 pp.

———. 1991. Pacific coast nudibranchs: A guide to the opisthobranchs of the northeastern Pacific, 2nd ed. Sea Challengers, Monterey, California. 107 pp.

———. 1992. Pacific coast nudibranchs. Supplement I – Radula. Sea Challengers, Monterey, California. 11 pp.

BERGH, R. 1880. On the nudibranchiate gastropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Scientific Results of the Exploration of Alaska 1(Art. 6):189–276, pls. 9–16.

COOPER, J. G. 1863. Some genera and species of California Mollusca. Proceedings of the California Academy of Natural Sciences 2:202–207.

IREDALE, T. AND C. H. O'DONOGHUE. 1923. List of British nudibranchiate Mollusca. Proceedings of the Malacological Society of London 15:195–233.

MACFARLAND, F. M. 1966. Studies of the Opisthobranchiate Mollusks of the Pacific coast of North America. Memoirs of the California Academy of Sciences, No. 6. 546 pp., 71 pls.

MARCUS, ER. 1961. Opisthobranch mollusks from California. Veliger 3(Supp):1–85.

MCDONALD, G. R. 1983. A review of the nudibranchs of the California coast. Malacologia 24:114–276.

———. 1997. A review of the nudibranchs of the California coast. Master's thesis, California State University, Hayward. 337 pp.

MCDONALD, G. R. AND J. W. NYBAKKEN. 1981. Guide to the nudibranchs of California, 2nd ed. American Malacologists Inc., Melbourne, Florida. 72 pp.

O'DONOGHUE, C. H. 1922. Notes on the Nudibranchiate Mollusca from the Vancouver island region. III. Records of species and distribution. Transactions of the Royal Canadian Institute 14:145–167.

SPHON, JR., G. G. AND J. R. LANCE. 1968. An annotated list of the nudibranchs and their allies from Santa Barbara County, California. Proceedings of the California Academy of Sciences 36:73–84.

STEINBERG, J. E. 1963. Notes on the opisthobranchs of the west coast of North America – III. Further nomenclatural changes in the order Nudibranchia. Veliger 6:63–67.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of the Soft Coral Genus *Eleutherobia* Pütter, 1900, (Octocorallia: Alcyoniidae) from South Africa

by

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The alcyoniid soft coral genus *Eleutherobia* was previously known to contain sixteen valid species, distributed from southern Africa to the south central Pacific Ocean. A new species is here described from the KwaZulu-Natal coast of South Africa, thereby making a total of seventeen species, with four of these restricted to southern Africa. The new taxon is superficially similar to *Eleutherobia rubra* (Brundin, 1896), originally described from Japan, but differs from it and all other species of the genus by a unique complement of sclerite types.

Williams (2000b:159) summarized recent discoveries concerning natural products biochemistry and the soft coral genus *Eleutherobia*. In the same paper, *Eleutherobia zanahoria* was described from the Tonga Islands, thus extending the known geographic range of the genus approximately 3000 km to the southeast into the central South Pacific. Four species of the genus are known from southern Africa, including the new species described below. The other taxa are *Eleutherobia studeri* (J. S. Thomson, 1910), *E. rotifera* (J. S. Thomson, 1910), and *E. aurea* Benayahu and Schleyer, 1995 (Williams 1992a, 2000a, 2000b). Together with thirteen species from the Indo-West Pacific, a total of seventeen species of the genus *Eleutherobia* are presently considered valid. The geographic range of the genus extends from the southeastern fringe of the Atlantic Ocean (Cape Peninsula), around South Africa, through the Indian Ocean, and as far as Japan, Palau, and Tonga in the Pacific Ocean (Fig. 1). A revision, which will add other taxa for southern Africa, is currently in progress by the authors.

METHODS

Material was collected by SCUBA or dredge and preserved in 70% ethanol. Sclerites were isolated using sodium hypochlorite (household bleach). Micrographs and photographs for Figures 2 and 3 were taken using a Nikon Coolpix 990 digital camera, a Nikon SMZ-10 dissecting microscope, and an Olympus CH-2 compound microscope. Scanning electron micrographs were taken using a Leo 1400 Series scanning electron microscope. Sclerites were examined and drawn using an Olympus CH-2 compound microscope with an attached drawing tube. Digital images and plates of photographs, micrographs, and scanning electron micrographs were made using Adobe Photoshop software. The abbreviation used for the South African Museum, Cape Town, is SAM.

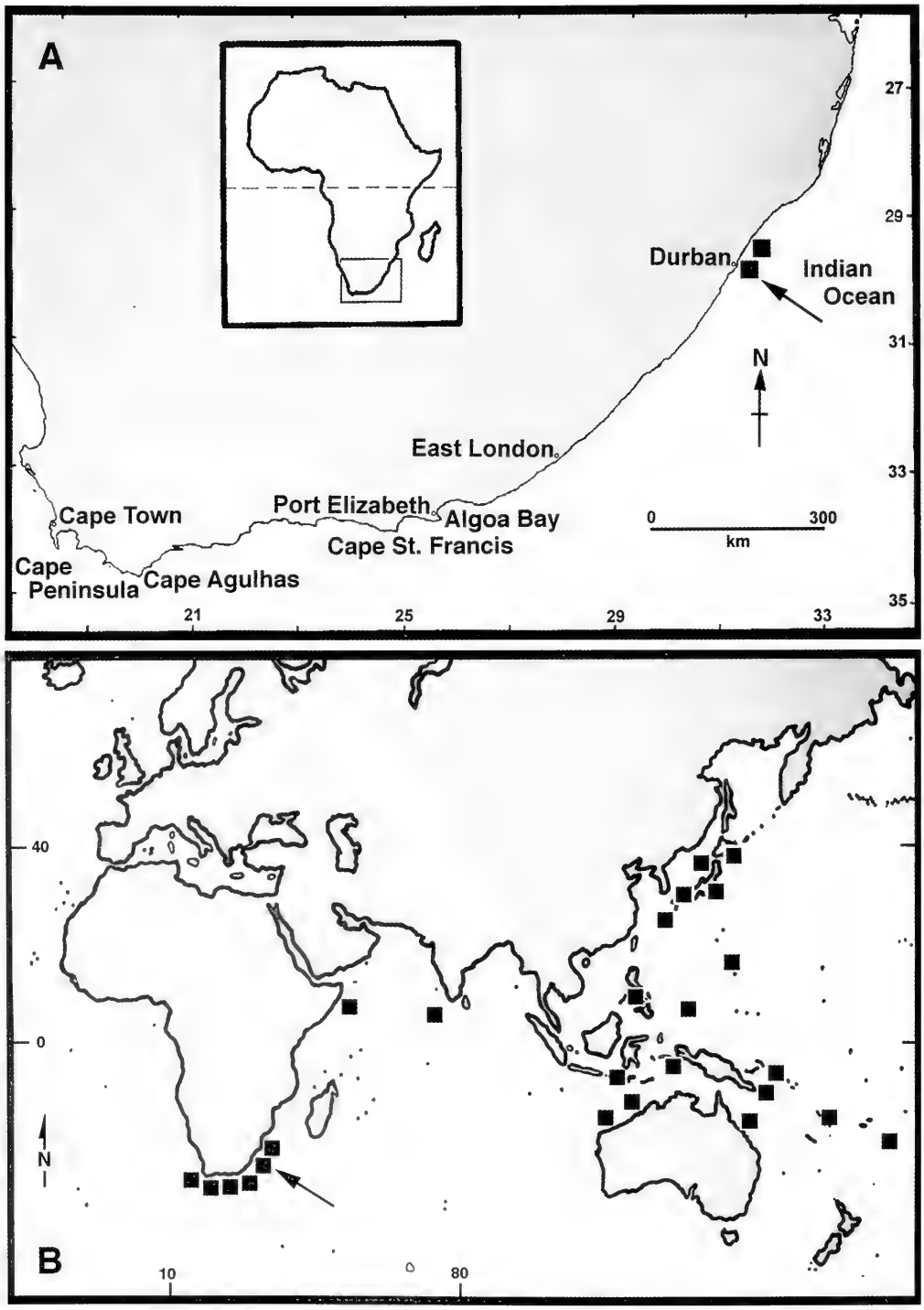

FIGURE 1. A. Map of southern Africa showing collecting stations for *Eleutherobia vinadigitaria* sp. nov. B. Map of the Indo-West Pacific showing geographic distribution of the genus *Eleutherobia*. Arrows show type locality of *Eleutherobia vinadigitaria* sp. nov. Numbers along axes represent degrees of longitude and latitude.

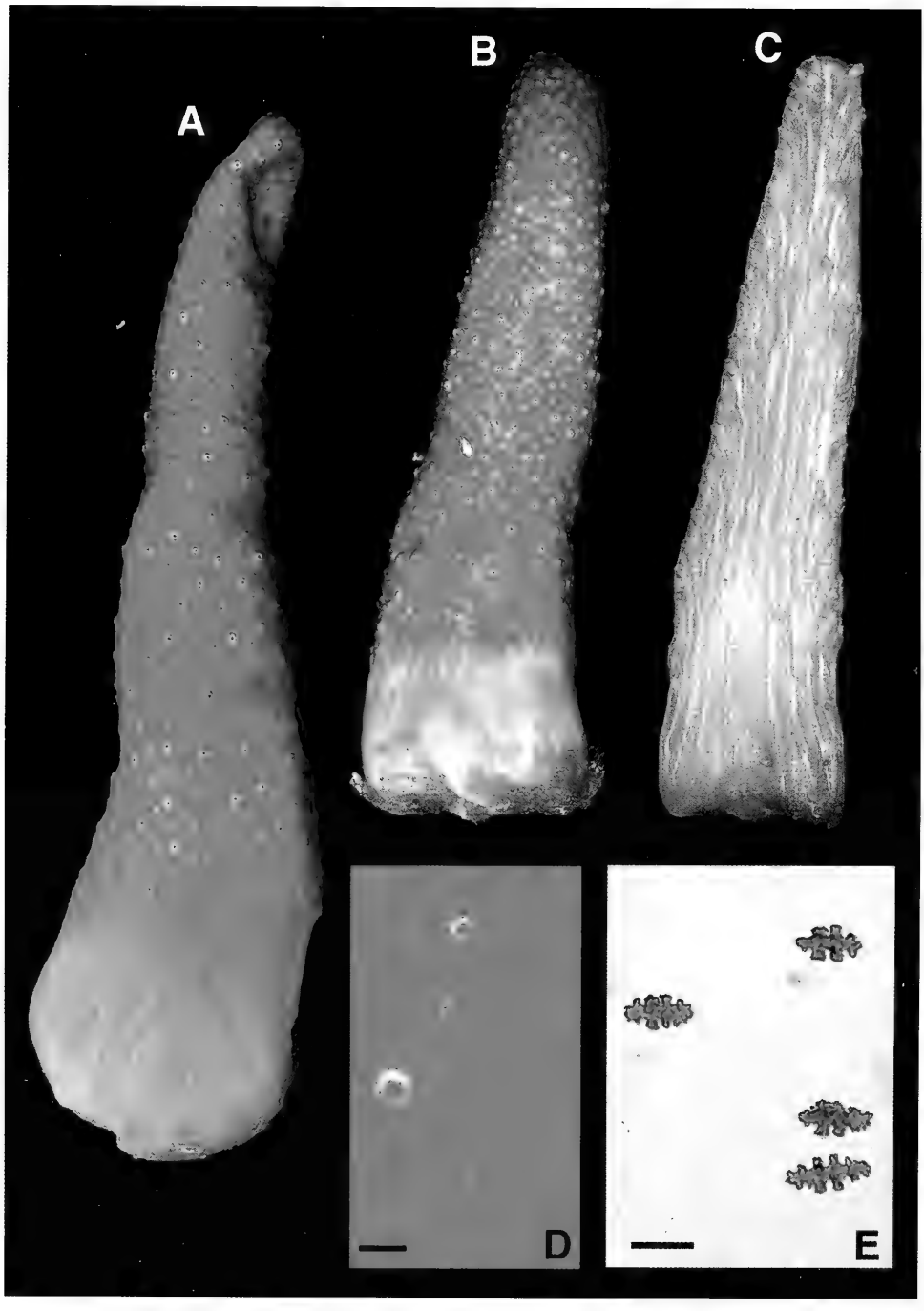

FIGURE 2. *Eleutherobia vinadigitaria* sp. nov. A. Holotype, total length 97 mm. B. Paratype exterior, total length 88 mm. C. Paratype interior, longitudinal section; total length 88 mm. D. Holotype, detail of surface of polyparium showing retracted polyps; scale bar = 0.50 mm. E. Holotype, sclerites from the surface of the polyparium; scale bar – 0.07 mm.

SYSTEMATIC ACCOUNT

Family Alcyoniidae Lamouroux, 1812

Eleutherobia Pütter, 1900

Eleutherobia Pütter, 1900:449. Verseveldt and Bayer, 1988:27. Williams, 1992a:306. 2000b:160.
Nidalia (in part): *non* Gray, 1835.
Bellonella (in part): *non* Gray, 1862.
Metalcyonium (in part): *non* Pfeffer, 1889.

DIAGNOSIS.—Alcyoniid soft corals with colonies digitiform, finger-shaped, often conical and tapering, rarely multilobate. Polyps monomorphic. Calyces absent, although retracted polyps often form low rounded to conspicuous protuberances. Sclerites mostly derived from radiates although spindles, crosses, barrels, or tuberculate spheroids may also be present. Polyp sclerites often present as eight points, or crown and points, or totally absent. Zooxanthellae absent.

TYPE SPECIES.—*Eleutherobia japonica* Pütter, 1900, by monotypy.

DIVERSITY AND DISTRIBUTION.—Seventeen species of the Indo-West Pacific (southern and eastern Africa to Japan and Tonga).

Eleutherobia vinadigitaria sp. nov.

Figs. 1-10

MATERIAL EXAMINED.—HOLOTYPE: SAM-H4877, station number DEEP No. 1, South Africa, KwaZulu-Natal, outer anchorage off Durban Bluff, 52 m depth, 13–14 December 1984, collected by W. R. Liltved with aid of SCUBA, one whole specimen (97 mm in length). PARATYPE: SAM-H4878, same data as holotype, one specimen (cut longitudinally into two halves; each half 88 mm in length). OTHER MATERIAL: SAM-H792, station number P. F. 11538, South Africa, KwaZulu-Natal, Thukela (Tugela) River Mouth, NW by N 22 1/2 miles, 86 m depth, 29 January 1901, collected by S.S. *Pieter Faure* survey with aid of dredge, one whole specimen (20 mm in length). SAM H-4835, same data as holotype, three whole specimens (18 mm, 72 mm, and 100 mm in length); the latter specimen partly cut transversely, thus partially separating the polypary from the stalk (Fig. 4B).

DIAGNOSIS.—Alcyoniid soft corals with digitiform colony shape, tapering distally to a rounded apex. Stalk conspicuous, comprising 20 to 50% of total colony length. Retracted polyps form moundlike protuberances. Sclerites of the eight polyp wall ridges with longitudinal rows of mostly sparsely-set, elongated, needle-like spindles (up to 0.30 mm long), sometimes arranged more or less in a chevroned fashion. Coenenchymal sclerites restricted to a thin surface layer of the polypary and stalk, primarily radiates and spindles, with a few clubs also present (0.03–0.20 mm in length). Interior sclerites absent. Color of stalk pink; polypary pink, red, or deep wine red. Sclerite color primarily reddish, rarely colorless.

DESCRIPTION OF THE HOLOTYPE.—**Growth form and size**. The wet-preserved holotype is 97 mm in length, and varies from 10 mm in width near the distal tip to 25 mm in width at the base of the stalk. It is finger-shaped, not branched or lobate. The length of the polypary is 77 mm, and comprises 79% of the total colony length, while the stalk is approximately 20 mm long and represents about 21% of the total colony length. The specimen is digitiform and tapers markedly from the holdfast to the distal terminus, which is conspicuously rounded (Fig. 2A).

Polyps. The polyps are tightly retracted in the available specimens, including the holotype. A small portion of the surface coenenchyme of the holotype was cut away to expose the retracted polyps. Many of the exposed polyps contain several mature gonads in their gastric cavities. These are pale yellow in color and mostly vary from 0.2 – 0.4 mm in diameter. The size of retracted polyps on the sur-

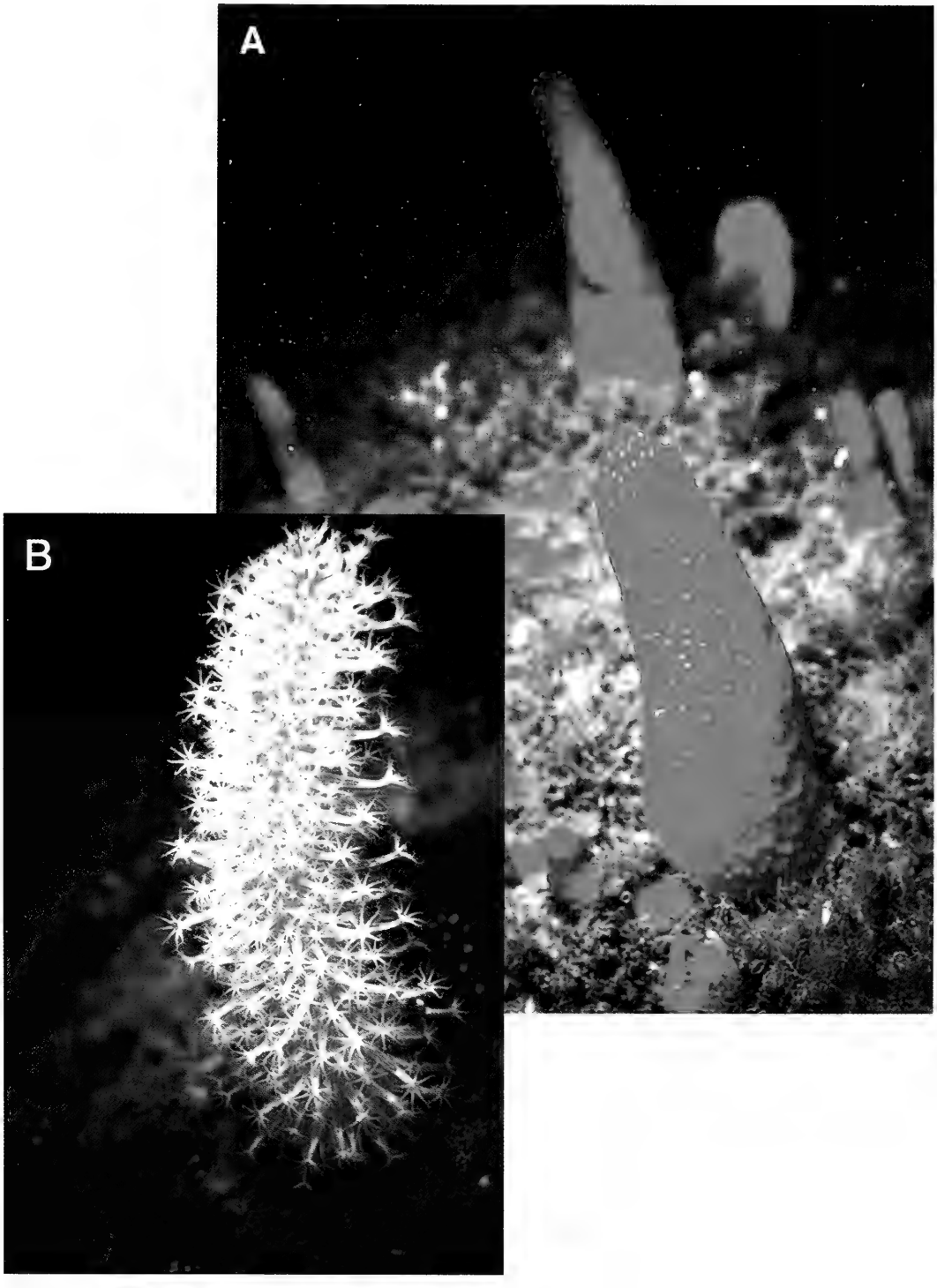

FIGURE 3. *Eleutherobia vinadigitaria* sp. nov. Living soft corals. A. Several colonies with polyps retracted (Photograph by Michael Schleyer). B. A single colony with polyps expanded (Photograph by Michael Schleyer).

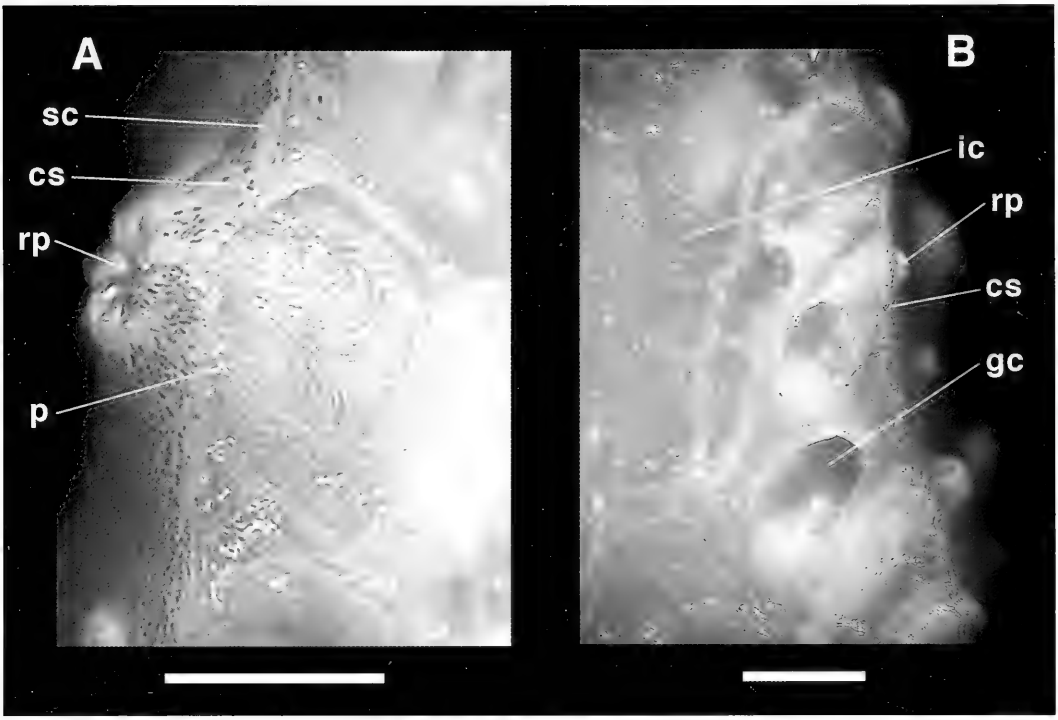

FIGURE 4. *Eleutherobia vinadigitaria* sp. nov. Micrographs of surface region of paratype; longitudinal section of polypary. A. A single retracted polyp showing chevroned arrangement of needle-like sclerites in polyp wall, and thin layer of sclerites of mostly radiates in the surface coenenchyme. B. Three adjacent polyps. Scale bars each represent 1.0 mm. Abbreviations: cs – coenenchymal sclerites, gc – gastric cavity, ic – interior coenenchyme, p – points of enchevroned needle-like sclerites, rp – retracted polyp, sc – surface coenenchyme.

face of the polypary varies from 0.3 to 0.8 mm in diameter (Fig. 2D). Observation of living non-type material at the type locality shows that the polyps are generally retracted in bright daylight (Fig. 3A) and are expanded in early hours of the morning (Fig. 3B) (M. H. Schleyer, pers. comm.). Polyp sclerites are arranged in eight longitudinal rows along the ridges of the polyp walls, relatively sparsely placed. In some polyps, the sclerites may be disposed in a chevroned fashion, forming eight points.

Sclerites. Sclerites from the polyp body walls are needle-like spindles, mostly with tuberculation restricted to the opposite margins, as the flattened faces of the sclerites are for the most part smooth and devoid of ornamentation (Figs. 6A, 7A-B, 8A). They vary in length from 0.17 to 0.30 mm. Sclerites are lacking in the tentacles and pinnules. Coenenchymal sclerites are restricted to a very thin surface layer of the polypary and stalk (Fig. 4B). Sclerites of the surface of the polypary, as well as the bases of the polyps, are radiates and spindles (0.03–0.20 mm in length). Some of the spindles may be somewhat club-shaped (Fig. 6B, 10B). Sclerites from the surface of the stalk and holdfast are radiates (0.05–0.11 mm in length). Sclerites are altogether absent from the interior of the colonies.

Color. The interior of the wet-preserved holotype is cream colored to pale yellow (Fig. 2C), but crisp white in life (M. H. Schleyer, pers. commun.). The polyps are white to cream white (Fig. 3B). The color of the coenenchymal sclerites varies from deep red (Fig. 2E) to pale red, while the polyp sclerites vary from pale red to colorless.

INTERNAL ANATOMY OF THE PARATYPE.—The paratype specimen was cut longitudinally to reveal aspects of internal anatomy (Figs. 2C; 4A, B). The mature polyps have gastric cavities that extend throughout the entire length of the colony (Fig. 2C). The surface coenenchyme containing sclerites is

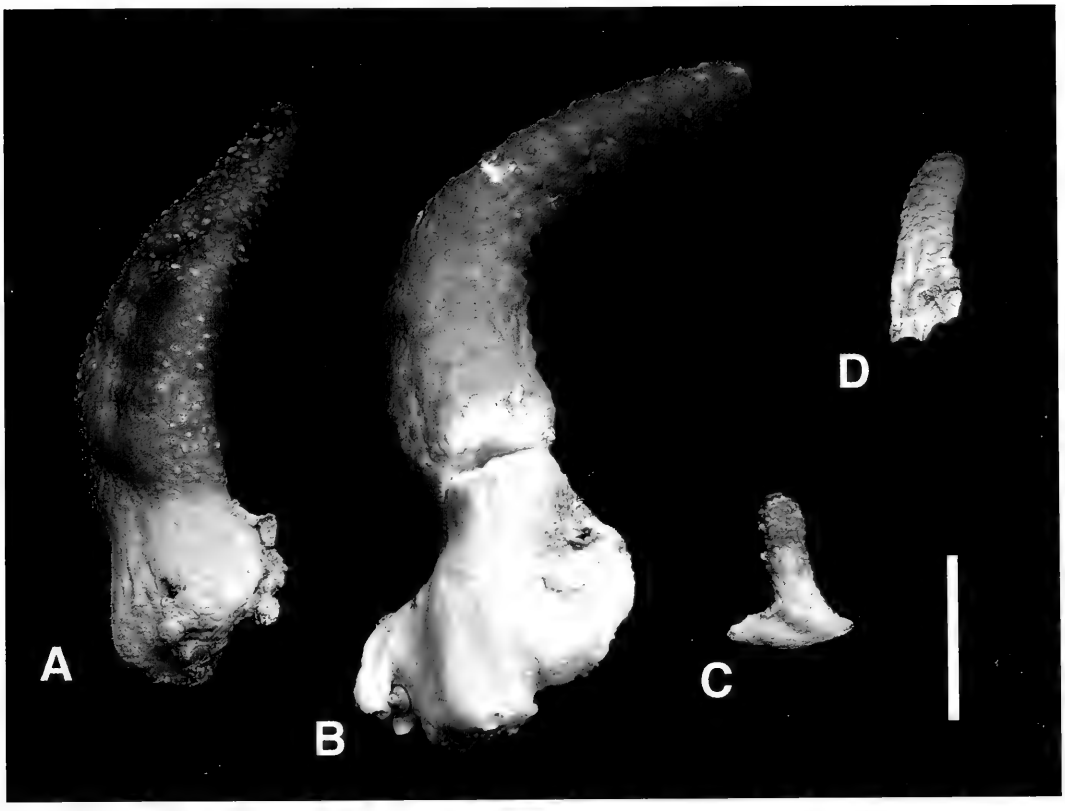

FIGURE 5. *Eleutherobia vinadigitaria* sp. nov. Variation in colony shape and size (non type material, wet preserved). A. SAM-H4835, 72 mm length. B. SAM-H4835, 100 mm. C. SAM-H4835, 18 mm. D. SAM-H792, 20 mm. Scale bar = 20 mm.

very thin, mostly < 0.2 mm in thickness (Fig. 4). The interior coenenchyme is firm but lacks sclerites (Fig. 4B). Conspicuous points formed by enchevroned sclerites from the polyp walls of the anthocodial neck zones can clearly be observed. However, transversely disposed sclerites forming a distinctive crown are lacking or at most are very sparsely distributed below the points (Fig. 4A).

ETYMOLOGY.—The specific epithet of the new species is derived from the Latin, *vinum* (wine), *digitus* (a finger), and the suffix, *-aria* (like); in reference to the wine red, finger-shaped colonies of this species of soft coral.

DISTRIBUTION.—The new species is known only from two localities in KwaZulu-Natal, South Africa (Fig. 1).

VARIATION.—The six available specimens range in size from 18–100 mm in length. The polypary comprises approximately 50–80% of the total colony length (Figs. 2, 5). The stalk and the polypary are approximately equal in length in the smallest specimens (Fig. 5C, D).

DISCUSSION

The rachises of the larger specimens of *Eleutherobia vinadigitaria* sp. nov. have retracted polyps exhibiting a variety of diameters (Fig. 2A, B, D). These all appear to be autozooids in various intermediate states of growth—each with eight equal-sized lappets closing over the opening of the retracted polyps, anthocodiae, and well-developed gastric cavities (Figs. 2C, 4B). In dimorphic taxa such as the

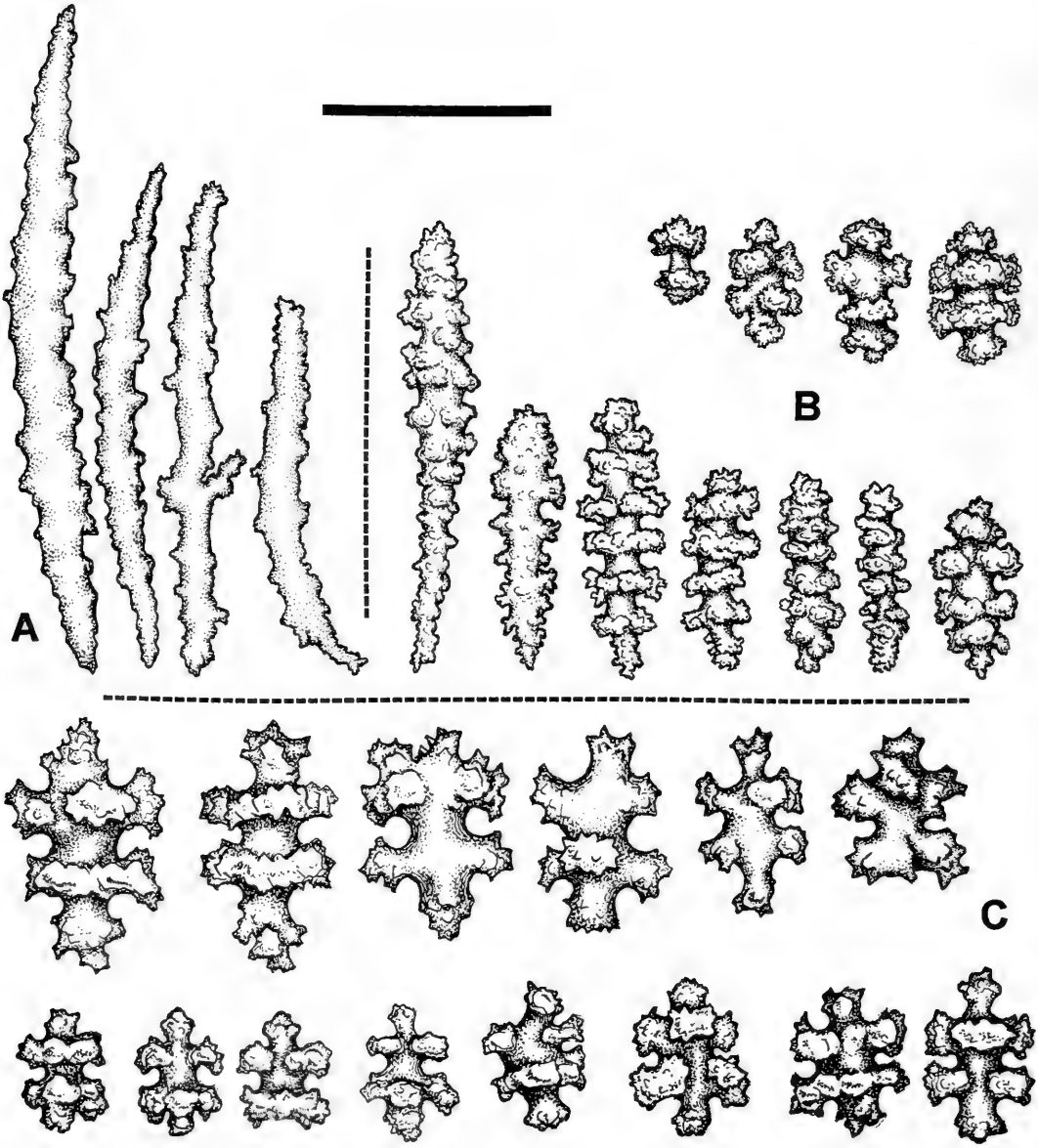

FIGURE 6. *Eleutherobia vinadigitaria* sp. nov., holotype. Variation in sclerite shape and size. A. Sclerites from the polyp walls. B. Coenenchymal sclerites from the surface of the polypary. C. Coenenchymal sclerites from the surface of the holdfast region of the stalk. Scale bar = 0.10 mm.

various species of the superficially similar soft coral genus *Paraminabea* Williams and Alderslade, 1999, the siphonozooids and autozooids display two distinct sizes without intermediates (Williams 1992b; Williams and Alderslade 1999). An additional aspect of distinction between the two genera is as follows: *Eleutherobia vinadigitaria* sp. nov., as in most other species of the genus, has distinctive longitudinal rows of needle-like sclerites in the neck zone of the anthocodiae (often enchevroned), while all species of *Paraminabea* apparently lack polyp sclerites (Fabricius and Alderslade, in press; Williams 1992b; Williams and Alderslade 1999).

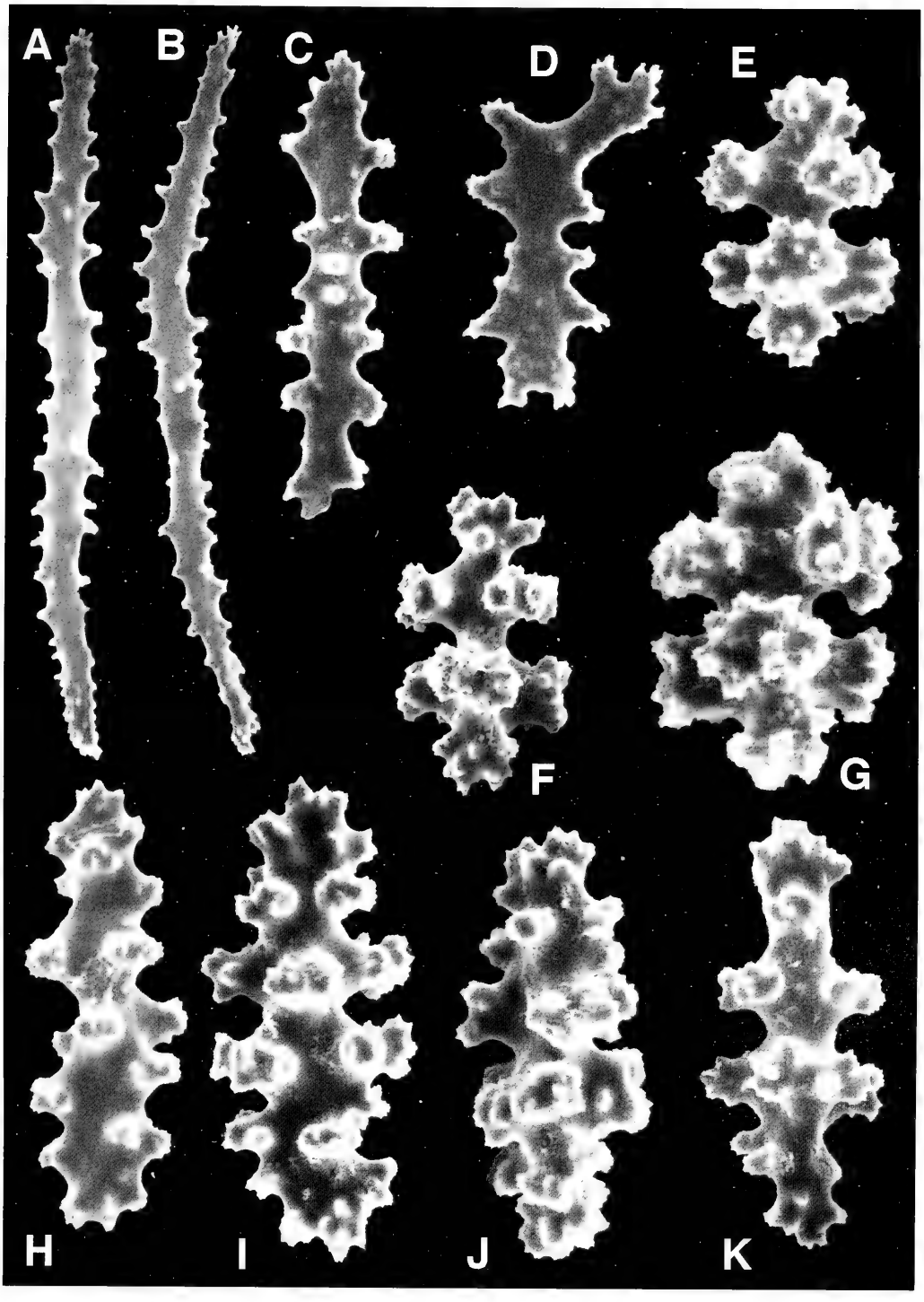

FIGURE 7. *Eleutherobia vinadigitaria* sp. nov. Scanning electron micrographs of sclerites from the holotype. A-B. Sclerites from the polyp walls, each 0.27 mm. C-K. Coenenchymal sclerites from the surface of the polypary and polyp bases. C. 0.09 mm. D. 0.07 mm. E. 0.05 mm. F. 0.06 mm. G. 0.05 mm. H. 0.08 mm. I. 0.09 mm. J. 0.06 mm. K. 0.08 mm.

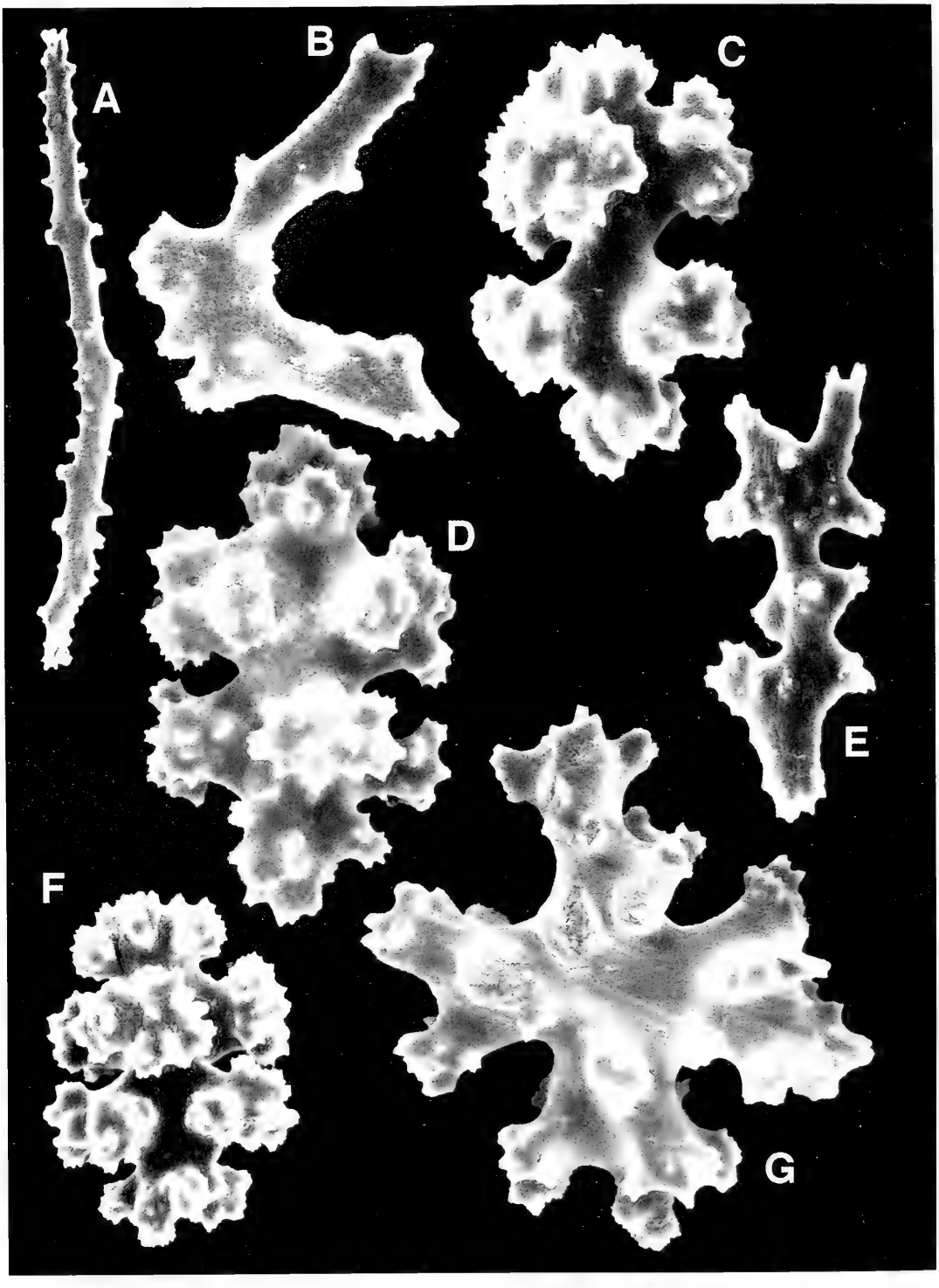

FIGURE 8. *Eleutherobia vinadigitaria* sp. nov. Scanning electron micrographs of sclerites from the holotype. A. A polyp wall sclerite, 0.20 mm. B–G. Coenenchymal sclerites from the surface of the polypary and polyp bases. B. 0.04 mm. C. 0.04 mm. D. 0.06 mm. E. 0.05 mm. F. 0.05 mm. G. 0.07 mm.

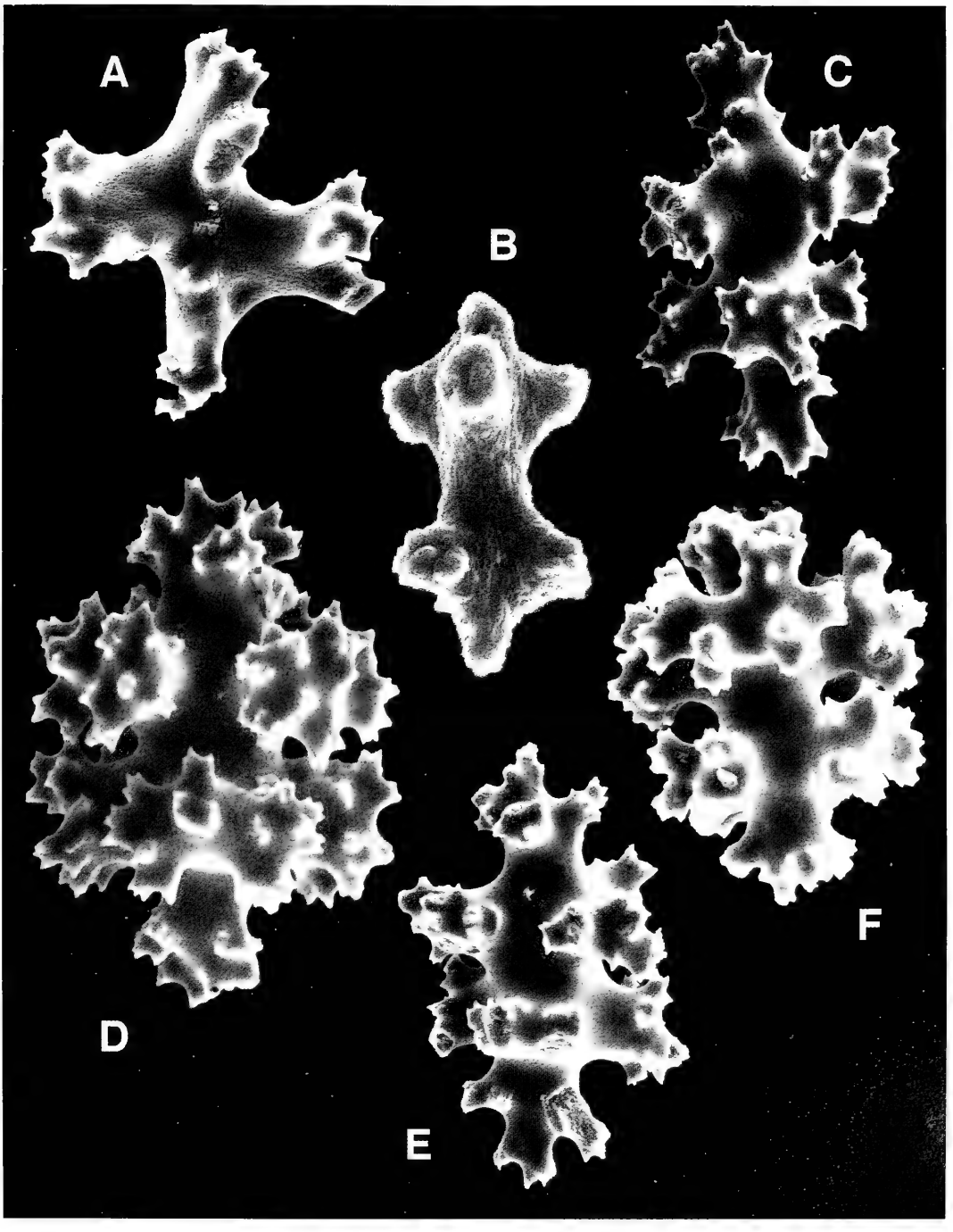

FIGURE 9. *Eleutherobia vinadigitaria* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the surface of the stalk of the holotype. A. 0.05 mm. B. 0.01 mm. C. 0.10 mm. D. 0.03 mm. E. 0.09 mm. F. 0.05 mm.

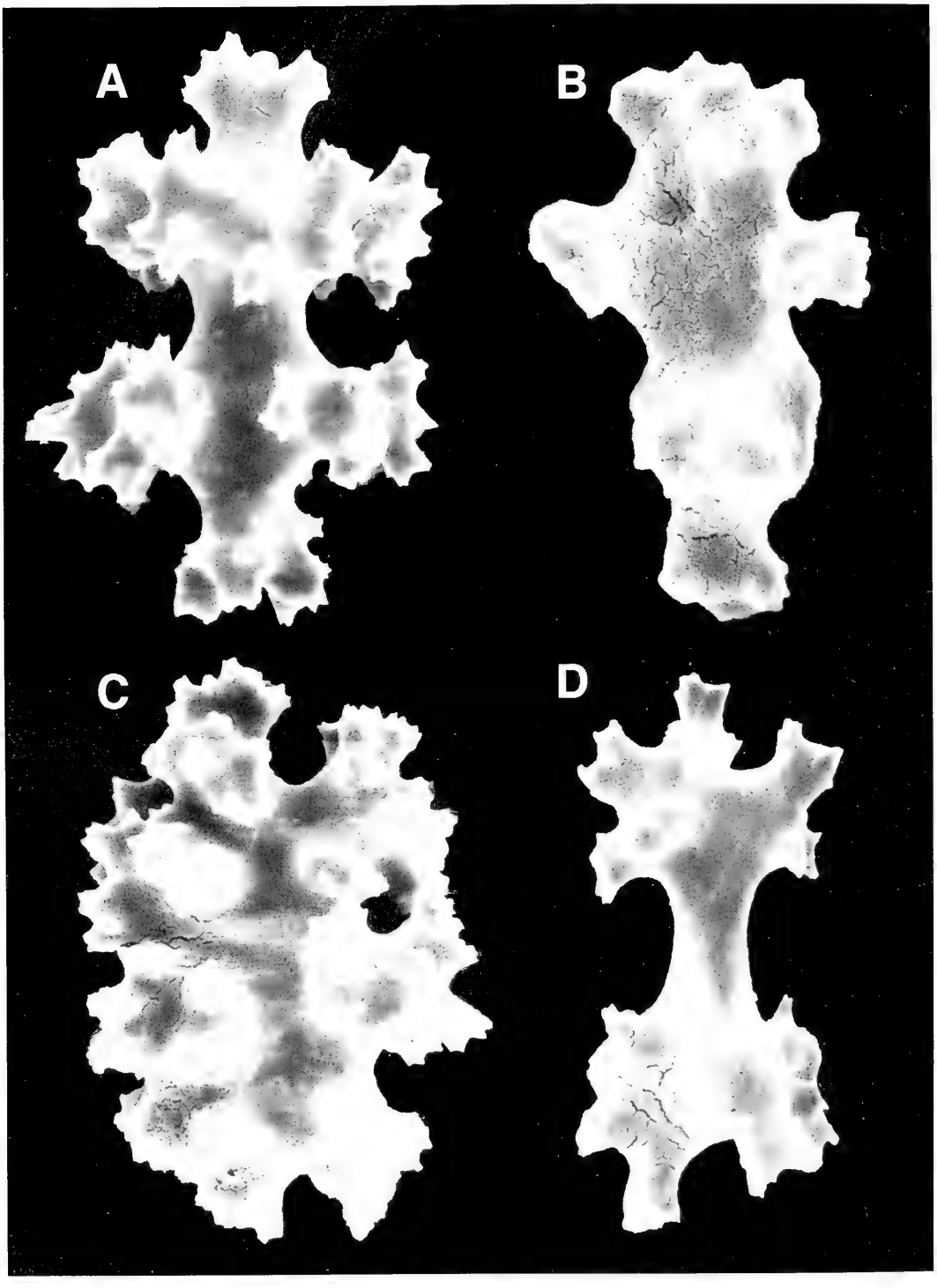

FIGURE 10. *Eleutherobia vinadigitaria* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the surface of the stalk of the holotype. A. 0.07 mm. B. 0.06 mm. C. 0.06 mm. D. 0.09 mm.

Eleutherobia vinadigitaria sp. nov. superficially resembles *Eleutherobia rubra* (Brundin, 1896) from Japan and northwestern Australia (compare Figs. 1 and 3 with Verseveldt and Bayer 1988, fig. 32e–h). However, *Eleutherobia rubra* can be differentiated from the new species by the following characters: well-developed crown and points with densely set sclerites in the anthocodiae, sclerites in the tentacles, and highly ornamented polyp wall spindles with elongated tubercles (Verseveldt and Bayer 1988, figs. 30–31). *Eleutherobia vinadigitaria* sp. nov., on the other hand, has weakly developed points (without the development of a crown), lacks tentacle sclerites, and has polyp wall sclerites that are sparsely ornamented spindles with low tubercles.

Eleutherobia aurea Benayahu and Schleyer (1995), also from Natal, South Africa, is similar in colony shape to *Eleutherobia vinadigitaria* sp. nov., but differs by having bright yellow coloration, a lack of polyp sclerites, and coenenchymal sclerites that are compact radiates and spheroids.

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Literature Cited

Benayahu, Y. and M. H. Schleyer. 1995. Corals of the south-west Indian Ocean II. *Eleutherobia aurea* spec. nov. (Cnidaria, Alcyonaria) from deep reefs on the KwaZulu-Natal Coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report 68:1–12.

Fabricius, K. and P. Alderslade. In press. Soft corals and sea fans—a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville.

Gray, J. E. 1835. Characters of a new genus of corals (*Nidalia*). Proceedings of the Zoological Society of London 3:59–60.

———. 1862. Description of two new genera of zoophytes (*Solenocaulon* and *Bellonella*) discovered on the north coast of Australia by Mr. Rayner. Proceedings of the Zoological Society of London 1862:34–37.

Pfeffer, G. 1889. Zur Fauna von Sud-Georgien. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 6(2):49–55.

Pütter, A. 1900. Alcyonaceen des Breslauer Museum. Zoologische Jahrbücher (Systematik)13(5):443–462.

Thomson, J. A. and L. M. I. Dean. 1931. The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga Expedition Monographs 13d:1–227.

Thomson, J. S. 1910. The Alcyonaria of the Cape of Good Hope and Natal. Alcyonacea. Transactions of the Royal Society of Edinburgh 47(3):549–589.

Verseveldt, J. and F. M. Bayer. 1988. Revision of the genera *Bellonella*, *Eleutherobia*, *Nidalia* and *Nidaliopsis* (Octocorallia:Alcyoniidae and Nidalliidae), with descriptions of two new genera. Zoologische Verhandelingen 245:1–131.

Williams, G. C. 1992a. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Annals of the South African Museum 100(3):249–358.

———. 1992b. Revision of the soft coral genus *Minabea* (Octocorallia: Alcyoniidae) with new taxa from the Indo-West Pacific. Proceedings of the California Academy of Sciences 48(1):1–26.

———. 1996. Octocorallia – Octocorals. Pp. 32–60 *in* Coral reef animals of the Indo-Pacific—animal life from Africa to Hawai'i exclusive of the vertebrates, T. M. Gosliner, D. W. Behrens, and G. C. Williams. Sea Challengers, Monterey. 314 pp.

———. 2000a. Two new genera of soft corals (Anthozoa: Alcyoniidae) from South Africa, with a discussion of diversity and endemism in the southern African octocorallian fauna. Proceedings of the California Academy of Sciences 52(6):65–75.

———. 2000b. A new species of the soft coral genus *Eleutherobia* Pütter, 1900 (Coelenterata: Alcyonacea) from the Tonga Islands. Proceedings of the California Academy of Sciences 52(13):159–169.

WILLIAMS, G. C. AND P. ALDERSLADE. 1999. Revisionary systematics of the western Pacific soft coral genus *Minabea* (Octocorallia: Alcyoniidae), with descriptions of a related new genus and species from the Indo-Pacific. Proceedings of the California Academy of Sciences 51(7):337–364.

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First Record of a Bioluminescent Soft Coral: Description of a Disjunct Population of *Eleutherobia grayi* (Thomson and Dean, 1921) from the Solomon Islands, with a Review of Bioluminescence in the Octocorallia

by

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A population of alcyoniid soft corals assignable to the species *Eleutherobia grayi* (Thomson and Dean, 1931) is described from the Solomon Islands in the southwestern Pacific Ocean, a taxon previously known only from the Indonesian and Ryukyuan Archipelagos. The species is remarkable in that the anthocodiae are strikingly bioluminescent. This represents the first record of a bioluminescent soft coral, other than a dubious record for *Alcyonium*. Other octocorals for which bioluminescence has been verified are restricted to the gorgonian family Isididae and the Pennatulacea. A table of all octocorallian taxa in which bioluminescence has been recorded (along with newly presented data) is also included, along with a brief review of bioluminescence in the Octocorallia. Two additional species of *Eleutherobia*, which are presently unidentified and presumably undescribed, one from Palau, and the other from the Philippine and Mariana Archipelagos, are here reported to also bioluminesce.

Previously, bioluminescence in octocorals has been presumed to be restricted to many, but not all, sea pens (Pennatulacea) and two to four species of gorgonians (Alcyonacea: Isididae) (Harvey 1952; Muzik 1978). The present paper reports the discovery of bioluminescence in a species of the alcyoniid genus *Eleutherobia* from the Solomon Islands. The discovery represents the first record of bioluminescence in a soft coral.

The genus *Eleutherobia* was last revised by Verseveldt and Bayer (1988). Three species of *Eleutherobia* have recently been described: *E. lutea* Benayahu and Schleyer, 1995, from Natal, South Africa; *E. zanahoria* Williams, 2000, from the Tonga Islands; and *E. vinadigitaria* Williams and Little, 2001, also from Natal, South Africa. Seventeen described species of the genus (considered valid taxa) are known from southern Africa and the Indo-West Pacific—four from southern Africa and thirteen from the Indo-West Pacific (Somalia to Japan and Tonga). Bioluminescence has not been reported in any previously described species of the genus.

Material collected from a disjunct population of a soft coral species identified as *Eleutherobia grayi* (Thomson and Dean, 1931) is described from the Solomon Islands. The specimens do not differ morphologically from the lectotype (redescribed by Verseveldt and Bayer 1988), which was clearly illustrated with scanning electron micrographs of sclerites. However, the Solomon Islands material differs ecologically in one respect from the type material and other known specimens. The previously known material: type specimens from Indonesia, and a record from the Ryukyu Islands (Verseveldt and Bayer 1988:33), was collected from sandy or rubbly bottom substrata (sand with small stones and shells or pieces of dead coral), whereas specimens from the newly discovered population in the Solo-

mon Islands have been observed only on hard substrata (floors, walls and ceilings of limestone caves, alcoves, and overhangs). The populations also differ bathymetrically. The Indonesian and Ryukyuan populations are known from 30–73 m, while the Solomon Islands population has been observed at shallower depths, 5–18 m.

Williams (2000:159) has summarized recent discoveries pertaining to natural products biochemistry and the genus *Eleutherobia*.

Material and Methods

Material for this study was collected by SCUBA and preserved directly in 70% ethanol. Sclerites were isolated by disassociating them from the coenenchyme with household bleach (sodium hypochlorite). Underwater photographs for Figure 1 were made with a Nikonis-V camera and Nikonis SB 103 flash unit. Other photographs and micrographs were made using a Nikon Coolpix 990 digital camera and a Nikon SMZ-10 dissecting microscope. Scanning electron micrographs were made with a Leo 1400 series scanning electron microscope. Sclerite drawings were made using an Olympus CH-2 compound microscope with an attached drawing tube. Digital images and plates of photographs, micrographs, and scanning electron micrographs were made using Adobe Photoshop software. An abbreviation used in the text is CAS (California Academy of Sciences, San Francisco).

Systematic Account

Family Alcyoniidae Lamouroux, 1812

Eleutherobia Pütter, 1900

Eleutherobia Putter, 1900:449. Verseveldt and Bayer, 1988:27. Williams, 1992:306; 2000:160. Williams and Little, 2001.

Diagnosis. — Alcyoniid soft corals, colonies digitiform (finger-like), conical or cylindrical, rarely lobate to subglobular. Polyps monomorphic with calyces absent, however, retracted polyps may form low rounded or conspicuous and mound-like protuberances of the coenenchyme. Sclerites predominantly derived from radiates, with spindles, barrels, tuberculate spheroids, rod-like forms, or crosses sometimes present. Anthocodial sclerites present as crown and points, or as eight points only, or altogether absent. Color variable.

Type Species. — *Eleutherobia japonica* Pütter, 1900, by monotypy.

Diversity and Distribution. — Seventeen species in the Indo-West Pacific and South Africa (eastern and southern Africa to Japan, Saipan, and Tonga) (Fig. 10B).

Eleutherobia grayi **(Thomson and Dean, 1931)**
Figs. 1-10

Nidalia grayi Thomson and Dean, 1931:37, pl. 2 fig. 2. Type locality: Indonesia.
Eleutherobia grayi : Verseveldt and Bayer, 1988:33, figs. 24, 25.
Eleutherobia sp.: Williams, 1996:34 (color photographs taken both at night and during the day).

Material Examined. — CAS 101096, station number 35, Solomon Islands, Mborokua Island (Murray's Island), 18 m depth, 9 November 1994, collected by G. C. Williams with aid of SCUBA, one whole specimen, 22 mm in length. CAS 147475, same data as CAS 101096, one specimen cut longitudinally into two halves, 29 mm in length. CAS 147476, station number 16, Solomon Islands,

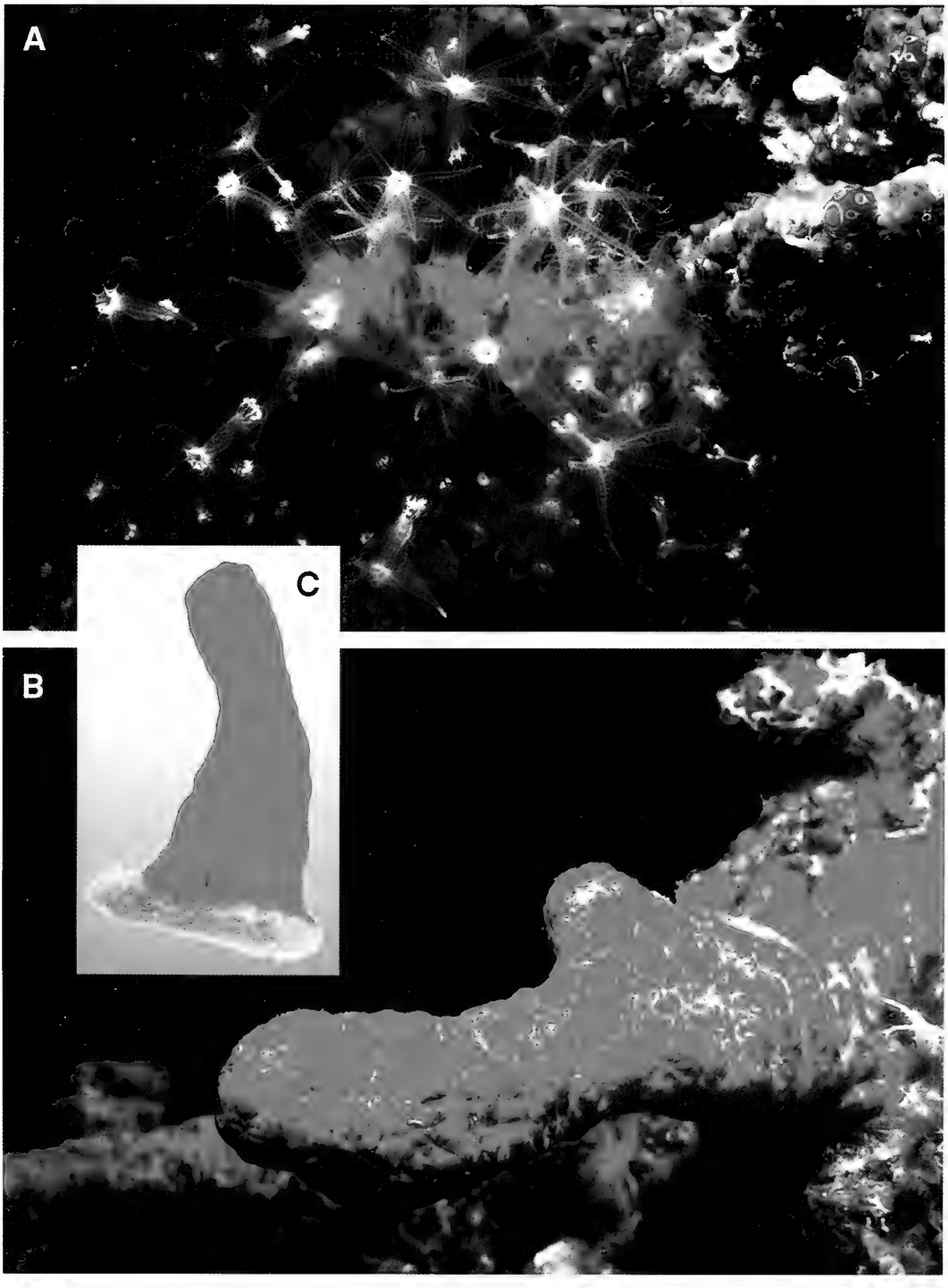

FIGURE 1. *Eleutherobia grayi*. A-B. Underwater photographs of living soft corals, Solomon Islands. Colonies (excluding polyps) are approximately 25 mm in length. A. Photograph taken at night. B. Photograph taken during midday. C. Lectotype, approximately 33 mm in length (from Thomson and Dean 1931, pl. 2 fig. 2).

Mborokua Island (Murray's Island), 10 m depth, 12 September 1998, collected by G. C. Williams with aid of SCUBA, one whole specimen, 24 mm in length. CAS 101095, station number 20, Solomon Islands, Mborokua Island (Murray's Island), 16 m depth, 4 November 1994, collected by G. C. Williams with aid of SCUBA, three whole specimens: 22 mm, 24 mm, and 27 mm in length.

DESCRIPTION. — **Growth form and size**. Alcyoniid soft corals in which the colonies are digitiform (Figs. 1A, 2E) or somewhat lobate (Figs. 1B, 2A–D), mostly cylindrical in shape (Fig. 2E), not markedly tapered, distal apex bluntly rounded (Figs. 1B, 2B–E), somewhat truncate (Figs. 1C, 2A) or somewhat clavate (Fig. 2A, C, D), not pointed. The stalk is very short, as the polyps are distributed over approximately 95% of surface of colony (Figs. 1, 2). The polyparies of most colonies arise directly from a broad holdfast (Figs. 1C, 2A). Wet-preserved colonies vary in length from 11 to 29 mm.

Polyps. The polyps are arranged uniformly over the surface of the colonies. They are monomorphic and do not have calyces, although the retracted polyps may form low rounded or mound-like protuberances on the surface of the polypary in some preserved or tightly retracted colonies (Fig. 1C). These protuberances are formed from the coenenchyme and hence cannot be defined as true calyces. In most cases, the retracted polyps are often more or less flush with the surface of the polypary (Figs. 1B, 2). Polyp sclerites are absent (Figs. 1A, 3, 4).

The living expanded polyps are colorless and translucent, 9–12 mm in length. The length of pharynx is approximately one-third the length of the body of the polyp (Figs. 1A, 3). The peristome is a lustrous and reflective opaque white, while the glandular uppermost portions of the mesenterial filaments are pale yellowish or cream-colored (Fig. 1A). The narrow elongate tentacles are mostly 6–8 mm in length, gradually taper to a point, and have two opposite rows of approximately 12–16 pinnules. (Figs. 1A, 3, 4). Wet-preserved expanded polyps are opaque white (Fig. 2B).

Sclerites. Sclerites are of several distinct types varying from 0.05 to 0.15 mm in length. In the surface coenenchyme of the polypary and holdfast are seven-radiates (Figs. 5C; 6G; 7E, O; 8I), eight-radiates (Figs. 5A, C; 6C, I; 7I, K; 8B, F, N), crosses (Figs. 7J, 8D), quadriradiates with three tubercles in one plane and one tubercle vertically disposed in the center (Fig. 6A), and triradiates (Fig. 6K). In the subsurface coenenchyme and deep interior of the colonies are tuberculate rods and irregularly-shaped, somewhat flattened, rod-like forms (Figs. 5B, D; 7G, L, P).

Color. Most colonies are brick red (Fig. 1A), but some have varying amounts of yellow coloration (Fig. 1B). Sclerite color varies from red to orange, or colorless.

DISTRIBUTION. — Solomon Islands (5–18 m depth) (present study) plus the type localities: Ceram Sea, between Misool and the western end of New Guinea; Indonesia (32 m depth) (lectotype, designated from two syntypes by Verseveldt and Bayer, 1988); and Flores Sea, northwestern end of Sumbawa, Indonesia (73 m depth) [paralectotype, designated from two syntypes by Verseveldt and Bayer (1988)]. They also reported the species from the region of Okinawa in the Ryukyu Islands, Japan (30 m depth). I have examined a large number of specimens of material assignable to the genus *Eleutherobia* from Okinawa. These specimens differ in several respects from *Eleutherobia grayi*, and are here considered to represent another (as yet undetermined) species of the genus. I therefore consider the occurrence of *Eleutherobia grayi* in the Ryukyu Archipelago as unverified (Fig. 10).

VARIABILITY. — Colony shape is variable—digitiform, or bilobate, to somewhat globular. Color is also variable depending on the proportions of red, orange, and colorless sclerites present in the coenenchyme. Some colonies are a uniform brick red, or red with yellowish polyp mounds, while others are very pale pink with cream-colored mounds created by the retracted polyps. These calyx-like mounds are usually uniformly colored, but may be bicolored in some colonies—yellow with eight radiating red stripes, or red with yellow stripes (Fig. 1).

BIOLUMINESCENCE. — During night dives on three occasions (November 1993, November 1994, and September 1998), a vivid green bioluminescence (bright green flash) was observed immediately upon tactile contact with the fully expanded polyps of *Eleutherobia grayi*. This light seems to

FIGURE 2. *Eleutherobia grayi*. A. Wet-preserved specimen (CAS 101096); 22 mm in length. B. Wet-preserved specimen with expanded polyps (CAS 147476); 24 mm in length. C. Wet-preserved specimen (CAS 147475), external view; 29 mm in length. D. Wet-preserved specimen (CAS 147475), cut longitudinally to show internal aspects; 29 mm in length. E. Wet-preserved specimen (CAS 101095); 27 mm in length. Scale bar = 12 mm.

emanate from the region of the peristome (oral disc) and the distal-most region of the pharynx (Figs. 1A, 3, 4), although the precise origin of luminescence remains uncertain. The peristome appears lustrous white under the white-light of an underwater camera flash unit, and thus displays a striking contrast to other parts of the soft coral colony (Fig. 1A). Research using epiflourescence microscopy to determine the location of photocytes in this species is in progress.

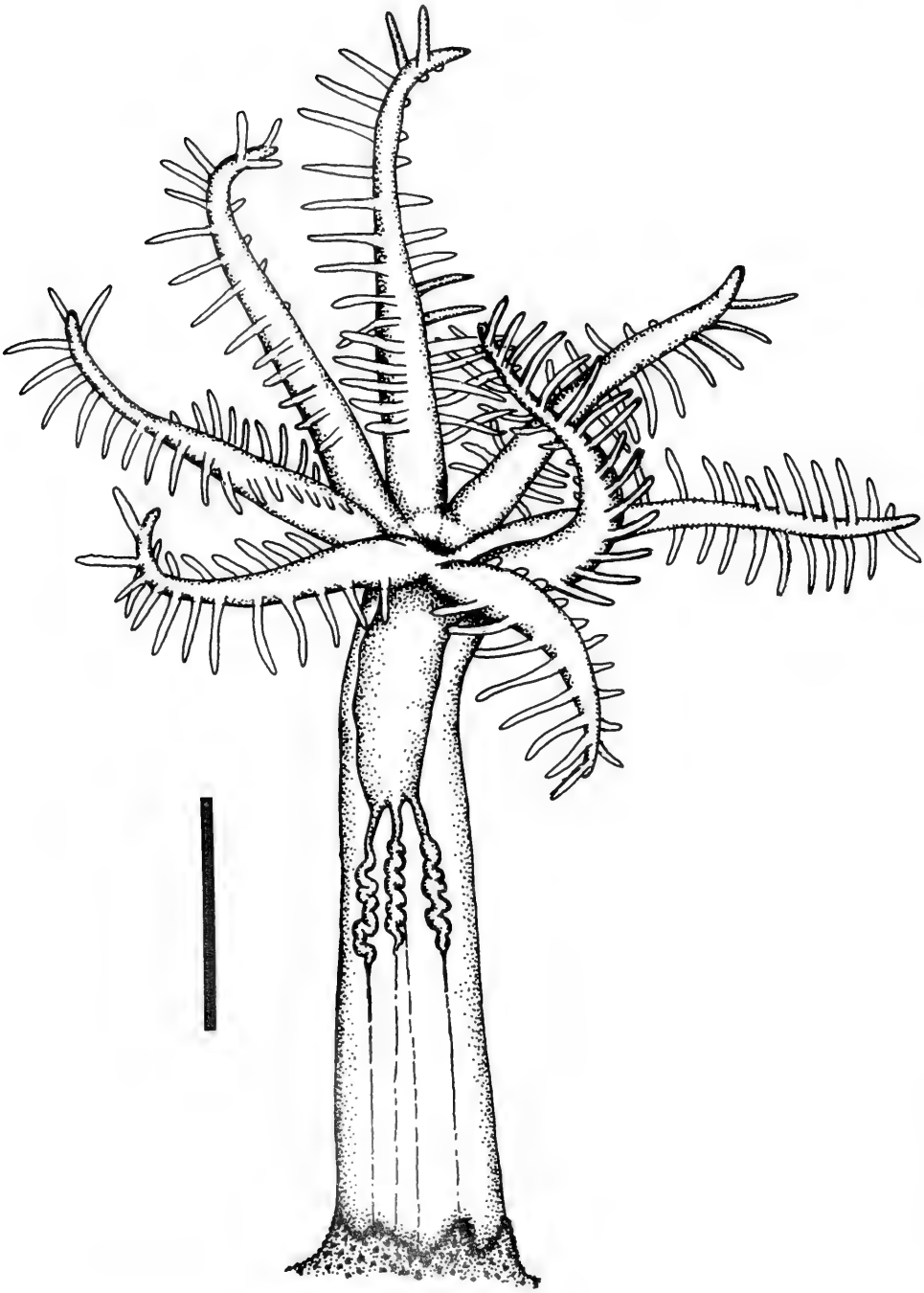

FIGURE 3. *Eleutherobia grayi*. A single polyp, fully extended; scale bar = 3 mm.

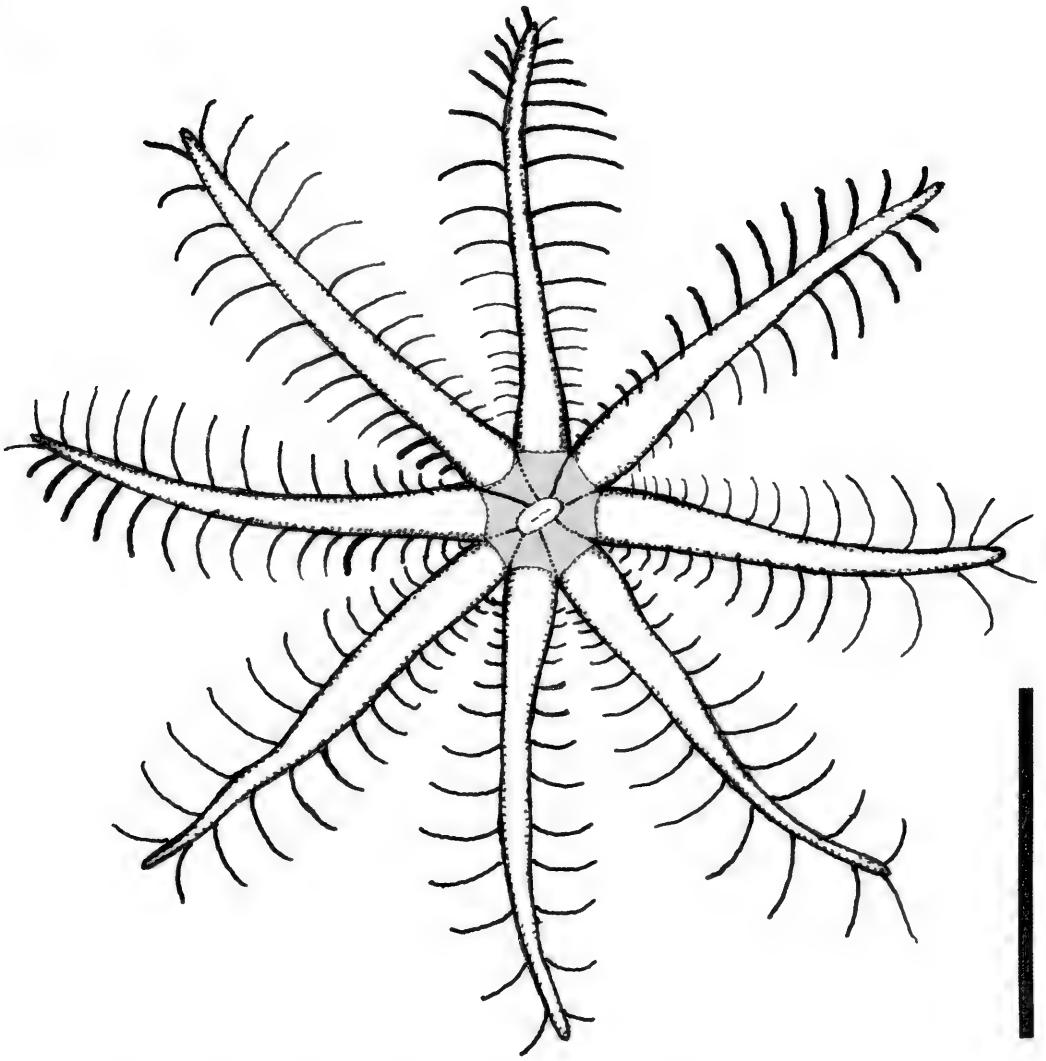

FIGURE 4. *Eleutherobia grayi*. Mouth and tentacles showing oral disc surrounding the mouth (peristome), which is the suspected region of bioluminescence; scale bar = 5 mm.

Since the polyps of *Eleutherobia grayi* are bioluminescent and devoid of scleritic armature as well, it is possible that the attribute of bioluminescence precludes the need for anthocodial armature, and may be regarded as a defense against potential predators of the soft coral polyps. Only one other described species of *Eleutherobia* (*E. zanahoria* Williams, 2000) is known to lack polyp armature, but the presence or absence of bioluminescence in this taxon is not known.

ECOLOGICAL OBSERVATIONS. — Much of the shallow water, hard coral cover at the type locality was dramatically altered between 1994 and 1998, presumably by a combination of warming events and a series of severe storms. Physical decimation of hermatypic as well as ahermatypic scleractinians took place, together with a substantial amount of bleaching (predominantly on the distal-most extremities of the coral colonies). On the exposed reef flats and slopes, replacement of hermatypic scleractinians by soft corals such as *Paralemnalia* spp. and various taxa of coralline algae, was ob-

served during this period. In the limestone caves, alcoves, and overhangs (Fig. 9), a physical replacement of *Tubastraea faulkneri* Wells, 1982 (which provided the dominant cover in 1993 and 1994) by the soft coral *Eleutherobia grayi*, was also observed during the same period.

The polyps of the soft coral are retracted into the body of the soft coral during daylight hours (Fig. 1B), gradually expand at dusk, and remain fully expanded (in feeding mode) for the duration of the night (Fig. 1A).

Several colonies of *Eleutherobia grayi* were observed to have minute epizoites (mostly tunicates or bryozoans) growing on the surface of the polyparies, between the polyps.

REMARKS. — Morphologically, material from the Solomon Islands population fully agrees with the original description of *Eleutherobia grayi* by Thomson and Dean (1931), and the well-illustrated redescription of the designated lectotype by Verseveldt and Bayer (1988). Several important points of concurrence are listed below.

1. Total lack of sclerites in the anthocodiae.
2. Red or yellow coloration due to varying amounts of red and yellow sclerites.
3. Deep interior of colonies with many sclerites, almost exclusively rod-like forms.
4. Size range of sclerites: 0.05–0.15 mm (present study); 0.03–0.18 mm (Verseveldt and Bayer, 1988).
5. Sclerite types: Eight-radiates, seven-radiates, triradiates, crosses, quadriradiates with three tubercles in one plane and one tubercle arising vertically from the center, and irregularly-shaped tuberculate rods.

DISCUSSION

BIOLUMINESCENCE IN OCTOCORALS (Table 1). — For the sake of the following discussion, the various groups of octocorals are defined as follows. **Stoloniferous octocorals** have separate polyps connected at their bases by membranous or ribbon-like stolons. **Soft corals** have polyps embedded in a common coenenchyme and are attached to hard substrata by basal holdfasts, they have no axial development, and only free sclerites comprise the skeletal elements. **Gorgonians**, like the soft corals, have polyps embedded in a common coenenchyme and are attached to the substratum by basal holdfasts, but unlike soft corals, in addition to free sclerites, have some form of internal axial development composed of calcium carbonate, gorgonin, or a combination of the two. **Sea pens** or **pennatulaceans** have the coral colony divided into a proximal muscular peduncle that is anchored in soft substrata, and a distal rachis that contains several kinds of polyps. They may or may not have a calcareous axial skeleton.

Williams (1999:23, 49–50) provided a historical review and comprehensive bibliography pertaining to pennatulacean bioluminescence. The scientific literature regarding bioluminescence in octocorals is relatively rich, extending back to the sixteenth century with the works of Gesner, Boussuet, Imperato, Rondelet, and others. Important modern contributions include: Panceri (1871, 1872a, b); Parker (1920); Harvey (1940, 1952); Nicol (1958); Titschak (1965, 1966); Morin (1974, 1976); Muzik (1978); and Herring (1991). Harvey (1952:168) stated, "... but among the Alcyonaria are to be found some of the most brilliant and striking luminous animals. Of the three groups of Alcyonaria, the Alcyonacea, the Gorgonacea, and the Pennatulacea, only luminescence of the Pennatulacea has been carefully studied." Pertaining to alcyonaceans, only a few species in the gorgonian family Isididae have been known to luminesce. Mangold's (1910) record of Leuckart's luminescent *Alcyonium* is considered by Harvey (1952:169–170) to be "very dubious." No subsequent records of bioluminescence in the genus *Alcyonium*, or any other soft coral taxon for that matter, are known in the previous literature.

The only records of bioluminescent soft corals are represented by new data presented here of *Eleutherobia grayi* from the Solomon Islands, as well as observations made on two other species of

TABLE 1. Records of bioluminescence in octocorals.

Taxon	Depth	Color of light	References on bioluminescence
Order Alcyonacea			
Soft corals			
ALCYONIIDAE			
Eleutherobia grayi	5–18 m	green	present study
Eleutherobia sp. indet. #1 (Luzon and Saipan)	12–23 m	green	Gosliner and Starmer - pers. commun.; Williams - pers. observ.
Eleutherobia sp. indet. #2 (Palau)	20 m	—	Starmer - pers. commun.
Gorgonians			
ISIDIDAE			
Lepidisis olapa	400–450 m	white	Muzik (1978:735; 1981[82]:56)
Isidella elongata	564 m	—	Muzik (1978:735)
Keratoisis sp.	—	—	Harvey (1952:169)
Primnoisis sp.	—	—	Harvey (1952:169)
Order Pennatulacea			
Sea Pens			
VERETILLIDAE			
Cavernularia habereri	—	—	Harvey (1917)
Cavernularia pusilla	65–75 m	—	Panceri (1872a)
Veretillum cf. *manillense*	10–25 m	green	Williams - pers. observ.
Veretillum cynomorium	13–91 m	—	Bujor (1901); Titschak (1965)
ECHINOPTILIDAE			
Actinoptilum molle	12–333 m	green	Williams (1990:63)
RENILLIDAE	0–70 m		
Renilla muelleri	—	—	Parker (1920)
Renilla koellikeri	—	—	Morin (1976:632)
Renilla reniformis	—	—	Ward and Cormier (1978)
FUNICULINIDAE			
Funiculina quadrangularis	60–2600 m	lilac	Thomson (1874:149); Herring (1991)
PROTOPTILIDAE			
Distichoptilum gracile	650–4300 m	—	Herring (1991)
UMBELLULIDAE	210–6100 m		
Umbellula huxleyi	—	—	Herring (1991)
Umbellula thomsoni	—	—	Tizard et al. (1885:49)
VIRGULARIIDAE			
Stylatula elongata	9–50 m	—	Morin (1976:632)
Acanthoptilum gracile	10–146 m	—	Morin (1976:630)
Virgularia mirabilis	9–400 m	—	Herdman (1913); Nicol (1958)
PENNATULIDAE			
Ptilosarcus gurneyi	0–68 m	—	Morin (1976:630)
Pennatula phosphorea	300–3609 m	—	Herdman (1913); Titschak (1966)
Pennatula rubra	—	—	Panceri (1871); Titschak (1966)
Pteroeides spinosum	—	—	Panceri (1871); Titschak (1966)

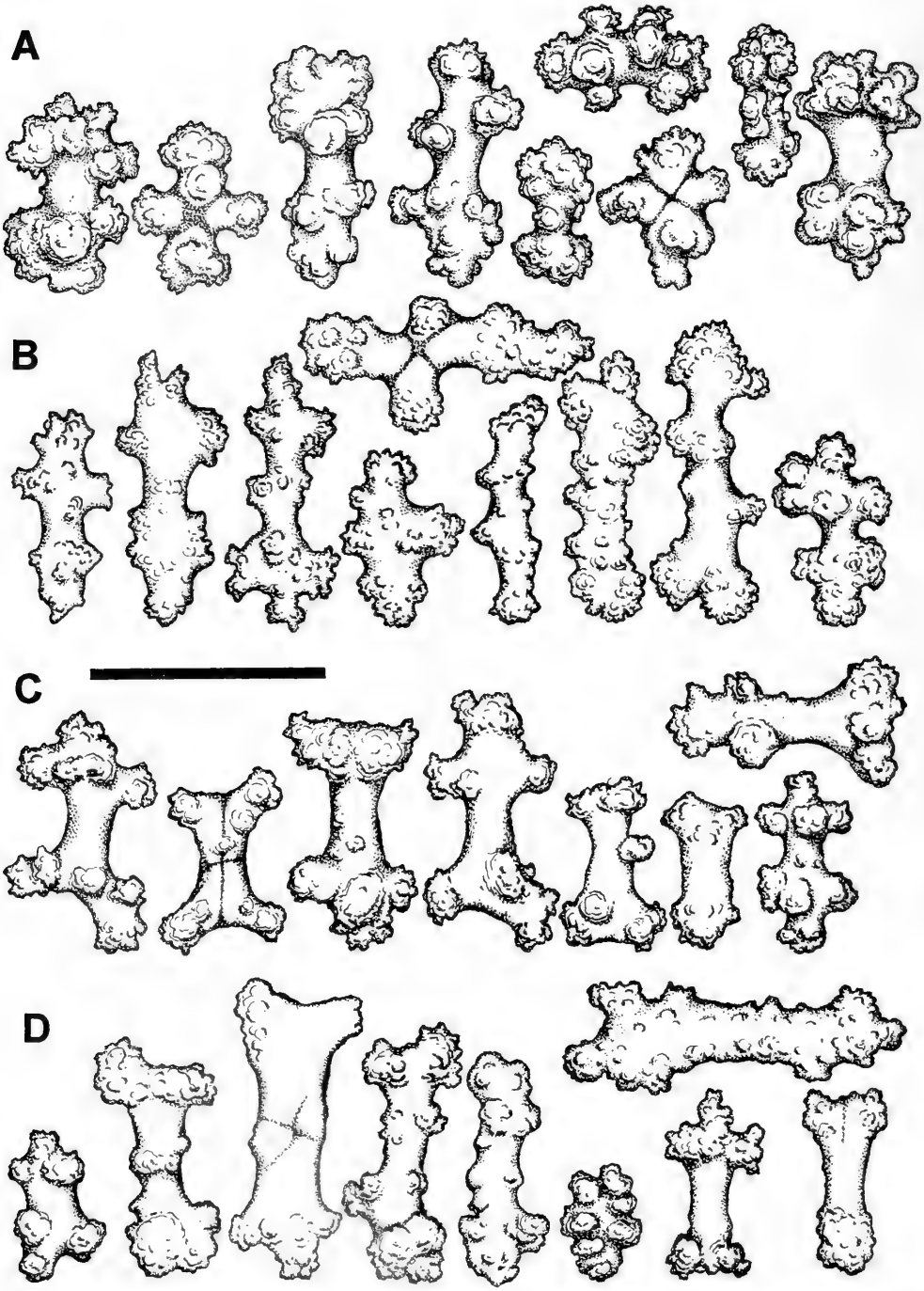

FIGURE 5. *Eleutherobia grayi* sp. nov. Sclerites. A. Polypary surface. B. Polypary interior. C. Stalk surface. D. Stalk interior. Scale bar = 0.1 mm.

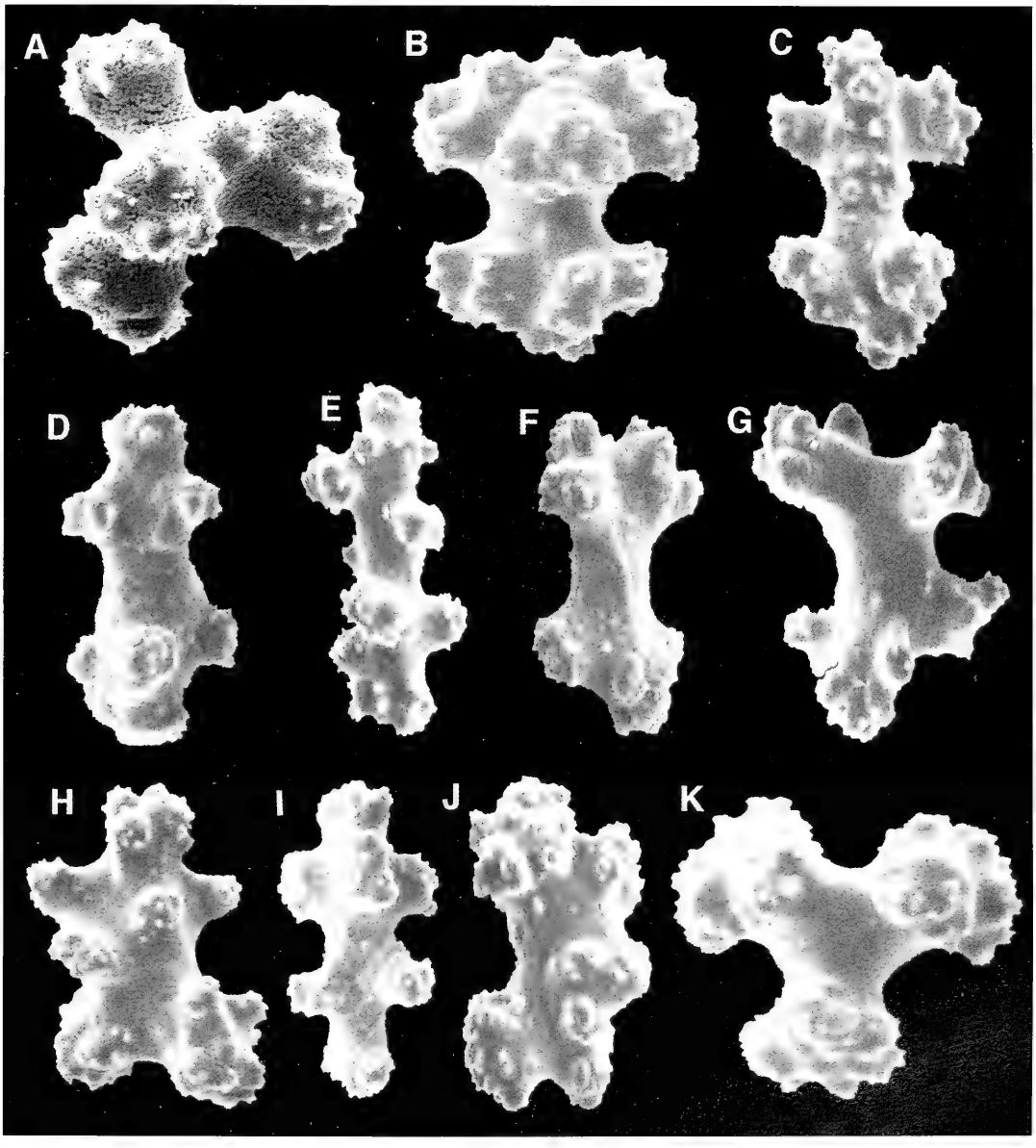

FIGURE 6. *Eleutherobia grayi* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the mound-like protuberances formed by the retracted polyps. A. 0.04 mm. B. 0.05 mm. C. 0.06 mm. D. 0.05 mm. E. 0.07 mm. F. 0.06 mm. G. 0.07 mm. H. 0.07 mm. I. 0.07 mm. J. 0.07 mm. K. 0.04 mm.

Eleutherobia (*Eleutherobia* spp. indet.). One of these is found on vertical surfaces at 12 m depth in southern Luzon, Philippines (pers. observ., and pers. commun. T. M. Gosliner), and Saipan (pers. commun. J. Starmer), and the other has been collected from Palau (pers. commun. J. Starmer). These observations presented here are the first records of bioluminescent soft corals (outside of the dubious record of Leuckart's *Alcyonium*).

The phenomenon of bioluminescence in the Pennatulacea, although commonly encountered in bathymetrically diverse habitats and supported by a relatively rich literature, is by no means universal,

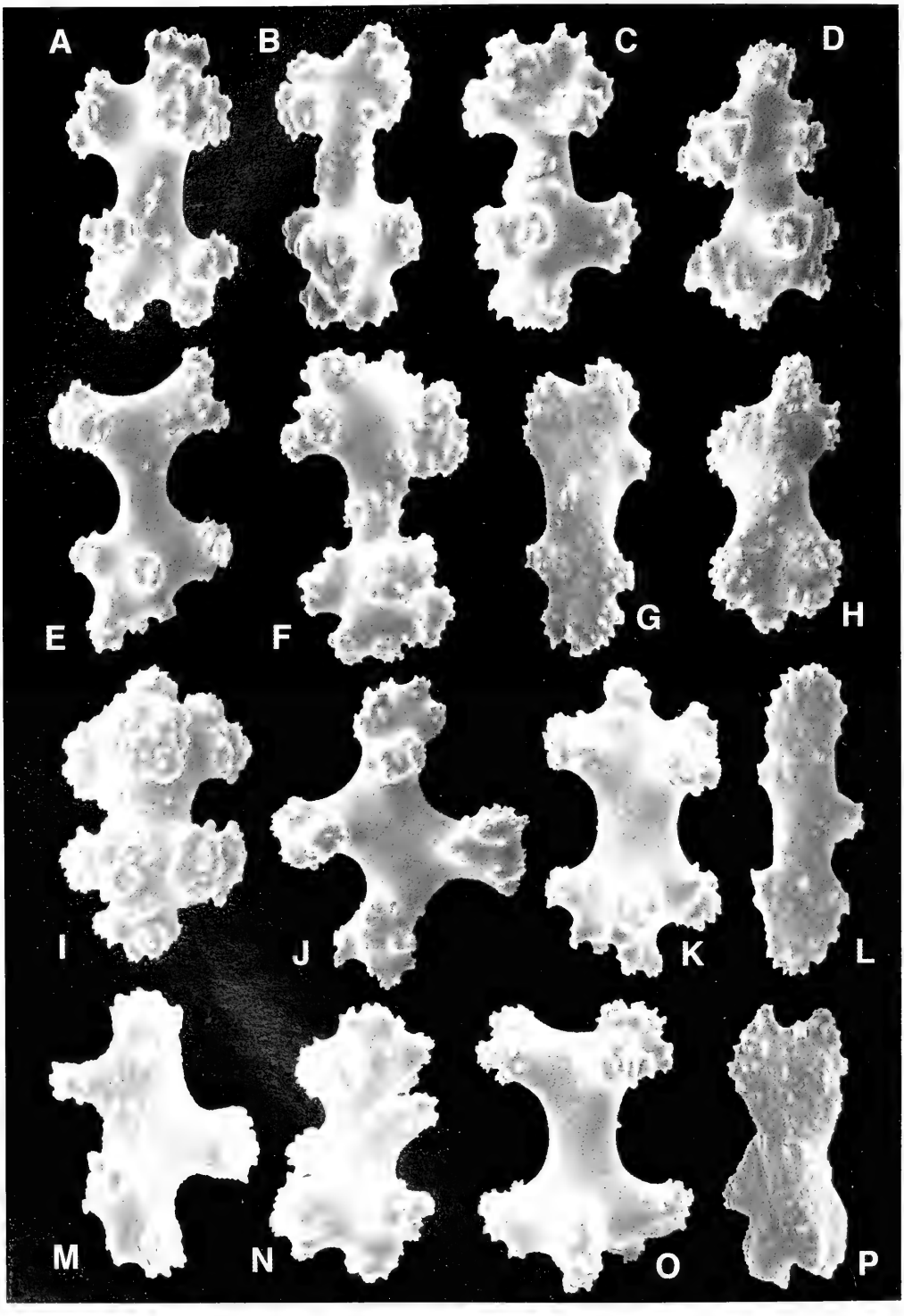

FIGURE 7. *Eleutherobia grayi* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the surface and subsurface of the polypary. A. 0.09 mm. B. 0.08 mm. C. 0.05 mm. D. 0.08 mm. E. 0.09 mm. F. 0.08 mm. G. 0.08 mm. H. 0.07 mm. I. 0.06 mm. J. 0.10 mm. K. 0.08 mm. L. 0.09 mm. M. 0.05 mm. N. 0.05 mm. O. 0.08 mm. P. 0.07 mm.

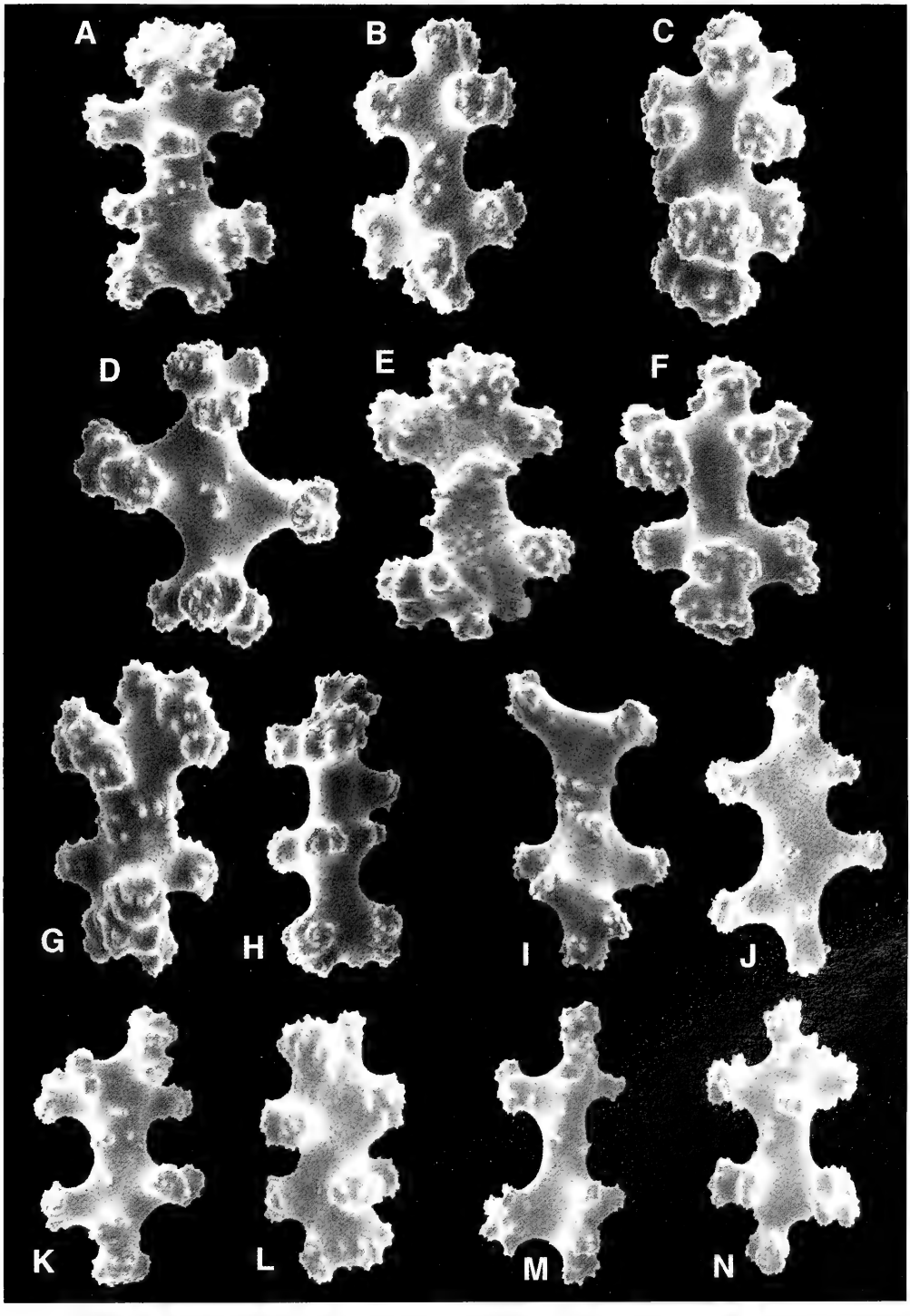

FIGURE 8. *Eleutherobia grayi*. Scanning electron micrographs of coenenchymal sclerites from the surface of the holdfast region of the stalk. A. 0.09 mm. B. 0.08 mm. C. 0.07 mm. D. 0.08 mm. E. 0.08 mm. F. 0.08 mm. G. 0.05 mm. H. 0.08 mm. I. 0.10 mm. J. 0.11 mm. K. 0.10 mm. L. 0.07 mm. M. 0.13 mm. N. 0.11 mm.

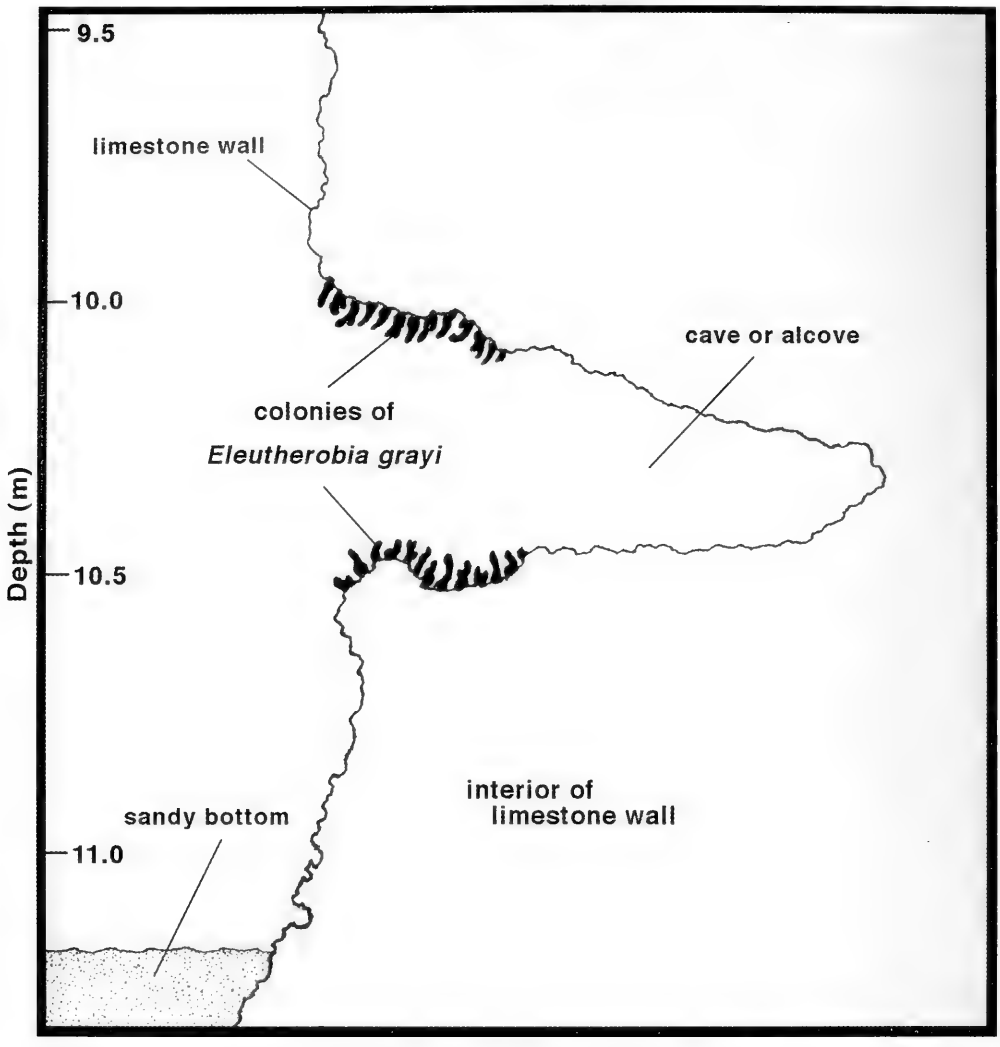

FIGURE 9. Habitat Section. Diagram of longitudinal section through a limestone wall at approximately 10 meters in depth, Mborokua Island, Solomon Islands, showing disposition of densely-set colonies of *Eleutherobia grayi*. Depths shown at left are in meters.

as some taxa are definitely not luminescent. For example, Herring (1978:204) stated that some species of *Virgularia* have been shown to be non-luminous.

Bioluminescence has thus far been recorded in only 53% of the pennatulacean families (8 of 15), 40% of the genera (13 of 32), and 10% of the estimated number of valid species (19 of 186). If the total number of described species in the literature are taken into account, then the latter percentage drops to approximately 4% (19 of 436). These estimates represent minimum values, but could be much higher, and are based on numbers of taxa in Williams (1995:93) and Table 1 of the present paper.

It is surprising that after nearly 450 years of published observations resulting in more than eighty published accounts of pennatulacean bioluminescence, a mere nineteen species (or approximately 10% of the valid species) have been recorded. This number seems especially low considering the introduction of modern technological means to make observations—such as SCUBA, remote operational vehicles (ROV's), and manned deep-sea submersibles. Only a few sea pens are diurnal and/or

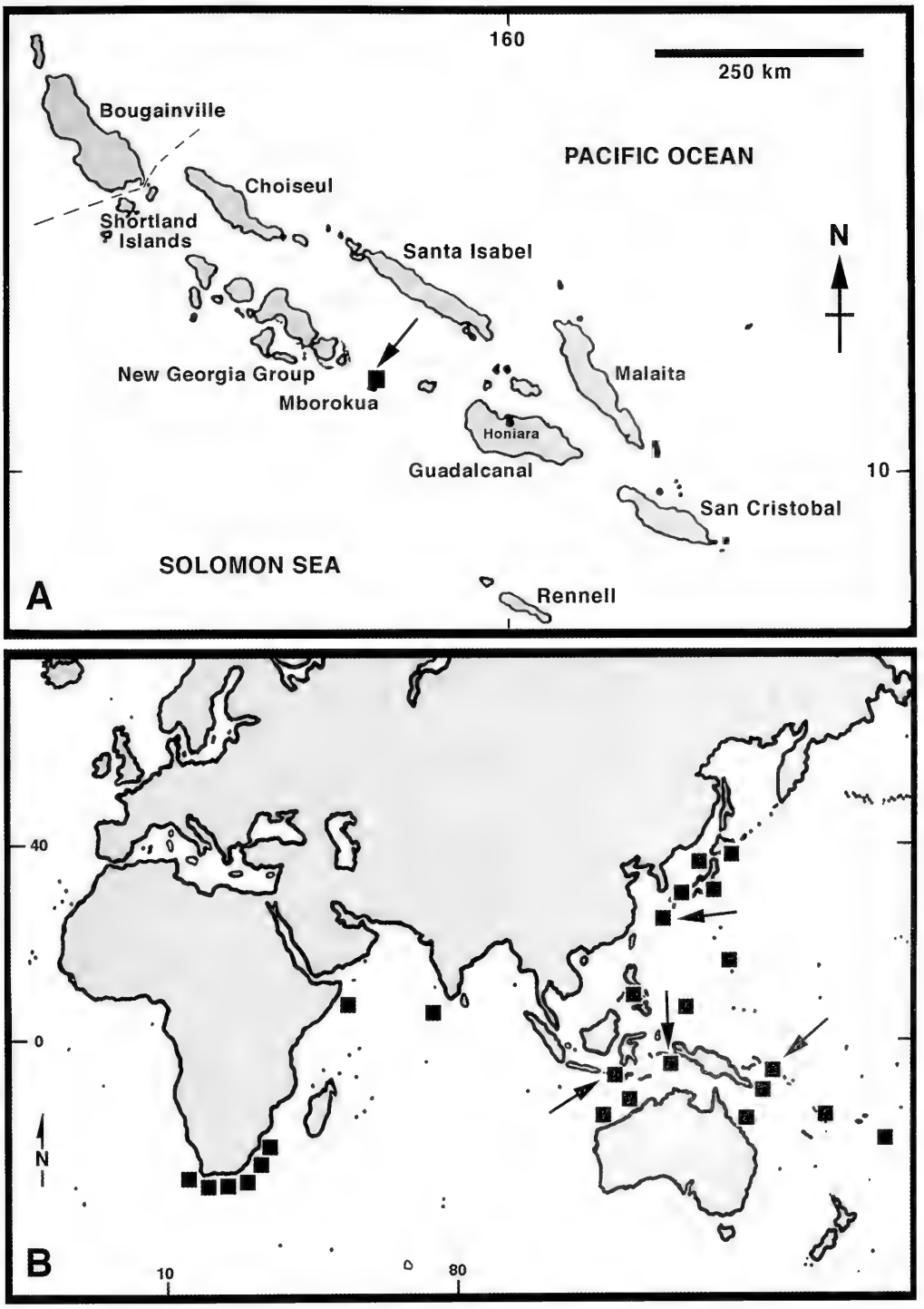

FIGURE 10. A. Map of the Solomon Archipelago, southwestern Pacific Ocean; dotted line marks the political boundary between Papua New Guinea (upper left) and the Solomon Islands. B. Map of the Indo-West Pacific showing geographic distribution of the genus *Eleutherobia*; ■ = collecting stations; arrows show collecting stations for *Eleutherobia grayi*.

zooxanthellate, and are not known to bioluminesce. The majority of shallow water species (at least in the Indo-Pacific) are nocturnal and azooxanthellate (Williams, pers. observ.). One South African species, *Actinoptilum molle*, appears to be active both during the day and night, and is at the same time azooxanthellate and bioluminescent (Williams, 1990:63). In addition, a remarkable diversity of deep-water taxa are known (Williams 1993:733–734; 1997:499, 503) that live in perpetual darkness. It is therefore assumed that the actual number of bioluminescent sea pens could be much higher than is presently documented.

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I am grateful to James Kasson (Menlo Park, California), John Starmer (Koror, Palau), and Terrence M. Gosliner, Alan Dekelboum, and Roy Eisenhardt (California Academy of Sciences) for their underwater observations. I thank James Morin (Cornell University) and Stephen Cairns (Smithsonian Institution) for their insight and useful comments.

LITERATURE CITED

BENAYAHU, Y. AND M. H. SCHLEYER. 1995. Corals of the south-west Indian Ocean II. *Eleutherobia aurea* spec. nov. (Cnidaria, Alcyonaria) from deep reefs on the KwaZulu-Natal Coast, South Africa. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report 68:1–12.

BUJOR, P. 1901. Sur l'organisation de la Vérétille. Archives de zoologie expérimentale et générale, notes et revur (Ser. 3) 9: No. 4, xlix–lx.

HARVEY, E. N. 1917. Studies on bioluminescence. 6. Light production by a Japanese pennatulid *Cavernularia habereri*. American Journal of Physiology 42:349–358.

———. 1940. Living Light. Princeton University Press, Princeton, New Jersey. 328 pp.

———. 1952. Bioluminescence. Academic Press, New York. 649 pp.

HERDMAN, W. A. 1913. "Phosphorescence" of Pennatulida. Nature, London 91:582.

HERRING, P. J., ed. 1978. Bioluminescence in action. Academic Press, London. 570 pp.

———. 1991. Observations on bioluminescence in some deep-water anthozoans. Hydrobiologia 216/217:573–579.

MANGOLD, E. 1910. Die Produktion von Licht. Pp. 225–392 *in* Handbuch der vergleichende Physiologie, Jena 3 (2nd half), H. Winterstein, ed.

MORIN, J. G. 1974. Coelenterate bioluminescence. *In* Coelenterate Biology: Reviews and New Perspectives, L. Muscatine and H. Lenhoff, eds. Academic Press, New York. 501 pp.

———. 1976. Probable functions of biolumninescence in the Pennatulacea (Cnidaria, Anthozoa). *In* Coelenterate ecology and behavior, G.O. Mackie, ed. Plenum, New York. 744 pp.

MUZIK, K. 1978. A bioluminescent gorgonian, *Lepidisis olapa*, new species (Coelenterata: Octocorallia), from Hawaii. Bulletin of Marine Science 28(4):735–741.

———. 1981(82). Proceedings of the Fourth International Coral Reef Symposium 2:756 [abstract].

NICOL, J. A. C. 1958. Observations on the luminescence *of Pennatula phosphorea*, with a note on the luminescence of *Virgularia mirabilis*. Journal of the Marine Biological Association of the United Kingdom 37:551–563.

PANCERI, P. 1871. Gli organi luminoi e la luce delle Pennatule. Rendiconto dell' Accademia della scienze, Napoli 10(1):204–211.

———. 1872a. Études sur la Phosphorescence des Animaux Marins. II. Du siège du mouvement lumineux dans les Méduses; III. Organes lumineux et lumière des Pennatules; VI. Sur un Pennatulaire phosphoresenct encore inconnu dans les environs de Naples (*Cavernularia pusilla*); IX. Des organes lumineux et de la lumière des Béroidiens. Annales des Sciences Naturelles, sér. 5 (Zoologie)16 (8):1–66.

———. 1872b. The luminous organs and light of the Pennatulae. Quarterly Journal of Microscopical Science, London 12:248–254. [English translation of Panceri, 1871]

PARKER, G. H. 1920. The phosphorescence of *Renilla*. Proceedings of the American Philosophical Society 19:171–175.

THOMSON, C. W. 1878. 1874. The depths of the sea—an account of the general results of the dredging cruises of H.M.S. "Porcupine" and "Lightning" during the summers of 1868, 1869, and 1870, under the scientific direction of Dr. Carpenter, F.R.S., J. Gwyn Jeffreys, F.R.S., and Dr. Wyville Thomson, F.R.S., 2nd ed. Macmillan and Company, London. 527 pp.

THOMSON, J. A. AND L. M. I. DEAN. 1931. The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga Expedition Monographs 13d:1–227.

TITSCHAK, H. 1965. Untersuchungen über das Leuchten der Seefeder *Veretillum cynomorium* (Pallas). Vie et Milieu 15:547–563.

———. 1966. Über die Lumineszenz und ihre Lokalisation bei Seefedern. Zoologischer Anzeiger, Supplementband 29, 1965(1966):120–131.

TIZARD, T. H., H. N. MOSELEY, H. Y. BUCHANAN, AND J. MARRAY. 1885. Narrative of the cruise of H.M.S. Challenger with a general account of the scientific results of the expedition. Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873–76, Narrative, Vol. 1 (first part):1–509.

VERSEVELDT, J. AND F. M. BAYER. 1988. Revision of the genera *Bellonella*, *Eleutherobia*, *Nidalia* and *Nidaliopsis* (Octocorallia: Alcyoniidae and Nidalliidae), with descriptions of two new genera. Zoologische Verhandelingen 245:1–131.

WARD, W. W. AND M. J. CORMIER. 1978. Energy transfer via protein protein interaction in *Renilla* bioluminescence. Photochemistry and Photobiology 27(4):389–396.

WILLIAMS, G. C. 1990. The Pennatulacea of southern Africa (Coelenterata, Anthozoa). Annals of the South African Museum 99(4):31–119.

———. 1992. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Annals of the South African Museum 100(3):249–358.

———. 1993. Biotic diversity, biogeography, and phylogeny of pennatulacean octocorals associated with coral reefs in the Indo-Pacific. Proceedings of the Seventh International Coral Reef Symposium 2:729–735.

———. 1995. Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. Zoological Journal of the Linnean Society, London 113:93–140.

———. 1996. Octocorallia—Octocorals. *In* Coral reef animals of the Indo-Pacific, animal life from Africa to Hawai'i exclusive of the vertebrates, T. M. Gosliner, D. W. Behrens, and G. C. Williams. Sea Challengers, Monterey, California. 314 pp.

———. 1997. Preliminary assessment of the phylogeny of Pennatulacaea (Anthozoa: Octocorallia), with a reevalutation of Ediacaran frond-like fossils, and a synopsis of the history of evolutionary thought regarding the sea pens. Proceedings of the Sixth International Conference on Coelenterate Biology: 497–509.

———. 1999. Index Pennatulacea—annotated bibliography and indexes of the sea pens (Coelenterata: Octocorallia) of the world 1469–1999. Proceedings of the California Academy of Sciences 51(2):19–103.

———. 2000. A new species of the soft coral genus *Eleutherobia* Pütter, 1900 (Coelenterata: Alcyoniidae) from the Tonga Islands. Proceedings of the California Academy of Sciences 52 (13):159–169.

WILLIAMS, G. C. AND S. A. LITTLE. 2001. A new species of the soft coral genus *Eleutherobia* Pütter, 1900 (Octocorallia: Alcyoniidae) from South Africa. Proceedings of the California Academy of Sciences 52(16):193–206.

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Four New Species of *Forcepia* (Porifera, Demospongiae, Poecilosclerida, Coelosphaeridae) from California, and Synonymy of *Wilsa* de Laubenfels, 1930, with *Forcepia*, Carter, 1874

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Four new species of the marine sponge genus *Forcepia* (Porifera, Demospongiae, Poecilosclerida, Myxillina, Coelosphaeridae), are described and *Wilsa hymena* de Laubenfels, 1930, which is now designated as *Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930), is redescribed on the basis of new material found in the collections of the Scripps Institution of Oceanography. As a result of detailed comparison of this material with de Laubenfels' type, *Wilsa* is synonymized with *Forcepia*. Heretofore, only one species of this group (*Wilsa hymena*) had been described from California. Full descriptions, figures and relevant morphological and habitat information have been included.

While the rich coastal waters along the California coast support a vast and varied invertebrate fauna, our knowledge of the organisms found in this region remains disappointingly poor. A prime example is the marine sponge fauna. Those studying sponges must rely largely on a publication from 1932 by de Laubenfels and a field manual on intertidal invertebrates last published in 1975 by Hartman as their main source of information. Scattered papers, of which only a few are recent, provide the remainder of the available information.

Five years ago, the David and Lucile Packard Foundation generously funded the author for a study of the sponges of California. That study has been completed (Lee, Elvin, Reiswig, in preparation). Over 250 species have been found in Californian waters, many of these new to science. The present paper represents the first of an anticipated series describing the newly discovered species.

In the past, sponges bearing forceps as microscleres have been variously placed in different taxa. From recent investigations by Van Soest (pers. commun.) and Hajdu and Vacelet (pers. commun.) forceps-bearing taxa are now largely relegated to the genus *Forcepia* Carter, 1874 (family Coelosphaeridae). An exception is the genus *Asbestopluma,* Norman, 1882 (family Cladorhizidae), which consists largely of abyssal sponges with forceps of different structure, not considered homologous with the forceps of *Forcepia.* The papers by the above mentioned authors are part of a worldwide effort to review and revise all presently used taxonomic categories through a re-examination of the type material on which these taxa are based. The papers will be compiled in the *Systema Porifera* to be published this year (Hooper and Van Soest, in press). The revision of *Forcepia* includes two newly defined subgenera, *Forcepia* and *Leptolabis,* the latter distinguished by the presence of basal acanthostyles and a hymedesmoid-like skeletal architecture. The California sponges described here all belong to the subgenus, *Forcepia.*

To date only two forceps-bearing sponges have been reported from California, *Asbestopluma lycopodium* (Levinsen, 1886) and *Wilsa hymena* de Laubenfels, 1930. The first is a member of the family Cladorhizidae, and will not be discussed here. The genus *Wilsa* was erected by de Laubenfels

in 1930 for a single forceps-bearing specimen. Recent review of newly found material suggests that this species belongs to the genus *Forcepia* and de Laubenfels' *Wilsa* is synonymized with *Forcepia.* Besides a redescription of *Wilsa hymena,* four new species of *Forcepia* are described in this paper.

MATERIALS AND METHODS

Material examined in this study was predominantly taken from museum collections. Abbreviations for specimens in these collections are as follows: NHM, The Natural History Museum, London; CASIZ, California Academy of Sciences; BIC-SIO, Scripps Institution of Oceanography, Invertebrate Collection; SBMNH, Santa Barbara Natural History Museum; U.S.N.M., U.S. National Museum, Smithsonian Institution; YPM, Peabody Museum, Yale University.

Spicule preparations and cross-sections were routinely made according to the procedures of Hartman (1975). Slide preparations were mounted in Permount. All measurements, including spicules, were made with a stage micrometer directly through a compound microscope. Width measurements for megascleres were taken at the thickest point of the spicule shaft. Isochela lengths were taken from the apices of alae; length measurements of other spicules refer to maximum lengths. No less than 50 measurements were made for each spicule type and the data subjected to statistical analyses of range and mean. These measurements were displayed graphically to determine if distinct spicule size classes were present. Distinctive size classes are deemed legitimate only when these graphs show either non-overlapping, or distinct bi- or tri-modal distributions.

Spicule measurements are shown in this paper with the lowest size listed first and the greatest size listed last. In cases where only one specimen was measured, the mean is given in between these two extremes and underlined (234–<u>268</u>–295 μm). If more than a single specimen is measured then the range of means [from lowest to highest] is given and underlined (234–<u>259–271</u>–295 μm).

Spicules were prepared for the scanning electron microscope (SEM) as described above but mounted and dried on 1.5 cm round slides. These were mounted on stubs with double-sided tape, sputter coated with gold-paladium, and examined on an Hitachi S-520 scanning electron microscope.

SPECIES DESCRIPTIONS

Family Coelosphaeridae Hentschel, 1923
Genus *Forcepia* Carter, 1874
Wilsa de Laubenfels, 1930:27

***Forcepia* (*Forcepia*) *acanthostylosa* sp. nov.**
Figs. 1 and 2

MATERIAL. — **Holotype**: SBMNH 345543, U.S.A. California, San Miguel Island, Cuyler Harbor, Depth 10.7 to 12.2 m, Collectors: B. Scronce, M. Conboy, C. Carreon, and L. Bray, 19 February 1964. G. E. and N. Macginitie Port Hueneme Collection. **Paratype**: CASIZ 154368, U.S.A., California, Santa Barbara County, Santa Cruz Island, small cove midway between Chinese Harbor and Prisoners Harbor. Depth 10.3 to 12.2 m. Collectors: B. Scronce, M. Conboy, and L. Bray, 3 July 1963. G. E. and N. Macginitie Port Hueneme Collection.

DISTRIBUTION. — Known only from two localities in southern California: San Miguel Island (holotype) and Santa Cruz Island (paratype).

HABITAT. — Habitat descriptions were not included in the collection data.

SHAPE. — Holotype, thickly encrusting, 1.5–3.3 cm thick. Sponge irregular in shape, 6 cm long by 2.0–3.8 cm wide. The sponge appears to have encrusted a mat of bottom material, including algae, other invertebrates and sand. Paratype, thinly encrusting on a shell of the bivalve *Hinnites*

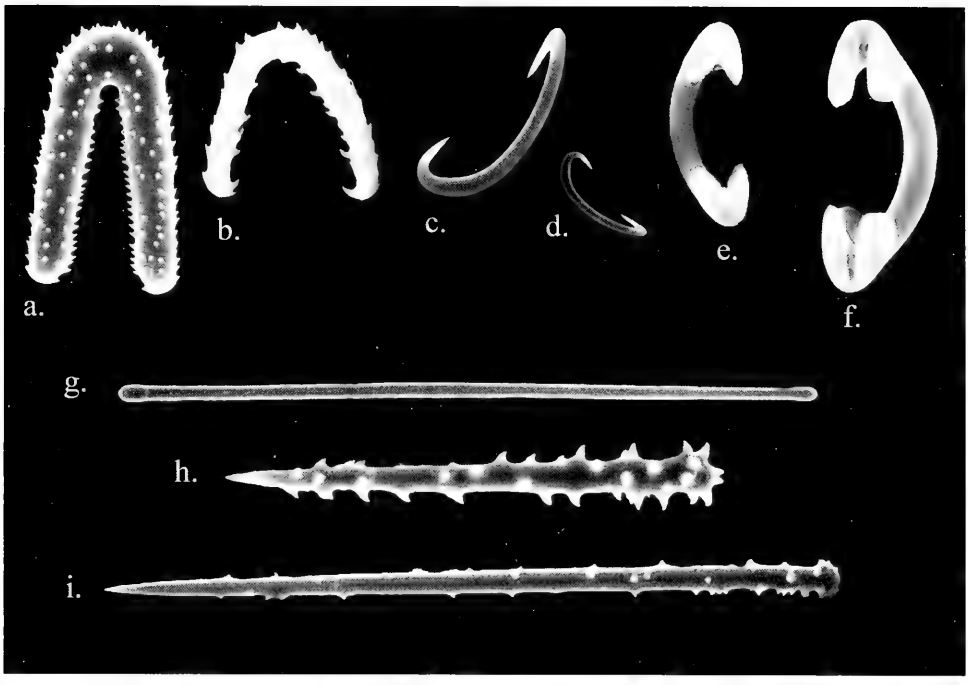


FIGURE 1. Scanning electron micrographs of the spicules of *Forcepia* (*Forcepia*) *acanthostylosa*, sp. nov. Holotype (SBMNH 345543) a. Forceps 4,000×, b. Forceps 7,000×, c. Large sigma 2,000×, d. Small sigma 3,000×, e. Small arcuate isochela 7,000×, f. Large arcuate isochela 4,000×, g. Substylote 500×, h. Small acanthostyle 1500×, i. Large acanthostyle 500×.

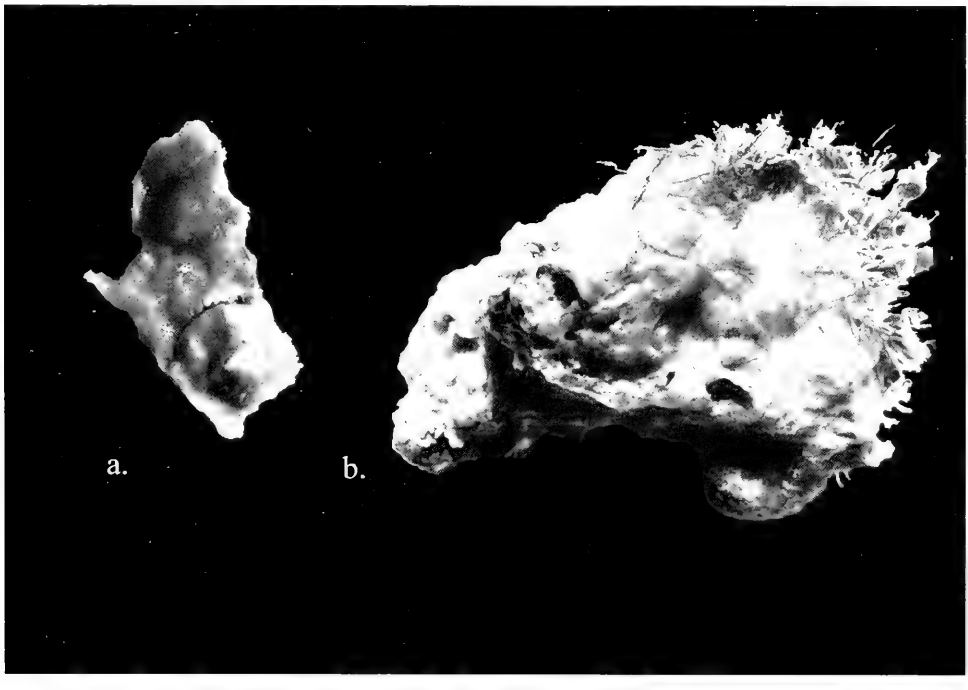


FIGURE 2. *Forcepia* (*Forcepia*) *acanthostylosa*, sp. nov. a. Paratype (CASIZ 154368), on fragments of *Hinnites multirugosus* 1.0–1.5 mm thick. b. Holotype (SBMNH 345543), dimensions.1.5–3.25 cm thick, 6.0 × 2.0–3.75 cm wide.

multirugosus, which had been broken into several pieces. The sponge thickness was up to 1.5 mm in a few places, but mostly 1.0 mm or less.

COLOR. — Live—yellow to orange; preserved in ethanol—light tan.

OSCULA. — On surface, randomly distributed on the holotype. Only one seen on the largest piece of the paratype. Oscula oval or nearly so, with no rims, but appear sunken below the surface. These range from 0.5 to 1.5 mm in diameter. A few large surface openings are also present. These are somewhat oblong and roughly 2.0 by 4.0 mm; they are probably not oscula.

TEXTURE AND SURFACE CHARACTERISTICS. — Texture firm, but soft, elastic to somewhat compressible. Surface smooth, opaque, somewhat irregularly lobate to verrucose. These surface features never of a high profile and prominent but usually of low profile and gently undulating.

ECTOSOME. — Made up of parallel tylotes to subtylotes very closely and tightly packed making the ectosome exceedingly firm. The thickness of this layer ranges from 182 to 200 μm. The strength of the ectosome almost always leads to the tearing of cross-sections.

CHOANOSOME. — Difficult to assess since the firm ectosome tends to drastically disrupt the choanosome in any cross-sections. Furthermore, presence of dirt, algae and other extraneous material (less noticeable in the smaller paratype) makes sectioning difficult. What is apparent in the choanosome is a very loose reticulation of acanthostyles of two size classes which often changes to a disorganized dispersal of the same. In many cases the choanosome becomes very thick, heavy and difficult to characterize. In the few relatively open spaces that do exist there is a plethora of microscleres of all kinds, with sigmas dominating in both numbers and size. Superimposed on the reticulation or disorganized dispersal of acanthostyles within the choanosome one can often find thick tracts varying from 46 to 72 μm, consisting mostly of acanthostyles of both size classes and, sometimes, tylostyles to styles. The smaller acanthostyles tend to be either echinating these tracts or involved in the formation of the reticulation. These tracts appear thickest near the ectosome and dominate the subectosomal area.

The paratype is relatively free of extraneous material. The holotype is completely invaded by dirt, algae and other material, making the overall structure difficult to determine. On occasion, areas of some cross-sections show a basal layer of spongin in which acanthostyles seem to have their heads imbedded but this is not at all clear.

MEGASCLERES. — Acanthostyles of two size classes. **Small**: 68–77–84–101 μm. × 2.4–3.9–5.8–7.3 μm (Fig. 1h). Spicule straight. Head tends to be flattened and covered with many spines. Many spines also on the upper third of the shaft. However, some spines occur almost to the tip. Spines large and robust. With the exception of those spines on the head, almost all are slightly recurved toward the head end. Tip spineless, sharply angled and pointed. **Large**: 181–220–236–265 μm. × 2.4–4.4–7.0–9.7 μm (Fig 1i). Spicules straight or with upper third slightly curved. Heads often flattened. Most spines are on the head and upper fifth of the spicule, a few occurring to near the tip. Spines mostly small, erect and sharply pointed. Those on the head tend to be crowded and may be blunt or irregular in shape. Tip free of spines, long and gently angled to a sharp point. Tylotes to subtylotes of a single size class. 195–227–233–258 μm. × 3.6–5.0–5.6–6.0 μm (Fig. 1g). Spicules straight, heads usually smoothly rounded but sometimes somewhat elongated. Frequently the shaft is gently tapered to one end, giving rise to a spicule with unequal ends, one smaller than the other. Sometimes one end is stylote while the other is subtylote.

MICROSCLERES. — Arcuate isochelae of two distinct size classes. **Small**: 22–26–29–36 μm (Fig.1e). Shaft thick and strongly curved. Alae small with edges gently rounded. The lateral alae attached to the shaft most of their length. **Large**: 46–51–58–68 μm (Fig. 1f). Shaft thick and strongly curved. Alae somewhat elongate with edges either nearly square (lateral alae) or somewhat pointed (frontal alae). Lateral alae clearly detached from the shaft for at least half their length.

Sigmas of two distinct size classes. Both occur in S and C configurations. **Small**: 26–38–47 μm (Fig. 1d). More or less even to slightly asymmetric curvature forming a medium arch. Tips thin,

sharply pointed and angled inwards. One end often twisted out of the plane of the other. **Large**: 53–68–72–78 μm (Fig. 1c). More or less even to slightly asymmetric. Much shallower arch. Tips thin, sharply pointed and angled inwards.

Forceps of two distinct size classes. **Small**: 7–10–11–13 μm (Fig. 1b). Legs not parallel but angled to about 30° from the median between the two equally long legs. Covered with spines with those at the tip of the legs largest and strongly recurved. Spines on the inner edges of the legs more strongly recurved than those on the outer edges. **Large**: 21–24–29 μm (Fig. 1a). Legs not parallel, slightly angled to about 10° from the median between the two equally long legs. Covered with numerous small, angled, erect spines, looking like the teeth of a saw. Those on the inner edge of the legs tend to be larger than those on the outer edges. The tips of the legs have caps delineated by a ring of small spines.

ETYMOLOGY. — The species is named *acanthostylosa* to recognize that it is the first *Forcepia* from California with acanthostyles.

REMARKS. — This species is the only *Forcepia* species with acanthostyles reported from the west coast of North America from Baja California to Canada. Only one *Forcepia* species has been noted from this region (Austin and Ott 1987). These authors describe a species similar to *Forcepia* (*Forcepia*) *japonica* Koltun, 1959, which has styles, but not acanthostyles. However the Canadian species was noted as having styles to acanthostyles with few spines. This species has only single size classes of all microsclere types and differs in almost all other respects.

Van Soest (pers. commun.) proposes two subgenera for this genus: *Leptolabis* for species with a hymedesmoid kind of structure, with the acanthostyles embedded in a basal layer of spongin, and *Forcepia* for those in which the styles or acanthostyles are structural megascleres making up the choanosomal reticulation. This new species appears to have most of its megascleres involved as structural elements in a reticulation. It has a thick choanosome showing a reticulate pattern and the observations of acanthostyles possibly embedded in a basal layer of spongin are too inconclusive to allow transfer to the subgenus *Leptolabis*.

***Forcepia* (*Forcepia*) *elvini* sp. nov.**
Figs. 3 and 4

MATERIAL. — **Holotype**: CASIZ 108399, U.S.A., California, Marin Co., Cordell Bank, approximately 20 miles due west of Pt. Reyes. Depth 82.3 m, Collectors: Swift, Smith, Hanna, September 1940.

DISTRIBUTION. — To date only known from the type locality, Central California, Marin Co., Cordell Bank.

HABITAT. — Habitat information was not included in the collection data.

SHAPE. — Sponge, thick, encrusting, irregular but somewhat rounded; 3.7 cm at the widest point, 3.5 cm at the narrowest point; 1.5 to 2.5 cm high.

COLOR. — Color in life not recorded; cream white in ethanol.

OSCULA. — Difficult to interpret. Openings, 1–3 mm in diameter, round to nearly so with irregular distribution, abundant at, and flush with the surface. These appear to penetrate well into the interior of the sponge where smaller, round openings may be seen.

TEXTURE AND SURFACE CHARACTERISTICS. — Texture firm, slightly compressible. Surface superficially smooth, some areas with irregularly shaped lobes and others which appear layered with thin, flat plates. The edges of the lobes and plates are distinctly hispid; the general surface is likewise hispid, but to a lesser degree.

ECTOSOME. — (Fig. 4a). The ectosome consists of a very thin layer of tightly packed subtylotes from 24 to 36 μm thick; occasionally to 48 μm thick. Superimposed over the subtylotes is a layer approximately 24 μm thick, packed with microscleres of which isochelae of both size classes appear to dominate. The presence of the layer of isochelae and the smaller size of the subtylote as compared to

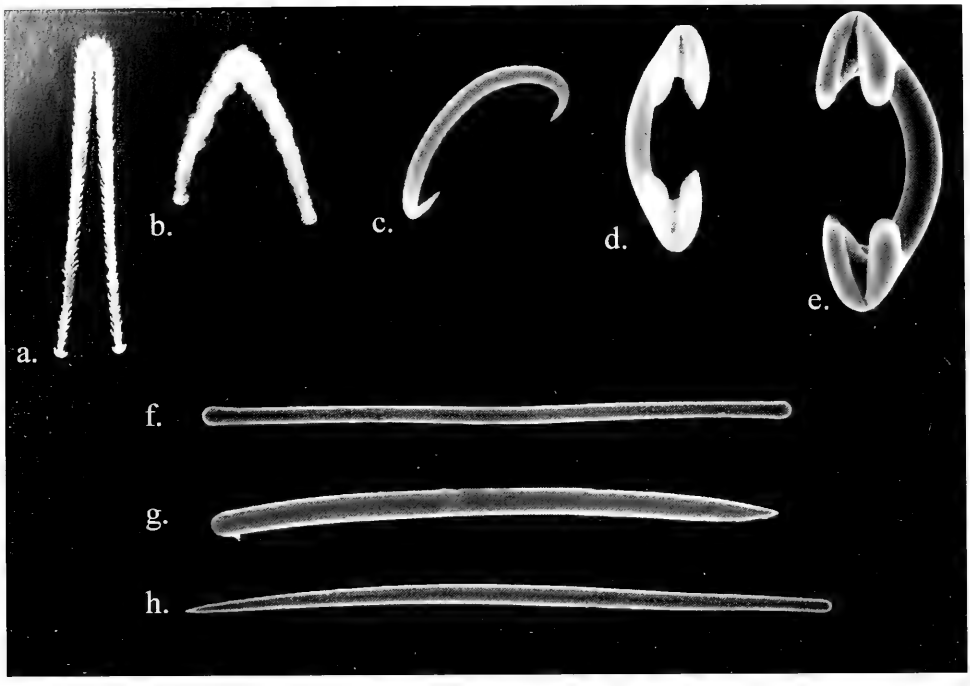
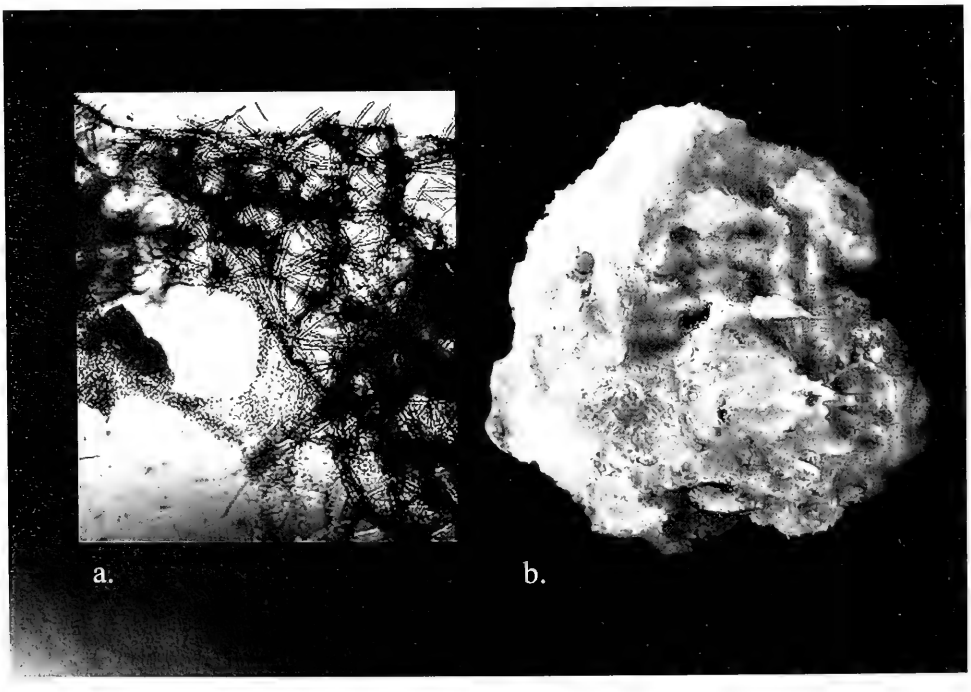


FIGURE 3. Scanning electron micrographs of the spicules of *Forcepia* (*Forcepia*) *elvini* sp.nov. Holotype (CASIZ 108399) a. Large forceps 2,000×, b. Small forceps 2,000×, c. Sigma 1500×, d. Small isochela 4,000×, e. Large isochela 2,000×, f. Substylote 500×, g. Style with spine 300×, h. Style 300×.



Forcepia (*Forcepia*) *elvini* sp. nov. a. Cross-section 40×. b. Holotype (CASIZ 108399), dimensions 3.5 × 3.7 cm × [illegible]

the styles in the choanosome make it difficult to see the subtylotes, such that one may initially assume that the ectosome is made up of microscleres only. The tips of the thick tracts of styles in the choanosome frequently push through the ectosome and form brushes on the surface.

CHOANOSOME. — (Fig. 4a). The choanosome is formed of a robust reticulation of styles. The reticulation is dominated by thick tracts, normally ranging from 121 to 133 μm but sometimes as thick as 182 μm. Superimposed over these tracts and connecting them is a reticulation of smaller tracts, 61 to 91 μm thick. The nodes of this reticulation are particularly thick and noticeable.

MEGASCLERES. — Styles of a single size class. 257–338–393 μm × 15–16–18 μm (Fig. 3g, h). Spicules almost always smooth, a few with a very small spine; almost always gently curved near the center. Shaft thick, slightly thicker near the center. Heads gently rounded, a few may approach a subtylostyle configuration. Point somewhat sharp.

Subtylotes of a single size class (Fig. 3f). 222–251–335 μm × 6–7–10 μm. Spicule smooth, straight to slightly undulate; shaft moderately thick, often slightly wider at one end. Heads very slightly inflated and smoothly rounded.

MICROSCLERES. — Arcuate isochelae of two size classes. **Small**: 16–19–21 μm (Fig. 3d). Shaft thin with well rounded, gentle arch. Alae somewhat smoothly pointed and well separated. Lateral alae directed rather sharply back towards the shaft; two thirds of their length is attached to the shaft. **Large**: 26–44–49 μm (Fig 3e). Shaft thick and strongly arched. Central ala somewhat narrowed with rounded but even more narrowed tip. Lateral alae wider and well rounded but short relative to length of shaft. One half of their length is attached to the shaft.

Sigmas of one size class (Fig. 3c). 39–49–56 μm. Arch shallow, mostly eccentric with one end rounded, the other not. Tips sharp; the tip of the rounded end slightly bent inward, the tip on the opposite end sharply bent inward.

Forceps of two size classes. **Small**: 11–15–28 μm (Fig. 3b). Legs often unequal in length, noticeably thickest where they join; not parallel but angled to about 30° from the median between the two legs. Surface not spined but gently undulate. Small caps at the ends of the legs are but slightly inflated bulbs. **Large**: 36–49–55 μm (Fig. 3a). Legs equal to subequal, very thin except for where they join; nearly parallel, angled to about 10° to 12° from the median between the two legs. Both interior and exterior surfaces covered with spines, these pointed away from the tip of the foot. Spines sharpest and most numerous near tip of feet. Distinct saucer shaped caps present.

ETYMOLOGY. — This species is named after Dr. David Elvin, a sponge biologist, computer specialist, and a long time friend and colleague.

REMARKS. — This species appears to be unique, especially in regard to its two size classes of forceps. The larger appears very similar to those frequently seen in other species, showing numerous teeth on the legs on both exterior and interior surfaces. The smaller size class is quite different in that it has an undulating surface with no apparent spines at all. Noteworthy also, is the presence of tiny spines on some of the styles making up the distinct choanosomal reticulation.

***Forcepia* (*Forcepia*) *macrostylosa* sp. nov.**
Figs. 5 and 6

MATERIAL. — **Holotype**: CASIZ 146074, U.S.A., California MET Sta. 105. Catalina Basin, 33°10′N, 118°36′W, 1271–1280 m, 25′ otter trawl. January 29, 1981, 2400–0230. R/V *New Horizon*. Coll. K. Smith, S. Luke.

DISTRIBUTION. — This species is presently known only from its type locality, Southern California, Catalina Basin, California.

HABITAT. — Habitat information was not included in the collection data.

SHAPE. — Thick, massive, somewhat domed-bulbous, 5.0 by 3.5 cm and height to 23 mm.

COLOR. — Color in life unknown; light tan in ethanol.

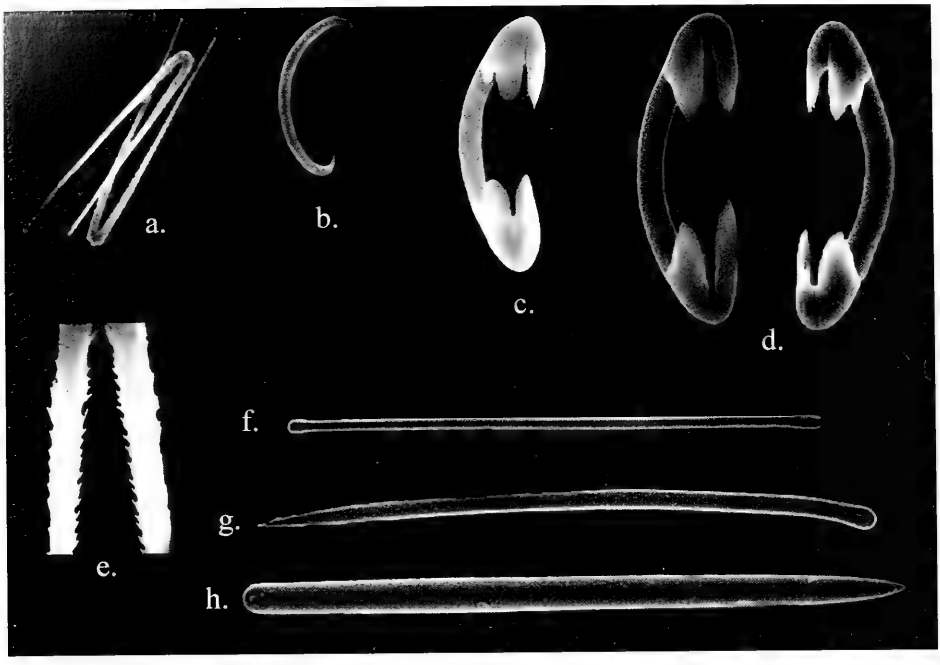


FIGURE 5. Scanning electron micrographs of the spicules of *Forcepia* (*Forcepia*) *macrostylosa* sp. nov. Holotype (CASIZ 146074) a. Forceps 1500×, b. Sigma 1500×, c. Small arcuate isochela 4000×, d. Large arcuate isochelae 2500×, e. Legs of forcep 5000×, f. Substylote 300×, g. Subtylostyle 300×, h. Style 300×.

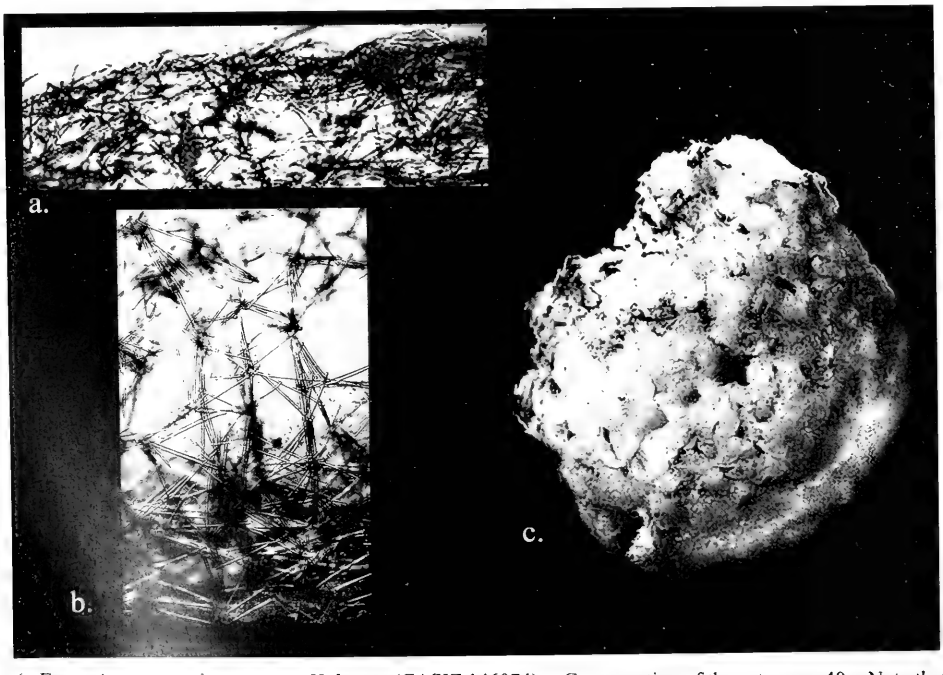


FIGURE 6. *Forcepia macrostylosa* sp. nov. Holotype (CASIZ 146074) a. Cross-section of the ectosome 40×. Note that the bundles of subtylotes are worn away except at the extreme right of the photograph. b. Cross-section of the choanosome, 80×. Note the ladderlike skeleton. c. Holotype, dimensions 5.0 × 3.5 cm, 23 mm high.

OSCULA. — Difficult to discern. May be situated below the surface where the platelike surface creates openings ranging from 3.0 to 12.5 mm or greater.

TEXTURE AND SURFACE CHARACTERISTICS. — Superficially smooth; some areas totally smooth, others layered with overlapping thin, flat plates. Consistency spongy, compressible.

ECTOSOME. — (Fig. 6a) Formed of a thin layer of packed subtylotes which is easily removable. The thickness is usually 48 to 60 μm, but sometimes reaches 72 μm. In places the ectosomal layer of subtylotes is worn away.

CHOANOSOME. — (Fig. 6b) The choanosome consists of a ladderlike reticulate skeleton with tracts of subtylostyles about 91 μm. thick. These tracts support a loose reticulation of thinner bundles ranging up to 24 μm thick of from 2 to 5 or more subtylostyles. The thick tracts and ladderlike reticulation becomes less obvious as the ectosome is approached. Near the surface, tracts may become bent almost parallel to the surface and the reticulation gets more confused, complicated and random.

MEGASCLERES. — Subtylostyles to styles of a single size class (Fig 5g, h). 268–499–593 μm × 18–20–22 μm. Smooth, most curved close to the head end. Shaft thick, of more or less even width except slightly wider just below the head. Tip hastate to tornote-like, often with a slight expansion of the shaft before narrowing to the tip.

Subtylotes of a single size class. 309–372–540 μm × 6–8–9 μm (Fig. 5f). Shaft thin, either straight or somewhat sinuous with heads abruptly and slightly expanded. Heads often unequal in size, the smaller set off by a slight constriction of the shaft.

MICROSCLERES. — Arcuate isochelae of two size classes. **Small**: 19–23–29 μm (Fig. 5c). Shaft with slight or moderate curvature. Alae only somewhat separated. Central ala is the longest; often angled or pointed. Lateral alae smaller, rounded and most often with an obvious, very small, rounded incipient ala next to the shaft. **Large**: 36–44–50 μm (Fig. 5d). Sharply arched. Alae well separated, thin and pointed, often sharply. Sometimes the central or lateral alae are bifurcated.

Sigmas of a single size class. 45–60–66 μm (Fig. 5b). Arch shallow, may be even or eccentric. Shaft moderately thick. Points very sharp with one bent out of the plane of the shaft.

Forceps of a wide range of sizes or more probably of a single size class, but may appear as multiple size classes. 9–50–87 μm (Fig. 5a, e). Shape highly variable, from V-shaped with legs nearly parallel to legs almost toxa-like. The most common form is long, slender, with legs nearly parallel. Spines small but obvious on inner edge, all pointing upwards. Outer edge with few, somewhat blunt spines with the exception of those on the upper edge where the legs join. Here the spines are erect, obvious and sharp.

ETYMOLOGY. — This species was named *macrostylosa* in recognition of the large size of its styles.

REMARKS. — This species is distinguished by the large size of its styles and tylotes and the extreme size range of its forceps. In some respects it resembles *Forcepia* (*Forcepia*) *topsenti* Lundbeck, 1905, which has large styles and tylotes and forceps of a similar range of shapes. However, in all other respects it differs. In *F. topsenti*, isochelae are of one size class, sigmas are significantly larger and surface features are quite different from those detailed for the new species.

***Forcepia* (*Forcepia*) *hartmani* sp. nov.**
Figs. 7 and 8

MATERIAL. — **Holotype**: CASIZ 53463, U.S.A., California, Monterey County, Pescadero Point, 17 Mile Drive, April 28, 1982. Three pieces. Depth, intertidal. Coll. W. Lee. **Paratypes**: CASIZ 53465, U.S.A., California, Monterey County, Point Lobos, March 1984. Coll. D. Chivers and W. Lee; CASIZ 35911, U.S.A., California, Sonoma County, Bodega Bay, Bodega Marine Labs, August 9, 1983. Two pieces. Depth 0.5 m, rocky intertidal; CASIZ 017311, U.S.A., California, Farallon Islands, Southeast Farallon Island, April 4, 1977. Coll. B. Bowman and C. Chaffee. Numerous pieces.

Depth intertidal, +0.4 m under overhang; CASIZ 35961, U.S.A., California, Sonoma County, Bodega Bay Marine Laboratory, August 9, 1983, open coast west of aquaculture building, Depth, intertidal, -0.5 m, rocky intertidal. Coll. S. Ward and A. Miller. **Other Material**: CASIZ 18, CASIZ 31, CASIZ 3662, CASIZ 4593, CASIZ 6923, CASIZ 20358, CASIZ 31282, CASIZ 35961, CASIZ 53411, CASIZ 53461, CASIZ 53464, CASIZ 59662, CASIZ 78254, CASIZ 108925, YPM 1540 and YPM 1697A.

DISTRIBUTION. — Present known range: Point Lobos, Monterey Co. to Bodega Bay Headlands and Farallon Islands, California. Type locality: Pescadero Point.

HABITAT. — Rocky intertidal, in deep pools or rocky overhangs from about + 0.4 m to encrusting rocks, -0.4–0.5 m.

SHAPE. — Thin to thick encrusting with a more or less flat surface. Incrustations up to 1.6 cm thick. Size of largest piece of holotype 4.8 cm long × 4.2 cm wide × 1.6 cm high. Incrustations may cover a much larger area.

COLOR. — In life, honey yellow, yellow gold, yellow, gold tan, buffy citron, buff; light tan in ethanol.

OSCULA. — Oscula numerous, 1.0 to 4.0 mm across, round or somewhat irregular with slightly raised membranous lips. In the thickest specimens the oscula tend to be within the surface grooves where their shape and the membranous lips may not be easily seen.

TEXTURE AND SURFACE CHARACTERISTICS. — Consistency slightly compressible, friable. Surface nodular and ridged, ridges somewhat hispid and delineating shallow grooves. In larger specimens the grooves are deeper.

ECTOSOME. — (Fig. 8a) Exceedingly dense, crustlike. Made up of tightly bound masses of tylotes to subtylotes parallel to the surface. Generally 85 to 91 μm in thickness but may reach over 200 μm in some places due to additional, looser, accumulation of tylotes underneath.

CHOANOSOME. — (Fig. 8a) A reticulation of wide tracts of styles with an overlying, looser, less structured reticulation of random styles and tylotes. The tracts range in size from small, 24 to 28 μm to large, 60 to 72 μm. Within the choanosome are large strands of tissue with massive numbers of microscleres, most notably sigmas.

MEGASCLERES. — Styles to subtylostyles of a single size class. 169–<u>202–221</u>–281 μm × 7–<u>8–9</u>–10 μm (Fig. 7e). These vary from straight to strongly curved, the curvature occurring on the upper 1/2 to 1/3 of the spicule. Most are simple styles but some may have tiny spines on either head or tip. Even when some spines occur, the spicules look more like a normal style than an acanthostyle. The shaft is equally wide throughout most of its length. The head is evenly and well rounded but may appear slightly swollen. The tip end often has a small indentation which temporarily reduces the shaft width just prior to a long, sharp, tornote-like tip. The appearance is as though the shaft was pinched inward before the tip, leaving a slight indentation.

Tylotes to subtylotes of a single size class. 137–<u>166–185</u>–205 μm × 4–<u>5</u>–6 μm (Fig. 7d). Mostly straight to very slightly bent. Shaft of even width or slightly wider centrally. The heads are distinctly tylote or strongly subtylote. There is a tendency for the swollen heads to be elongated, with nearly parallel sides. This is especially noticeable on the smallest spicules. Spicules with ends often unequal in size.

MICROSCLERES. — Arcuate isochelae of a single size class. 18–<u>23–34</u>–38 μm (Fig. 7b). Thick shaft with moderate curvature. Alae tend to be short, well separated, with rounded tips which may be slightly flared. Lateral alae fused to shaft 3/4 of their length.

Sigmas of a single size class. 30–<u>42–48</u>–55 μm (Fig. 7c). Sigmas with low arch and tending to be elongate with a relatively thick shaft. One end has a wider curvature than the other end and with a somewhat curved, sharp point. The opposite end is narrower and more compact, with a very sharp and sharply bent spine, usually bent out of the plane of the shaft.

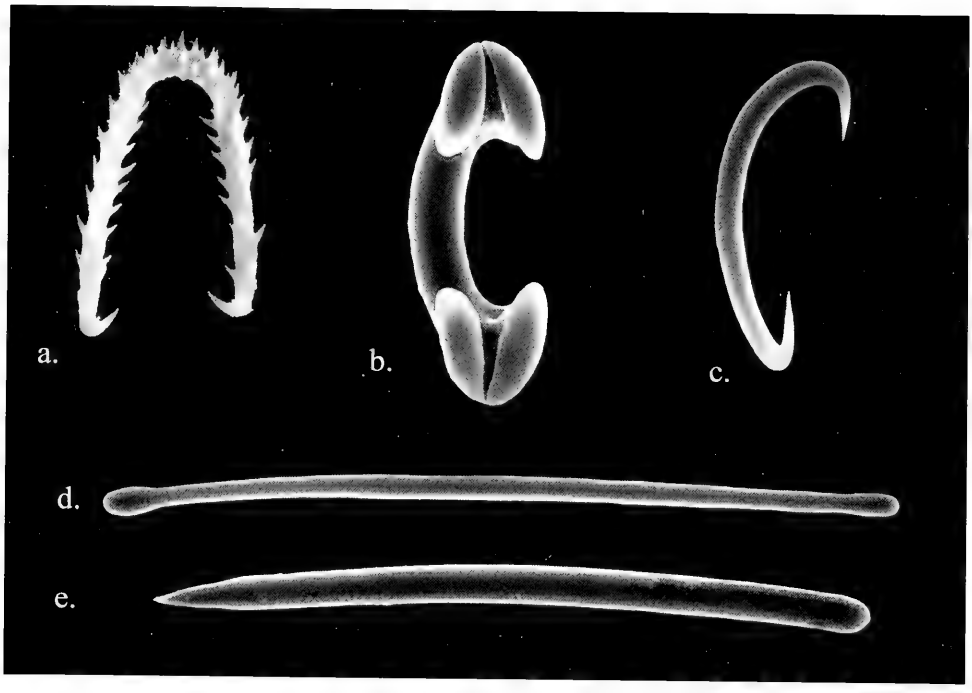


FIGURE 7. Scanning electron micrographs of the spicules of *Forcepia* (*Forcepia*) *hartmani* sp. nov. a. Forceps 10,000×, b. Isochela 3,000×, c. Sigma 2,000×, d. Tylote to substylote 700×, note the difference in the two ends, e. Style 500×.

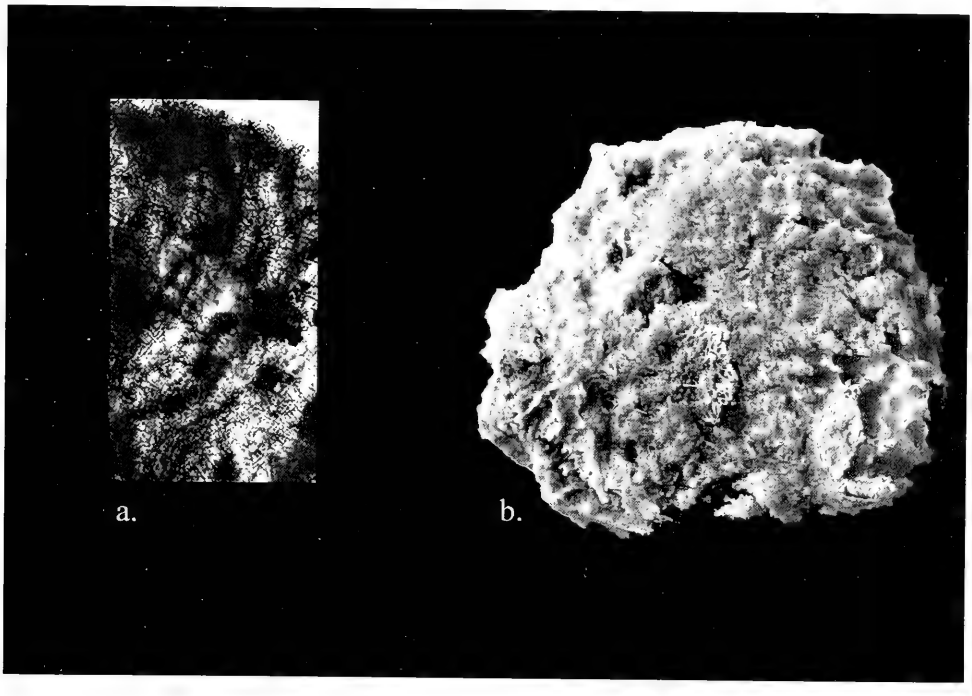


FIGURE 8. *Forcepia* (*Forcepia*) *hartmani* sp. nov. a. Cross-section 40×, b. Holotype (CASIZ 053463), dimensions 4.8 × 4.2 cm wide and 1.6 cm high.

Forceps of a single size class. 5–8–9–11 μm (Fig. 7a). These are generally horseshoe-shaped with a narrow to moderate range in the angle of the two legs from the median between them. The legs are heavily spined, the spines all curved upward and well spaced. There are three rows of spines seen on each side; one facing inwards, one along the middle of the leg and one on the outer edge. The tips of the legs are widened and set off by three large spines.

ETYMOLOGY. — This species is named after the sponge systematist and biologist, Doctor Willard Hartman. Hartman introduced me to the marvelous world of sponges and has been a colleague in producing the sponge chapter in the latest edition of the Light's Manual (Lee, Hartman, and Diaz, in prep.). Doctor Hartman has done much for our understanding of the systematics and biology of the Porifera. He has likewise become a valued friend.

REMARKS. — This species originally appeared in material reviewed in Hartman's 1975 description of *Lissodendoryx firma* where he described the occasional occurrence of forceps in this species. This is a very understandable error, likewise initially made by this author, since the spicule complement of these two species is so similar. In fact, it was only by separating out all supposed *L. firma* with forceps and comparing this group with those that had no forceps, that it became obvious that the forceps-bearing specimens were clearly different from *L. firma*. While the spicule complement (other than forceps) is superficially similar between the two species, the details of their structure differ significantly. Most important are the obvious but subtle differences in skeletal structure, especially in the nature of the ectosome and the details of the choanosomal tracts.

The ectosome of *Forcepia* (*Forcepia*) *hartmani* is exceedingly thick and tightly bound with tylotes to subtylotes parallel to the surface but with few, if any, spicules penetrating the surface. In *Lissodendoryx*, this area is made up of palisades of subtylotes that may be perpendicular, parallel or at an angle to the surface. Spicule penetration of the surface and the formation of brushes is common.

The choanosome of *Forcepia* (*Forcepia*) *hartmani* is made up of obvious, bold, thick tracts that form a reticulation over which can be found a looser, more random reticulation with many random spicules. In *Lissodendoryx firma* there are distinct to vague tracts just under the ectosome. These are far less dominant than those in *Forcepia*. Also, in *Forcepia* the choanosome is made up of a distinct reticulation of thin tracts. The deeper one looks, the more random the reticulation appears.

While these differences are consistent, they nevertheless are subtle. However, even more subtle is the occurrence of forceps. These microscleres are tiny in *Forcepia* (*Forcepia*) *hartmani* and are exceedingly difficult to find unless one is well aware that they may be present. Thus, the similarities between the two species can lead to a hurried, and incorrect, identification.

***Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930) n. comb.**
Figs. 9, 10, and 11

Wilsa hymena de Laubenfels, 1930 (Fig. 10)

MATERIAL. — **Holotype**: U.S.N.M. 21515, California, Monterey Co. Monterey Bay, May 9, 1929, Depth 700 m, Coll. E. F. Ricketts; **Paratype**: B.M. 29.8.22.62, California, Monterey Co., Monterey Bay, May 9, 1929, Depth 700 m, Coll. E. F. Ricketts. **Reference specimen**: BIC-SIO P-1366, BIC-SIO P-1367, CASIZ 146075, R-12. San Diego Trough, California. 32°34.5′N, 117°33′W, 1170–1216 m, 25′ otter trawl. Mud. October 29, 1970, 1900–2147. R/V *Agassiz*. Coll. F. Rokop, S. Luke.

DISTRIBUTION. — San Diego Trough to Monterey Bay, California.

HABITAT. — Possibly mud, 700–1216 m.

SHAPE. — Globular, massive; BIC-SIO P-1366, 5.3 × 2.0 × 3.5 cm. high. BIC-SIO P-1367, 2.1 × 1.3 × 0.8 cm. high, 1.7 × 1.5 × 0.6 high, and 3.0 × 2.0 × 1.4 cm high.

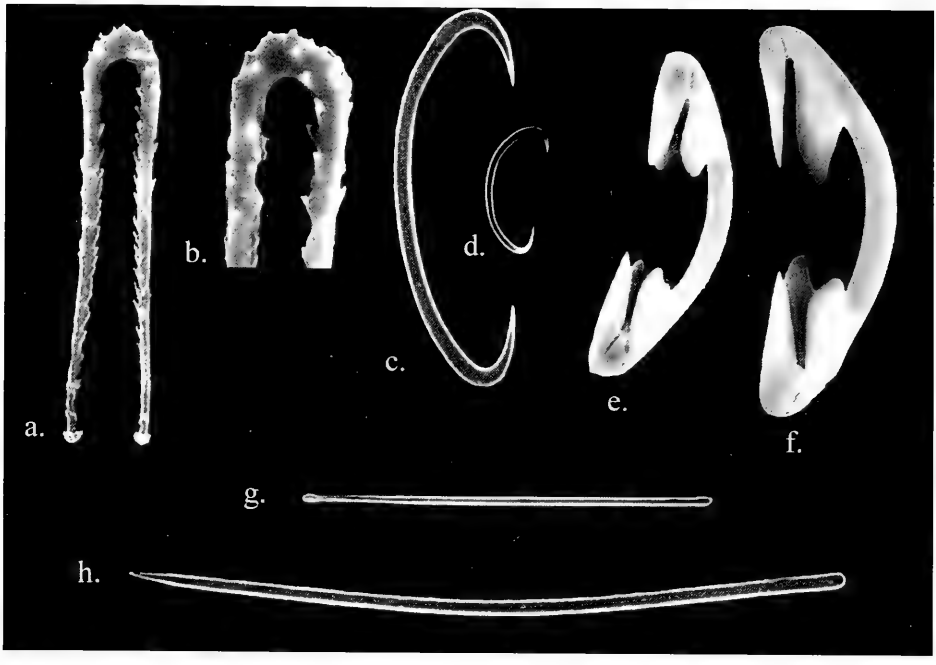


FIGURE 9. Scanning electron micrographs of the spicules of *Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930). a. Forcep 5,000×, b. Forceps upper end showing fewer and smaller spines, c. Large sigma 500×, d. Small sigma 500×, e. Isochela 3,000×, f. Isochela 4,000×, g. Substylote 400×, h. Style 200×.

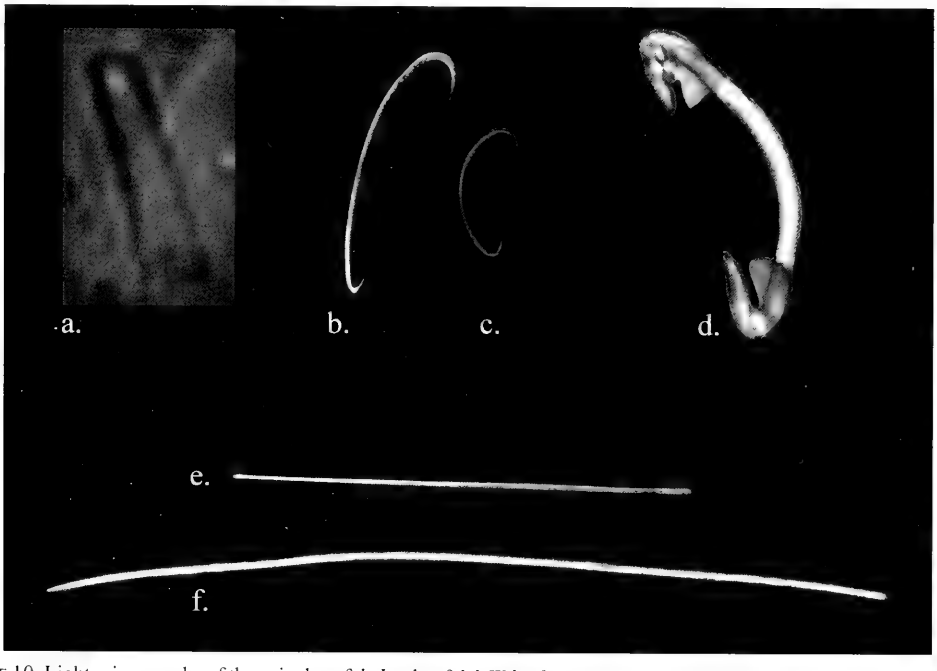


FIGURE 10. Light micrographs of the spicules of de Laubenfels' *Wilsa hymena*, 1930 (Holotype USNM 21515). a. Forceps 600×, b. Large sigma 500×, c. Small sigma 500×, d. Isochela 600×, e. Substylote 400×, h. Style 200×. Note: The quality of these images was largely influenced by the poor condition of de Laubenfels' slides.

FIGURE 11. *Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930). Reference specimen CASIZ 146075, dimensions 5.3 × 2.0 cm wide × 3.5 cm high.

COLOR. — In life, not recorded for reference specimen; holotype recorded as "pale drab." Dark tan to brown in ethanol.

OSCULA. — Numerous, round to somewhat elongate or irregular, 1.5 to 4.0 mm across. Flush with surface or somewhat recessed, no lip or rim.

TEXTURE AND SURFACE CHARACTERISTICS. — Soft, compressible, spongy. Surface with some areas superficially smooth but mostly slightly roughened, verrucose. Surface with shallow grooves delineated by smooth ridges and small rounded conules.

ECTOSOME. — The ectosome is delineated by a dermal membrane, 48 to 72 μm thick which contains microscleres in abundance, especially the macro-sigmas. Below is a compact bundle of subtylotes reaching up to 96 μm in thickness. The subtylotes are tightly bound together and parallel to the surface.

CHOANOSOME. — The choanosome is dominated by a rugged reticulation of styles between tracts of styles. The larger tracts range from about 45 to 95 μm thick. Smaller tracts of more loosely bound styles may also be found, these ranging from 19 to 24 μm. The entire choanosome appears as a very rugged, almost random reticulation with more or less parallel tracts running through it. The choanosome is also packed with sand grains and detritus. The combination of a soft, compressible texture with the presence of sand grains and detritus made it impossible to obtain good cross-sections. Accordingly, the structure detail had to be pieced together from observations of numerous slides of varying quality.

MEGASCLERES. — Styles of a single size class. 533–<u>601</u>–697 × 13–<u>14</u>–16 μm (Figs. 9h, 10f). Smooth, width even throughout. Most somewhat curved near middle. Tip tornote-like with sharp point.

Subtylotes of a single size class. 273–<u>327</u>–448 × 5.5–<u>6.9</u>–7.0 μm (Figs. 9g, 10e). Straight, smooth, slightly wider near center. Ends mostly subtylote, or tylote with head somewhat elongate. Frequently ends unequal, one subtylote, the other tylote, and of different sizes.

MICROSCLERES. — Arcuate isochelae of a single size class. 24–<u>38</u>–48 μm (Figs. 9e, f; 10d). Strong arch with alae long and well separated. Frontal ala long, narrow and sharply pointed, often divided into two or three small or independent alae. Lateral alae longer, attached to shaft by 1/2 to 3/4 of

their length and curved toward the shaft with a narrowed but rounded tip. Lateral alae tend to have hints of additional divisions, but these are never complete but seen only at the outer edge. Frequently, one end differs from the other relative to such divisions.

Sigmas of two size classes. **Small**: 60–77–99 μm (Figs. 9d, 10c). Somewhat elongate, with relatively deep and eccentric arch. Both ends with tips moderately bent inwards in the same plane as the shaft. **Large**: 169–208–243 μm (Figs. 9c, 10b). Elongate with moderate arch. Arch not eccentric but with one end with a rounder curvature than the other and a sharp point which is only moderately bent. The other end with a point more obviously bent. Both points in the same plane as the shaft.

Forceps of a single size class. 11–19–26 μm (Figs. 9a, b;10a). Legs long, parallel to about 2/3 the distance from the tips where they are very slightly angled outwards. Wide spines which point upwards, mostly on the inner side of the legs. Many fewer spines on the outer edge. The legs terminate in saucer-like caps. Spines on upper edge where the legs join, fewer and smaller than elsewhere.

REMARKS. — In 1930, de Laubenfels described a new genus and species, *Wilsa hymena*, from a single specimen found on the macerated skeleton of a hexactinellid sponge. The specimen had an intact ectosomal membrane containing abundant macro-sigmas. The choanosome was so enmeshed with the hexactinellid on which it was residing that its structure could not be determined, although some styles were found. Adjacent to the specimen and presumably contaminating it with its spicules, was a specimen of *Lissodendoryx kyma*. De Laubenfels described *Wilsa* as containing styles, palmate isochelae, macro-sigmas, sigmas of a smaller size class, and forceps. The forceps were described through light microscopy as appearing smooth with only the faintest traces of spination. In addition to these spicules, de Laubenfels noted the presence of some tornotes and arcuate isochelae.

In reviewing material from the Scripps Museum the author discovered in a mixed lot, several pieces of a sponge that were obviously in the genus *Forcepia*. On preliminary examination it was found that in many respects this material matched de Laubenfels' *Wilsa hymena*. While it was possible to get reasonable cross-sections and scanning electron micrographs from the Scripps specimen, this was not the case for the holotype of *Wilsa hymena*. The only material available were two de Laubenfels microscope slides, one of which had little material on it. Fifty measurements were taken of each spicule type for both the *Wilsa* type (U.S.N.M. 21515) and the Scripps material. The spicules from these are compared in Table 1. Note that the de Laubenfels measurements are designated by an asterisk. Spicule widths for the de Laubenfels type are not given.

The palmate isochelae noted by de Laubenfels may well have been a contaminant. However, most all of the isochelae seen on the de Laubenfels slide appeared to be arcuate. The arcuate isochelae were thought to be a contaminant from *Lissodendoryx kyma* which de Laubenfels noted was living adjacent to his specimen. Interestingly, the isochelae of *L. kyma* and those measured from the Scripps specimens totally overlap in size range. Close comparison of the morphologies of the spicules that are shared between the de Laubenfels type and the Scripps specimens show them to be very close or identical.

De Laubenfels erected the genus *Wilsa* for this single species, noting that it was most similar to *Esperiopsis forcipula*, Lundbeck, 1905. *Esperiopsis forcipula* was later transferred to *Leptolabis* (Topsent, 1904). In recent work for the *Systema Porifera*, Van Soest (pers. commun.) designated this species as *Forcepia* (*Forcepia*) *forcipula* (Lundbeck, 1905). There is indeed a close resemblance between the two species, but it is clear that they are not the same. Among some of the differences, the macro-sigmas of *Forcepia* (*Forcepia*) *hymena* are much larger and it has only a single size class of isochelae, not two.

Given our present understanding of this group of sponges and the fact that the genus *Wilsa* was erected for a single, incomplete and contaminated specimen, *Wilsa* is hereby synonymized with *Forcepia* and de Laubenfels' holotype should be referred to *Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930). Since de Laubenfels' holotype is both incomplete and contaminated, the reference specimen may act as a subsidiary source of information on this species.

DISCUSSION

Five species of *Forcepia* are now known to occur in California. Four of these are newly described herein; the fifth represents the assignment of *Wilsa hymena* de Laubenfels, 1930 to *Forcepia* and a redescription based on newly found material. The family Coelosphaeridae Hentschel, 1923, to which these species belong, may be generally distinguished by having an ectosomal tangential crust of smooth diactinal (usually tylote) spicules, a reduced choanosomal skeleton composed of a reticulation of smooth or acanthose styles, with or without tracts and having sigmas, arcuate isochelae, and no toxas. The genus *Forcepia* is the only forceps-bearing genus in the family. In addition, the ectosomal spicules are always tylote or subtylote, the choanosomal spicules may be styles and may have ectosomal spicules (tylotes or subtylotes) involved as well. In encrusting forms, one may sometimes find a hymedesmoid structure replacing the reticulation, or elements of both. Van Soest (pers. commun.) has used choanosomal skeletal structure to erect two subgenera. Species with a hymedesmoid arrangement and acanthostyles with their heads embedded in a basal spongin layer are placed in the subgenus *Leptolabis*. Those with styles or acanthostyles which are involved in a choanaosomal reticulation are placed in the subgenus *Forcepia*.

In the genus *Asbestopluma* (family Cladorhizidae) some species also contain forceps but these are structurally different than, and considered non-homologous with, the forceps of *Forcepia*. In addition, *Asbestopluma* differs from *Forcepia* in other significant ways. *Asbestopluma* tends to be abyssal, with erect stalked growth forms and basal root adaptations. The upper part is penniform or with side branches; the skeleton with a spicule axis divided into parallel fibers. Megascleres are styles or subtylostyles in the axial and extra-axial skeleton and minutely spined tylostyles to tylostrongyles in the coat of the stalk. Microscleres may be large, asymmetric palmate isochelae, sigmas, and forceps.

The California species of *Forcepia* are quite distinctive and can be readily separated.

KEY TO THE SPECIES OF *FORCEPIA* FROM CALIFORNIA

1a. Monacts are acanthostyles . . . . . *Forcepia* (*Forcepia*) *acanthostylosa* sp. nov.
1b. Monacts are styles, subtylostyles or tylostyles 2

2a. Isochelae of 2 distinct size classes 3
2b. Isochelae of 1 distinct size class 4

3a. Tylotes small to moderate, 222–335 μm. Forceps of 2 distinct size classes, 11–28 μm, 36–55 μm . . . . . *Forcepia* (*Forcepia*) *elvini* sp. nov.
3b. Tylotes large, 309–540 μm. Forceps either of many size classes or of wide range, 9–87 μm . . . . . *Forcepia* (*Forcepia*) *macrotylota* sp. nov.

4a. Styles small, 169–281 μm. Sigmas 1 size class . . . . . *Forcepia* (*Forcepia*) *hartmani* sp. nov.
4b. Styles large 533–697 μm. Sigmas of 2 size classes, the larger being of exceptional size 169–243 μm . . . . . *Forcepia* (*Forcepia*) *hymena* (de Laubenfels, 1930)

Of the species discussed, most need no further explanation as they clearly possess the usual characteristics of *Forcepia* and have no circumstances surrounding them that would complicate their taxonomic placement. However two species, *Forcepia* (*Forcepia*) *hartmani* and *Forcepia* (*Forcepia*) *hymena* do merit further discussion.

As noted earlier, *F.* (*Forcepia*) *hartmani* was originally described as a forceps-bearing variant of *Lissodendoryx firma*. Once forceps-bearing specimens were separated from those without, it was clear that the two could be readily separated in other ways as well. Both genera are in the family Coelosphaeridae and are closely related. In addition, their spicule complements other than forceps are amazingly similar. In a like manner, while their skeletal structures are distinct, they are close enough in detail to be confused if not examined carefully. To complicate these problems, the forceps in *F.* (*Forcepia*) *hartmani* are extremely small and not easily seen unless specifically sought for, or sub-

TABLE 1. Comparison of the spicule complement of *Wilsa hymena* de Laubenfels, 1930 (holotype) with *Forcepia* (*Forcepia*) *hymena* (BIC-SIO 1366). All measurements in micrometers (μm); measurements by de Laubenfels (1930) with asterisk (*). Underlined = mean.

Morphological feature	*Wilsa hymena* (holotype)	*Forcepia* (*Forcepia*) *hymenia* (BIC-SIO 1366)
Smooth styles	(330–600 × 10–15)* 436–619–770	533–601–697 × 13–14–16
Subtylotes (not noted or interpreted as tornotes)	255–300–333	273–327–448 × 5.5–6.9–7.0
Palmate isochelae	17–20*	not seen
Arcuate isochelae in ectosome	19–26–39	24–38–48
Macro-sigmas	approx. 250* 205–220–239	169–208–243
Sigmas	55–75* 55–75–108	60–77–99
Forceps	10–12* faint spination 8–15–21	with shallow spines 11–19–25
Acanthostyles (not mentioned)	47–53–62	not seen
Small styles (the larger with microspined heads)	present	not seen
Dermal membrane	30–70*	48–72

jected to SEM analysis. Given these similarities, the geographic and depth distributions given for this new species are probably incomplete. Accordingly, it will be important that current museum specimens and newly collected material be carefully reviewed and the distribution data amended.

Forcepia (*Forcepia*) *hymena* is a prime example of the problems that can be generated by formally describing a new species on the basis of a tiny fragment, which is admittedly contaminated. The type of *Wilsa hymena* is sufficiently minuscule that further examination cannot take place without its destruction, leaving it virtually useless. Only two slides were available of this material, with but one being of any substantial use. It is always difficult to try to redescribe a species as poorly represented as this one. However, extensive comparisons appear to strongly match those of the original material. Noteworthy is the fact that *Wilsa hymena* as specifically described by de Laubenfels has never been recorded since.

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LITERATURE CITED

AUSTIN, W. C. AND B. OTT. 1987. Phylum Porifera. Pp. 6–29 *in* Marine invertebrates of the Pacific Northwest, R. N. Kozloff, and L. H. Price, eds. University of Washington Press, Seattle.

CARTER, H. J. 1874. Descriptions and figures of deep sea sponges and their spicules from the Atlantic Ocean, dredged up on board H.M.S. "Porcupine," chiefly in 1869; with figures and descriptions of some remarkable spicules from the Agulhos Shoal and Colon, Panama. Annals and Magazine of Natural History, ser. 4, 14:207–221, 245–257.

HADJU, E. AND J. VACELET. In press. Family Cladorhizidae de Laubenfels, 1936. *In* Systema Porifera. A Guide to the Supraspecific Classification of Sponges and Spongiomorphs (Porifera), J. N. A. Hooper and R. W. M. Van Soest, eds. Plenum, New York.

HARTMAN, W. D. 1975. Phylum Porifera. Pp. 32–54 *in* Light's Manual: Intertidal invertebrates of the Central California Coast, 3rd ed., R. I. Smith and J. T. Carlton, eds. University of California Press, Berkeley.

HENTSCHEL, E. 1923. Erste Unterabteilung der Metazoa. Parazoa. Einziger Stamm und einzige Klasse der ersten Unterabteilung: Porifera = Schwämme. Handbuch der Zoologie 1:307–417.

HOOPER, J. N. A AND R. W. M. VAN SOEST. In press. Systema Porifera. A Guide to the Supraspecific Classification of Sponges and Spongiomorphs (Porifera). Plenum, New York.

LAUBENFELS, M. W. DE. 1930. The Sponges of California. Stanford University Bulletin 5(98):24–29.

———. 1932. The marine and fresh water sponges of California. Proceedings of the United States National Museum 81:1–140.

LEE, W., D. ELVIN, AND H. REISWIG. In manuscript. The Sponges of California. n.p.

LEE, W., W. HARTMAN, AND C. DIAZ. In press. Phylum Porifera. *In* Light's Manual: Intertidal Invertebrates of the Central California Coast, 4th ed, J. T. Carlton, ed. University of California Press, Berkeley.

LEVINSEN, G. M. R.1886. Kara-Haverts Svampe (Porifera). Dijmpha-Togtets zool. bot. Udbytte 341–372, pl. xxix–xxx.

LUNDBECK, W. 1905. 2. Porifera (Part II). Desmacidonidae (Pars.). The Danish Ingolf Expedition, vol. 6, pp.1–219 (Bianco) Luno, Copenhagen.

SOEST, R. W. M. VAN. In press. Family Coelosphaeridae Hentschel, 1923. *In* Systema Porifera. A Guide to the Supraspecific Classification of Sponges and Spongiomorphs (Porifera), J. N. A. Hooper and R. W. M. Van Soest, eds. Plenum, New York.

TOPSENT, E. 1904. Spongiaires des Açores. Résultats des Campagnes Scientifiques accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco 25:1–280.

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The Green Lacewings (Neuroptera: Chrysopidae) of Brazilian Agro-ecosystems

By

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Universidade Estadual Paulista, Jaboticabal, São Paulo, Brazil

and

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Eighty-one species of Chrysopidae in six genera and two subgenera are described from Brazilian agricultural systems. Forty-one of these are new species. They are: *Nacarina aculeata* de Freitas and Penny (type locality: Birigui, São Paulo, Brazil); *N. gladius* de Freitas and Penny (type locality: Birigui, São Paulo, Brazil); *N. lavrasana* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *N. sagitta* de Freitas and Penny (type locality: Ibitinga, São Paulo, Brazil); *Ceraeochrysa dislepis* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *C. dolichosvela* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *C. squama* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *Chrysoperla raimundoi* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *Chrysopodes* (*Chrysopodes*) *adynatos* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *C.* (*C.*) *copia* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil);*C.* (*C.*) *crocinus* de Freitas and Penny (type locality: Birigui, São Paulo, Brazil); *C.* (*C.*) *delicata* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *C.* (*C.*) *elongata* de Freitas and Penny (type locality: Luis Antonio, São Paulo, Brazil); *C.* (*C.*) *nigropicta* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *C.* (*Neosuarius*) *karinae* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *Plesiochrysa alytos* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *Leucochrysa* (*Leucochrysa*) *bruneola* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *L.* (*L.*) *catarinae* de Freitas and Penny (type locality: Fraiburgo, Santa Catarina, Brazil); *L.* (*Nodita*) *affinis* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *L.* (*N.*) *barrei* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *L.* (*N.*) *confusa* de Freitas and Penny (type locality: Fraiburgo, Santa Catarina, Brazil); *L.* (*N.*) *cornuta* de Freitas and Penny (type locality: Guaira, São Paulo, Brazil); *L.* (*N.*) *forciformis* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *L.* (*N.*) *furcata* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *L.* (*N.*) *guataparensis* de Freitas and Penny (type locality: Luis Antonio, São Paulo, Brazil); *L.* (*N.*) *ictericus* de Freitas and Penny (type locality: Birigui, São Paulo, Brazil); *L.* (*N.*) *incognita* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); *L.* (*N.*) interata de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *L.* (*N.*) *lineata* de Freitas and Penny (type locality: Luis Antonio, São Paulo, Brazil); *L.* (*N.*) *maculata* de Freitas and Penny (type locality: Taquaritinga, São Paulo, Brazil); *L.* (*N.*) *michelini* de Freitas and Penny (Jaboticabal, São Paulo, Brazil); *L.* (*N.*) *parallela* de Freitas and Penny (type locality: Jaboticabal, São Paulo, Brazil); *L.* (*N.*) *retusa* de Freitas and Penny (type locality: Balsamo, São Paulo, Brazil); *L.* (*N.*) *robusta* de Freitas and Penny (type locality: Itiquira, São Paulo, Brazil); *L.* (*N.*) *santini* de Freitas

(type locality: Jaboticabal, São Paulo, Brazil); *L.* (*N.*) *scomparini* de Freitas and Penny (type locality: Itiquira, São Paulo, Brazil); *L.* (*N.*) *squamisetosa* de Freitas and Penny (type locality: Birigui, São Paulo, Brazil); *L.* (*N.*) *tabacinus* de Freitas and Penny (type locality: Itiquira, São Paulo, Brazil); *L.* (*N.*) *tenuis* de Freitas and Penny (type locality: Luis Antonio, São Paulo, Brazil); *L.* (*N.*) *vignisi* de Freitas and Penny (type locality: Itiquira, Mato Grosso, Brazil); and *L.* (*N.*) *vittata* de Freitas and Penny (type locality: Ribeirão Preto, São Paulo, Brazil). Information about crops on which these species were collected is given when known.

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Brazilian agricultural production is among the largest and most diverse in the world, generating about $777 billion annually in foodstuffs and fiber and accounting for 8% of total gross domestic product (Ministério de Agricultura, 1999). Agriculture is also the largest source of export revenues for the country, producing $11.788 billion annually, or 24.55% of all export products (idem). For example, Brazil is the largest producer of coffee, orange juice, and sugar in the world, and is second only to the United States in soybean production. It has been said that the weather in São Paulo will materially affect futures markets in Chicago and New York for such commodities as soybeans, coffee, and orange juice. A more colorful way of phrasing this interdependence is that when a farmer sneezes in São Paulo, a trader in Chicago catches a cold.

To protect these crops against pest damage a variety of strategies have evolved. As in North America, there is a growing desire to rely less on pesticides and increase use of natural predators and parasites. Two components of natural predator protection are inundative releases and oviposition augmentation. However, in order for either of these strategies to be successful it is necessary for researchers to know what species of predators and parasites can exist in these ecosystems and how they interact with each other. A first step in this direction is to document the species of predators and parasites which naturally coexist with pests in the fields, orchards, and plantations.

In the United States, the most frequently utilized natural predators for inundative release programs are members of the green lacewing genus *Chrysoperla* (M. J. Tauber et al. 2000), which as

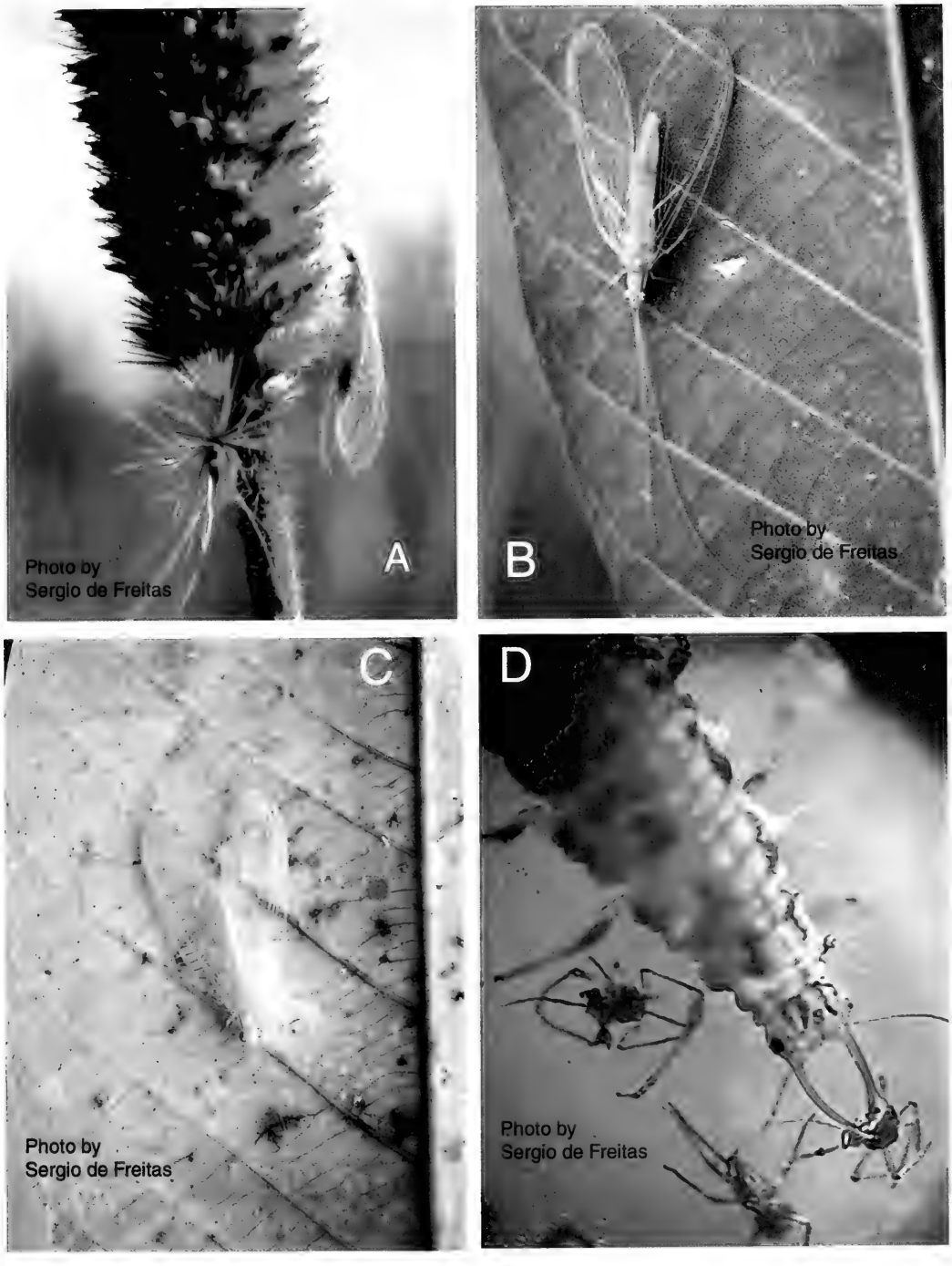

PLATE A. Adult *Ceraeochrysa cincta* on sorghum. B. Adult *Ceraeochrysa caligata* on rubber tree leaf. C. Adult *Ceraeochrysa caligata* on rubber tree leaf. D. Third instar of *Chrysoperla externa* feeding on aphids.

adults feed on grass pollen and naturally occur most frequently in grasslands. Other green lacewings are more frequently found in orchards (*Ceraeochrysa* spp.) and forests (*Leucochrysa* spp.).

Green lacewings often are voracious and aggressive predators as larvae, being quite effective in feeding on phytophagous insects under ideal conditions. Neumark (1952) found that female *Chrysoperla carnea* (Stephens) in Israel will lay up to 679 eggs. Smith (1921, 1922) counted up to 617 eggs per female of *Chrysopa oculata* Say in North America. Withycombe (1923) recorded larval *Chrysoperla* and *Chrysopa* in Europe feed on an average of about 100 aphids during their development, while Matsuda (1928) recorded as many as 900 aphids or 3,780 scale insects for each larva of Japanese species. Neumark (1952) fed *Chrysoperla carnea* 6,487 scale insect eggs during the 14 day cycle of its larval development. Larval green lacewings are known to feed on adult aphids (Aphidoidea), scale insects (Coccoidea), mealy-bugs (Pseudococcidae), saw-fly larvae (Diprionidae), mites (Acari), Lepidoptera larvae and eggs, syrphid fly larvae (Syrphidae), dusky-wing larvae (Coniopterygidae), thrips (Thysanoptera), and small Coleoptera larvae. However, although known as general predators, there often is a strong link between host plant and associated species of green lacewing indicating a more specific association with prey items than is generally believed.

Brazil produces a tremendous number of crops in many different vegetation structures from open fields of gramineous crops (barley, maize, oats, wheat) to vines (grapes, guarana), to tree crops (oranges, coffee, cacão), to selective harvesting of forest products (rubber, cupuaçu). These crops often contain a rich assemblage of chrysopid species, some of which have never been formally described. Previous studies have almost always listed chrysopids as *Chrysopa* sp., a genus which is now restricted to the Northern Hemisphere. Because of the rapidly evolving state of chrysopid taxonomy, all previous identifications must be treated with a great deal of caution. Formal names and descriptions are herein provided to facilitate studies of species biologies, interactions, and the role each species plays in protecting these food plants. This monograph is primarily intended for use by taxonomists attempting to identify species collected in these agricultural systems. Other crop protection specialists may be able to identify the included species, but this should be done with caution. The male and female genitalic sclerites and membranes illustrated herein are tiny (often much less than one mm in length) and require careful dissection and staining to observe clearly. A considerable amount of experience is needed to confidently recognize these structures properly.

Materials and Methods

For this study 579 adults were collected by the senior author and his students on nine crops from 35 different localities in seven different states using several different methods throughout the year. These methods included sweep net sampling, lights, flight intercept traps (Malaise traps), and Molasses traps. Molasses traps were small plastic water bottles suspended from trees. Each bottle had a 10% molasses solution inside and two 2 cm holes cut in the sides of the bottle. Chrysopids would enter through the holes and could not find their way back out. While the number of crops and number of localities collected during this study was not comprehensive, in a country the size of Brazil the number of potential crops and collecting localities is enormous. It was felt that enough information had accumulated that this monograph was warranted. Certainly, future collecting on additional crops and in additional localities will reveal further information about these and perhaps other species.

Many specimens were pinned and others were preserved in 75% ethyl alcohol. To study the wings, they were detached from the body and mounted dry on microscope slides. Abdomens were detached, macerated in warm 10% KOH, then stained with Chlorazol Black E. After study, wings were glued to a small card on the pin below the specimen and abdomens were placed in small vials of glycerin below each specimen. Drawings were made using dissecting and compound microscopes with camera lucida attachments. Inked drawings were then scanned, using Abode Photoshop, and arranged into composite plates.

This study relies much more heavily on elements of the female genitalia than most previous studies. We have found that the form of the spermatheca (vela and ventral impression), spermathecal ducts, subgenitale and surrounding area are much more diverse and reliable for species recognition than previously thought.

Types of designated new species will be deposited in the Museu de Zoologia/USP, São Paulo, SP, Brazil. Other material examined specifically for this study is deposited in the Sergio de Freitas Collection, Departamento de Fitossanidade, Universidade Estadual Paulista, Jaboticabal, São Paulo (SDF), unless specifically indicated as deposited at California Academy of Sciences (CAS), San Francisco, California, U.S.A.

CROP ASSOCIATIONS

Specimens were collected and examined from the following crops: rubber, orange, corn (maize), guava, apple, cotton, cashew nut, cantaloupe and eucalyptus.

The insects collected in rubber tree (*Hevea brasiliensis*) plantations were identified as members of 42 species in 4 genera, as follows: *Leucochrysa* (*Leucochrysa*) *ampla*, *L.* (*L.*) *pretiosa*, *L.* (*L.*) *varia*, *L.* (*L.*) *bruneolus*; *L.* (*Nodita*) *affinis*, *L.* (*N.*) *camposi*, *L.* (*N.*) *cruentata*, *L.* (*N.*) *heriocles*, *L.* (*N.*) *lancala*, *L.* (*N.*) *lateralis*, *L.* (*N.*) *marginalis*, *L.* (*N.*) *marquezi*, *L.* (*N.*) *melanocera*, *L.* (*N.*) *rodriguezi*, *L.* (*N.*) *barrei*, *L.* (*N.*) *forciformis*, *L.* (*N.*) *furcata*, *L.* (*N.*) *guataparensis*, *L.* (*N.*) *ictericus*, *L.* (*N.*) *incognita*, *L.* (*N.*) *interata*, *L.* (*N.*) *retusa*, *L.* (*N.*) *robusta*, *L.* (*N.*) *scomparini*, *L.* (*N.*) *tabacinus*, *L.* (*N.*) *vignisi*; *Ceraeochrysa cincta*, *C. caligata*, *C. claveri*, *C. cubana*, *C. everes*, *C. sanchezi*, *C. tenuicornis*, *C. pennyi*; *Plesiochrysa elongata*, *P. alytos*; *Chrysopodes adynatus*, *C. delicata*, *C. nigropicta*, *C. polygonica*; *Chrysoperla externa*, and *C. defreitasi*.

In orange groves (*Citrus sinensis*) the following species were encountered: *Leucochrysa* (*N.*) *camposi*, *L.* (*N.*) *clepsydra*, *L.* (*N.*) *cruentata*, *L.* (*N.*) *walkerina*, *L.* (*N.*) *lancala*, *L.* (*N.*) *rodriguezi*, *L.* (*N.*) *affinis*, *L.* (*N.*) *ictericus*, *L.* (*N.*) *maculata*, *L.* (*N.*) *michelini*, *L.* (*N.*) *vittata*; *Chrysopodes lineafrons*, *C. polygonica*, *C. spinella*, *C. divisa*; *Nacarina pletorica*, *N. lavrasana*; *Plesiochrysa brasiliensis*; *Ceraeochrysa cincta*, *C. caligata*, *C. claveri*, *C. cubana*, *C. dolichosvela*, *C. everes*, *C. paraguaria*, *C. sanchezi*, *C. scapularis*, *C. tucumana*, *C. citrinus*, *C. pennyi*, *Chrysoperla externa*, and *C. raimundoi*.

In corn fields (*Zea mays*) the following were found: *L.* (*N.*) *lancala*, *L.* (*N.*) *cornuta*, *L.* (*N.*) *ictericus*, *L.* (*N.*) *rodriguezi*, *L.* (*N.*) *squamisetosa*; *Chrysopodes indentata*, *C. crocinus*; *Nacarina panchlora*, *N. aculeata*, *N. sagitta*, *N. gladius*; *Plesiochrysa brasiliensis*, *P. elongata*, *P. alytos*; *Ceraeochrysa cincta*, *C. claveri*, *C. cubana*, *C. everes*; and *Chrysoperla externa*.

Guava (*Psidium guajava*) yielded the following species: *L.* (*N.*) *camposi*, *L.* (*N.*) *cruentata*; *Chrysopodes lineafrons*, *C. karinae*; *Plesiochrysa brasiliensis*, *P. alytos*; *Ceraeochrysa cincta*, *C. claveri*, *C. cubana*, *C. everes*, *C. montouana*, *C. paraguaria*, *C. sanchezi*, *C. squamma*; *Chrysoperla externa*, and *C. raimundoi*.

The following species were found in apple (*Malus pumila*) orchards: *Leucochrysa* (*L.*) *boxi*, *L.* (*L.*) *catarinae*, *L.* (*N.*) *intermedia*, *L.* (*N.*) *confusa*; and *Chrysoperla externa*.

Cotton (*Gossypium* spp.) fields yielded the following species: *Leucochrysa* (*N.*) *interata*, *L.* (*N.*) *parallela*; *Ceraeochrysa cincta*, *C. cubana*; and *Chrysoperla externa*.

In cashew nut (*Anacardium occidentale*) plantations the following species were found: *Leucochrysa* (*N.*) *rodriguezi* and *Chrysoperla externa*.

The following species were found in cantaloupe (*Cucumis melo*) fields: *Ceraeochrysa sanchezi* and *Chrysoperla externa*.

Eucalyptus plantations contained the following species: *Leucocrysa* (*N.*) *aurantiacus*, *L.* (*N.*) *guataparensis*, *L.* (*N.*) *lineata*, *L.* (*N.*) *robusta*, *L.* (*N.*) *santini*, *L.* (*N.*) *tenuis*; *Chrysopodes divisa*, *C. elongata*; *Ceraeochrysa cubana*, *C. pennyi*, *C. scapularis*; *and Chrysoperla externa*.

SYSTEMATIC TREATMENT

The identification of Neotropical Chrysopidae is difficult. Of the 489 species described from the New World south of the U.S.A. border, 290 of them were described by Padre Longinos Navás during the first third of the 20th century (Penny 1978). His descriptions were brief, often not diagnostic, and usually not accompanied by useful illustrations. To complicate matters, he sometimes placed type material in his private collection, much of which has subsequently been destroyed. To understand the species he described, it is necessary to visit many of the European museums where types exist, as well as study the remnants of the Navás collection. The late Phillip A. Adams studied almost all of Navás' remaining types, frequently macerated and stained the abdomens, took notes, and made pencil sketches of male and female genitalia. These notes and sketches are now in the Entomology Department of the California Academy of Sciences and have proven invaluable in the preparation of this manuscript. In the individual species descriptions of this monograph, where no indication is given that types have been studied, the species have been identified using Adams' notes and sketches of the type specimens. Additionally, in 1992 the junior author received an Ernst Mayr grant from the Museum of Comparative Zoology to study Banks and Schneider types at that museum. A set of specimens from the California Academy of Sciences was compared with types at Harvard University at that time and has provided valuable comparative material. Less detailed studies have been made by the junior author of some Navás types in the British Museum (Natural History) (London) and Muséum national d'Histoire Naturelle (Paris) but have not been included in the material examined section of species descriptions.

Three publications have also exceptionally useful for interpretation of the Neotropical chrysopid fauna. Adams and Penny (1987) covered not only part of the region under consideration, but also one of the two main tribes involved in the present study. This paper provides keys to all species and includes known synonymy. Adams (1982a) described one of the major genera under discussion and listed the 27 species known at that time, along with considerable synonymy. Finally, Brooks and Barnard (1990) have provided a modern generic framework for many disparate species previously placed together in the genus "*Chrysopa*."

The most problematic group remains *Leucochrysa* (*Nodita*). This subgenus contains over 200 described species, and no modern treatments of the individual species exist. Thus, we have relied almost exclusively on the type specimens that we have seen and Phillip Adams' notes and drawings for species identification. The key included here is the first key of any *Leucochrysa* (*Nodita*) species in more than 55 years.

We are following the classification and terminology used by Brooks and Barnard (1990) in their world generic revision of Chrysopidae. We have included all species that we have found in agricultural production areas, but have not intended this to be a complete treatment of all green lacewings found in Brazil. Numerous other species are to be found in natural ecosystems and these probably occasionally will stray into the more disturbed agricultural ecosystems. We hope eventually to publish monographic revisions for the different tribes and genera of the Neotropics, but we intend this treatment to be used for the specific habitat types indicated until more comprehensive studies can be completed. For the Amazonian region, a systematic treatment of Chrysopini is available (Adams and Penny 1987).

Since we are relying so strongly on elements of the male and female terminalia for identification, a few words of explanation of these structures are merited. A full complement of sclerites at the apex of the male abdomen would include: a small quadrate sclerite directly below the anus (subanal plate), followed in order by a thin arched structure (tignum) usually with a small medial projection (acumen); an arched structure (gonarcus) with broadened apices (lateral arms), sometimes with a dorsal plate (dorsal hood), a pair of dorsally projecting lobes (gonocornua), or caudo-ventrally projecting lobes (entoprocesses) which partially wrap laterally around a membranous apical sac (gonosaccus); the

gonarcus usually has a caudally projecting medial lobe (mediuncus) which ends in medial point (arcessus) which often is tripartite and decurved; below (and not connected to) the gonarcus and above the gonosaccus there may be a long medial sclerite (pseudopenis); the gonosaccus often bears setae (gonosetae) or small toothed plates (gonocristae) on its surface; lateral to the gonosaccus in Belonopterygini there may be an elongate, pointed sclerite (paramere); finally, there may be a sclerite above the fused eighth and ninth sternite (gonapsis), which in New World species takes the form of a long rod. All elements of the male genitalia are never present, and the combination of presence or absence of these components is the best available criterion for generic recognition.

Female genital elements include a spermatheca consisting of heavily scleritized vela with a ventral impression at its anterior end and connected near the mouth of this impression is a long duct (spermathecal duct) ending in an appendix-like projection which is often hairy (see Fig. 30). At the posterior end of the vela is a constricted and less sclerotized duct (bursal duct) which connects to an expanded, membranous copulatory bursa. Two membranous accessory glands (bursal glands) empty into the bursa. Above the bursa is a second set of membranous accessory glands (colleterial glands), which terminate separately between the lobes of the lateral gonapophyses. On the body surface below the lateral gonapophyses and above the seventh sternite is a sclerite (subgenitale) with paired dorsal lobes and ventromedial lobe. In the Belonopterygini, the subgenitale can be protracted by an elongate, membranous stalk. The ventromedial lobe may be quite small, or occasionally quite elongate. Often, in the middle of this ventral lobe is a small, more heavily sclerotized indentation (crumena). In Belonopterygini at the caudal apex of the seventh sternite there is a small medial sclerite (praegenitale) with a central crumena. This probably reflects a migration and separation of the apex of the subgenitale ventromedial lobe.

At present all known green lacewings found in agro-ecosystems in Brazil belong to three tribes, all in the subfamily Chrysopinae. Adults can be distinguished using the following key.

KEY TO THE TRIBES OF CHRYSOPIDAE FOUND IN BRAZILIAN AGRO-ECOSYSTEMS

1. Adults thick-bodied with prothorax wider than long (Fig. 1A); antennomeres wider than long beyond the first few basal segments; larvae associated with ant nests . . . . . Belonopterygini

1'. Adults thinner-bodied with prothorax usually as long as wide (Fig. 9A); antennomeres longer than wide beyond the first few basal segments; larvae free-living on vegetation, often with bodies covered with debris and skins of prey 2

2. Forewings bearing dark spot at base of pterostigma; outer gradate series of crossveins at narrow angle (less than 45°) to pseudomedial vein (Fig. 41B); antennae longer than wings . . . . . Leucochrysini

2'. Forewing pterostigmal area completely pale; outer gradate series of crossveins at broad angle (greater than 60°) to pseudomedial vein (Fig. 37B); antennae shorter than wings . . . . . Chrysopini

TRIBE BELONOPTERYGINI NAVÁS, 1913a

These green lacewings, when first seen, are remarkably robust. They are wider bodied than other chrysopids. The pronotum is always wider than long and antennal segments are wider than long (Adams and Penny 1987). However, the species found in Brazil are among the least robust of the tribe and some species can be confused with members of Chrysopini. Other species in the region, however, are large and thick-bodied. We have seen some females from Rio Doce in Minas Gerais that are so big that they can momentarily appear similar to some of the large, yellow megalopterans of the genus *Chloronia*.

The tribe is worldwide in distribution. Most of the Old World species are in the genus *Italochrysa* (Tjeder 1966). The dominant New World genus is *Nacarina* and all known Brazilian species are in this genus. There are two additional New World genera (Adams 1978): *Belonopteryx* is a monotypic genus with long, narrow wings known from only three specimens from Argentina; and *Abachrysa* is a

genus with dark wings and dark maculations on the wings found in southeastern U.S.A. and the Caribbean (Brooks and Barnard 1990).

All known species of Belonopterygini are ant nest associates as larvae (Brooks and Barnard 1990). Their main contribution to agricultural ecosystems is probably to reduce the numbers of certain species of ants in the fields. Their more frequent occurrence in corn fields may be an indication of preference for ants living in a more open habitat.

Genus *Nacarina* Navás, 1915

Brooks and Barnard (1990) reported 14 species of *Nacarina*, all restricted to the New World with 11 of them found in South America. During this study, three of the 11 South American species were seen, as well as four undescribed species. Adults can be distinguished using the following key.

KEY TO THE SPECIES OF *NACARINA* FOUND IN BRAZILIAN AGRO-ECOSYSTEMS

1. Apical segment of maxillary palps swollen, bulbous (Fig. 1D) 2
1′. Apical segment of maxillary palps tubular, apically tapering (Fig. 3A) 3

2. Head and pronotum completely pale, without markings (Fig. 2A) . . . . . *N. pletorica*
2′. Vertex and gena with red marks; pronotum with lateral red stripe (Fig. 1A) . . . . . *N. panchlora*

3. Head without dark markings; lateral arms of gonarcus with funnel-shaped cavity (Fig. 7C) . . . . . *N. sagitta*
3′. Head with some dark markings (Fig. 5A); lateral arms of gonarcus without cavity (Fig. 4F). 4

4. Forewing inner and outer gradate veins parallel (Fig. 5B). 5
4′. Forewing inner and outer gradate veins divergent (Fig. 3B) . . . . . *N. wagneri*

5. No red markings on central raised area of vertex (Fig. 4A); parameres adherent to gonosaccus (Fig. 4G); gonosaccus with numerous, small gonocristae (Fig. 4F, G) . . . . . *N. aculeata*
5′. Two crescent-shaped red marks on raised central area of vertex (Fig. 5A); parameres adjacent to gonosaccus (Fig. 5F); gonosaccus with few long setae, no small gonocristae (Fig. 5F). 6

6. Intramedian cell quadrate (Fig. 6B); gena red; maxillary palps pale (Fig. 6C); inner margins of gonocornua form V-shaped (Fig. 6H). . . . . *N. lavrasana*
6′. Intramedian cell triangular (Fig. 5B); gena pale; maxillary palps dark (Fig. 5C); inner margins of gonocornua form U-shaped (Fig. 5E) . . . . . *N. gladius*

Nacarina panchlora (Gerstaecker, 1888)

DIAGNOSIS. — This is one of two species with bulbous maxillary and labial palpi, short faces, and broad bodies. There also appears to be the beginnings of a second intramedial cell. *Nacarina panchlora* has much more red coloration on gena and pronotum than *N. pletorica*. The lateral digitiform lobes of the female genitalia also appear distinctive. So far, we have only found this species associated with corn fields.

HEAD. — Yellow and green. Vertex yellow, rugose, posteriorly elevated; two small, red postocular spots at hind margin. Frons yellow with red marks below antennal bases. Clypeus and labrum green. Gena red (Fig. 1C). Maxillary and labial palpi pale, last segment basally bulbous, apically rounded (Fig. 1D). Antenna pale, first segment of flagellum larger than others.

THORAX. — Green with yellow mid-line. Pronotum twice as wide as long; anterior margin arched; brown stripes laterally (Fig. 1B). Meso- and metanotum unmarked. Tarsal claws elongate without basal expansion. **Wings**: Forewing green, with anterior endings of Radius (R)-Radial Sector (Rs) and gradate veins dark. Subcosta (Sc) and Rs veins swollen. Intramedian cell (imc) quadrangular. Incomplete second intramedian cell. Partial third gradate series present (Fig. 1B). Forewing length (2.55 cm): width (0.92 cm) = ratio (2.77). Hindwing length (2.28 cm): width (0.82 cm) = ratio (2.78).

ABDOMEN. — Green with yellow mid-line. **Female**: Subgenitale with central projection (Fig. 1G). Spermatheca short, membranous posterior part folded upon itself. Bursa copulatrix acute anteriorly, with pair of accessory glands (Fig. 1E). Lateral to subgenitale a membranous lobe with two flat pockets (Fig. 1F).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Birigui, 6 April 1996, Scomparin, C. H. J. (1♀)(corn); 3 September 1996, Scomparin, C. H. J. (1♀)(corn); Jaboticabal, 11 August 1991, Scomparin, C. H. J. (1♀)(corn); Franca, 19 October 1994, Montovani, R.C. (1♀)(corn).

***Nacarina pletorica* (Navás, 1919)**

DIAGNOSIS. — This is one of two species with quite broad bodies, short faces, and bulbous apices of palps. *Nacarina pletorica* can be separated from *N. panchlora* by the lack of genal and pronotal red coloration and somewhat narrower wings, without partial third gradate series.

HEAD. — Pale yellow. Gena, clypeus, labrum, frons, vertex and antenna pale, without marks. Face short (Fig. 2D). Maxillary and labial palpi pale, last segment large, bulbous, tapered to rounded apex (Fig. 2C). Vertex rugose and raised posteriorly.

THORAX. — Pale yellow, unmarked. **Wings**: Venation pale, except anterior intersections of first costal crossveins, basal subcostal crossvein, posterior endings of first R-Rs crossveins, gradates, ends of Pseudomedius (Psm)-Pseudocubitus (Psc) crossveins, and apex of anal veins brown (Fig. 2B). Imc quadrate. Pterostigma pale, unmarked. Rs, Psm and Psc swollen. Forewing slender; length (17.8 mm): width (0.56 cm) = ratio (3.18). Hindwing green, except anterior ending of first costal crossveins, posterior endings of first Rs-Psm crossveins, gradates, endings of Psm-Psc crossveins, and endings of anal veins pale brown (Fig. 2B). Gradates, Psm, and Psc swollen. Hindwing slender, length (1.6 cm), width (0.5 cm) = ratio (3.14).

ABDOMEN. — Yellow, unmarked. Ectoproct ventro-posterior angle tapering to sclerotized point. Setae of callus cerci angled medially. **Male genitalia**: Eighth and ninth sternites fused; ninth smaller than eighth and strongly tapered to apex; microtholi present (Fig. 2E). Gonarcus short and broad; lateral arms short, with lateral lobe. Gonocornua plate-like with two apical lobes, the inner acute. Arcessus short, apical lobe with medial hook flanked by short, rounded, lateral lobes. Gonosaccus with many long setae (Fig. 2F, G).

MATERIAL EXAMINED. — **BRAZIL: São Paulo**: Jaboticabal, 18 December 1995, Franco, E. (1♂).

REMARKS. — The male specimen that we have available appears to have somewhat aberrant wing venation in that the forewing has a second intramedial vein.

***Nacarina wagneri* Navás, 1924a**

DIAGNOSIS. — Characterization was made from a faded, pinned specimen. This species is a member of a species group having elongate, tubular, apical palp segments. The quadrate intramedian cell separates *N. wagneri* from *N. aculeata* and *N. gladius*. The red head and pronotal markings separate *N. wagneri* and *N. lavrasana* from *N. sagitta*, while the concave curvature of the inner gradates separates *N. wagneri* from *N. lavrasana*.

HEAD. — Antennae pale. Red mark around antennal bases. Maxillary and labial palpi pale, last palpimere slender, tapered and not inflated (Fig. 3A).

THORAX. — Pronotum twice as wide as long, with lateral red stripe. Mesonotum with lateral red stripe. **Wings**: Forewing length (1.95 cm): width (0.69 cm) = ratio (2.83). Venation completely pale. Intramedian cell quadrangular (Fig. 3B). Hindwing length (1.67 cm): width (0.60 cm) = ratio (2.78).

ABDOMEN. — Pale. **Female**: Seventh sternite with apical knob (Fig. 3C). Spermatheca a large chamber and several convoluted coils (Fig. 3E); accessory glands with huge sac which extends anteriorly to sixth segment (Fig. 3F). Subgenitale with medial projection with ventral cremena (Fig. 3D).

MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Salabra, March 1940, collector unknown.

Nacarina aculeata de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museum de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled: "Birigui, SP, Fz. São Joaquim, 11/Jun/94, Scomparin, C. H. J., SP66" (on corn).

DIAGNOSIS. — This is a member of a species group having tubular, tapering palps. It has ovate intramedian cell and dark palpi, which separates it from all other species, except *N. gladius*. *Nacarina aculeata* can be separated from *N. gladius* by the shorter face, lack of red markings on the vertex, shorter inner gradate series of the hindwing, shorter setae on ectoproct and sternite 8 + 9, shape and longer length of the parameres, and spiny apex and dorsal margin of sternite 8 + 9.

The name "aculeata" comes from the Latin *aculeatus* meaning sharp-pointed. This name refers to the field of spines along lateral margin of sternite 8 + 9 and the teeth at the apex of this sternite.

HEAD. — Golden yellow. Vertex, frons and clypeus glabrous. Face short. Gena pale, unmarked. Vertex deeply depressed laterally near eye margin. Scape and pedicel with dorsal brownish red stripes; basal segments of flagellum black striped on inner surface (Fig. 4A), more distal segments fuscous, with setae black. Maxillary and labial palpi with black markings; last segment tapered and slender. (Fig. 4C).

THORAX. — Yellow. Pronotum glabrous with lateral pale reddish brown stripe (Fig. 4A). **Wing**: Venation pale, except R-Rs crossveins, Rs-Psm crossveins, Rs-inner gradate (Ig) crossveins, gradates, Psm-Psc crossveins, marginal forked and unforked veins dark. Pterostigma unmarked. Forewing length (1.6 cm): width (0.52 cm) = ratio (3.08). Intramedian cell triangular. Hindwing venation pale except costal crossveins, R-Rs transverse vein endings and gradates dark. Length (1.38 cm): width (0.43 cm) = ratio (3.2) (Fig. 4B).

ABDOMEN. — **Male**: Densely covered by short and pale setae (Fig. 4D). Sternite 7 much larger than sternite 8 + 9. Apex of ectoproct rounded (Fig. 4D). Sclerotized melanic band at anterior margin of ectoproct with branch leading downward to melanic callus cerci, unlike the pale apodemes found in all other species. Apex of sternite 8 + 9 with several heavily sclerotized teeth; subapical dorsal margin of sternite with spiny lobe (Fig. 4E); without microtholi. Arcessus short, broad with dorso-medial projection terminating in decurved hook flanked by two rounded lobes (Fig. 4F, G, H). Lateral arms of gonarcus with posterio-ventral portion extending below arcessus. Gonosaccus with few long setae; ventral portion with field of numerous small gonocristae. Parameres parallel curved rods adherent to gonosaccus (Fig. 4F).

MATERIAL EXAMINED. — Known only from the holotype.

Nacarina gladius de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled: "Birigui, SP, 6 April 1996, Scomparin, C. H. J." (on corn).

DIAGNOSIS. — This is a member of a species group having tubular, apically tapered palps and a triangular intramedian cell. It can be separated from *N. aculeata* by the presence of a double crescent red mark on the vertex, much longer inner gradate series of the hindwing and characteristics of the male genitalia such as a more narrow arcessus, lack of spines on sternite 8 + 9 and lack of gonocristae on the gonosaccus in *N. gladius*.

The name "gladius" comes from the Latin word for sword, and refers to the shape of the parameres.

HEAD. — Golden yellow. Vertex raised, rugose, with red double crescent marking. Scape and pedicel with wide dorsal red stripe (Fig. 5A); first 37 flagellomeres with black stripe along medial margin; more apical segments fuscous. Frons with red spot below antennal base and above anterior tentorial pit. Gena black-banded near frons. Maxillary and labial palpi pale, apical segment tubular, apically tapering (Fig. 5C).

THORAX. — Yellowish green. Pronotum with short and slender brown stripe at anterior angle; posterior angle weakly red spotted. Meso- and metanota without markings (Fig.5A). **Wings**: Venation green, except costal crossveins, R-Rs crossveins and gradates dark (Fig. 5B). Pterostigma pale, unmarked. Forewing length (2.23 cm): width (0.69 cm) = ratio (3.23). Hindwing length (1.8 cm): width (0.6 cm) = ratio (3.0). Venation green, except middle costal crossveins dark.

ABDOMEN. — Green without marks. Ectoproct dorso-apical angle acute. Sternite 8 + 9 evenly tapered, triangular; suture not visible, no microtholi (Fig. 5D). Gonarcus not vertically arched; lateral arms ovate. Bases of gonocornua proximal to each other; inner margins U-shaped. Arcessus short, narrow; with medial decurved hook and tiny rounded lateral lobes. Gonosaccus with few long gonosetae. Parameres long, sword-shaped, conical, adherent to gonossacus.

MATERIAL EXAMINED. — Known only from the holotype.

***Nacarina lavrasana* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP; Abril/93, Murtati, G."

DIAGNOSIS. — This species can be separated from other South American species by the tubular, apically tapered maxillary palpi and quadrangular intramedian cell. The only other species of *Nacarina* in the region with these characteristics is *N. sagitta*, which has no red markings on head and thorax. The male genitalia are also quite different, with the gonocornua of *N. lavrasana* much more approximated basally and much shorter, and not having dorsal pockets of the lateral arms of the gonarcus. This species also resembles *N. cordillera* from northern South America and Central America, but that species has the apex of male sternite 8 + 9 bluntly truncated.

The name of this species is derived from the town of Lavras in Minas Gerais State.

HEAD. — Yellow, marked with red. Vertex glabrous with red, double crescent-shaped marks (Fig. 6A). Scape and pedicel with narrow red stripe dorsally; flagellum with medial dark stripe on basal flagellomeres and completely brown apical ones. Gena with red spot bordering frons (Fig. 6C). Maxillary and labial palpi pale, last segment slender and narrow, apically tapered (Fig. 6D).

THORAX. — Green. Pronotum with red lateral stripe. Meso- and metanota green without marks. **Wings**: Venation green, except posterior endings of R-Rs crossveins and gradates of forewing dark. Transverse vein between first and second median cells inflated (Fig. 6B). Forewing length (2.28 cm): width (0.74 cm) = ratio (3.08). Hindwing length (2.02 cm): width (0.65 cm) = ratio (3.1).

ABDOMEN. — Green without markings. No microtholi. **Male genitalia**: Gonarcus arcuate, thick. Bases of gonocornu proximal, apically decurved. Arcessus long, with small, rounded lateral lobes and medial decurved hook. Cluster of setae on gonosaccus below gonocornu. Paramere slender, adherent to gonosaccus (Fig. 6H, I). **Female genitalia**: Spermatheca short, extended as long wrinkled expansion to bursa copulatrix. Spermathecal duct short, coiled. Two sets of colleterial glands long and filamentous, extended to fifth segment (Fig. 6E, G). Subgenitale heavily-sclerotized, extended anteriorly as sclerotized medial lobe (Fig. 6F).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: São João da Boa Vista, 12 October 1994, Mello, S. R. C. (1♀ paratype)(orange); Jaboticabal, April 1993, Murtati, G. (1♀ paratype); **Minas Gerais**: Lavras, 10 October 1990, Carvalho, C. F.

Nacarina sagitta de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Ibitinga, SP; 19-12-88, Maia, A. M."

DIAGNOSIS. — This species is a member of the group having slender, tapering pale palpi and sharply tapered male sternite 8 + 9. It is close to *Nacarina gladius*, but can be differentiated by a suite of characteristics: *N. gladius* has a triangular intramedian cell; gonarcus less vertically arched; bases of gonocornua more closely approximated, lateral arms of gonarcus not inflated with internal pocket.

The name "sagitta" comes from the Latin word for arrow, and refers to the shape of the male parameres.

HEAD. — Vertex, frons, clypeus, labrum and gena pale yellow. Antenna pale, unmarked.

THORAX. — Yellow. Pro-, meso- and metanota unmarked. **Wings**: Wing apex missing. Transverse vein between first and second median cells and contiguous parts of Psc swollen. Intramedian cell quadrangular (Fig. 7B).

ABDOMEN. — Apex of ectoproct truncate. **Male genitalia**: Dorsal apodeme of ectoproct forked near base; ventral fork continues ventrally below ectoproct and terminates acutely (Fig. 7A). Sternite 8 + 9 partially fused with visible suture; microtholi present (Fig. 7A). Medial arch of gonarcus short and strongly curved; lateral arms swollen with inner pocket which opens dorsally (Fig. 7C). Gonocornua slender, with bases well separated. Arcessus elongate; apical lateral lobes as vertically oriented plates and medial decurved hook. Group of little lobes below arcessus and laterad of gonosaccus with long setae. Large, sclerotized, conical, apically arrowhead-shaped parameres extend to arcessus (Fig. 7C, D).

MATERIAL EXAMINED. — Known only from the holotype.

TRIBE CHRYSOPINI SCHNEIDER, 1851

Chrysopini are the green lacewings most often seen in fields and on windows and store fronts at night. Adults of some species, such as those in the Holarctic genus *Chrysopa,* can emit a foul-smelling odor in self-defense. Adults of Chrysopini are small to medium-sized (8–20 mm forewing length) and basically green in color with four similar transparent wings. Larvae of some genera, such as *Chrysoperla,* have naked larvae, while larvae of other genera, such as *Ceraeochrysa,* cover their bodies with debris and dried bodies of prey. As a group, they are indigenous to all temperate and tropical parts of the world, except New Zealand.

Adult Chrysopini are morphologically conservative, so that the generic classification is based primarily on sclerotized elements of the male genitalia. Adults of genera of Brazilian Chrysopini can be distinguished using the following key:

KEY TO MALES OF CHRYSOPINI GENERA FOUND IN BRAZILIAN AGRO-ECOSYSTEMS
(modified from Adams and Penny 1987)

1. Tignum present (Fig. 25E) 2
1′. Tignum absent (Fig. 31B) 3

2. Pseudopenis present; pronotum with four red spots or lateral stripes (Fig. 37A, H) . . . . . *Plesiochrysa*
2′. Pseudopenis absent; pronotum without red marks (Fig. 24A, I) . . . . . *Chrysoperla*

3. Gonapsis elongate (Fig. 8C); two hornlike structures on gonarcus or arcessus (Fig. 9E) . . . . . *Ceraeochrysa*
3′. Gonapsis absent (Fig. 31B); hornlike structures absent from gonarcus-arcessus (Fig. 31E) 4

4. Mandibles blunt-tipped; wings with narrow costal area in most species (Fig. 30B) . . . . . *Chrysopodes* (*Neosuarius*)
4′. Mandibles with fanglike tip (Fig. 32E); wings with wide costal area in most species (Fig. 36B) . . . . . *Chrysopodes* (*Chrysopodes*)

Genus *Ceraeochrysa* Adams, 1982a

Adults of *Ceraeochrysa* are among the most colorful of all New World Chrysopini and most easily characterized. Individuals often have lateral or dorsal stripes on the scape and the pronotum usually has stripes or dark spots. Dark marks can also occur on the meso- and metanota. Dark margining of veins can occur on the wing membrane and some species have swelling and darkening of veins at the base of the posterior margin of the forewing. Females have a simple U-shaped spermatheca. Males of all species have an elongate rod (gonapsis) above sternite 8 + 9. Adams and Penny (1987) recorded the occurrence of a triangular gonapsis in one species of *Chrysopodes*. However, Brooks and Barnard (1990) regarded a gonapsis as absent from *Chrysopodes* and we have never observed a gonapsis in other species of *Chrysopodes*. *Ceraeochrysa* is the most speciose genus of Chrysopini in the New World with more than 50 described species. We add an additional four species in the current treatment. The genus is distributed from southern Canada (Penny et al. 1997) to northern Argentina (Penny 1978), although it is most abundant and speciose in the tropics. *Ceraeochrysa cincta* has been collected on bananas and citrus in Honduras (Adams and Penny 1987) and must be considered a prime candidate for biological control programs. In fact, many species of this genus are found in association with orchards and probably contribute significantly to natural pest control. López-Arroyo et al. (1999) recommended three species of *Ceraeochrysa* as biological control agents showing great potential in tropical America. Considerable recent work has been done on larval taxonomy of this genus by C. A. Tauber et al. (2000) and Tauber and de León (2001). Fifteen species have been collected in Brazilian agro-ecosystems and adults can be distinguished using the following key.

Key to Males of the Species of *Ceraeochrysa* found in Brazilian Agro-ecosystems

1. Pronotum with dark lateral stripes (Fig. 10A) 2
1′. Pronotum with two pair of dark circular marks (Fig. 15A); apex of sternite 8 + 9 with a pair of forcipate projections (Fig. 15C) . . . . . *C. paraguaria*

2. Antennal scape without dark markings (Fig. 21A); spermatheca long (Fig. 21C) . . . . . *C. dolichosvela*
2′. Antennal scape with stripes or spots (Fig. 11A) 3

3. Antennal scape with lateral spots (Fig. 13A) 4
3′. Antennal scape with dark stripes (Fig. 11A) 5

4. Dorsal apodeme of ectoproct extended ventrally as apically-expanded projection (Fig. 8C). . . . . *C. acmon*
4′. Dorsal apodeme of ectoproct not extended ventrally as projection (Fig. 12C); gonarcus with dorso-medial, platelike projection (Fig. 13D) . . . . . *C. everes*

5. Scape with dorso-medial dark stripe (Fig. 11A) 6
5′. Scape with dorso-lateral dark stripe (Fig. 16A) 9

6. Scape stripe not extended basally onto antennal fossa (Fig. 10A) . . . . . *C. cincta*
6′. Scape stripe extended basally onto antennal fossa (Fig. 11A) 7

7. Antennal flagellum pale (Fig. 10A) . . . . . *C. caligata*
7′. Antennal flagellum dark (Fig. 11A) 8

8. Scape with two dark stripes (Fig. 14A); spermatheca U-shaped (Fig. 14C); dorsal apodeme of ectoproct not prolonged ventrally beyond ectoproct (Fig. 12C); gonapsis unforked (10F). . . . . *C. montoyana*
8′. Scape with single dark stripe (Fig. 12A); spermatheca not U-shaped (Fig. 10E); dorsal apodeme of ectoproct extended ventrally beyond ectoproct (Fig. 11C); gonapsis forked caudally (Fig. 11F). . . . . *C. claveri*

9. Antennal flagellum pale (Fig. 12A) 10
9′. Antennal flagellum dark (Fig. 20A) 12

10. Gonarcus with dorso-medial projection (Fig. 12G); gonosaccus with several large gonocristae (Fig. 12C) . . *C. cubana*
10′. Gonarcus without dorso-medial projections (Fig. 19I); gonosaccus without gonocristae (Fig. 19J) 11

11. Apical hook of arcessus twice as long as wide (Fig. 19I); apex of sternite 8 + 9 with scattered setae not in well-defined field (Fig. 19D); forewing gradates not heavily shaded (Fig. 19B) . . . . . *C. tucumana*
11′. Apical hook of arcess five times as long as wide (Fig. 18D); apex of sternite 8 + 9 with two lateral fields of long setae (Fig. 18C); forewing gradates heavily shaded (Fig. 18B) . . . . . *C. tenuicornis*

12. Gonarcus with dorsal plate-like projection (Fig. 20C); mesonotum pale, without spots (Fig. 18A) 13
12′. Gonarcus without dorsal projection (Fig. 16I); paired dark spots on mesonotum (Fig. 17A) 14

13. Dorsal apodeme of ectoproct prolonged ventrally as projection; a group of scales on lateral membrane of gonosaccus adjacent to ventral projection of ectoproct (Fig. 22E); posterior apex of gonapsis smooth (Fig. 22G) . . . . *C. squama*
13′. Dorsal apodeme of ectoproct not prolonged ventrally as projection; no scales on lateral aspect of gonosaccus (Fig. 20F); gonapsis with teeth at posterior apex (Fig. 20E) . . . . . *C. dislepis*

14. Dorsal apodeme of ectoproct prolonged ventrally as projection (Fig. 16C); gonosaccus with gonosetae on enormous basal tubercles (Fig. 16I) . . . . . *C. sanchezi*
14′. Dorsal apodeme of ectoproct not forming ventral projection (Fig. 17C); gonosaccus with long setae on small basal tubercles (Fig. 17H). . . . . *C. scapularis*

Ceraeochrysa acmon Penny, 1998

DIAGNOSIS. — Males of this species are distinctive because of the expanded ventral tip of the ventral fork of the dorsal apodeme of the ectoproct. The often anvil-shaped form of this expansion gives this species a characteristic appearance and makes males of this species immediately recognizable.

HEAD. — Vertex greenish yellow, unmarked. Frons and gena yellow, unmarked. Scape straw yellow, darkened dorso-laterally (Fig. 8A); pedicel with dark band laterally; flagellum black. Maxillary and labial palpi pale, unmarked.

THORAX. — Green. Pronotum green with dark red stripe laterally (Fig. 8A). Meso- and metathorax unmarked. **Wings**: Forewing venation mostly green, except costal crossveins 1–11, origin of Rs, R-Rs crossveins, inner and outer gradates and endings of anal veins dark. Length (1.4–1.5 cm); width (0.45–0.48 cm). Hindwing venation green, except costal crossveins and gradates dark (Fig. 8B). Hindwing length (3.25 cm): width (1.03 cm) = ratio (3.16).

ABDOMEN. — Greenish yellow with small red spots on each side of tergites. **Male**: Dorsal apodeme of ectoproct with both dorsal and ventral branches widening apically (Fig. 8C). Membranous wall of genital atria juxtaposed against apex of ventral branch of dorsal apodeme bearing sclerotized plate with scales in several lines. Lateral arms of gonarcus long and triangular; medial arch bearing medial semicircular projection with two apical horns. Arcessus elongate, thin, ending in tripartite apex. Gonosaccus broad, with dense field of gonocristae and long setae (Fig. 8E, F). Gonapsis narrow and long, curved; subapically swollen; apex tapering to fine point (Fig. 8D). Apex of sternite 8 + 9 bearing lateral projections with setae having large, tubercle-like bases. **Female**: Subgenitale long, with lateral lobes and median projection (cremena) (Fig. 8H). Bursa copulatrix wrinkled with pair of large accessory glands. Spermatheca short, J-shaped (Fig. 8G).

MATERIAL EXAMINED. — **Costa Rica**: **Limón,** Amubri, A.C. Amistad, 4–21 December 1993, G. Gallardo, holotype male (deposited in INBIO). **Brazil**: **São Paulo**: Jaboticabal, 20 January 1998, Freitas, S. (2♀14♂); 10 September 1997, Freitas, S. (1♀); 9 December 1995, Freitas, S. (2♂); 23 March 1995, Freitas, S. (1♀); 22 February 1995, Freitas, S. (1♀); 12 October 1994, Gravena, R. (1♀); 13 November 1993, Jeronimo, E. (1♂); March 1999, Freitas, S. (1♀); São Simão, 2 January 1993, Freitas, S. (1♂)(eucalyptus); Birigui, 11 June 1994, Scomparin, C. H. J. (1♂); Balsamo, 20 December 1997, Freitas, S. (1♀); **Mato Grosso**: Corumba, 26 July 1995, Freitas, S. (1♀); Pontes e Lacerda, 14 July 1997, Freitas, S. (1♂)(rubber); Itiquira, 20 January 1994, Freitas, S. (1♀)(rubber).

***Ceraeochrysa caligata* (Banks, 1945)**

DIAGNOSIS. — This species is a member of the group of species with a recurved ventral projection of the male dorsal apodeme of the ectoproct. The pale antennae separate *C. caligata* from *C. claveri* and *C. scapularis*. *Ceraeochrysa caligata* is probably most similar to *C. cincta*, but males can be separated by the longer, more slender ventral projection of the dorsal apodeme (Figs. 9C, 10C) and longer gonocornua (Figs. 9E, F; 10H, I) of *C. caligata*.

HEAD. — Green; frons and gena pale without marks. Scape and pedicel with thin dark red stripe continued onto membranous base (Fig. 9A); flagellum pale.

THORAX. — Green; pronotum with dark red stripe laterally (Fig. 9C), mesoscutum with dark marks (Fig. 9A); metanotum unmarked. **Wing**: Venation green with some transverse veins black or darkened. Forewing: costal crossveins 4 to 10, origin of Rs, R-Rs crossveins 1 to 2, 4 to 8, inner and outer gradates, Psm-Psc crossveins 3 to 5 black. Length (1.5 cm): width (0.6 cm) = ratio (2.5). Hindwing venation green (Fig. 9B). Hindwing length (1.42 cm): width (0.45 cm) = ratio (3.16).

ABDOMEN. — Green, unmarked. **Male**: Ventral arm of dorsal apodeme of tergite 9 + ectoproct apically blunt and upturned (Fig. 9C). Gonarcus narrow, curved. Gonocornua long and decurved. Arcessus broad, with a pair of lateral and subapical horns, apically decurved. Gonosaccus with sparse elongate setae (Fig. 9E, F). Gonapsis thick and short (Fig. 9G). **Female**: Subgenitale short and thick, forming part of a heavily sclerotized plate (Fig. 9H); bursa large sac-like; spermatheca with short ventral impression (Fig. 9D).

MATERIAL EXAMINED. — **Panama**: Puerto Cabello, 11 June 1908, holotype male (deposited in Museum of Comparative Zoology, Harvard University). **Brazil**: **São Paulo**: Jaboticabal, 24 October 1990, Silva, A. D. (1♂)(orange); 2 September 1993, Narciso, R. (2♀)(orange); January 1995, Scomparin, C. H. J. (1♂)(orange); Taquaritinga 16 October 1993, Xavier, A. L. Q. (1♀)(CAS); 5 March 1994, Xavier, A. L. Q. (1♂)(orange), 4 October 1993, Xavier, A. L. Q. (2♀)(orange); Jaboticabal 7 April 1999, Freitas, S. (3♂); **Mato Grosso**: Itiquira, 13 January 1997, Freitas, S. (1♂1♀)(rubber).

***Ceraeochrysa cincta* (Schneider, 1851)**

DIAGNOSIS. — This species is a member of the group of species with a recurved ventral projection of the dorsal apodeme of the ectoproct. In Brazil, this species can be separated from *C. montoyana, C. scapularis* and *C. claveri* by their having dark antennae. Additionally, *C. scapularis* has dark spots on the mesonotum, *C. montoyana* has a double scape stripe and *C. claveri* has an apically bifurcate gonapsis. Though closely related, *C. caligata* males have a longer, thinner ventral projection of the dorsal apodeme of the ectoproct and longer gonocornua.

HEAD. — Vertex green; gena and frons pale yellow, unmarked; maxillary and labial palpi pale; antenna pale, apex fuscous; scape and pedicel with dorsal dark red stripe (Fig. 10A).

THORAX. — Green; pronotum with dark red stripe laterally (Fig. 10A); meso- and metanota unmarked. **Wings**: Forewing venation mostly yellowish green, except costal crossveins 5–11, origin of Rs, R-Rs crossveins 1–4, inner and outer gradates, Psm-Psc crossveins 1–4, and endings of anal veins dark. Length (1.4 cm): width (0.5 cm) = ratio (2.96). Hindwing costal crossveins, R-Rs crossveins, and middle part of Rs black (Fig. 10B). Length (1.11 cm): width (0.36 cm) = ratio (3.08).

ABDOMEN. — Green, unmarked. **Male**: Dorsal apodeme of tergite 9 + ectoproct heavily sclerotized bearing a posteriorly-directed ventral branch (Fig. 10C). Gonarcus with vertically flattened lateral arms and two caudally-directed, medial horns (gonocornua). Entoprocessus elongate, extending well below arcessus. Arcessus with a transverse basal sclerite with two latero-apical horns, apical sclerite with a decurved apical point. A field of tiny gonocristae arranged in rows above tergite 8 + 9 (Fig. 10H, I). Gonapsis long, slender, apically upturned (Fig. 10F). **Female**: Area between

subgenitale and 9th sternite heavily sclerotized (Fig. 10D). Subgenitale with ventral invagination without central projection (Fig. 10G). Spermatheca U-shaped, short, linked to bursa by short duct; bursa wrinkled, sac-like (Fig. 10E).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Taquaritinga, 5 March 1994, Xavier, A. L. Q. (3♂)(orange); 12 September 1992, Freitas, S. (1♀)(cotton); 20 September1993, Xavier, A. L. Q. (2♀); 12 September 1992, Freitas, S. (5♂); Jaboticabal, 9 December 1995, Freitas, S. (1♂2♀); 30 September 1997, Freitas, S. (1♀)(CAS); 2 October 1997, S. Freitas (1♂)(CAS); **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (1♂); 14 June 1997, Freitas, S. (1♀)(rubber).

***Ceraeochrysa claveri* (Navás, 1911)**

DIAGNOSIS. — This species is often more yellow in coloration than others of the genus. It is a member of the group of species with males having a recurved ventral projection of the dorsal apodeme of the ectoproct. This is one of three Brazilian species with dark antennae. However, *C. montoyana* has a double dorsal scape stripe, and *C. scapularis* has dark spots on the mesonotum. Males of *C. claveri* also have a distinctive thick apical fork of the gonapsis.

HEAD. — Vertex golden yellow; frons and gena pale, unmarked; pedicel and scape with a dorsal mid-line red stripe continued onto the antennal basal membrane as a triangular spot; flagellum black (Fig. 11A); maxillary and labial palpi pale.

THORAX. — Green; pronotum yellow with dark red stripe laterally (Fig. 11A); meso- and metanota unmarked. **Wings**: Venation mostly green with some crossveins black: forewing costal crossveins 4–12, origin of Rs base, R-Rs crossveins, Rs-Psm crossveins 1–4, gradates, Psm-Psc crossveins 6–8, unforked marginal veins, and cubital and anal vein endings dark. Length (1.4 cm): width (0.5 cm) = ratio (3.08). Hindwing costal crossveins 5–13, R-Rs crossveins, and gradates dark (Fig. 11B). Length (1.37 cm): width (0.42 cm) = ratio (3.26).

ABDOMEN. — Green, unmarked. **Male**: Dorsal apodeme of tergite 9 + ectoproct bearing ventral fork which is apically acute (Fig. 11C). Gonapsis long, slender, posteriorly forked (Fig. 11F). Gonarcus not arched. Entoprocessus long, caudally pointed. Arcessus short, membranous, triangular in dorsal view, without dorsal horns. Gonosaccus with sparse gonosetae (Fig. 11H, I); above apex of 9th sternite a field of gonocristae (Fig. 11E). **Female**: Area between subgenitale and 7th sternite heavily scletotized (Fig.11D). Bursa copulatrix with a pair of large glands (Fig. 11G). Spermatheca elongate, U-shaped, ventral impression elongate.

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Taquaritinga, 16 October 1993, (3♀2♂); 5 March 1994, Xavier, A. L. Q. (2♂2♀)(orange); 7 January 1993, Freitas, S. (2♂)(corn); 30 March 1993, Freitas, S. (2♂1♀)(guava); **Mato Grosso**: Itiquira, 7 September 1999, Freitas, S. (3♂4♀)(rubber)(SDF/CAS).

***Ceraeochrysa cubana* (Hagen, 1861)**

DIAGNOSIS. — This is a rather small species with pale antennae and considerable dark markings on the forewings. Females are indistinguishable from the more northern *C. valida*. Males have a number of autapomorphies: abdominal spiracles are unusually enlarged; the apex of sternite 8 + 9 is bifurcate and spiny; there are several large gonocristae on the gonosaccus; and the gonarcus has a vertical dorso-medial plate. Males also have a rugose vertex which is otherwise only found in *C. paraguaria* and *C. scapularis*.

HEAD. — Green; vertex glossy on female and rugose on male, unmarked; scape with a dark red, thin stripe dorso-laterally (Fig. 12A); flagellum pale; frons and gena unmarked.

THORAX. — Green. Pronotum with light red stripes laterally (Fig. 12A). Meso- and metanota unmarked. **Wings**: Venation green with black crossveins. Forewing costal crossveins 2–15, origin of Rs,

R-Rs crossveins 1–8, inner and outer gradates, Psm-Psc crossveins 3–8, and cubital and anal veins apical endings dark. Length (1.15 cm): width (0.37 cm) = ratio (2.97). Hindwing costal crossveins 4–12, R-Rs veins 1–4, and inner and outer gradates dark (Fig. 12). Length (1.06 cm): width (0.32 cm) = ratio (3.31).

ABDOMEN. — Green, unmarked. **Male**: Dorsal surface of 9th tergite + ectoproct deeply grooved; apex of 9th sternite with pair of lateral projecting forcipate lobes (Fig. 12D); dorso-laterally to ninth sternites two lobes bearing teeth and setae (Fig. 12C). Gonarcus broad with a dorso-medial, plate-like projection. Entoprocessus short. Arcessus large, apico-medially, decurved and acute. Gonosaccus with long setae (Fig. 12F, G). Gonapsis long and wide. **Female**: Spermatheca short. Bursa sac-like, wrinkled (Fig. 12E).

MATERIAL EXAMINED. — **Cuba**: Soledad, near Cienfuegos, 6–20 August, Banks, N., neotype male (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **São Paulo**: Taiuva, 23 July 1990, Scatolin, M. (2♀)(orange); 23 October 1990, Scatolin, M. (3♂)(orange); Taquaritinga, 8 January 1993, Xavier, A. L. Q. (3♂)(orange); 25 March 1993, Xavier, A. L. Q. (5♀); Jaboticabal, 22 February 1995, Freitas, S. (40♂35♀)(corn, guava, cotton, eucalyptus)(SDF/CAS); **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (3♂)(rubber).

***Ceraeochrysa everes* (Banks, 1920)**

DIAGNOSIS. — This species is a member of the *everes* species group with males having thick-based spines at the apex of sternite 8 + 9, a broad dorsal plate medially on the gonarcus; broad, vertically oriented entoprocesses; vertically elongate lateral arms of the gonarcus, and a field of gonocristae laterally below the apex of the ectoproct. Of these species, the more northern *C. costaricensis* has two dark spots on the pronotum rather than longitudinal stripes. *Ceraeochrysa everes* has a field of gonosetae which line up in rows and evenly curved ventral margin of the ectoproct, while *C. squama* has a randomly arranged field of gonosetae and a sclerotized ventrally projecting arm of the ectoproct at the apex of the dorsal apodeme.

HEAD. — Greenish yellow; frons and gena unmarked; maxillary and labial palpi pale; scape and pedicel green with middle of lateral surface bearing reddish brown diffuse spot, sometimes poorly defined; flagellum black (Fig. 13A).

THORAX. — Green. Pronotum somewhat yellowish with lateral reddish to chocolate brown stripe (Fig. 13A). Meso- and metanota unmarked. **Wings**: Venation mostly green, except for some crossveins dark (Fig 13B): Forewing costal crossveins in middle part, R-Rs crossveins at apical ends, and inner and outer gradates dark. Length (1.52 cm): width (0.46 cm) = ratio (3.0) Hindwing inner gradates dark. Length (1.35 cm): width (0.43 cm) = ratio (3.14).

ABDOMEN. — Green, unmarked; **Male**: Tergite 9 + ectoproct without visible ventral projection of apodeme (Fig. 13I). Gonapsis flattened, apex plate-like and upturned with row of small apical teeth and one larger dorso-apical tooth (Fig. 13H). Gonarcus strongly arched horizontally with a vertically oriented, medio-dorsal plate; lateral arms crescent-shaped. Arcessus membranous basally with a pair of hooks and two inflated lobes; apex bearing a medial hook and pair of lateral, decurved and medially-curved sclerotized lobes. Gonosaccus large with dense medial field of stout setae; two lateral lobes of gonosaccus with long setae, and between medial field of short gonosetae and lateral field of long gonosetae a field of tiny gonocristae. Lateral to the genital atria a field of tiny scales arranged in several lines. Apex of sternite 8 + 9 with large basal tubercles bearing setae arranged on two lateral lobes (Fig. 13C, D, E). **Female**: Spermatheca elongate, twisted, opening into a transversally wrinkled bursa (Fig. 13G). Subgenitale heavily sclerotized with a median projection (cremena), attached to bursa by a sclerotized plate.

MATERIAL EXAMINED. — **French Guiana**: Roches de Kourou, July, Le Moult, lectotype female (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **São Paulo**:

Jaboticabal, 20 January 1998, Freitas, S. (4♂)(corn)(SDF/CAS); 12 February 1995, (1♂)(guava); Luiz Antonio, 8 December 1993, Freitas, S. (1♂)(eucalyptus); Taquaritinga, 20 November 1992, Freitas, S. (1♂)(orange); 8 January 1993, Xavier, A. L. Q. (1♀)(orange); 5 March 1994, Xavier, A. L. Q. (1♂)(orange); Balsamo, 20 December 1997, Freitas, S. (1♂)(rubber); **Mato Grosso**: Itiquira, 10 September 1996, Scomparin, C. H. J. (2♀)(rubber); 23 September 1996, Scomparin, C. H. J. (1♀)(CAS).

Ceraeochrysa montoyana **(Navás, 1913a)**

DIAGNOSIS. — This species is closely related to other *cincta* group species that have dark antennae, such as *C. claveri*. However, in *C. claveri* the scape has a single stripe that continues onto the antennal basal membrane, and the spermatheca of *C. claveri* is not U-shaped. In addition, the two-striped scape of *C. montoyana* is a distinctive characteristic.

HEAD. — Vertex golden yellow; gena and frons pale yellow; scape yellow, with two red stripes, one dorso-laterally and the other dorso-centrally, the central one continuing onto antennal basal membrane (Fig. 14A); pedicel with red markings; flagellum black.

THORAX. — Green. Pronotum green with lateral dark red stripes (Fig. 14A). Meso- and metanota green, unmarked. **Wings**: Forewing venation mostly green, except costal crossveins, R-Rs crossveins, first Rs-Psm crossveins, Psm-Psc, apical and anal endings dark. Length (1.5 cm): width (0.54 cm) = ratio (2.78). Hindwing venation mostly green, except R-Rs crossveins dark (Fig. 14B). Length (1.38 cm): width (0.45 cm) = ratio (3.07).

ABDOMEN. — Green, without marks. **Female**: Spermatheca V-shaped, short, with long spermathecal gland (Fig. 14C). Subgenitale with two anterior lobes (Fig. 14D).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 25 March 1999, Freitas, S. (1♀)(guava).

Ceraeochrysa paraguaria **(Navás, 1920) new combination**

DIAGNOSIS. — This species is easily recognized by the four round small spots on the pronotum. Sometimes *C. paraguaria* is confused with *Plesiochrysa brasiliensis* when only external morphological characteristics are considered. However, *P. brasiliensis* is a larger, more robust species, with pronotum that is longer than wide. The pronotal spots of *C. paraguaria* are much darker and well-delimited, not diffuse. Finally, the bifurcate apex of sternite 8 + 9 in males is found only in *C. cubana* and *C. scapularis*.

HEAD. — Green; frons and gena unmarked; scape, pedicel and flagellum pale, unmarked.

THORAX. — Green. Pronotum with pair of dark red small spots laterally on either side (Fig. 15A). Meso- and metanota unmarked. **Wings**: Venation green, except for certain crossveins: forewing costal crossveins 4–10, origin of Rs, R-Rs crossveins, Psm-Psc crossveins 1–3, cubital and anal veins, imc lateral veins, and inner and outer gradates dark. Length (1.25 cm): width (0.41 cm) = ratio (3.04). Hindwing costal crossveins dark (Fig. 15B). Length (1.08 cm): width (0.33 cm) = ratio (3.27).

ABDOMEN. — Green, unmarked. **Male**: Tergite 9 + ectoproct deeply grooved dorsally forming two separate lobes. Sternite 8 + 9 apically bifurcate. Gonarcus narrow, lateral arms projecting vertically. Entoprocessus short and wide. Gonocornua long, tapered, reaching apex of arcessus. Arcessus triangular; apically acutely decurved. Gonosaccus with many long setae (Fig. 15H, I). Gonapsis slender with multi-pronged apical appendage (Fig. 15E). **Female**: Subgenitale short and wide (Fig.15F). Spermatheca short, with thick, twice-coiled spermathecal gland.

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Taquaritinga, 7 January 1993, Freitas, S. (9♂12♀)(orange); Jaboticabal, 17 February 1995, Freitas, S. (12♂)(orange); 20 October 1994, Cha-

gas, A. (2♀)(orange); 7 August 1996 Freitas, S. (4♂4♀) (guava); 20 October 1996, Freitas, S. (1♂1♀)(CAS).

REMARKS. — Navás described *Chrysopa paraguaria* in 1920. Later, Navás (1924) modified the name to *C. paraquaria*. However, Article 32.5.1 of the International Code of Zoological Nomenclature (ICZN 1999) states that "If there is in the original publication itself, without recourse to any external souce of information, clear evidence of an inadvertent error, such as a lapsus calami or a copyist's or printer's error, it must be corrected. Incorrect transliteration or latinization, or use of an inappropriate connecting vowel, are not to be considered inadvertent errors." Thus, without any indication in the original publication that this name was incorrectly spelled we have maintained the original spelling. Brooks and Barnard (1990) listed this species in *Plesiochrysa,* but the male genitalia, including elongate gonapsis, clearly indicate placement of this species in *Ceraeochrysa.*

***Ceraeochrysa sanchezi* (Navás, 1924b)**

DIAGNOSIS. — This is one of the species with dark antennae which can be separated most easily by characteristics of the male genitalia. The elongate ventral projection of the ectoproct and subapical dorsal projection of the ninth sternite are characteristic of this species, as is the pair of triangular fields of gonocristae projecting above and medial to the apex of the ninth sternite.

HEAD. — Yellow; frons and gena unmarked; maxillary and labial palpi pale; scape and pedicel yellow with lateral stripe brown, continued onto antennal basal membrane (Fig. 16A). Flagellum black. Maxillary and labial palpi pale.

THORAX. — Yellow. Pronotum with lateral stripe thick, red. Mesopraescutum and mesoscutum with lateral red spots (Fig. 16A). **Wings**: Venation mostly green with the following transverse veins black: forewing costal crossveins, origin of Rs, R-Rs crossveins; inner and outer gradates, Psm-Psc crossveins, anal and cubital vein apices, marginal forks and unforked apices. Length (1.35 cm): width (0.45 cm) = ratio (2.96). Hindwing veins: costal crossveins 4–10; R-Rs crossveins 5–8; inner and outer gradates dark (Fig. 16B). Length (1.14 cm): width (0.35 cm) = ratio (3.26).

ABDOMEN. — Yellow, without dark marks. **Male**: Tergite 9 + ectoproct with finger-like dorsal projection of dorsal apodeme above callus cerci and elongate ventral lobe of dorsal apodeme projecting ventrally from ectoproct (Fig. 16C). Sternite 8 + 9 with lateral concavities, which receive ventral ectoproct projection and subapical dorsally-projecting lobes (Fig. 16D). Gonapsis slender, apex with multi-lobed, spiny appendages (Fig. 16G). Gonarcus thick, lateral arms triangular in shape. Entoprocessus quite broad, apically obtusely pointed. Arcessus triangular, apex forming medial decurved point. Gonosaccus with three pair of long setae originating from stout bases. Posterior to gonosaccus a pair of triangular lobes with fields of gonocristae (Fig. 16I, J). **Female**: Bursa wrinkled, with a pair of large accessory glands (Fig. 16H). Spermatheca U-shaped with distal portion dilated (Fig. 16F). Subgenitale with median projection (cremena) and basal sclerotized plate (Fig. 16E).

MATERIAL EXAMINED. — **Cuba**: Havana, Playa Chivo, 18 December 1923, Cervera, holotype male (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **Rio Grande do Norte**: Assu, 6 June 1991, Freitas, S. (2♂2♀)(cantaloupe); **São Paulo**: Jaboticabal, 5 March 1992, Freitas, S. (1♀)(orange); 26 January 1995, Freitas, S. (1♀1♂)(guava); 2 May 1995, Seguin, L. D. (1♂); 4 December 1996, Freitas, S. (1♀)(CAS); 10 February 1998, Freitas, S. (1♂)(CAS); Taquaritinga, 7 January 1993, Freitas, S. (2♂)(orange); **Mato Grosso**, Itiquira, 7 September 1999, Freitas, S. (2♂1♀).

***Ceraeochrysa scapularis* (Navás, 1914)**

DIAGNOSIS. — This is a small species most closely related to *C. cubana* and *C. paraguaria.* All three species have a bifurcate apex of sternite 8 + 9 and gonosetae with large bases. Of the three, *C. scapularis* is the only one with dark antennae and two dark spots on the mesonotum.

HEAD. — Yellowish green. Gena and frons unmarked. Scape with lateral dark red stripe, pedicel dark-ringed; flagellum black (Fig. 17A). Maxillary and labial palpi pale.

THORAX. — Greenish yellow. Pronotum as long as wide with lateral red stripe (Fig. 17A). Mesonotum with pair of small dark red spots (Fig. 17A). **Wings**: Green longitudinal veins and black crossveins. Forewing crossveins darker than hindwing veins: costal crossveins 1–15, origin of Rs; R-Rs crossveins 1–9; inner and outer gradates; Psm-Psc crossveins 1–7; anals, cubitals and unforked marginal endings black (Fig. 17B). Length (1.1 cm): (0.35 cm) = ratio (3.03). Hindwing costal crossveins; R-RS crossveins, Rs-Psm crossveins, inner and outer gradates, and bases of Psm-Psc crossveins black. Length (0.99 cm): width (0.29 cm) = ratio (3.41).

ABDOMEN. — Greenish yellow. **Male**: Tergite 9 + ectoproct deeply grooved dorsally. Apex of sternite 8 + 9 with two forcipate lobes (Fig.17D). Gonarcus thick. Gonocornua slender and upturned. Arcessus triangle-shaped, apex tapered into a medial point. Gonosaccus with apical field of long setae (Fig. 17H, I). Posterior to gonosaccus two large lateral lobes with strong gonocristae and medial field of small gonocristae (Fig. 17C). Gonapsis elongate, narrow, widening subapically (Fig.17E). **Female**: Subgenitale without median projection (Fig. 17G). Bursa with two large accessory glands (Fig. 17F). Spermatheca U-shaped with broad spermathecal duct.

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Catanduva, January 1995, Silva, J. L. (1♂)(orange); Luiz Antonio, 9 December 1991, Freitas, S. (1♂)(eucalyptus); 5 October 1993, Crispolin, F. (3♀)(eucalyptus); Jaboticabal, 17 February 1995, Freitas, S. (10♂)(orange); 23 March 1995, Freitas, S. (1♂)(orange); 14 July 1995, Freitas, S. (1♂)(orange); 17 February 1995, Freitas, S. (4♀)(orange); 7 August 1996, Freitas, S. (2♂)(CAS).

Ceraeochrysa tenuicornis Adams and Penny, 1987

DIAGNOSIS. — This species cannot be separated with certainty from other species of *Ceraeochrysa* without study of the male genitalia. Of the male genital elements, the elongate gonocornua and ventral field of small gonosetae on the gonosaccus are most characteristic.

HEAD. — Yellowish green. Frons, gena and vertex unmarked. Scape, pedicel and flagellum pale; scape with a tiny dark spot on apico-lateral margin (Fig. 18A).

THORAX. — Pale green. Pronotum yellow with pale red stripe laterally (Fig. 18A). Meso- and metanota green, unmarked. **Wings**: Venation green, except some costal crossveins, R-Rs crossveins, gradates darkened; gradates darkly bordered. Forewing stigma unmarked. Length (0.96 cm): width (0.33 cm) = ratio (2.91). Hindwing venation green (Fig. 18B). Length (0.83 cm): width (0.25 cm) = ratio (3.32).

ABDOMEN. — Green. Tergites large, unmarked. **Male**: Dorsal apodeme of tergite 9 + ectoproct dark, forked at callus cerci, which has a few trichobothria (Fig. 18C). Sternite 8 + 9 densely covered by setae on conspicuous tubercles. Gonarcus thick, hardly arched, with fan-like lateral arms. Entoprocessus short and sharply decurved. Gonocornua straight, angled upward, reaching almost 2/3 length of arcessus. Arcessus divided: basal sclerite bearing two small horns and apical narrow, slender sclerite terminally decurved. Gonosaccus bearing laterally two pockets of long setae and ventrally a lobe with large field of tiny gonosetae, between them some small points in a vertical line (Fig. 18D, E). Gonapsis straight, unforked (Fig. 18F).

MATERIAL EXAMINED. — **Brazil**: **Amazonas**, Manaus, INPA campus, 23 April 1976, I. S. Goreyeb, holotype male (deposited at INPA), **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (1♂)(rubber).

REMARKS. — This is a species not known from south of the Amazon Basin and no females were collected during this project. For a description of the female, see Adams and Penny (1987).

Ceraeochrysa tucumana (Navás, 1919), new status

DIAGNOSIS. — *Ceraeochrysa tucumana* is a small species that resembles *Chrysoperla externa* in wing venation, but has stripes on the antennal scape and pronotum. The male genitalia and sternite 8 + 9 resemble *C. lineaticornis* (C. A. Tauber et al. 2000) and *C. berlandi* (Museum of Comparative Zoology material), but they have dark antennae and do not have the field of gonocristae below the gonosaccus.

HEAD. — Greenish yellow. Frons and gena without marks. Maxillary and labial palpi pale. Scape with lateral brown stripe, pedicel dark-ringed; flagellum pale (Fig. 19A).

THORAX. — Pale green. Pronotum with lateral stripe reddish brown (Fig. 19A). Meso- and metanota unmarked. **Wings**: Venation mostly green with some transverse veins black: forewing costal crossveins 1–13, origin of Rs, Rs-Psm crossveins 1–3, inner and outer gradates, and Psm-Psc crossveins. Length (1.09 cm): width (0.37 cm) = ratio (2.96). Hindwing costal crossveins 1–13, R-Rs crossveins; and inner and outer gradates dark (Fig. 19B). Length (0.92 cm): width (0.30 cm) = ratio (3.07).

ABDOMEN. — Greenish yellow with pale red spots on the tergites 2 and 3. **Male**: tergite 9 + ectoprocts deeply divided dorsally making two lateral lobes (Fig. 19E); apex of sternite 8 + 9 with pointed projection and thick-based setae (Fig. 19D). Gonarcus thick. Entoprocessus elongate, thin, decurved. Gonocornua vertically curved. Arcessus large, with medio-dorsal forked horn; apex upturned as sclerotized lobe with apical hook (Fig. 19I, J). Gonapsis slender (Fig. 19H). Gonosaccus with two lateral, protruding fields of long setae. Between gonosaccus and sternite 8 + 9 a membranous area with gonocristae. **Female**: Spermatheca short with thick spermathecal gland (Fig. 19F). Subgenitale with short median projection (Fig. 19G).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Taquaritinga, 8 January 1993, Xavier, A. L. (1♂)(orange); 1 June 1994, Narciso, R. (1♀)(orange); Luiz Antonio, 8 September 1993, Freitas, S. (1♂)(eucalyptus); 21 September 1993, Freitas, S. (3♂)(eucalyptus); 8 November 1993, Freitas, S. (2♂1♀)(eucalyptus); 21 December 1993, Freitas, S. (5♂3♀)(eucalyptus); 5 October 1993, Crispolin, F. (3♀)(eucalyptus); 13 July 1992, Freitas, S. (1♀)(eucalyptus); 29 April 1994, Freitas, S. (1♀)(CAS); 8 December 1998, Freitas, S. (1♀)(CAS).

REMARKS. — In his original description, Navás indicated that the type (sex not specified) was deposited in the museum at La Plata, Argentina. In their world list of chrysopid species, Brooks and Barnard (1990) placed this species as an "incertae sedis" at the end of the list. Phillip Adams found the type male at the Buenos Aires Museum, cleared and stained the genitalia, and made detailed sketches. These sketches were used to identify the above material. The genital elements include an elongate gonapsis, clearly placing this species in *Ceraeochrysa*.

Ceraeochrysa dislepis de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Bra-MT-Itiquira, P. E. Michelin 20/I/97, Freitas, S. Leg. 14♂."

DIAGNOSIS. — This species is a member of the *everes* species group with males having thick-based setae at the apex of sternite 8 + 9; a thick medial field of small gonosetae on the gonosaccus; a broad dorsal plate on the gonarcus; elongate, vertically-tapering, lateral arms to the gonarcus; and a pair of distinctive dorsal projections just posterior to the gonarcus. Of the four known species in the group, two [*C. costaricensis* (Penny 1997) and *C. squama*] have ventral projections from the ectoproct and gonapsis with lateral wings, while the other two species (*C. everes* and *C. dislepis*) have no ventral projection from the ectoproct and a gonapsis terminating in a vertical plate with teeth. Although similar, *C. dislepis* can be separated from *C. everes* by the central indentation of

the medial plate of the gonarcus and the lack of a field of tiny gonocristae laterally on the membrane below the ectoproct.

The name comes from "dis" meaning separated and "lepis" scales, describing the two lateral fields of small, scaly gonocristae on the gonosaccus.

HEAD. — Yellowish green. Vertex, frons and gena unmarked. Maxillary and labial palpi pale yellow, unmarked. Scape yellow with lateral brown stripe widening apically; pedicel as scape; flagellum black (Fig. 20A).

THORAX. — Green. Pronotum green with a dark red lateral stripe (Fig. 20A). Meso- and metanota unmarked. **Wings**: Forewing longitudinal veins green; costal crossveins, R-Rs crossveins, inner and outer gradates, anterior intersection of Psm-Psc crossveins, forked and unforked marginal veins, and margins near forks darkened. Length (1.3 cm): width (0.4 cm) = ratio (3.25). Hindwing apically acutely pointed, green except costal crossveins; R-Rs crossveins, apex of Rs, and outer gradates dark (Fig. 20B). Length (1.14 cm): width (0.37 cm) = ratio (3.08).

ABDOMEN. — Green, unmarked. **Male**: Dorsal apodeme of tergite 9 + ectoproct without ventral projection. Gonapsis flattened, anterior apex a vertical plate bearing two rows of teeth (Fig. 20E). Gonarcus lightly curved with dorsal medially-indented plate (Fig. 20C). Arcessus with dorso-lateral inflated lobes, a pair of small dorsal acute lobes, and decurved apical median hook with lateral lobes (Fig. 20D). Gonosaccus with lateral field of long setae and ventral fields of tiny gonocristae below setal fields (Fig. 20D). Apex of sternite 8 + 9 bearing setae with thick bases arranged on small lateral lobes (Fig. 20F). **Female**: Spermatheca twisted, but not coiled, apex with lateral alate projection (Fig. 20G). Bursa a large, transversely wrinkled sac with pair of large accessory glands.

OTHER MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 11 January1997, Freitas, S. (1♀ paratype)(rubber); 20 January 1997, Freitas, S. (1♂ paratype)(rubber); 14 September1998, Freitas, S. (1♂ paratype)(rubber); 10 September 1996, Scomparin, C. H. J. (1♀ paratype)(rubber); 4 November1996, Scomparin, C. H. J. (2♀1♂ paratypes)(rubber)(SDF/CAS); 30 December 1996, Scomparin, C. H. J. (1♂)(rubber); 18 July 1998, Freitas, S. (1♀ paratype)(rubber); 18 November 1996, Scomparin, C. H. J. (1♂ paratype)(rubber); **São Paulo**: Jaboticabal, 22 November 1995, Freitas, S. (1♀ paratype)(orange); 7 July 1996, Freitas, S. (1♂ paratype)(CAS); 30 September 1997, Freitas, S. (1♂ paratype)(orange); 7 July 1998, Freitas, S. (1♂ paratype)(orange); 17 November 1995, Freitas, S. (1♀ paratype)(orange); November 1995, Freitas, S. (1♂ paratype)(orange); Luiz Antonio, 8 December 1993, Freitas, S. (1♂ paratype)(eucalyptus); 21 December 1993, Freitas, S. (1♂ paratype)(eucalyptus); **Goias**: Cachoeira Alta, 10 June 1997, Freitas, S. (1♀ paratype)(rubber).

Ceraeochrysa dolichosvela de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled, "Bra-SP-Jaboticabal, FCAV, 20/I/98, 69, Freitas, S. Leg."

DIAGNOSIS. — The long, uncoiled shape of the spermatheca is not found in any other species.

The name "dolichovela" comes from the Greek *dolichos* meaning long, and refers to the long spermatheca and its vela in this species.

HEAD. — Vertex, gena and frons greenish yellow. Unmarked. Scape yellow-orange; pedicel black; flagellum black. Maxillary and labial palpi pale (Fig. 21A).

THORAX. — Green with a pale stripe on mid-line. Pronotum green with pale brown-red lateral stripe (diffuse in paratype) (Fig. 21A). Meso- and metanota unmarked. **Wings**: Venation mostly green, except costal crossveins, R-Rs transverse veins and gradates black. Length (1.49 cm): width (0.5 cm) = ratio (2.88). Hindwing venation mostly green, except R-Rs transverse veins and outer gradates black (Fig. 21B). Length (1.26 cm): width (0.41 cm) = ratio (3.07).

ABDOMEN. — Green with pale stripe along mid-line. **Female**: Spermatheca extremely long, slender, uncoiled; with long spemathecal duct (Fig. 21C). Posterior part of subgenitale bilobed, with large medial anterior projection.

OTHER MATERIAL EXAMINED. — **Brazil**: **Mato Grosso do Sul**: Corumba, 23 July 1995, Freitas, S. (1♀ paratype)(orange).

***Ceraeochrysa squama* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP, 20/01/95, SP14A, Freitas, S." (guava).

DIAGNOSIS. — This species is a member of the *everes* species group with character states listed under *C. dislepis*. The lateral arms of the gonapsis relate it most closely with *C. costaricensis* Penny, 1997, but it differs in having dark antennae and red stripes rather than spots laterally on the pronotum.

The name "squama" comes from the Latin for scale, and refers to the two fields of tiny gonocristae laterally on gonosaccus.

HEAD. — Vertex, frons and gena golden yellow, unmarked. Maxillary and labial palpi pale. Scape golden yellow, with small brown spot at apical dorso-lateral corner; pedicel with lateral brown stripe; flagellum black (Fig. 22A).

THORAX. — Green. Pronotum green with lateral dark red stripe. Meso- and metanota unmarked (Fig. 22A). **Wings**: Forewing venation mostly green with some transverse veins darkened, such as costal crossveins and R-Rs crossveins. Length (1.3 cm): width (0.46 cm) = ratio (2.83). Hindwing venation mostly green, except inner and outer gradates dark (Fig. 22B). Length (1.17 cm): width (0.36 cm) = ratio (3.25).

ABDOMEN. — Yellowish green, unmarked. **Male**: Dorsal apodeme of tergite 9 + ectoproct strongly sclerotized and with ventral projection (Fig. 22E). Gonapsis flattened, apex turned up as vertical plate-like lobe, but without teeth; subapical part with lateral alate projection apically decurved (Fig. 22G). Gonarcus strongly arched, with median plate-like projection as long as wide; lateral arms broadly rounded ventrally. Two inflated dorsal projections posteriad of gonarcus. Arcessus membranous basally with pair of small diverging lobes; apex medially acute and lateral membranous lobes. Gonosaccus large, with dense central field of small, stout setae; two lateral lobes with long setae flanked by a field of tiny gonocristae. Plate of randomly organized, sclerotized, pointed scales laterally on membranous wall of genital atrium, probably juxtaposed with ventral projection of ectoproct when depressed (Fig. 22A, B, C).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 30 September 1997, Freitas, S. (1♂ paratype); 24 April 1999, Takahashi, K. (1♂ paratype)(guava).

Genus *Chrysoperla* Steinmann, 1964

This is probably the most studied genus in the family. Adults are abundant in north temperate fields and yards, and are attracted to lights. They feed on grass pollen and are the most frequently considered candidates for inundative releases in fields and orchards for biological control. They are being mass-reared commercially for biological control programs in the U.S.A. (Tauber et al. 2000).

In a recent revision of the genus, Brooks (1994) found 35 species distributed world-wide, but with a preponderance of species in the Holarctic Region. Adult males of this genus have one distinctive structural feature. Sternite 8 + 9 of males is subapically constricted, giving the apex the appearance of a small apical lobe (Figs. 23E, 24D, 25C). All New World species have red genae, and lateral setae on the pronotum have thickened bases. However, other chrysopids have red genae and females must be identified with great caution. In this study we have found three species; the adults can be distinguished using the following key.

KEY TO THE SPECIES OF *CHRYSOPERLA* IN BRAZILIAN AGRO-ECOSYSTEMS
(modified from Brooks, 1994)

1. Forewing gradates green 2
1'. Forewing gradates black . . . . . *C. defreitasi*

2. Male arcessus only weakly decurved apically (Fig. 24I) . . . . . *C. externa*
2'. Male arcessus strongly decurved apically (Fig. 25E) . . . . . *C. raimundoi*

Chrysoperla defreitasi Brooks, 1994

DIAGNOSIS. — *Chrysoperla defreitasi* is closely related to *C. externa* and *C. raimundoi*. *Chrysoperla defreitasi* may be differentiated from the other two species by black gradate crossveins vs. green crossveins in *C. externa* and *C. raimundoi*.

HEAD. — Greenish yellow; red gena, lateral clypeus and lateral labrum; narrow red stripe on fronto-clypeal suture; antenna with scape and pedicel pale yellow, flagellum pale; maxillary palpi black, marked dorsally (Fig. 23C).

THORAX. — Yellowish green with yellow stripe on dorsal mid-line; Pronotum with narrow reddish lateral stripe (Fig. 23A); meso- and metanota unmarked. **Wings**: Forewing venation mostly green with black gradates, cubital and anal veins black; forewing length (1.3 cm): width (0.37cm) = ratio (3.5). Hindwing length (1.19 cm): width (0.37 cm) = ratio (3.22).

ABDOMEN. — Green with yellow stripe on mid-line. **Male**: long apodeme of tergite 9 forked on callus cerci; lip of sternite 8 + 9 short (Fig. 23E); many gonocristae; gonarcus large, arched; arcessus broad, tapered subapically, apex curved; gonosaccus with many gonosetae (Fig. 23F, G); tignum elongate, acumen long (Fig. 23D).

MATERIAL EXAMINED. — **Brazil**: Jaquaritingas, 15 November 1992, S. de Freitas, holotype male (MZ, USP), **São Paulo**: Jaboticabal, 7 August 1995, Seguim, L. D. (1♂); August 1996, Freitas, S. (1♀); 16 December 1998, Freitas, S. (1♂); **Mato Grosso**: Itiquira: 7 September 1999, Freitas, S. (5♂2♀)(rubber)(SDF/CAS).

Chrysoperla externa (Hagen, 1861)

DIAGNOSIS. — This species can be separated from *C. defreitasi* by the dark gradate veins of the forewing in *C. defreitasi*, and from *C. raimundoi* by the male's more exaggerated curvature of the tip of the arcessus in *C. raimundoi*.

HEAD. — Vertex, greenish yellow, flattened with several transverse striations (Fig. 24A); frons and clypeus unmarked; gena with red spot not reaching ventral margin near maxillae; black dorsal marks on maxillary palpi (Fig. 24C); scape and pedicel pale yellow; flagellum basally pale and apically fuscous.

THORAX. — Green with yellow stripe on dorsal mid-line; pronotum with grayish latero-anterior spot; base of setae black (Fig. 24A); meso- and metanota without marks. **Wings**: Venation yellowish green (Fig. 24B); forewing length (1.23 cm): width (0.31 cm) = ratio (4.0). Hindwing length (1.19 cm): width (0.36 cm) = ratio (3.31).

ABDOMEN. — Greenish yellow with yellow stripe on dorsal mid-line, unmarked. **Male**: Tignum elongate, narrow with medial acumen small, triangular (Fig. 24E); gonarcus hardly curved; arcessus narrow, apex slightly curved; gonosaccus with many long gonosetae (Fig. 24I, J); numerous gonocristae (Fig. 24H). **Female**: Long subgenitale (Fig. 24G); spermatheca short (Fig. 24F).

MATERIAL EXAMINED. — **Brazil: São Paulo**: Taiuva, 19 July 1990, Pazini, W. (6♂6♀)(orange); Jaboticabal, 10 August 1992, Freitas, S. (2♂)(guava); Taquaritinga, 7 January 1993 Freitas, S. (6♂1♀)(orange).

REMARKS. — *Chrysoperla externa* is probably the most common chrysopid in the Neotropical region and occurs associated with many graminous plants, apple trees, cotton, cantaloupe, eucalyptus, rubber and cashew nut.

***Chrysoperla raimundoi* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP, FCAV, 20-04-95, 1♂, Freitas, S."

DIAGNOSIS. — *Chrysoperla raimundoi* closely resembles *C. externa* and *C. defreitasi*. From *C. externa* it can be differentiated on cephalic characters: the vertex of *C. externa* is as long as wide and less striated. The head is also conspicuously different between them: *C. raimundoi* has a more elongate clypeus. The male genitalia also display some differences, e.g., the apex of the arcessus of *C. raimundoi* is quite curved and the gonosaccus bears longer gonosetae. *Chrysoperla defreitasi* can be differentiated from *C. raimundoi* by the smooth vertex, frons and red clypeus as well as the dark gradate veins of the forewing of *C. defreitasi*.

The name "raimundoi" is given in honor of Agricultural Engineer Raimundo José Ferreira who collected the type series.

HEAD. — Pale green; vertex raised with several transverse striations; diffuse red post-ocular spot; frons yellowish without marks, gena red throughout; dorsally black maxillary and labial palpi; scape and pedicel without marks (Fig. 25A).

THORAX. — Green with thick median yellow band; pronotum with lateral narrow reddish brown band not reaching the posterior corner. **Wings**: Venation green (Fig. 25B); forewing length (1.22 cm): width (0.40 cm) = ratio (3.02). Hindwing length (1.02 cm): width (0.31 cm) = ratio (3.29).

ABDOMEN. — Green with median yellow band. Tergite 9 + ectoproct apodeme branched below callus cerci; acumen of tignum, long slightly swollen apically; gonosaccus with numerous gonosetae; arcessus apex quite curved, lacking dorsal striation; gonarcus with narrow lateral arms; gonosaccus with numerous long gonosetae with crooked apices and ventral large gonocristae (Fig. 25C, D, E).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 8 June 1995, Ferreira, R. J. (5♂ paratypes)(guava), May 1995, Ferreira, R. J. (3♂ paratypes)(guava)(SDF/CAS).

Genus Chrysopodes Navás, 1913c

This is among the most diverse genera of New World Chrysopini. As with most genera in this tribe, the genus is usually defined by elements of the male genitalia, notably the lack of a tignum and gonapsis, presence of gonarcus with arcessus reduced to a curved, triangular, apically tapered sclerite. The ventral branch of the dorsal apodeme of the ectoproct is often acutely tapered apico-medially.

This is a New World genus distributed from south Florida, U.S.A. and Baja California, Mexico south to Argentina. The genus is usually divided into two subgenera (*Chrysopodes* and *Neosuarius* Adams and Penny, 1987) based principally on the shape of the adult mandibles. Members of *Chrysopodes* (*Chrysopodes*) have mandibles which are long and scythe-like, while members of *Chrysopodes* (*Neosuarius*) have mandibles which are considerably stouter than the nominate subgenus (Adams and Penny 1987). In most adult specimens, the mandibles are tucked under the labrum and difficult to see. The easiest way to view the mandibles is to separate the head from the body and macerate it in 10% KOH. Because this disarticulates the body and makes it more difficult to view other markings on the head, we have tried to avoid using mandibular characters in the species key. Most of the species of *C.* (*Neosuarius*) found west of the Andes in South America are dark in color, but species of *C.* (*Neosuarius*) found east of the Andes and in Central America are primarily green in color. Species of *C.* (*Chrysopodes*) generally have proportionally broader wings, a broader costal area, and longer forewing setae.

Brooks and Barnard (1990) listed 21 species in *C.* (*Chrysopodes*) and 11 species in *C.* (*Neosuarius*); Penny (1998) added two more species of *C.* (*Chrysopodes*), and Penny (2001) one additional species of *C.* (*Neosuarius*) from Costa Rica.

KEY TO THE SPECIES OF *CHRYSOPODES* OF BRAZILIAN AGRO-ECOSYSTEMS

1. Meso- and metanota with dark spots (Fig. 29A) 2
1′. Meso- and metanota without dark spots (Fig. 28A) 4

2. One pair circular spots (Fig. 29A) or completely pale (Fig. 28A) on mesonotum; frons mostly pale, at most with transverse dark stripe (Fig. 26C). 3
2′. Irregular spots forming partial stripe on mesonotum (Fig. 30A); clypeus, gena, part of frons and lateral margin of vertex red (Fig. 30C) . . . . . *C.* (*C.*) *copia*

3. Antenna with flagellum black; dorso-medial stripe of scape incomplete, dark; two pair of lateral spots on pronotum; mesopraescutum completely pale (Fig. 29A); forewing without crossvein shading (Fig. 29B) . . . . . *C* (*C.*) *adynatos*
3′. Antenna with flagellum pale; dorso-medial stripe of scape reaching both proximal and apical margins; single pair of elongate dark spots on pronotum, extending onto anterior margin of mesopraescutum (Fig. 34A); forewing crossveins and gradates extensively shaded (Fig. 34B) . . . . . *C.* (*C.*) *nigropicta*

4. Frons with semicircular red stripes below antennal pits (Fig. 26C) 8
4′. Frons without stripes (Fig. 32A) 5

5. Gena with two longitudinal dark stripes; clypeus and labrum laterally dark (Fig. 27D) 6
5′. Gena completely red; clypeus and labrum pale (Fig. 36C) 7

6. Apical forewing veins of male swollen (Fig. 27E); lateral arms of gonarcus longer than width between arms (Fig. 27H) . . . . . *C.* (*C.*) *polygonica*
6′. Apical forewing veins of male not swollen (Fig. 26B); lateral arms of gonarcus shorter than width between arms (Fig. 32F) . . . . . *C.* (*C.*) *delicata*

7. Scape with dark lateral spot (Fig. 36A); forewing with five inner and seven outer gradate veins (Fig. 36B); spermatheca short, with short, uncoiled spermathecal duct (Fig. 36E) . . . . . *C.* (*N.*) *karinae*
7′. Scape without dark lateral spot (Fig. 26A); forewing with three inner and six outer gradate veins (Fig. 31A); spermatheca long and multiply-coiled, as is spermathecal duct (Fig. 31F) . . . . . *C.* (*C.*) *crocinus*

8. Vertex and frons with dark marks between antennal bases (Fig. 33C) . . . . . *C.* (*C.*) *elongata*
8′. Vertex and frons without dark marks between antennal bases (Fig. 26A) 9

9. Male ectoproct with two ventral projections (Fig. 35D) 10
9′. Male ectoproct with single ventral projection, which is an extension of the dorsal apodeme (Fig. 26I) *C.* (*C.*) *lineafrons*

10. Lateral arm of gonarcus longer than high (Fig. 27I); small ventral peg on sternite 8 + 9 (Fig. 26I) . . . *C.* (*C.*) *spinella*
10′. Lateral arm of gonarcus much higher than long (Fig. 35H); sternite 8 + 9 without ventral peg (Fig. 35D) *C.* (*C.*) *divisa*

Chrysopodes (*Chrysopodes*) *lineafrons* Adams and Penny, 1987

DIAGNOSIS. — Of the species with reddish bands below the antennae and dark palpi, *C. lineafrons* males can be recognized by the strongly arched apex to the ninth sternite, the single ventral projection from the ectoproct, and the triangular shape of the lateral arms of the gonarcus. Females can be recognized by the heavily-sclerotized knob at the apex of sternite 7.

HEAD. — Vertex glossy green with two red marks lateral to central raised area (Fig. 26A). Frons green with narrow red crescentic band below each antenna (Fig. 26C). Gena red, palest on central part. Distal maxillary palpimere black; fourth palpimere dorsally black. Distal labial palpimere black (Fig. 26C). Scape and pedicel greenish yellow, unmarked; flagellum pale.

THORAX. — Green with yellow stripe along mid-line. Pronotum with lateral suffused pale brown stripe (Fig.26A). Meso- and metanota unmarked. **Wing**: Forewing venation mostly green with some transverse veins black, such as costal crossveins, R-Rs crossveins, base of Rs-Psm, inner and outer gradates and apices of anal veins (Fig. 26B). Length (1.4 cm): width (0.77 cm) = ratio 3.0. Hindwing

acute, venation green, except costal crossveins dark (Fig. 26B). Length (1.24 cm): width (0.39 cm) = ratio 3.18.

ABDOMEN. — Green with yellow stripe on dorsal mid-line. **Male**: Dorsal apodeme of tergite 9 + ectoproct heavily sclerotized with apical tooth projecting ventro-medially (Fig. 26I). Apex of sternite 9 with conical-based setae (Fig.26E), ventrally, deeply concave on posterior half (Fig. 26I). Gonarcus narrow, strongly arched with long triangular lateral arms. Arcessus short, thin, evenly tapered to pointed apex, which has heavily-sclerotized basal apodemes (Fig. 26F, G). Gonosaccus simple sac. **Female**: Posterior margin of sternite 7 with heavily-sclerotized knob. Spermathecal duct short (Fig. 26H).

MATERIAL EXAMINED. — **Brazil**: **Amazonas**, Manaus, 17 February 1977, N. D. Penny, holotype male (deposited at INPA, Manaus), **São Paulo**: Jaboticabal, 14 January 1999, Freitas, S. (2♂2♀)(guava); 26 April 1999, Takahashi, K. (1♂)(orange)(CAS); São Jose do Rio Preto, 20 April 1997, Freitas, S. (1♂); Taquaritinga, 5 March 1994, Xavier, A. L. (1♀)(CAS).

***Chrysopodes* (*Chrysopodes*) *polygonica* Adams and Penny, 1987**

DIAGNOSIS. — The male can be recognized by the swelling of the forewing apical gradates. Although males of other species of *Chrysopodes* have swollen veins, this usually involves the radial sector and associated veins more basal on the forewing. Only males of *C. polygonica* have an unswollen radial sector and swollen gradates and apical forks. The female also has a unique characteristic—a field of small setae on the knob at the apex of the seventh sternite.

HEAD. — Yellow with red and black markings. Gena with two black stripes continued onto lateral border of clypeus (Fig. 27C). Frons with small black spot close to gena. Vertex with postocular red spots at the posterior margin (Fig. 27A). Scape, pedicel and flagellum pale, unmarked. Maxillary and labial palpi black (Fig. 27C).

THORAX. — Green with yellow stripe on mid-line. Pronotum with pale brown stripe laterally (Fig. 27A). Meso- and metanotum without markings. **Wings**: Forewing venation green, except some costal crossveins, R-Rs crossveins, first five Rs-Psm crossveins, gradates and marginal forks dark. All transverse veins show at least a little shading. Apical gradate crossvein and apical branches of Rs swollen in male wings; female gradates normal. Forewing length (1.40 cm): width (0.47 cm) = ratio (2.98). Hindwing costal crossveins black; gradates black with brown shading (Fig. 27B). Length (0.86 cm): width (0.27) = ratio (3.18).

ABDOMEN. — Green with yellow stripe on mid-line. Tergites unmarked. **Male**: Sternite 8 + 9 with knob at mid-length and apical setae on conical bases (Fig. 27G). Ventro-caudal margin of ectoproct prolonged into an acute point. Large subanal plate densely setose. Gonarcus elongate, fragile, slender. Arcessus elongate, digitiform, apically decurved. Gonosaccus dorsally with few long gonosetae, and extended ventrally as lobe with numerous small setae (Fig. 27H, I). **Female**: Sternite 7 with terminal knob densely covered by small setae (Fig. 27F). Spermatheca bulbously inflated. Spermathecal duct short (Fig. 27J). Subgenitale with small rounded posterior lobes and no anterior prolongation (Fig. 27K).

MATERIAL EXAMINED. — **Brazil**: **Amazonas**, Manaus, Parque das Laranjeiras, 22 January 1981, J. R. Arias, holotype male (deposited at INPA, Manaus), **São Paulo**: Jaboticabal, 10 March 1999, Freitas, S. (1♂)(orange); 18 March 1998, Shinirara, A. (1♀); **Mato Grosso**: Itiquira, 14 December 1996, Scomparin, C. H. J. (1♀)(rubber); 11 January 1997, Freitas, S. (3♂1♀)(rubber); 13 January 1997, Freitas, S. (4♂1♀)(rubber)(SDF/CAS); 20 January 1997, Freitas, S. (1♀)(CAS); 23 February 1998, Freitas, S. (2♂3♀)(rubber).

Chrysopodes (*Chrysopodes*) *spinella* Adams and Penny, 1987

DIAGNOSIS. — The double ventral projections of the ectoproct appear to associate this species with *C. collaris* and *C. divisa* in *Chrysopodes* (*Neosuarius*) (Adams and Penny, 1987). However, *C. collaris* has a much broader body and neither of these species have the unique knob at mid-length on the ninth sternite. *Chrysopodes* (*Chrysopodes*) *lineafrons* has both subantennal red bands and knob at mid-length of the ninth sternite, but has only a single ventral projection of the ectoproct. Females of these four species can be separated only with great difficulty.

HEAD. — Yellow with red markings. Vertex glossy with red postocular spot from hind margin forward only to mid-length (Fig. 28A). Frons yellow with interrupted red band extending from eye margin medially below antennal sockets. Gena red. Maxillary distal palpimere black, fourth palpimere dorsally black and third darkened. Labial distal and basal palpimeres black. Scape and pedicel yellow, unmarked; flagellum stramineous (Fig. 28A, D).

THORAX. — Green with yellow stripe on mid-line. Pronotum longer than wide, with stripe dorsolaterally. Meso- and metanotum unmarked (Fig. 28A). **Wings**: Wing venation mostly green, including pterostigma. Forewing costal crossveins, basal R-Rs crossveins anterior and posterior intersections, origin of Rs, gradates, marginal forks and anterior ends of Psm-Psc all dark (Fig. 28B); forewing length (1.21 cm): width (0.41 cm) = ratio (2.95). Hindwing with costal crossveins and gradates dark (Fig. 28B). Length (1.06 cm): width (0.34 cm) = ratio (3.12).

ABDOMEN. — Green. **Male**: Dorsal apodeme of ectoproct with two ventral projections. Ninth sternite with small knob at mid-length. Gonarcus strongly arched horizontally, but with little vertical arch. Lateral arms of gonarcus elongate and apically rounded. Arcessus short, triangular (Adams and Penny 1987). **Female**: Spermatheca elongate with vela in form of crooked coil. Bursal duct elongate and multiply coiled (Fig. 28D).

MATERIAL EXAMINED. — **Brazil**: **Pará**, São Geraldo, 30 November to 8 December 1982, J. R. Arais, holotype male (deposited at INPA, Manaus), **São Paulo**: Jaboticabal, February 1992, Scomparin, C. H. J. (1♀)(orange).

Chrysopodes (*Chrysopodes*) *adynatos* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 12-VII-96 Scomparin, C. H. J." (rubber).

DIAGNOSIS. — Only two other species of *Chrysopodes* in the region have dark spots on the mesonotum. However, the spots on the other species are more diffuse and not as well delimited. The thin central arch of the gonarcus is also distinctive, as are the dark antennae.

The name "adynatos" is taken from the Greek meaning weak, or without strength, and refers to the thin medial arch of the gonarcus in this species.

HEAD. — Yellow. Gena, frons and vertex without marks. Scape with mid-dorsal, tapered black spot; pedicel and flagellum black.

THORAX. — Pronotum pale yellow, with two pairs of black marks, each pair appears as short lateral stripe (Fig. 29A). Mesonotum with pair of rounded black spots on scutum (Fig. 29A). Metanotum unmarked. **Wings**: Forewing venation green, except costal crossveins, R-Rs crossveins, first Rs-Psm veins; Psm-Psc crossveins and first two unforked marginal veins dark (Fig. 29B). Length (1.3 cm): width (0.45 cm) = ratio (3.25). Hindwing venation green. Length (1.18 cm): width (0.34 cm) = ratio (3.47).

ABDOMEN. — Yellow, unmarked. **Male**: Genitalia weakly sclerotized. Gonarcus thin with lateral projections similar to gonocornua but originate from lateral arms of gonarcus. Arcessus longer than wide, with broad medial decurved hook. Gonosaccus with long setae (Fig. 29C, D).

MATERIAL EXAMINED. — Known only from the holotype.

***Chrysopodes* (*Chrysopodes*) *copia* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP; FCAV Macadamia; 12/11/94; Freitas, S. SP70."

DIAGNOSIS. — The most distinctive characteristic of this species is the almost completely red coloration of the frons, as well as the extensive red coloration on meso- and metanota. The red coloration of the frons would appear to be an exaggerated extension of the transverse red bands found in several other species. However, these other species have dark palpi, not pale palpi as in this species.

This species appears most closely associated with *C.* (*Chrysopodes*) *indentata* Adams and Penny, 1987, because of the pale palpi and especially the short, broad gonarcus and arcessus. However, they can be separated because *C.* (*Chrysopodes*) *copia* has the almost completely red frons and clypeus, the ventral bump at mid-length of the male ninth sternite is not as developed, and the gonarcus is more laterally arched.

The name "copia" comes from the Latin for abundance or plenty and refers to the similarity to *C. indentata.*

HEAD. — Golden yellow with red markings. Clypeus, frons and gena completely red, except for restricted area below antennae sockets and between anterior tentorial pits (Fig. 30C). A red stripe runs from gena to posterior eye margin laterad of antennal sockets (Fig. 30A). Vertex yellow, except laterally close to eye margin red. Scape, pedicel and flagellum pale without marks. Maxillary and labial palpi pale, unmarked.

THORAX. — Slightly greenish yellow. Pronotum with diffuse red lateral stripes continuing onto meso- and metanotum (Fig. 30A). **Wings**: Forewing green with some crossveins totally or partially dark, such as posterior junctions of costal crossveins, R-Rs endings, Rs-Psm endings, inner and outer gradates, Psm-Psc crossveins, apex of marginal forked and unforked crossveins; and apical Psm-Psc crossveins shaded (Fig. 30B). Length (1.27 cm): width (0.43 cm) = ratio (2.95). Hindwing venation mostly green, except costal crossveins at subcostal juncture and outer gradates dark. Length (1.18 cm): width (0.36 cm) = ratio (3.28).

ABDOMEN. — Slightly greenish yellow, unmarked. **Male**: Ventral branch of dorsal apodeme of tergite 9 + ectoproct quite large (Fig. 30D). Sternite 8 + 9 with knob on ventro-medial area (Fig. 30D). Gonarcus evenly curved horizontally, barely curved vertically; lateral arms with long dorsal plate, slightly upturned apically (Fig. 30F, G). Arcessus short, broader than long, with a field of quite short setae distally on medial apex. Gonosaccus bearing scattered long setae dorsally and field of many small setae ventrally. **Female**: Spermatheca vela twice coiled, then extended as a convoluted coil. Bursal duct short, twisted (Fig. 30H); subgenitale bilobed without medial projection (Fig. 30E).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 22 January 1994, Freitas, S. (1♂ paratype)(on macadamia)(CAS); 22 February 1994, Freitas, S. (3♂1♀ paratypes)(corn); 22 February 1995, Freitas, S. (1♀ paratype)(guava)(CAS); 22 March 1995, Freitas S. (2♀ paratypes)(corn); 10 December 1996, Freitas, S. (1♂ paratype)(corn); Ribeirao Preto, October 1995, Pinotti, F. (2♀ paratypes); Bebedouro, 14 October 1995, Fonseca, C. (1♂ paratype); Birigui, 11 July 1994, Scomparin, C. H. J. (1♂ paratype)(corn).

***Chrysopodes* (*Chrysopodes*) *crocinus* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo.Brazil, labeled "Birigui, SP, 21-II-96, Scomparin, C. H. J." (corn).

DIAGNOSIS. — The most distinctive feature of this species is the lack of dark or red markings on head and thorax. The male gonarcus is similar to most species in the genus. However, a few features set this species apart. The dark antennal flagellum is found only in two other species of *C.* (*Chrysopodes*)—*C.* (C.) *adynatos* and *C.* (C.) *victoriae*—both of which have dark or red markings on

the thorax. Several South American species of *C.* (*Neosuarius*) have dark antennae, but again there are extensive dark markings on both the head and thorax, as well as dark maxillary palpi.

There appears to be no ventro-medial point to the male ectoproct of *C.* (*C.*) *crocinus*, unlike most species in this genus. (This character state could develop late in the maturation of the emerged adult). Most distinctive is the basal point on the male sternite 8 + 9. Less easily discernible are the hirsute tip of the arcessus and the two small patches of gonosetae on the gonosaccus.

The name "crocinus" comes from the Latin for saffronlike, referring to the coloration of the antennal scape and pedicel.

HEAD. — Yellow. Frons, clypeus and vertex pale yellow, unmarked. Gena slightly darkened. Scape, pedicel and basal membrane yellow-orange, without marks; flagellum black. Vertex without postocular marks. Labial and maxillary palpi pale.

THORAX. — Green with a pale stripe on mid-line. Pro-, meso- and metathorax unmarked. **Wings**: Forewing venation green, except costal crossveins and R-Rs crossveins somewhat darkened. Intramedian cell ovate, with swollen base. Base of Psc near intramedian cell swollen with many microtrichiae (Fig. 31C). Pterostigma unmarked. Length (1.18 cm): width (0.41) = ratio (2.88). Hindwing acute; venation green; stigma unmarked. Length (1.12cm): width (0.35 cm) = ratio (3.20)(Fig. 31A).

ABDOMEN. — Green with yellow stripe on middle line. Tergites unmarked. **Male**: Dorsal apodeme of ectoproct not apically forked. Sternite 8 + 9 with knob near anterior margin (Fig. 31B). Arcessus short, straight, triangular with dorsal setae most abundant. Gonosaccus with two groups of three setae, each with large conical base. Gonarcus wider than long, with thin, broadly lobate, parallel arms (Fig. 31D, E). **Female**: Sternite 7 with apical knob-like projection (Fig. 31G). Spermatheca long, coiled. Spermathecal gland and bursal accessory glands long, coiled (Fig. 31F). Subgenitale saccate (Fig. 31H).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Birigui, 2 February 1996, Scomparin, C. H. J. (2♂1♀ paratypes).

Chrysopodes (*Chrysopodes*) *delicata* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo. Brazil, labeled "Itiquira, MT, Seringueira, PEM-507, 31/12/96 Scomparin, C. H. J. Armadilha—melaco" (rubber).

DIAGNOSIS. — The double dark genal stripes, lack of subantennal bands, and dark palpi link *C. delicata* with *C. polygonica*. However, males of *C. polygonica* have much longer lateral arms of the gonarcus and swollen gradate and apical endings of forewing veins.

The name "delicata" comes from the Latin for delicate, tender, or dainty, and refers to the small size of the gonarcus.

HEAD. — Yellow. Frons and vertex pale yellow, unmarked. Gena with two large black stripes continuing onto margin of clypeus (Fig. 32A, C). Maxillary palpimeres 1–4 and half of fifth black. Scape, pedicel and flagellum pale (Fig. 32A). Mandibles scythe-like (Fig. 32E).

THORAX. — Green with yellow stripe on mid-line. Pro-, meso-, and metanotum unmarked. **Wings**: Forewing green, except most crossveins dark and with slight shading; gradates more shaded than other crossveins. Pterostigma green, unmarked. Forewing length (1.10 cm): width (0.38 cm) = ratio (2.89). Hindwing costal crossveins, gradates and origin of marginal forks dark (Fig. 32B). Length (0.96 cm): width (0.29 cm) = ratio (3.31).

ABDOMEN. — Green with yellow stripe on mid-line. Tergites unmarked. **Male**: Posterior margin of ectoproct with long setae on thick bases. Sternite 8 + 9 with large knob at midlength and narrowed apex (Fig. 32D). Male genitalia lightly sclerotized. Lateral arms of gonarcus reduced to tiny plates.

Arcessus more sclerotized than other genital structures; apex smooth, without setae, decurved. Gonosaccus with field of long setae (Fig. 32F,G).

MATERIAL EXAMINED. — Known only from the holotype.

***Chrysopodes* (*Chrysopodes*) *elongata* de Freitas and Penny, new species**

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil "Luiz Antonio, SP, Faz. Guatapara, 29-IV-94, Freitas, S." (eucalyptus).

DIAGNOSIS. — This species is a member of a group of species with interrupted transverse band across the frons and dark palpi. *Chrysopodes elongata* can be separated from *C. lineafrons* and *C. spinella* by the small dark spots between the antennal bases. Additionally, females can be separated by the long, narrow sternite 7 with no knobs, and especially by the long, thin spermatheca.

The name "elongata" comes from the Latin for prolonged, and refers to the long and narrow spermatheca.

HEAD. — Yellow, marked with red. Frons yellow with narrow, medially interrupted, transverse red line below antenna sockets; transverse line continued along ocular margin to posterior margin of vertex. Gena red. Tiny red spot between antenna on frons and anterior part of vertex. Scape, pedicel and flagellum pale. Fourth maxillary palpimere and half of fifth palpimere dark. Labial palpimeres dark (Fig. 33A, C).

THORAX. — Green with yellow stripe on mid-line. Cervical sclerite red. Pronotum with pale brown stripe dorso-laterally (Fig. 33A). Meso- and metanotum unmarked. **Wing**: Venation green, except costal crossveins, R-Rs crossveins, gradates, origin of Rs, Rs-Psm crossveins and marginal forks dark (Fig. 33B). Forewing pterostigma unmarked. Length (1.10 cm): width (0.38 cm) = ratio (2.89). Hindwing costal crossveins and gradates dark. Length (0.97 cm): width (0.30 cm) = ratio (3.23).

ABDOMEN. — Green with yellow stripe on mid-line. Tergites without markings. **Female**: Sternite 7 narrowed at apex. Spermatheca slender; duct extends as thin, filamentous tube to bursa copulatrix (Fig. 33D, F). Subgenitale with small, medial projection (Fig. 33G).

MATERIAL EXAMINED. — Known only from the holotype.

***Chrysopodes* (*Chrysopodes*) *nigropicta* de Freitas and Penny, new species**

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo Brazil, labeled "Bra-MT-Itiquira, P. E.Michelin; 18/VIII/98, Freitas, S. 78A" (rubber).

DIAGNOSIS. — The black marks on pro- and mesonotum are unusual, as is the heavy shading of forewing crossveins. Of the species having dark markings on the mesonotum, *C. adynatos* has dark antennae and well delimited dark mesonotal spots. Although *C. indentata* also has pale antennae, the dark markings of pro- and mesonotum are not found in this species. However, the two species appear related because they both have an exceptionally heavily-sclerotized spermathecal duct.

The name "nigropicta" comes from the Latin *nigra* for black or dark and *pictus* for painted or colored, referring to the dark markings of pro- and mesonota.

HEAD. — Greenish yellow. Vertex green, unmarked. Frons, clypeus and gena yellow. Scape yellow with mid-dorsal black stripe; pedicel and flagellum pale. Maxillary and labial palpi pale (Fig. 34A).

THORAX. — Green; pronotum with lateral black stripes from middle to posterior margin. Mesonotum with pair of dark spots laterally on prescutum and second pair of lateral circular spots on middle of scutum. Metanotum unmarked (Fig. 34A). **Wings**: Forewing veins green, with costal crossveins, R-Rs crossveins, first Rs-Psm crossvein, gradates, Psm-Psc crossveins after intramedian cell, apex of marginal forks, anterior marginal unforked veins and endings of anal veins dark. Almost all crossveins in posterior half of forewing heavily shaded. Length (1.41 cm): width (0.5 cm) = ratio

(2.83). Hindwing venation mostly green, except middle part of Rs and gradates dark (Fig. 34B). Length (1.24 cm): width (0.40 cm) = ratio (3.10).

ABDOMEN. — Greenish yellow. **Female**: Spermatheca U-shaped. Spermathecal gland with distal part exceptionally heavily sclerotized. Bursa sac-like, with two accessory glands (Fig. 34C).

MATERIAL EXAMINED. — Known only from the holotype.

Chrysopodes (*Neosuarius*) *divisa* (Walker, 1853)

DIAGNOSIS. — This is one of several species which has medially interrupted, red bands across the frons below the antennae. The double ventral projection of the ectoproct and tiny setae at the tip of the arcessus can be found in the closely related *C. collaris* (Schneider, 1851). However, *C. collaris* is a larger, thicker-bodied species with pronotum much wider than long; the apex of the sternite 8 + 9 is truncated and vertically thick, and the gonarcus + arcessus complex has an H-shaped supporting brace not found in *C. divisa* (see Adams and Penny 1987).

HEAD. — Yellow with red markings. Vertex with red lateral postocular marks from mid-length to posterior margin. Frons yellow with red band below antennal bases interrupted along mid-line. Gena red. Maxillary distal palpimere black; fourth palpimere dorsally black; and third fuscous. Third labial palpimere black. Scape and pedicel yellow, unmarked; flagellum pale yellow (Fig. 35A, C).

THORAX. — Green with yellow stripe on mid-line. Pronotum longer than wide, with weakly defined brown stripe laterally. Meso- and metanotum unmarked (Fig. 35A). **Wings**: Venation green, except costal crossveins, origin of Rs, R-Rs crossveins, gradates; Psm-Psc crossvein endings; and bifurcations of forked marginal veins dark. Pterostigma green, unmarked. Length (1.14 cm): width (0.39 cm) = ratio (2.92). Hindwing venation green except gradates and middle costal crossveins dark (Fig. 35B). Length (0.88 cm): width (0.28 cm) = ratio (3.14).

ABDOMEN. — Green, with mid-line yellow. Tergites without markings. **Male**: Tergite 9 + ectoproct triangularly angled at posterio-ventral margin, with basal lobe and apico-medially projecting hook (Fig. 35D). Sternite 8 + 9 deeply constricted posteriorly, without knob, with lateral setae with thick bases. Gonarcus mildly arched, with oblong, curved lateral arms. Arcessus evenly tapered, triangular, with apex decurved and bearing tiny setae (Fig. 35G, H). **Female**: Dorsally folded bursa with pair of ovate accessory glands. Long bursal duct extended into long and narrow spermatheca (Fig. 35E, F). Subgenitale broader than long, with small medial projection.

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Taquaritinga, 6 August 1993, Xavier, A. L. Q. (1♂)(orange); 8 January 1993, Xavier, A. L. Q. (1♂)(orange); 5 March 1994, Xavier, A. L. Q. (4♂1♀)(orange)(SDF/CAS); 19 November 1992, Freitas, S. (2♀)(orange); 10 January 1994, Xavier, A. L. Q. (1♀)(orange); 5 March 1994, Xavier, A. L. Q. (14♀)(orange); Monte Azul Paulista, November 1994, Silva, J. L. (1♂)(orange); Barretos, 11 February 1991, Freitas, S. (1♂)(orange); Jaboticabal, 20 August 1995, Freitas, S. (1♀); Luiz Antonio, 21 December 1994, Freitas, S. (1♀)(eucalyptus); Elisario, July 1994, Silva, J. L. (1♀)(orange); **Minas Gerais**: Peti, October 1988, coll. not named (1♂).

Chrysopodes (*Neosuarius*) *karinae* de Freitas and Penny, new species

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Bra-SP-Jaboticabal, FCAV, 24/IV/99, Takahashi, K. M., 82♀" (guava).

DIAGNOSIS. — This species is unlike other green species of *Chrysopodes* (*Neosuarius*) in having antennae with dark flagella, scapes with lateral mark, and labial and maxillary palpi pale. It can also be separated from *C. collaris* by having a pronotum as long as wide (Adams and Penny 1987). However, the most unique characteristic of this species is the subanal plate with numerous small setae and lateral pockets, which is found in no other species. The spermatheca is also thinner and more elongate than

most species. The spermathecae shape, long and crooked, the setae around the genitalia atria and the lateral pocket are not found in any other chrysopid species.

The name was given in honor of Agricultural Engineer Karina Manami Takahashi, enthusiastic entomologist who has studied and collected many chrysopids.

HEAD. — Golden yellow with red markings. Frons and clypeus unmarked. Gena red-tinged. Vertex with red spots on posterior margin near eyes. Scape yellow with dark spot at dorso-lateral apex; pedicel and flagellum dark (Fig. 36A, C). Maxillary and labial palpi pale.

THORAX. — Yellow. Pronotum with lateral pale brown stripe (Fig. 36A). Meso- and metanotum unmarked. **Wings**: Forewing venation green, except margin endings costal crossveins, R-Rs crossveins and gradates dark. Length (1.45 cm): width (0.5 cm) = ratio (2.9)(Fig. 36B). Hindwing venation green. Length (1.33 cm): width (0.43 cm) = ratio (3.09).

ABDOMEN. — Yellow, marked red laterally on first tergite. **Female**: Tergite 8 ventrally-prolonged laterally. Tergite 9 + ectoproct dorsally raised. Sternite seven with ventral knob apically (Fig. 36D). Proximal to genital atria a dorsal field of setae, a medial plate with densely clumped setae and two lateral pockets (Fig. 36F). Spermatheca elongate, twisted but not coiled, with long duct connected to bursa copulatrix. Bursa a membranous sac with pair of ovate accessory glands (Fig. 36E). Subgenitale simple, apically bilobed.

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**, Jaboticabal, 24 April 1999, Takahashi, K. M. (1♀ paratype)(guava).

Genus *Plesiochrysa* Adams, 1982b

Plesiochrysa adults are among the largest of South American Chrysopini, with forewing length of about 15 to 18 mm. They can usually be found in open fields, and at times can be quite common. Their male genital elements indicate a close relationship with the Holarctic genus *Chrysopa*. Brooks and Barnard (1990) listed 23 species in this genus, distributed in the Neotropics, Australia, Malay Archipelago, southern India to the Seychelles. Three species have been found during this study, including one new species. Unfortunately, male genital elements of all Brazilian species are virtually identical, but the species can be identified using the following key.

KEY TO THE SPECIES OF *PLESIOCHRYSA* FOUND IN BRAZILIAN AGRO-ECOSYSTEMS

1. Antennae dark (Fig. 39A) . . . . . *P. alytos*
1.′ Antennae pale (Fig. 37A). 2

2. Pronotum longer than wide; lateral stripes continuous or only slightly interrupted (Fig. 38A) . . . . . *P. elongata*
2′. Pronotum as wide as long; lateral spots widely separated (Fig. 37A) . . . . . *P. brasiliensis*

Plesiochrysa brasiliensis (Schneider, 1851)

DIAGNOSIS. — *Plesiochrysa brasiliensis* can be separated from the other two Brazilian species (*P. elongata* and *P. alytos*) by the dark antennal flagellum of *P. alytos* and longer pronotum with more continuous lateral red markings of *P. elongata*.

HEAD. — Yellow with red marks. Vertex yellow with small red spots on posterior part near eye margin (Fig. 37A). Frons unmarked. Gena with narrow red stripe close to frons continued onto lateral margin of clypeus (Fig. 37C). Maxillary palpi with dorsal black stripe. Labial palpi pale, unmarked. Scape and pedicel pale, unmarked; flagellum pale yellow.

THORAX. — Green with pale yellow stripe on mid-line. Pronotum marked with pair of well-delimited red spots laterally (Fig. 37A). Meso- and metanota unmarked. **Wings**: Forewing venation green, except posterior junctions of costal crossveins 3–7 and 8–13, origin of Rs, R-Rs crossveins

1–4, gradates, Psm-Psc crossveins, marginal unforked veins near anals and apices of anal veins dark (Fig. 37B). Length (1.5 cm): width (0.5 cm) = ratio (2.98). Hindwing venation green, except outer gradates dark (Fig. 37B). Length (1.30 cm): width (0.43 cm) = ratio (3.02).

ABDOMEN. — Green with yellow stripe on mid-line. **Male**:Tergite 9 + ectoprocts widely separated with medial indentation (Fig. 37D). Sternite 8 + 9 elongate, narrowed at apex (Fig. 37E). Tignum narrow, transverse band. Gonarcus wide and thick with small, medial gonocornua. Entoprocessus not fused to gonarcus, Y-shaped. Arcessus absent. Pseudopenis elongate, tapering, apically decurved. Gonosaccus large with numerous long setae on tubercules (smaller near pseudopenis) (Fig. 37G, H). **Female genitalia**: Spermatheca short. Bursa sac-like (Fig. 37F). Subgenitale with lateral lobes and small median projection.

MATERIAL EXAMINED. — **BRAZIL**: **São Paulo**: Jaboticabal, November 1991, Hungaro, C. M.; 24 October 1992, (1♀); Tanigawa, F. (1♀); October 1992, Mendes, M. B. (1♀); October 1992, Tannuri, L. (1♂); 5 November 1992, Scomparin, C. H. J. (1♀)(orange); 22 November 1994, Freitas, (1♂)(guava); 30 June 1995, Freitas, S. (1♂); 26 January 1995, Freitas, S. (1♂); 22 February 1995, Freitas, S. (1♂1♀)(orange); 24 February 1996, Rossi, R. M. (1♀); 28 August 1996, Silva, L. C. (1♂); 20 October 1996, Freitas, S. (1♂)(guava)(CAS); 21 October 1996, Fernandes, M. (1♀); 20 October 1996, Freitas, S. (2♂)(orange); 9 December 1996, Freitas, S. (1♂)(orange)(CAS); 17 June 1998, Freitas S. (1♂); Birigui, 26 January 1996, Scomparin, C. H. J. (1♂1♀)(corn); Atibaia, 15 November 1994, Onara, L. (1♀); Eng. Coelho, 10 August 1996, Poletti, M. (1♂); Matão, 15 October 1996, Yiagi, R. (1♂); Olimpia, 2 August 1996, Tolfo, A. L. T. (1♂).

Plesiochrysa elongata (Navás, 1913b)

DIAGNOSIS. — This species can be separated from *P. alytos* by its pale antennae and pale gradate crossveins, and from *P. brasiliensis* by its longer pronotum with more complete stripes.

HEAD. — Yellow with red markings. Vertex yellow with tiny red spots beside eye at posterior margin. Frons unmarked. Gena with red stripe on half closest to frons, not extended onto clypeus (Fig. 38A, C). Maxillary palpi with dorsal black stripe. Labial palpi unmarked. Scape, pedicel and flagellum pale yellow, unmarked.

THORAX. — Green with pale yellow stripe on mid-line. Pronotum marked with red stripe narrowed or interrupted at midlength. Meso- and metanota unmarked (Fig. 38A). **Wings**: Venation and size similar to *P. brasiliensis*.

ABDOMEN. — Male and female as *P. brasiliensis*.

MATERIAL EXAMINED. — **BRAZIL**: **São Paulo**: Jaboticabal, October 1993, Furuhashi, S. (1♂); 10 October 1996, Ferreira, A. (1♂); 15 November 1996, Freitas, S. (1♀)(corn)(CAS); October 1993, Fernandes, F. (1♀); **Minas Gerais**: Viçosa, 28 December 1988, Abrantes, C. V. M. (1♂1♀); 27 January 1989, Abrantes, C. V. M. (2♂)(SDF/CAS); 28 February 1988, Abrantes, C. V. M. (1♂); **Mato Grosso**: Itiquira, 10 September 1996, Scomparin, C. H. J. (1♀)(rubber).

Plesiochrysa alytos de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, PEM, 7-IX-99, Freitas, S." (guava).

DIAGNOSIS. — This is the only species of *Plesiochrysa* in South America which has a continuous pronotal band, showing no signs of restriction or broken lines at mid-length. In the other species, occasional specimens will appear to have stripes rather than spots, sometimes because of pigment "bleeding," but there is virtually always an indication of restriction at mid-length. This is also the only species with dark antennae.

This name "alytos" comes from the Greek, meaning continuous or unbroken, and refers to the continuous, unbroken, lateral stripes on the pronotum.

HEAD. — Yellow with red markings. Vertex yellow with small red spots beside eye at posterior margin (Fig. 39A). Frons and clypeus unmarked. Gena red-tinged. Maxillary palpi with dorsal black stripe. Labial palpi unmarked (Fig. 39C). Scape and pedicel unmarked, flagellum black basally and fuscous apically (Fig. 39A).

THORAX. — Greenish yellow. Pronotum longer than wide, glabrous, with pale red lateral stripe. **Wings**: Venation green, except darkened gradates in fore- and hindwings (Fig. 39B). Forewing length (1.56 cm): width (0.49 cm) = ratio (3.18). Hindwing length (1.40 cm): width (0.43) = ratio (3.26).

ABDOMEN. — Greenish yellow. Male and female genitalia, as in *P. brasiliensis*.

OTHER MATERIAL EXAMINED. — **BRAZIL**: **São Paulo**: Jaboticabal, November 1996, Manzini, J. P. (1♀ paratype); 1 November 1990, Camargo, R. (1♂ paratype); 13 November 1994, Lopez, C. C. (1♂1♀ paratypes)(SDF/CAS); 12 September 1995, Gomes, R. G. (1♂ paratype); 20 November 1995, Ferreira, R. J. (1♂ paratype); 12 September 1996, Britto, L. F. (1♀ paratype)(CAS); 4 December 1996, Freitas S. (1♀ paratype); Birigui, 26 January 1996, Scomparin, C. H. J. (1♀ paratype)(corn); Pirangi, 15 December 1996, Fernandes, E. (1♂ paratype); Franca, October 1990, Cunha, L. S. A. (1♂ paratype); **Mato Grosso**: Itiquira, 4 November, 1996, Scomparin, C. H. J. (1♂ paratype)(rubber); 7 September 1996, Freitas, S. (1♂ paratype)(rubber).

TRIBE LEUCOCHRYSINI ADAMS, 1978

Adult members of the tribe Leucochrysini are distinctive. They have a dark spot along the anterior margin of the forewing at the base of the pterostigma, a rather low angle of juncture between the pseudomedia and the outer gradate series of crossveins, and antennae which are longer than the wings. Males have a broad gonarcus which is only weakly arched and lacks entoprocesses. Female genitalia often include an elongate subgenitale, which is likely the precursor for a praegenitale (Brooks and Barnard 1990).

This tribe is only found in the New World, ranging from as far north as Iowa and Massachusetts in North America (Penny et al. 1997) south to Argentina (Penny 1978). Members of Leucochrysini are found primarily in tropical forests where they are the dominant tribe in this habitat. *Leucochrysa,* with its two subgenera, is the most speciose genus of the family. Leucochrysini consists of seven genera, and is most diverse in South America. All genera are known from Brazil, except *Neula,* which is known only from its type specimen collected in Colombia. All known larvae are trash-bearers, known locally as "bicho de lixo." Probably because of their preference for forest habitat, only *Leucochrysa* has been collected in Brazilian agro-ecosystems.

Genus *Leucochrysa* McLachlan, 1868

Much of what has been said about Leucochrysini applies equally well to *Leucochrysa.* It is the largest genus in the family with nearly 170 described species and many still undescribed. Like the tribe, *Leucochrysa* is distributed from northern U.S.A. to Argentina, although the greatest diversity and numbers occur in the tropical forests. Within the tribe, *Leucochrysa* is currently delimited by the lack of diverse derived character states of the other genera. A phylogenetic analysis of the tribe will probably split *Leucochrysa* into several lineages. As currently constituted, *Leucochrysa* has two subgenera. Adults can be distinguished using the following key.

KEY TO THE SUBGENERA OF *LEUCOCHRYSA*

1. Forewing intramedian cell quadrangular, Rs straight (Fig. 40A) . . . . . *L.* (*Leucochrysa*)
1′. Forewing intramedian cell triangular, Rs sinuous (Fig. 47B) . . . . . *L.* (*Nodita*)

Subgenus *Leucochrysa* (*Leucochrysa*) McLachlan, 1868

This subgenus is usually characterized by having forewings with a quadrate intramedian cell, rather than an ovate or triangular one, and straight radial sector rather than sinuous. However, as is frequently pointed out (Banks 1945; Adams 1977; Brooks and Barnard 1990), a small percentage of individuals of either subgenus will have the shape of the intramedian cell of the other subgenus. Individuals of *Leucochrysa* (*Leucochrysa*) are large, with a forewing length of more than 20 mm and at times more than 30 mm. The shape of the intramedian cell may in part be correlated with large wing size, although large species of *Leucochrysa* (*Nodita*) maintain a triangular shape. The shape of the forewing radial sector is also probably an artifact of larger wings of *Leucochrysa* (*Leucochrysa*), as larger species of *Leucochrysa* (*Nodita*) also appear to have a straighter Rs. Brooks and Barnard (1990) recorded 41 species in *Leucochrysa* (*Leucochrysa*) distributed from northern U.S.A. to Argentina. Seven species are recorded here, two were previously undescribed. Adults can be distinguished using the following key.

KEY TO SPECIES OF *LEUCOCHRYSA* (*LEUCOCHRYSA*) FOUND IN BRAZILIAN AGRO-ECOSYSTEMS

1. Two longitudinal dark stripes on meso- and metanota; pronotum with two red spots near posterior margin (Fig. 41A) . . . . . *L.* (*L.*) *boxi*
1′. Meso- and metanota pale or dark, but without longitudinal stripes; pronotum pale green without markings (Fig. 40C). 2

2. Head, thorax and abdomen without markings. . . . . *L.* (*L.*) *catarinae*
2′. Head with thick red markings and suffusions (Fig. 40B, C); abdomen with large dark marks on Tergites 5 and 6 (Fig. 40D). 3

3. Dark spot at base of forewing intramedia vein (Fig. 40A) 4
3′. No dark spot at base of forewing intramedia vein (Fig. 44A). 5

4. Frons suffused with red (Fig. 43D); female spermatheca coiled about five times, with short spermathecal duct (Fig. 43E) . . . . . *L.* (*L.*) *varia*
4′. Frons pale, without markings (Fig. 40B); female spermatheca short, S-shaped, with long spermathecal duct coiled dozens of times (Fig. 40E). . . . . *L.* (*L.*) *ampla*

5. Male gonocornua short, separated by more than five times their length (Fig. 44D) . . . . . *L.* (*L.*) *walkeriana*
5′. Male gonocornua longer, separated by less than twice their length (Fig. 42D) 6

6. Lateral arms of male gonarcus oriented vertically; inner margins of gonocornua diverging (Fig. 42D). . *L.* (*L.*) *pretiosa*
6′. Lateral arms of male gonarcus oriented at 45° to vertical; inner margins of gonocornua parallel (Fig. 45C) . . . . . *L.* (*L.*) *bruneola*

Leucochrysa (*Leucochrysa*) *ampla* (Walker, 1853)

DIAGNOSIS. — This is a member of a group of species having heavy red markings and red pigmentation suffused over the frons and vertex, no markings on the pronotum, general (but variable) dark suffusion of the meso- and metascuta, and dark marks on the 5th and 6th abdominal tergites. Within this group, *L. ampla* can be separated from all others, except *L. varia*, by the dark spot at the base of the intramedian cell. From *L. varia* it is separated by distinctly different female genitalia: *L. varia* having a long, multiply coiled spermatheca and short, uncoiled spermathecal duct, while *L. ampla* has an S-shaped spermatheca and long spermathecal duct coiled three to four dozen times.

HEAD. — Pale yellow, broadly tinged reddish brown; vertex reddish along posterior ocular margin, lateral of raised medial area and base of antenna; frons dark brown between scape and eye and through antennal sockets to ventral margin with gena; gena dark brown at frons and clypeus and otherwise red; scape light red-tinged throughout; flagellum pale, basal segments fuscous; maxillary and labial palpi pale (Fig. 40B).

THORAX. — Cervical sclerites red; pronotum pale yellow, unmarked; most of meso- and metanota dark red and chocolate brown (Fig. 40C). **Wings**: Pterostigma marked with prominent dark brown spot. Forewing bases of longitudinal veins dark brown; outer gradates with conspicuous brown spots; inner gradates brownish; most costal cross veins brown at apex; base of Rs and ventral corner of intramedian cell brown with bordering; marginal forks of veins brown at apex. Length (2.11 cm): width (0.83cm) = ratio (2.54). Hindwing veins predominately pale, only costal crossveins brown (Fig. 40A). Length (1.87 cm): width (0.63 cm) = ratio (2.97).

ABDOMEN. — Yellowish green with a broad yellow stripe along dorso-medial line; tergites 5 and 6 dark brown (Fig. 40D). **Female genitalia**: Spermatheca long; spermathecal duct long, convoluted; subgenitale bears extra plate with pit; long accessory glands (Fig. 40 E, F).

MATERIAL EXAMINED. — **BRAZIL**: **Mato Grosso**: Itiquira, 13 January 1997, Freitas, S. (1♀)(rubber).

***Leucochrysa* (*Leucochrysa*) *boxi* Navás, 1930**

DIAGNOSIS. — The characteristic of a medial dark stripe on the meso- and metanota is shared by *L.* (*L.*) *longicornis* and *L.* (*L.*) *boxi.* In characters of the male genitalia they are also similar, including the subapical constriction of sternite 8 + 9. However, the two species differ in that *L.* (*L.*) *longicornis* has a tapering dark medial stripe on the pronotum, while *L.* (*L.*) *boxi* is pale medially and has two short, dark, lateral marks on the pronotum. The inner gradate series of the forewing of *L.* (*L.*) *boxi* is also distinctive, extending quite far basally and parallels the pseudomedius for a long distance.

HEAD. — Yellow; frons, clypeus, vertex and gena pale; scape and pedicel dark laterally and dorso-laterally; first 17 antennomeres (including pedicel) black on anterior surface; maxillary and labial palpi pale.

THORAX. — Pronotum dark at anterio-lateral margin; meso- and metanota dark at mid-line (Fig. 41A). **Wings**: Venation mostly green; pterostigma dark; intramedian cell quadrangular; inner gradates curved medially to level of origin of fifth radial cross veins; dark oblique band at wing apex. Length (2.42 cm): width (0.84 cm) = ratio (2.88). Hindwing costal crossveins black, remainder of wing green (Fig. 41B). Length (2.21 cm): width (0.71 cm) = ratio (3.11).

ABDOMEN. — Dorsal surface and tergites dark-tinged (Fig. 41C). **Male genitalia**: Gonarcus lateral arms broad; gonarcus hardly curved and thick; gonocornua short, upturned with broad base; arcessus short with lateral lobes, medial lobe of arcessus decurved; gonosaccus without gonosetae (Fig. 41E, G). Dorsal apodeme of ectoproct forked posteriorly (near callus cerci)(Fig. 7D); sternites with many microtholi; sternites 8 + 9 narrow at apex, bearing setae (Fig. 41F).

MATERIAL EXAMINED. — **BRAZIL**: **Santa Catarina**: São Joaquim, 20 August 99, Borges, R. (1♂)(apple).

***Leucochrysa* (*Leucochrysa*) *pretiosa* (Banks, 1910)**

DIAGNOSIS. — This species forms part of the *varia* species group having extensive red suffusion of the frons and vertex, completely pale pronotum, and heavy, dark, poorly delimited markings of the meso- and metanota. It is one of three species having no dark spot at the base of the intramedian cell. Amongst these three species male genital characters are the most reliable. *Leucochrysa bruneola* has lateral arms of the gonarcus angled at about 45° and closely spaced gonocornua which are short and

parallel. *Leucochrysa walkeriana* has vertically oriented lateral arms of the gonarcus, but the short, parallel gonocornua are widely separated. *Leucochrysa pretiosa* has lateral arms of the gonarcus vertically oriented, and more massive, closely-spaced gonocornua which appear to diverge at their inner margins.

HEAD. — Yellow, but broadly red-tinged; vertex wine red, raised medial area pale, between antennal sockets brown-tinged; frons, clypeus and labrum wine red with some clear areas; gena red; maxillary and labial palpi pale; scape and pedicel red; flagellum pale (Fig. 42A).

THORAX. — Cervical sclerites red; pale pronotum yellow unmarked; most of mesonotum brown; metanotum brown except scutellum and borders of scutum (Fig. 42E); pterostigma faintly black marked. **Wings**: Forewing black-tinged basally; longitudinal veins (costa, Rs, pseudomedia, pseudocubitus, and anals) black at base; inner and outer gradates black; four apical Psm–Psc crossveins black and outer gradates with brown shading; basal Rs crossveins black at intersections. Hindwing venation mostly pale; costal crossveins black. Forewing length (2.03 cm): width (0.72 cm) = ratio (2.82). Hindwing length (1.81 cm): width (0.60 cm) = ratio (3.02)(Fig. 42B).

ABDOMEN. — Green, dorso-medial line pale yellow, tergites 5, 6 marked with brown (Fig. 42J); **Male**: Ventral fork of dorsal apodeme of ectoproct long, with acute apex (Fig. 42C). Gonarcus slightly arched, lateral arms large, vertically oriented (Fig. 42G); gonocornua slender, decurved; arcessus medial point decurved with thin lateral lobes, not seen in dorsal view; few gonosetae on gonosaccus (Fig. 42D, G). **Female**: genitalia with convoluted spermatheca, vela large, gland short; two long filamentous bursal glands present (Fig. 42F); subgenitale divided into two parts (Fig. 42H, I); two sclerotized plates close to base of subgenitale with cerci and two irregular sclerotized structures can be seen (Fig. 3H, I).

MATERIAL EXAMINED. — **Venezuela**: San Esteban, 1 January, Anduze, syntype male (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **Mato Grosso**: Itiquira, 23 January 97, Freitas, S. (3♂2♀)(rubber); 5 April 97, Freitas, S. (1♂)(rubber); 4 November 96, Scomparin, C. H. J. (1♂)(rubber).

Leucochrysa (*Leucochrysa*) *varia* (Schneider, 1851)

DIAGNOSIS. — *Leucochrysa varia* forms part of a species complex with character states mentioned above for other species. The dark spot at the base of the intramedian cell help distinguish this species from all others in the complex, except *L. ampla*. The most distinctive characteristics separating these two species are the multiply-coiled spermatheca and short, uncoiled spermathecal duct of *L. varia*.

HEAD. — Yellow with red markings. Vertex, frons, clypeus, genae, labrum, scape and pedicel marked pale red. Maxillary and labial palpi unmarked (Fig. 43B, D).

THORAX. — Cervical sclerite red; pronotum yellow unmarked; meso- and metanotum brown-tinged (Fig. 43B). **Wings**: Pterostigma faintly black marked; marginal endings of costal crossveins black; apex of Rs dark; inner gradates pale, outer gradates black and shaded, first and second ones more evident; third and apical psm-pscu crossveins black and shaded (Fig. 43A); length (2.08–2.13 cm); width (0.72–0.83). Hindwing middle costal crossveins, black; apex of Rs faintly dark; length (1.83–1.86 cm); width (0.54–0.56 cm) (Fig. 43A).

ABDOMEN. — Yellowish, 5th and 6th tergites marked with brown (Fig. 43C). **Male**: Dorsal apodeme of ectoproct well-sclerotized and prolonged posteriorly into an acute apex; few microtholi present; callus cerci with few trichobothria, whose setae are strong and short (Fig. 43E); Male genitalia with stout gonarcus and vertically elongate lateral arms; gonocornua short, not extended to apex of arcessus; arcessus a heavily sclerotized sac from which apex of gonocornua extends; apical lobes laterally rounded, medial hook decurved, heavily sclerotized; gonosaccus with a few gonosetae (Fig.

43G, H). **Female**: Genitalia with spermatheca long and convoluted; gland short; bursa sac-like (Fig. 43E); subgenitale bilobed, with short ventral projection (Fig. 43F).

MATERIAL EXAMINED. — **Brazil**: unknown locality, holotype male (deposited in Museum of Comparative Zoology, Harvard University), **São Paulo**: Jaboticabal, April 1993, Murtati, G. (1♂); Luiz Antonio, 29 April 1994, Freitas, S. (1♀)(eucalyptus). **Mato Grosso**: Itiquira, 23 January 1997, Freitas, S. (1♂)(rubber).

***Leucochrysa* (*Leucochrysa*) *walkerina* Navás, 1913**

DIAGNOSIS. — This species is a member of the *varia* species complex. The lack of a dark spot at the base of the intramedian cell groups it with two other species: *L. bruneola* and *L. pretiosa*. The most distinguishing feature of *L. walkeriana* is the widely spaced gonocornua of the male genitalia. It also has smaller gonocornua than *L. pretiosa* and more vertically aligned lateral arms of the gonarcus than *L. bruneolus*.

HEAD. — Yellow, marked with red. Raised medial area of vertex with anterior converging stripes extended to antennal bases; lateral area red-tinged. Scape and pedicel red-tinged; flagellum pale, first five antennomeres with small black spot along anterior surface. Gena red. Frons with pair of small red spots below antennae. Clypeus red-tinged medially (Fig. 44C).

THORAX. — Pronotum bright green, without marks. Meso- and metanota dark; mesonotum with brown marks along anterior prescutum and lateral scutum (Fig. 44B). **Wings**: Venation pale, except basal area, marginal junctions of costal crossveins, first radial crossvein, gradates, apical Psm-Pscu crossveins dark. forewing length (2.15 cm): width (0.85 cm) = ratio (2.52). Hindwing costal crossveins and middle part of Rs dark (Fig. 44A). Length (1.88 cm): width (0.67 cm) = ratio (2.81). Pterostigma of fore- and hindwing with dark mark basally.

ABDOMEN. — Green, unmarked. **Male**: Gonarcus lateral arms slightly higher than long. Gonocornua short, slightly decurved. Entoprocessus sharply decurved at base of gonarcus. Arcessus broad with lateral lobes; medial hook apically decurved. Gonosaccus without gonosetae (Fig. 44D, E).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Campinas, 22 July 1991, Chinchilla, C. (1♂)(orange).

***Leucochrysa* (*Leucochrysa*) *bruneola* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 10-V-96, Seringueira, PEM 811, Scomparin, C. H. J." (rubber).

DIAGNOSIS. — This is a member of a group of species having extensive red suffusion of the head, completely pale pronotum, and extensive dark markings on the mesonotum. The lack of a dark spot at the base of the intramedian cell is characteristic of this and two other species: *L. pretiosa* and *L. walkeriana*. The most distinctive feature of *L. bruneola* is the lateral arms of the gonarcus oriented at a 45° angle to vertical, as opposed to the more usual 90° angle in other species (Fig. 45C, E). Additionally, the gonocornua are more widely spaced in *L. walkeriana*, and gonocornua are larger and more divergent along the inner margins in *L. pretiosa* (Fig. 42D).

The name "bruneola" comes from the Medieval Latin *brunneus* for brown and Greek *olos* for mud or dirt and refers to the brown meso- and metanota.

HEAD. — Pale green. Gena red. Frons and clypeus lightly red-tinged. Vertex with red A-shaped mark with legs expanded near eye margins; pair of small red spots along posterior margin near eye (Fig. 45B). Scape and pedicel completely suffused with red; antennal fossa red.

THORAX. — Cervical sclerites red. Pronotum pale, unmarked. Meso- and metanota pale with dark brown tinge; mesoprescutum and scutum with amorphous dark spots; second axillary sclerite

dark (Fig. 45B). **Wings**: Forewing venation pale, costal crossvein apices, first four R-Rs crossveins, gradates, and apical Psm-Psc crossveins dark. Length (2.1 cm): width (0.82 cm) = ratio (2.56). Hindwing venation pale, except costal crossveins dark (Fig. 45A). Length (1.81 cm): width (0.63 cm) = ratio (2.87). Pterostigma of both fore- and hindwing with dark basal spot.

ABDOMEN. — Yellow, unmarked. **Male**: Gonarcus thick, wide and short. Gonocornua conical, apically decurved. Arcessus with heavily-sclerotized median, decurved, apical hook; lateral lobes not projecting posteriorly. Gonosaccus with few large gonosetae (Fig. 45C, D, E).

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Leucochrysa*) *catarinae* de Freitas and Penny, new species

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Catarina, SC, Fraiburgo, 26-09-99, Borges, R." (apple).

DIAGNOSIS. — This species is unique amongst *Leucochrysa* (*Leucochrysa*) species in several ways. There are virtually no dark markings anywhere on the body. Amongst species found in Brazilian agro-ecosystems only *L. boxi* has no dark markings on the abdomen, and yet it has dark longitudinal stripes on the meso- and metanota. The female genitalia are also unique. The spermathecal duct is long, yet only moderately coiled at its apex. The vela of the spermatheca is long and flattened in its apical half, unlike the tubular structure of most other species. These genitalic structures are so distinctive that we are departing from the usual procedure in describing the species based only on a female specimen.

The name "catarinae" refers to the state of Santa Catarina, which in English is Saint Catherine.

HEAD. — Yellow, without markings. Labial and maxillary palpi pale. Scape, pedicel and flagellum pale.

THORAX. — Pro-, meso-, and metanota pale, without markings. **Wing**: Venation pale, except first eleven costal crossveins, first three radial crossveins, middle part of Rs and last six crossveins, gradates and marginal forks dark. Forewing length (1.81 cm): width (0.56 cm) = ratio (3.1) (Fig. 46A). Hindwing length (1.73 cm): width (0.55 cm) = ratio (3.15). Pterostigma with slightly dark pigmentation at basal margin.

ABDOMEN. — Green, unmarked. **Female**: Spermatheca apically slender, with basal half flattened, coiled. Spermathecal duct long, apically coiled. Subgenitale wide with small anterio-medial projection (Fig. 46B).

MATERIAL EXAMINED. — Known only from the holotype.

Genus *Leucochrysa* (*Nodita*) Navás, 1916

The subgenus *Leucochrysa* (*Nodita*) can be defined by the forewing triangular or ovate intramedian cell, sinuous radial sector, and short basal extension of the female subgenitale (Brooks and Barnard 1990). The male genitalia are inseparable from the nominate subgenus and the two groups remain close. Species of *Leucochrysa* (*Nodita*) are generally smaller than *Leucochrysa* (*Leucochrysa*) with forewing length ranging from 9 mm to about 30 mm, although a few of the larger species, such as *L.* (*Nodita*) *amazonica* rival species of *Leucochrysa* (*Leucochrysa*) in size. This is the most speciose group of chrysopids in the New World, with Brooks and Barnard (1990) listing 120 species and several more having been subsequently described (Penny 1998, 2001). Herein we describe 24 more, previously undescribed, taxa. This subgenus will probably eventually contain more than 200 species. They are distributed from the southern U.S.A. (Penny et. al 1997) to northern Argentina (Penny 1978). We have found 36 species in Brazilian agro-ecosystems, adults of which can be distinguished using the following key.

KEY TO SPECIES OF *LEUCOCHRYSA* (*NODITA*) FOUND IN BRAZILIAN AGRO-ECOSYSTEMS

1. Scape with one longitudinal stripe (Fig. 81A) 2
1′. Scape with two stripes (Fig. 53A), completely dark (Fig. 49A), or of other form (Fig. 51A) 20

2. Scape with dorsal longitudinal stripe (Fig. 81A) . . . . . *L.* (*N.*) *vittata*
2′. Scape with lateral longitudinal stripe (Fig. 47A) 3

3. Lateral stripe of scape well defined and wide, attaining both the anterior and posterior sides of the scape (Fig. 47A) 4
3′. Lateral stripe of scape narrow, not attaining the anterior and posterior sides of the scape (Fig. 62A) 14

4. Flagellum pale (Fig. 77C) 5
4′. Flagellum completely (Fig. 55A) or partially dark (Fig. 47A) 7

5. Forewing with base of Rs, MA and inner gradate veins dark and darkly margined (Fig. 61B) . . . . . *L.* (*N.*) *confusa*
5′. Forewing with base of Rs, MA and inner gradate veins dark, but without margining or shading (Fig. 47B) 6

6. Central arch of gonarcus elongate and thin, gonocornua small (Fig. 79D, E) . . . . . *L.* (*N.*) *tenuis*
6′. Central arch of gonarcus short and thick; gonocornua long (Fig. 60E, F) . . . . . *L.* (*N.*) *barrei*

7. Forewing with dark spots on crossveins (Fig. 70B); dark spot on the dorsal surface of the basal antennal cavity; first two flagellar segments dark; pronotal stripes not reaching anterior margin (Fig. 70A) . . . . . *L.* (*N.*) *maculosa*
7′. Forewing without dark spots on crossveins (Fig. 47B); basal antennal cavity without dorsal mark; flagellum totally dark or dark on one side; pronotal stripes reaching anterior margin (Fig. 57A) 8

8. Flagellum with only one side darkened (Fig. 47A) 9
8′. Flagellum completely dark (Fig. 52A) 10

9. Forewing with medial part of Rs and contiguous crossveins dark; marginal forks dark; hind margin of hindwing darkened (Fig. 47B) . . . . . *L.* (*N.*) *camposi*
9′. Forewing with Rs completely pale; marginal forks pale; hind margin of hindwing pale (Fig. 68B) . . . *L.* (*N.*) *interata*

10. One or two circular dark spots on mesonotum (Fig. 66A) 11
10′. No circular dark spots on mesonotum (Fig. 52A) 12

11. A single pair of dark spots on mesonotum (Fig. 66A); no dark spots on 2nd axillary sclerite; small dark spot on lateral surface of scape (Fig. 66D) . . . . . *L.* (*N.*) *ictericus*
11′. Two pair of dark spots on mesonotum; a dark spot at base of 2nd axillary sclerite (Fig. 57A); lateral surface of scape completely pale (Fig. 56D) . . . . . *L.* (*N.*) *melanocera*

12. Lateral stripe of pronotum well defined, straight, wide, reaching the anterior and posterior margins (Fig. 58A) . . . . . *L.* (*N.*) *rodriguezi*
12′. Lateral stripe of pronotum undulating and not reaching posterior margin; inner and outer margins of flagellum equally darkened (Fig. 55 A) 13

13. Gena pale yellow; posterior margin of hindwing pale (Fig. 52B); spermatheca short, broad, with a small lateral projection opposite juncture with spermathecal duct (Fig. 52D) . . . . . *L.* (*N.*) *intermedia*
13′. Gena red (Fig. 55C); posterior margin of hindwing darkened (Fig. 55B); spermatheca elongate and coiled (Fig. 55I) . . . . . *L.*(*N.*) *marginalis*

14. Gena with dark markings (Fig. 49C) 15
14′. Gena completely pale (Fig. 64F) 19

15. Pronotal stripe broken into small spot at anterior margin and larger spot at mid-length (Fig. 62A); arcessus bearing pair of dorsal horns (Fig. 62F) 16
15′. Pronotal stripe continuous, even if constricted at mid-length (Fig. 72A); arcessus not bearing pair of dorsal horns (Fig. 72F) 17

16. Maxillary palps pale (Fig. 62C); dark spot on mesoscutum barely visible (Fig. 62A); dorsal horns of arcessus projecting posteriorly (Fig. 62D) . . . . . *L.* (*N.*) *cornuta*
16′. Maxillary palps dark apically (Fig. 48C); dark spot on mesoscutum well developed (Fig. 48C); dorsal horns of arcessus projecting dorsally (Fig. 48E) . . . . . *L.* (*N.*) *clepsydra*

17. Mesonotum bearing pair of well-developed dark spots (Fig. 72A) . . . . . *L.* (*N.*) *parallela*
17′. Mesonotum completely pale (Fig. 73A) 18

18. Maxillary palps dark; gena completely red (Fig. 75D) . . . . . *L. (N.) santini*
18′. Maxillary palps pale; gena red only near frons (Fig. 74D) . . . . . *L. (N.) robusta*

19. Gonarcus narrow, gonocornua in the form of a broad plate with small apical point (Fig. 73C) . . . . . *L. (N.) retusa*
19′. Gonarcus broad; gonocornua narrower, with more elongate point (Fig. 80E) . . . . . *L. (N.) vignisi*

20. Scape with two dark stripes (Fig. 53A) 21
20′. Dorsal surface of scape completely dark (Fig. 49A) 24

21. Pronotum with two pair of stripes (Fig. 53A) 22
21′. Pronotum with a single pair of lateral stripes (Fig. 49A) 23

22. Forewing with Rs and adjacent veins dark (Fig. 53B); a single pair of dark marks on abdominal tergites (Fig. 53G) . . . . . *L. (N.) lancala*
22′. Forewing with most veins pale, including Rs and adjacent veins (Fig. 56B); abdomen with five pairs of dark marks on tergites (Fig. 56E) . . . . . *L. (N.) marquezi*

23. Hindwing apically pale (Fig. 76B); vertex with lateral dark stripes and two central crescent-shaped marks (Fig. 76A); pronotum marks confined to two pair of small spots (Fig.76A) . . . . . *L. (N.) scomparini*
23′. Hindwing apically dark (Fig. 51B); vertex pale, except for continuation of scape stripe; pronotum with complete dark lateral stripe (Fig. 51A) . . . . . *L. (N.) herioles*

24. Gonocornua elongate, in the form of spines (Fig. 67D) 25
24′. Gonocornua forming shorter flat plates (Fig. 65E) 29

25. Forewing pterostigma weakly darkened (Fig. 67A); gonocornua twisted (Fig. 67D) . . . . . *L. (N.) incognita*
25′. Forewing pterostigma with well-developed dark mark (Fig. 49B); gonocornua slender, straight (Fig. 50F) 26

26. Base of Rs in the forewing darkened (Fig. 49B) 27
26′. Base of Rs in the forewing pale (Fig. 54B) 28

27. Flagellum dark (Fig. 52A); gonarcus strongly arched anteriorly; gonocornua forcipate; dorsal horns of arcessus apically pointed (Fig. 49F) . . . . . *L. (N.) cruentata*
27′. Flagellum pale (Fig. 68A); gonarcus only weakly arched anteriorly; gonocornua straight; dorsal horns of arcessus apically rounded (Fig. 50 E, F) . . . . . *L. (N.) gossei*

28. Vertex with Y-shaped dark mark behind antennal bases (Fig. 54A); a2–a3 crossvein not darkly margined; base of forewing darkened (Fig.54B) . . . . . *L. (N.) lateralis*
28′. Vertex bearing dark lateral stripes beside eyes and two medial crescent-shaped marks (Fig. 77A); a2–a3 crossvein darkly margined, but base of forewing pale (Fig. 77B) . . . . . *L. (N.) squamisetosa*

29. Medial margin of pronotal stripes not straight, not well defined (Fig. 65A); abdomen bearing series of crescent-shaped dark marks (Fig. 65C) 30
29′. Medial margin of pronotal stripes straight, well-defined (Fig. 69A); abdomen bearing longitudinal dark medial stripe (Fig. 64C) 31

30. Gonocornua apically directed, widest at base (Fig. 65F) . . . . . *L. (N.) guataparensis*
30′. Gonocornua apico-laterally directed, widest at mid-length (Fig. 59E) . . . . . *L. (N.) affinis*

31. Gonocornua much shorter than apex of arcessus (Fig. 64G) . . . . . *L. (N.) furcata*
31′. Gonocornua elongate, reaching to apex of arcessus (Fig. 69E) 32

32. Gonarcus narrow (Fig. 69E); pterostigma only weakly darkened (Fig. 69B) 33
32′. Gonarcus broad (Fig. 63E); pterostigma heavily pigmented (Fig. 63B) 34

33. Rs of forewing and adjacent veins dark; basal cavity of antennae without dorsal dark mark (Fig. 69C); apical intersection of costal crossveins darkened; apex of gonocornua with a single point (Fig. 69E) . . . . . *L. (N.) lineata*
33′. Rs of forewing pale; basal cavity of antennae with dorsal dark mark (Fig. 78C); apical intersection of costal crossveins pale; apex of gonocornua forked (Fig. 78E) . . . . . *L. (N.) tabacinus*

34. Complete, dark transverse band directly behind antennal base (Fig. 63D); apex of gonocornua bifurcate (Fig. 63E) . . . . . *L. (N.) forciformis*
34′. No transverse band on vertex behind antennal bases (Fig. 71D); apex of gonocornua with a single point (Fig. 71E) . . . . . *L. (N.) michelini*

***Leucochrysa* (*Nodita*) *camposi* Navás, 1933**

DIAGNOSIS. — This species is one of several that have a dorso-lateral stripe on the scape, paired marks on the raised medial portion of the vertex, submedial dark markings on meso- and metanota, middle region of the Rs darkened, pale apex to the hindwing, and paired dark markings on each abdominal segment. *Leucochrysa* (*Nodita*) *melanocera* can be separated by its pale gena, completely dark flagellum, and pale metanotum. *Leucochrysa* (*N.*) *cruentata* has dark palpi and dark scape marking covering entire dorsal surface. *Leucochrysa* (*N.*) *scomparini* has a medial dark spot on the scape, longitudinal lateral stripes on the vertex, and metascutellum completely dark. *Leucochrysa* (*N.*) *vittata* has no dark lateral stripe on the pronotum, scape stripe is medial rather than lateral, and no dark markings on metascutellum. *Leucochrysa* (*N.*) *affinis, L.* (*N.*) *guataparensis*, and *L.* (*N.*) *rodriguezi* have dark antennae and much reduced dark markings on meso- and metanota. *Leucochrysa* (*N.*) *furcata*, *L.* (*N.*) *lineata*, *L.* (*N.*) *michelini*, and *L.* (*N.*) *tabacinus* form a group of species which have pale gena, broader and more extended lateral pronotal stripes, and dark abdominal markings completely covering tergites. However, the most distinctive feature of *L.* (*N.*) *camposi* is the subapical, truncate plate of the arcessus. This feature is found in no other species encountered in agro-ecosystems, but is found in the more northern *L.* (*N.*) *amazonica.* Both species have other characteristics in common, such as large size (forewing length > 20 mm), crescent-shaped markings on the vertex, and dark Rs vein at mid-length. However, *L.* (*N.*) *amazonica* bears no scape stripe, nor does it have dark metanotal and abdominal tergal markings.

HEAD. — Yellow. Frons without marks. Gena with thin red stripe. Maxillary and labial palpi pale (Fig. 47A, C). Vertex yellow, raised, marked with two medial, crescent-shaped red bands. Antennal scape and pedicel with dark red, dorso-lateral stripe continued onto antennal fossa; flagellum basally dark on lateral margin, apically pale.

THORAX. — Green with yellow dorsal median stripe. Pronotum with anterio-lateral darkened band (Fig. 47A). Mesonotum marked with red spots on prescutum and scutum. Metanotum with red spots on scutum and scutellum (Fig. 47G). **Wings**: Venation green, except marginal endings of costal crossveins, middle part of Rs, Psm-Psc crossveins 1–7, forks of marginal veins and anal veins dark. Pterostigma slightly darkened basally. Length (2.08–2.15 cm); width (0.64–0.76 cm) (Fig. 47B). Hindwing pterostigma well marked. Hindwing green, except last radial crossvein, last costal crossvein, middle part of Rs, and posterior marginal area darkened (Fig. 47B). Length (1.78 cm): width (0.59 cm) = ratio (3.02).

ABDOMEN. — Green, with red marks on all tergites (Fig. 47I). **Male**: Sternite 8 + 9 not completely fused; microtholi present (Fig. 47H). Gonarcus thick with triangular lateral arms. Gonocornua long and apically decurved. Entoprocessus absent. Arcessus with subapical dorsal plate and apical ventrally-folded plate with medial point (Fig. 47D, E, F). **Female**: Subgenitale with short, anterio-medial projection (Fig. 47J). Bursa sac-like, folded at apex, with pair of filamentous, multiply-forked accessory glands. Spermatheca long, ventral impression short.

MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 18 July 1998, Freitas, S. (1♂)(rubber)(CAS); **São Paulo**: Taquaritinga, 8 June 1993, Xavier, A. L. Q. (1♂)(orange); 21 October 1992, Freitas, S. (1♀)(orange); Catanduva, May 1994, Silva, J. L. (1♂)(orange); Taquaral, 13 March 1991, Freitas, S. (1♂)(orange); 5 March1991, Freitas, S. (1♀)(orange); Jaquariuna, May 1992, Kubo, R. K. (5♂)(orange); Jaboticabal, 26 August 1995, Freitas, S.(1♂)(guava); Taiuva, 27 May 1992, Pessoa, R. (1♂)(orange); 8 June 1990, Freitas, S. (1♀)(orange); 11 September 1995, Ferreira, R. J. (2♀)(guava); 21 October 1995, Ferreira, R. J. (1♀)(guava); October 1989, Fernandes, O. D. (1♀); 10 July 1998, Freitas, S. (1♀)(CAS).

Leucochrysa (*Nodita*) *clepsydra* Banks, 1918

DIAGNOSIS. — *Leucochrysa* (*N.*) *clepsydra* is associated with *L.* (*N.*) *cornuta* by the thin, red stripe of the gena; pale antennae with thin, incomplete dorsal stripe of the scape; pair of dark lateral spots on either side of pronotum of unequal size; pair of dark mesonotal spots; forewing Rs with dark area at mid-length, and pale apex of hindwing. Differences between the two species include dark maxillary palpi; two small dark spots on vertex; small gonarcus with vertically elongate lateral arms and longer pair of subapical dorsal horns in *L.* (*N.*) *clepsydra*.

HEAD. — Yellowish green. Gena with reddish stripe near frons. Apical maxillary palpimeres dark. Vertex marked with two, diverging, elongate, red spots (Fig. 48A,C). Antennae pale with short red stripe dorso-laterally on scape.

THORAX. — Cervical sclerites red. Pronotum with two red spots laterally on either side. Mesonotum with pair of red spots (Fig.48A). Metanotum unmarked. **Wings**: Forewing venation green, except both junctures of costal crossveins, apex of Rs, gradates and marginal forks dark (Fig. 48B). Pterostigma weakly darkened basally. Forewing length (1.46 cm): width (0.50 cm) = ratio (2.92).

ABDOMEN. — Green, marked with red. **Male**: Gonarcus short, poorly defined, with small, ovate lateral arms. Gonocornua well developed, apically decurved, surface with tiny setae. Arcessus poorly sclerotized, with pair of large, dorsal, subapical horns between gonocornua and apico-medial point and two, small, rounded, lateral lobes. Gonossacus with few, scattered, lateral gonosetae (Fig. 48D, E, F).

MATERIAL EXAMINED. — **Colombia**: Caldas, May, 4900 ft. [1490 m], Fassl, four syntypes (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **São Paulo**: Taquaritinga, 8 January 1993, Xavier, A. L. Q. (1♂)(orange).

Leucochrysa (*Nodita*) *cruentata* (Schneider, 1851)

DIAGNOSIS. — This species is part of the complex having red gena, crescent-shaped marks on the vertex, dark submedial markings on meso- and metanotum, and extensive dark markings on abdominal tergites. However, the combination of dark palpi, completely red dorsal surface of the scape, shading of the origin of Rs on the forewing, and large, incurved gonocornua will separate this from all other species.

HEAD. — Green. Gena red. Frons unmarked. Clypeus laterally marked with red (Fig. 49C). Maxillary and labial palpimeres dark. Vertex with divergent red stripes on medial raised area. Scape completely red dorsally, the red coloration extends onto basal membrane, pale ventrally; pedicel with red ring not shown on illustration; flagellum pale (Fig. 49A).

THORAX. — Green, marked with red. Pronotum as wide as long, with lateral red stripes, broader at mid-length and converging anteriorly. Meso- and metanotum with variegated red marks (Fig. 49A). **Wings**: Forewing venation pale, except costal crossveins, R-Rs crossveins, Rs-Psm, inner and outer gradates, marginal forks, and Rs dark. Origin of Rs with brown shading. Wing base with linear red mark (Fig. 49B). Pterostigma with basal dark spot. Length (2.50 cm): width (0.98 cm) = ratio (2.55). Hindwing venation pale, except costal crossveins, and inner and outer gradates dark (Fig. 49B). Pterostigma with heavy dark mark basally. Length (2.13 cm): width (0.73 cm) = ratio (2.92).

ABDOMEN. — Tergites 3, 5, 6, 7, and 8 with reddish brown crescent-shaped marks (Fig. 49D). **Male**: Microtholi absent. Lateral arms of gonarcus ovate. Gonocornua large, widely separated basally, apically incurved at a sharp angle. Arcessus broad; dorsal surface poorly sclerotized, with pair of subapical, dorsal horns, apical portion decurved, with medial hook and membranous, rounded lateral lobes (Fig. 49E, F, G, H). **Female**: Subgenitale with apical sclerotized sac with many gonocristae

(Fig. 49J). Spermatheca large, thick. Vela and bursal duct well developed. Spermathecal duct thin, with apical brush (Fig. 49I).

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 21 December 1993, Freitas, S., (1♂)(rubber); 17 August 1995, Freitas, S. (2♂1♀)(orange); 11 October 1995, Freitas, S. (1♂)(rubber); 10 February 1998, Freitas, S. (1♂)(guava); 5 July 1998, Freitas, S. (1♀)(CAS); 5 August 1998, Freitas, S. (1♀)(guava); 10 March 1999, Freitas, S. (1♀)(CAS).

Leucochrysa (*Nodita*) *gossei* (Kimmins, 1940)

DIAGNOSIS. — This species appears to be closely related to *L.* (*N.*) *cruentata* because of the completely red dorsum of the scape, red gena, dark lateral markings of both meso- and metanota, dark shading of the origin of Rs on the forewing. However, *L.* (*N.*) *gossei* has pale palpi and the tergal marks on the abdomen are quite different. In the male genitalia, the gonocornua of *L.* (*N.*) *gossei* are slightly turned outward, while in *L.* (*N.*) *crentata* they are strongly medially curved.

HEAD. — Yellow. Gena red. Apical maxillary palpimeres dark. Vertex with pair of small, thin red marks. Scape completely red dorsally, pale ventrally; pedicel pale; flagellum pale (Fig. 50A, C).

THORAX. — Green. Pronotum longer than wide, with lateral stripes dark red. Meso- and metanotum yellow with brown spots (Fig. 50A). **Wings**: Forewing venation green, except gradates, R-Rs crossveins, apices of Rs-inner gradates, marginal forked and unforked veins, and Psm-Psc crossveins dark. Gradates not darkly bordered. Pterostigma with dark basal mark. Length (1.47 cm): width (0.56 cm) = ratio (2.63). Hindwing with acute apex. Pterostigmal dark spot well defined. Venation green, except apex of Rs, gradates, and marginal forks dark (Fig. 50B). Length (1.27 cm): width (0.41 cm) = ratio (3.10).

ABDOMEN. — Yellow with large dark spot on tergite 3, two small ones on tergite 4, large one on tergite 6, and two small dark marks on tergite 7 (Fig. 50D). **Male**: Dorsal apodeme of ectoproct forked near callus cerci. Microtholi absent. Gonarcus arcuate; lateral arms short. Gonocornua elongate, parallel and apically decurved. Arcessus broad; with pair of dorsal plates elongate, upturned, apically truncate; apex with small medial horn and acute lateral lobes. Gonosaccus with few gonosetae (Fig. 50E, F, G). **Female**: Spermatheca twice-recurved. Bursa wrinkled with a pair of long accessory glands. Subgenitale with short, rounded lateral lobes and elongate medial projection (Fig. 50H, I).

MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 14 September 98, Freitas, S. (1♂)(rubber); **São Paulo**: Luis Antonio, 9 August 1993, Freitas, S. (1♀)(CAS); 8 June 1994, Freitas, S. (1♂)(CAS).

REMARKS. — This species was originally described by Walker (1853) as *Chrysopa conformis*. However, Walker's name is an objective junior homonym of *Hemerobius conformis* Rambur, 1842, a name which was subsequently transferred to the genus *Chrysopa* by Walker himself in 1853.

Leucochrysa (*Nodita*) *heriocles* Banks, 1944

DIAGNOSIS. — *Leucochrysa* (*Nodita*) *heriocles* is distinctive in being the only species with a dark apex to the hindwing found in the agro-ecosystem. Several other species found further north have this trait. Of these species only *L.* (*N.*) *apicata*, *L.* (*N.*) *indiga*, and *L.* (*N.*) *postica* have dark palpi, apically expanded stripe on the scape, and lateral red pronotal stripe (see Penny 2001). However, *L.* (*N.*) *indiga* has a complete dark band across the frons and *L.* (*N.*) *postica* has an almost complete band. Neither of these species have dark markings on meso- and metanotum. *Leucochrysa* (*N.*) *apicata* and *L.* (*N.*) *heriocles* are close, and may in fact be the same species, both having elongate gonocornua which approximate or cross apically, but *L.* (*N.*) *heriocles* males have a distinctive scalloping and apical point to sternite 9, which is not nearly so accentuated in *L.* (*N.*) *apicata*.

HEAD. — Yellow. Narrow red band across clypeus under and between anterior tentorial pits. Gena red. Apical labial and maxillary palpi dark. Vertex pale, unmarked. Scape with red stripe dorso-laterally expanded to complete ring apically, basally extended onto basal membrane; pedicel with apical dark ring; flagellum pale, except for dark stripe along medial margin of antennomeres 1–3 (Fig. 51A, C).

THORAX. — Yellowish green. Pronotum longer than wide with lateral dark red stripe. Mesonotum with diffuse reddish marks, especially pronounced along anterior margin. Metanotum pale, unmarked (Fig. 51A). **Wings**: Forewing longitudinal and some associated crossveins dark. Dark pterostigmal spot quite evident. Gradates, Psm–Psc crossveins; and forked marginal veins bordered (Fig. 51B). Length (1.18 cm): width (0.42 cm) = ratio (2.81). Hindwing acute; apex with diffuse dark spot. Dark pterostigmal spot well defined. Rs, costal crossveins black; outer gradates, and forked marginal veins dark. Outer gradates darkly margined (Fig. 51B). Length (0.97 cm): width (0.30 cm) = ratio (3.23).

ABDOMEN. — Green with two small dark spots on tergite 1 and other larger ones covering tergites 3 and 6 (Fig. 51H). **Male**: Sternites 2–8 with dense microtholi. Erect setae on apical sternite stouter than on tergites and arising from pit in cuticle. Apex of sternite 9 scalloped laterally, forming medial point lined dorsally by band of gonocristae (Fig. 51 I, J). Gonarcus arcuate, with short, ovate lateral arms. Gonocornua elongate, medially angled, apically approximated. Arcessus broad basally, with pair of small, dorsal, subapical horns and small apico-medial hook flanked by two small rounded lobes. Gonosaccus with sparse gonosetae. **Female**: Spermatheca elongate, distally coiled (Fig. 51G).

MATERIAL EXAMINED. — **Surinam**: Paramaribo, Charlesburg, 5 May 1941, Geijskes, syntype male (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **Mato Grosso**, Itiquira, 23 March 97 (1♂)(rubber); 18 February 1996, Scomparin, C. H. J. (1♂)(rubber); 10 November 97, Scomparin, C. H. J. (3♂4♀)(rubber).

Leucochrysa (*Nodita*) *intermedia* (Schneider, 1851)

DIAGNOSIS. — The combination of dark antennae, lack of dark markings on meso- and metanotum, and dark markings only on tergites 1 and 2 will separate this species from all others. The lateral projection of the spermatheca vela and tiny pits on the accessory glands are also distinctive for *L.* (*Nodita*) *intermedia*. The closest species is probably *L.* (*N.*) *marginalis,* from which *L.* (*N.*) *intermedia* can be separated by its larger size (forewing length 19 mm) and pale posterior margin of the hindwing.

HEAD. — Yellow, somewhat red-tinged on clypeus, frons and vertex. Vertex with V-shaped medial dark mark. Scape with red stripe dorso-laterally; pedicel dark-ringed subapically; flagellum dark (Fig.52A).

THORAX. — Pronotum yellowish green with pale red stripe laterally. Meso- and metanotum pale, unmarked. **Wing**: Fore- and hindwing pterostigma heavily pigmented basally. Venation pale, except origin of Rs, costal crossveins, middle part of Rs and contiguous veins, inner gradates, pseudocubital crossveins and branches of forked marginal veins dark. Length (1.89 cm): width (0.70 cm) = ratio (2.70). Hindwing venation pale, except middle costal crossveins, Rs-inner gradate crossveins and contiguous veins dark (Fig. 52B). Length (1.71 cm): width (0.54 cm) = ratio (3.17).

ABDOMEN. — Green. Tergites 1 and 2 with dark red markings (Fig. 52C). **Female**: Bursa copulatrix sac-like with pair of filamentous accessory glands bearing tiny, circular, sclerotized pits on the surface (Fig. 52D). Subgenitale two short lateral lobes and large anterio-medial projection (Fig. 52E). Spermatheca short, thick; vela with small lateral projection (Fig. 52D).

MATERIAL EXAMINED. — **Brazil**: **Santa Catarina**: São Joaquim, March 1999, Borges, R. (1♀)(apple).

***Leucochrysa* (*Nodita*) *lancala* Banks, 1944**

DIAGNOSIS. — The most distinctive characteristic of this species is the bird's-head-shaped apical projection of the arcessus. This species appears to be most closely related to *L.* (*N.*) *guataparensis* which also has the distinctively shaped apex of the arcessus, but the dark palpi, unconnected red stripes on the scape, and thinner gonocornua sets *L.* (*N.*) *lancala* apart.

HEAD. — Pale yellow. Frons with small, reddish brown spot between and below antennae. Third and fourth maxillary palpimeres and basal half of fifth segment dark. Gena red. Vertex yellow with thin, red, medial, V-shaped mark; on raised medial area two faint, widely-spaced, red, crescent-shaped marks. Scape pale with dorsolateral red stripe, continued onto antennal base and short dorso-medial red spot; pedicel pale with dark subapical ring; flagellum pale with dark medial stripe basally (Fig. 53A, C).

THORAX. — Cervical sclerites red. Pronotum yellow medially; green submedially; red stripe on lateral margin, tapering posteriorly; posterio-medial half with thin black stripe. Mesonotum pale with red tinge, more pronounced along anterior margin. Metanotum pale with red stripe laterally (Fig. 53A). **Wing**: Fore- and hindwing pterostigma dark. Venation green, except middle costal crossveins, origin of Rs, fourth Rs and contiguous veins, gradates, marginal forks and posterior ends of outer pseudocutibal veins 4–5 dark. Eight inner and nine outer gradate veins. Length (1.72–1.86 cm); width (0.55–0.67cm). Hindwing apically acute. Venation pale, except middle of Rs and contiguous crossveins, gradates, and marginal forks dark. Length (1.55–1.74 cm); width (0.44–0.53 cm) (Fig. 53B).

ABDOMEN. — Green; mid-line yellow (Fig. 53G). **Male**: Apex of ectoproct truncated obliquely. Anterior half of sternite 8 + 9 with microtholi and posterior half with dense, short, black setae. Gonarcus thick, short, with ovate lateral arms. Gonocornua long, tapering, dorsally ridged, nearly straight, but with slight apical twist, and somewhat angled medially. Arcessus narrow, bilobed apodeme basally, strongly arched apically, with well-sclerotized apico-medial hook without lateral lobes (Fig. 53D, E, F). **Female**: Spermatheca thick, sinuous; ventral impression short. Bursa convoluted. Subgenitale with swollen lateral lobes forming medial groove; anterio-medial projection finely rugose (Fig. 53H, I, J) .

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 19 April 1993, Freitas, S. (1♂)(orange); 10 September 1999, Freitas, S. (1♀); 10 October 1995, Freitas, S. (1♂)(orange); March 1996, Freitas, S. (1♀)(guava)(CAS); 6 February 1997, Freitas, S. (1♀); March 1996, Freitas, S. (1♀); Birigui, 21 February 1996, Scomparin, C. H. J. (1♀)(corn); **Mato Grosso**: Itiquira, 18 September 1996, (3♀2♂)(rubber); 18 November 1996, Scomparin, C. H. J. (1♀)(CAS); 30 December 1996, Scomparin, C. H. J. (1♂)(rubber); 23 January 1997, Scomparin, C. H. J. (1♂)(rubber).

***Leucochrysa* (*Nodita*) *lateralis* Navás, 1913c**

DIAGNOSIS. — This is one of several species with completely dark dorsal surface of the scape, V- or Y-shaped dark mark behind antennae on vertex, and dark markings on the meso- and metanotum. Of these species, *L.* (*N.*) *gossei* has dark maxillary palpi; *L.* (*N.*) *cruentata* has forewing shading at the origin of Rs; and *L.* (*N.*) *cruentata* and *L.* (*N.*) *affinis* have much larger lateral stripes on the pronotum. Perhaps the most closely related species is the more northern *L.* (*N.*) *virginiae,* which also has a pale pronotum, although with a small red spot in the anterio-lateral corner (Penny 1998). However, *L.* (*N.*) *virginiae* has a complete, broad dark band across the frons, which is not present in *L.* (*N.*) *lateralis.* The most distinctive feature of this species is the lateral projection of the bursal vela.

HEAD. — Yellow with red markings. Gena red. Clypeus pale with slight red tinge. Maxillary and labial palpi pale. Frons pale with short red bands below antennal bases and small medial red mark be-

tween antennal bases. Anterior part of vertex with Y-shaped mark (Fig. 54C). Scape dark brown throughout; pedicel pale with subapical dark ring (Fig. 54A); flagellum pale.

THORAX. — Pronotum green with pair of small red spots on anterio-lateral corners. Anterior margin of mesoprescutum and mesoscutum laterally reddish brown (Fig. 54A). **Wing**: Pterostigma with slight indication of dark mark basally. Forewing base and second axillary sclerite with brownish red spot. Venation pale, except ends of first eight costal crossveins, all of remaining costal crossveins; radial sector crossveins, gradates, Psm-Psc crossveins, and forked and unforked marginal veins dark (Fig.54B). Forewing length (1.73 cm): width (0.59 cm) = ratio 2.93. Hindwing venation pale, except costal crossveins and gradates dark. Length (1.45 cm): width (0.44) = ratio 3.30.

ABDOMEN. — Green, with reddish brown marks on tergites 2, 3, 6, and 7 (Fig. 54A). **Female**: Spermatheca short, pill-box-shaped; vela with lateral projection. Spermathecal duct moderately long, twisted but not coiled, becoming wider near spermatheca. (Fig. 54D). Subgenitale broad, without medial projection (Fig. 54E).

MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 18 October 1996, Scomparin, C. H. J. (1♀)(rubber).

Leucochrysa (*Nodita*) *marginalis* Banks, 1915

DIAGNOSIS. — This is one of a group of species with pale palpi, red gena, dorso-lateral stripe on the scape, pair of crescent-shaped marks on the vertex, dark lateral stripes on the pronotum, and darkened area in the middle of the Rs of the forewing. However, only a few other species in the group have dark antennae: *L.* (*N.*) *intermedia*, *L.* (*N.*) *lineata*, *L.* (*N.*) *melanocera*, *L.* (*N.*) *michelini*, *L.* (*N.*) *rodriguezi*, and *L.* (*N.*) *tabacinus*. Of these species, all have abdominal markings and more extensive meso- and metanotal markings than *L.* (*N.*) *marginalis*. Males of none of the other species have the subapical truncate plate of the arcessus of *L.* (*N.*) *marginalis*.

HEAD. — Yellow. Frons with tiny red spot below and between antennae. Gena red. Maxillary and labial palpi pale. Vertex with pair of medial, short, red, crescent-shaped stripes. Scape with red dorso-lateral stripe; pedicel pale with subapical dark ring; first 17 segments of flagellum black and more apical segments fuscous (Fig. 55A, C).

THORAX. — Pronotum pale with lateral dark stripe, which is restricted at mid-length (Fig. 55A). Mescutum pale with pair of small red spots. Metanotum pale, unmarked. **Wings**: Forewing venation green, except marginal junctions of costal crossveins, origin of Rs, and middle part of Rs and contiguous crossveins dark. Gradates pale. Length (1.63 cm): width (0.59 cm) = ratio (2.76). Hindwing venation green, except endings of basal costal crossveins, middle part of Rs and contiguous veins, and branched endings of forked marginal veins dark. Shading along hind margin at forked marginal veins. Length (1.41 cm): width (0.45 cm) = ratio (3.13). Fore- and hindwing pterostigma dark basally (Fig. 55B).

ABDOMEN. — Tergites without dark markings. **Male**: Sternites 8 and 9 not fused. Microtholi present. Dorsal apodeme of ectoproct thick, well sclerotized near callus cerci (Fig. 55D). Gonarcus thick, arched; lateral arms well developed, triangular. Gonocornua elongate but not reaching apex of arcessus, thick at base. Arcessus large with subapical medial plate and small, depressed apico-medial hook (Fig. 55E, F, G). Gonosaccus with few gonosetae, continued as second sac-like structure above sternite 9. **Female**: Spermatheca short with short spermathecal duct; ventral impression short. Bursa sac-like with pair of filamentous accessory glands (Fig. 55I). Subgenitale rounded with small median projection (Fig. 55H).

MATERIAL EXAMINED. — **Bolivia**: Rio Longo, 750 m, Fassl, holotype male (deposited in Museum of Comparative Zoology, Harvard University), **Brazil**: **São Paulo**: Balsamo, 15-X-97, Bergman, E. (1♀1♂)(rubber).

***Leucochrysa* (*Nodita*) *marquezi* Navás, 1913a**

DIAGNOSIS. — The oblique dark stripes at the posterior margin of the pronotum link *L.* (*N.*) *marquezi* with *L.* (*N.*) *affinis, L.* (*N.*) *guataparensis, L.* (*N.*) *internata,* and *L.* (*N.*) *lancala.* Of these species, *L.* (*N.*) *marquezi* is probably most closely related to *L.* (*N.*) *lancala*, with which it shares dark palpi and a dark mark on the medial surface of the scape. They also share sigmoidally curved gonocornua and quadrate lateral arms of the gonarcus of the male genitalia. However, *L.* (*N.*) *lancala* has more extensive dark markings on the meso- and metanotum, no dark markings on abdominal tergites 2 and 3, and a distinctively curved, bird's head shape to the apex of the arcessus (Fig. 53D).

HEAD. — Yellow. Frons with small reddish brown spot between and below antennae (Fig. 56C). Gena red (Fig. 56D). Apical maxillary palpimeres dark. Vertex pale with red, V-shaped mark behind antennal bases; posteriorly pair of crescent-shaped red stripes on raised medial area (Fig. 56A, C). Scape yellow with dorso-lateral red stripe continued onto antennal fossa, and short dorso-lateral red mark along medial margin (Fig. 56A); pedicel pale with subapical dark ring; flagellum pale.

THORAX. — Cervical sclerites red (Fig. 56C, D). Pronotum yellow medially, green submedially, with red stripe on lateral margin which tapers toward posterior margin; postero-medial region with pair of oblique, curved, black stripes about halfway between center line and margin. Mesonotum yellow with dark marks on prescutum and scutum (Fig. 56A). **Wings**: Forewing pterostigma with slightly dark pigmentation basally. Venation green, except first, second and last radial crossvein, apex of Rs, Rs-Psm crossveins 2–4; Psm-Psc crossveins, gradates, marginal forked and unforked veins dark (Fig. 56B). Forewing length (1.8–2.1 cm); width (0.64–0.72 cm). Hindwing acute. Pterostigma with well-developed basal dark mark. Venation green, except apex of Rs, gradates, marginal forked branches and apical costal crossveins dark (Fig. 56B). Length (1.44 cm): width (0.46 cm) = ratio (3.13).

ABDOMEN. — Green with yellow mid-line and red marks on tergites 2, 3, 6 and 7 (Fig. 56E). **Male**: Ectoproct apically truncate. Sternites 8 and 9 not fused; with many microtholi. Gonarcus thick, with vertically quadrate lateral arms. Gonocornua long, slightly sinuous, medially slanted. Arcessus short, double apodemes basally and with strong apical hook without small lateral lobes (Fig. 56H, I). **Female**: Spermathecae curved, ventral impression short. Bursa convoluted with pair of filamentous accessory glands (Fig. 56F, G). Subgenitale sclerotized, anterio-medial part elevated above membrane.

MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 10 February 1998, Freitas, S. (1♂1♀); 10 March 1999, Freitas, S. (1♂); **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (3♂1♀)(rubber)(SDF/CAS); 23 January 1997, Freitas, S. (1♂1♀)(rubber); 13 September 1998, Freitas, S. (1♀)(CAS).

***Leucochrysa* (*Nodita*) *melanocera* Navás, 1916**

DIAGNOSIS. — This species is most notable for the lack of markings—both on the face and metanotum. Also, abdominal markings, although present on all segments, are quite small. The distinctive spotting pattern of the mesonotum and second axillary sclerite indicate a fairly close relationship with *L.* (*N.*) *barrei* and *L.* (*N.*) *parallela*, but *L.* (*N.*) *barrei* has dark palpi and gena, and both have pale antennae. The pentagonal-shaped subgenitale and distinctly two-parted spermathecal vela can also help distinguish this species.

HEAD. — Yellow. Frons, clypeus and gena without dark markings. Maxillary and labial palpi pale. Vertex with two dark marks anteriorly and weak red marks on raised medial area. Scape and pedicel with broad, dorso-lateral dark stripes; flagellum dark.

THORAX. — Pronotum greenish yellow with thin, lateral, red stripes widening at apices. Mesoprescutum with black spots laterally; mesoscutum with pair of dark spots medially. Second

axillary sclerite with dark spot (Fig. 57A). **Wings**: Pterostigma with faint dark spot basally. Forewing venation pale with costal crossvein endings, origin of radial sector, first Rs-Psm crossveins, middle part of Rs and adjacent veins, gradates, and forked marginal veins dark. Length (1.77 cm): width (0.65 cm) = ratio (2.72). Hindwing acute. Venation pale, except costal crossveins, middle part of Rs and some marginal forks dark (Fig. 57B). Length (1.52 cm): width (0.50 cm) = ratio (3.04).

ABDOMEN. — Yellowish green. Tergites with lateral dark red spots (Fig. 57A). **Female**: Spermatheca with vela divided into two parts (Fig. 57C). Bursa with pair of filamentous accessory glands. Subgenitale pentangular (Fig. 57D).

MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 18 February 1996, Freitas, S. (1♀)(rubber).

***Leucochrysa* (*Nodita*) *rodriguezi* (Navás, 1913a)**

DIAGNOSIS. — This is one of a large group of species with red gena, dorso-lateral stripes on the scape, crescent-shaped marks on the vertex, dark red lateral stripes on the pronotum, and dark area at mid-length of forewing Rs. It is one of six species of this group with dark antennae found in Brazilian agro-ecosystems. Of these species, only *L.* (*N.*) *marginalis* has similar small linear dark markings on the mesoscutum. However, *L.* (*N.*) *marginalis* has no abdominal tergite markings and has a distinctive subapical, truncate plate on the arcessus. The gonocornua with dorso-basal tooth is a distinctive feature of *L.* (*N.*) *rodriguezi* found in no other species.

HEAD. — Yellow with red markings. Vertex with pair of oblique, crescent-shaped red marks on medial raised area. Small red spot between antennal bases. Gena red. Maxillary and labial palpi pale. Scape with dark red dorso-lateral stripe; pedicel with small dorso-lateral dark spot; flagellum black, basal antennomeres laterally more intensively black (Fig. 58A, D).

THORAX. — Yellowish green. Pronotum with lateral red stripes. Mesoscutum pale with pair of medial red spots and premesoscutum with pair of lateral, diffuse, pale red spots. Metanotum pale, without marks (Fig. 58A). Pterostigma with dark basal mark. Forewing venation green, except costal crossveins 5–15, origin of Rs, Rs-Psm crossveins 1–6, apex of Rs, inner gradates 5–7 and outer gradates 7–9, and Psm-Psc crossveins dark. Length (16.9–17.8 mm); width (5.3–6.4 mm). Hindwing venation pale, except costal crossveins 7–10, and outer gradates dark Fig. 58B). Length (1.44 cm): width (0.47 cm) = ratio (3.06).

ABDOMEN. — Yellow with pair of small red stripes on each tergite (Fig. 58C). **Male**: Apex of ectoproct with several long setae. Sternites 8 + 9 fused and apically bilobed; with many microtholi (Fig. 58E). Gonarcus thick, only slightly arched; lateral arms short, ovate. Gonocornua elongate, forcipate with dorso-basal tooth. Arcessus with dorso-medial, subapical, acute projection and ventrally decurved apical hook flanked by small, rounded lateral lobes. Gonosaccus with few scattered setae (Fig. 58G, H). **Female**: Cavity between subgenitale and sternite 8 large and sclerotized, with tiny microtrichia. Subgenitale apically bilobed, with anterio-medial projection. Spermatheca short with ventral impression short. Apex of spermathecal duct strongly dilated (Fig. 58I).

MATERIAL EXAMINED. — **Brazil**: **São Paulo** – Jaboticabal, 27 August 1996, Domenici, M. G. (1♀); 29 August 1995, Ferreira, R. J. (1♂)(CAS); 3 November 1989, Jacob, M. (1♂)(orange); 9 October 1989, Carmo, O.B. (1♀); 23 March 1996, Fernandes, O. A. (1♀); 9 August 1996, Freitas, S. (1♂); Taquaritinga, 4 September 1993, Xavier, A. L. Q. (1♀)(orange); 4 September 1993, Narciso, R. (1♂)(orange); Birigui, 21 February 1996, Scomparin, C. H. J. (1♂)(corn); **Mato Grosso**: Itiquira, 9 November 1999, Freitas, S. (1♂)(rubber); 10 September 1996, Scomparin, C. H. J. (1♀)(rubber); 14 December 1996, Scomparin, C. H. J. (1♀)(rubber); **Bahia**: Juazeiro, 6 March 1996, Ferreira, R. J. (2♂)(cashew nut).

***Leucochrysa* (*Nodita*) *affinis* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "São Paulo: Jaboticabal, 5 June 1995, Freitas, S." (orange).

DIAGNOSIS. — This is a member of a group of species with the dorsal surface of the scape completely red, while the ventral surface is completely pale. All species in this group appear to have at least some dark markings on the mesonotum. *Leucochrysa* (*N.*) *affinis* appears intermediate with the group of species having oblique dark marks at the posterior part of the pronotum, and is the only species with completely red dorsal scape to have oblique dark marks on the pronotum. A similar species is *L.* (*N.*) *cruentata*, which has the dark dorsal side of the scape, dark flagellum, and extensive segmental markings on the abdominal tergites. It also has large, angled gonocornua, but they are forcipate and rather evenly tapered in *L.* (*N.*) *cruentata*, whereas the gonocornua of *L.* (*N.*) *affinis* are distinctively flattened, widened at mid-length, and apically divergent. *Leucochrysa* (*N.*) *affinis* actually appears most closely related to *L.* (*N.*) *guataparensis,* which does not have a completely red dorsal surface on the scape, but has markings more like two longitudinal stripes partially fused along the mid-line. The male gonocornua of both species are highly flattened, but in *L.* (*N.*) *guataparensis* they are triangular, while in *L.* (*N.*) *affinis* they are strongly elbowed. *Leucochrysa* (*N.*) *affinis* also has dark antennae, which are pale in *L.* (*N.*) *guataparensis.*

The name *affinis* is Latin for "related to" and refers to the close relationship of this species to *L.* (*N.*) *guataparensis.*

HEAD. — Yellow. Gena red. Vertex with V-shaped red mark behind antennal bases. Maxillary and labial palpi pale. Scape red dorsally, pale ventrally; pedicel and flagellum black (Fig. 59A,D).

THORAX. — Pronotum pale green with lateral red stripe, fused at posterio-lateral margin with second, oblique, thin, red mark on posterior half (Fig. 59A). Meso and metanotum pale, unmarked. **Wings**: Forewing pterostigma with faint dark mark basally. Venation green; except costal crossveins, R-Rs crossveins, gradates, and apices of marginal forks dark. Length (1.76 cm): width (0.64 cm) = ratio (2.75). Hindwing pterostigma with well-developed dark mark basally. Venation pale, except middle part of Rs and contiguous veins, gradates, and apices of marginal forks dark (Fig. 59B). Length (1.47 cm): width (0.48 cm) = ratio (3.06).

ABDOMEN. — Green with red marks (Fig. 59C). **Male**: Microtholi on sternite 8 + 9. Gonarcus short and broad, with ovate lateral arms. Gonocornua dorso-ventrally flattened and broadly expanded at mid-length, apically pointed with divergent apices. Arcessus basally broad, without dorsal horns; decurved apical hook without well-developed lateral lobes (Fig. 59E,F). **Female**: Spermatheca short; ventral impression short. Bursa convoluted with pair of filamentous accessory glands.

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 4 December 1996, Freitas, S. (3♂ paratypes)(orange)(SDF/CAS); **Mato Grosso**: Itiquira, 5 April 1996, Scomparin, C. H. J. (1♂ paratype)(rubber); 20 January 1997, Freitas, S. (1♀ paratype)(CAS); 16 August 1997, Freitas, S. (8♂2♀ paratypes)(rubber).

***Leucochrysa* (*Nodita*) *barrei* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 2-IX-97, Scomparin, C. H., SP79 ♂" (rubber).

DIAGNOSIS. — This is one of the species with well-defined dark spots on the mesoscutum. Of these species, *L.* (*N.*) *clepsydra* has a small spot rather than dorso-lateral stripe on the scape, dark red spots rather than lateral stripe on pronotum, and prominent dorsal horns of the arcessus. Unlike *L.* (*N.*) *barrei*, *L.* (*N.*) *ictericus* has pale palpi, no second axillary sclerite markings, and basally and apically toothed gonocornua. *Leucochrysa* (*N.*) *melanocera* has pale palpi, thin lateral pronotal stripes, and

small dark markings on all abdominal tergites. The highly arched form of the arcessus and gonocornua, as well as small ventral lobe at mid-length of the gonocornua are unique to *L.* (*N.*) *barrei.*

This species is dedicated to Lionel Barré, who enthusiastically initiated the use of chrysopids for biological control of rubber tree pests in Brazil.

HEAD. — Yellow. Frons and clypeus pale, unmarked. Gena with small red stripe near frons. Maxillary palpi basally pale, dark in middle, and apical half of apical segment pale. Labial palpi pale (Fig. 60C, D). Vertex yellow, unmarked. Scape with dorsolateral red stripe; pedicel with apical dark ring; flagellum pale.

THORAX. — Pronotum pale with irregular, lateral, thin, dark red stripe. Mesonotum with pair of dark circular spots submedially. Mesonotal second axillary sclerite red basally. Metanotum pale, unmarked (Fig. 60A). **Wing**: Forewing pterostigma faintly darkened basally. Venation green, except costal, radial and Psm-Psc crossveins, gradates, and apices of marginal forks dark. Length (2.75 cm): width (1.0 cm) = ratio (2.75). Hindwing pterostigma with well-developed dark basal spot. Venation green, except apex of Rs and outer gradates dark (Fig. 60B). Length (2.30 cm): width (0.75 cm) = ratio (3.07).

ABDOMEN. — Green with dark marks on tergites 3 and 4. **Male**: Abdominal sternites without microtholi. Gonarcus short, with no vertical arch; lateral arms ovate, longer than high (Fig. 60E). Gonocornua slender, forcipate and decurved, with small ventral lobe at mid-length (Fig. 60F). Arcessus strongly arched high above gonocornua, with subapical lateral ridge and decurved apical hook. Gonosaccus without gonosetae.

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Nodita*) *confusa* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Fraiburgo, SC, 26-IX-99, Maçã, SP83, Borges R." (apple).

DIAGNOSIS. — This is one of four species in the region which have the origin of the radial sector heavily shaded. Two of these, *L.* (*N.*) *cruentata* and *L.* (*N.*) *gossei*, have darkened dorsal surface of the scape and belong to another species group. *Leucochrysa* (*N.*) *confusa* appears to be closely related to *L.* (*N.*) *maculata*, but *L.* (*N.*) *maculata* has heavy dark markings below the antennae on the frons which forms a complete or interrupted band across the frons and the male gonarcus has a short vertical plate dorso-medially.

The name "confusa" comes from the Latin *confusio* meaning mixture or disorder, and refers to the difficulty in interpreting the male genitalia of this species.

HEAD. — Yellow with red markings. Vertex pale, without markings, except red spot behind each antennal base. Gena with red stripe extending slightly onto frons. Frons pale, without markings. Scape with dorso-lateral dark brown stripe; pedicel pale with apical dark ring; flagellum pale.

THORAX. — Cervical sclerite red (Fig. 61A,C). Pronotum green with thin lateral red stripe on anterior half. Mesonotum with irregular dark marks on prescutum and scutum. Metanotum pale, without markings (Fig. 61A). **Wing**: Forewing pterostigma with well-developed dark spot basally. Venation pale, except costal and R-Rs crossveins, origin of Rs and Ma, inner gradates, Psm-Pscu crossveins, apex of forked and unforked marginal veins, and anal veins dark. Origin of Rs, inner gradates, and last Psm-Pscu crossvein shaded. Forewing length (1.3 cm): width (0.41 cm) = ratio (3.17). Hindwing venation pale, except costal, R-Rs crossveins and inner gradates dark. Length (1.12 cm): width (0.34 cm) = ratio (3.29) (Fig.61B).

MALE ABDOMEN. — Green with red markings on tergites 2, 6, and 7 (Fig. 61G); densely covered by long setae on tergites and sternites (Fig. 61H). Microtholi absent. Gonarcus arched, thick with short, narrow lateral arms. Gonocornua elongate, apically forcipate and embracing arcessus. Arcessus

slender and apically decurved with apical hook flanked by vertical plate-like lobes. Gonosaccus with numerous tiny gonosetae with large bases (Fig. 61, D, E, F).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *cornuta* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Guaira, SP, 12-XII-97, Angelini, M. R." (corn).

DIAGNOSIS. — This is one of a group of species best defined by elements of the male genitalia. The gonocornua are long and relatively straight, and the arcessus has a pair of subapical dorsal horns and sharply decurved apex. Other members of this group include: *L.* (*N.*) *clepsydra, L.* (*N.*) *cruentata, L.* (*N.*) *lenora* Banks (1944), and *L.* (*N.*) *nictheroyana* (Navás, 1926). Of these species *L.* (*N.*) *cruentata* and *L.* (*N.*) *nictheroyana* have a completely dark dorsal surface of the scape, complete lateral pronotal stripe, dark palpi, and curved, forcipate gonocornua. *Leucochrysa* (*N.*) *lenora* is a more northern species with red spots below each antenna on the frons, but unlike *L.* (*N.*) *cornuta* the antennal scape dorsally is heavily marked with a dorso-lateral stripe that expands apically to encompass the whole surface, the pronotum only has a pair of small dark spots at the anterio-lateral margins, and the mesonotum has extensive dark markings along the anterior margin of the prescutum and laterally on the scutum. However, the male genitalia are almost identical. Even so, the non-genitalic character states are so different as to preclude these being regional variants.

The name "cornuta" comes from the Latin *cornutus,* which means horned, and refers to the cone-like shape of the lateral arms of the gonarcus.

HEAD. — Green. Gena with dark red mark near frons (Fig. 62C). Frons pale, without markings. Maxillary and labial palpi pale. Vertex pale, except for dark red continuation of scape stripe onto antennal base. Scape with dorso-lateral dark red stripe; pedicel pale with apical dark ring; flagellum pale (Fig. 62A).

THORAX. — Green. Pronotum pale with thin, lateral dark red stripe on anterior half. Mesonotum pale with pair of small irregular dark marks on prescutum and scutum (Fig. 62A). **Wings**: Forewing pterostigma with faintly dark basal spot. Venation green, except anterior junction of costal crossveins, apical radial crossveins, middle part of Rs, inner and outer gradates, vertex of intramedian cell, Psm-Pscu crossveins, and hind marginal crossveins dark (Fig. 62B). Length (1.54 cm): width (0.56 cm) = ratio (2.75). Hindwing venation green, except costal and R-Rs crossveins dark (Fig. 62B). Length (1.30 cm): width (0.43 cm) = ratio (3.02).

ABDOMEN. — Green; tergites with red markings; sternites 2–8 with numerous microtholi. **Male**: Gonarcus strongly arched, with ovate lateral arms. Gonocornua elongate, evenly tapered, slightly sinuous at mid-length. Arcessus with two well-developed subapical horns and decurved, apico-medial hook. Gonosaccus with few scattered setae (Fig. 62D, E, F).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *forciformis* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Bra-MT-Itiquira, P. E.Michelin, 20/I/97, SP41B, ♂, Freitas, S." (rubber).

DIAGNOSIS. — This species is a member of a group of species with bifurcate apices to the gonocornua. Members of the group also have pale palpi, a dark dorsal abdominal stripe and dark markings at the lateral margins of the meso- and metascutellum. However, *L.* (*N.*) *forciformis* can be distinguished from *L.* (*N.*) *forcipata* and *L.* (*N.*) *furcata* by the broad lateral pronotal stripe, by the dark transverse band behind the antennal bases, and broadly contiguous bases of the gonocornua.

The name comes from the Latin *forceps* meaning pincer-like, and *forma* meaning form, referring to the shape of the bifurcate apices of the gonocornua.

HEAD. — Yellow. Clypeus and frons with diffuse red coloration. Gena pale, unmarked. Vertex with broad, transverse brown band behind antennal bases; pair of indistinct parallel red stripes on raised medial area (Fig. 63D). Maxillary and labial palpi pale. Scape with diffuse reddish brown spot; pedicel pale with apical dark ring; flagellum black.

THORAX. — Yellow. Pronotum pale with broad, dark, lateral stripe. Meso- and metanota with dark lateral stripe and lateral margin of meso- and metascutellum (Fig. 63A). **Wings**: Forewing pterostigma with large dark spot basally. Venation green, except apex of Rs and adjacent crossveins, gradates, forked and unforked marginal veins, anal veins, and hind margin dark. Veins in anal area more intensively darkened. Length (1.88 cm): width (0.62 cm) = ratio (3.03). Hindwing venation green, except apex of Rs, gradates, apices of forked and unforked marginal veins, and hind margin dark. Anal region more intensively darkened (Fig. 63B). Length (1.65 cm); width (0.50 cm) = ratio (3.30).

ABDOMEN. — Microtholi present. Tergites dark, forming dark medial stripe (Fig. 63C). **Male**: Gonarcus thick; strongly arched in broad V-shape; lateral arms broadly flattened. Gonocornua with broad, contiguous bases and bifurcate, decurved hooks apically. Arcessus short, without subapical horns or plate, apico-medial decurved hook with poorly developed lateral lobes. Gonosaccus with gonosetae on conspicuous conical bases in two lateral pockets, most medial gonosetae longer and most lateral gonosetae shorter; area beneath gonocornua with small sclerotized pits on membrane (Fig. 63E, F). **Female**: Spermatheca short, with many coils. Bursa with pair of filamentous accessory glands (Fig. 63G).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 17 July 1995, Freitas, S. (1♀ paratype); **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (2♀ paratypes)(rubber).

Leucochrysa (*Nodita*) *furcata* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 20-I-97, Scomparin, C. H., V.216, SP41D" (rubber).

DIAGNOSIS. — This species is a member of the group of species easily distinguished by the bifurcate gonocornua. Within the group, this species has a shorter arcessus, and shorter gonocornua with apical teeth of unequal length. Additionally, it does not have the development of dark coloration on meso- and metascutellum that the nominate species has. It can be separated from *L.* (*N.*) *forciformis* by the lack of dark band behind the antennae, lack of dark lateral stripes on meso- and metanota, and widely separated bases of the gonocornua of *L.* (*N.*) *furcata*. However, the most distinctive feature (found in no other species) is the pair of sclerotized sacs at the apex of sternite 8 + 9 in males of of *L.* (*N.*) *furcata*.

The name "furcata" is derived from the Latin *furca*, meaning fork-bearing, which refers to the bifurcate apex of the gonocornua.

HEAD. — Yellow. Clypeus and frons with diffuse red pigmentation. Gena pale, unmarked. Vertex diffuse red with anterior pair of short, convergent, dark stripes (Fig. 64F). Maxillary and labial palpi pale. Scape with broad reddish spot; pedicel pale with apical dark ring; flagellum dark.

THORAX. — Green. Pronotum green with reddish brown stripe laterally. Mesoscutum and scutellum pale with small lateral red mark. Metascutellum pale with dark red lateral mark, remainder of metanotum pale green (Fig. 64A). **Wings**: Forewing pterostigma with well-developed dark mark basally. Venation pale, except costal crossveins, R-Rs crossveins, Rs-Psm crossveins, Psm-Psc crossveins, apex of Rs, gradates, marginal forks and anal veins dark. Length (0.93 cm): width (0.31 cm) = ratio (3.00). Six inner and eight outer gradate crossveins (Fig. 64B). Hindwing acute. Pterostigma with well-developed dark mark basally. Venation pale, except R-Rs crossveins, gradates,

marginal forks, apex of Rs, and hind marginal veins dark (Fig.64B). Length (0.81 cm): width (0.25 cm) = ratio (3.24). Five inner and eight outer gradate crossveins.

ABDOMEN. — All tergites dark, forming longitudinal dark stripe (Fig. 64C). **Male**: Apex of sternite 8 + 9 with pair of laterally raised, sclerotized sacs and tiny medial denticles (Fig. 64 D, E). Gonarcus slightly arched, thick, with rounded lateral arms. Gonocornua short, with divided, two-pronged apex. Arcessus narrow, elongate, without subapical horns or plate, with apical decurved, medial hook, but lateral lobes not well developed. Gonosaccus with numerous gonosetae (Fig. 64G, H). **Female**: Spermatheca short, once coiled. Bursa with tiny denticles and pair of filamentous accessory glands (Fig. 64I, J).

OTHER MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 18 August 1998, Freitas, S. (1♀ paratype)(rubber).

***Leucochrysa* (*Nodita*) *guataparensis* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Luiz Antonio, SP, Faz. Guatapara, T. 22, Celpav, 27/07/92, Freitas, S." (eucalyptus)

DIAGNOSIS. — This species has a bird's-head-shaped arcessus. The only two other species with this shape are *L.* (*N.*) *lancala*, from which it can be distinguished by the pale palpi and broad and apically decurved gonocornua, and *L.* (*N.*) *affinis*. The oblique pronotal markings and flattened gonocornua probably indicate a close relationship between these two species. They can be separated by the dark flagellum and broadly triangular shape of the gonocornua of *L.* (*N.*) *guataparensis*.

The name "guataparensis" refers to the small town of Guatapara, in which the primary type specimen was collected.

HEAD. — Yellow. Gena red. Vertex pale with V-shaped red mark behind antennal bases. Frons pale with small red spot between and below antennae. Maxillary and labial palpi pale. Scape pale with two dorsal red stripes medially fused; pedicel pale with apical dark ring; flagellum pale, but basal antennomeres darkly shaded on anterior surface (Fig. 65A, D).

THORAX. — Green. Pronotum pale with dark red lateral stripe; pair of thin, oblique dark lines fused to lateral stripes at posterio-lateral corners. Mesonotum pale with red mark at lateral margin of prescutum (Fig. 65A). Metanotum pale yellow, without markings. **Wings**: Forewing pterostigma heavily pigmented basally. Venation green, except costal crossveins, middle part of Rs and adjacent crossveins, inner and outer gradates, apices of unforked and first forked marginal veins dark (Fig. 65B). Length (1.58–1.78 cm); width (0.53–0.64 cm). Hindwing pterostigma darker basally than in forewing. Venation green, except costal crossveins, middle part of Rs, inner and outer gradates and forked marginal veins dark (Fig. 65B). Length (1.47 cm): width (0.50 cm) = ratio (2.94).

ABDOMEN. — Tergites pale, with red markings (Fig. 65C). **Male**: Microtholi present. Gonarcus only slightly arched, lateral arms small, elongate triangular. Gonocornua, in lateral view, sharply elbowed and broadly expanded at mid-length, apically decurved; in dorsal view, a broad triangular plate with apical point. Arcessus short, broadly triangular, with subapical bird's-head-shaped curve, in lateral view; apically decurved as small medial hook and undeveloped lateral lobes (Fig. 65E, F). **Female**: Subgenitale well-sclerotized, with pair of heavily sclerotized lateral tubercles caudally. Spermathecae short, sinuous. Bursa with pair of filamentous accessory glands (Fig. 65G, H, I).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Luiz Antonio, 1 June 1994, Freitas, S. (1♂ paratype)(eucalyptus); Jaboticabal, S. (1♀ paratype), 30 March 1996, Freitas, S. (1♀ paratype); 4 December 1996, Freitas, S. (1♀ paratype); **Mato Grosso**: Itiquira, 20 January 1997, Freitas, S. (1♂ paratype)(rubber); 17 February 1997, Scomparin, C. H. J. (4♂ paratypes)(rubber).

Leucochrysa (*Nodita*) *ictericus* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Birigui, SP, 21-I-96, Scomparin, C. H. J." (corn).

DIAGNOSIS. — *Leucochrysa* (*N.*) *ictericus* is closely related to *L.* (*N.*) *rodriguezi*. Both species have a basal tooth on the gonocornua, which is found in no other species. They can be separated by the more dorsal stripe on the scape and larger, more circular spot on the mesoscutum of *L.* (*N.*) *ictericus*. However, the most apparent differences are in the male genitalia, where *L.* (*N.*) *ictericus* has an unusual gonarcus with lateral arms that project laterally, not anteriorly, with no arch, and the presence of a medio-dorsal lobe. Neither of these characteristics is found in any other species of *Leucochrysa* (*Nodita*). The gonocornua are also distinctively elongate, with an apical notch.

The name comes from the Greek *ikterikos* meaning jaundiced or yellow and refers to the basic body coloration.

HEAD. — Yellow with red markings. Vertex pale with pair of oblique crescent-shaped red marks on raised medial area. Frons pale with small red spot between antennal bases. Gena red, extending as red suffusion on clypeus. Maxillary and labial palpi amber. Scape with mid-dorsal red stripe, pedicel pale with apical black ring; flagellum dark, with basal antennomeres intensely black ventro-laterally (Fig. 66A, C, D).

THORAX. — Yellow. Legs pale. Pronotum pale with lateral red stripes extending to lateral tip of mesoprescutum. Mesoscutum with submedial, circular red spot (Fig. 66A). Metanotum pale, without markings. **Wings**: Forewing pterostigma with faint dark spot basally. Venation pale, except costal crossveins, R-Rs crossveins, Rs-Psm and Rs-Ig crossveins, and gradates dark. Gradate series divergent. Length (1.55–1.69 cm); width (0.5 cm). Hindwing pterostigmatic spot faint. Venation pale, except middle costal crossveins, R-Rs transverse veins, middle part of Rs and posterior inner gradates dark; darkness of crossveins not as intense as on forewing. Length (1.33–1.47 cm); width (0.39–0.47 cm) (Fig. 66B).

ABDOMEN. — Yellow with faint red spots. **Male**: Gonarcus not arched; lateral arms flat, ovate, at right angle to arcessus; dorso-medial, caudally-directed lobe with apical tooth. Gonocornua elongate, tips bifid; large, apically-directed basal tooth. Arcessus broad, with decurved apical hook flanked by apically truncate membranous lobes. Gonosaccus with sparse gonosetose (Fig. 66E, F, G). **Female**: Spermatheca short with long spermathecal duct (Fig. 66I). Subgenitale with posterio-lateral lobes and long anterio-medial projection (Fig. 66J, H).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Birigui, 21 November 1996, Scomparin, C. H. J. (1♂ paratype)(corn); Taquaritinga, 4 September 1993, Xavier, A. L. Q. (1♂1♀ paratypes)(orange); Jaboticabal, 13 February 1991, Freitas, S. (1♀ paratype)(CAS); 9 August 1996, Freitas, S. (1♂ paratype)(orange); March 1996, Freitas, S. (1♂3♀ paratypes)(SDF/CAS); 30 June 1992, Pessoa, R. (1♂ paratype); 27 October 1995, Freitas, S. (1♀ paratype); 23 March 1996, Fernandes, O. A. (1♀ paratype); 18 March 1998, Freitas, S. (1♀ paratype); 14 March 1995, Seguim, L. D. (1♀ paratype); Nova Europa, 21 October 1996, Bergman, L. G. (1♀ paratype)(rubber).

Leucochrysa (*Nodita*) *incognita* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 30-XII-96, Scomparin, C. H. J." (rubber).

DIAGNOSIS. — The short, twisted shape of the gonocornua is distinctive. We have not seen this form in any other species and this feature should be sufficient for recognition of the species.

The name "incognita" comes from the Latin *incognitus* meaning unknown or strange, and refers to the bizarre shape of the male gonocornua.

HEAD. — Yellow. Frons and vertex without markings. Gena red (Fig. 67C). Maxillary palpimeres pale, except four and basal half of five dark. Scape faintly darkened; pedicel pale with apical dark ring; flagellum dark.

THORAX. — Pale, unmarked. **Wing**: Forewing pterostigma with dark mark basally. Venation green, except first 15 costal crossveins, base and apex Rs, and inner and outer gradates dark. Length (1.47 cm): width (0.55 cm) = ratio (2.67). Hindwing pterostigma with well-developed, dark mark basally. Venation pale, except gradates and costal crossveins somewhat dark (Fig. 67A). Length (1.19 cm): width (0.39 cm) = ratio (3.05).

ABDOMEN. — Pale, unmarked. Dorsal apodeme of ectoproct heavily sclerotized and forked near callus cerci. Apical half of sternite 8 + 9 strongly tapered (Fig. 67B). **Male**: Lateral arms of gonarcus ovate, with irregular margins; strongly arched and curved. Gonocornua short, twisted. Arcessus narrow with straight medial hook flanked by small lateral lobe. Gonosaccus with sparse gonosetae (Fig. 67D).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *interata* de Freitas and Penny, new species**

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP, 20-X-93, Marucci, R. (cotton).

DIAGNOSIS. — The combination of character states which help define this species include: thin, red marks from frons to tentorial pits, dark spots on mesonotum, and pronotum with medial spots or lateral stripe extensions. Three other species also share this suite of character states: *L.* (*N.*) *affinis*, *L.* (*N.*) *camposi*, and *L.* (*N.*) *parallela*. Unlike *L.* (*N.*) *interata*, *L.* (*N.*) *affinis* has dark dorsum of the scape, dark antennae, and no dark metanotal markings. *Leucochrysa* (*N.*) *parallela* also has no dark metanotal markings and no medial spots on the pronotum. Probably the most closely related species is *L.* (*N.*) *camposi*, which has more extensive markings of meso- and metanotum and abdominal tergites than *L.* (*N.*) *interata*. Additionally, the slender elongate spermatheca and broad antero-medial projection of the subgenitale are distinctive for *L.* (*N.*) *interata*.

The name "interata" comes from the Latin *inter* meaning between and *atus* meaning pertaining to, and refers to the apex of the spermathecal gland which is neither hairy (the usual state for chrysopids) nor bearing small plates.

HEAD. — Yellow. Frons and clypeus unmarked. Gena with small red spot near frons. Maxillary and labial palpi pale. Vertex yellow with pair of crescent-shaped red stripes on raised medial area. Scape and pedicel with red stripe dorso-laterally; flagellum pale, with basal antennomeres dark on lateral margin (Fig. 68A, C, D).

THORAX. — Pronotum green, with pair of black punctures at mid-length; red stripe weakly defined laterally. Mesoprescutum and scutum pale, with pair of diffuse red marks. Metanotum pale, with pair of pale red marks (Fig. 68A). **Wing**: Pterostigma with faint dark mark basally. Forewing venation green, except apical forks and basal radial and medial crossveins dark. Inner and outer gradates pale (Fig. 68B). Forewing length (1.93 cm): width (0.72 cm) = ratio (2.68). Hindwing length (1.64 cm): width (0.54 cm) = ratio (3.04).

ABDOMEN. — Pale; tergites 1 and 2 with red marks (Fig. 68E). **Female**: Spermatheca long; ventral impression short. Surface of spermathecal duct apex smooth, neither hairy nor with tiny plates. Subgenitale with broad, heavily-sclerotized antero-medial projection (Fig. 68F, G).

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Nodita*) *lineata* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Luiz Antonio, SP, Fz. Guatapara, T.25, Celpav, ♂, 1-X-92, SP41, Freitas, S." (eucalyptus).

DIAGNOSIS. — There is a group of species that has dark abdominal tergites that form a continuous dark dorsal stripe and apically bifurcate gonocornua of the male genitalia. Among these species there appears to be a progression from *L.* (*N.*) *rodriguezi* which has only crescent-shaped marks on the abdomen, arched gonarcus, and narrow gonocornua with only a slight indication of apical bifurcation; to *L.* (*N.*) *ictericus* with a complete abdominal stripe, flattened gonarcus with lateral arms at right angles to the arcessus, and narrow gonocornua with slightly bifurcate apices; to *L.* (*N.*) *lineata* with gonocornua greatly swollen basally and apically cleft (or hooked). Intermediate stages of this development can be observed in the male genitalia of *L.* (*N.*) *michelini*, *L.* (*N.*) *retusa*, and *L.* (*N.*) *tabacinus*. However, the differences among individual species in this grouping are so striking that they could not be considered as variants of a single species. This group of species appears to be confined to southern South America.

The name "lineata" is derived from the Latin *linea* meaning line or thread, and refers to the dark medial line on the abdominal tergum of this species.

HEAD. — Yellow. Maxillary and labial palpi amber. Gena pale, unmarked. Indistinct reddish brown transverse band at clypeal-frontal suture; small dark red spot below antennae on mid-line. Vertex with pair of divergent red stripes, which at anterior end form dark red double spot. Scape suffused red dorsally, pale ventrally; pedicel pale with apical dark ring; flagellum black (Fig. 69C).

THORAX. — Pronotum green, with broad brown stripe laterally. Mesoprescutum brown laterally along prescutal-scutal suture; scutum with two interconnected brown marks on either side; scutellum with post-lateral brown dot. Metascutum and scutellum with large brown marks submedially (Fig. 69A). **Wing**: Forewing pterostigmal spot faint. Venation green, except origin of Rs, Rs vein for first five cells and contiguous crossveins, gradates and marginal forks dark. Length (1.58 cm): width (0.56 cm) = ratio (2.82). Hindwing venation pale, except apex of Rs and contiguous crossveins, gradates and marginal forks dark (Fig. 69B). Length (1.41 cm): width (0.45 cm) = ratio (3.13).

ABDOMEN. — Tergites dark, forming dark mid-line (Fig. 69D). Microtholi present on sternite 8 + 9. **Male**: Tiny lanceolate gonocristae at apex of sternite 8 + 9. Gonarcus slender, only slightly arched; lateral arms almost in straight line. Gonocornua basally greatly swollen, with medially curved, apico-lateral hook. Arcessus with apically-decurved medial hook flanked by pair of rounded, membranous lobes. Gonosaccus with gonosetae on conspicuous conical bases in pair of lateral pockets; anterior to field of gonosetae, field of tiny linear pits below gonocornua on lateral margins of gonosaccus (Fig. 69E, F).

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Nodita*) *maculosa* de Freitas and Penny, new species

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Taquaritinga, SP, Brasil, I-93, Fz. São Jose, Xavier, A. L. Q." (orange).

DIAGNOSIS. — Almost all species of *L.* (*Nodita*) with heavy shading of forewing crossveins [e.g., *L.* (*N.*) *postica*] also have a dark apex of the hindwing. The heavy shading of forewing crossveins combined with pale apex of the hindwing is unusual. Of the species with heavy shading of the forewing crossveins, only *L.* (*N.*) *maculosa* has a flagellum which is basally dark and pale after the first two segments. The short spermatheca is also unknown in other species of *Leucochrysa*. In this respect, it more closely resembles species of Chrysopini with cordate spermatheca, such as *Chrysoperla externa* and *Plesiochrysa brasiliensis*.

The name "maculosa," from the Latin *macula* meaning spot or mark, refers to the heavily margined crossveins in the forewing, which gives this species the appearance of having spotted forewings.

HEAD. — Pale yellow. Frons green with wine red marks below antennal bases from eye margin to medial margin of antennae and ventrally to below anterior tentorial pit. Vertex green with antennal fossa wine red. Maxillary palpi pale basally, dark on fourth and basal half of apical segment, pale on apical half (Fig. 70D). Scape with dorso-lateral and medial red stripes fused dorsally; pedicel pale with apical dark ring; first two antennomeres dark, apical segments pale (Fig.70A).

THORAX. — Cervical sclerites red. Pronotum green with pair of oblique wine red marks on posterior 2/3. Mesoprescutum pale with brick red mark along lateral margin, extending onto scutum near wing base. Metanotum pale, without markings (Fig. 70A). **Wings**: Fore- and hindwing pterostigma with well-developed dark mark basally. Venation green, except origin of Rs, apical radial crossveins, Psm-Psc crossveins, gradates and apical forks dark and heavily shaded. Length (1.47 cm): width (0.54 cm) = ratio (2.72). Hindwing venation green (Fig. 70B). Length (1.24 cm): width (0.40 cm) = ratio (3.10). Tarsal claws without basal expansion.

ABDOMEN. — Green, with red spot on second tergite. **Female**: Spermatheca short, thick, not coiled; ventral impression broad basally (Fig. 70C).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *michelini* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP, XI-96, Tosi, E. ♂".

DIAGNOSIS. — This species is a member of a group having dark abdominal tergites and flattened gonocornua with apical hook [see discussion under *L.* (*N.*) *lineata*]. Of the members of this group with swollen bases of the gonocornua, *L.* (*N.*) *tabacinus* has less enlarged gonocornua with bifid apex (not hooked), and broadly widened arch of the gonarcus. The marks on the vertex also appear smaller and on metanotum much more developed in *L.* (*N.*) *tabacinus*. The most similar species to *L.* (*N.*) *michelini* is *L.* (*N.*) *lineata*, which has the same inflated gonocornua, but the lateral arms of the gonarcus have no arch, forming a straight line perpendicular to the arcessus. *Leucochrysa* (*N.*) *lineata* also appears to have more dark pigmentation on the mesonotum than *L.* (*N.*) *michelini*.

The name was given in honor of P. E. Michelin who has given financial support to the senior author for chrysopid research.

HEAD. — Yellow. Vertex pale with U-shaped red mark on raised medial area interrupted at mid-line and darker anteriorly. Scape with diffuse red spot dorsally; pedicel pale with apical dark ring; flagellum black. Maxillary and labial palpi amber. Gena pale, unmarked. A diffuse red transverse band on either side of clypeal-frontal suture. Small red spot below and between antennae (Fig. 71D).

THORAX. — Pronotum green with broad brown lateral stripe. Middle part prescutum dark; two crescent-shaped marks on mesoscutum. Submedial part of metascutum and lateral portion of scutellum dark brown (Fig. 71A). **Wing**: Forewing pterostigma slightly darkened basally. Venation green; except most of costal crossveins, apex of Rs and contiguous veins, gradates and marginal forks dark. Length (1.68 cm): width (0.58 cm) = ratio (2.90). Hindwing apically acute. Pterostigma with faint darkening basally. Venation green, except apex of Rs and contiguous veins black (Fig. 71B). Length (1.44 cm): width (0.45 cm) = ratio (3.20).

ABDOMEN. — Microtholi present. Tergites dark, forming dark mid-line (Fig. 71C). **Male**: Gonarcus strongly arched with rounded lateral arms. Gonocornua broadly expanded plates with apical decurved hook. Arcessus short; subapical horns and plate absent; decurved apico-medial hook present with lateral lobes flattened or absent. Gonosaccus with numerous setae on large conical bases

arranged in two lateral fields; field of tiny linear marks present near gonocornua, and directly below gonocornua field of tiny punctures (Fig. 71E, F).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 26 October 1995, Ribeiro, M. C. (1♂ paratype)(orange).

***Leucochrysa* (*Nodita*) *parallela* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Bra-SP-Jaboticabal, FCAV, 10-III-99, SP58, ♂, Freitas, S." (cotton).

DIAGNOSIS. — The lateral arms of the gonarcus of this species are flattened, rather than vertical, as in other species. The lack of extensive dark markings on the thorax, especially the lateral portion of the metascutellum and minimal abdominal tergite markings also suggest a distant relationship with the *forcipata* group. We know of no other species with such strikingly flattened lateral arms.

The name "parallela" comes from the Latin *parallelus* meaning side by side equidistantly, and refers to the parallel, flattened arms of the gonarcus.

HEAD. — Yellow. Frons and clypeus pale, unmarked. Gena pale with small red spot along frontal suture. Maxillary and labial palpi pale (Fig. 72A, D). Vertex pale, unmarked. Antennal scape pale, with red lateral stripe thin at midlength; flagellum pale.

THORAX. — Pronotum green with lateral red stripe thinner at mid-length. Mesoscutum pale with pair of circular red spots; second axillary sclerite with small red spot (Fig.72A). **Wings**: Forewing pterostigma faintly darkened basally. Venation green, except costal ends of costal crossveins, middle of R- Rs crossveins, first five Rs-Psm crossveins, gradates, Psm-Psc crossveins, forked and unforked marginal veins, and apices of anal veins dark (Fig. 72B). Length (1.40 cm): width (0.50 cm) = ratio (2.80). Hindwing pterostigma heavily pigmented basally. Venation green, except middle part of Rs and gradates dark (Fig. 72B). Length (1.19 cm): width (0.40 cm) = ratio (2.98).

ABDOMEN. — Tergites pale, with red spots on tergites 2 and 3. **Male**: Gonarcus short, with lateral arms large, rounded, truncate posteriorly, with latero-apical, decurved point. Arcessus angulate in lateral view; distal half with thin, semimembranous and apically divergent ridges; terminal hook flanked by paired membranous lobes (Fig.72E, F). Ectoproct heavily sclerotized; ventral branch of dorsal apodeme extends to postventral corner of ectoproct as highly sclerotized, obtuse point. Microtholi absent.

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, October 1992, Delfino, T. H. (1♂ paratype)

***Leucochrysa* (*Nodita*) *retusa* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, "Balsamo, SP, 29-IX- September 1997, Bergman, E." (rubber).

DIAGNOSIS. — Males of this species appear to have a less developed state of swollen gonocornua and hooked or bifurcate apex, such as found in *L.* (*N.*) *lineata* and *L.* (*N.*) *tabacinus*. Perhaps the most similar species is *L.* (*N.*) *furcata,* which is part of the group of species with bifid gonocornua. Like *L.* (*N.*) *retusa*, *L.* (*N.*) *furcata* has short, relatively broad gonocornua, and relatively few meso- and metanotal markings. However, *L.* (*N.*) *retusa* does not have the darkened abdominal tergites of this species. The thin, quadrate-shaped gonarcus with small lateral arms and broad arcessus are distinctive for *L.* (*N.*) *retusa*.

The name "retusa" comes from the Latin *retusus* meaning blunted or notched, and refers to the unusual squared arch of the gonarcus.

HEAD. — Yellow, without marks. Maxillary palpimeres basally pale; third, fourth and half of fifth segments dark. Scape pale with dark dorso-lateral mark; pedicel pale with dorso-lateral dark mark; flagellum pale (Fig. 73A).

THORAX. — Cervical sclerite red. Pronotum with thin dark red stripe laterally on anterior 2/3. Meso- and metanotum pale, unmarked (Fig. 73A). **Wings**: Forewing pterostigma faintly darkened basally. Venation green, except junctures of costal crossveins, R-Rs crossveins, gradates, and marginal forked veins dark (Fig. 73B). Length (1.44 cm): width (0.53 cm) = ratio (2.72). Hindwing pterostigma dark basally. Venation pale, except middle part of Rs and gradates dark. Length (1.24 cm): width (0.41 cm) = ratio (3.02).

ABDOMEN. — Pale, except tergite 2 with pair of triangular red spots. **Male**: Medial arch of gonarcus thin, quadrate. Gonocornua widely spaced, flattened, with apico-lateral hook. Arcessus broad, with subapical transverse ridge; decurved apico-medial hook with poorly developed lateral lobes. Gonosaccus with few, scattered, large gonosetae (Fig. 73C, D).

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Nodita*) *robusta* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, SP, 7-IX-99, PEM, 28, Freitas, S." (rubber).

DIAGNOSIS. — This species shares with *L.* (*N.*) *santini* a dorsal scape stripe, dark pronotal stripe which expands posteriorly, absence of meso- and metanotal markings, and quite short gonocornua. However, *L.* (*N.*) *santini* has dark basal palpimeres and almost straight gonocornua in dorsal view, which are also slightly larger and more closely spaced than in *L.* (*N.*) *robusta*.

The name "robusta" comes from the Latin word *robustus*, meaning hard and strong like an oak, and refers to the thick arch of the gonarcus with broad arcessus.

HEAD. — Pale yellow. Gena pale, with transverse red band close to frons. Frons green, without markings. Maxillary palpimeres pale (Fig. 74A). Vertex green, without marks (Fig. 74A, D). Scape pale, with dorso-latersal red stripe not reaching dorsal and ventral margins; pedicel pale, with dark marks; flagellum pale.

THORAX. — Green. Pronotum pale, glabrous, with irregular red mark on lateral margin expanded posteriorly (Fig. 74A). Mesonotum and metanotum pale, without markings. **Wings**: Forewing pterostigma faintly darkened basally. Venation green, except crossvein endings, and inner and outer gradates dark. Apex of intramedian vein reaches Psm after first Rs-Psm crossvein. Length (1.33–1.51 cm); width (0.5–0.56 cm). Hindwing pterostigma darkened basally. Venation green, except costal crossveins, radial crossveins 7–9, apex of Psm, and inner and outer gradates dark. Length (1.17–1.25 cm); width (0.30–0.43 cm) (Fig. 74B).

ABDOMEN. — Green. Tergites with dark red marks. Sternites 2–8 with microtholi. **Male**: Gonarcus large, thick, strongly-arched, with ovate lateral arms. Gonocornua small, laterally curved. Arcessus broad; without subapical horns or plate; decurved apico-medial hook with lateral lobes forming two small ridges (Fig.74F). **Female**: Spermatheca cordate at apex, continuing to mass of convoluted tubes; spermathecal duct contorted, terminally expanded; ventral impression wide, swollen; accessory glands short, stout, tubular. Subgenitale short; with thin-walled, pocket-like medial extension (Fig. 74G, H).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, 19 November 1995, Freitas, S. (1♀ paratype); Luiz Antonio, 13 August 1992, Freitas, S. (1♂ paratype)(corn); 27 July 1992, Freitas, S. (1♂2♀ paratypes); **Mato Grosso**: Itiquira, 7 September 1999, Freitas, S. (1♂ paratype)(rubber).

Leucochrysa (*Nodita*) *santini* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Jaboticabal, SP, 28-VII-1995, Freitas, S."

DIAGNOSIS. — This species has few distinctive characteristics. The shape of the lateral pronotal stripe, similar abdominal markings and small unmodified gonocornua would indicate a closer relationship with *L.* (*N.*) *robusta* than with other species. The two species can be separated by the dark palpi and straight shape of the gonocornua of *L.* (*N.*) *santini.*

The name was given in honor of Prof. Santin Gravena who provided some specimens for this study.

HEAD. — Pale yellow. Gena red. Frons green, without dark markings. Maxillary palpimeres pale basally; palpimeres 3–4 and basal part of 5 dark; apex of palpimere 5 pale. Vertex green, without markings (Fig. 75A, D). Scape with dorso-lateral red stripe, not reaching basal or apical margins (Fig. 75A); pedicel pale with dark marks; flagellum pale.

THORAX. — Green. Pronotum pale with bright red marginal stripe abruptly broadened posterior to mid-length (Fig. 75A). Mesonotum pale with dark red markings. Metanotum pale, without markings. **Wings**: Forewing pterostigma faintly darkened basally. Venation green, except junctions of crossveins, and inner and outer gradates dark. Apex of intramedian cell reaches Psm after the first Rs-Psm crossvein. Length (1.28–1.58 cm); width (0.47–0.58 cm) (Fig. 75B). Hindwing pterostigma strongly darkened basally. Venation green, except costal crossveins and gradates dark (Fig.75B). Length (1.21 cm): width (0.40 cm); ratio = (3.03).

ABDOMEN. — Green. Tergites with dark red markings on segments 3, 4, 5, 7, and 8 (Fig. 75C). Sternites 2–8 with many microtholi. **Male**: Gonarcus thick, strongly arched, with vertically oriented, ovate lateral arms. Gonocornua small, straight, apically decurved. Arcessus without subapical horns or plate; apically decurved hook flanked by small, lateral ridges. Gonosaccus with scattered gonosetae (Fig. 74E, F). **Female**: Spermatheca multiply-coiled, ventral impression small with many turns (Fig. 34G).

OTHER MATERIAL EXAMINED. — **Brazil**: **São Paulo**: Jaboticabal, August 1996, Freitas, S. (1♀ paratype)(CAS); Luiz Antonio, 25 August 1992, Freitas, S. (2♂ paratypes)(eucalyptus); 27 July 1992, Freitas, S., (1♂ paratype)(eucalyptus)(CAS); **Minas Gerais**: Belo Horizonte, 2 September 1991, Kumagai, A. (2♂ paratypes).

Leucochrysa (*Nodita*) *scomparini* de Freitas and Penny, new species

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 18-XI-96, Scomparin, C. H. J." (rubber).

DIAGNOSIS. — Females of this species are immediately recognizable and separable from all other known species by the apical, tight double coil, which forms a knob at the end of the spermatheca (Fig. 76E). The extensive dark meso- and metanotal markings and dark abdominal tergites relate this species to a group in which males have enlarged, flattened gonocornua that are apically bifid or hooked [see discussion of *L.* (*N.*) *lineata*].

This species is dedicated to the enthusiastic entomologist Cassio Henrique Junqueira Scomparin, who has attempted to use chrysopids in biological control of agricultural pests.

HEAD. — Yellow with red markings. Vertex pale, with lateral red stripe close to ocular margins; convergent crescentic stripes on raised medial area (Fig. 76A). Scape pale, with red dorso-lateral stripe and short medial stripe; pedicel pale with red ring; flagellum pale. Gena red. Frons pale with small red spot below and between antennal bases. Maxillary and labial palpi pale (Fig. 76C).

THORAX. — Pronotum yellowish green, with red spots at the anterio-lateral corner and pair of red spots at posterio-medial margin. Mesonotum pale with extensive red and brown marks, prescutum

medially with red spots and laterally brown; scutum and postscutum with reticulate brown marks; mesoscutellum pale medially, brown laterally. Metanotum broadly brown (Fig. 76A). **Wings**: Forewing and hindwing pterostigma with dark brown spot basally. Venation pale, except costal juncture of costal crossveins, origin of radial sector, middle part of Rs, gradates, forked marginal veins, and apices of marginal unforked veins dark. Length (1.66 cm): width (0.66 cm) = ratio (2.52). Hindwing venation pale, except costal crossveins, middle part of Rs, gradates and forked marginal veins dark (Fig. 76B). Length (1.44 cm): width (0.48 cm) = ratio (3.00).

ABDOMEN. — Green. Tergites 4–7 with large, dark spots (Fig. 76A). **Female**: Spermatheca short, vela with two tight apical rings. Bursa much folded, with pair of filamentous accessory glands. Subgenitale wide, with short anterio-medial projection (Fig. 76D, E).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *squamisetosa* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, "Birigui, SP, Fz. São Joaquim, 11/June/94, SP68, Scomparin, C. H. J." (corn).

DIAGNOSIS. — The swollen and darkened, second anal vein of the forewing is similar to the basal markings of *Ceraeochrysa tauberae* from Costa Rica (Penny 1997), but is otherwise unknown in *L.* (*Nodita*). The contorted subapical ridges of the arcessus is also a characteristic unique to this species. The extensive red markings of the head are not often seen in this subgenus, but there are a few other species with similar markings, such as *L.* (*N.*) *aleura* (Banks, 1944), *L.* (*N.*) *morrisoni* (Navás, 1914), and *L.* (*N.*) *trifurcata* (Banks, 1948). However, no other species of *L.* (*Nodita*) has the distinctive, thickened gonosetae, some of which have basal plates.

The name "squamisetosa" comes from the Latin *squama* and *seta* meaning scaly hairs, and refers to the scattered large gonosetae on large conical bases or flat plates of the gonosaccus.

HEAD. — Pale yellow. Clypeus pale, marked with narrow red band between eyes through clypeus under anterior tentorial pit; broader medially. Frons pale with narrow, red, double concentric ring below antennal sockets fused at mid-line and continued dorsally as a narrow median stripe. Vertex pale, with red partial ring at base of each scape continued postero-laterally as a narrow stripe along eye margin; pair of submedial, parallel, red stripes. Labial and maxillary palpi pale. Scape with dorsal surface red, ventral surface pale; pedicel and flagellum pale (Fig. 77A, C).

THORAX. — Pronotum wider than long, yellow-green, unmarked. Meso and metanotum pale with diffuse reddish markings; no pale median stripe (Fig. 77A). **Wings**: Fore- and hindwings with dark basal spot. Venation green, except crossveins and bases of longitudinal veins dark; no bordering. Basal fork of second anal veins swollen, darkened and bordered. Forewing with five inner, and seven outer gradates, the series converging posteriorly (Fig. 77B). Forewing length (1.20 cm): width (0.50 cm) = ratio (2.40). Hindwing length (1.08 cm): width (0.34 cm) = ratio (3.18).

ABDOMEN. — Pale. Tergites 3, 4, 6 and 7 with broad dark marks (Fig. 77D). Apex of sternite 9 truncate. Dorsal apodeme of ectoproct extended dorso-medially at apex. Callus cerci black posteriorly. **Male**: Microtholi large, dense on sternites 3–8. Gonarcus thick, broadly arcuate; lateral arms triangular. Gonocornua short, straight, apically obtuse and decurved. Arcessus broad basally, little sclerotized laterally; with low, contorted dorsal ridges at subapical angle, apical hook small, with lateral lobes transverse. Gonosaccus with gonosetae borne subapically on sclerotized, conical projections; ventral pair of thick gonosetae on oval scleritized bases (Fig. 77E, F, G).

MATERIAL EXAMINED. — Known only from the holotype.

Leucochrysa (*Nodita*) *tabacinus* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, 20-I-97, Scomparin, C. H. J." (rubber).

DIAGNOSIS. — This species is a member of the group of species with completely darkened abdominal tergites and flattened, apically bifid gonocornua. The gonocornua, while well developed in *L.* (*N.*) *tabacinus*, are not as swollen as in some other species in the group, such as *L.* (*N.*) *lineata* and *L.* (*N.*) *michelini*. The lateral arms of the gonarcus, although broadly angled with respect to the medial arch in *L.* (*N.*) *tabacinus*, do not form a straight line, as is found in *L.* (*N.*) *ictericus* and *L.* (*N.*) *lineata*. The extensive brown coloration of thorax and abdomen is also seen in *L.* (*N.*) *scomparini*, but unlike *L.* (*N.*) *tabacinus*, that species has red gena, completely dark metascutellum, and a distinctive doubly-coiled knob on the spermatheca.

The name "tabacinus" comes from the New Latin for *tabacum* for tobacco and *inus* meaning pertaining to, referring to the extensive tobacco brown coloration of the body.

HEAD. — Yellow. Clypeus and frons without markings, except a small dark spot between and below antennal bases. Gena pale, unmarked. Vertex with short dark stripes antero-medially near antennal bases. Antennal fossa dorsally red. Maxillary and labial palpi pale (Fig. 78C). Scapes pale with diffuse reddish brown spot; pedicel pale, with apical dark ring; flagellum dark.

THORAX. — Pronotum yellow with lateral brown stripe not extended to anterior or posterior margins (Fig. 78A). Mesoprescutum pale with red mark antero-laterally; scutum pale with brown mark posteriorly; mesoscutellum pale with lateral dark suffusion. Metascutum pale with pair of broad submedial brown marks; metascutellum pale medially, with progressively darker suffusion laterally (Fig. 78A). **Wings**: Fore- and hindwing faintly darkened basally. Venation green, except posterior part of costal margin, outer gradates, marginal forks and unforked marginal veins, and anal veins dark; posterior juncture of anal veins and hind margin intensely black. Length (3.06 cm): width (1.06 cm) = ratio (2.89). Hindwing venation green, except apex of Rs and contiguous veins, and apical part of fore- and hind margins dark; marginal junctures of anal veins and base of hind margin dark (Fig.78B). Length (2.66 cm): width (0.84 cm) = ratio (3.17).

ABDOMEN. — Pale green, except all tergites with dark medial sclerites (Fig.78G). **Male**: Gonarcus thin, curved, lateral arms continuation of same plane as medial arch. Gonocornua flattened, with apex bifid, decurved. Arcessus short; subapical horns and plate absent; apical decurved medial hook, flanked by rounded, enlarged lateral lobes. Gonosaccus with scattered gonosetae (Fig. 78E, F). **Female**: Spermatheca short. Bursa convoluted and two thick accessory glands (Fig. 78I). Subgenitale highly sclerotized, with long antero-medial projection above large, round sclerotized lobe (Fig. 78D, J)

OTHER MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**: Itiquira, 20 June 1997, Scomparin, C. H. J." (2♂2♀ paratypes)(rubber).

Leucochrysa (*Nodita*) *tenuis* de Freitas and Penny, new species

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Luiz Antonio, SP, Faz. Guatapara, T.25, Celpav, 6/12/93, Freitas, S." (eucalyptus).

DIAGNOSIS. — This is a relatively pale species with few distinctive markings. However, the gonarcus is quite distinct. No other species has the exaggerated, long, parallel lateral sides of the medial arch of this species. The almost complete absence of gonocornua is also quite distinctive.

The name "tenuis" comes from the Latin meaning thin, and refers to incredibly long, thin, lateral sides of the medial arch of the gonarcus.

HEAD. — Yellow. Gena pale, with diffuse red spot near frons (Fig. 79C). Frons pale, with small red spot below and between antennal bases. Maxillary palpimeres basally pale; fourth and base of fifth

segments dark; apex pale. Vertex pale, unmarked (Fig. 79C). Scape pale, with dark brown dorso-lateral stripe; pedicel and flagellum pale.

THORAX. — Green. Pronotum with dorso-lateral dark red stripe (Fig. 79A). Meso- and metanotum pale, unmarked. **Wings**: Forewing pterostigma faintly darkened basally. Venation green, except costal crossveins 7–13, apex of Rs, posterior apices of radial crossveins, and forked marginal veins dark (Fig. 79B). Length (1.51 cm): width (0.56 cm) = ratio (2.70). Hindwing pterostigma with well-developed dark spot basally. Venation green, except apex of Rs and forked marginal veins dark. Length (1.34 cm): width (0.41 cm) = ratio (3.27).

ABDOMEN. — Green, without markings. **Male**: Sternites 2–8 with many microtholi. Gonarcus medial arch quadrate, extremely long, thin, and parallel; lateral arms ovate. Gonocornua reduced to small, rounded, basal lobes. Arcessus large, broad; subapical horns and plate absent; apical hook well-sclerotized, not decurved, with lateral lobes well-developed, rounded. (Fig. 79D, E).

MATERIAL EXAMINED. — Known only from the holotype.

***Leucochrysa* (*Nodita*) *vignisi* de Freitas and Penny, new species**

TYPE. — Male holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Itiquira, MT, 10-V-96, Scomparin, C. H. J." (rubber).

DIAGNOSIS. — There are few distinctive features to this species. It appears to be part of a group of species with poorly developed gonocornua and broad, bulging bases to the arcessus. The two species most similar to *L.* (*N.*) *vignisi* appear to be *L.* (*N.*) *retusa* and *L.* (*N.*) *santini*, which also have thin, incomplete stripes on the scape; pale vertex; pale meso- and metanotum; somewhat thin, incomplete lateral pronotal stripes; and sparse, scattered gonosetae. Of the three, *L.* (*N.*) *santini* has dark palpi and gena. The gonarcus of *L.* (*N.*) *retusa* is much thinner and more quadrate-shaped than in *L.* (*N.*) *vignisi*. The shape of the gonocornua separates the three species most easily. The gonocornua of *L.* (*N.*) *retusa* are relatively broad, with an apical hook along the lateral edge. The bases of the gonocornua of *L.* (*N.*) *santini* are spaced much closer together than in *L.* (*N.*) *vignisi*.

This species was dedicated to Berthrand Vignis, who along with L. Barré enthusiastically opened the way for chrysopid use for biological control of rubber plant pests.

HEAD. — Yellow. Frons, palpi, gena and vertex pale, unmarked. Scape pale, with incomplete, thin dorso-lateral black stripe; pedicel and flagellum pale (Fig. 80A).

THORAX. — Pronotum green with medial yellow stripe and thin, lateral red stripe. Meso- and metanotum pale, unmarked (Fig. 80A, C). **Wings**: Fore- and hindwing pterostigma with well-developed dark spot basally. Venation green, except costal junctures of costal crossveins, radial crossveins, apex of Rs, anterior juncture of last medial crossvein, inner and outer gradates, Psm-Psc crossveins, and forked and unforked marginal veins dark. Length (1.48 cm): width (0.56 cm) = ratio (2.64). Hindwing venation green, except costal crossveins, radial crossveins, apex of Rs and forked marginal veins dark (Fig. 80B). Length (1.30 cm): width (0.44 cm) = ratio (2.95).

ABDOMEN. — Green, with yellow mid-dorsal line. Tergites 3, 4, and 7 with dark spots (Fig. 80D). **Male**: Gonarcus strongly arched medially; lateral arms ovate. Gonocornua small, widely spaced, apically forcipate. Entoprocessus broad, well developed; without subapically horns or plate; apico-medial, decurved hook flanked by well-developed rounded ridges. Gonosaccus with many long gonosetae (Fig 80E, F).

OTHER MATERIAL EXAMINED. — **Brazil**: **Mato Grosso**, Itiquira, 23 March 1997, Scomparin, C. H. J." (1♂ paratype)(rubber).

***Leucochrysa* (*Nodita*) *vittatus* de Freitas and Penny, new species**

TYPE. — Female holotype, deposited at Museu de Zoologia/USP (MZUSP), São Paulo, Brazil, labeled "Rib. Preto, SP, 2/11/91, Vieira, D. A." (orange).

DIAGNOSIS. — This species has a rather atypical appearance for this subgenus. Usually, any dark markings of the pronotum are in the form of lateral stripes and spots, sometimes coupled with oblique stripes. Submedial pronotal stripes seem to be unique to this species. In many ways *L.* (*N.*) *vittata* resembles *L.* (*N.*) *scomparini* with more extended and exaggerated submedial stripes. Both species have extensive, similar dark markings of head and mesonotum. More extensive darkening of the abdominal stripes found in *L.* (*N.*) *vittata* would create the condition seen in *L.* (*N.*) *scomparini.* However, there are some significant differences between the two species. The metascutellum on *L.* (*N.*) *vittata* is pale, while that of *L.* (*N.*) *scomparini* is dark. The dark scape stripe is dorsolateral in *L.* (*N.*) *scomparini* and dorsomedial in *L.* (*N.*) *vittatus* while *L.* (*N.*) *scomparini* has an additional medial spot. The most distinct differences are in the female genitalia, where *L.* (*N.*) *scomparini* has a spermatheca with tightly-coiled knob and non-glandular duct, whereas *L.* (*N.*) *vittata* has a larger, unknobbed spermatheca and glandular spermathecal duct. *Leucochrysa* (*N.*) *vittata* also has an inner gradate series of the hindwing which runs close to the radial sector, while that of other species is more equidistant between Rs and the outer gradate veins.

The name "vittatus" comes from the Latin *vitta* for ribbon, band or stripe and *atus* for provided with, referring to the unusual number of brown stripes on the head and thorax.

HEAD. — Pale green. Gena brown. Frons pale, without markings. Maxillary and labial palpi pale (Fig. 80A, D). Vertex pale with pair of dark parallel stripes on raised medial area, tapered antero-medially to point between antennal bases; lateral pair of dark stripes along eye margin to posterior margin of vertex. Scape with dorso-medial brown stripe continued briefly onto fossa; pedicel and flagellum pale.

THORAX. — Pronotum with submedial brown stripes and small lateral spot each side halfway to posterior margin. Mesoprescutum with three dark marks on either side, continued onto mesoscutum and mesoscutellum, which have additional lateral stripes. Metanotum pale with submedial pair of dark spots and postero-lateral oblique dark stripe. Pleura and metacoxae brown; metafemur pale fuscous, brown banded apically (Fig. 80A). **Wings**: Pterostigma of both wings dark basally. Venation green, except junctures of first ten costal crossveins and all of distal crossveins, radial crossveins distal to stigma, longitudinal veins at juncture with crossveins, and three cells of Rs at mid-length dark. Forewing gradates parallel. Hindwing venation marked as in forewing. Inner series of gradates closer to Rs than in forewing (Fig. 80B). Forewing length (1.59 cm): width (0.53 cm) = ratio (3.00). Hindwing length (1.43 cm): width (0.43 cm) = ratio (3.33).

ABDOMEN. — Pale green. Tergites 2–8 with pair of submedial brown stripes (Fig. 80C). **Female**: Spermatheca short, wide, with constriction between upper and lower chamber; vela region lightly-sclerotized, moderately short; ventral impression short. Spermathecal duct wide, gently undulated, glandular-walled region; longer than spermatheca. Bursa small. Bursal accessory glands not seen. Subgenitale broadly rounded, dorsal lobes deeply incised medially; postero-medial lobe with broad indentation and transverse lip (Fig. 80E, F, G).

MATERIAL EXAMINED. — Known only from the holotype.

FIGURES

A list of abbreviations used with the figures is as follows:

acu = acumen
g = accessory glands
al = apical lobe
arc = arcessus
atp = anterior tentorial pit
b = copulatory bursa
bd = bursal duct
cc = callus cerci
cru = crumena
dapo = dorsal apodeme
dh = dorsal hood of the gonarcus
ent = entoprocessus
gc = gonarcus (medial arch)
gcn = gonocornua
gcr = gonocristae
gps = gonapsis
gsc = gonosaccus
gst = gonosetae
ig = inner gradates
imc = intramedian cell
la = lateral arm of the gonarcus
lg = lateral gonapophyses
m1 = first median cell
m2 = second median cell
mm = millimeters
mp = maxillary palpi
u = mediuncus
og = outer gradates
pa = paramere
Psc = pseudocubitus vein
Psm = pseudomedia vein
psp = pseudopenis
Rs = radial sector
S6 = sixth sternite
S7 = seventh sternite
S8 + 9 = fused eighth and ninth sternite
sap = subapical projection
sd = spermathecal duct
T7 = seventh tergite
T8 = eighth tergite
T9 + ect = ninth tergite and ectoproct
v = vela
vapo = ventral apodeme
vb = ventral branch of the dorsal apodeme
vi = ventral impression

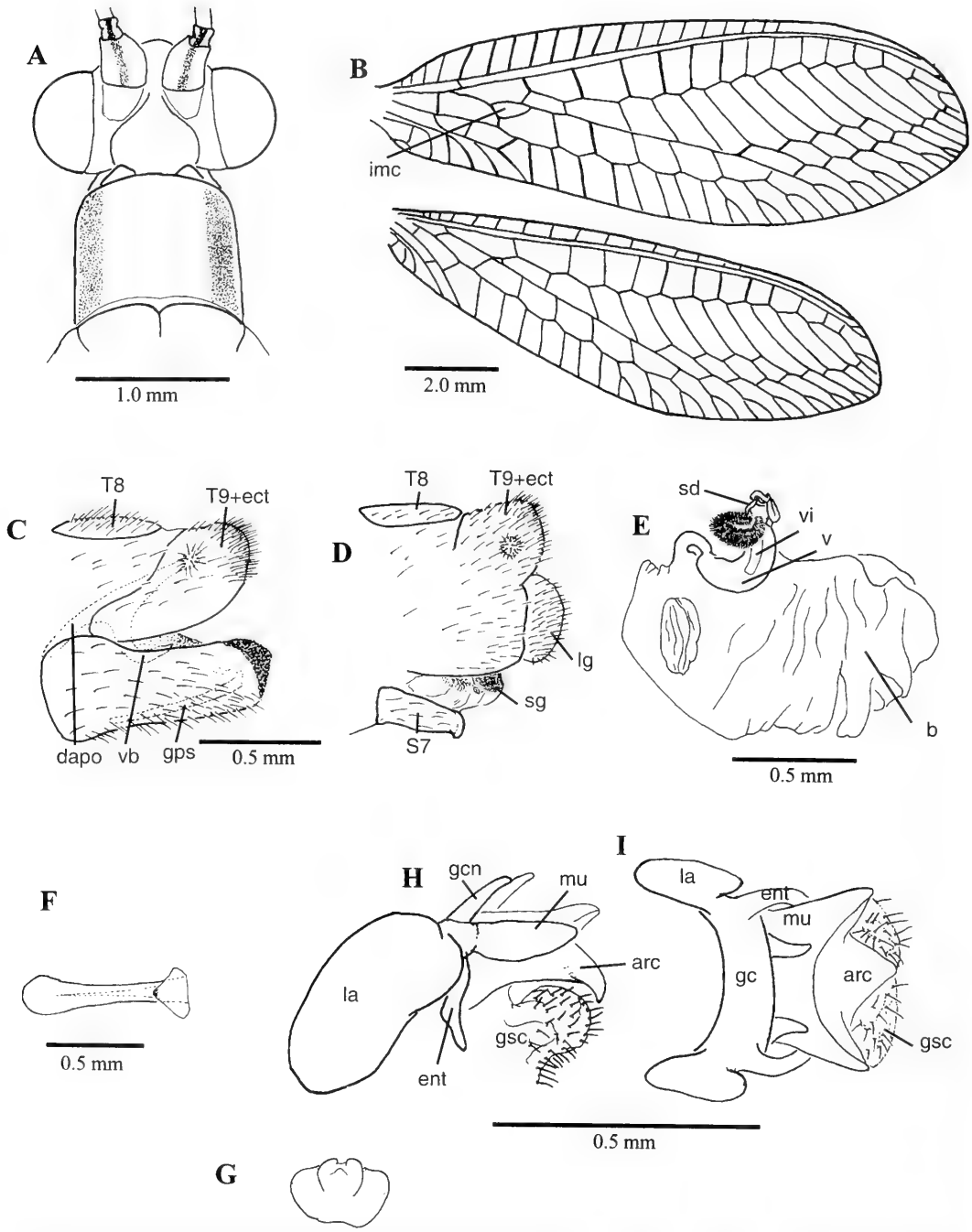

FIGURE 1. *Nacarina panchlora* (Gerstaecker, 1888). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Maxillary palpi; E. Female genitalia; F. Apex of abdomen; G. Subgenitale.

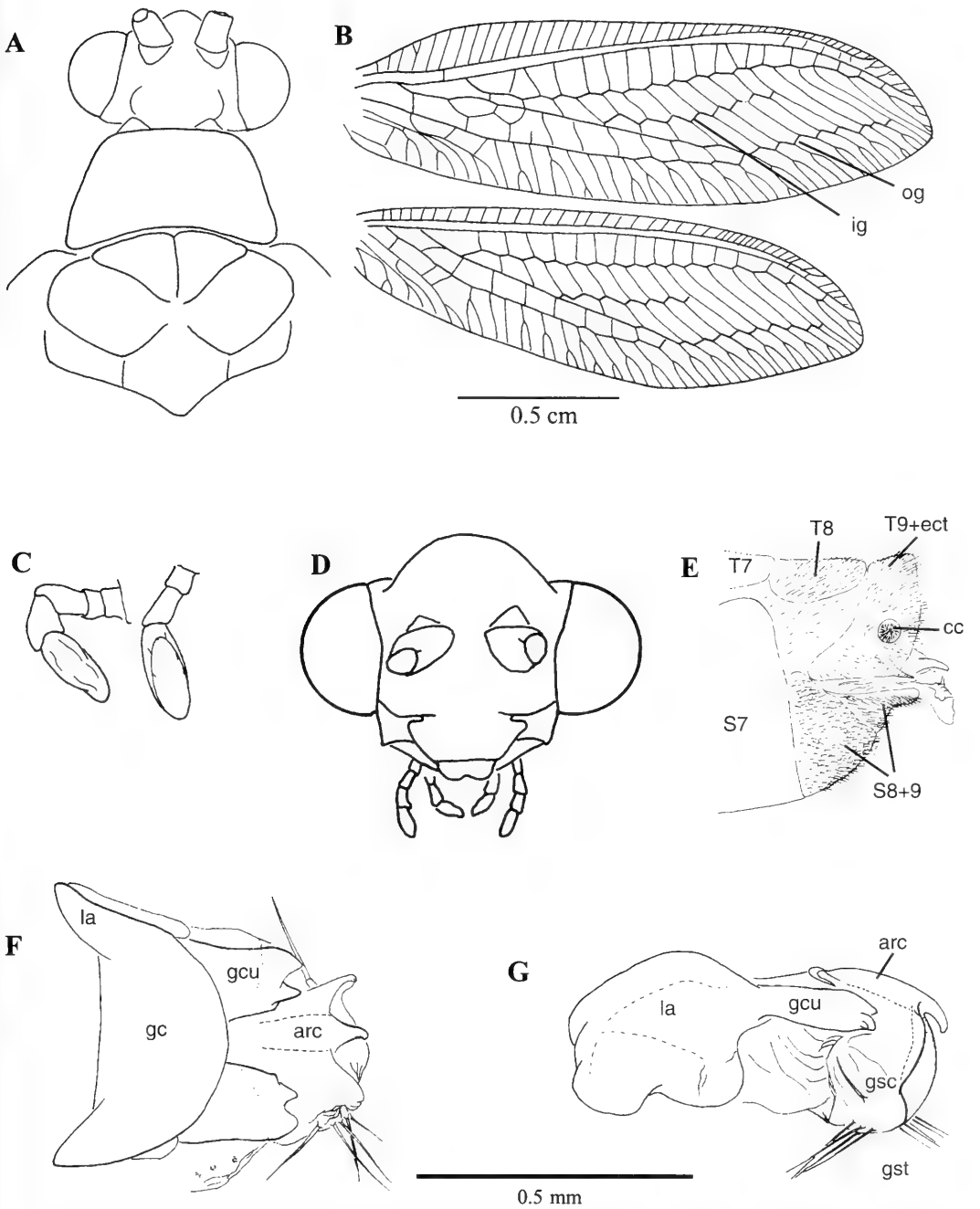

FIGURE 2. *Nacarina pletorica* (Navás, 1919). A. Head and thorax: dorsal view; B. Wings; C. Maxillary palpi; D. Head, frontal view; E. Apex of male abdomen; F, G. Male genitalia, dorsal and lateral view.

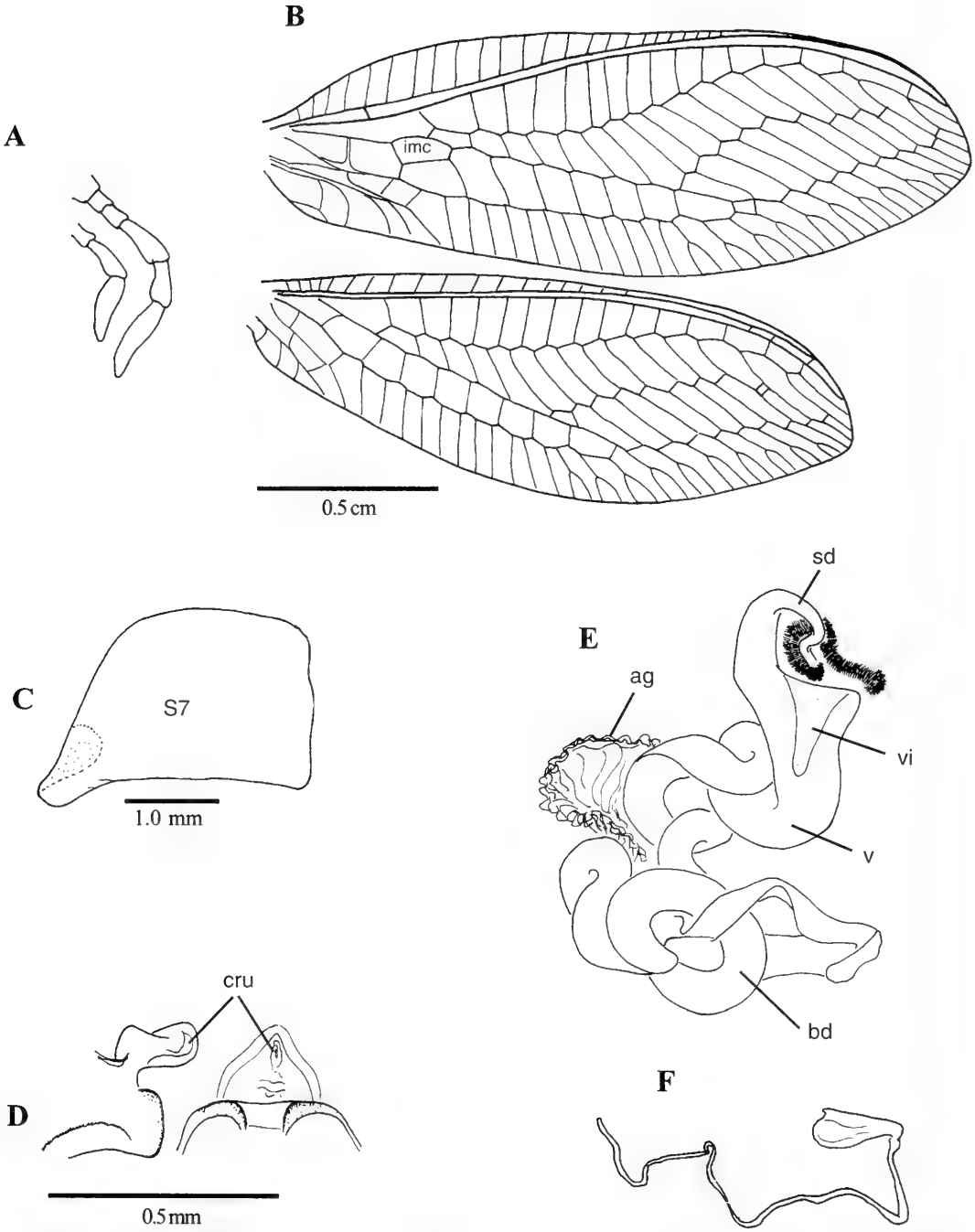

FIGURE 3. *Nacarina wagneri* (Navás, 1924). A. Maxillary and labial palpi; B. Wings; C. Sternite 7; D. Subgenitalia; E. Spermatheca; F. Colleterial gland.

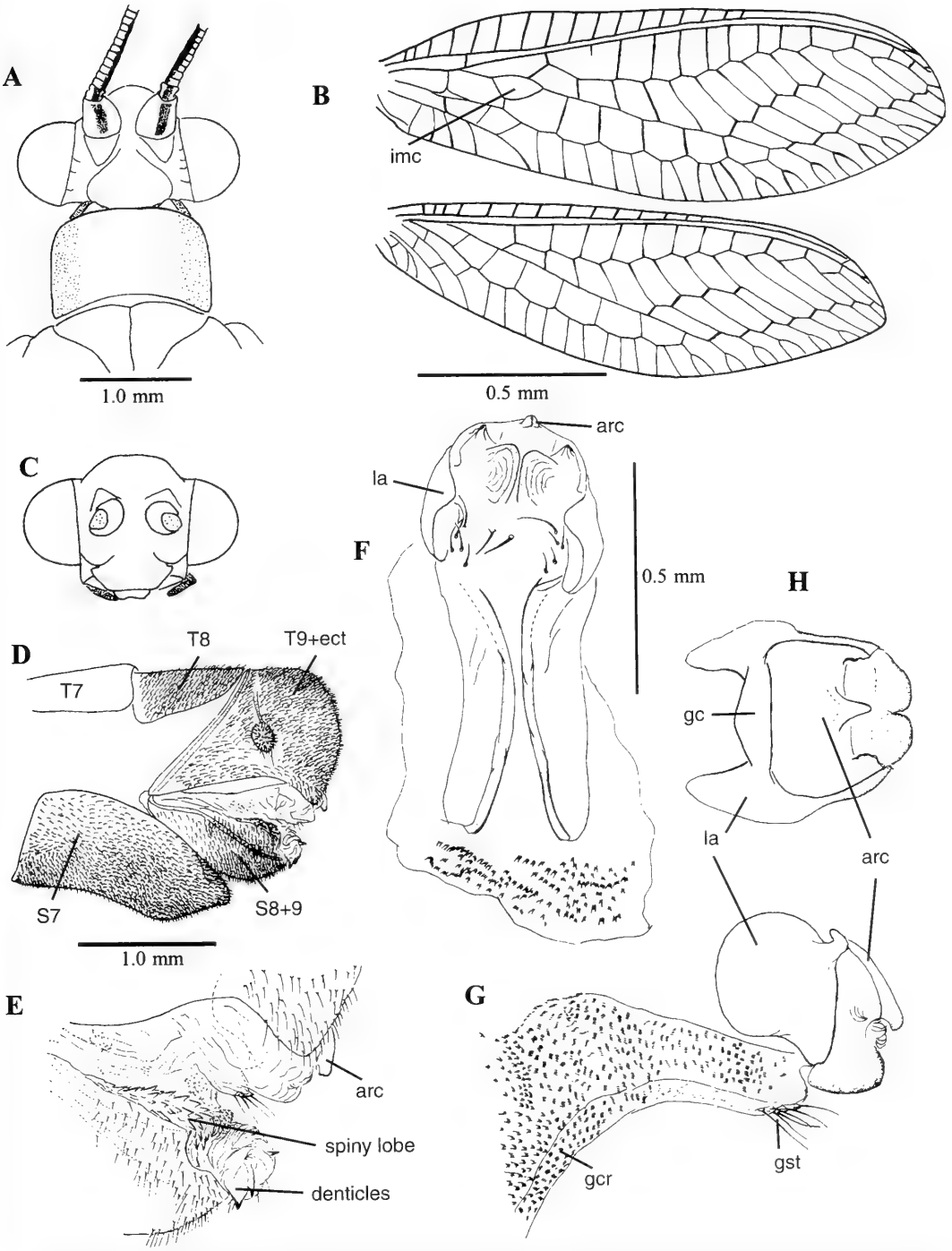

FIGURE 4. *Nacarina aculeata*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen; E. Part of abdominal apex showing the denticles; F, G, H. Male genitalia, ventral, lateral and dorsal view, respectively.

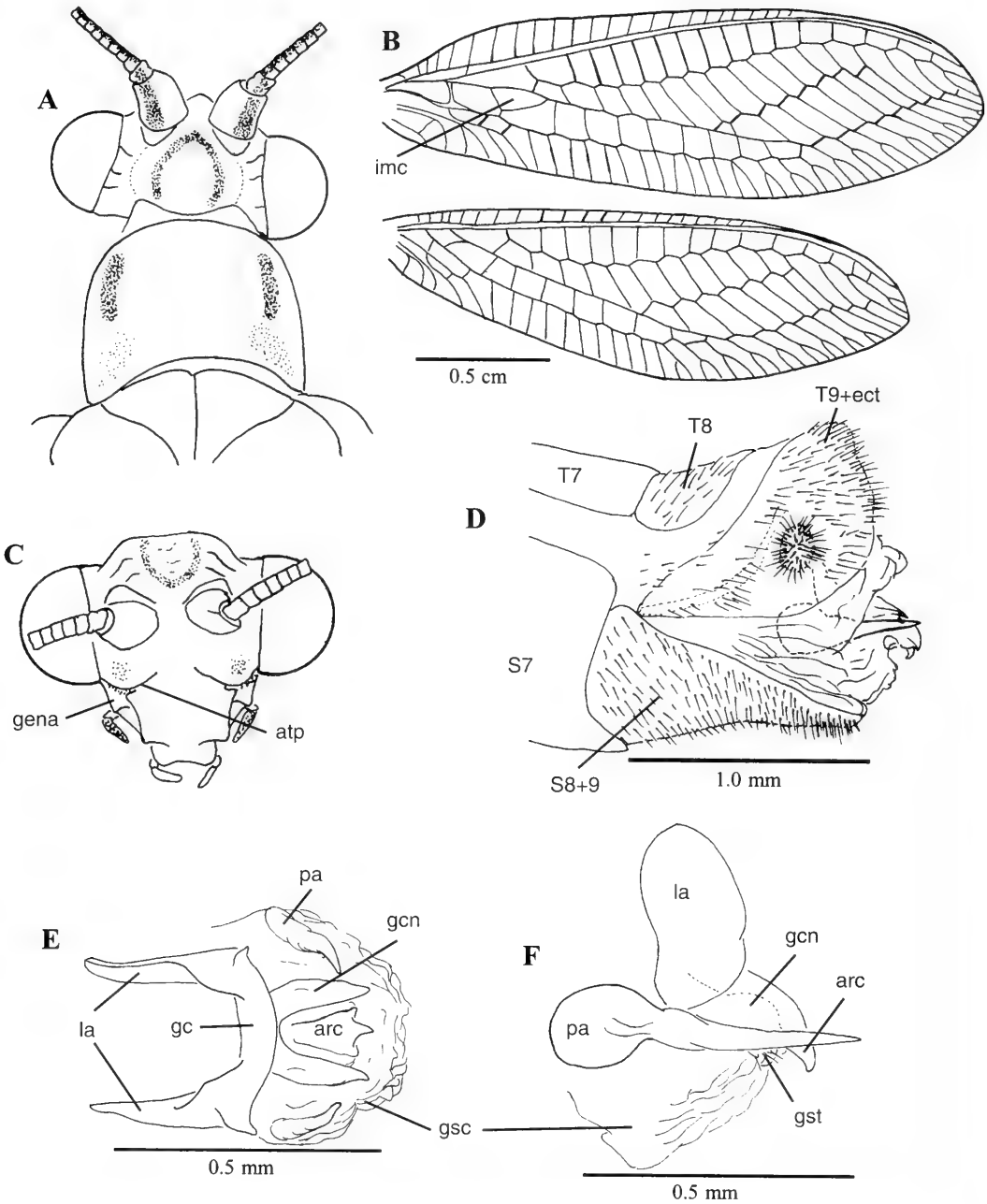

FIGURE 5. *Nacarina gladius,* new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen; E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

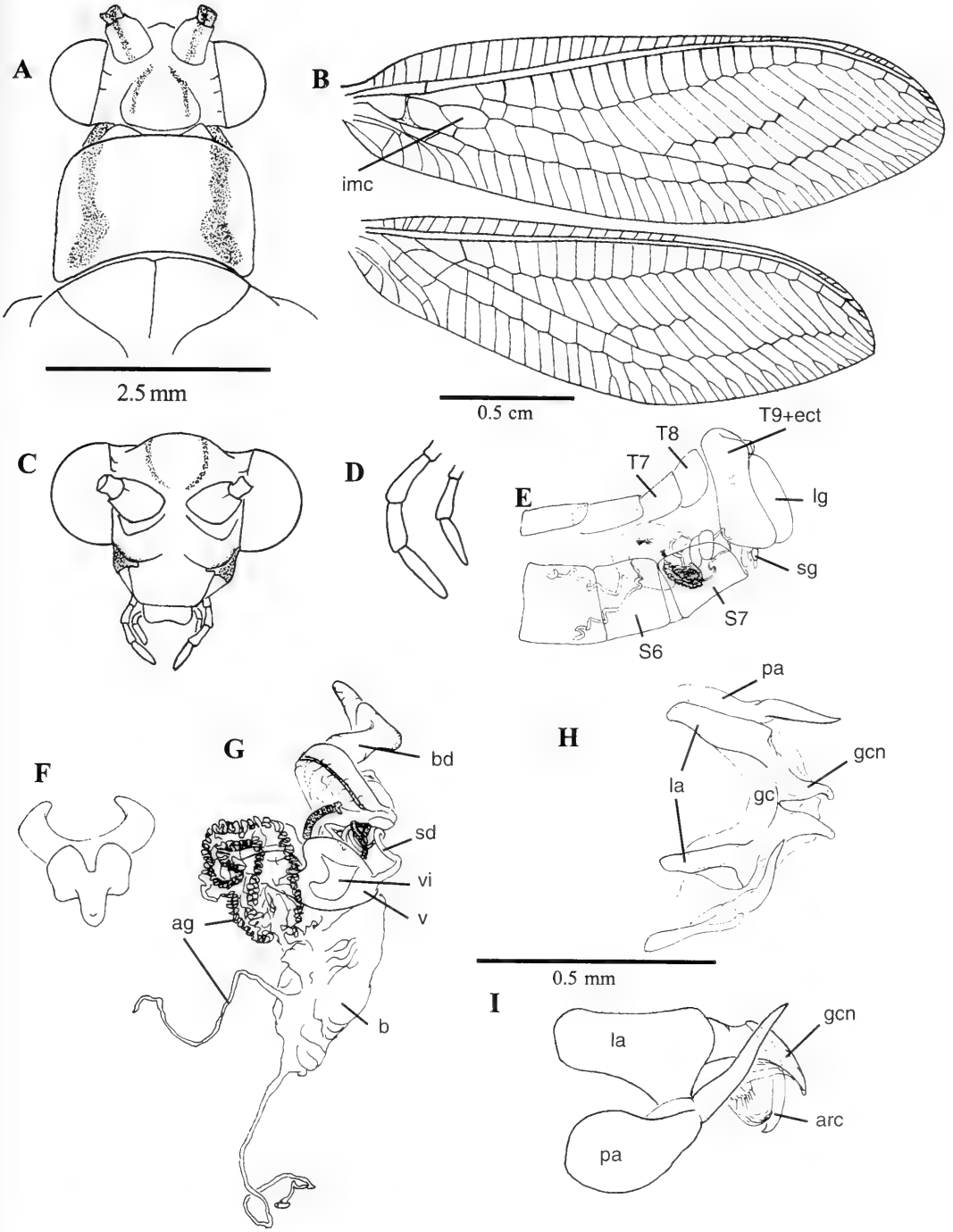

FIGURE 6. *Nacarina lavrasana*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Maxillary and labial palpi; E. Apex of female abdomen; F. Subgenitale; G. Female genitalia; H. Male genitalia, dorsal view; I. Male genitalia, lateral view.

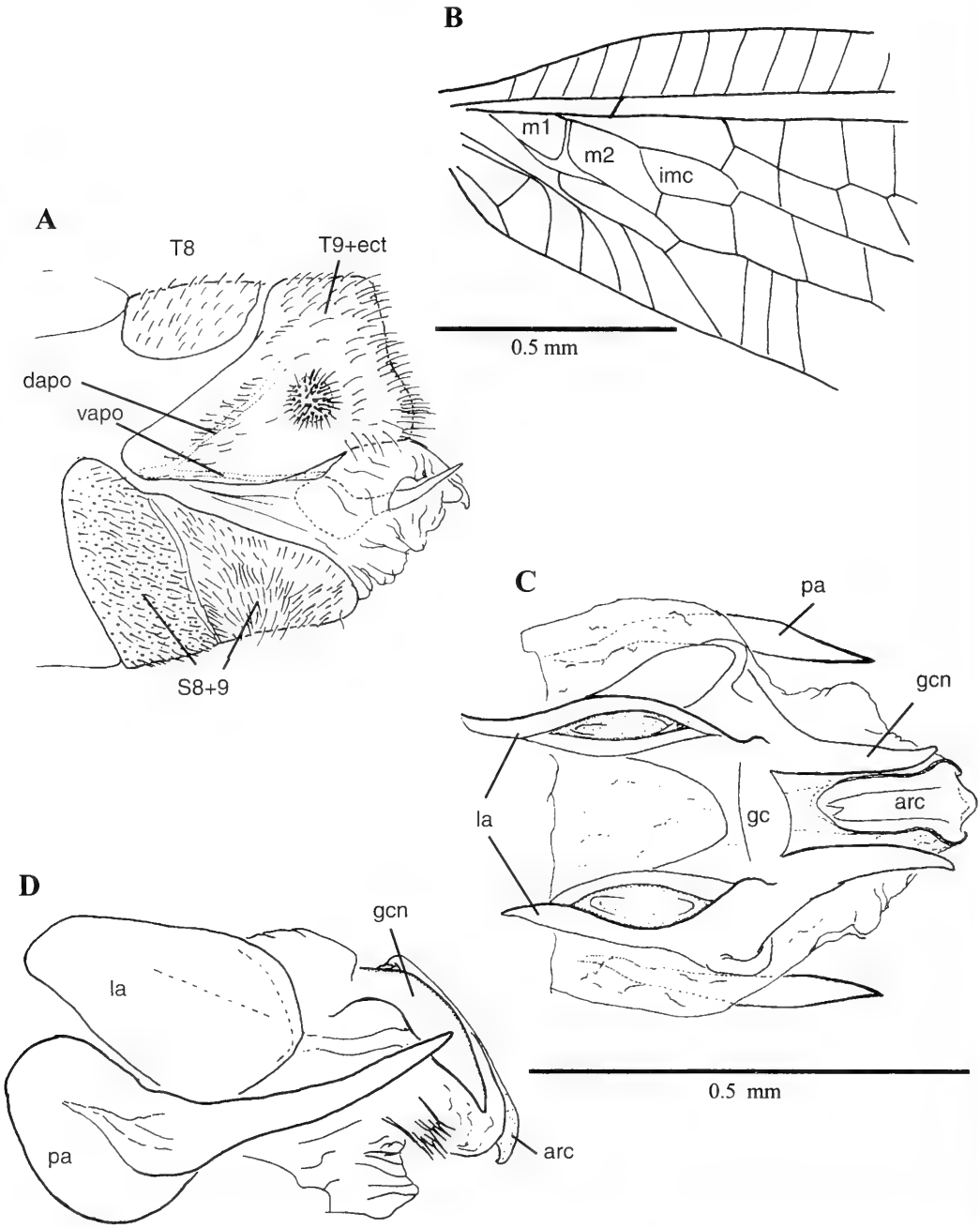

FIGURE 7. *Nacarina sagitta*, new species. A. Apex of male abdomen; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view.

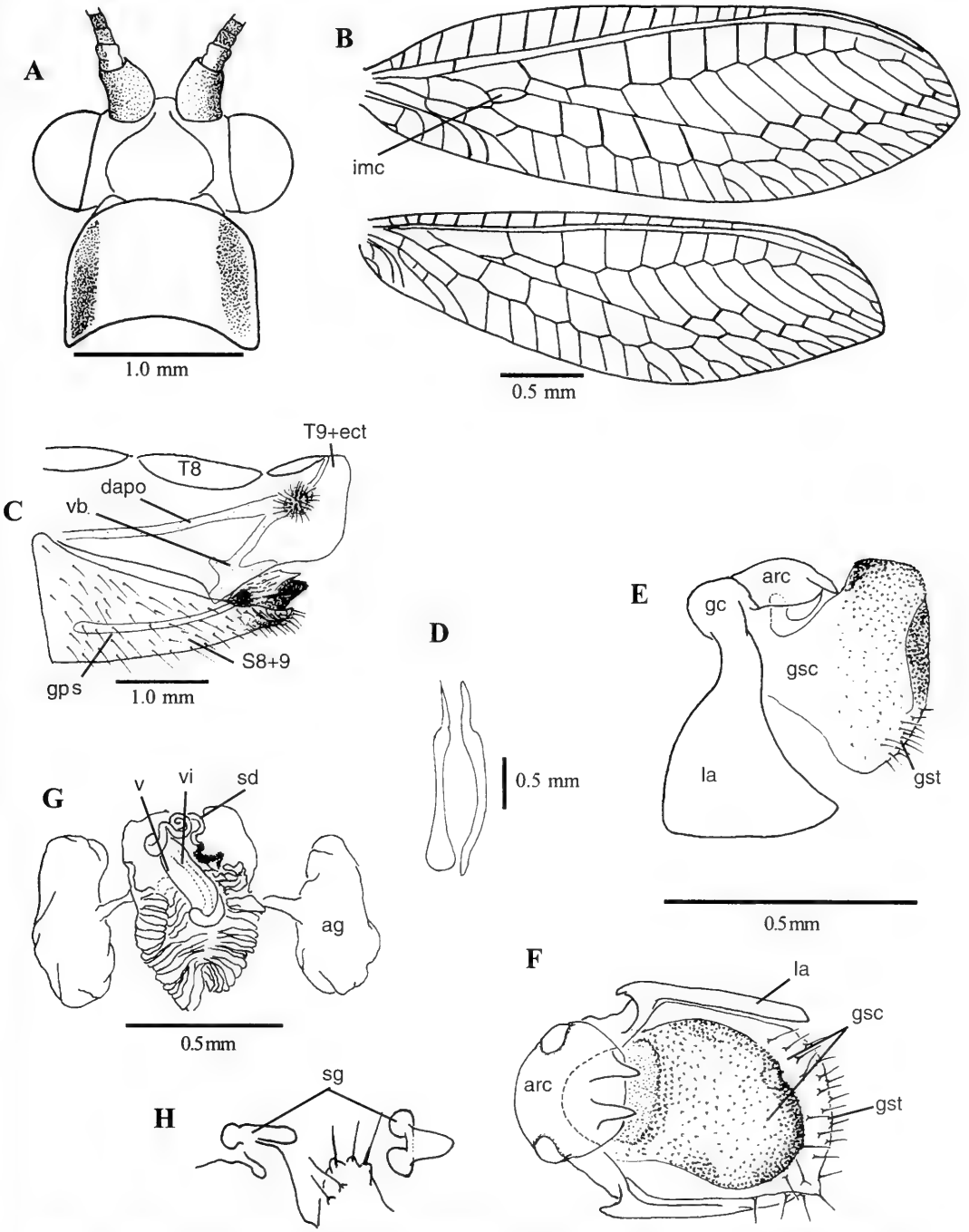

FIGURE 8. *Ceraeochrysa acmon* Penny, 1998. A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen; D. Gonapsis; E. Male genitalia, lateral view; F. Male genitalia caudal view; G. Female genitalia; H. Subgenitale.

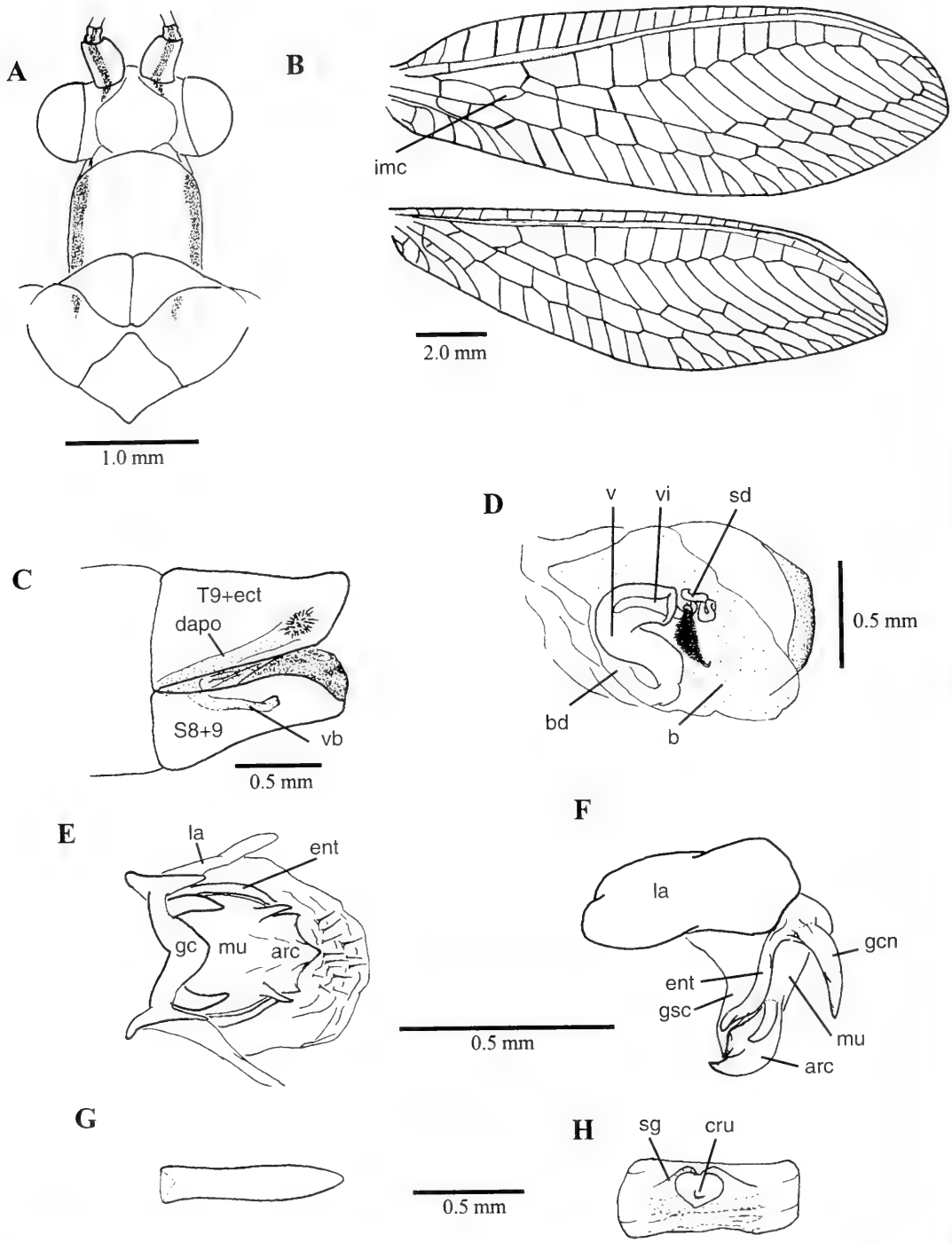

FIGURE 9. *Ceraeochrysa caligata* (Banks, 1945). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen; D. Female genitalia; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonapsis; H. Subgenitale.

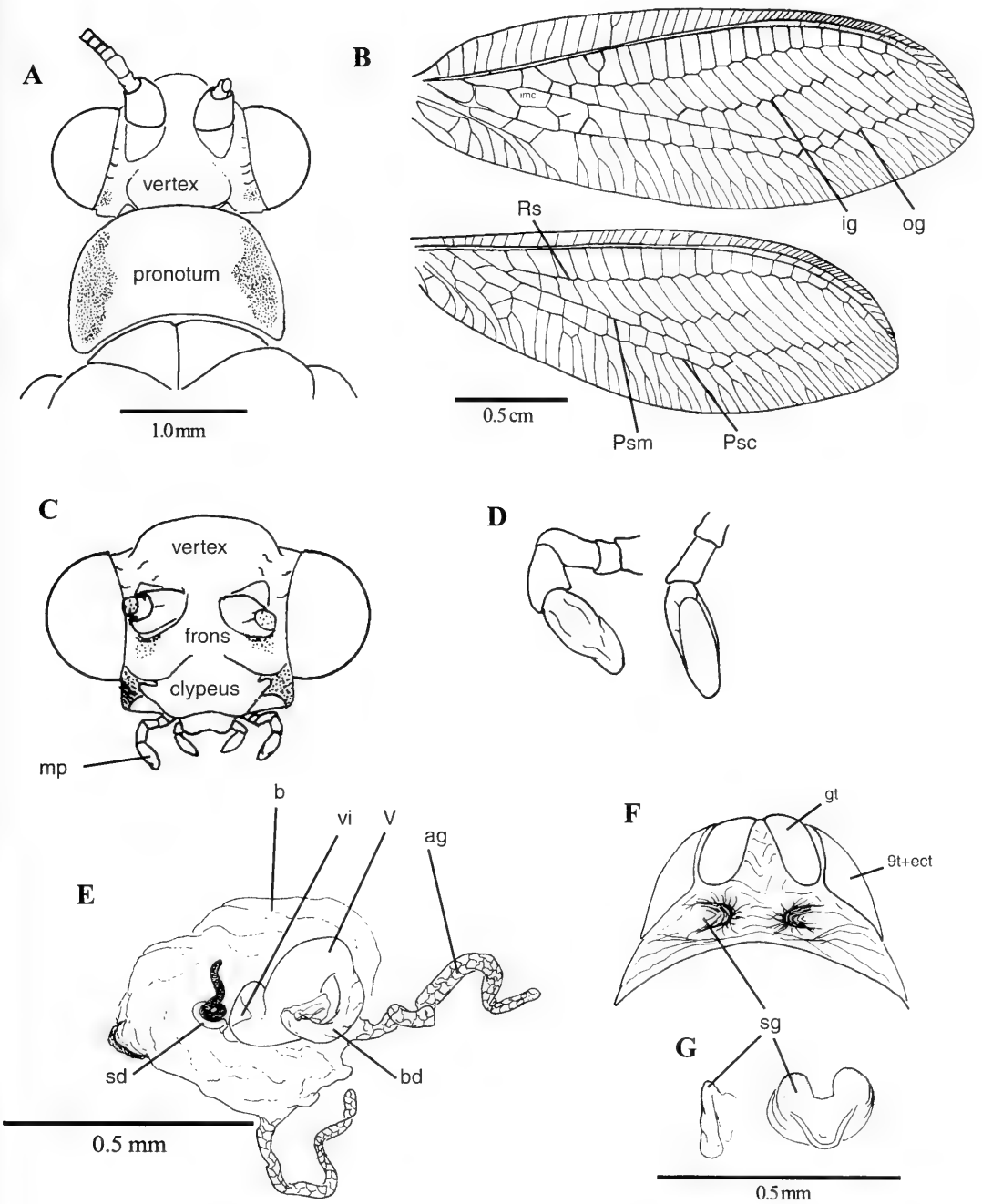

FIGURE 10. *Ceraeochrysa cincta* (Schneider, 1851). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Apex of female abdomen; E. Female genitalia; F. Gonapsis; G. Subgenitale; H. Male genitalia, lateral view; I. Male genitalia, dorsal view; da= dorsal apodeme of ectoproct, ent= entoprocessus, gps= gonapsis, vb= ventral branch of dorsal apodeme.

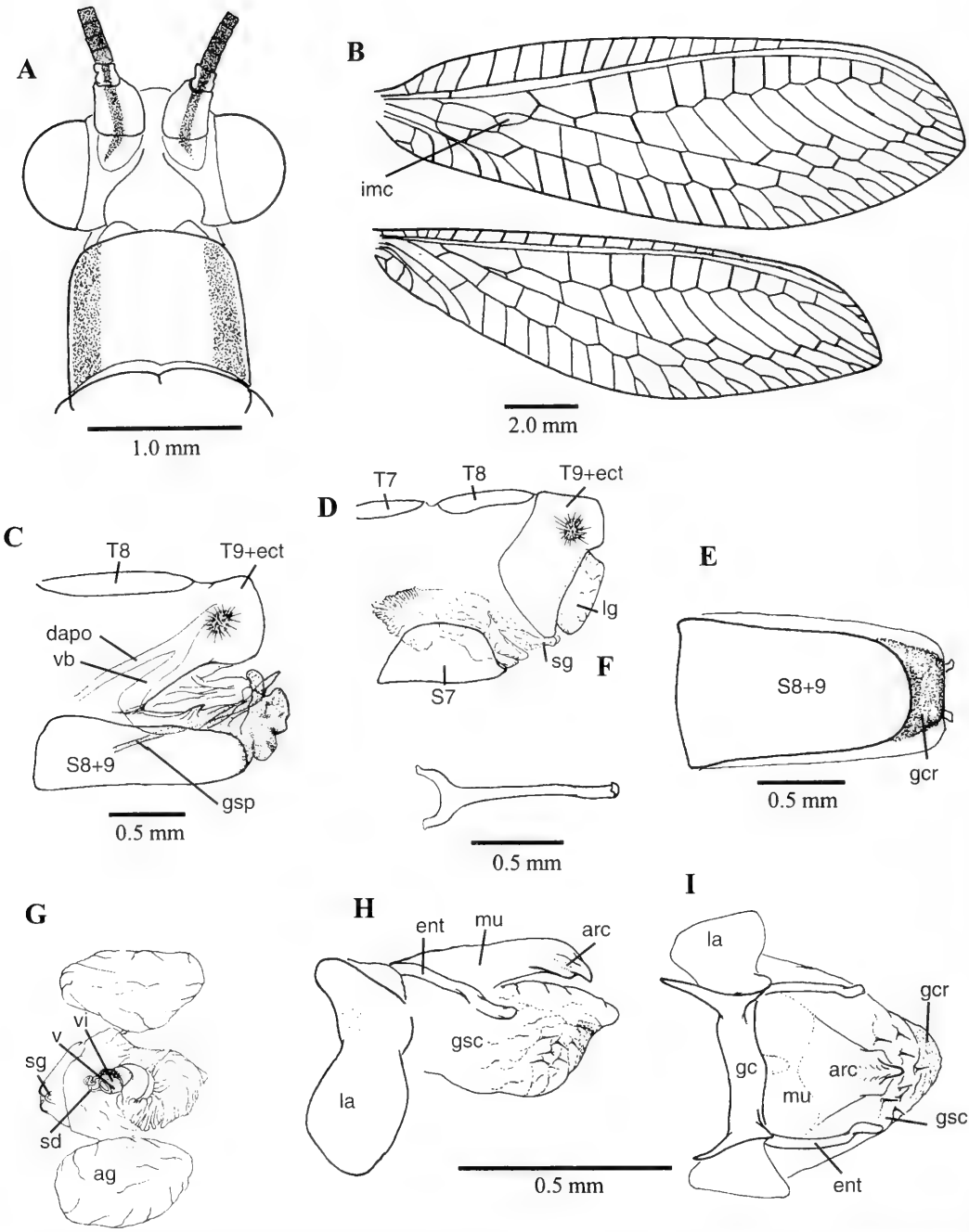

FIGURE 11. *Ceraeochrysa claveri* (Navás, 1911). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen; D. Apex of female abdomen; E. Sternite 8 + 9, ventral view; F. Gonapsis; G. Female genitalia; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

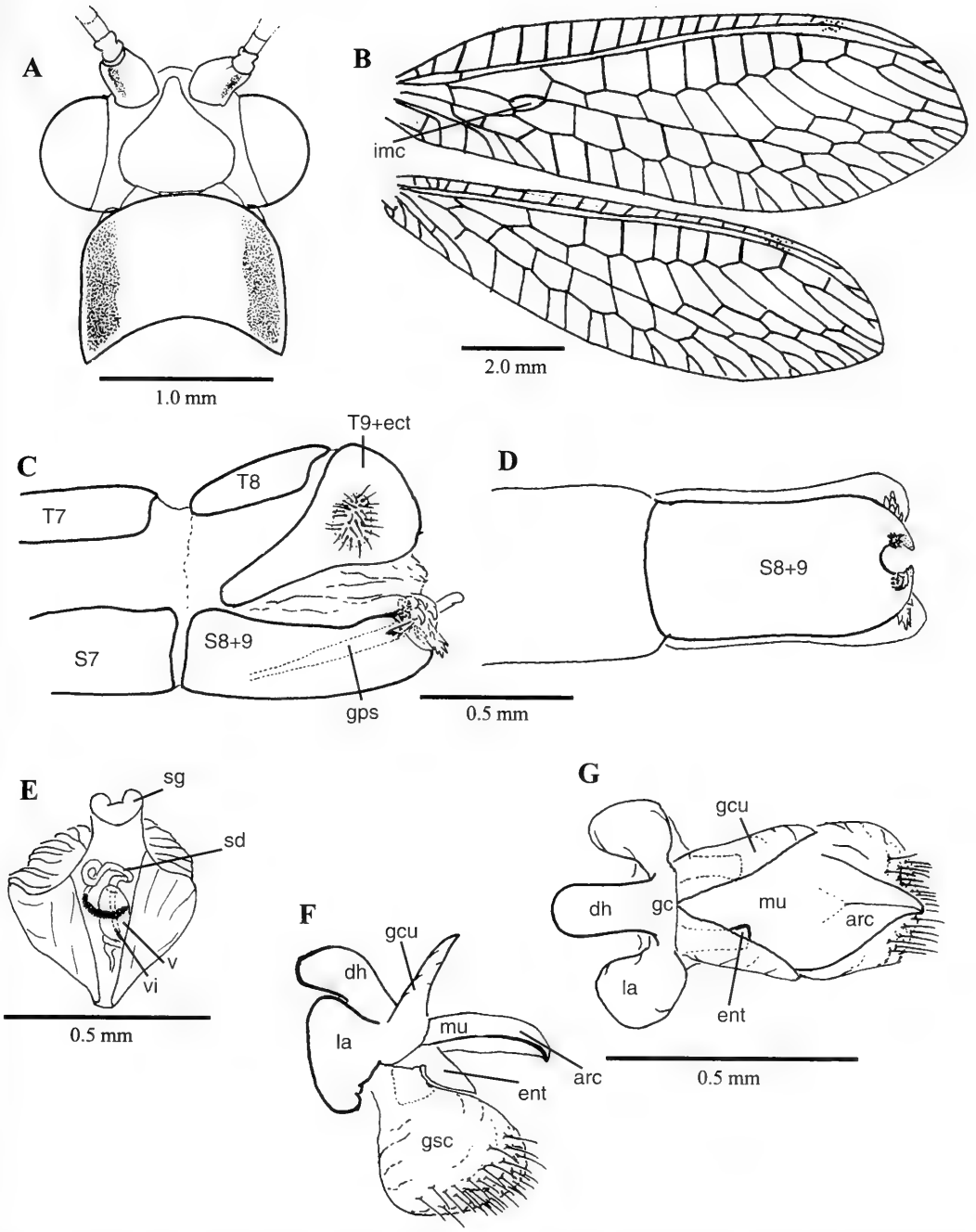

FIGURE 12. *Ceraeochrysa cubana* (Hagen, 1861). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Apex of male abdomen, ventral view; E. Female genitalia; F. Male genitalia, lateral view; G. Male genitalia, dorsal view.

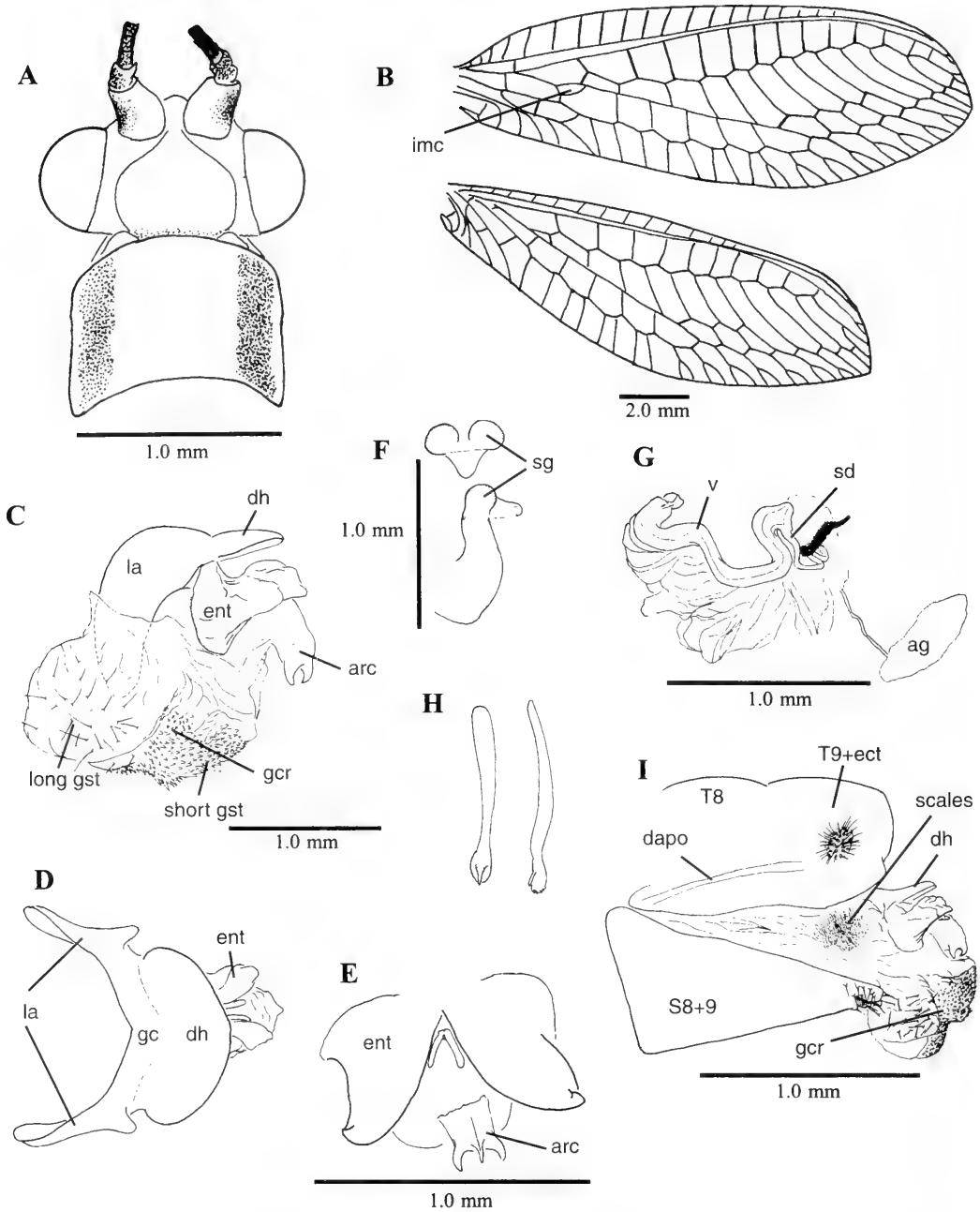

FIGURE 13. *Ceraeochrysa everes* (Banks, 1920). A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, lateral view; D. Male genitalia, dorsal view; E. Detail of apex of arcessus; F. Subgenitale; G. Spermatheca; H. Gonapsis; I. Apex of abdomen.

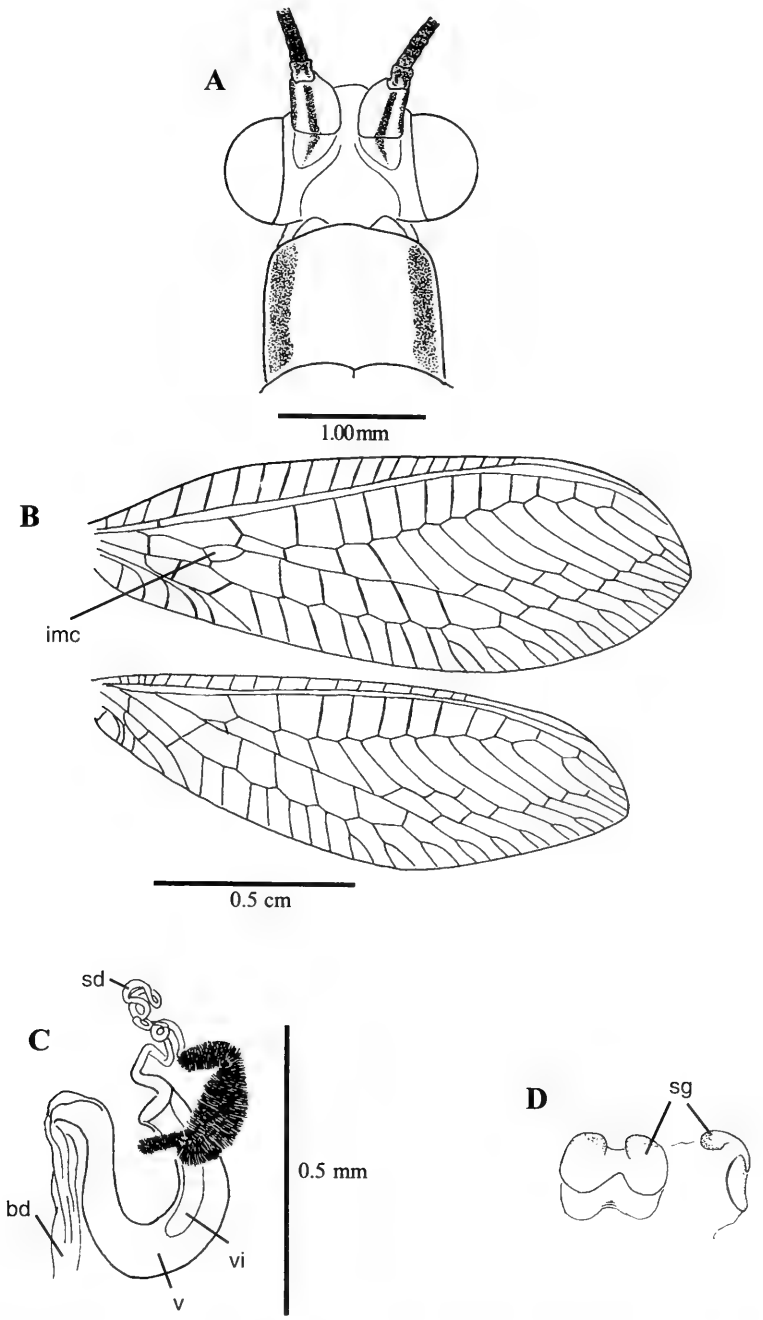

FIGURE 14. *Ceraeochrysa montoyana* (Navás, 1913). A. Head and prothorax, dorsal view; B. Wings; C. Spermatheca; D. Subgenitale.

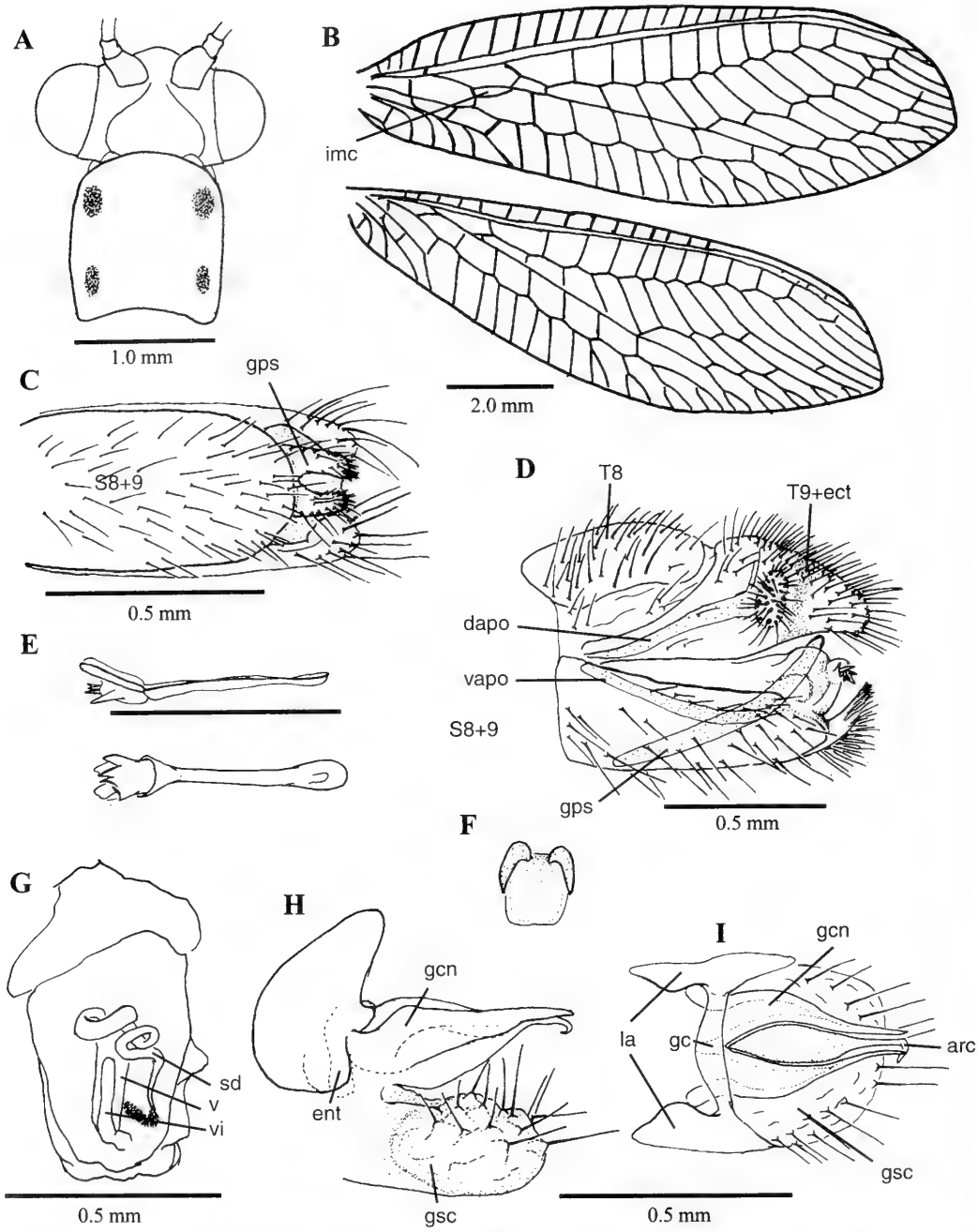

FIGURE 15. *Ceraeochrysa paraguaria* (Navás, 1919). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, ventral view; D. Apex of male abdomen, lateral view; E. Gonapsis; F. Subgenitale; G. Female genitalia; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

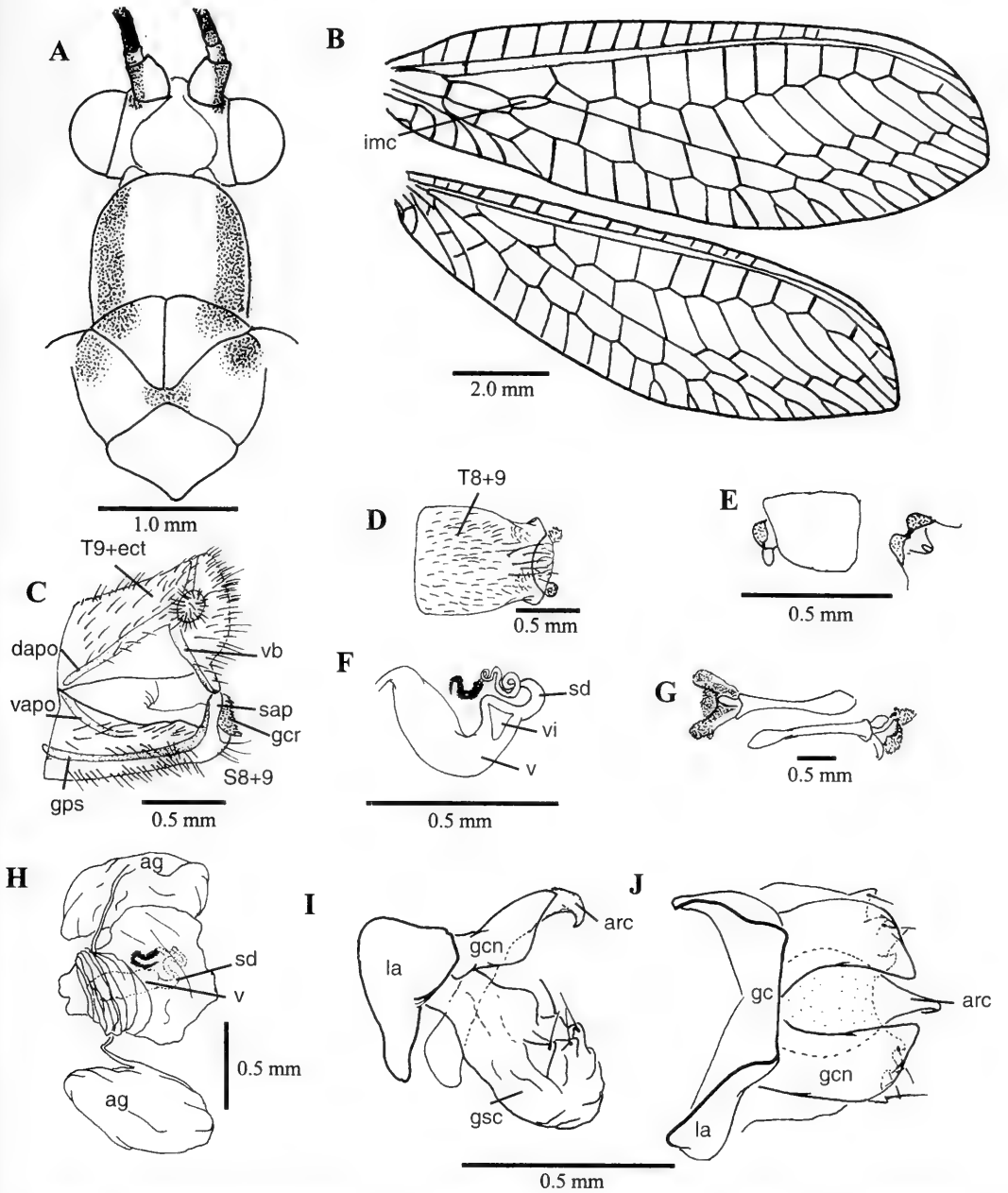

FIGURE 16. *Ceraeochrysa sanchezi* (Navás, 1924). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Sternite 8 + 9; E. Subgenitale; F. Spermatheca, G. Gonapsis; H. Female genitalia; I. Male genitalia, lateral view; J. Male genitalia, dorsal view.

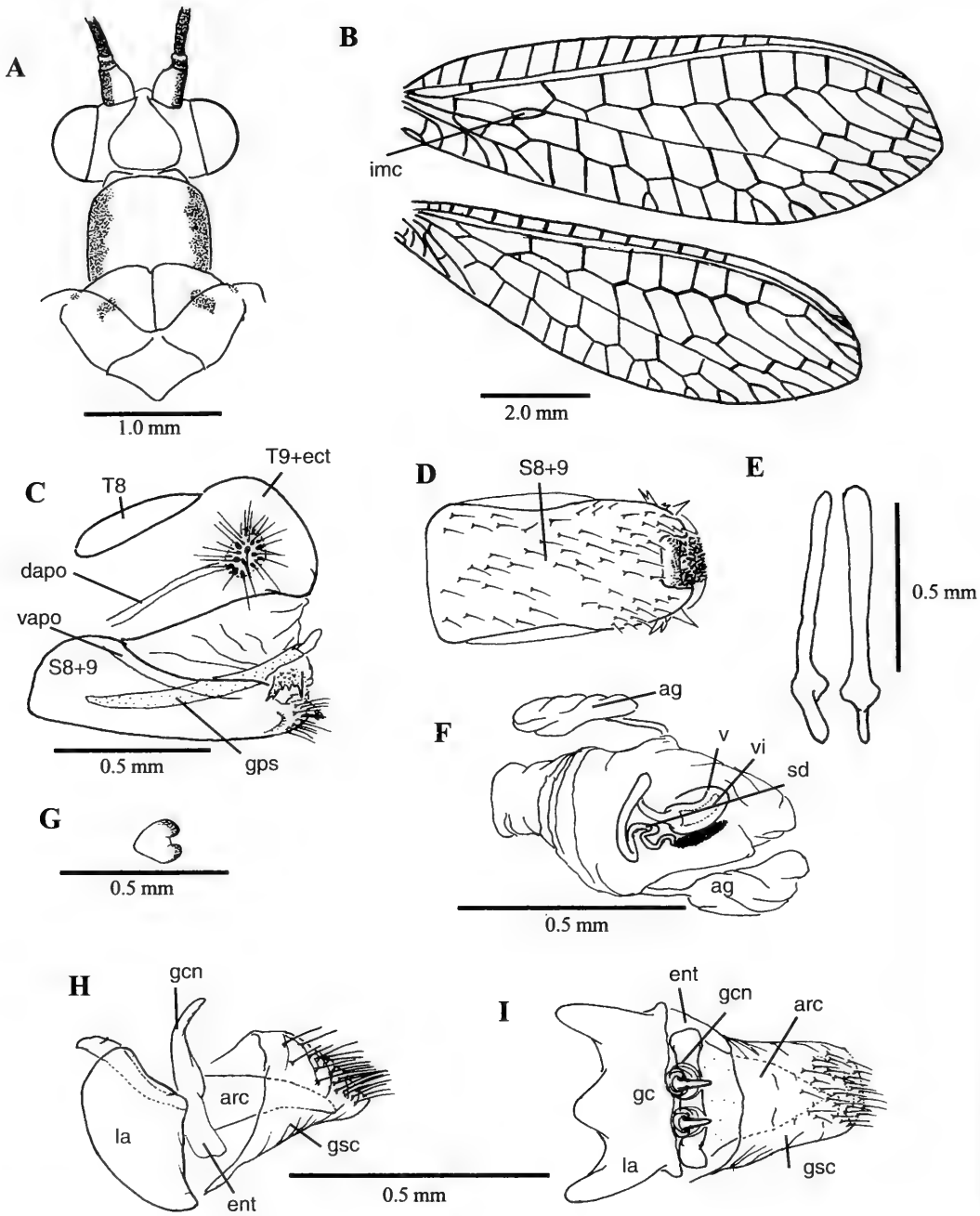

FIGURE 17. *Ceraeochrysa scapularis* (Navás, 1914). A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Sternite 8 + 9; E. Gonapsis; F. Female genitalia; G. Subgenitale; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

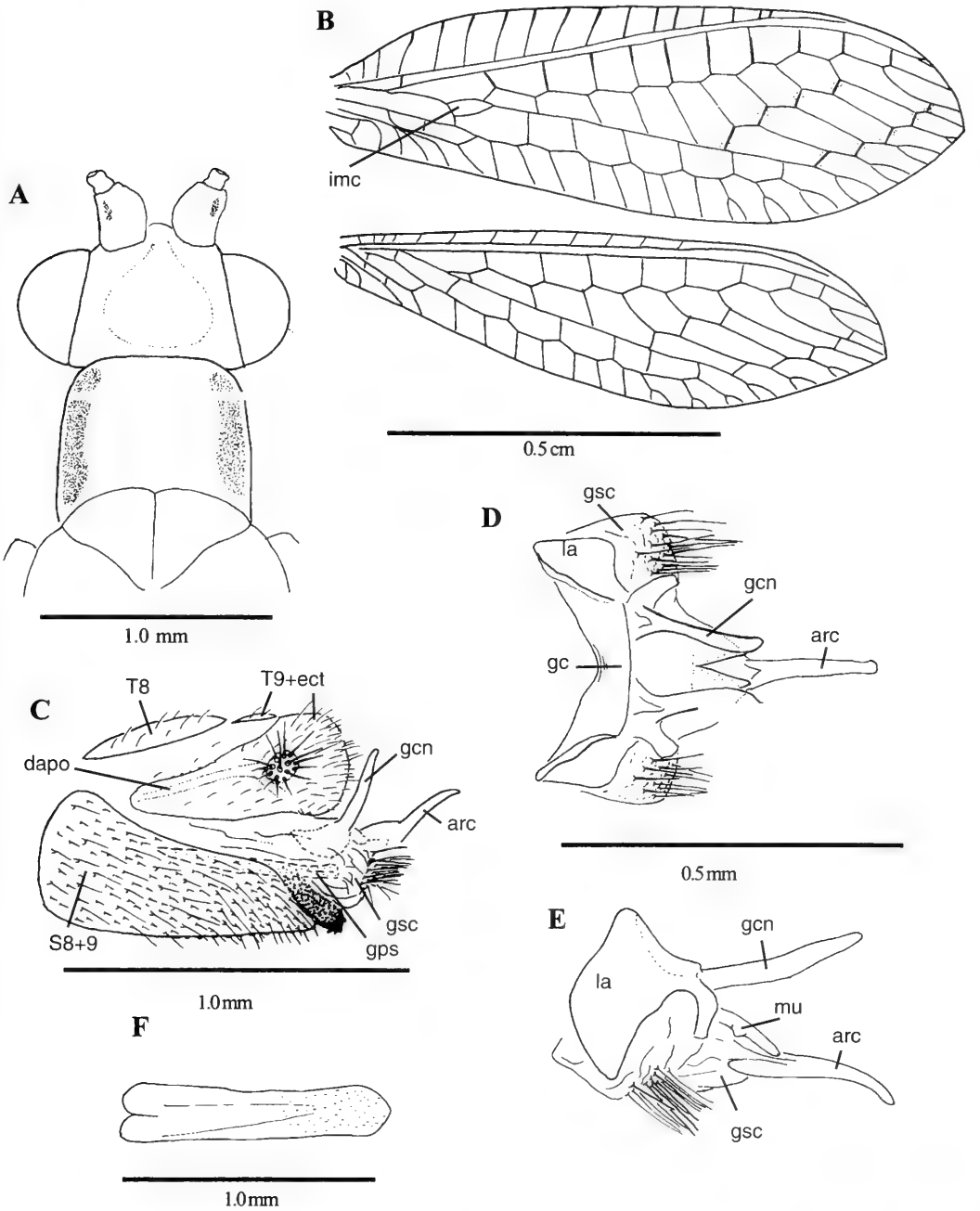

FIGURE 18. *Ceraeochrysa tenuicornis* Adams and Penny, 1987. A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis.

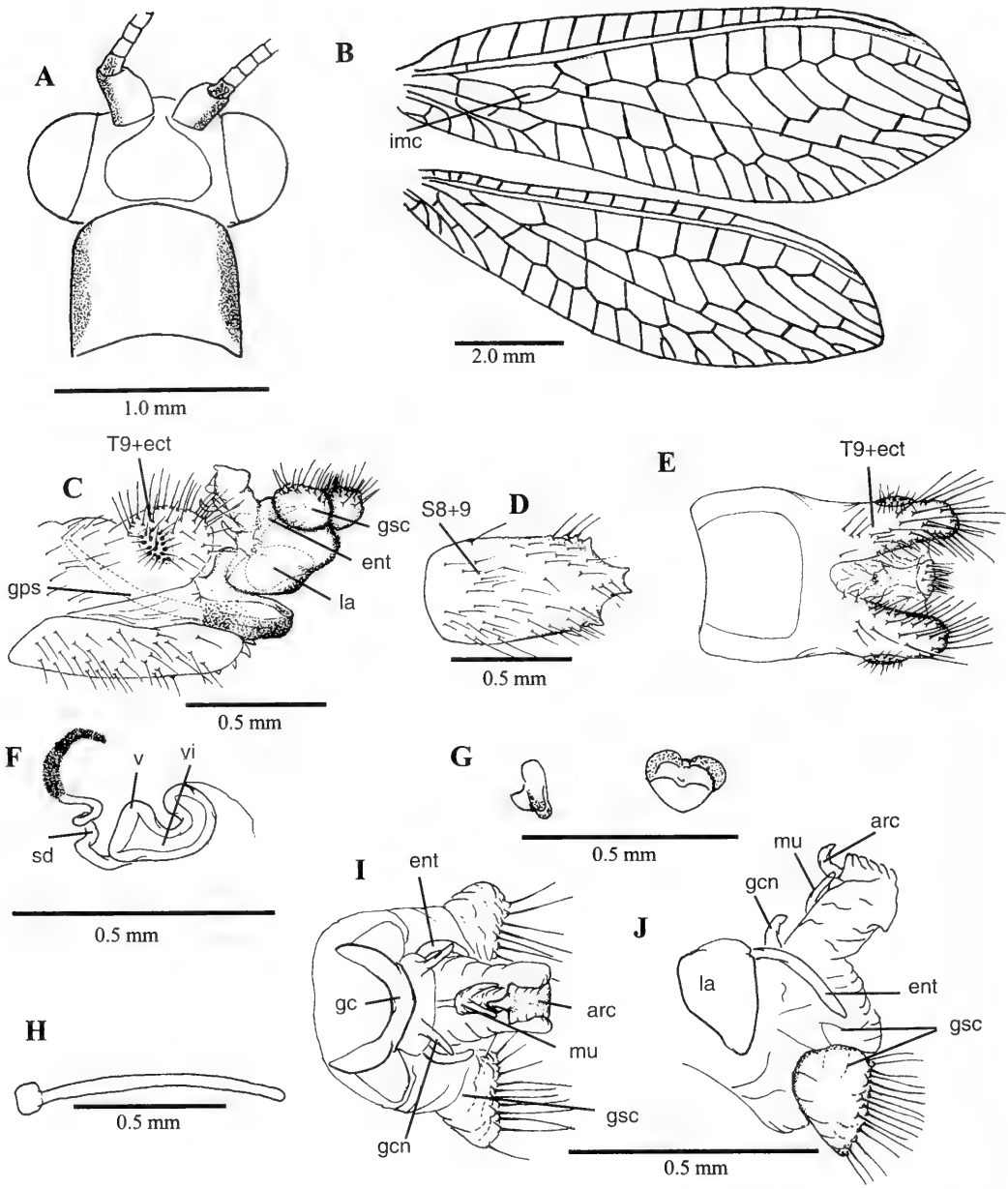

FIGURE 19. *Ceraeochrysa tucumana* (Navás, 1919). A. Head and prothorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Sternite 8 + 9; E. Apex of male abdomen, dorsal view; F. Spermatheca; G. Subgenitale; H. Gonapsis; I. Male genitalia, dorsal view; J. Male genitalia, lateral view.

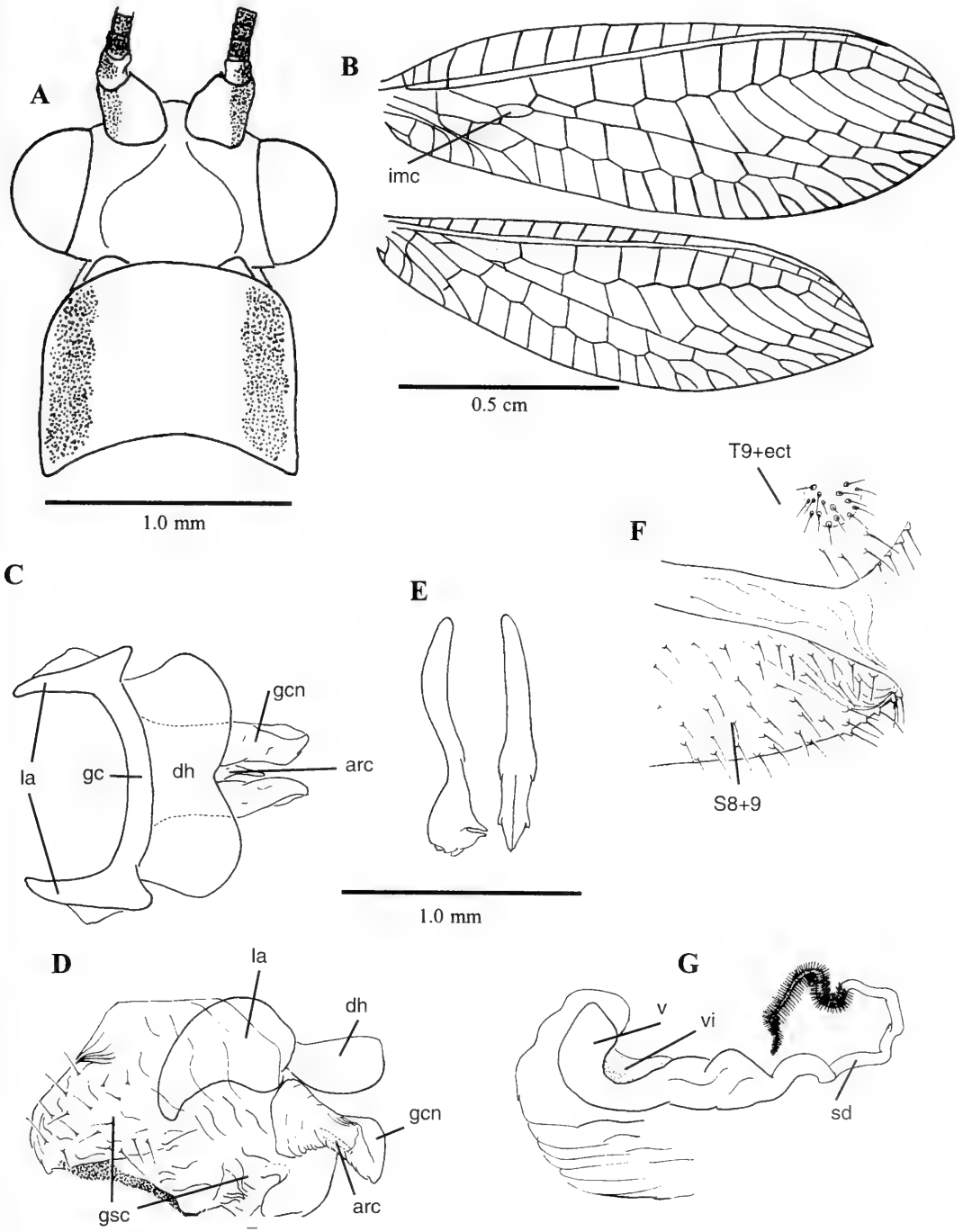

FIGURE 20. *Ceraeochrysa dislepis*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Gonapsis; F. Apex of male abdomen, detail; G. Spermatheca.

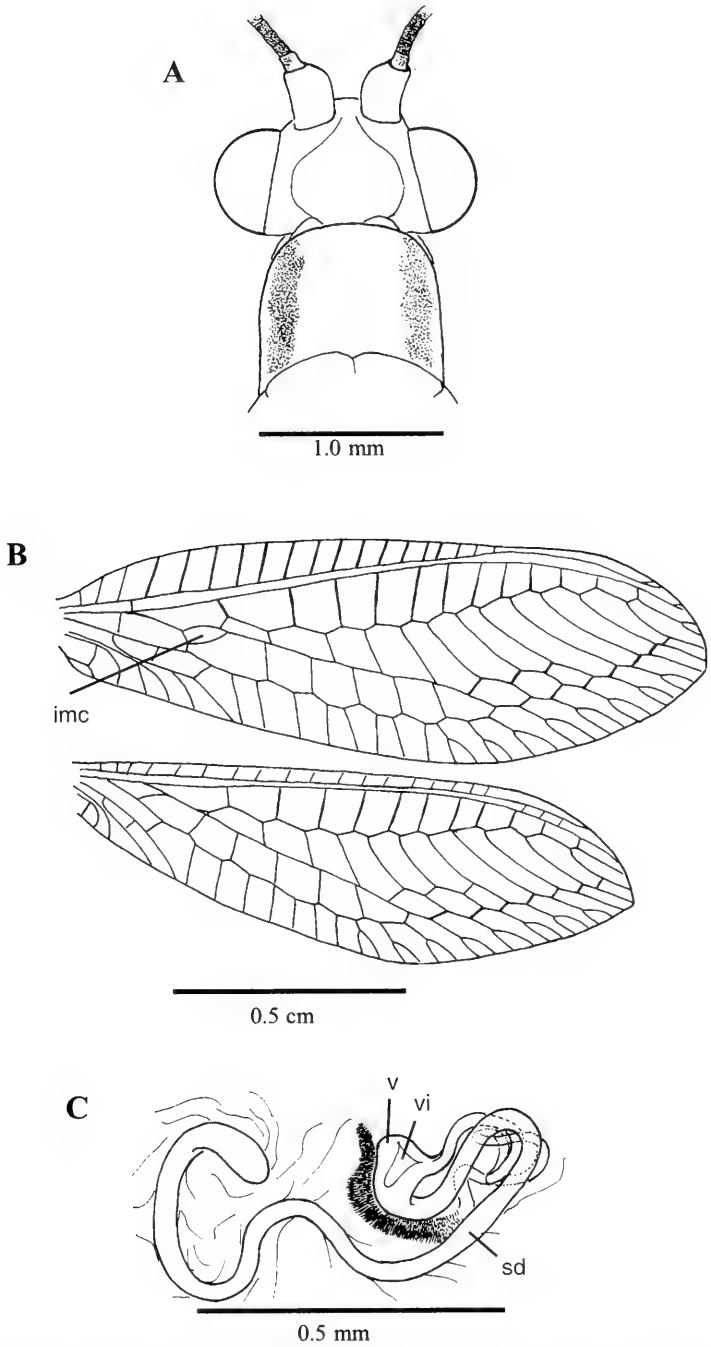

FIGURE 21. *Ceraeochrysa dolichosvela*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Female genitalia.

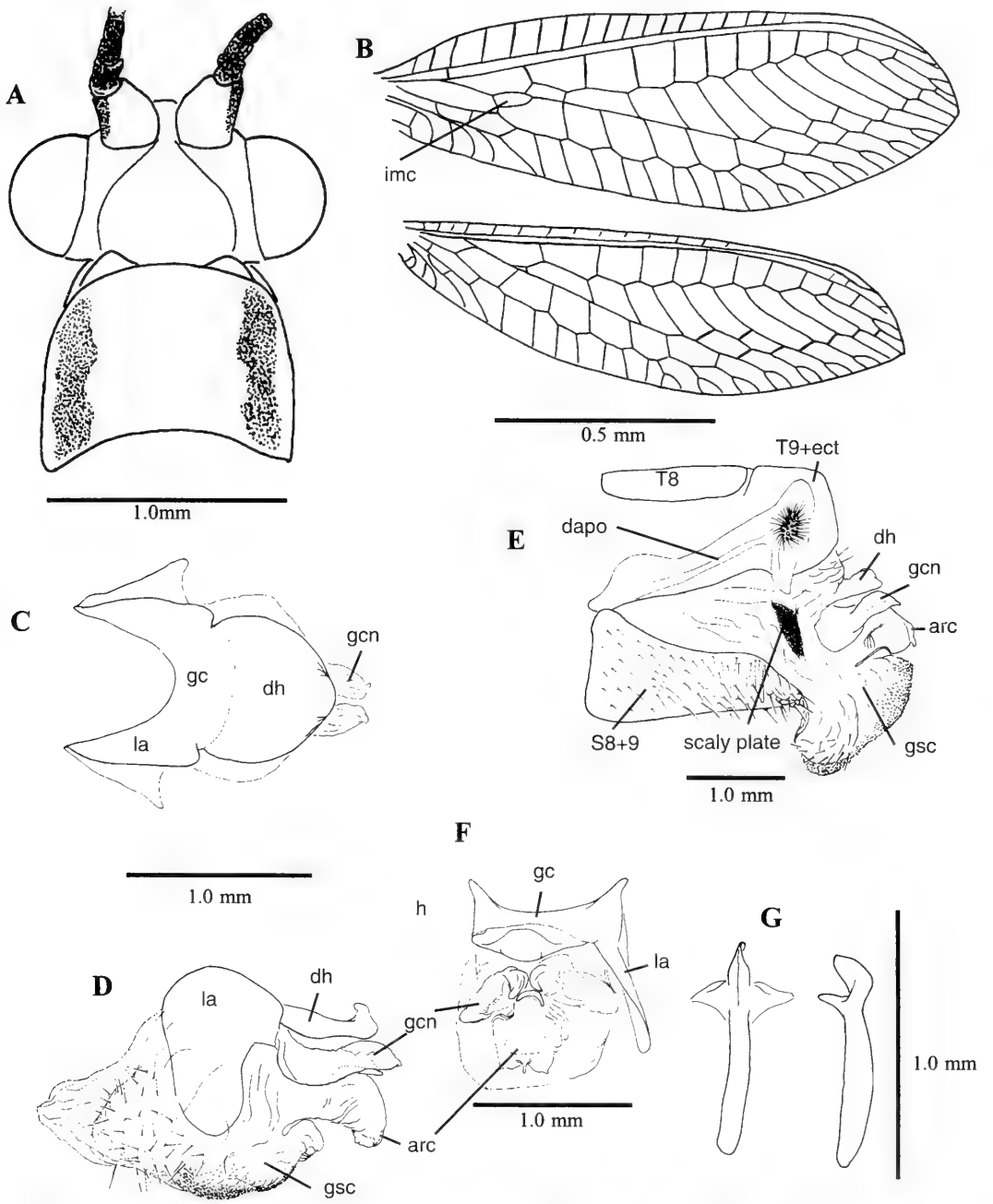

FIGURE 22. *Ceraeochrysa squama*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Apex of male abdomen apex, lateral view; F. Male genitalia, caudal view; G. Gonapsis.

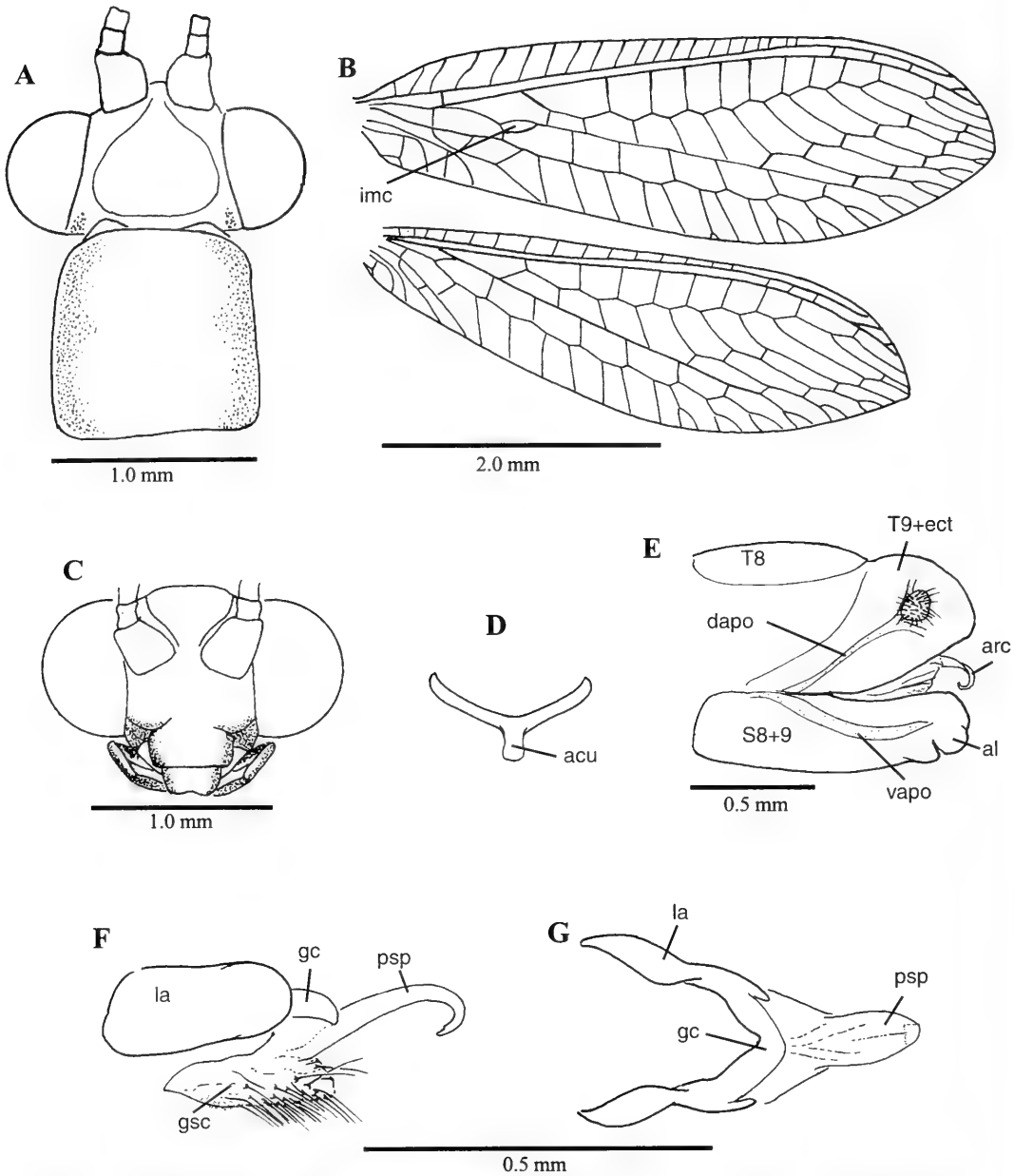

FIGURE 23. *Chrysoperla defreitasi* Brooks, 1994. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Tignum; E. Apex of male abdomen; F. Male genitalia, lateral view; G. Male genitalia, dorsal view.

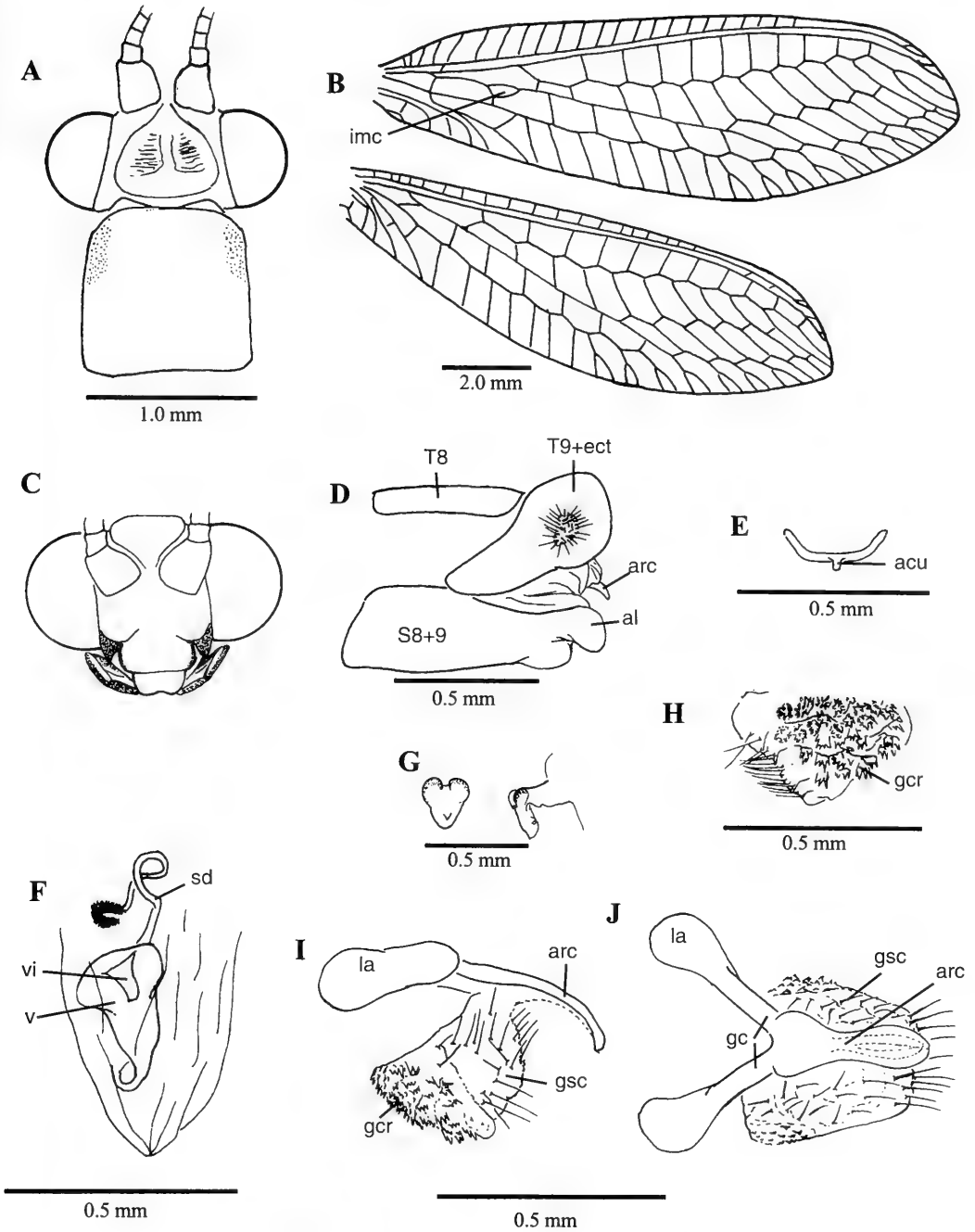

FIGURE 24. *Chrysoperla externa* (Hagen, 1861). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen, lateral view; E. Tignum; F. Female genitalia; G. Subgentiale; H. Gonosaccus; I. Male genitalia, lateral view; J. Male genitalia, dorsal view.

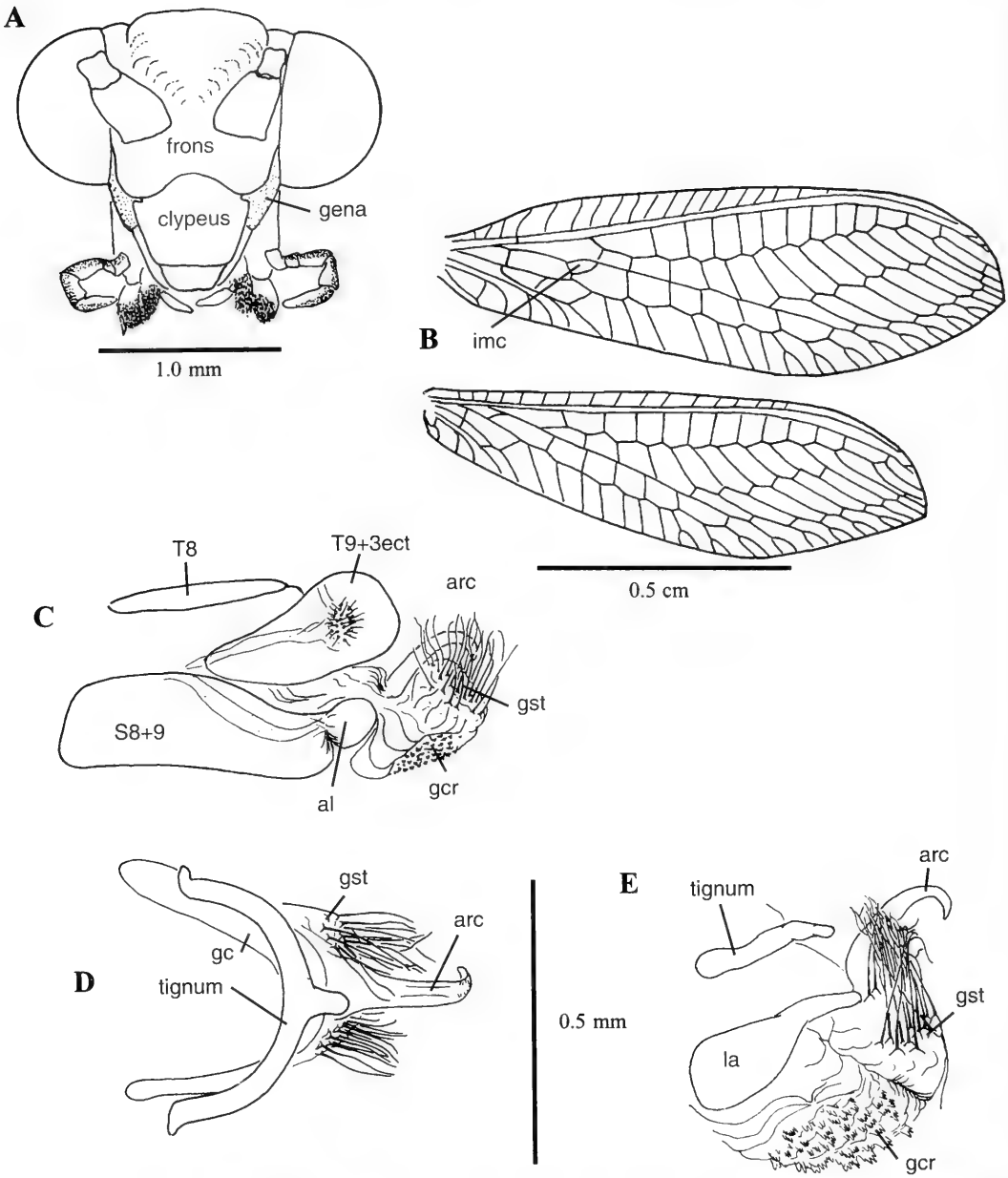

FIGURE 25. *Chrysoperla raimundoi*, new species. A. Head, frontal view; B. Wings; C. Apex of male abdomen; D. Male genitalia, dorsal view; E. Male genitalia, lateral view.

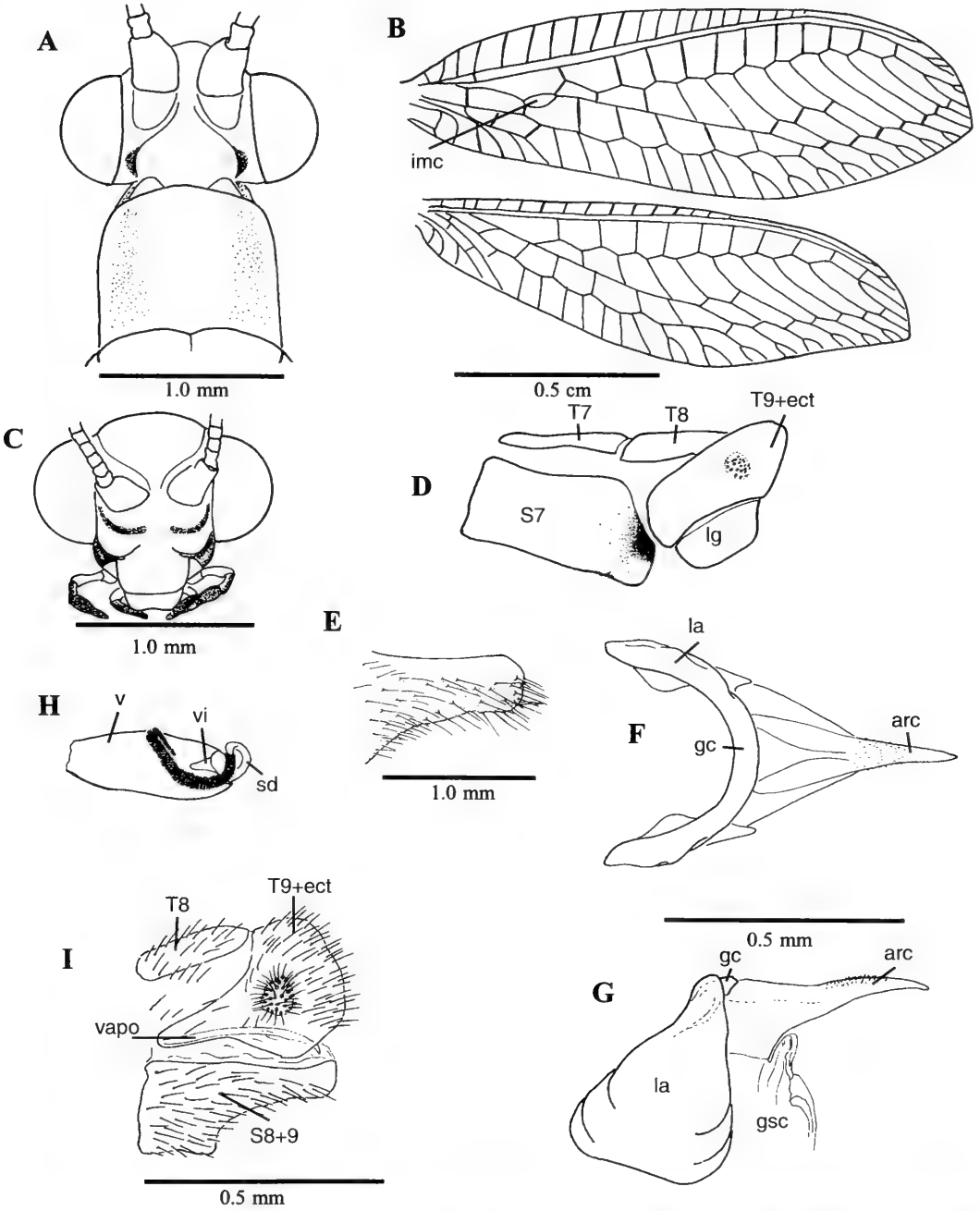

FIGURE 26. *Chrysopodes* (*Chrysopodes*) *lineafrons* Adams and Penny, 1987. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of female abdomen, lateral view; E. Male sternite 8 + 9 apex; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Spermatheca; I. Apex of male abdomen, lateral view.

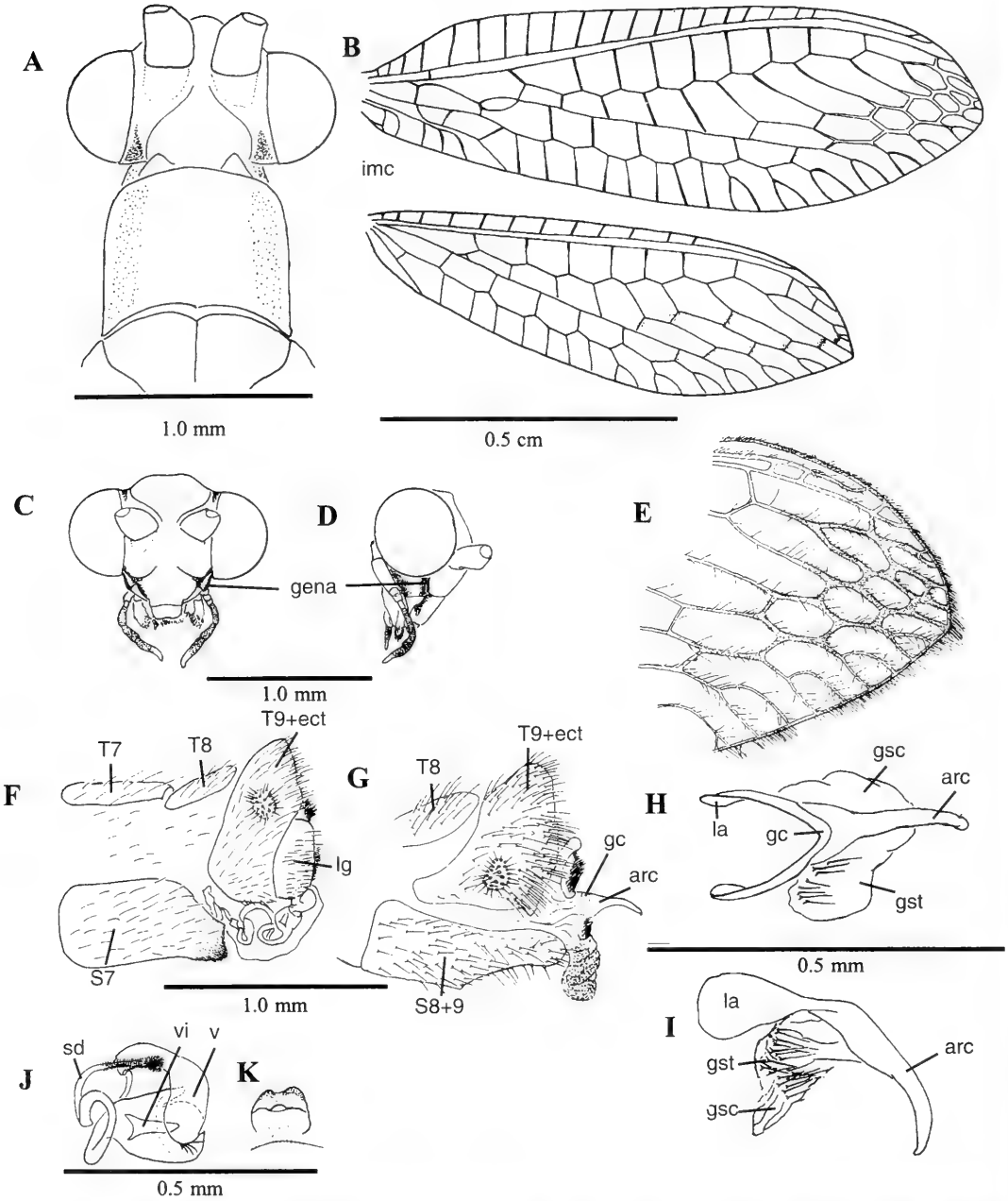

FIGURE 27. *Chrysopodes* (*Chrysopodes*) *polygonica* Adams and Penny, 1987. A. Head and prothorax, dorsal view; B. Wings: C. Head, frontal view; D. Head, lateral view; E. Apex of forewing; F. Apex of female abdomen; lateral view; G. Apex of male abdomen, lateral view; H. Male genitalia, dorsal view; I. Male genitalia, lateral view; J. Female genitalia; K. Subgenitale.

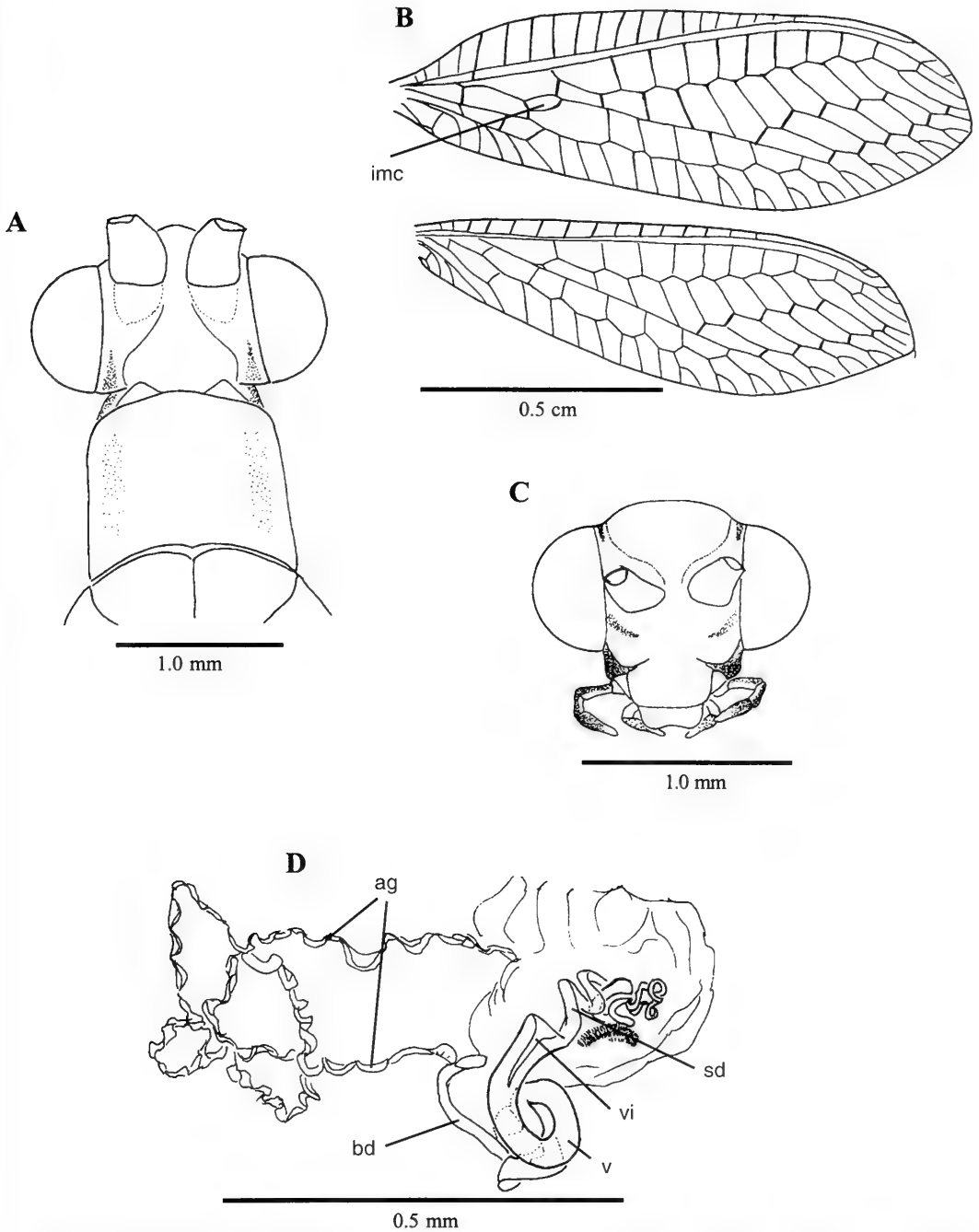

FIGURE 28. *Chrysopodes* (*Chrysopodes*) *spinella* Adams and Penny, 1987. A. Head and prothorax, dorsal view; B. Wings: C. Head, frontal view; D. Female genitalia.

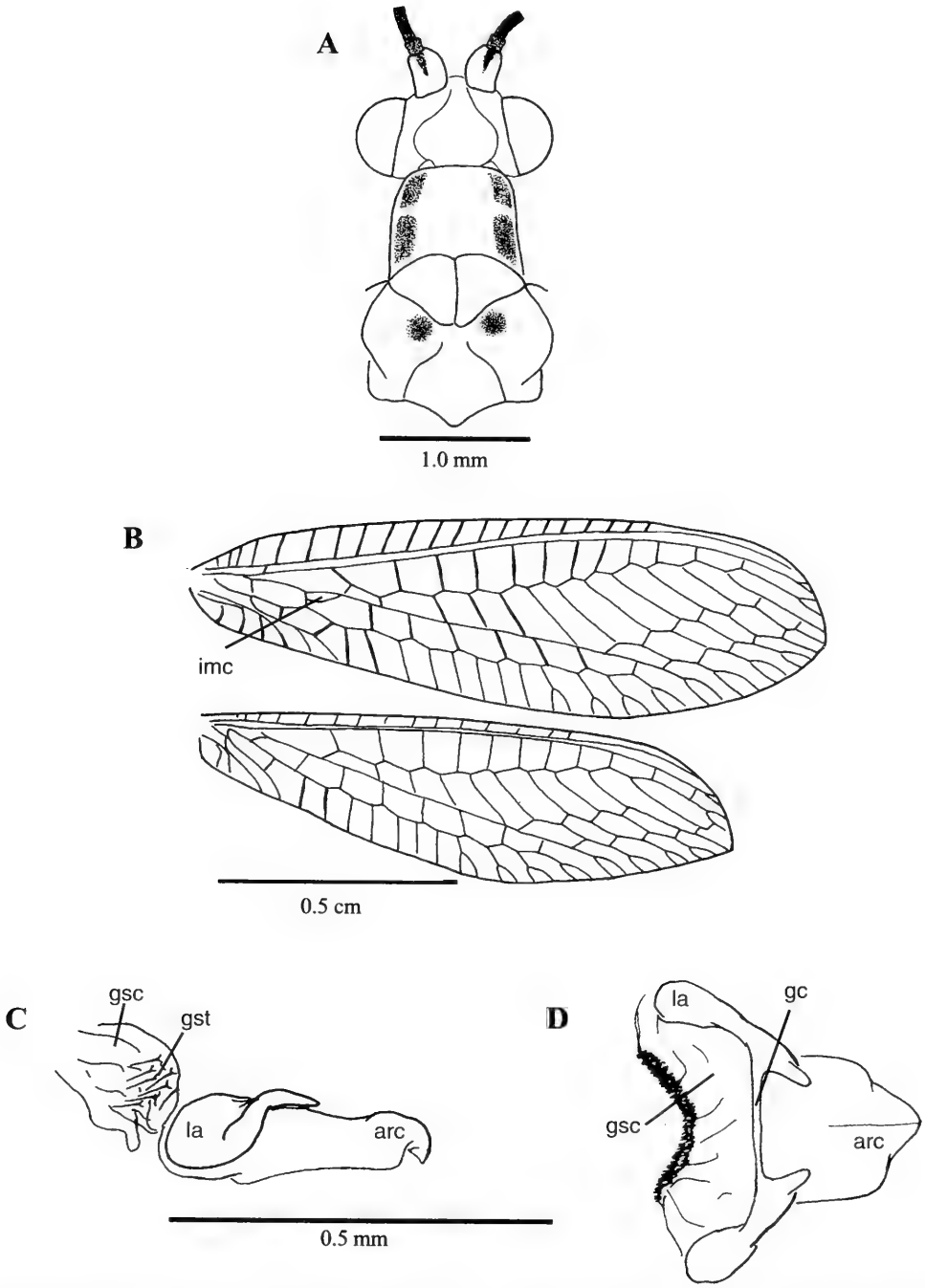

FIGURE 29. *Chrysopodes* (*Chrysopodes*) *adynatos*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, lateral view; D. Male genitalia, dorsal view.

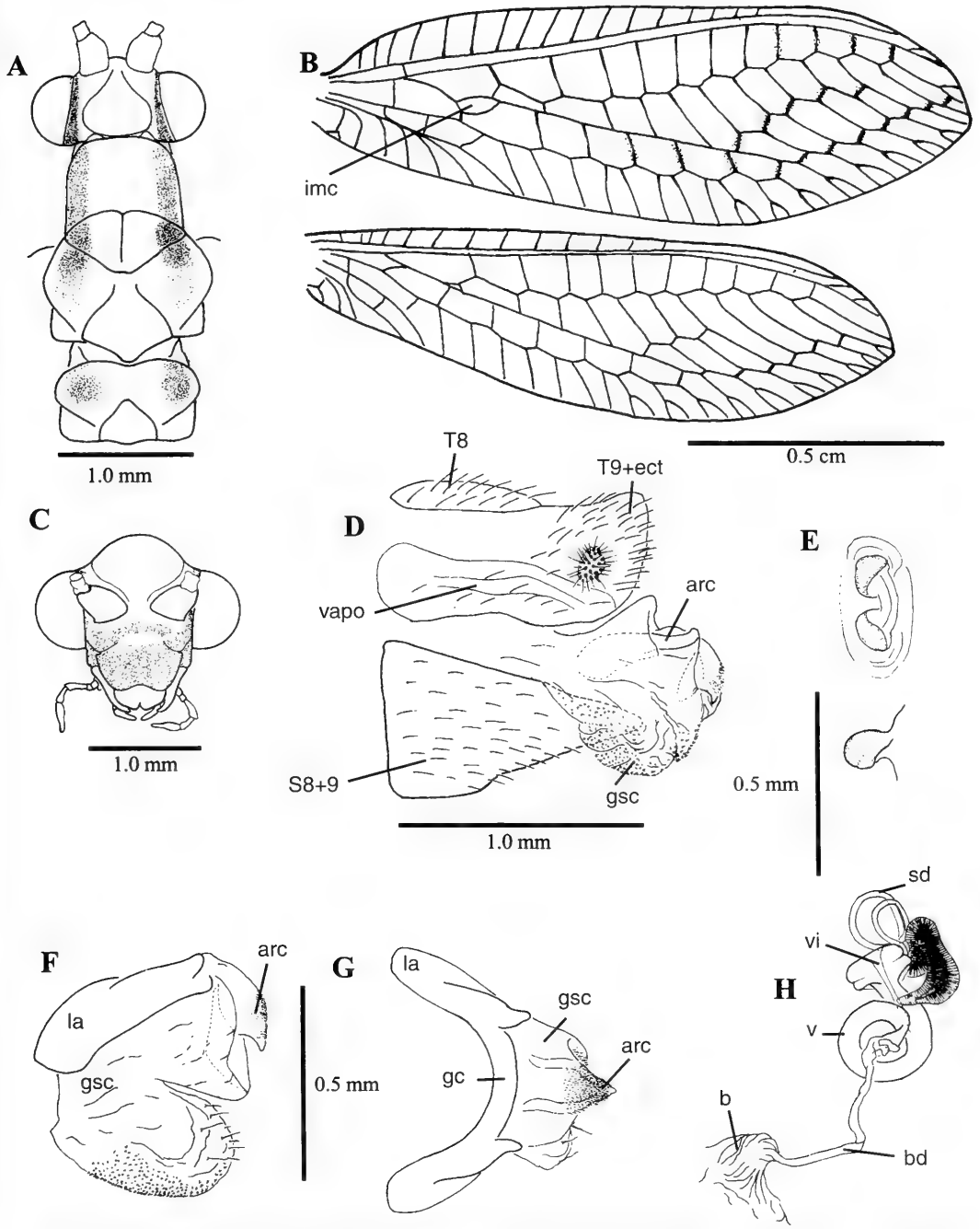

FIGURE 30. *Chrysopodes* (*Chrysopodes*) *copia*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen, lateral view; E. Subgenitale; F. Male genitalia, lateral view; G. Male genitalia, dorsal view; H. Spermatheca.

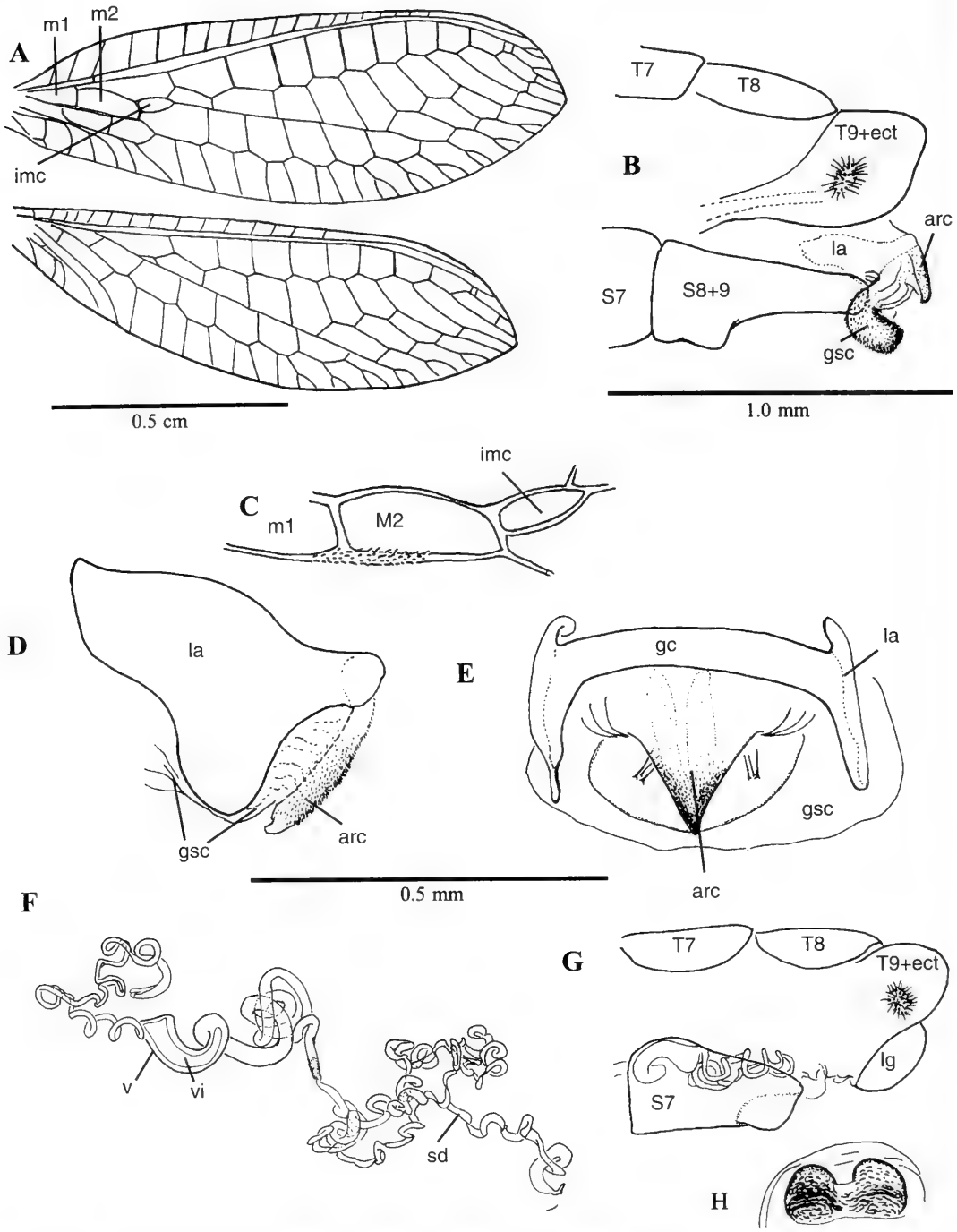

FIGURE 31. *Chrysopodes* (*Chrysopodes*) *crocinus*, new species. A. Wings; B. Apex of male abdomen, lateral view; C. Encrassate median cell; D. Male genitalia, lateral view; E. Male genitalia, dorsal view; F. Spermatheca; G. Apex of female abdomen, lateral view; H. Subgenitale.

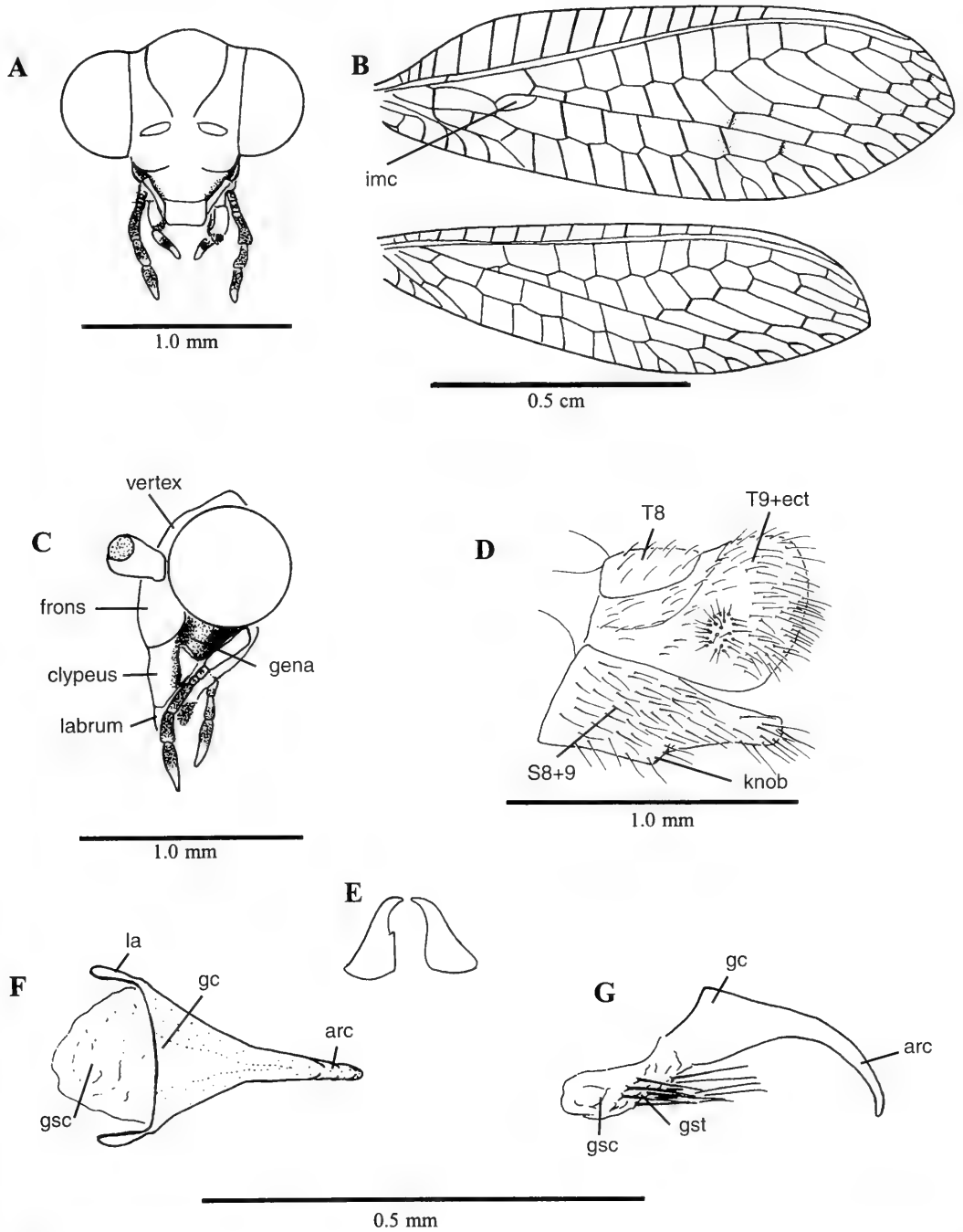

FIGURE 32. *Chrysopodes* (*Chrysopodes*) *delicata*, new species. A. Head, frontal view; B. Wings; C. Head, lateral view; D. Apex of male abdomen, lateral view; E. Mandibles; F. Male genitalia, dorsal view; G. Male genitalia, lateral view.

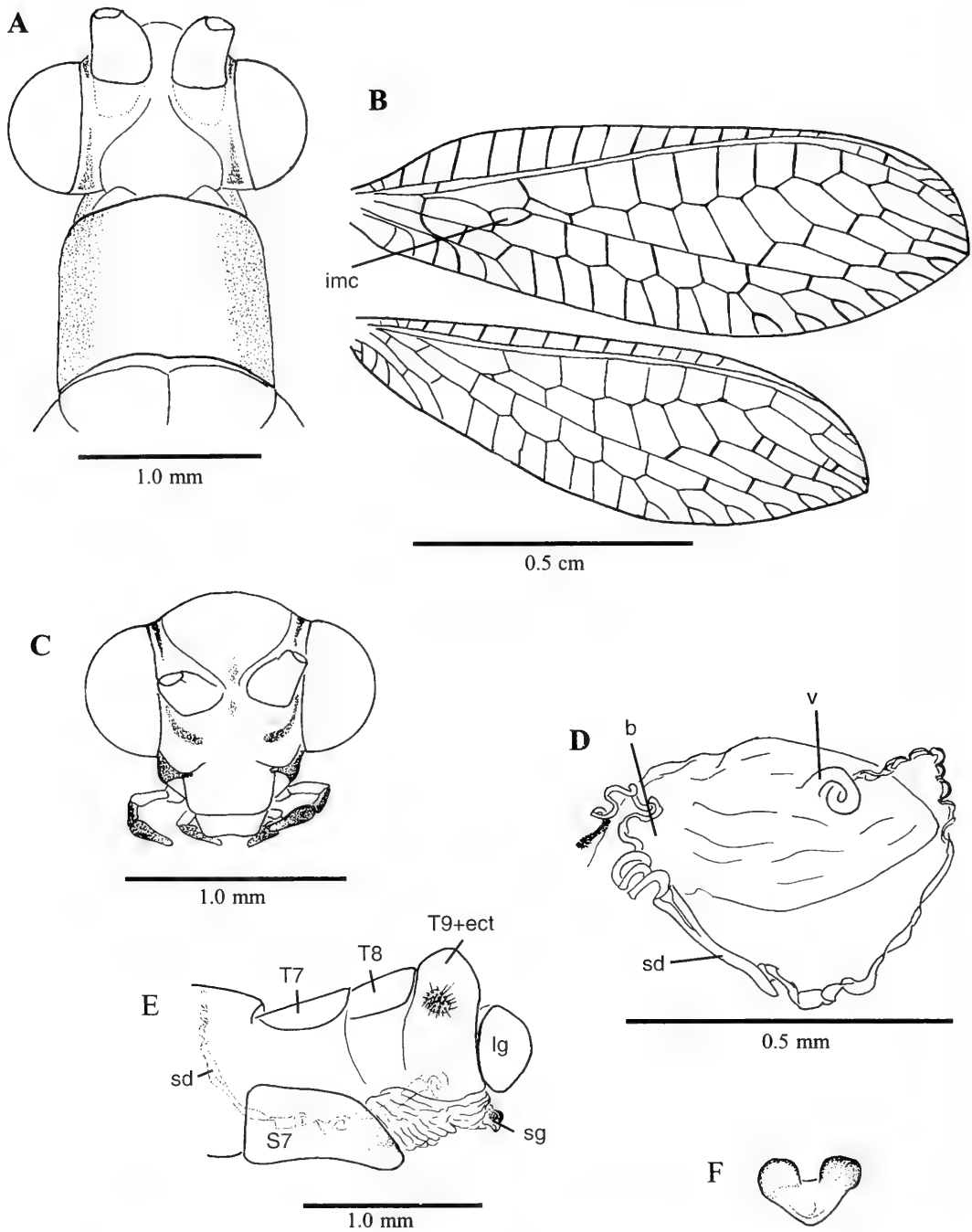

FIGURE 33. *Chrysopodes* (*Chrysopodes*) *elongata*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Female genitalia; E. Apex of female abdomen; F. Subgenitale.

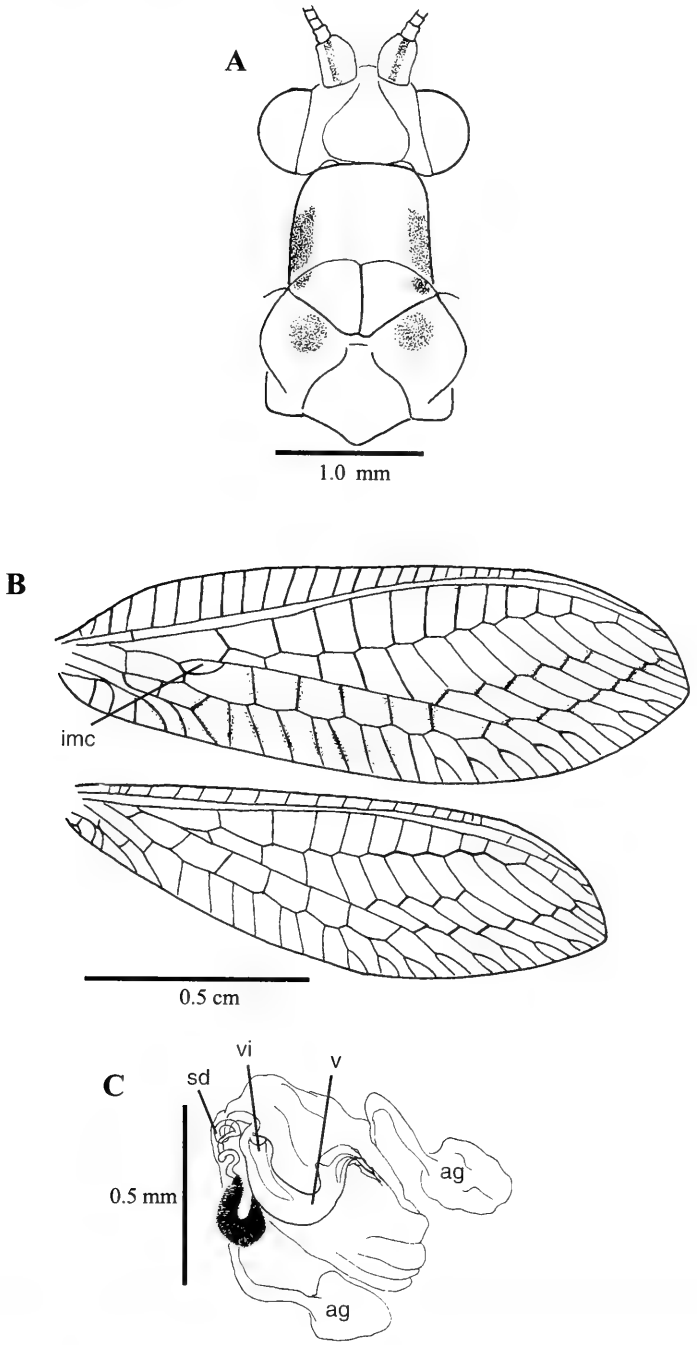

FIGURE 34. *Chrysopodes* (*Chrysopodes*) *nigropicta*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Female genitalia.

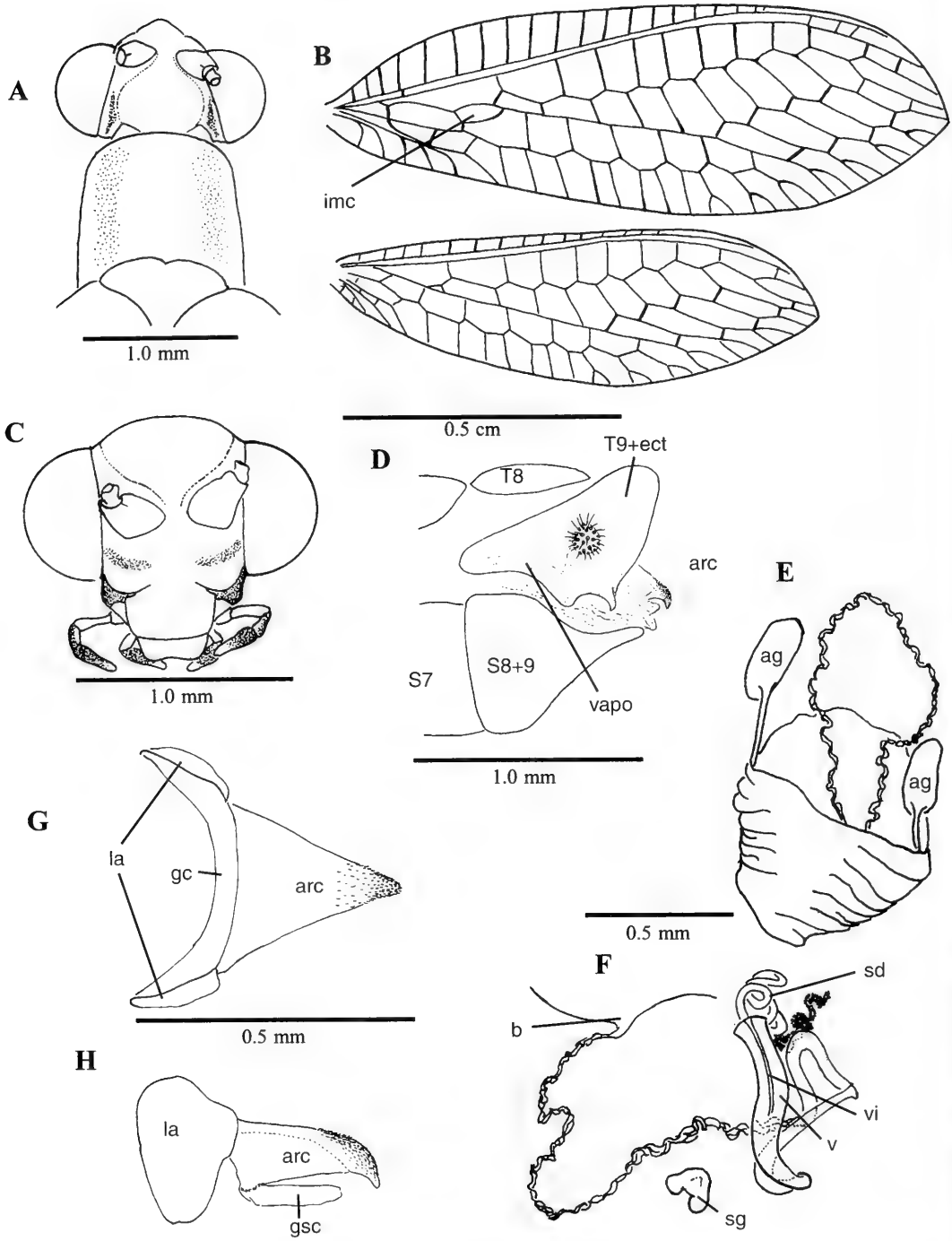

FIGURE 35. *Chrysopodes* (*Neosuarius*) *divisa* (Walker, 1853). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen; E. Female genitalia; F. Spermatheca; G. Male genitalia, dorsal view; H. Male genitalia, lateral view.

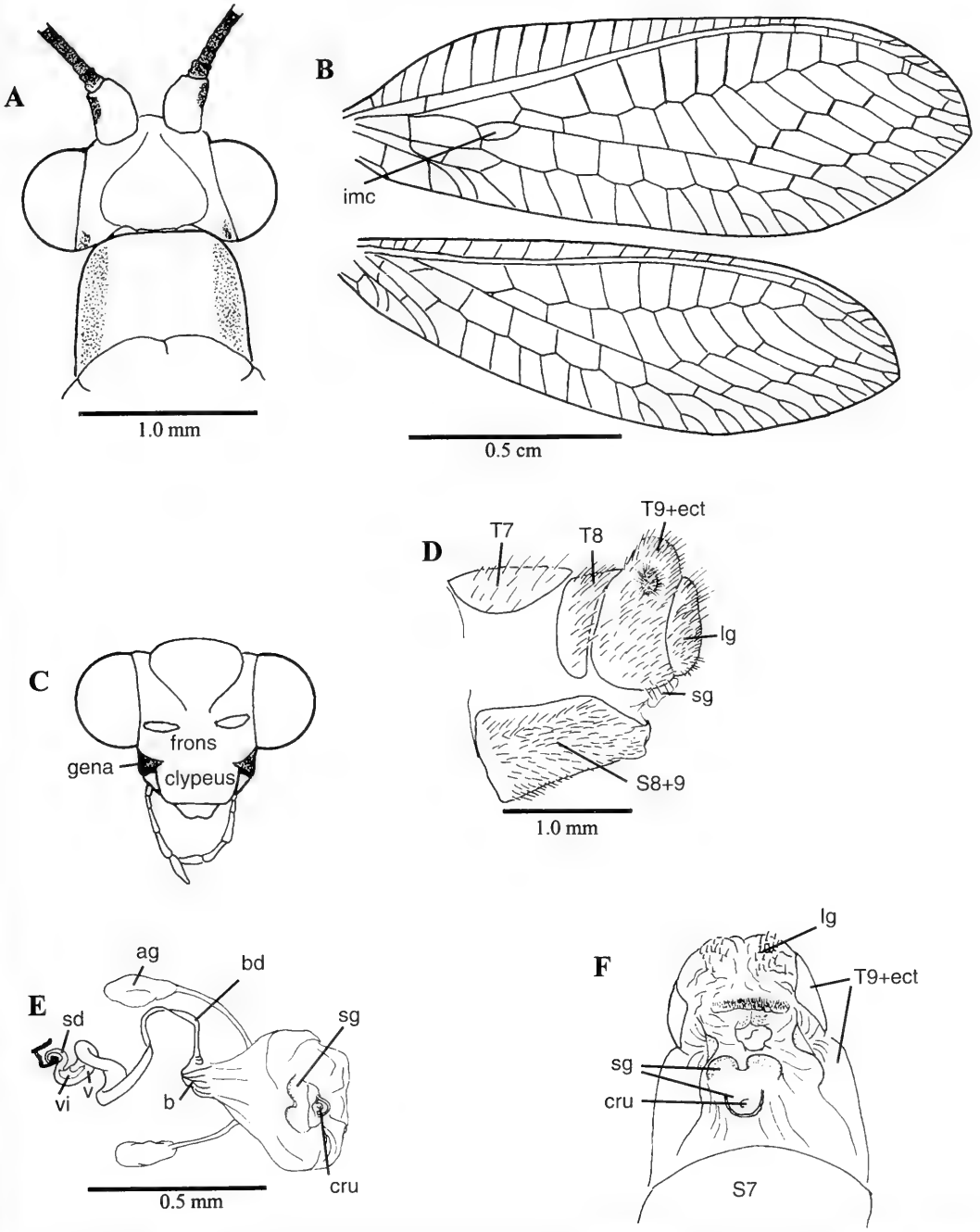

FIGURE 36. *Chrysopodes* (*Neosuarius*) *karinae* Adams and Penny. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen, lateral view; E. Female genitalia; F. Apex of female abdomen, ventral view.

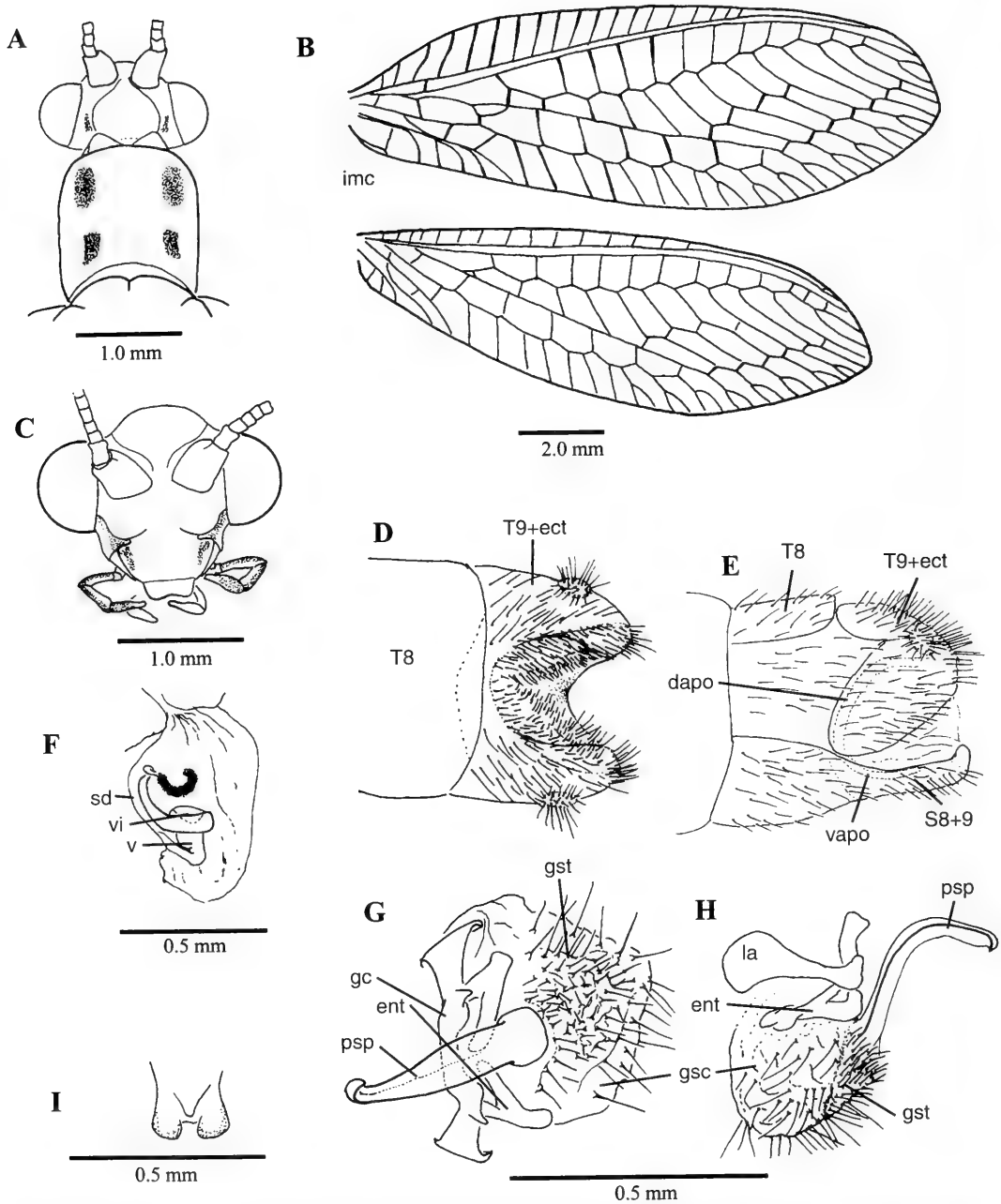

FIGURE 37. *Plesiochrysa brasiliensis* (Schneider, 1851). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen, dorsal view; E. Apex of male abdomen, lateral view; F. Female genitalia; G. Male genitalia, dorsal view; H. Male genitalia, lateral view; I. Subgenitale.

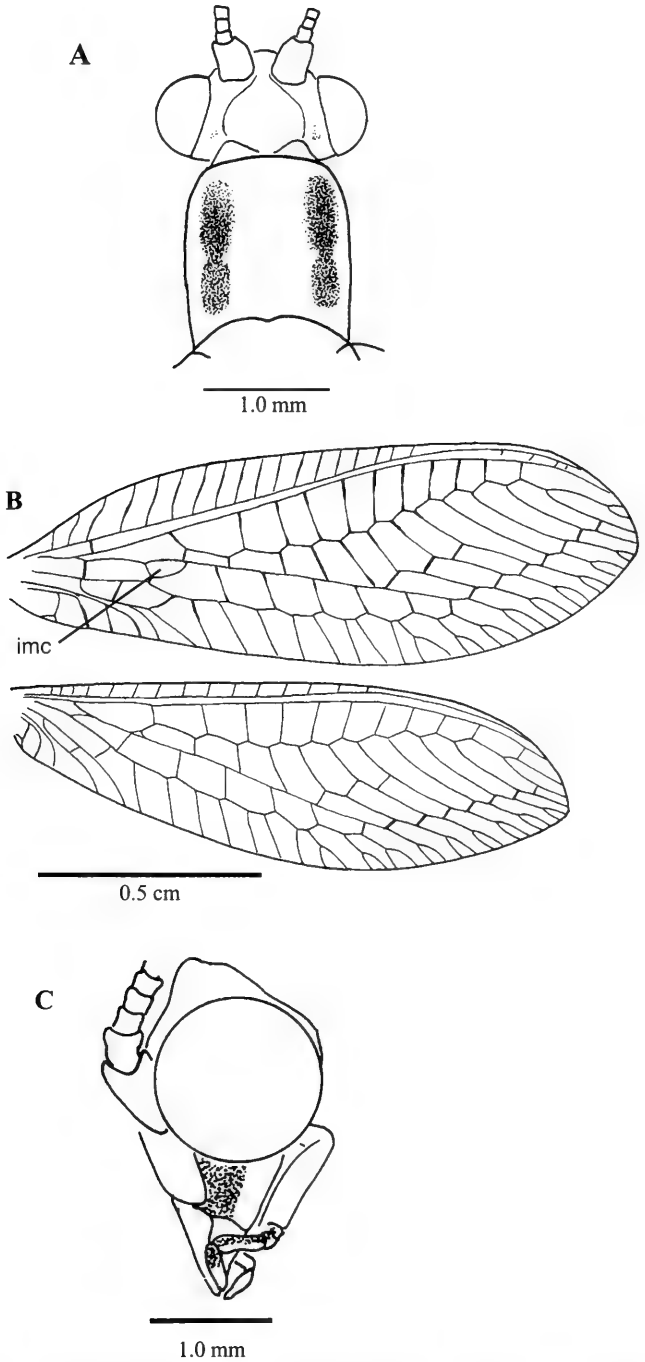

FIGURE 38. *Plesiochrysa elongata* (Navás, 1913). A. Head and prothorax, dorsal view; B. Wings; C. Head, lateral view.

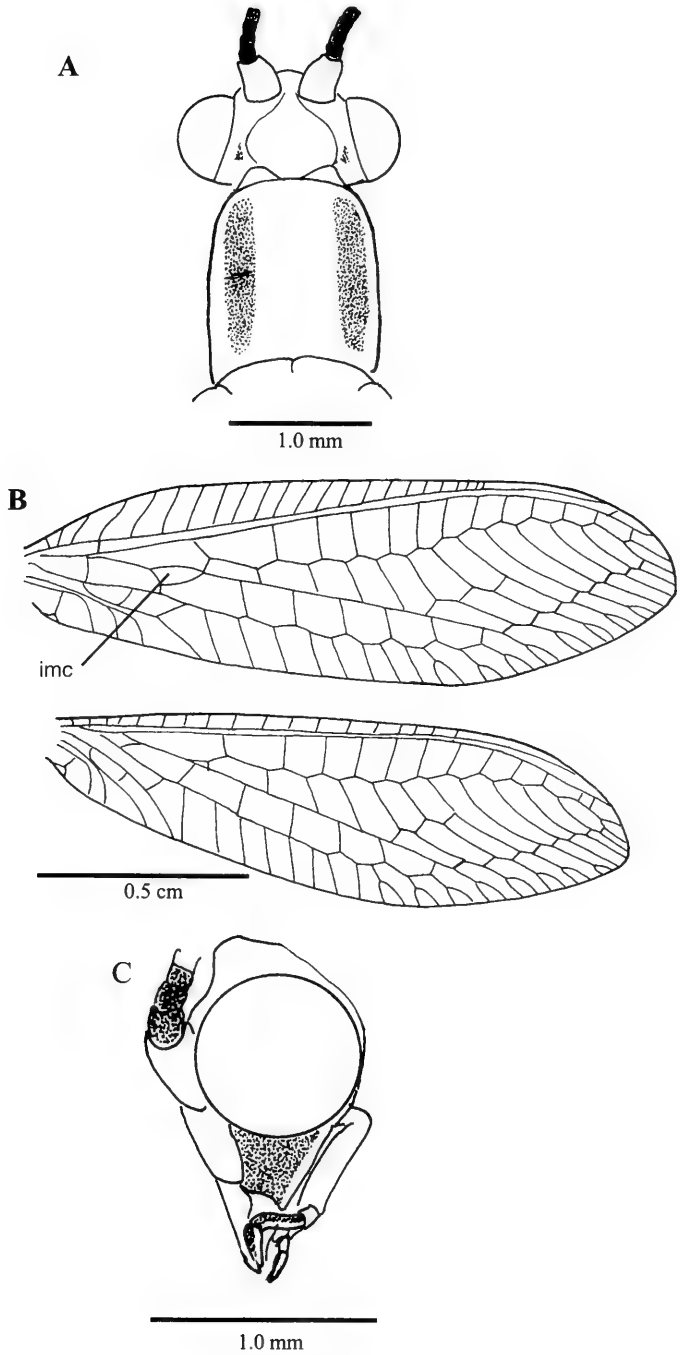

FIGURE 39. *Plesiochrysa alytos,* new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, lateral view.

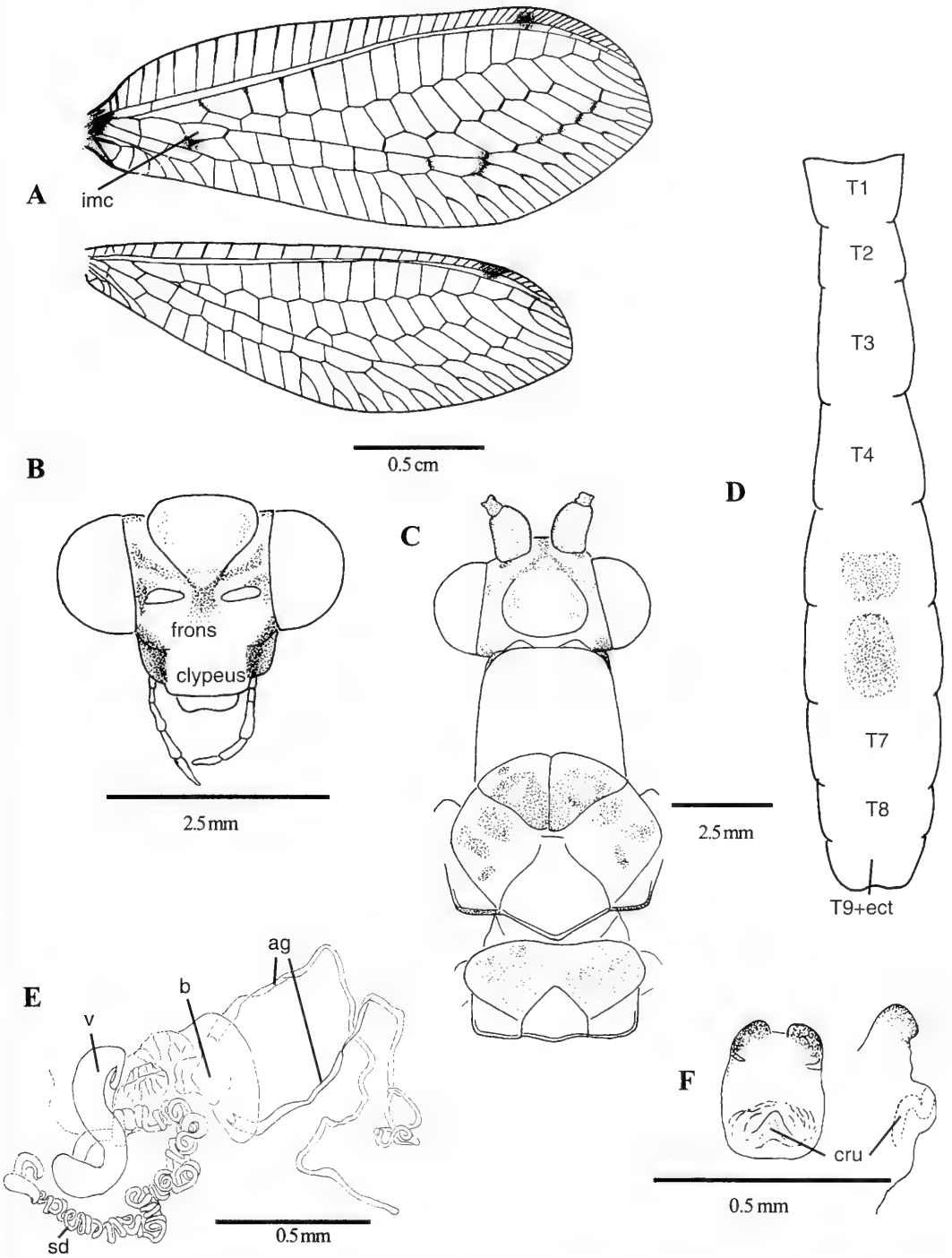

FIGURE 40. *Leucochrysa* (*Leucochrysa*) *ampla* (Walker, 1853). A. Wings; B. Head, frontal view; C. Head and prothorax, dorsal view; D. Abdomen, dorsal view; E. Female genitalia; F. Subgenitale.

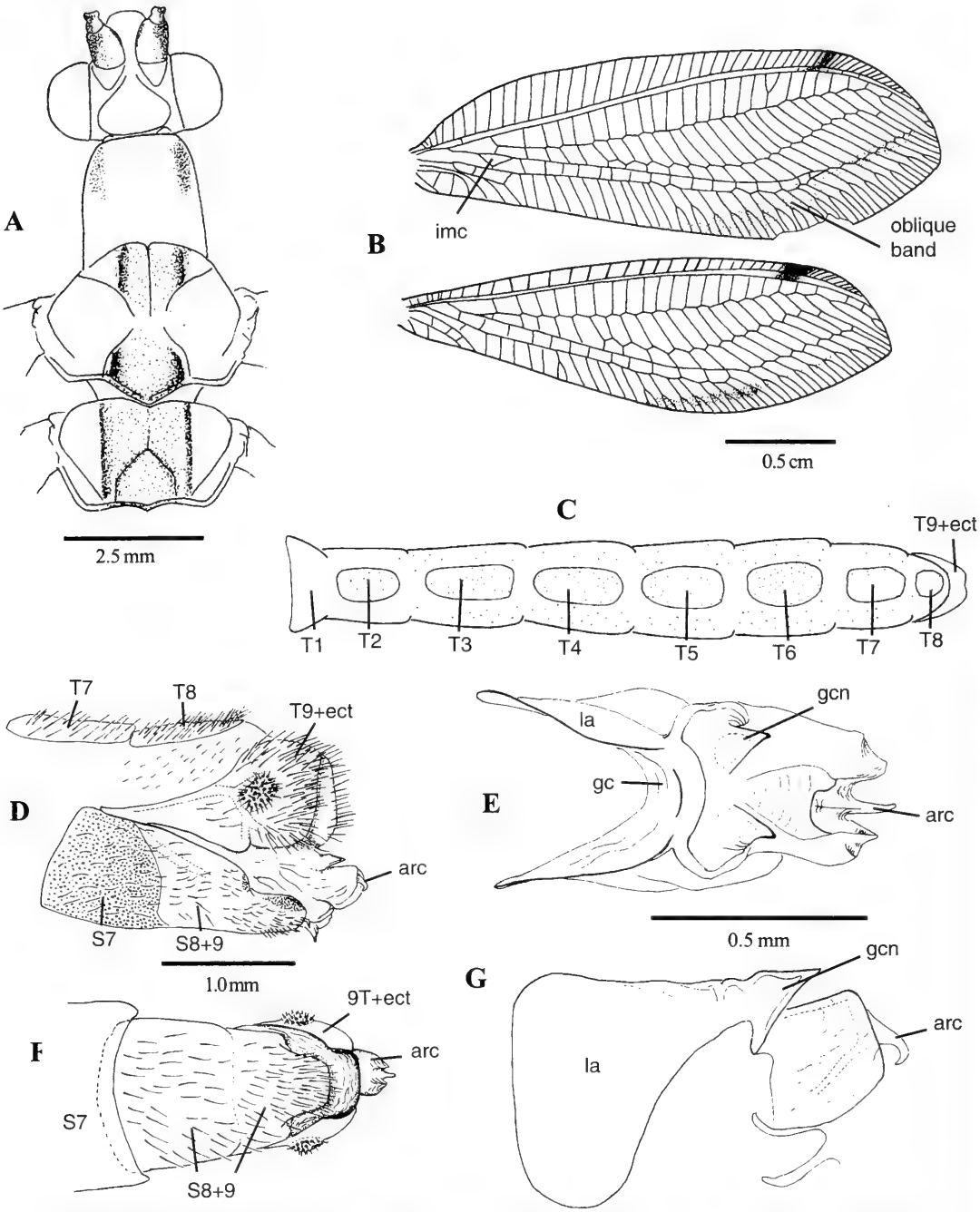

FIGURE 41. *Leucochrysa* (*Leucochrysa*) *boxi* Navás, 1930. A. Head and prothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Apex of male abdomen, lateral view; E. Male genitalia dorsal; F. Sternite 8 + 9; G. Male genitalia, lateral view.

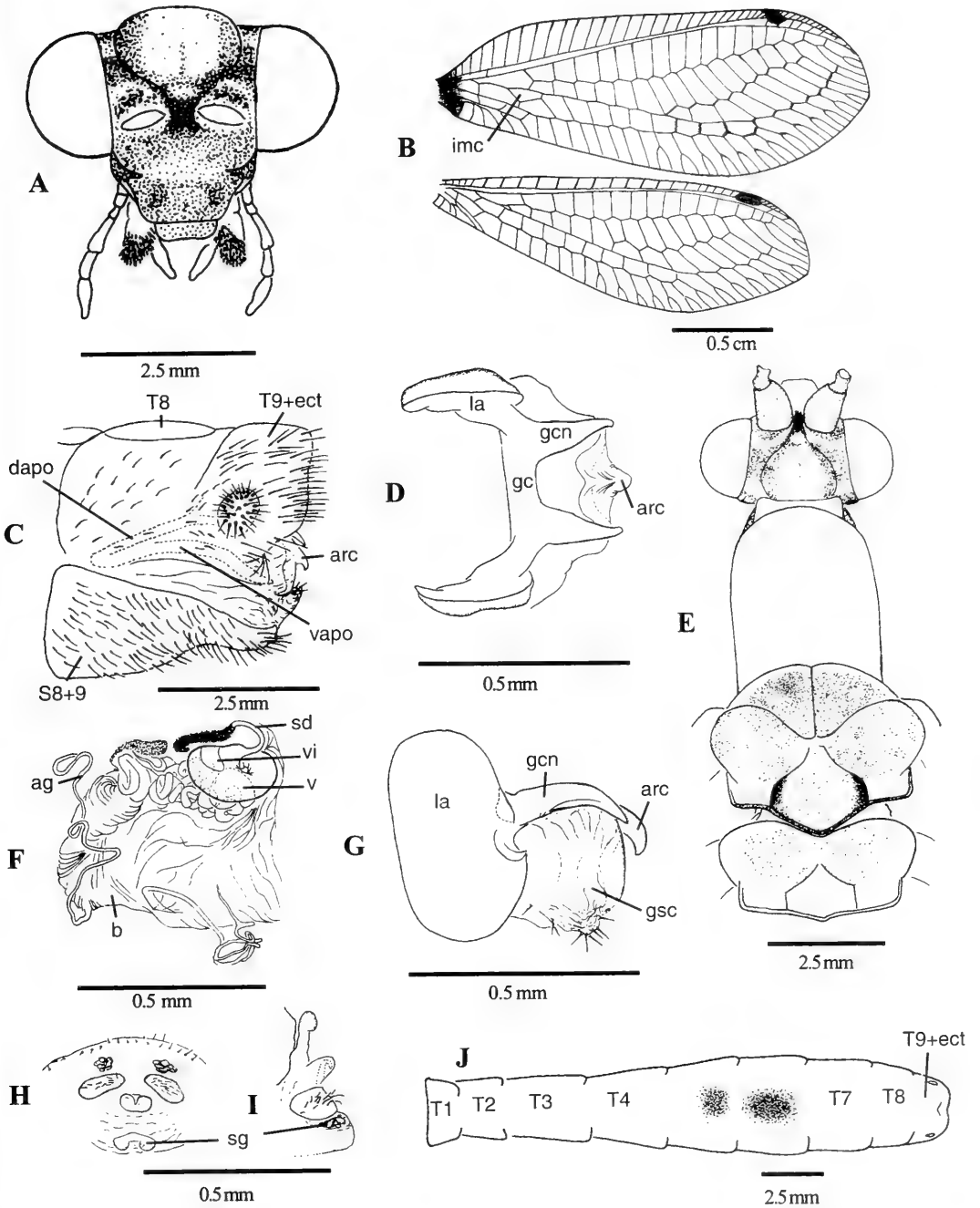

FIGURE 42. *Leucochrysa* (*Leucochrysa*) *pretiosa* (Banks, 1910). A. Head, frontal view; B. Wings; C. Apex of abdomen, lateral view; D. Male genitalia, dorsal view; E. Head and prothorax, dorsal view; F. Female genitalia; G. Male genitalia, lateral view; H. Subgenitale, dorsal view; I. Subgenitale, lateral view; J. Abdomen, dorsal view.

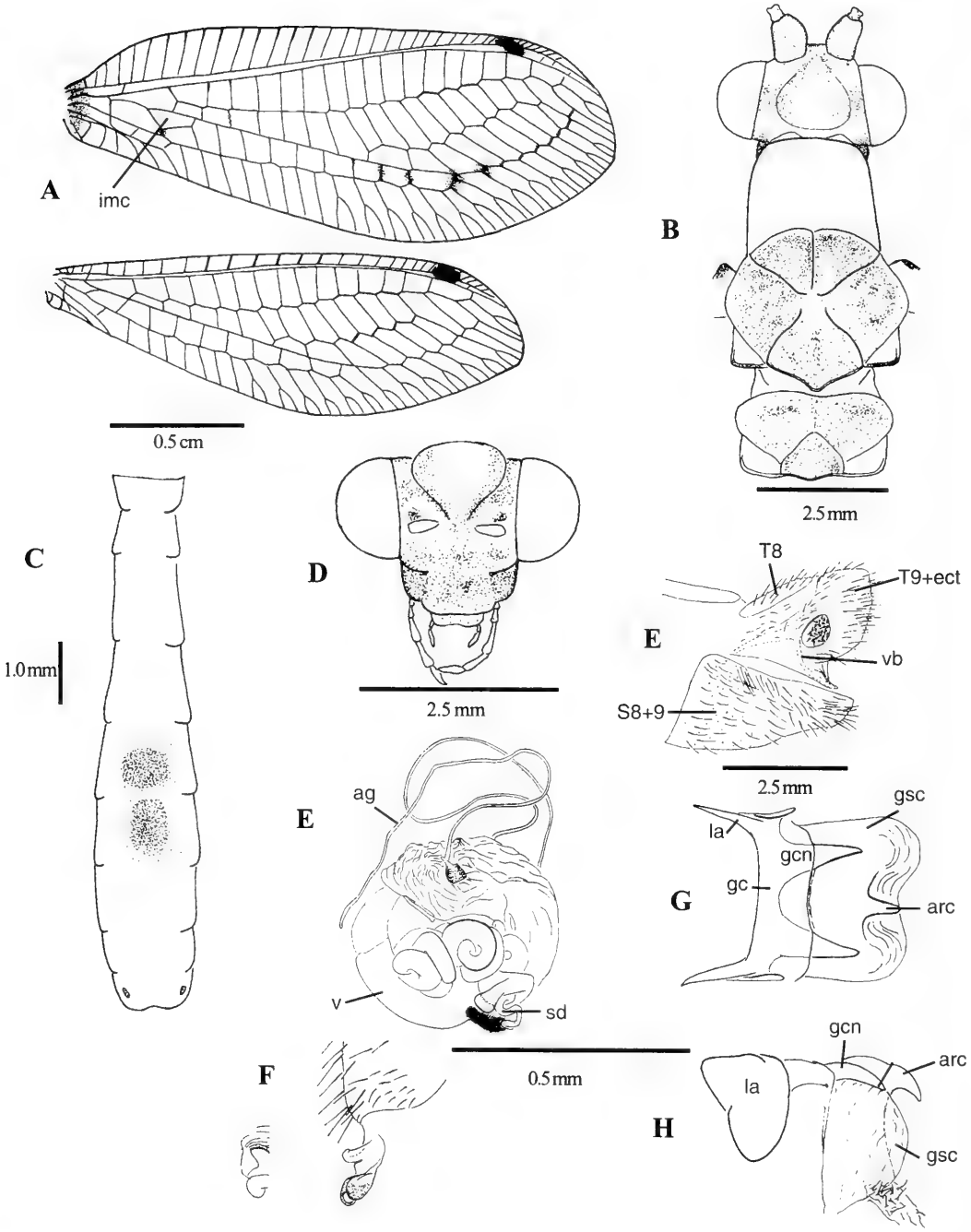

FIGURE 43. *Leucochrysa* (*Leucochrysa*) *varia* (Schneider, 1851). A. Wings; B. Head and pro- and mesothorax, dorsal view; C. Abdomen, dorsal view; D. Head, frontal view; E. Female genitalia; F. Subgenitale; G. Male genitalia, dorsal view; H. Male genitalia, lateral view.

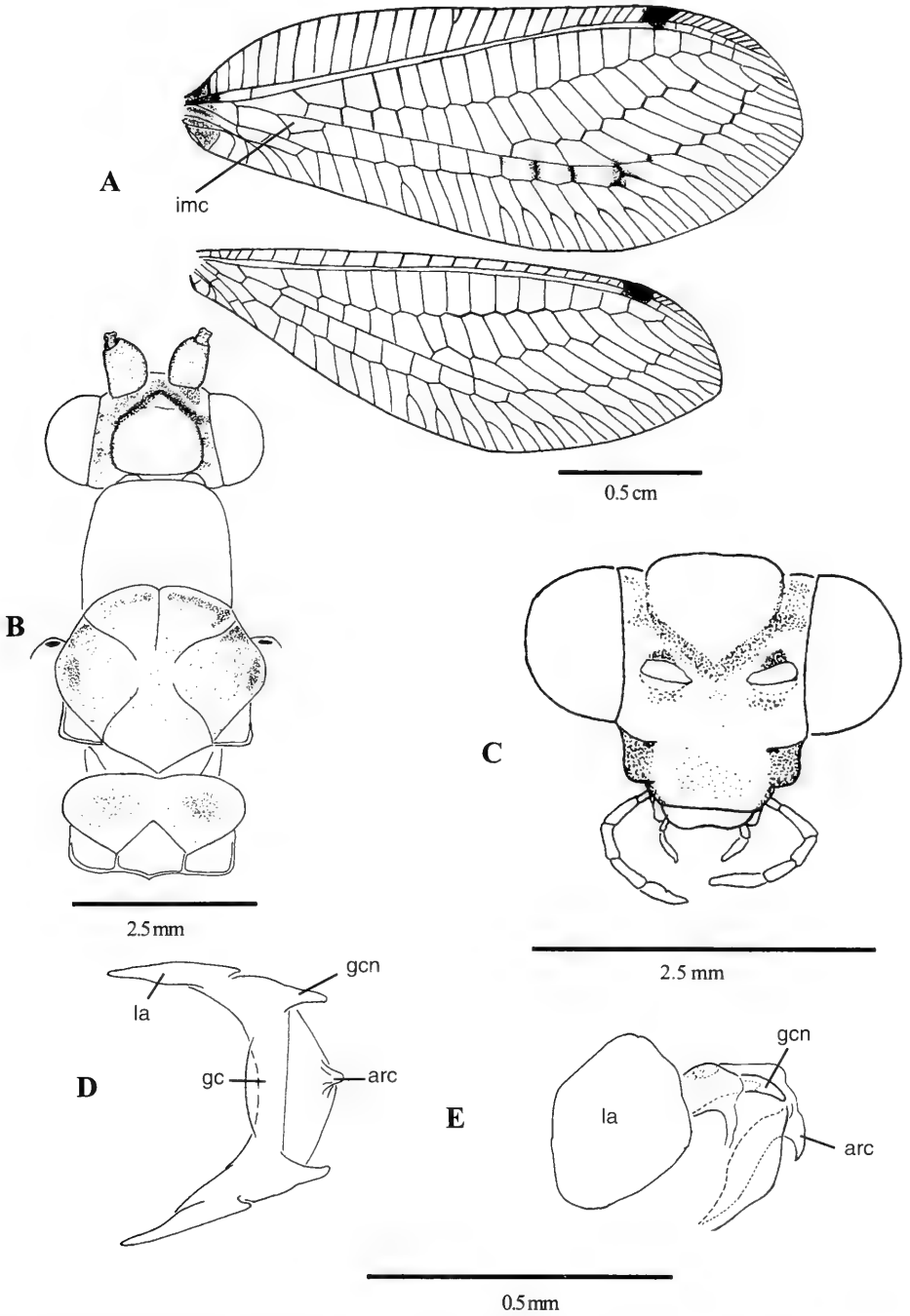

FIGURE 44. *Leucochrysa* (*Leucochrysa*) *walkerina* Navás, 1913. A. Wings; B. Head, pro- and mesothorax, dorsal view; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view.

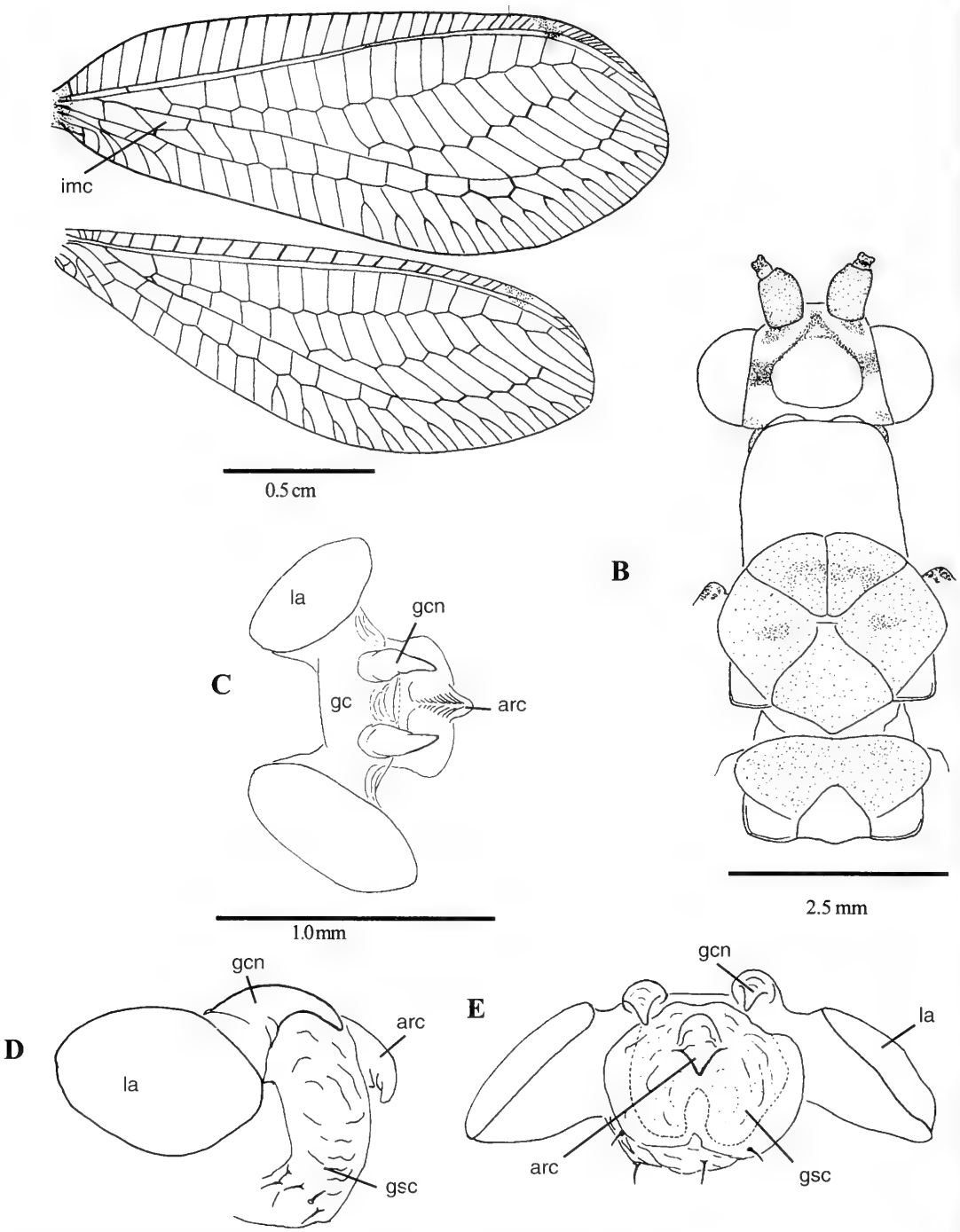

FIGURE 45. *Leucochrysa* (*Leucochrysa*) *bruneolus*, new species. A. Wings; B. Head, pro- and mesothorax, dorsal view; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Male genitalia, caudal view.

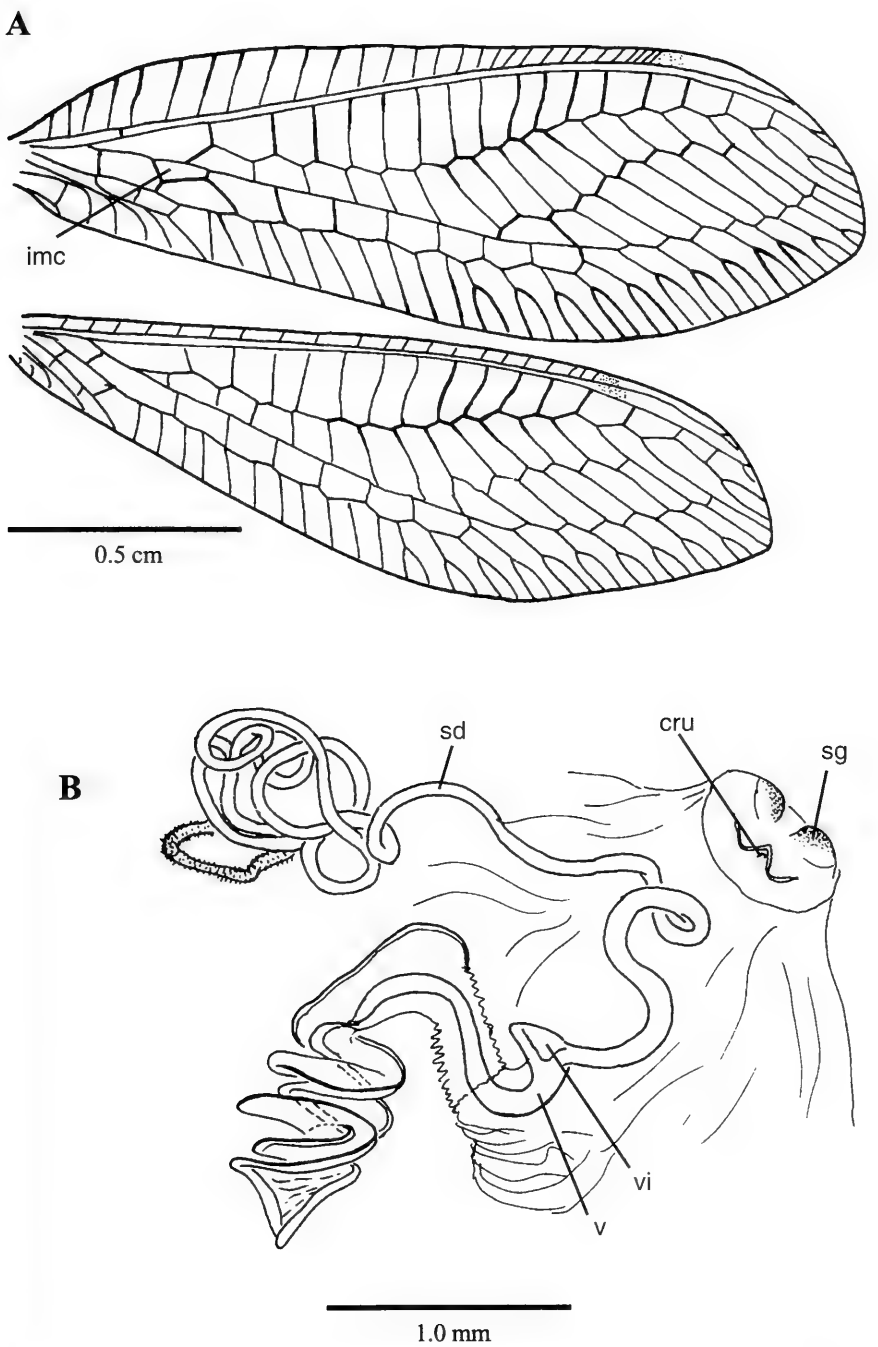

FIGURE 46. *Leucochrysa* (*Leucochrysa*) *catarinae* new species. A. Wings; B. Female genitalia.

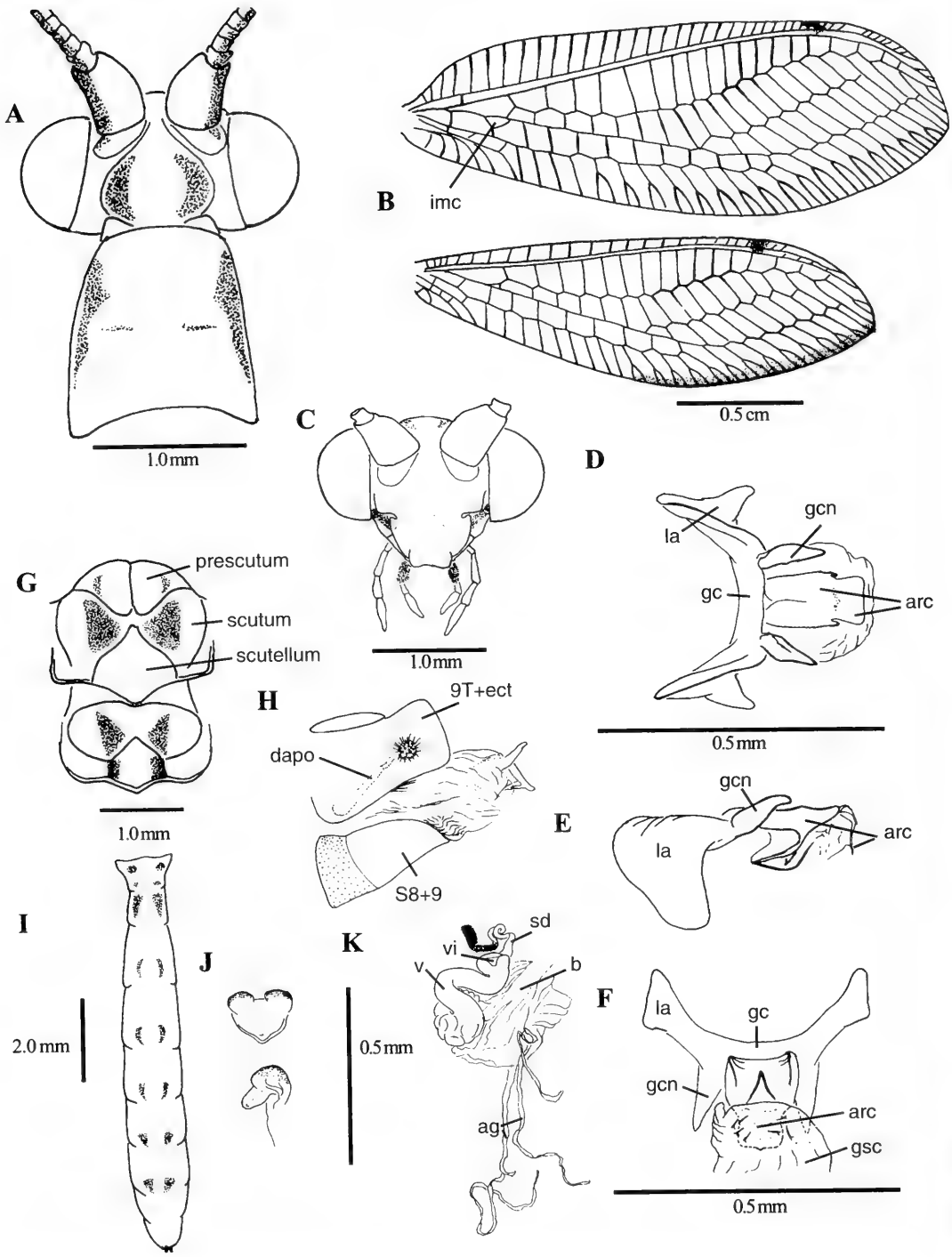

FIGURE 47. *Leucochrysa* (*Nodita*) *camposi* Navás, 1933. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Male genitalia, ventral view; G. Meso- and metanotum; H. Apex of abdomen, lateral view; I. Abdomen, dorsal view; J. Subgenitale; K. Female genitalia.

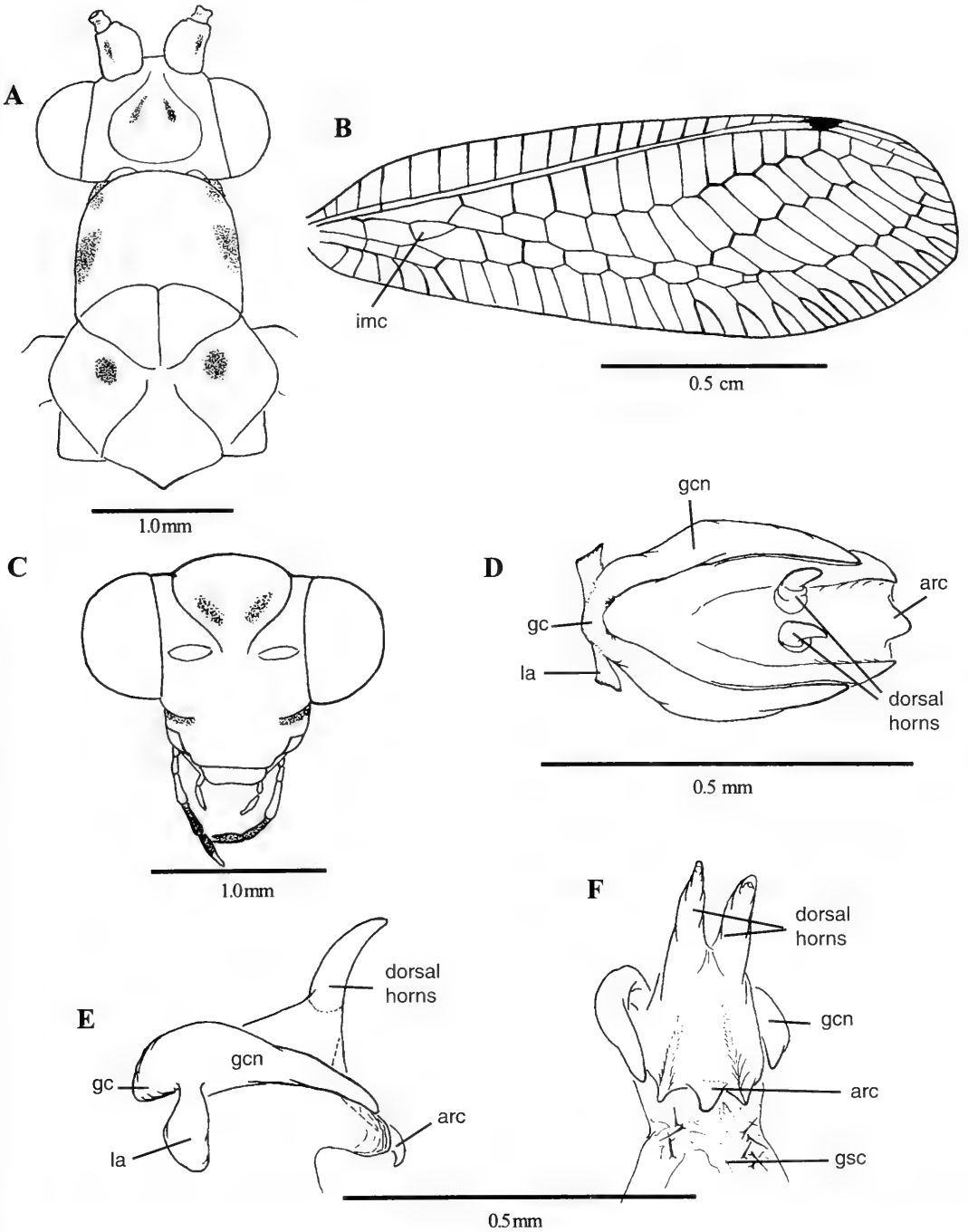

FIGURE 48. *Leucochrysa* (*Nodita*) *clepsydra* Banks, 1918. A. Head and prothorax, dorsal view; B. Forewing; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Male genitalia, caudal view.

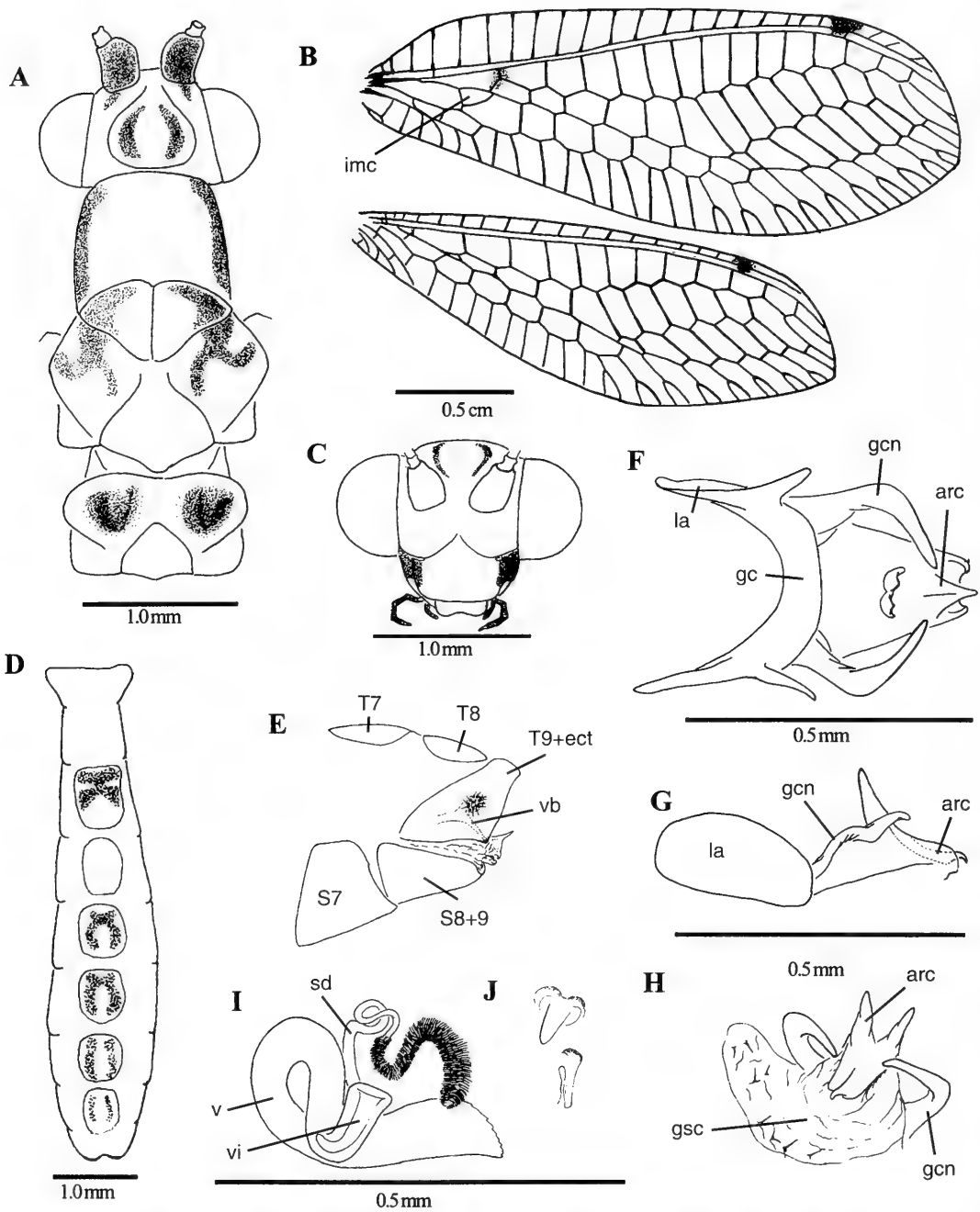

FIGURE 49. *Leucochrysa* (*Nodita*) *cruentata* (Schneider, 1851). A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Abdomen, dorsal view; E. Apex of male abdomen, lateral view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Male genitalia, caudal view; I. Spermatheca; J. Subgenitale.

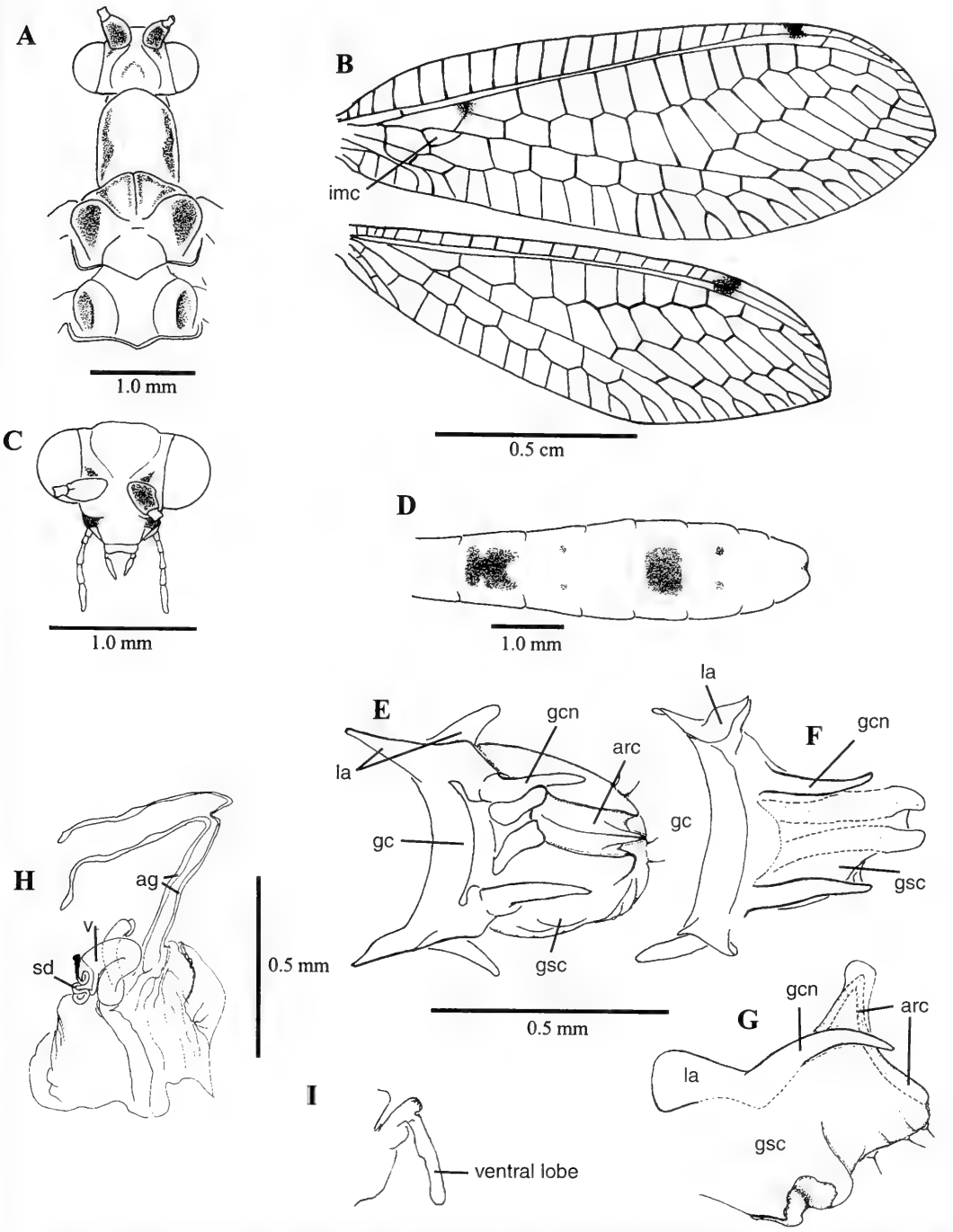

FIGURE 50. *Leucochrysa* (*Nodita*) *gossei* (Kimmins, 1940). A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Abdomen, dorsal view; E. Male genitalia, dorso-caudal view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Female genitalia; I. Subgenitale.

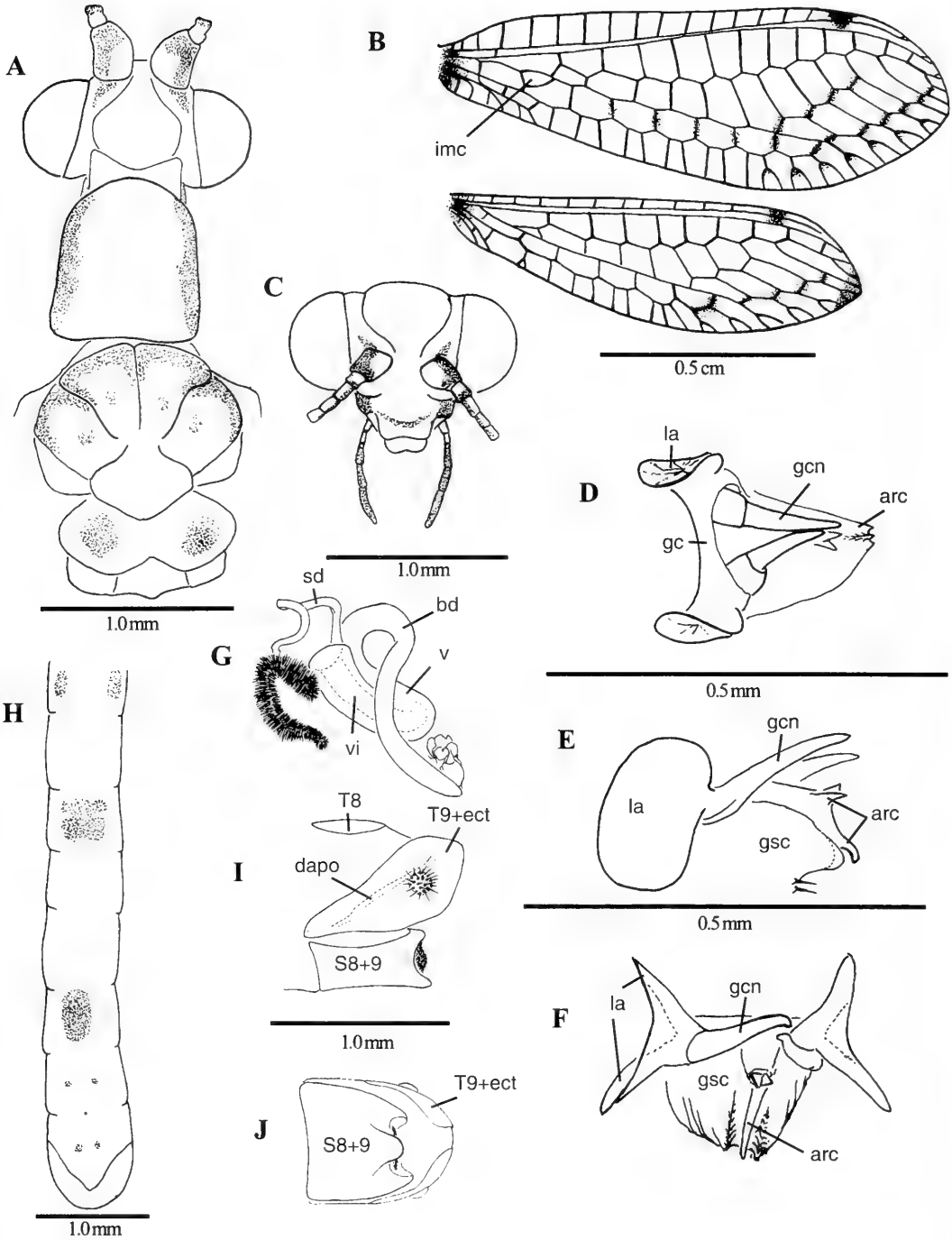

FIGURE 51. *Leucochrysa* (*Nodita*) *heriocles* Banks, 1944. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Male genitalia, caudal view; G. Spermatheca; H. Abdomen, dorsal view; I. Apex of male abdomen, lateral view; J. Sternite 8 + 9.

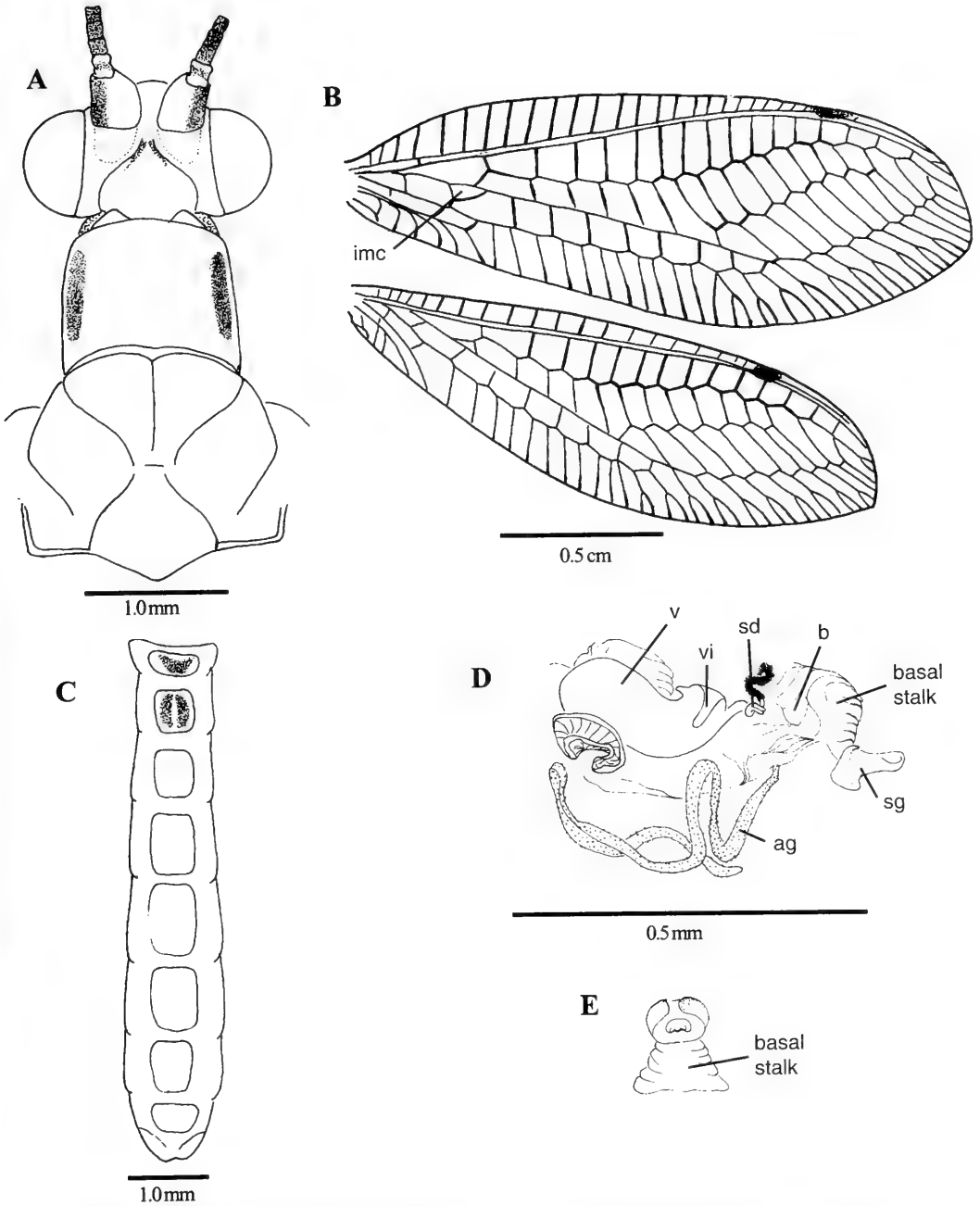

FIGURE 52. *Leucochrysa* (*Nodita*) *intermedia* (Schneider, 1851). A. Head and prothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Female genitalia; E. Subgenitale.

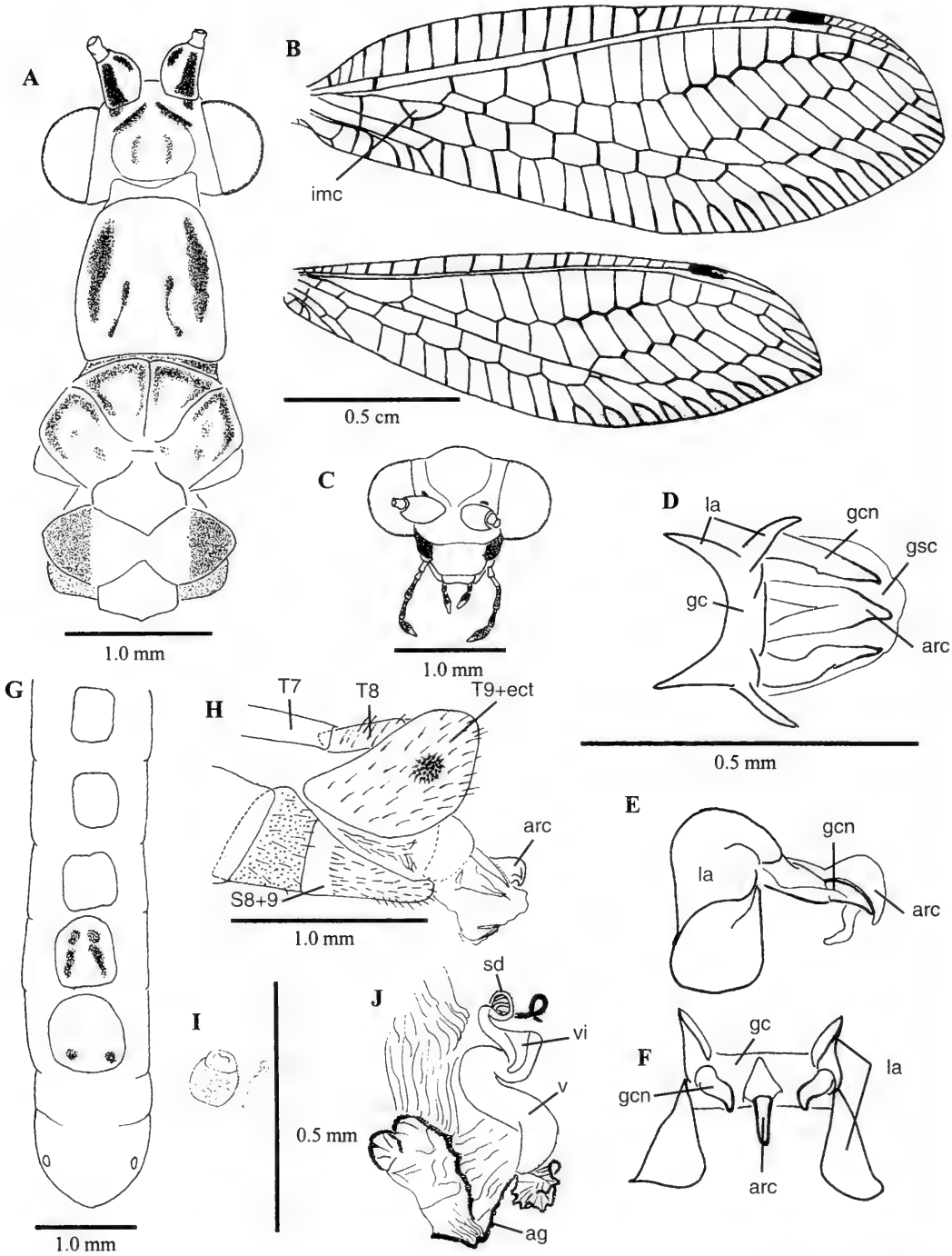

FIGURE 53. *Leucochrysa* (*Nodita*) *lancala* Banks, 1944. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Male genitalia, caudal view; G. Abdomen, dorsal view; H. Apex of male abdomen, lateral view; I. Subgenitale; J. Spermatheca.

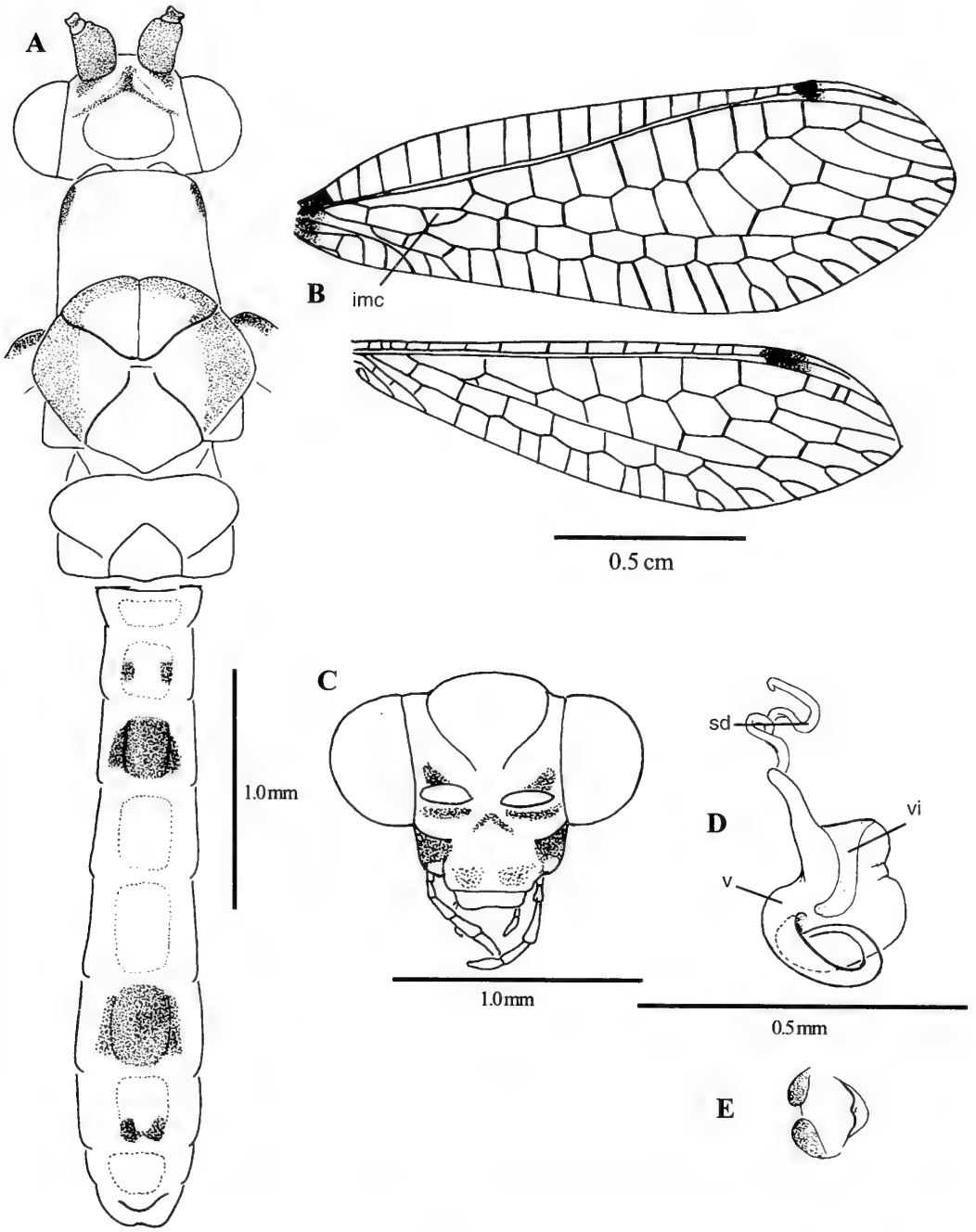

FIGURE 54. *Leucochrysa* (*Nodita*) *lateralis* Navás, 1913. A. Head, thorax and abdomen, dorsal view; B. Wings; C. Head, frontal view; D. Spermatheca; E. Subgenitale.

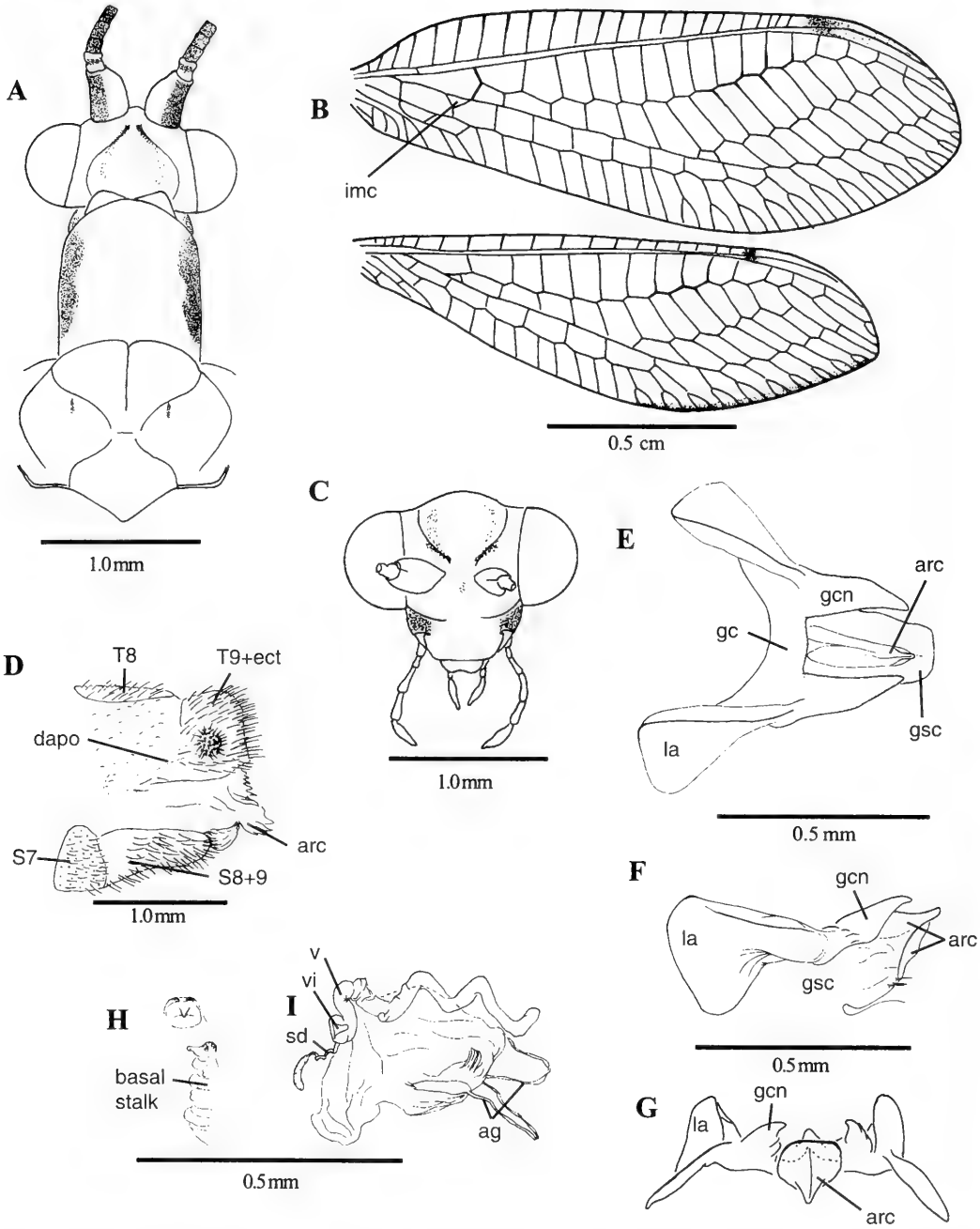

FIGURE 55. *Leucochrysa* (*Nodita*) *marginalis* (Banks, 1915). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of male abdomen, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Male genitalia, caudal view; H. Subgenitale; I. Female genitalia.

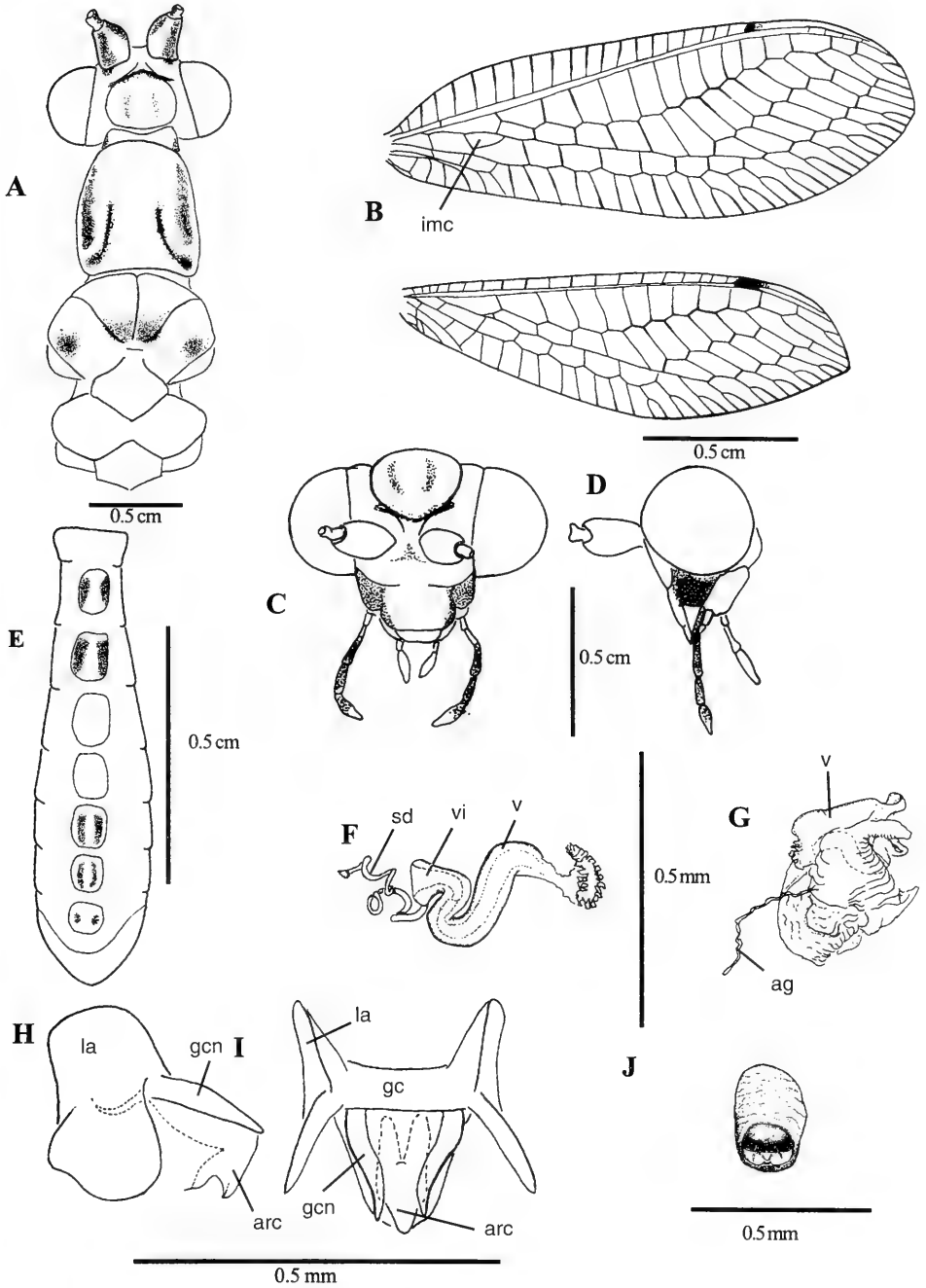

FIGURE 56. *Leucochrysa* (*Nodita*) *marquezi* Navás, 1917. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head, lateral view; E. Abdomen, dorsal view; F. Spermatheca; G. Female genitalia; H. Male genitalia, lateral view; I. Male genitalia, dorsal view; J. Subgenitale.

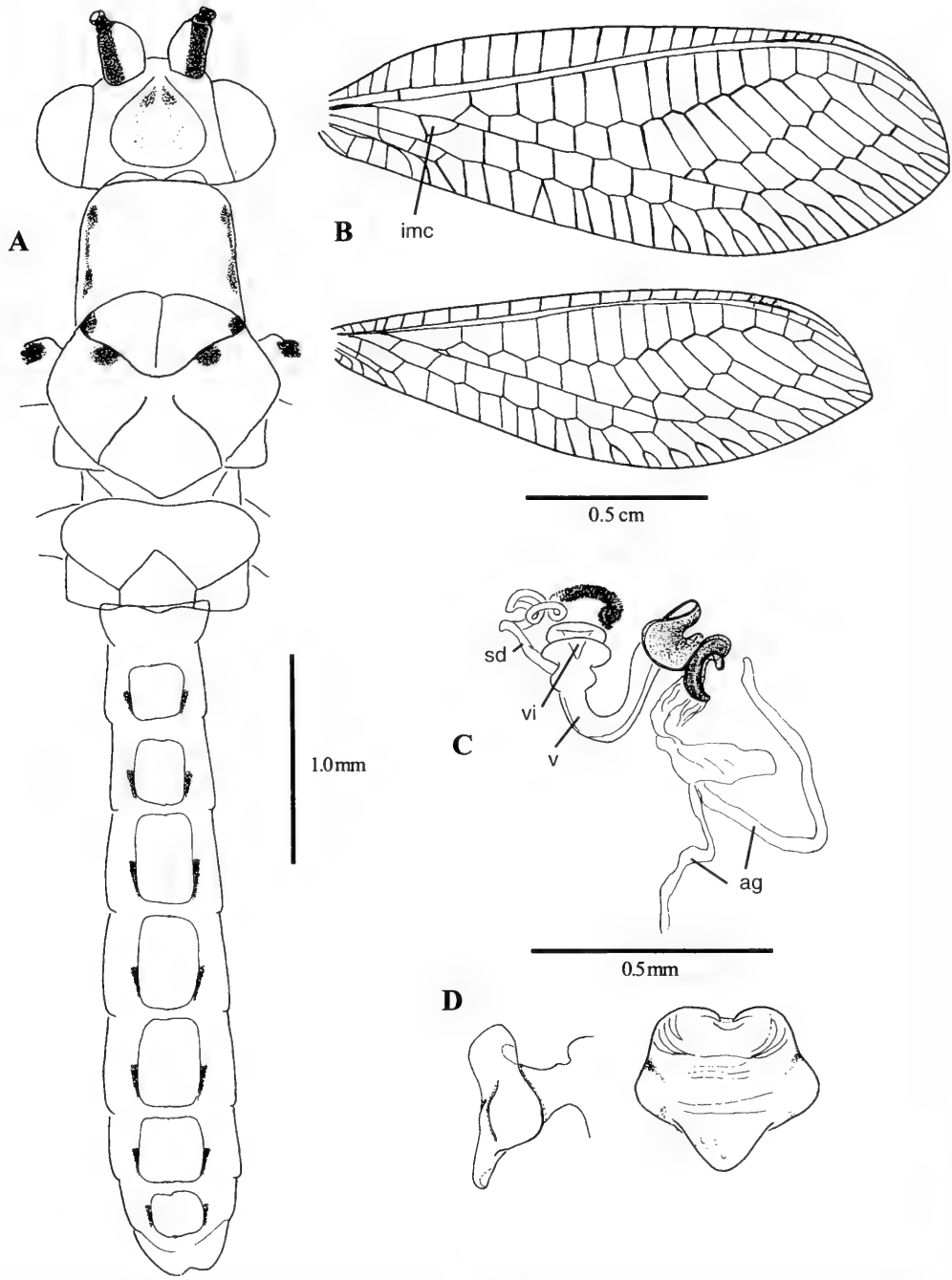

FIGURE 57. *Leucochrysa* (*Nodita*) *melanocera* Navás, 1916. A. Head, prothorax and abdomen, dorsal view; B. Wings; C. Female genitalia; D. Subgenitale.

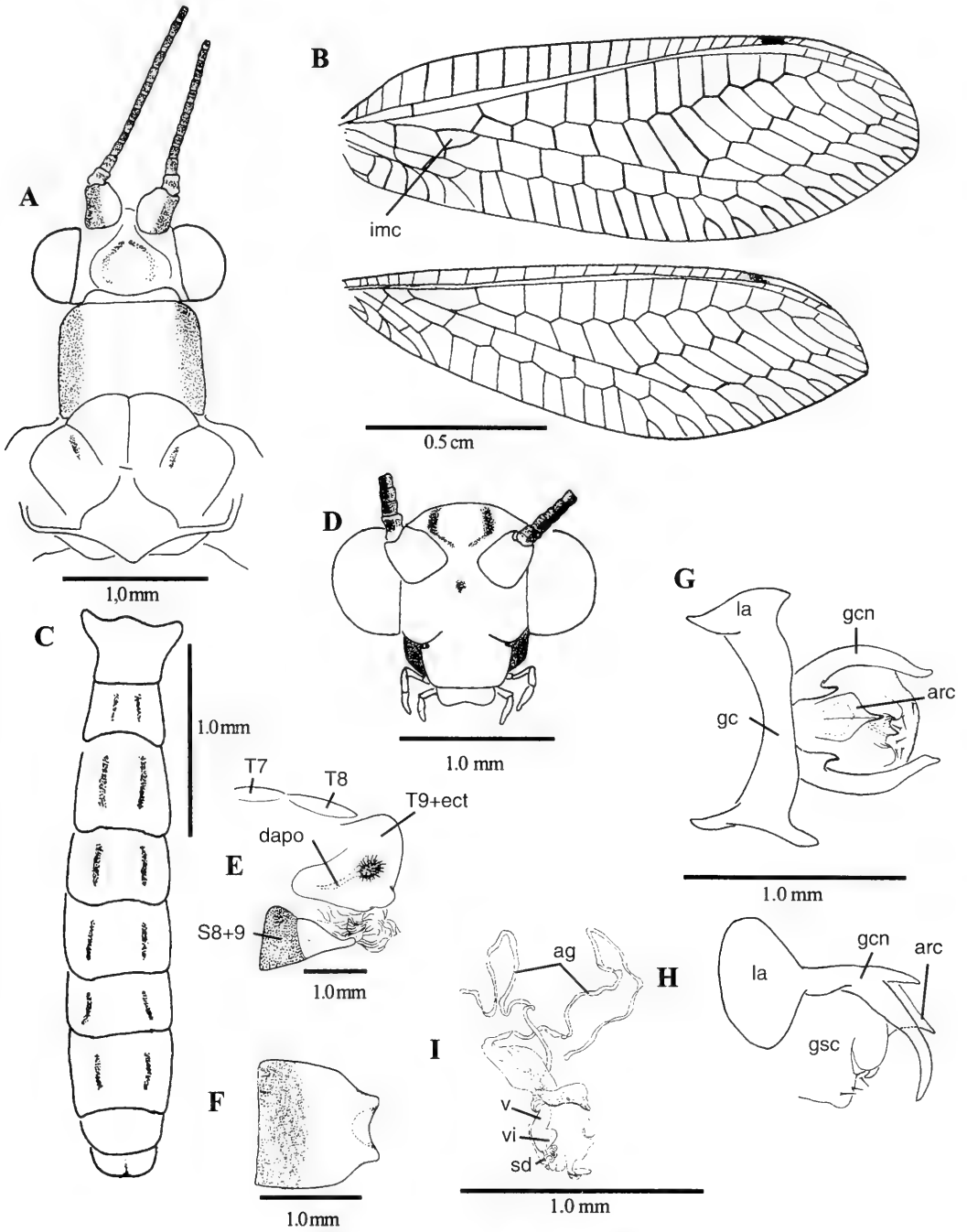

FIGURE 58. *Leucochrysa* (*Nodita*) *rodriguezi* (Navás, 1913) A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Apex of male abdomen, lateral view; F. Sternite 8 + 9; G. Male genitalia, dorsal view; H. Male genitalia, lateral view.

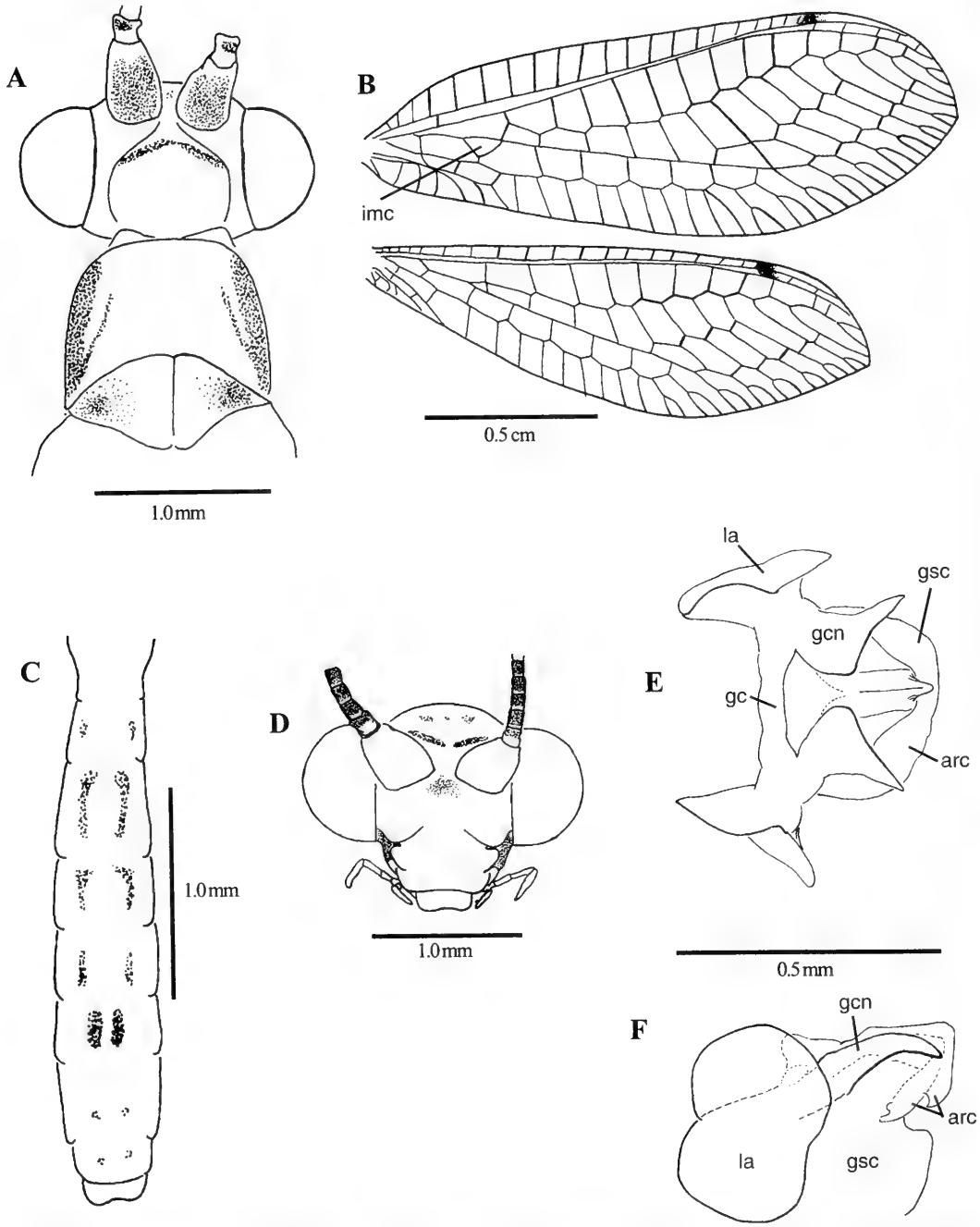

FIGURE 59. *Leucochrysa* (*Nodita*) *affinis*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

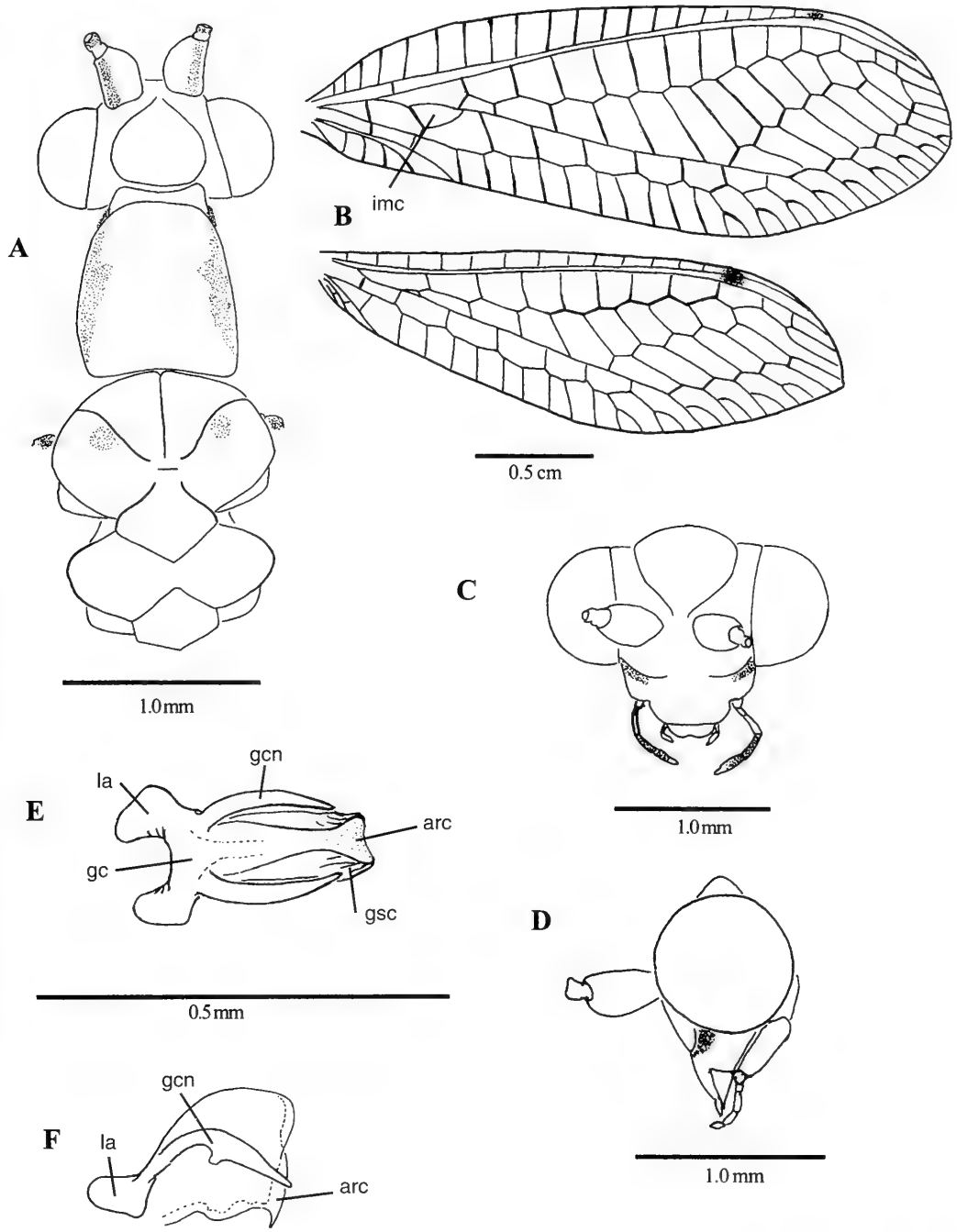

FIGURE 60. *Leucochrysa* (*Nodita*) *barrei*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

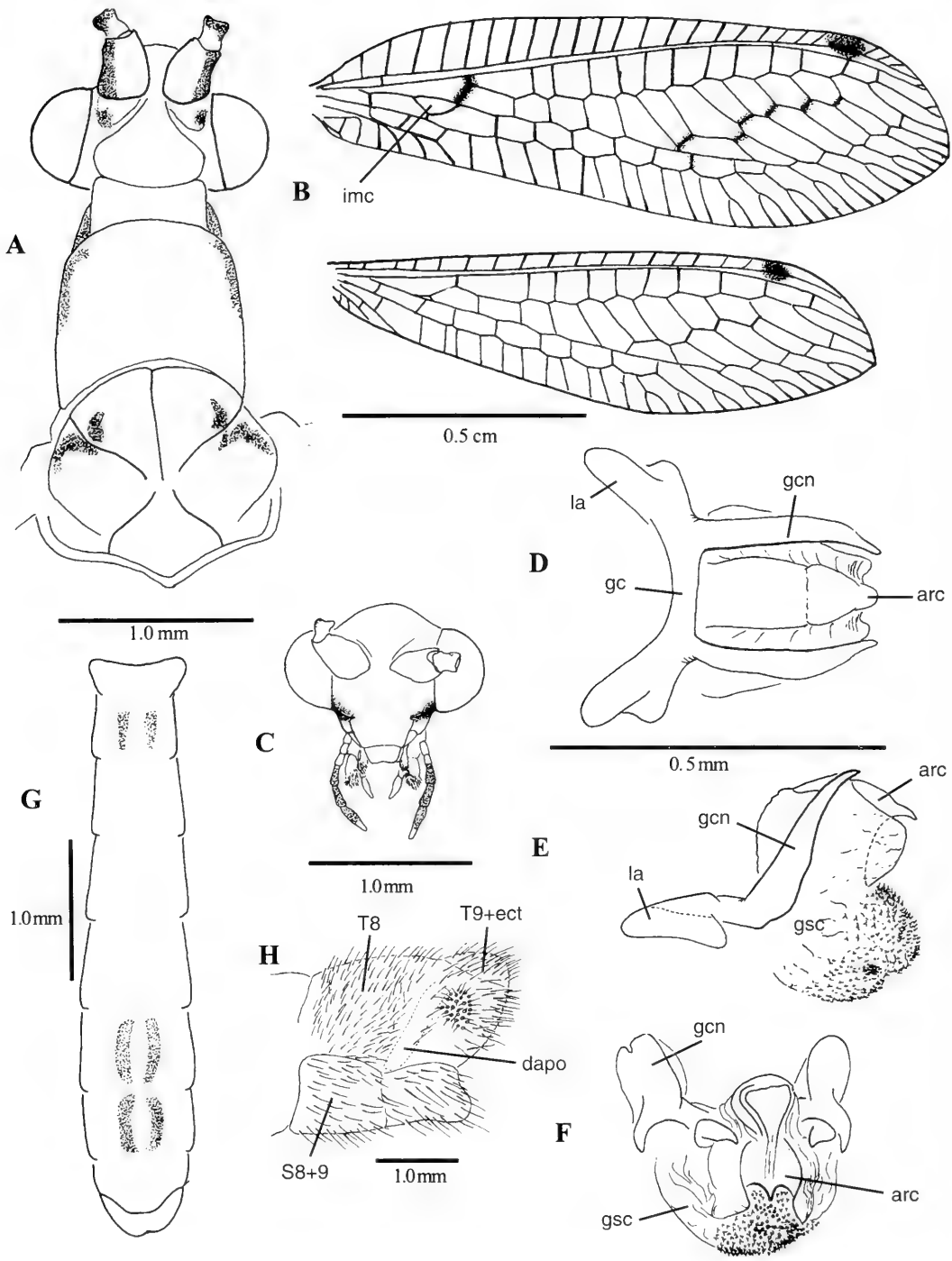

FIGURE 61. *Leucochrysa* (*Nodita*) *confusa*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Male genitalia, caudal view; G. Abdomen, dorsal view; H. Apex of male abdomen, lateral view.

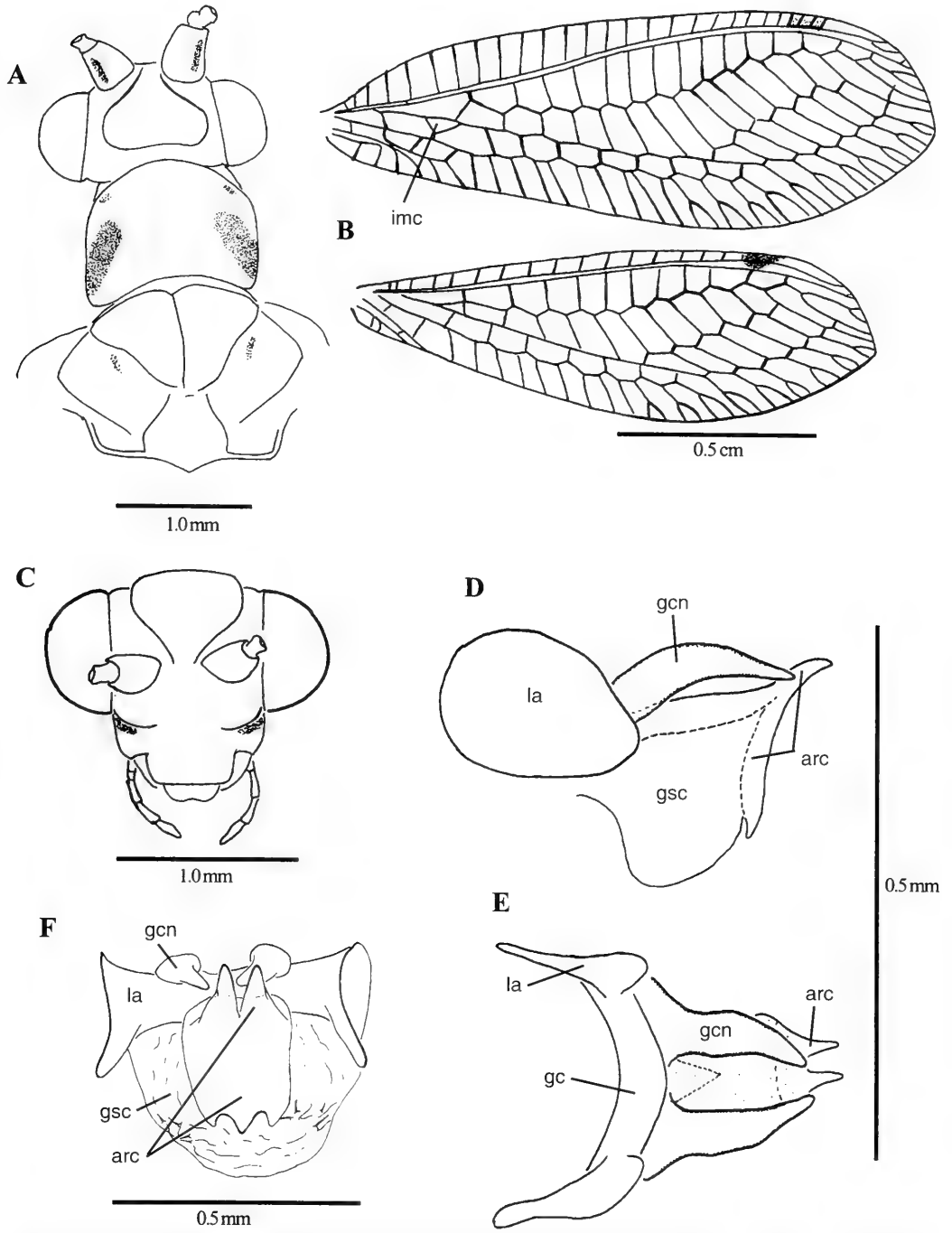

FIGURE 62. *Leucochrysa* (*Nodita*) *cornuta*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male genitalia, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, caudal view.

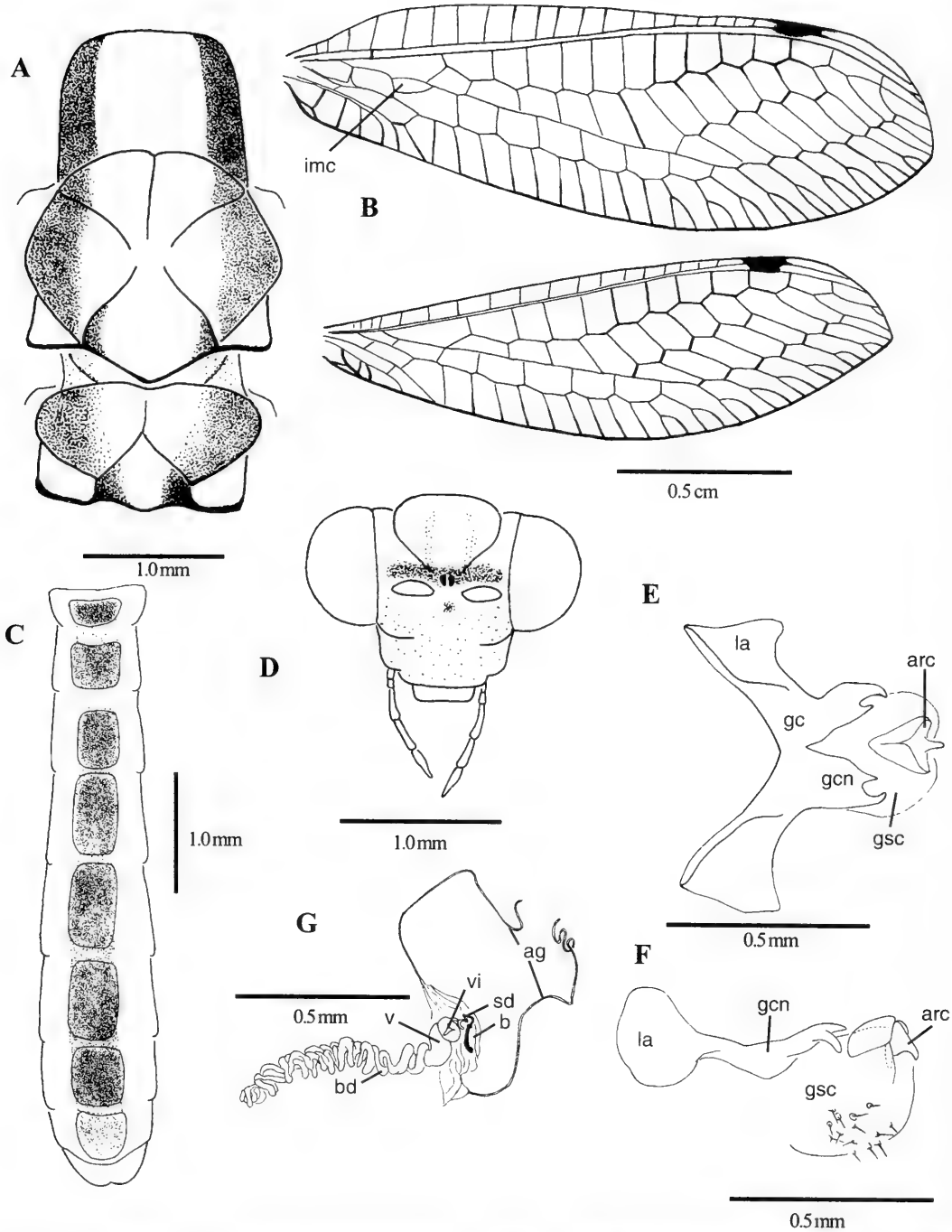

FIGURE 63. *Leucochrysa* (*Nodita*) *forciformis*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Female genitalia.

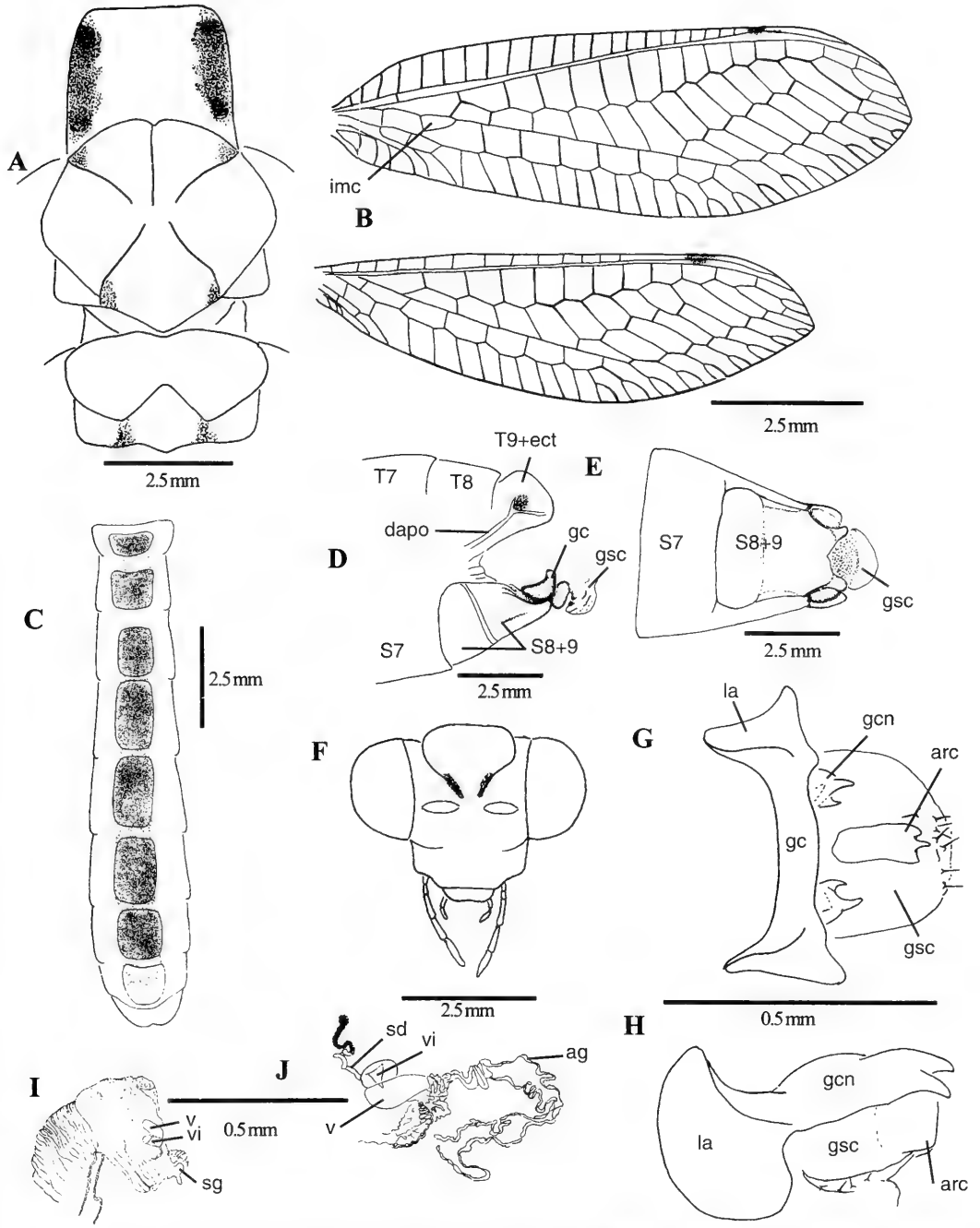

FIGURE 64. *Leucochrysa* (*Nodita*) *furcata*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Apex of male abdomen; E. Sternite 8 + 9; F. Head, frontal view; G. Male genitalia, dorsal view; H. Male genitalia, lateral view; I. Female genitalia; J. Spermatheca.

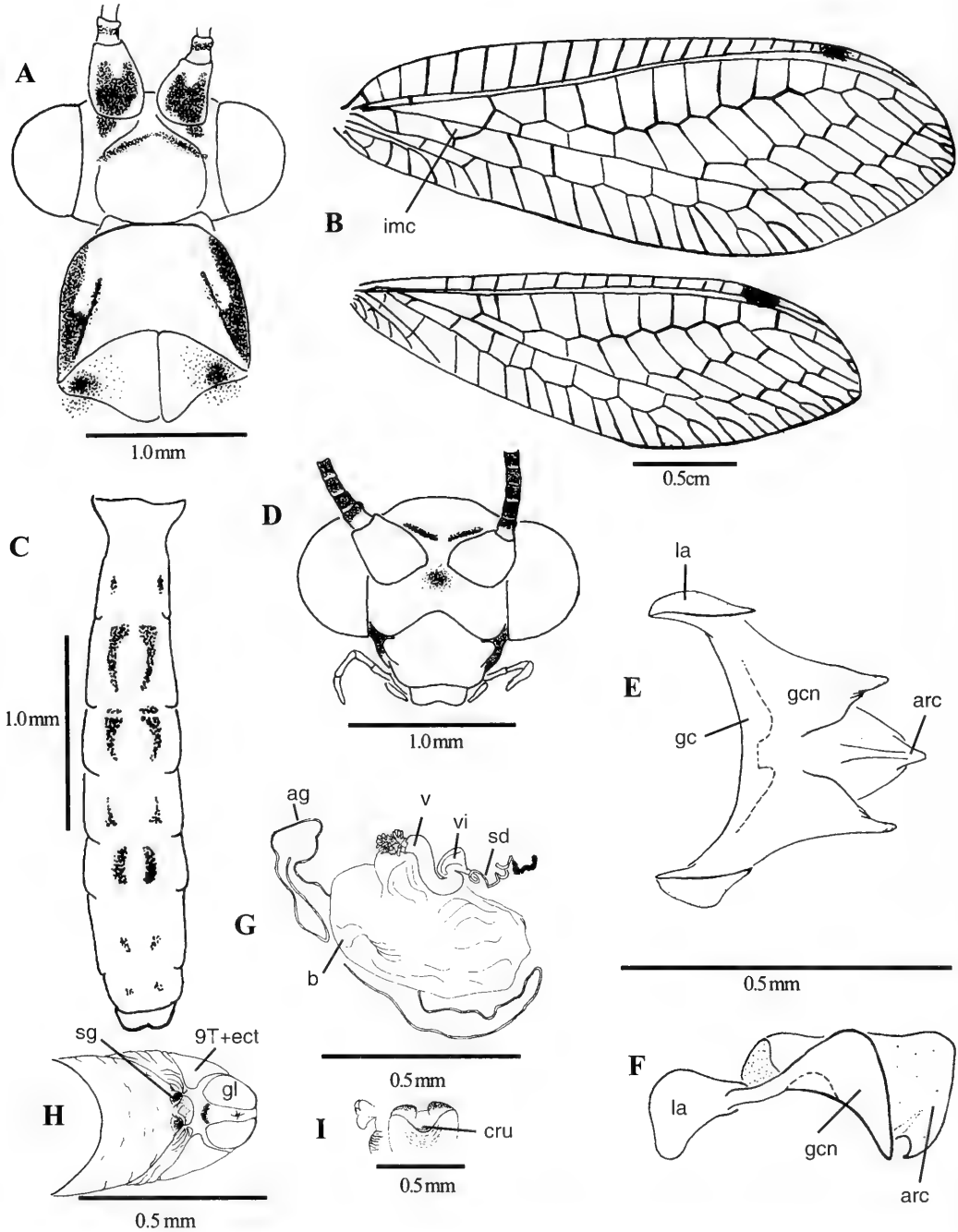

FIGURE 65. *Leucochrysa* (*Nodita*) *guataparensis*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings, C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Female genitalia; I. Subgenitale.

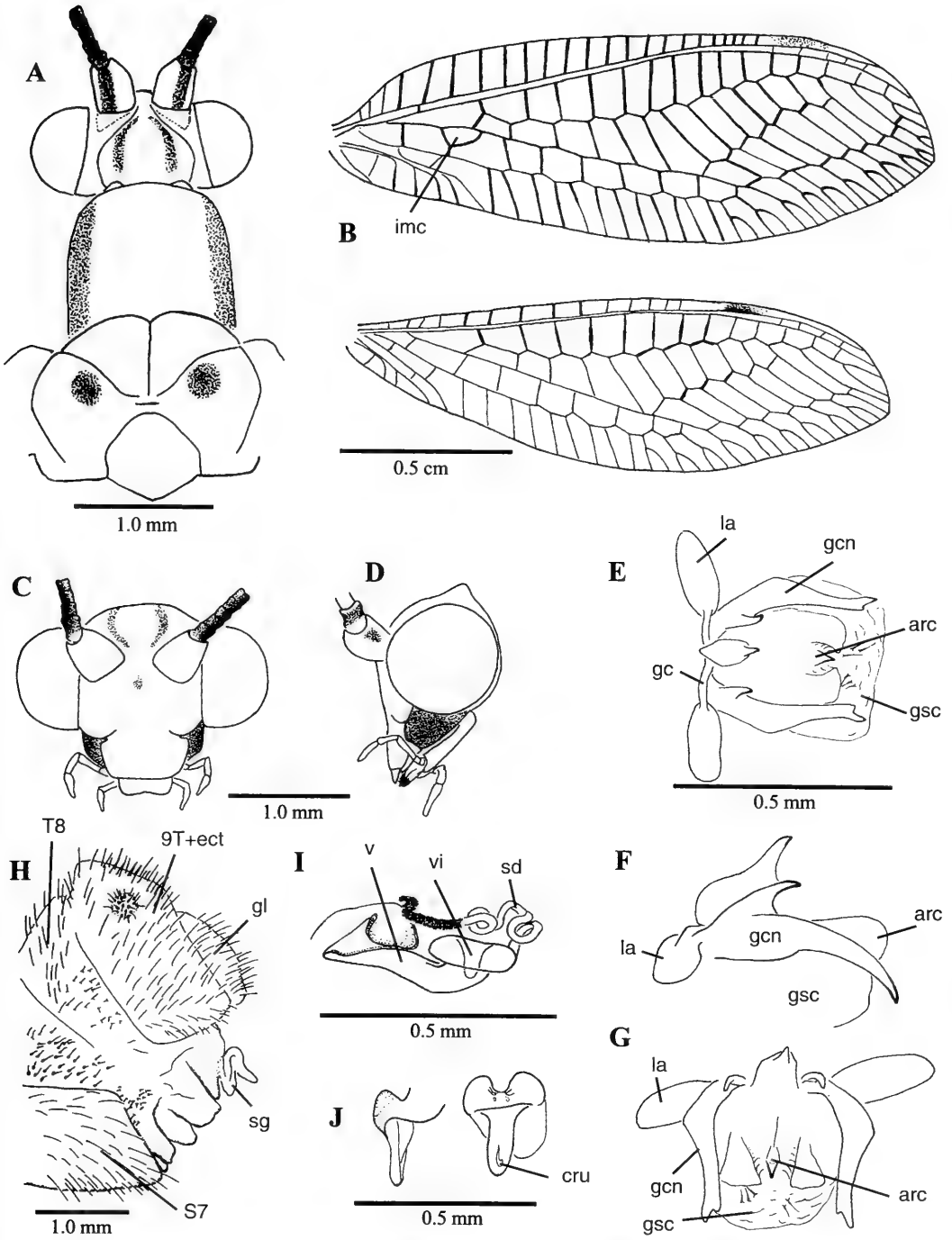

FIGURE 66. *Leucochrysa* (*Nodita*) *ictericus*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head, lateral view; E. Male genitalia, dorsal view, F. Male genitalia, lateral view; G. Male genitalia, caudal view; H. Apex of female abdomen, lateral view; I; Spermatheca; J. Subgenitale.

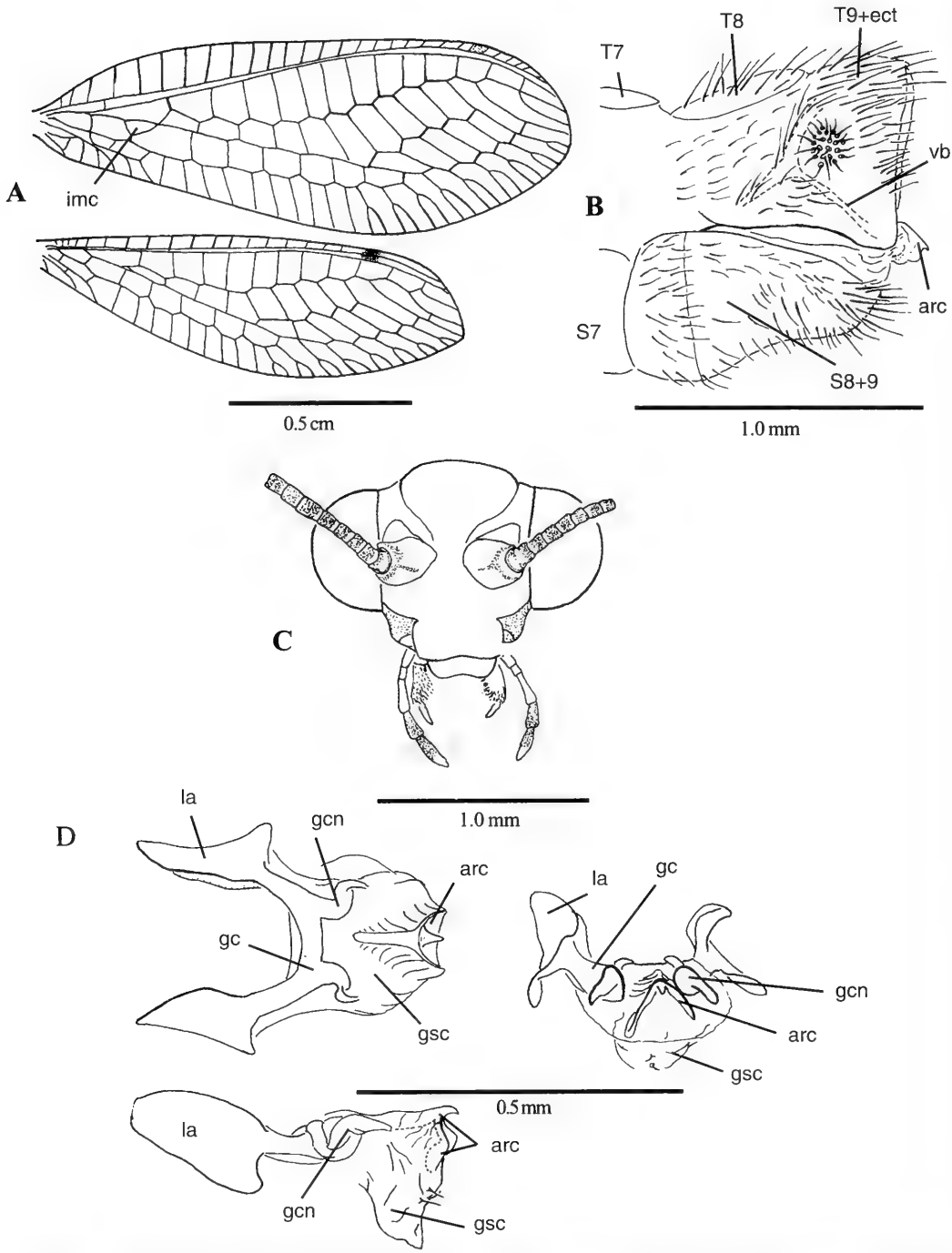

FIGURE 67. *Leucochrysa* (*Nodita*) *incognita*, new species A. Wings; B. Apex of male abdomen, lateral view; C. Head, frontal view; D. Male genitalia, dorsal, lateral and caudal view.

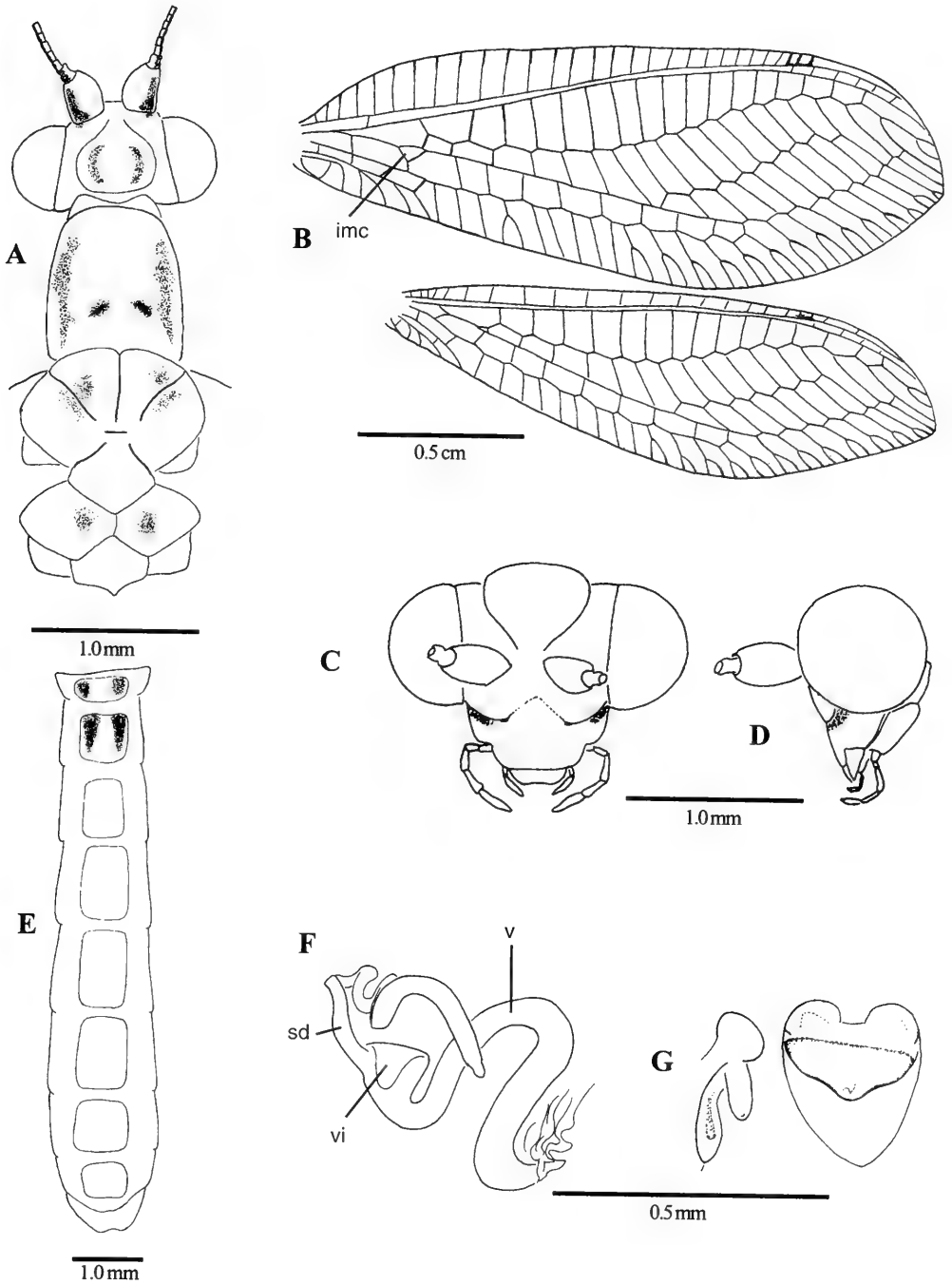

FIGURE 68. *Leucochrysa* (*Nodita*) *interata*, new species. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head, lateral view; E. Abdomen, dorsal view; F. Spermatheca; G. Subgenitale.

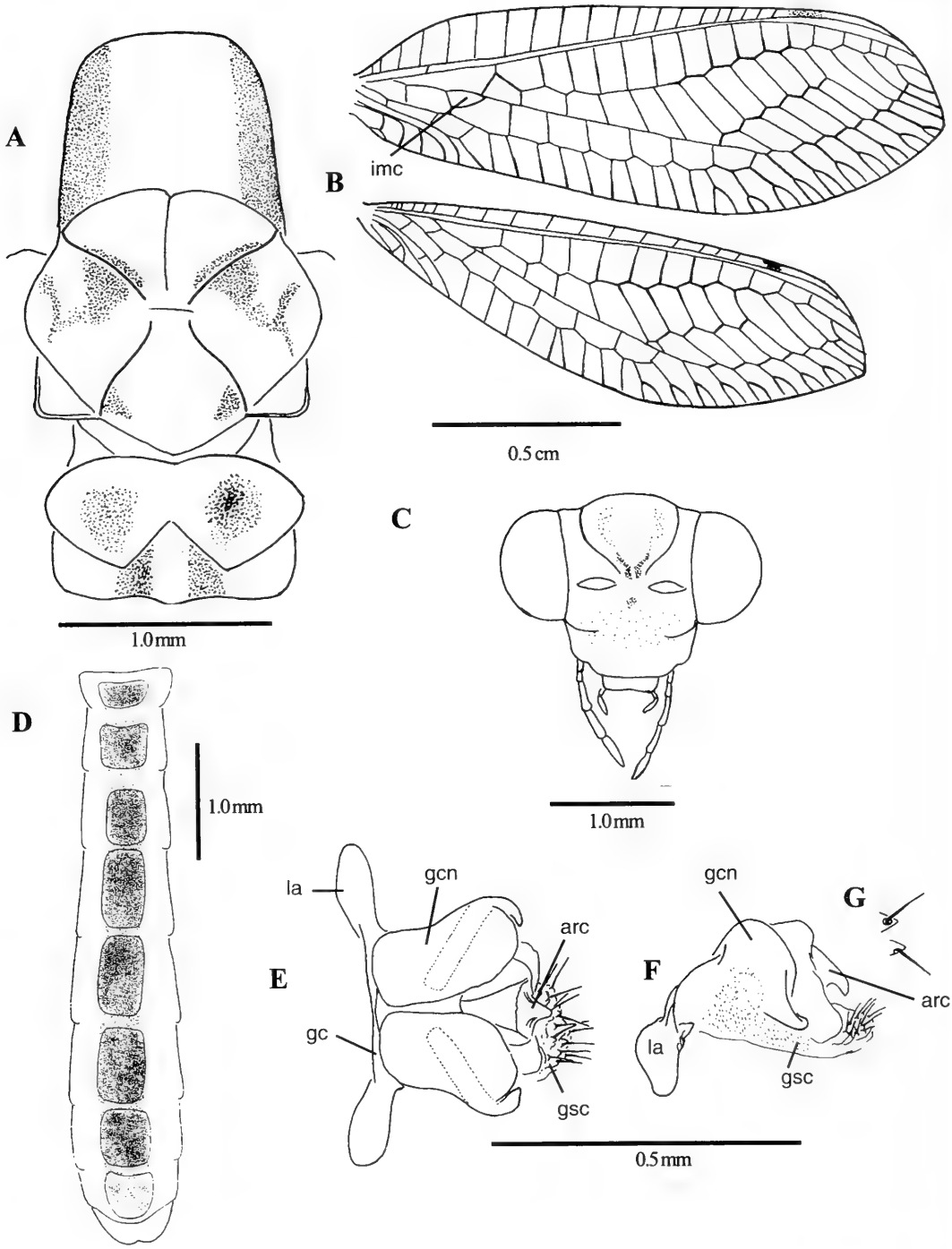

FIGURE 69. *Leucochrysa* (*Nodita*) *lineata*, new species. A. Pro-, meso- and metanota; B. Wings; C. Head, frontal view; D. Abdomen, dorsal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonosetae.

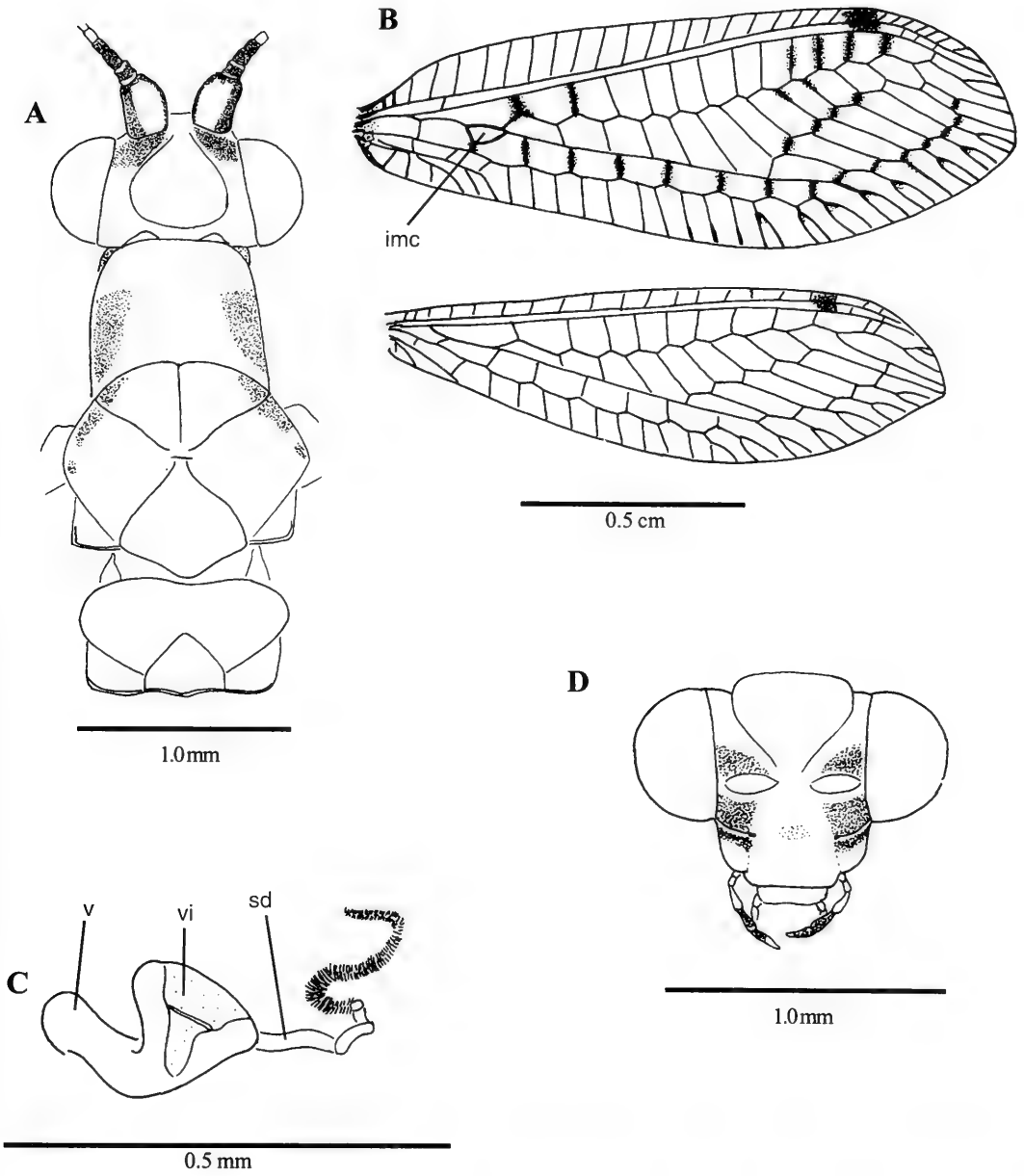

FIGURE 70. *Leucochrysa* (*Nodita*) *maculata* new species. A. Head and thorax, dorsal view; B. Wings; C. Spermatheca; D. Head, frontal view.

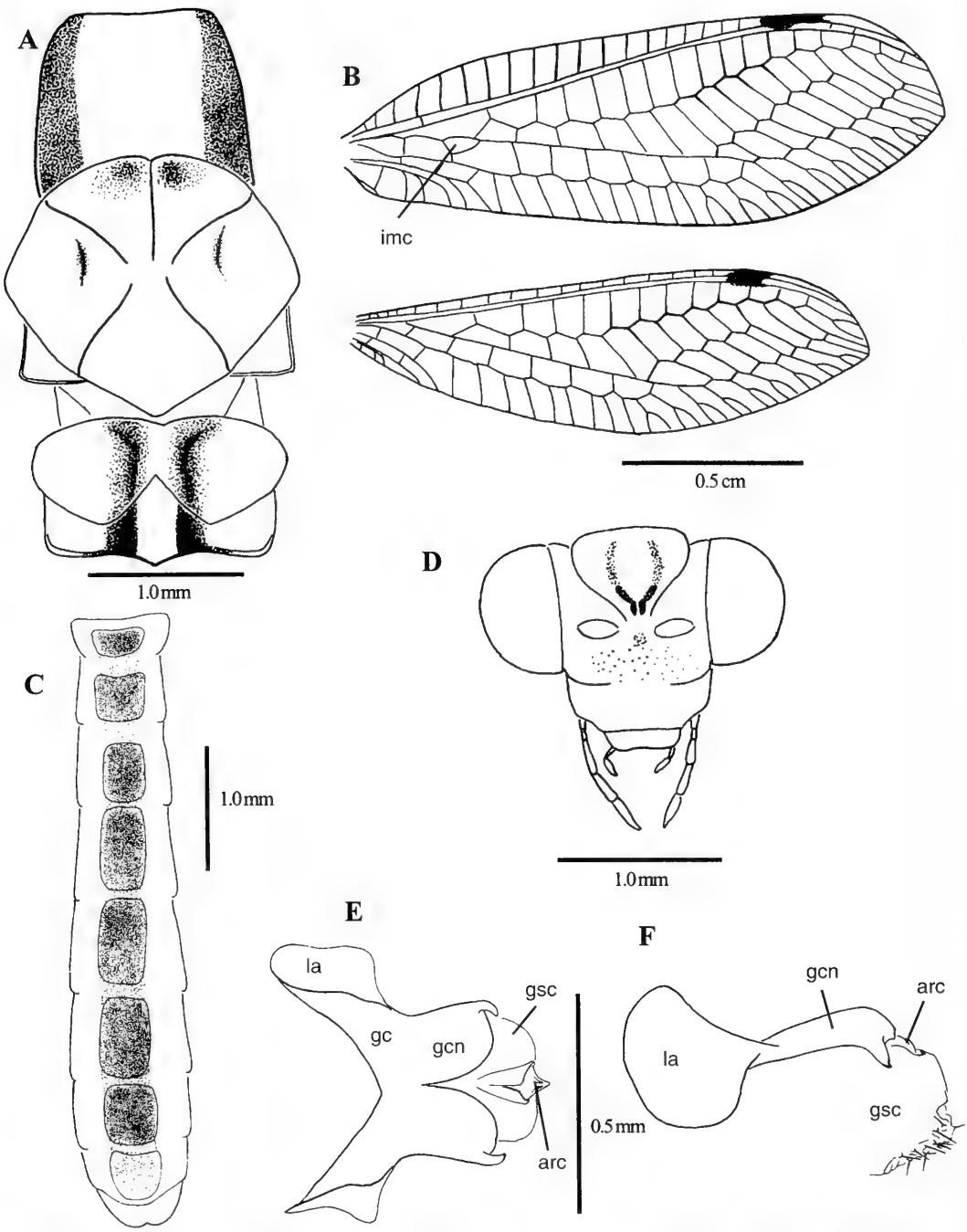

FIGURE 71. *Leucochrysa* (*Nodita*) *michelini*, new species. A.Thorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

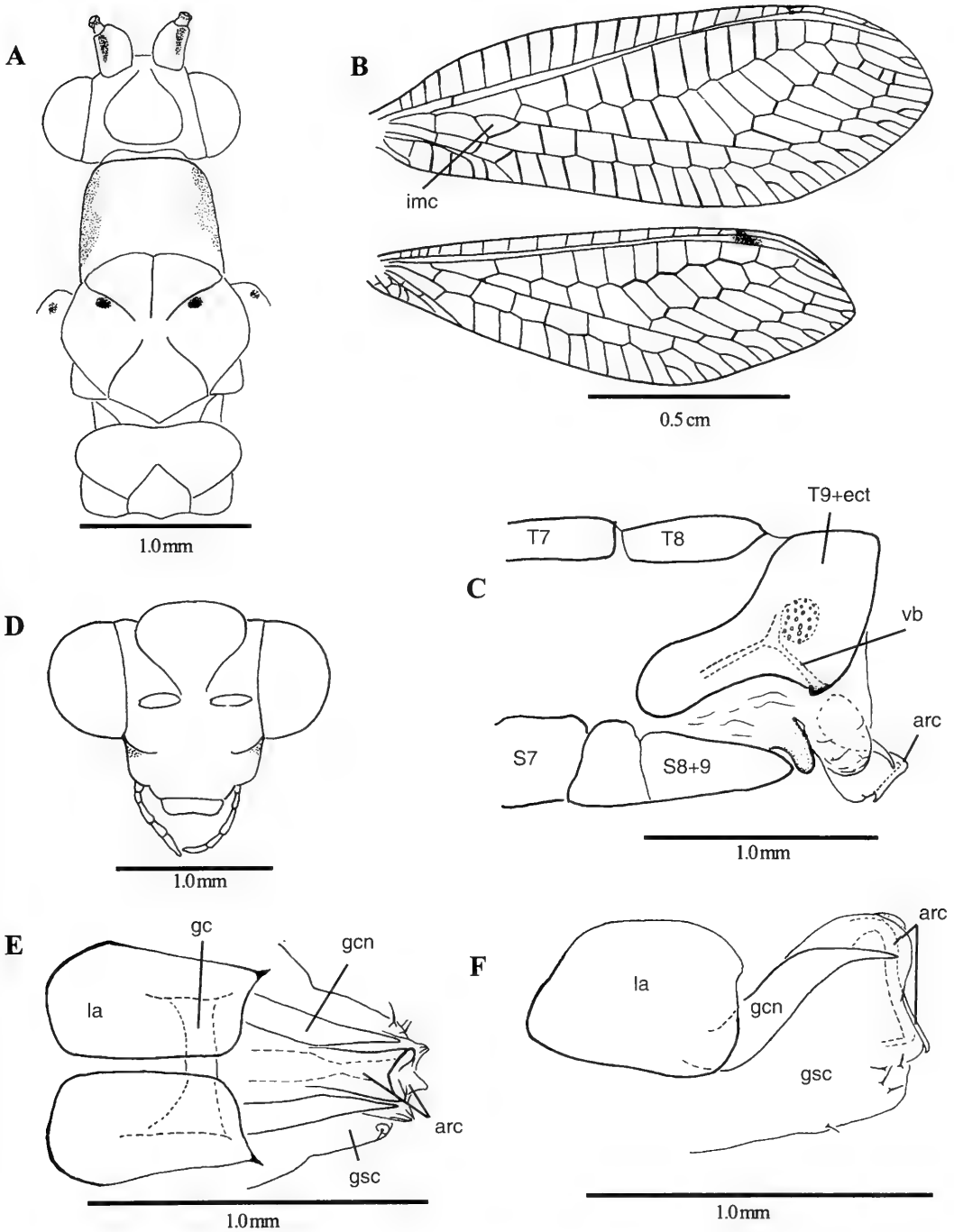

FIGURE 72. *Leucochrysa* (*Nodita*) *parallela* new species A. Head and thorax, dorsal view; B. Wings; C. Apex of male abdomen, lateral view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

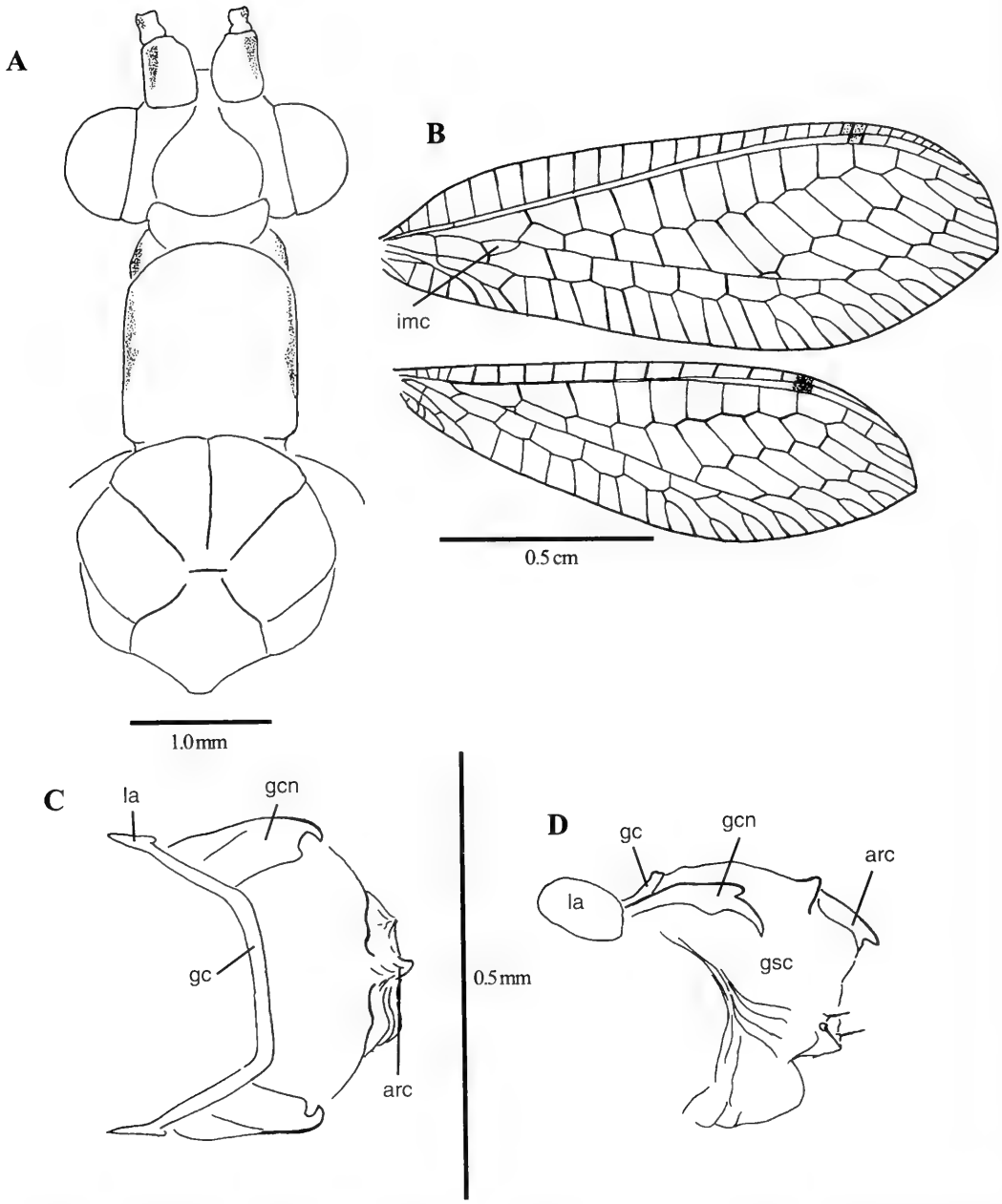

FIGURE 73. *Leucochrysa* (*Nodita*) *retusa*. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view.

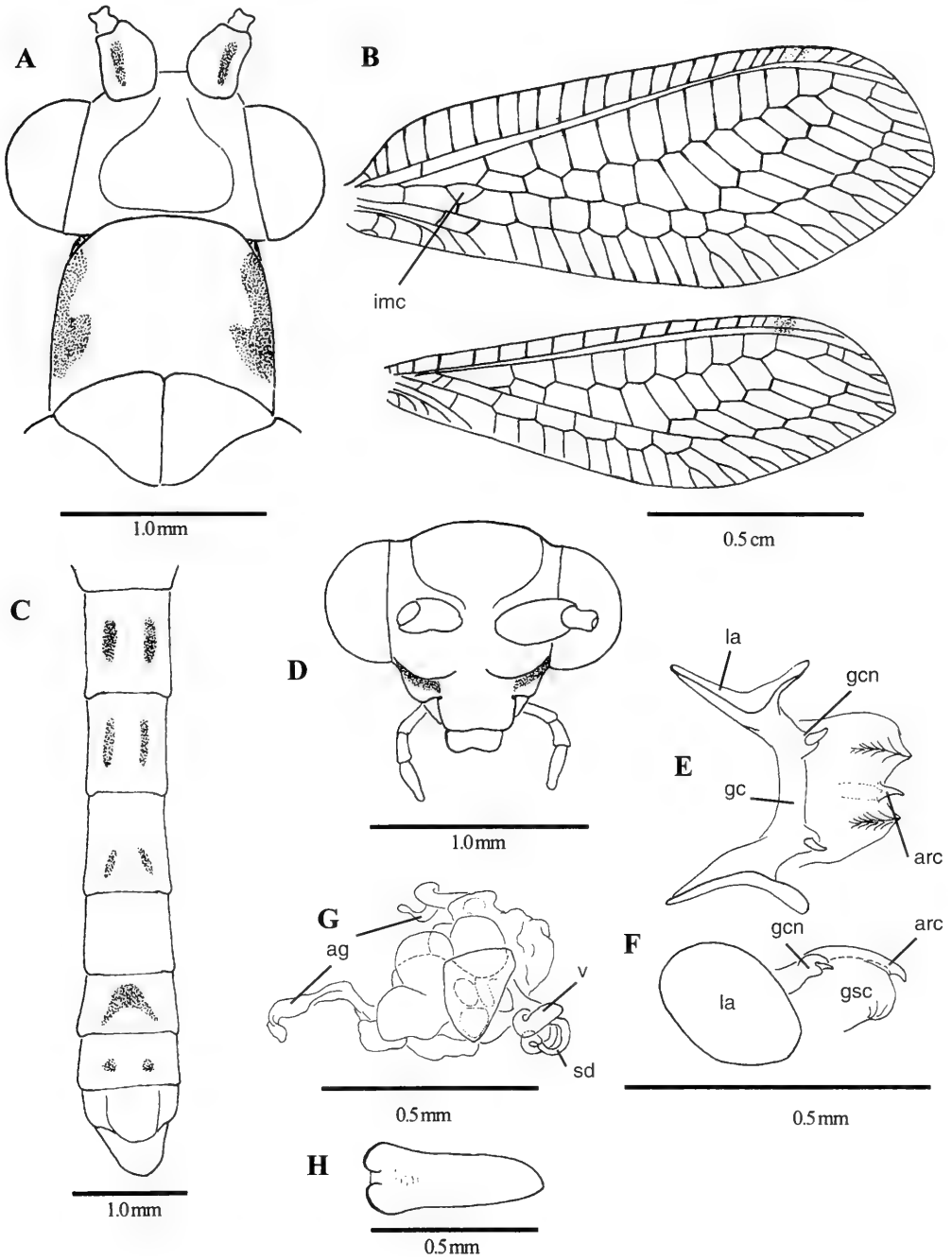

FIGURE 74. *Leucochrysa* (*Nodita*) *robusta*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Female genitalia; H. Subgenitale.

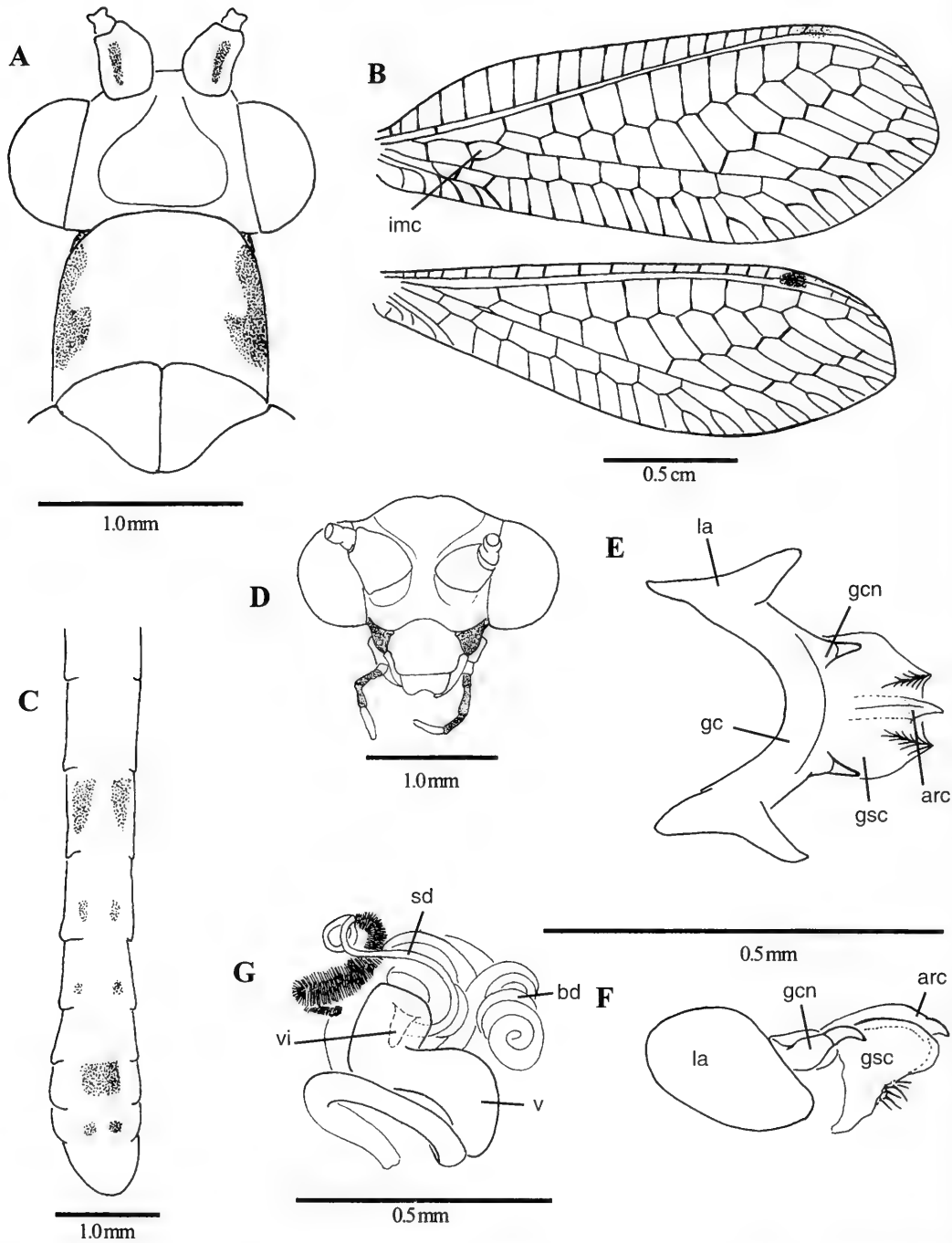

FIGURE 75. *Leucochrysa* (*Nodita*) *santni*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Subgenitale.

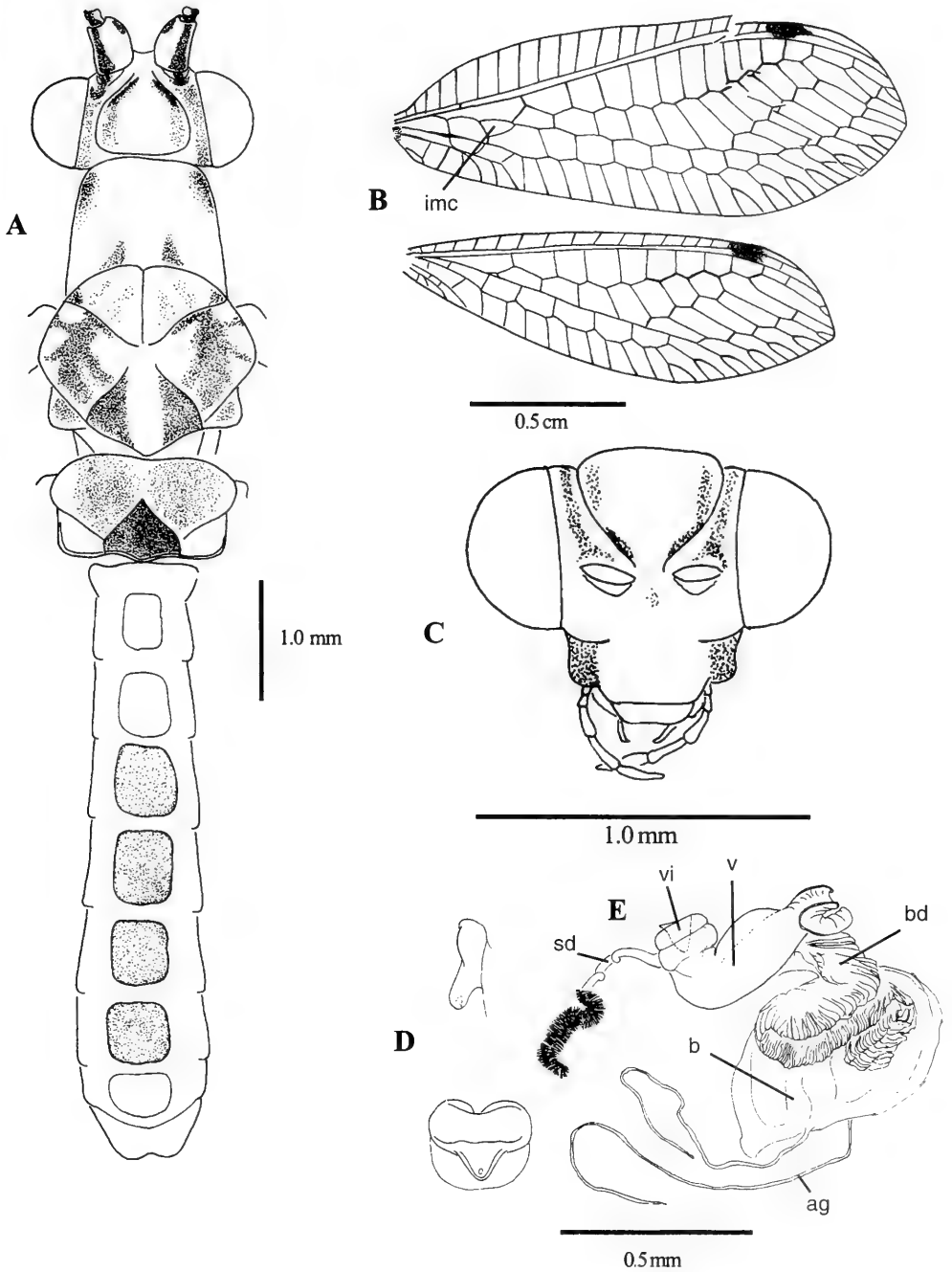

FIGURE 76. *Leucochrysa* (*Nodita*) *scomparini*, new species. A. Head and thorax, dorsal view; B. Wings; C. Head, frontal view; D. Subgenitale; E. Female genitalia.

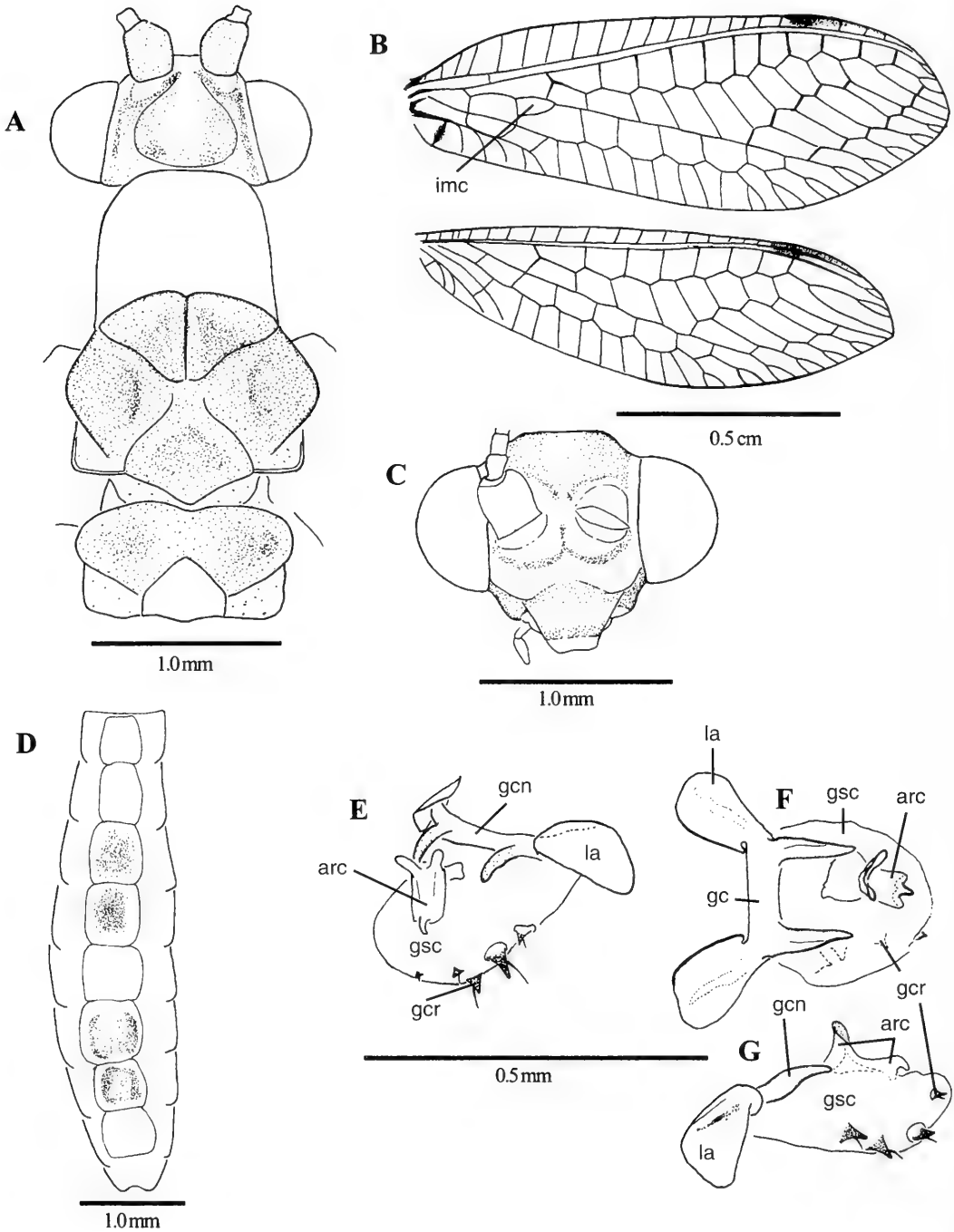

FIGURE 77. *Leucochrysa* (*Nodita*) *squamisetosa*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Abdomen, dorsal view; E. Male genitalia, dorso-caudal view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view.

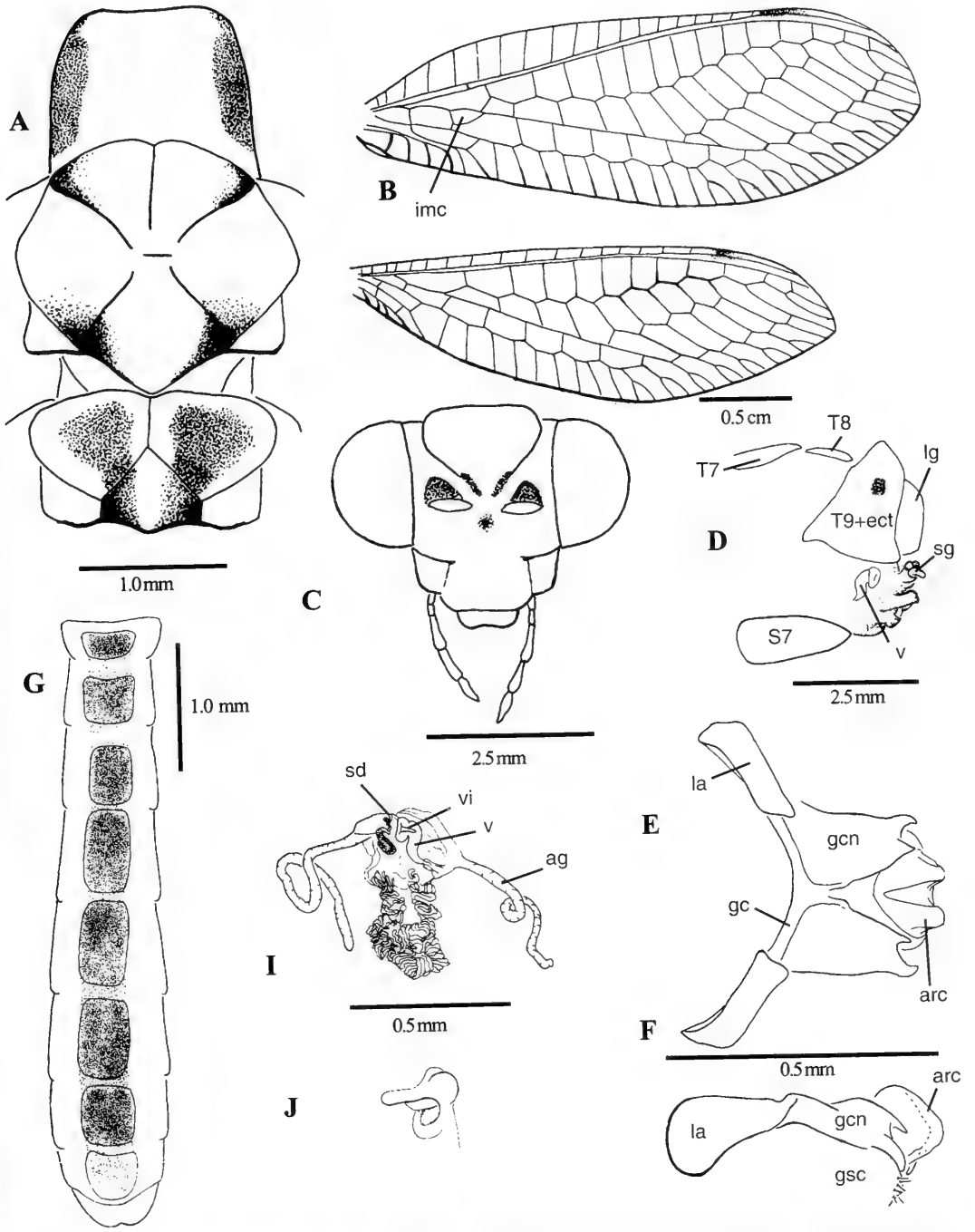

FIGURE 78. *Leucochrysa* (*Nodita*) *tabacinus*, new species A. Head and thorax, dorsal view; B. Wings; C. Head, frontal view; D. Apex of female abdomen, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Abdomen, dorsal view; H. Female genitalia; I. Subgenitale.

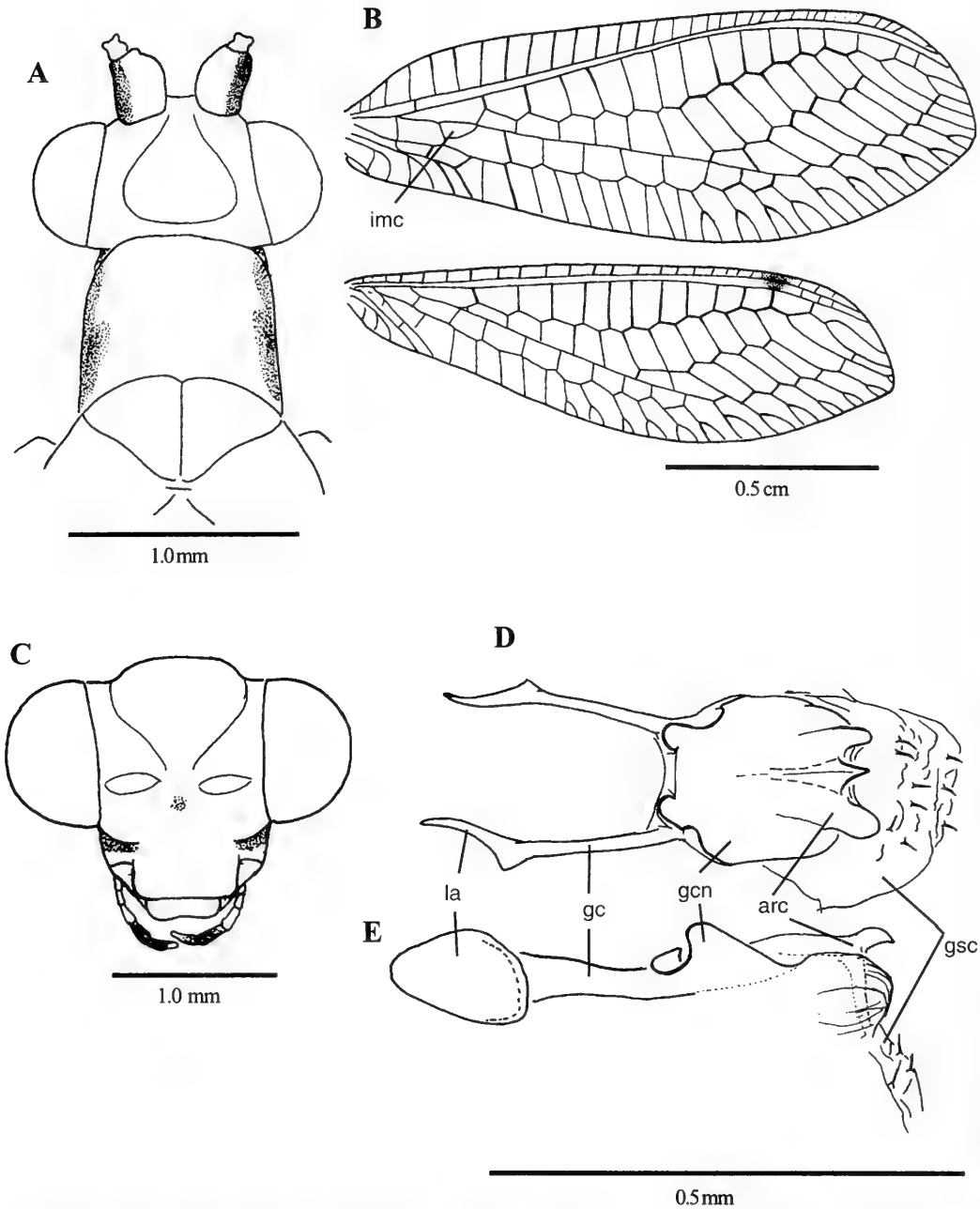

FIGURE 79. *Leucochrysa* (*Nodita*) *tenuis*, new species. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view.

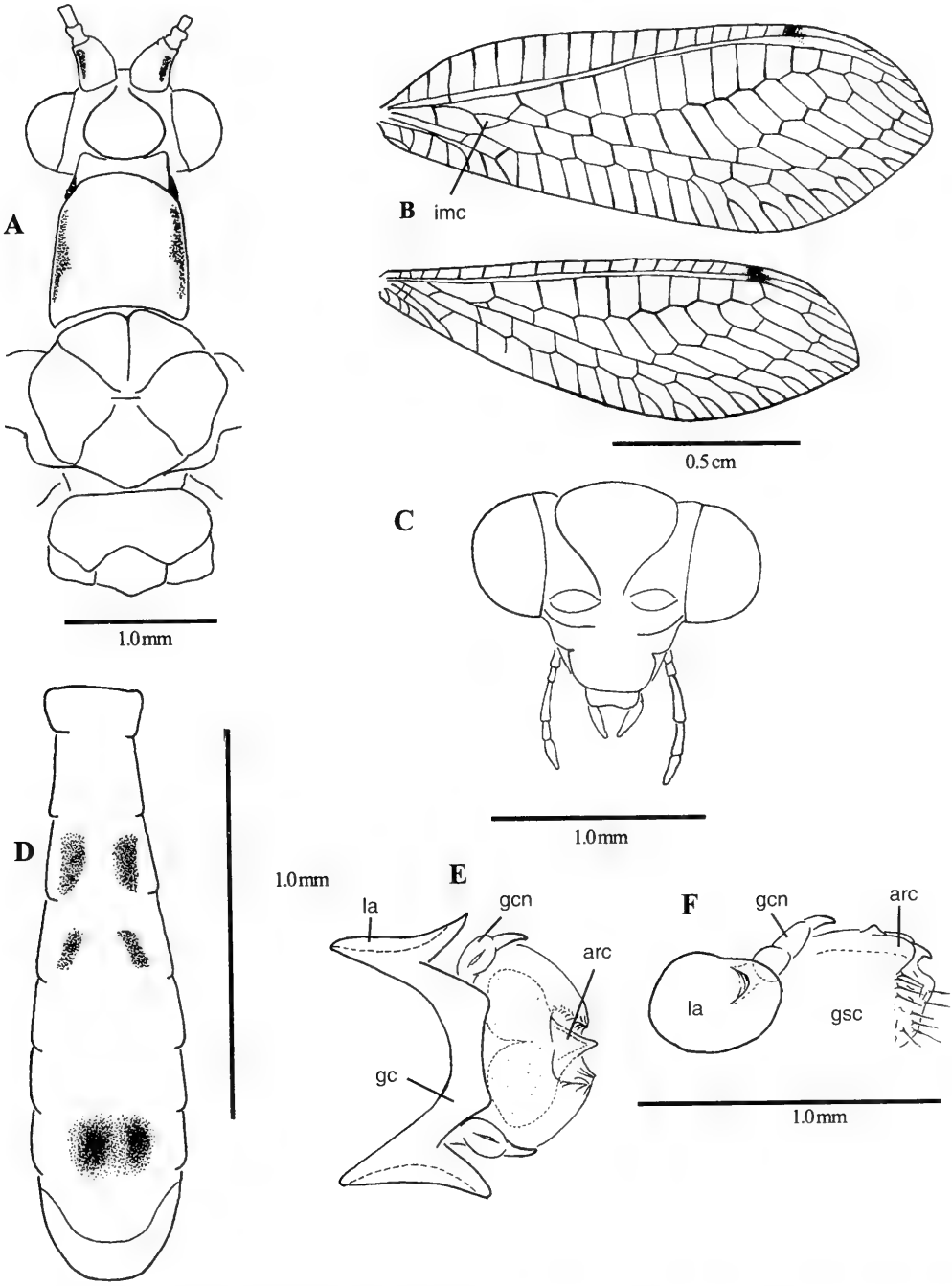

FIGURE 80. *Leucochrysa* (*Nodita*) *vignisi*, new species. A. Head and thorax, dorsal view; B. Wings; C. Head, frontal view; D., E. Male genitalia, dorsal view; F. Male genitalia, lateral view.

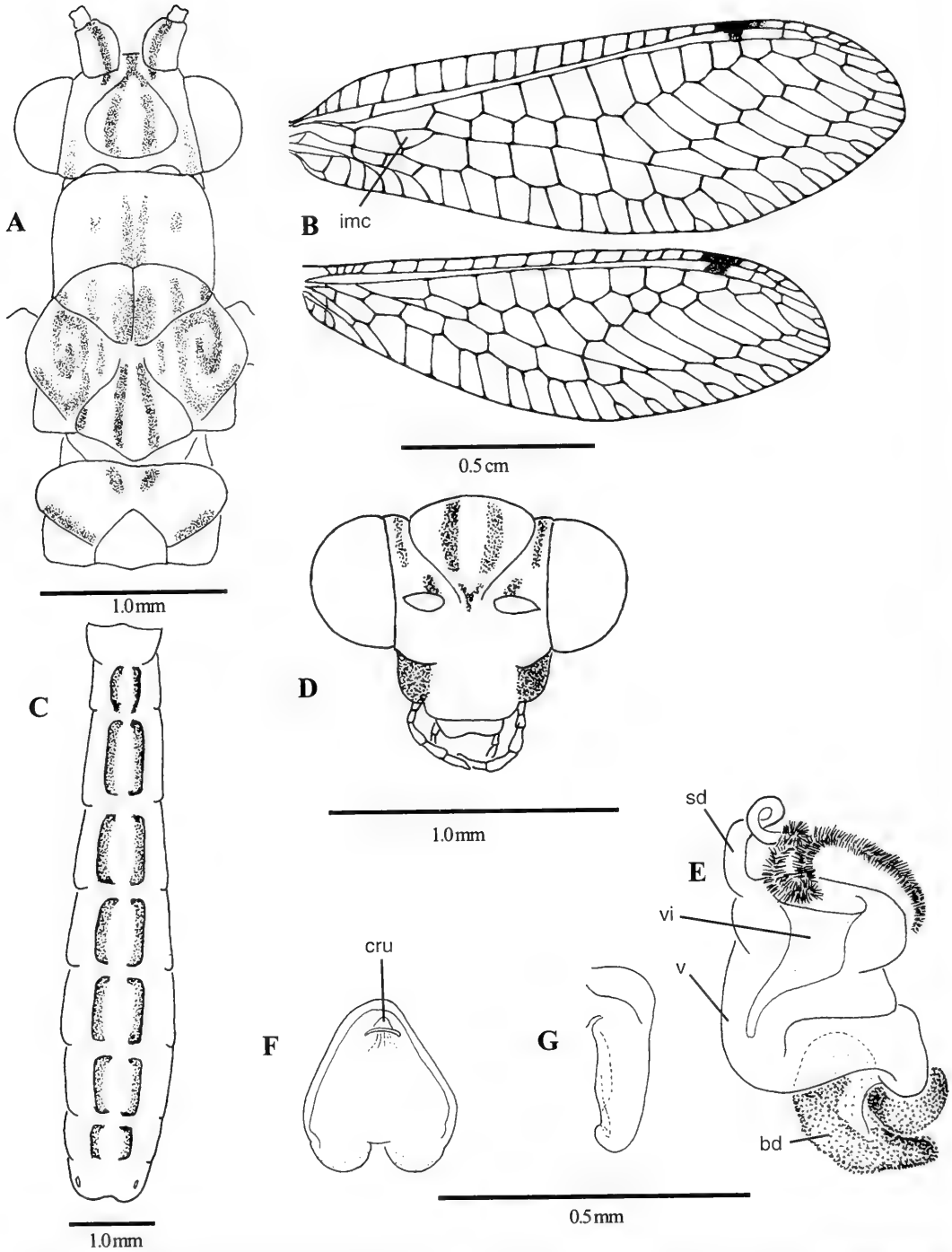

FIGURE 81. *Leucochrysa* (*Nodita*) *vittata*, new species. A. Head and thorax, dorsal view; B. Wings; C. Abdomen, dorsal view; D. Head, frontal view; E. Spermatheca; F. Subgenitale, dorsal view; G. Subgenitale, lateral view.

ACKNOWLEDGMENTS

This project could not have been accomplished without the extensive help provided by a series of notebooks of detailed drawings and notes of type specimens developed by Phillip A. Adams. These notes cover almost all existing types of Neotropical chrysopids in European and North American collections. However, any errors in interpretation of these notes are our responsibility. We gratefully acknowledge a grant from the Ernst Mayr Fund at the Museum of Comparative Zoology, Harvard University for allowing the junior author to study types and determined Neotropical material in that museum. This work was also supported by Fundação de Amparo a Pesquisa do Estado de São Paulo – FAPESP, Project No. 99/05245-2.

LITERATURE CITED

ADAMS, P. A. 1977. Taxonomy of United States *Leucochrysa* (Neuroptera: Chrysopidae). Psyche, Camb. 84(1):92–102.

———. 1978. Zoogeography of New World Chrysopidae, a progress report. Folia Entomologica Mexicana 39/40:210–211.

———. 1982a. *Ceraeochrysa*, a new genus of Chrysopinae (Neuroptera) (Studies in New World Chrysopidae, Part II). Neuroptera International 2:69–75, 12 figs.

———. 1982b. *Plesiochrysa,* a new subgenus of *Chrysopa* (Neuroptera) (Studies in New World Chrysopidae, Part I). Neuroptera International 2:27–32, 13 figs.

ADAMS, P. A. AND N. D. PENNY. 1987. Neuroptera of the Amazon Basin. Part 11a. Introduction and Chrysopini. Acta Amazônica 15:413–479. 213 + 29 figs., 1 table.

BANKS, N. 1910. New South American neuropteroid insects. Proceedings of the Entomological Society of Washington 12:146–160.

———. 1915. New neuropteroid insects, native and exotic. Proceedings of the Academy of Natural Sciences of Philadelphia 66:608–632, 1 pl. with 26 figs.

———. 1918. New neuropteroid insects. Bulletin of the Museum of Comparative Zoology 62:1–22, 2 pls. with 26 figs.

———. 1920. New neuropteroid insects. Bulletin of the Museum of Comparative Zoology 64:297–362, 7 pls. with 110 figs.

———. 1944. Neuroptera of northern South America. Part III. Chrysopidae. Boletin de Entomologia Venezolana 3:1–34.

———. 1945. A review of the Chrysopidae (Nothochrysidae) of Central America. Psyche, Camb. 52:139–174.

———. 1948. Chrysopidae (Nothochrysidae) collected in Mexico by Dr. A. Dampf (Neuroptera). Psyche, Camb. 55:151–177, 3 pls. with 37 figs.

BROOKS, S. J. 1994. A taxonomic review of the common green lacewing genus *Chrysoperla* (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History, Entomology Series 63(2):137–210.

BROOKS, S. J. AND P. C. BARNARD. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History, Entomology Series 59:117–286, 578 figs., 1 table.

GERSTAECKER, A. 1888. Weitere Beiträge zur artenkenntniss der Neuroptera Megaloptera. Mitteilungen des Naturwissenschaftlichen Vereins für Neu-Vorpommern und Rugen in Greifswald 19:89–130.

HAGEN, H. 1861. Synopsis of the Neuroptera of North America, with a list of the South American species. Smithsonian Miscellaneous Collections 49(1):xx + 1–347.

KIMMINS, D. E. 1940. Notes on some types of Chrysopidae (Neuroptera) in the British Museum Collections. Annals and Magazine of Natural History (11)5:442–449.

LÓPEZ-ARROYO, J. I., C. A. TAUBER AND M. J. TAUBER. 1999. Comparative life-histories of the predators *Ceraeochrysa cincta, C. cubana,* and *C. smithi* (Neuroptera: Chrysopidae). Annals of the Entomological Society of America 92:208–217.

MATSUDA, M. 1928. Observations on *Chrysopa vulgaris* Schn. var. *ampingensis*, Petersen. Transactions of the Natural History Society of Formosa 18:97–114. [in Japanese]

McLachlan, R. 1868. New genera and species, &c., of neuropterous insects; and a revision of Mr. F. Walker's British Museum Catalogue of Neuroptera, part ii. (1853), as far as the end of the genus *Myrmeleon*. Journal of the Linnean Society of London, Zoology 9:230–281, 1 pl. with 3 figs.

Ministerio de Agricultura. 1999. www.minagric.br.

Navás, L. 1911. *Chrysopides nouveaux* (Ins. Neur.). Annales de la Société Scientifique de Bruxelles 35 (pt. 2):266–282, 7 figs.

———. 1913a. Crisópidos sudamericanos. Brotéria (Zoológica) 11:73–104, 149–168. 8 and 5 figs.

———. 1913b. Névroptères nouveaux de l'Amérique du Nord [I]. Entomologische Zeitschrift, Frankfurt am Main 27:19–20, 2 figs.

———. 1913c. Les Chrysopides (Ins. Névr.) du Musée de Londres [1a]. Annales de la Société Scientifique de Bruxelles 37 (pt. 2):292–330, 19 figs.

———. 1914. Les Chrysopides (Ins. Névr.) du Musée de Londres [1b]. Annales de la Société Scientifique de Bruxelles 38 (pt. 2)73–114, 15 figs.

———. 1915. Neurópteros nuevos o poco conocidos. (Sexta [VI] serie). Memorias de la real Academia de Ciencias y Artes de Barcelona (3)12:119–136, 9 figs.

———. 1916. Neurópteros sudamericanos. (Trecera [III] serie). Neurópteros del Brasil recogidos por el R. P. Joaquín da Silva Tavares S. J. Brotéria (Zoológica) 14:14–35, 15 figs.

———. 1919. Algunos insectos Neurópteros de la República Argentina. (Trecera [III] serie). Revista de la Real Academia de Ciencias Exactas Físicas y Naturales de Madrid 17:287–305, 6 figs.

———. 1920. Insectos Sudamericanos (3a serie). Anales de la Sociedad Cientifica Argentina 90:52–72, 11 figs.

———. 1924a. Insectos de la Argentina y Chile. Estudios. Revista Mensual (Academia literaria del Plata, Buenos Aires) 22:358–368. 4 figs.

———. 1924b. Crisópidos (Neur.) de Cuba. Boletín de la Sociedad Entomologica de España 7:51–53.

———. 1926. Algunos insectos del Brasil (3.a serie) [IIIb]. Brotéria (Zoológica) 23:5–15, 5 figs.

———. 1930. Insectos de la Argentina. (Sexta [VI] serie). Revista de la Sociedad Entomologica Argentina 3:125–132, 5 figs.

———. 1933. Insectos suramericanos. (Sexta [VI] serie). Revista de la Real Academia de Ciencias Exactas Fisicas y Naturales de Madrid 29:191–198, 7 figs.

Neumark, A. 1952. *Chrysopa carnea* Steph. and its enemies in Israel. Forest Research Station, Ilanoth 1:vii + 1–127, 68 figs.

Penny, N. D. 1978. Lista de Megaloptera, Neuroptera e Raphidioptera do México, América Central, ilhas Caraíbas e América do Sul. Acta Amazônica 7(4)(Suplemento):1–61.

———. 1997. Four new species of Costa Rican *Ceraeochrysa* (Neuroptera: Chrysopidae). Pan-Pacific Entomologist 73(2):61–69.

———. 1998. New Chrysopinae from Costa Rica (Neuroptera: Chrysopidae). Journal of Neuropterology 1:55–78. 68 figs.

———. 2001. New species of Chrysopinae (Neuroptera: Chrysopidae) from Costa Rica, with selected taxonomic notes and a neotype designation. Entomological News 112(1):1–14.

Penny, N. D., P. A. Adams, and L. A. Stange. 1997. Species catalog of the Neuroptera, Megaloptera, and Raphidioptera of America north of Mexico. Proceedings of the California Academy of Sciences 50(3):39–114.

Schneider, W. G. 1851. Symbolae ad monographiam generis Chrysopae, Leach. Hirt, Vratislaviae. 178 pp., 60 pls.

Smith, R. C. 1921. A study of the biology of the Chrysopidae. Annals of the Entomological Society of America 14:27–35.

———. 1922. The biology of the Chrysopidae. Memoirs of the Cornell University Agricultural Experiment station 58:1287–1372, 10 text figs. and 14 pls. with 122 figs.

Steinmann, H. 1964. The *Chrysopa* species (Neuroptera) of Hungary. Annales Historico-Naturales Musei Nationalis Hungarici (Zoologica) 56:257–266, 1 fig.

Tauber, C. A. and T. de León. 2001. Systematics of green lacewings (Neuroptera: Chrysopidae): Larvae of *Ceraeochrysa* from Mexico. 94(2):197–209.

Tauber, C. A., T. de León, N. D. Penny, and M. J. Tauber. 2000. The Genus *Ceraeochrysa* (Neuroptera: Chrysopidae) of America north of Mexico: Larvae, adults, and comparative biology. Annals of the Entomological Society of America 93(6):1195–1221.

TAUBER, M. J., C. A. TAUBER, K. M. DANNE, AND K. S. HAGEN. 2000. Commercialization of predators: Recent lessons from green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). American Entomologist 46(1):26–38.

TJEDER, B. 1966. Neuroptera-Planipennis. The Lace-wings of Southern Africa. 5. Family Chrysopidae. Pp. 228–534 *in* South American Animal Life. B. Hanström, P. Brinck, and G. Rudebeck, eds. Vol. 12. Swedish Natural Science Research Council, Stockholm.

WALKER, F. 1853. List [Catalogue] of the specimens of neuropterous insects in the collection of the British Museums. Part II. (Sialidaes – Nemopterides). British Museum [Natural History], London. Pp. 193–476.

WITHYCOMBE, C. L. 1923. Notes on the biology of some British Neuroptera (Planipennis). Transactions of the Entomological Society of London 1922:501–594, 6 pls. with 72 figs.

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A New *Lycodon* (Serpentes: Colubridae) from Northeast India and Myanmar (Burma)

by

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A new species of the colubrid snake genus *Lycodon* is described from western Myanmar and Northeast India. Morphologically, the new species is most similar to *L. laoensis*, but is distinguishable from it by its brownish black and white dorsal coloration (vs. brownish black and yellow in *L. laoensis*) and the absence of a well-developed nape band (present in *L. laoensis*). The new species increases the diversity of *Lycodon* to four in Myanmar and to five in Northeast India.

Lycodon H. Boie in Fitzinger (1826) is a genus of small colubrid snakes characterized by an arched maxillary generally with three sets of teeth separated by two diastemata, a dorsoventrally compressed head, and a vertically elliptical pupil (Smith 1943; Taylor 1965; Leviton 1965). Approximately 25 species occur in Asia (Lanza 1999). Recently, herpetofaunal surveys in Myanmar and Northeast India (by Slowinski, Htun Win, Thin Thin, Sai Wanna Gyi, San Lwin Oo, and Hla Tun in Myanmar; Pawar in Northeast India) yielded specimens of *Lycodon* from western Myanmar and Northeast India that represent a new species. Four other species, viz., *L. aulicus/capucinus*, *L. fasciatus*, *L. kundui*, *L. laoensis,* and *L. jara*, occur in Myanmar and Northeast India (Smith 1943; Dowling and Jenner 1988).

All specimens were hand collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Comparative material was examined at the CAS (California Academy of Sciences), BMNH (Bombay Museum of Natural History), and ZSI (Zoological Survey of India). In addition, information was collected from private collections in India and field stations in various protected areas in Northeast India.

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[1] Dr. Joseph Slowinski died in Myanmar on September 12, 2001, while leading a biological expedition to the extreme northeast of that country. He will be deeply missed by his academic colleagues, his students and friends, and by his many co-workers in Myanmar.

Species Description

***Lycodon zawi* sp. nov.**
Zaw's wolf snake

Material Examined. — Holotype: CAS 210323 (Fig. 1), a male from Alaungdaw Katapha National Park (AKNP) (22°19′N, 94°29′E), Sagaing Division, Myanmar, collected 17 July, 1999, by Htun Win, Thin Thin, K. Wiseman, J. Lovette, and J. Vindum. Paratypes: CAS 210223, a male from AKNP (22°19′N, 94°24′E), Sagaing Division, Myanmar, collected 10 July, 1999, by J. Slowinski, K. Wiseman, J. Lovette, and J. Vindum; CAS 215494, a male from AKNP (22°19′N, 94°24′E), Sagaing Division, Myanmar, collected 30 May, 2000, by Htun Win, Thin Thin, San Lwin Oo, Sai Wanna Gyi, and Hla Tun; CAS 215570, a male from AKNP (22°19′N, 94°29′E), Sagaing Division, Myanmar, collected 12 June, 2000, by Htun Win, Thin Thin, and San Lwin Oo; CAS 215599, a male from AKNP (22°19′N, 94°29′E), Sagaing Division, Myanmar, collected 14 June, 2000, by Htun Win, Thin Thin, and San Lwin Oo; CAS 216505, a male from the Gwa Township (17°39′N, 94°39′E), Rakhine State, Myanmar, collected 29 November, 2000, by J. Slowinski, Htun Win, and Hla Tun. ZSI 25346, a male from Ngengpui Wildlife Sanctuary (NgWS; 22°29′N, 92°48′E), Mizoram, Northeast India, collected 17 April, 1999, by S. Pawar; ZSI 25347, a male from Nongkhyllem Wildlife Sanctuary (NWS; 25°56′N, 91°31′E), Meghalaya, Northeast India, collected 8 May, 2000, by M. F. Ahmed; ZSI 25348, a female from Garbhanga Reserve Forest (GRF; 26°09′N, 91°33′E), Assam, Northeast India, collected 30 March, 1998, by S. Sengupta. Additional Specimens: Two more specimens, a male near Kaifung (23°39′N, 92°57′E), North Mizoram, Northeast India, and another male from Balphakram Tiger Reserve (BTR; 25°30′N, 90°45′E), Meghalaya, Northeast India, not housed in a permanent depository.

Diagnosis. — *Lycodon zawi* differs from other *Lycodon* of the Asian mainland by the following combination of character states: 17 dorsal scale rows at mid-body, preocular scale present (Fig. 1), loreal scale not in contact with internasal (Fig. 1), anal scale divided, poorly-developed white crossbands on a brownish black dorsum, and without a well-developed nape band (Fig. 1). In terms of scale characteristics, *L. zawi* is similar to *L. laoensis* (Figs. 2–4), known from Northeast India, China, Malaysia, Thailand, Laos, Vietnam, and Cambodia (Lanza 1999), but differs by its brownish black and white dorsal coloration (brownish black and yellow in *L. laoensis*), the poorly-developed light crossbands (well-developed in *L. laoensis*), and the lack of a nape band. *Lycodon zawi* differs from other Myanmar and Northeast India congeners as follows: from *L. aulicus/capucinus* (Figs. 2–4) in lacking a nape band, in lacking a sharply defined white lip margin, and in having a loreal scale that does not contact the internasal scale; from *L. kundui* in lacking a nape band, having 17 mid-body scale rows (15 in *L. kundui*), and in having 8 or 9 supralabials (7 in *L. kundui*); from *L. fasciatus* (Figs. 2–4) in lacking loreal contact with the eye, in lacking well-developed light crossbands, and in having smooth dorsal scales; from *L. jara* (Figs. 2–3) in having light bands and in having a loreal scale that does not contact the internasal scale. *Lycodon zawi* resembles *L. travancoricus* (Western Ghats and southern Pakistan) and *L. tiwarii* (Andaman and Nicobar Islands; Biswas and Sanyal 1965) in scalation. From *L. travancoricus*, *L. zawi* differs by its divided anal and weakly developed light bands (*L. travancoricus* has well-developed yellow bands which bifurcate on the sides). *Lycodon zawi* differs from *L. tiwarii* in having white bands on a dark dorsum (white reticulations on a dark dorsum in *L. tiwarii*).

Description of Holotype (Adult male). — Body dimensions: SVL 395 mm; tail length 85 mm; total length 480 mm. Body scalation: 183 ventrals; 45 subcaudals; 17-17-15 dorsal scale rows. Head scalation: loreal well separated from internasal and from the eye border by the preocular and 3rd supralabial; 8 supralabials, 3rd, 4th, and 5th touching eye; 1 postocular; 2+3 temporals; 9/10 infralabials, 1st to 5th infralabials contacting chin shields.

FIGURE 1. The holotype (CAS 210323) of *Lycodon zawi*.

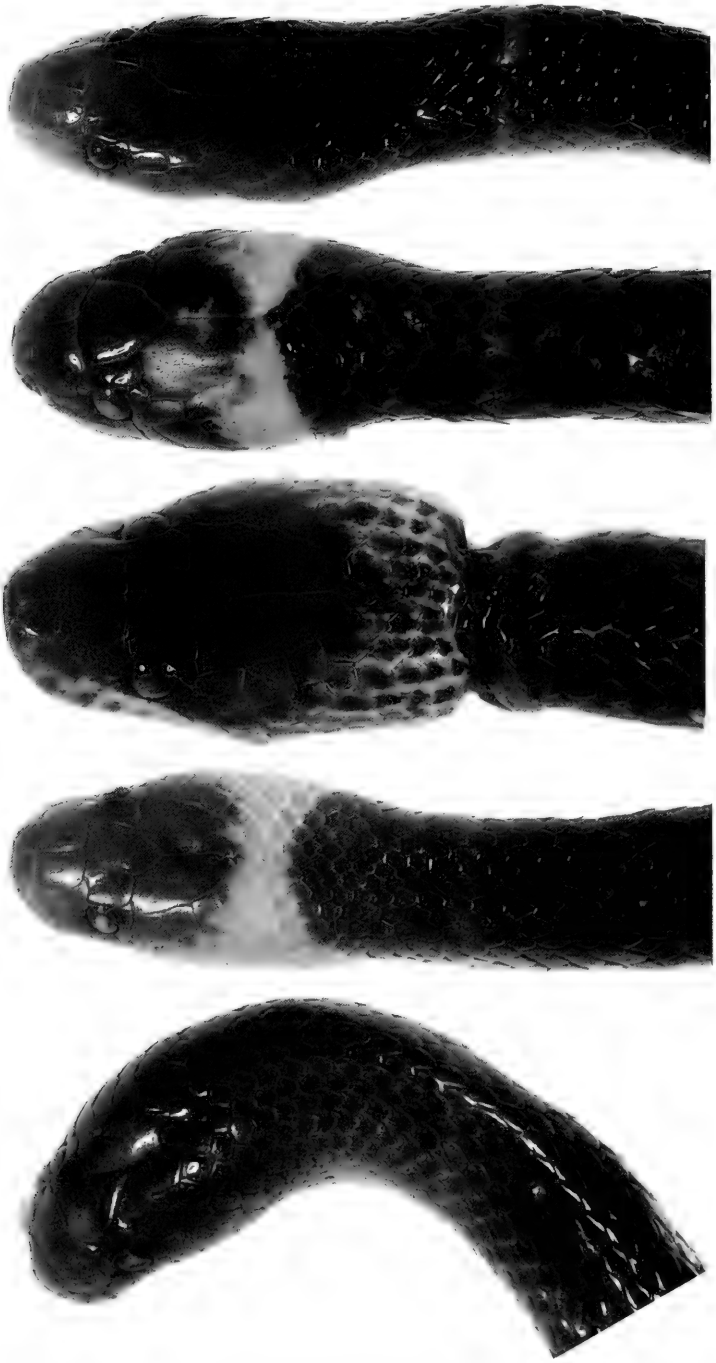

FIGURE 2. Dorsal views of heads of (top to bottom) *Lycodon zawi* (CAS 210323), *Lycodon fasciatus* (CAS 55147) from western China, *L. aulicus* (CAS 216278) from Mandalay Division, Myanmar, *L. laoensis* (CAS 73679) from Thailand, and *L. jara* (CAS 12395) from Assam, India.

FIGURE 3. Lateral views of heads of (top to bottom; same snakes as in Fig. 2) *Lycodon zawi*, *L. fasciatus*, *L. aulicus*, *L. laoensis*, and *L. jara*.

The maxilla (right maxilla examined) is arched and similar in form to that illustrated by Smith (1943, fig. 88) for *L. aulicus*. Two diastemata separate the maxillary teeth into three groups. The anterior group is composed of three small teeth followed posteriorly by two enlarged teeth; the middle group is composed of five equal teeth; the posterior group is composed of two enlarged teeth.

Everted hemipenis extending to 8th subcaudal; unforked; distal half characterized by longitudinal flounces perpendicular to the long axis of organ; proximal half of organ with large spines; sulcus single, terminating in expanded trough at tip.

Coloration in life (same as in preservative): brownish black dorsally with irregularly shaped white transverse bands, the bands well developed anteriorly (one scale row in width) but fading posteriorly; faint, diffuse light band on nape; head dark brown dorsally, fading to light brown on lips; tail uniform brown dorsally without white bands; venter cream with dark lateral corners on each ventral scale.

VARIATION. — Four of six Myanmar specimens have 8 supralabials on both sides, but two have 9/8 supralabials. All five Northeast India specimens have 9 supralabials on both sides. Five of the six Myanmar specimens have 9 infralabials on both sides, but the holotype has 9/10. All five Northeast India specimens have 10 infralabials. The holotype, a paratype from Northeast India (ZSI 25348), and two other specimens from Northeast India have 2+3 temporals on both sides. Another paratype from Northeast India (ZSI 25347) has 2+3 temporals on the left and 3+4 on the right. The third paratype from Northeast India (ZSI 25346) has 2+1 temporals on the left and 2+2 on the right. All other specimens, from Myanmar, have 1+2+3 temporals. The holotype and two other Myanmar specimens (CAS 210223, 1/1 postocular; CAS 216505, 2/1 postocular) have one postocular; all other specimens have two postoculars. Ventrals in males range from 179 to 186 in the Myanmar specimens and 190 to 194 in the Northeast India specimens; the single female specimen (ZSI 25348) from India has 207 ventrals; subcaudals in males range from 45 to 67 in the Myanmar specimens and 70 to 75 in the Northeast India specimens; the single female from India has an incomplete tail.

The general color pattern is identical in all specimens, except for some white bands on the tail in several specimens. Three Northeast India specimens have a faint spot on the nape. The ventral coloration of the female paratype (ZSI 25348) consists of erratically distributed dark patches on the ventral scales, not seen in the others.

ETYMOLOGY. — The specific name is a patronym in the genitive singular, honoring U Khin Maung Zaw, Director of the Myanmar Nature and Wildlife Conservation Division, who has provided critical assistance to our survey of the herpetofauna of Myanmar.

DISTRIBUTION AND NATURAL HISTORY. — In Myanmar, *Lycodon zawi* is currently known from two localities in the west (Fig. 5): five specimens collected from AKNP in the Sagaing Division, and one specimen collected from a locality on the western slope of the southern Rakhine (Arakan) Mountains, over 470 km south of the first locality. Alaungdaw Katapha National Park is in the Sagaing Division in west-central Myanmar, approximately 160 km west of Mandalay. This is an area of low mountains with a maximum elevation of 1000 m. Rainfall at AKNP averages 1500 mm per year (Tun Nyo 1997), and the park consists of a mosaic of deciduous forest types, from closed canopy moist deciduous forest to indaing, a savanna of stunted dipterocarp trees. The single Rakhine Yoma specimen came from the forests near Gwa in the Rakhine State, approximately 170 km west of Yangon (Rangoon). Rainfall in the southern Rakhine mountains is quite high, averaging over 5000 mm per year (data from Myanmar government). Owing to this, the habitat is quite different from that in AKNP. Originally evergreen forest (Stamp 1924, 1930), logging and shifting cultivation has reduced most of the forest to extensive bamboo stands (Collins et al. 1991).

In Northeast India, *L. zawi* has been collected at five localities (Fig. 5). All localities are in low to mid-elevation hill tracts receiving medium to high precipitation (above 2000 mm per year); all sites harbor, or formerly harbored, low to mid-elevation moist tropical evergreen to semi-evergreen forest. Four of the five localities, viz., NgWS, NWS, BTR, and GRF, are protected. As in Myanmar, habitat

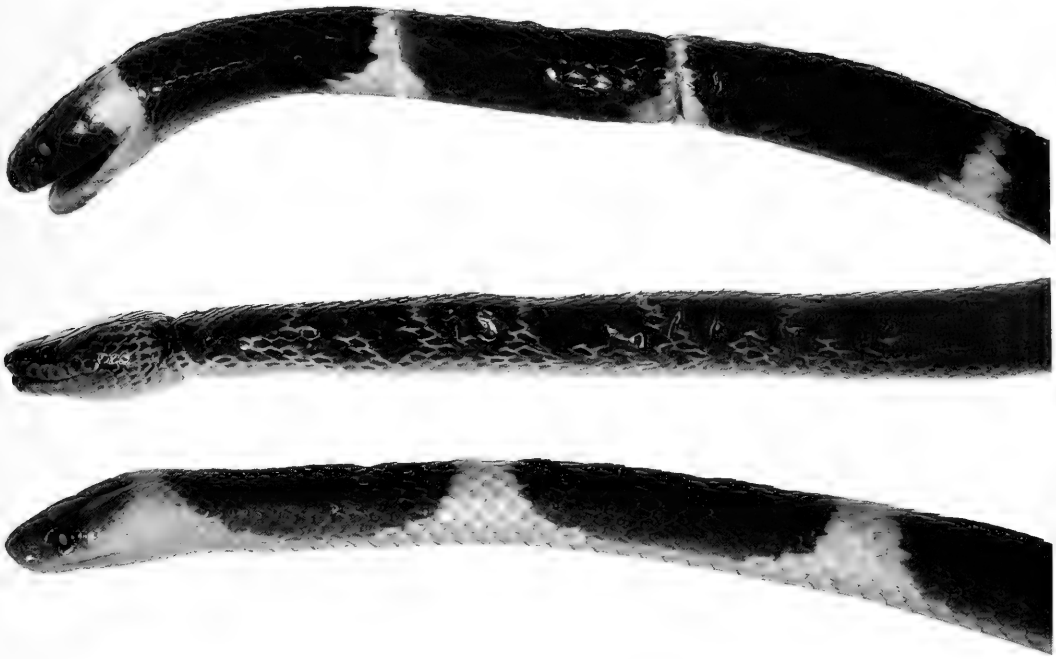

FIGURE 4. Anterior bodies of (top to bottom; same snakes as in Fig. 2) *Lycodon fasciatus, L. aulicus,* and *L. laoensis.*

alteration due to slash-and-burn cultivation is a major problem for habitat conservation in Northeast India (Ramakrishnan 1992). In fact, the specimen (ZSI 25346) from NgWS was caught while fleeing a burning slash-and-burn plot near the sanctuary boundary.

All evidence suggests that *L. zawi* is a nocturnal species, apparently preferring riparian forests. Most specimens were found active at night along streams at elevations less than 500 m. Although there are extensive tracts of bamboo in Northeast India-Myanmar, no specimens were found in bamboo habitats.

In both Myanmar localities, as well as most of the localities in Northeast India, *L. zawi* is sympatric with *L. aulicus* and/or *L. fasciatus*. All localities of *L. zawi* from Northeast India are south of the Brahmaputra river, which is an important biogeographical barrier in that region (Mani 1974; Ripley and Beehler 1990). Despite recent surveys (Pawar, unpublished data), no specimens have been obtained north of the Brahmaputra river, including the eastern Himalayas. If found there, *L. zawi* may be sympatric with as many as three other species of *Lycodon*: *L. jara*, *L. aulicus*, and *L. laoensis*.

Three specimens of *Lycodon zawi* from Myanmar had prey items in their alimentary tracts: CAS 210223 contained the partially digested head of a small skink; CAS 215494 contained the rear torso and tail of a small skink; CAS 215599 contained a hind limb and the tail of a small skink. In each case, the skink appears to be *Sphenomorphus maculatus*, which is common along streams in Myanmar. One specimen (ZSI 25346) kept by Pawar in captivity for 28 days fed on geckos (*Hemidactylus frenatus* and *H. garnoti*).

DISCUSSION

Lycodon zawi seems to be common where it occurs. Its recent discovery is not surprising, because western Myanmar and Northeast India remain very poorly surveyed. Recent surveys of this region by the authors have brought to light new records and species for the region (Slowinski and Wuster 2000;

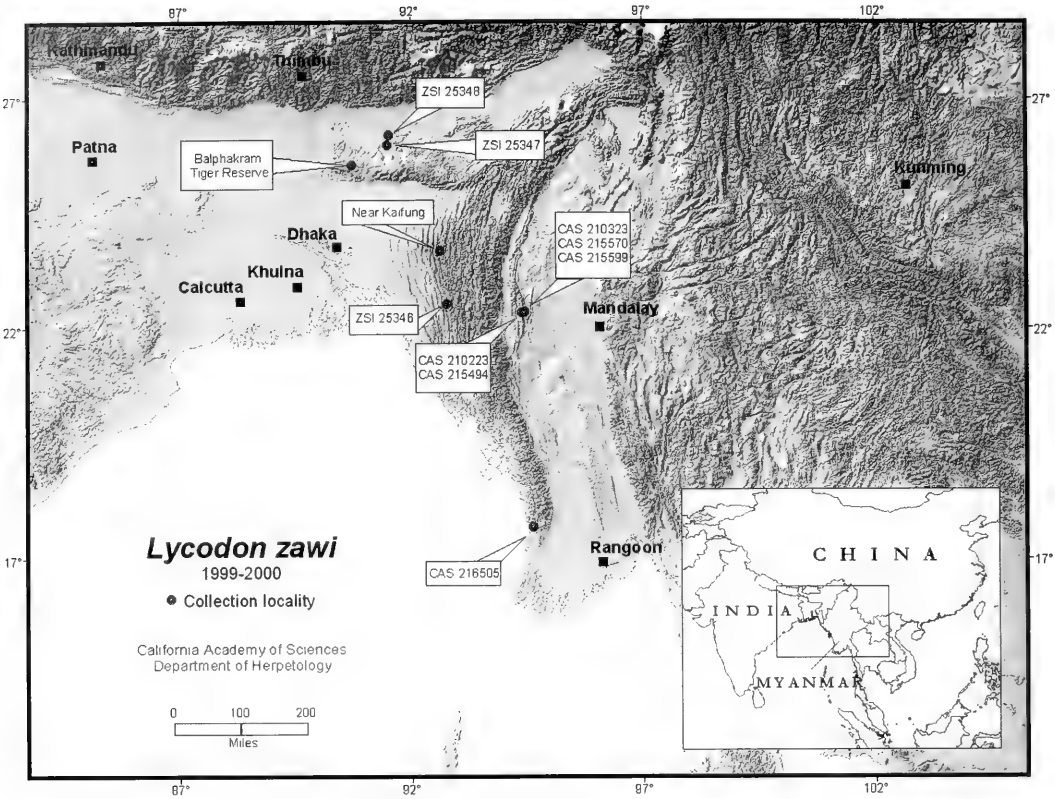

FIGURE 5. Distribution of *Lycodon zawi* in Myanmar and India.

Pawar and Biswas 2001; Pawar and Choudhury 2000). It is also possible that specimens of this species exist in local museums in India, perhaps misidentified as *L. aulicus* or *L. laoensis*, to which the new species bears superficial resemblance. In general, *L. zawi* is easily differentiated by its combination of morphology and color pattern. It is apparent from the above description that there is some variation both within and between Northeast India and Myanmar samples. The apparent differences between the ventral scale counts of the Myanmar and Northeast India populations suggests geographic differentiation.

ADDITIONAL MATERIAL EXAMINED

Lycodon laoensis.—CAS 73679 (Thailand), CAS-SU 8523 (Penang, Malaysia), CAS 15966 (Kerala, India).

Lycodon aulicus.—CAS 216278 (Mandalay Division, Myanmar), CAS 215387 (Sagaing Division, Myanmar), CAS 215396 (Sagaing Division, Myanmar), CAS 215422 (Sagaing Division, Myanmar).

Lycodon fasciatus.—CAS 55147 (China), CAS 172715 (Chiang Mai Province, Thailand).

Lycodon jara.—CAS 17210 (Orissa, India), CAS-SU 12395 (Assam, India).

Lycodon tiwarii.—ZSI 20849 (no locality available), CAS 20851 (no locality available).

Lycodon travancoricus.—CAS-SU 15967 (Kerala, India).

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LITERATURE CITED

ATHREYA, R. M., A. S. CAPTAIN, AND V. R. ATHREYA. 1997. A faunal survey of Namdapha Tiger Reserve, Arunachal Pradesh, India. July, 1997. Unpublished report.

BISWAS, S. AND D. P. SANYAL. 1965. A new species of wolfsnake of the genus *Lycodon* Boie [Reptilia: Serpentes: Colubridae] from the Andaman and Nicobar Islands. Proceedings of the Zoological Society, Calcutta 18:137–141.

COLLINS, N. M., J. A. SAYER, AND T. C. WHITMORE. 1991. Atlas of tropical forests: Asia and the Pacific. Simon and Schuster, New York. 256 pp.

DOWLING, H. G. AND J. V. JENNER. 1988. Snakes of Burma: Checklist of reported species & bibliography. Smithsonian Herpetological Information Service No. 76. 19 pp.

FITZINGER, L. J. F. J. 1826. Neue Classification de Reptilien nach ihren naturlichen Verwandtschaften. Wien. 66 pp.

LANZA, B. 1999. A new species of *Lycodon* from the Philippines, with a key to the genus (Reptilia Serpentes Colubridae). Tropical Zoology 12:89–104.

LEVITON, A. E. 1965. Contributions to a review of Philippine snakes, VIII. The snakes of the genus *Lycodon* H. Boie. Phillipine Journal of Science 94:117–140.

MANI, M. S. 1974. Ecology and biogeography in India. W. Junk, The Hague, Netherlands. 773 pp.

PAWAR, S. S. AND B. C. CHOUDHURY. 2000. An inventory of Chelonians from Mizoram, North-east India: New records and some observations on threats. Hamadryad 25:144–158.

PAWAR, S. AND S. BISWAS. 2001. First record of the parachute gecko *Ptychozoon lionotum* Annandale 1905 from the Indian mainland. Asiatic Herpetological Research (in press).

RAMAKRISHNAN, P. S. 1992. Shifting agriculture and sustainable development: an interdisciplinary study from northeastern India, 1st ed. UNESCO, Paris.

RIPLEY, S. D. AND B. M. BEEHLER. 1990. Patterns of speciation in Indian birds. Journal of Biogeography 17:639–648.

SLOWINSKI, J. B. AND W. WÜSTER. 2000. A new cobra (Elapidae: *Naja*) from Myanmar (Burma). Herpetologica 56:257–270.

SMITH, M. A. 1943. Fauna of British India, Ceylon, and Burma, including the whole of the Indo-Chinese sub-region. Reptilia and Amphibia. Vol. III. Serpentes. Taylor and Francis, London. 583 pp.

STAMP, L. D. 1924. Notes on the vegetation of Burma. Geography Journal 64:231–237.

———. 1930. Burma: an undeveloped monsoon country. Geographic Review 20:86–109.

TAYLOR, E. H. 1965. The serpents of Thailand and adjacent waters. University of Kansas Science Bulletin 45:609–1096.

TUN NYO. 1997. Alaungdaw Katapha National Park (brief notes). Report to Nature and Wildlife Conservation Division, Forest Department, Ministry of Forestry, Myanmar. 20 pp.

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Grenadiers (Families Bathygadidae and Macrouridae, Gadiformes, Pisces) of New South Wales, Australia

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Twenty-six years of extensive trawling off New South Wales (NSW) by the FRV *Kapala*, supplemented by opportunistic sampling by ORV *Franklin*, revealed a grenadier fauna comprising 60 species in 21 genera. Despite a relatively limited coastline (600 nautical miles), the diversity in NSW is comparable to those off Western Australia (63 spp.), New Caledonia (63 spp.), and New Zealand (about 67 spp.). Of the 60 species, none are endemic to NSW, but 12 are the only Australian records. Most of the material used in this study and data on abundance, depth, and distribution were collected on the *Kapala* during fishery resource surveys. Between 1972 and 1997, *Kapala* surveyed shelf and slope depths along the whole NSW coast, although most trawling was on the more extensive and commercially productive grounds off central and southern NSW. The maximum depth trawled was about 1200 m. Grenadiers were present in about 10% of tows on the outer-shelf (about 100–200 m), about half of all tows between 200 and 300 m, and in almost every trawl deeper than 300 m. Smaller-meshed nets caught on average two more species per station than those with larger mesh, and the mean number of species increased with depth. The data also suggested that the NSW grenadier fauna is relatively rich in species at depths beyond those sampled by *Kapala*. Depth-distribution data separated the species into two groups, an upper-slope group in about 200–700 m, and a lower-slope group in 700–1300 m. Many species that were rarely caught by *Kapala* appeared to be at the fringes of their geographic or depth distributions in NSW. The large genus *Caelorinchus* was represent by 15 species, while *Coryphaenoides* had 11 species. All other genera had four or fewer representatives. Keys, figures, and brief accounts are provided for all NSW genera and species, with emphasis in the species accounts placed on their abundance and distribution in NSW.

Fishes of the families Bathygadidae and Macrouridae, often referred to as grenadiers, whiptails, and rattails, are among the most abundant members of the demersal fish fauna at continental slope depths of the world's oceans. The rich grenadier fauna of the southwestern Pacific has only recently come to the attention of the scientific world, mainly through the research and development of deep-water trawl fisheries around Australia and New Zealand. McCann and McKnight (1980) made the first major study of the New Zealand grenadier fauna and recognized 25 species from the area. That number has been increased by the addition of new records and new species described by McMillan and Paulin (1993)[*Caelorinchus*], McMillan (1995) [*Trachyrincus*], Iwamoto and McMillan (1997) [*Trachonurus*], and McMillan (1999) [*Coryphaenoides*]. Current research by McMillan and Iwamoto

suggests that the number will exceed 65. The New Caledonian grenadiers were treated by Iwamoto and Merrett (1997) and Merrett and Iwamoto (2000). They recorded 63 species belonging to 20 genera.

Australia's rich fauna was documented little more than a decade ago by Paxton et al. (1989) as having about 57 species of grenadiers. Unpublished records of Iwamoto suggest that there are more than 100 species in all of Australia's waters. Iwamoto and Williams (1999) found 63 species (17 new species; 20 genera) off the western and northwestern coasts of Australia. On the southeast coast of Australia, extensive deep-water trawling by the fisheries research vessel *Kapala* over a period of 26 years is principally responsible for revealing an extremely diverse grenadier fauna off New South Wales (NSW). The number of species now known from NSW is 60 in 21 genera.

The diversity of the NSW fauna is unusually large given the limited extent of coastline [600 nautical miles (n. mi.)] and is probably attributable to the geographic position of NSW, between the species-rich tropical waters to the north and the productive temperate waters to the south. The grenadier fauna of NSW includes species known from the Coral and Tasman seas as well as from the Indian and Southern oceans. Our knowledge of this diversity results from the extensive sampling by the *Kapala* on the NSW slope over a prolonged period, which provided a unique opportunity for the collection of grenadiers.

The purposes of this paper are threefold: (1) to record the species of grenadiers of New South Wales; (2) to provide a key to the species and brief descriptions as an aid to their identification; and (3) to record aspects of their distribution and abundance off NSW, so far as information is available.

Historical Perspective. Most of the grenadiers collected off NSW are housed in the Australian Museum, Sydney (AMS). The earliest AMS specimens were collected in 1906 by the government vessel *Woy Woy* from "a single cast of a small trawl which was built on the principal of one designed and successfully used by the Prince of Monaco. It was lowered in 800 fathoms at a point thirty-five miles due east of Sydney, on the 152nd Meridian" (McCulloch 1907). Grenadiers collected from this trawl were *Caelorinchus innotabilis* (2 specimens), *C. "fasciatus" [maurofasciatus]* (1), *"Macrourus" [Lucigadus] nigromaculatus* (5), and *"Optonurus" [Lepidorhynchus] denticulatus* (6). *Caelorinchus innotabilis* and *Lucigadus nigromaculatus* were subsequently described by McCulloch as new species. It should be noted that the grenadiers and other teleosts collected with them (see McCulloch 1907) are all upper-slope species, which suggests that the depth of this station was, in fact, much less than the stated 800 fathoms and probably around 300 fathoms (550 m).

Between 1920 and 1968, a further 27 grenadier specimens were registered in the AMS collection; these were *C. australis* (3), *C. mirus* (22), and *L. denticulatus* (2), all upper-slope species. The holotype and four paratypes of *C. mirus* are included in this collection (see McCulloch 1926).

In 1970 the collection and study of NSW deep-water fishes was given great impetus with the commissioning of FRV *Kapala* (Plate 1) by the NSW State Government. The 26 m *Kapala* was built as a research vessel designed principally for trawling. Betweeen 1971 and 1997, *Kapala* conducted numerous research surveys on continental shelf and slope trawling grounds between southern Queensland and eastern Victoria. During this period, about 1260 grenadier specimens (55 spp.) from 217 *Kapala* stations in depths between 130 and 1240 m were registered in the AMS collection.

A further 40 grenadiers from off NSW were deposited in AMS by other collectors between 1970 and 1999; these included specimens of *Coryphaenoides striaturus* and *C. filicauda* from depths of 1590 and 2450 m. Additional NSW grenadiers are held by the Museum of Victoria (NMV) in Melbourne (69 specimens, 16 spp.); included are four species not represented in the AMS collections. The I.S.R Munro Ichthyological Collection at the Commonwealth Scientific and Industrial Research Organization, Marine Research Laboratories, Hobart (CSIRO), also has a small collection of grenadiers caught off NSW between 1975 and 1993 (41 specimens, 11 spp.), but this collection contains no additional species to those in AMS and NMV.

PLATE 1. The 26-meter fishery research vessel *Kapala*.

This paper describes the NSW grenadier fauna as represented in the AMS and NMV collections. As the great majority of NSW grenadiers were collected from *Kapala* stations, much of the discussion relates to observations made during *Kapala's* offshore surveys. Relative abundance, depth, and distribution data were collected by Graham on *Kapala* between 1972 and 1997, and during subsequent trawling on a commercial trawler off the southern NSW port of Bermagui in 1999–2001.

MATERIALS AND METHODS

Study Area. New South Wales is on the east coast of Australia between latitudes 28°10′S and 37°45′S (Fig. 1). New South Wales waters extend to the edge of the Australian Fishing Zone (AFZ; 200 n. mi. from land) and include the area around Lord Howe Island (31°30′S, 159°05′E). Apart from a few isolated seamounts and reefs, most of the seabed beyond the continental slope is deeper than 2000 m; some parts of the Lord Howe Rise within the AFZ are as shallow as 1000 m. The NSW continental shelf is narrow, with the shelf break mostly between 15 and 25 n. mi. offshore at a depth of about 200 m. The continental slope (between the 200 and 2000 m isobaths) can be arbitrarily divided into three depth zones. The upper-slope (200–700 m) is mostly between three and five n. mi. in width, with a gradient between 1:10 and 1:20, while the mid-slope (700–1300 m) and lower slope (>1300 m) are relatively much narrower and steeper.

The *Kapala* collected grenadiers from shelf and slope waters between 27°50′S and 38°15′S over a depth range of 130 to 1240 m. Collections were also made from a few mid-slope and lower-slope stations between 800 and 2500 m off Nowra by CSIRO's oceanographic research vessel *Franklin* (NMV specimens). A small number of grenadiers at AMS were collected by *Franklin* with a beam trawl and epibenthic sled on the Lord Howe Rise.

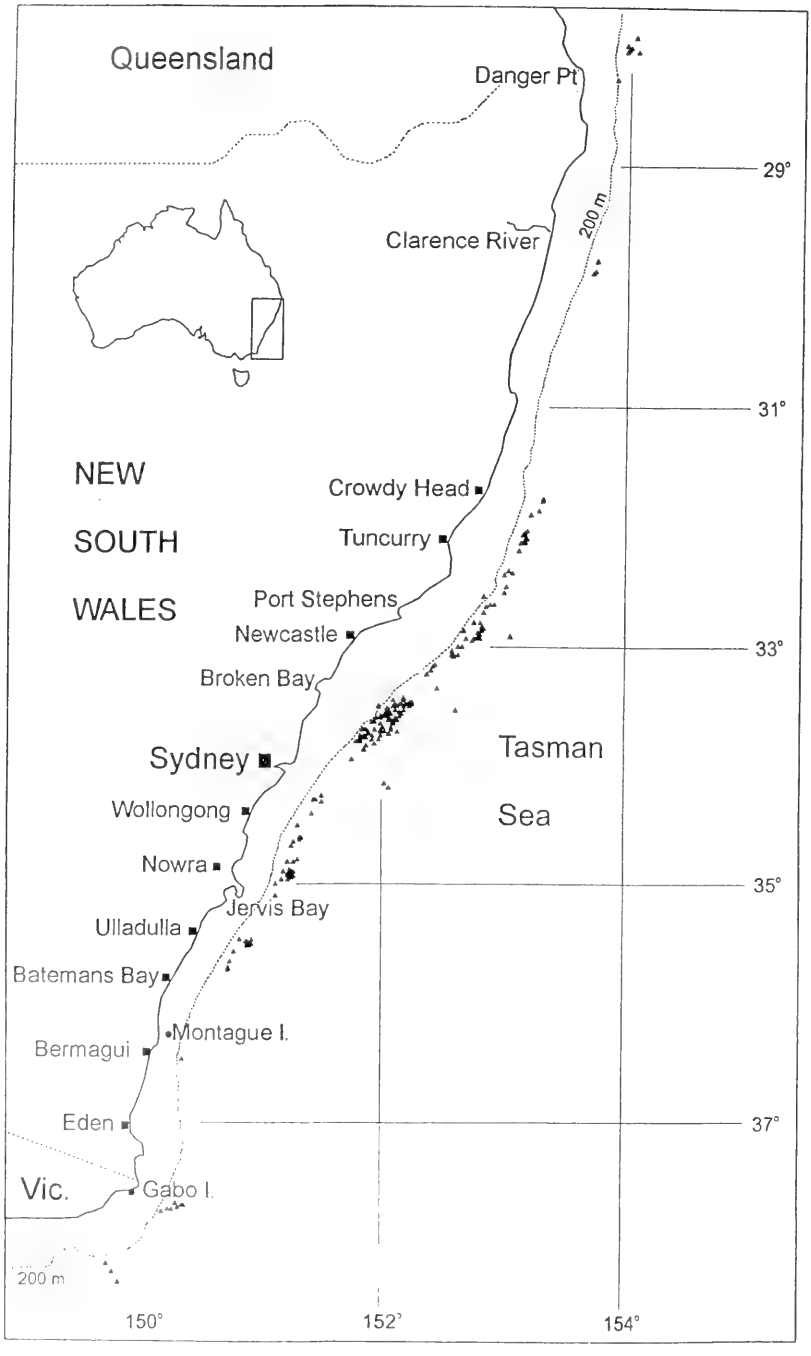

FIGURE 1. Map of New South Wales coast showing FRV *Kapala* stations where grenadiers were collected for AMS.

***Kapala* Trawl Gear and Survey Methods**. A range of net sizes and styles was used during the many *Kapala* exploratory and stock-assessment surveys, with the choice dependent on the purpose of each study. Nets for the capture of prawns ranged in size between 20 and 30 m headline length and were constructed throughout with 45 mm mesh netting. Fish trawls had headline lengths between 20 and 56 m, and were made with relatively large-mesh panels in the front of the net (100–200 mm mesh) and usually with codends of 90 mm mesh. During some surveys, fish trawls were fitted with 45 mm mesh codend liners. Towing speed in upper-slope depths was between 2.5 and 3.5 knots; mid-slope trawling was usually 1.8–2.5 knots. The maximum depth trawled by *Kapala* (1240 m) was limited by the amount of trawl warp carried on her main winch (2500 m). A large mid-water trawl was also deployed in oceanic waters off Sydney-Newcastle on a few occasions in 1977–79 for the capture of bathypelagic species.

Normal practice for exploratory and stock-assessment trawling was to tow along a selected depth for one to two hours. The depth range of upper-slope tows was usually within ± 20 m of the target depth, while on the steeper mid-slope the range was often greater, around ± 40 m of the target. Recorded fishing depths were for the period the trawl was fishing the seabed. Catches were sorted into commercial and non-commercial species for assessment; all grenadiers caught off NSW were considered to be part of the non-commercial component of the catch. A list of all fishes (with approximate numbers) was compiled for each station. Any rarely caught specimens were retained for AMS.

TAXONOMIC DESCRIPTIONS

In the descriptive section of this work, general features of the family, subfamily, and genera are provided separately under each section and in the key. Detailed characters that distinguish the species are given under the species descriptions, although characters previously given in the keys are generally not repeated except for necessary elaboration. For synonymies and additional figures and descriptions of most of the species and genera treated here, the reader is referred to Last et al. (1983), Gomon et al. (1994), Iwamoto and Merrett (1997), Iwamoto and Williams (1999), Merrett and Iwamoto (2000), and references cited in the last three publications. Methods of taking measurements and counts are described in detail in Iwamoto and Sazonov (1988) and in a condensed version in Iwamoto and Williams (1999).

Abbreviations for fins are 1D = first dorsal, 2D = second dorsal, P = pectoral, V = pelvic. Spinous rays in the first dorsal fin are designated with Roman numerals, segmented rays are given in Arabic numerals (e.g., II,10). The splintlike uppermost ray of the pectoral fin is designated with a small *i* (e.g., i16). Counts of gill rakers (GR) are distinguished as to which gill arch the rakers are counted (e.g., first or outermost arch = GR-I, second arch = GR-II) and whether the outer or inner series is counted. Gill-raker counts are usually made on the right side of the fish, with the gill covers pulled back to expose the rakers, which are often quite small. In some species, the upper connection of the gill cover to the body must to severed in order to pull the cover back far enough to expose the rakers. Scale rows are counted in a diagonal series from the first dorsal origin ("below 1D"), mid-base of 1D, and below 2D origin, to, but not including, the lateral-line scale. The count of lateral-line scales includes those from the anterior origin of the lateral line to a point marking the distance equal to that from the snout tip to the origin of the first dorsal fin (viz., the predorsal length) (Fig. 2). Size given is maximum total length, rounded up to the nearest 5 cm. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988). Australian states are abbreviated as follows: New South Wales, NSW; Queensland, Qld; South Australia, SA; Tasmania, Tas.; Victoria, Vic.; Western Australia, WA.

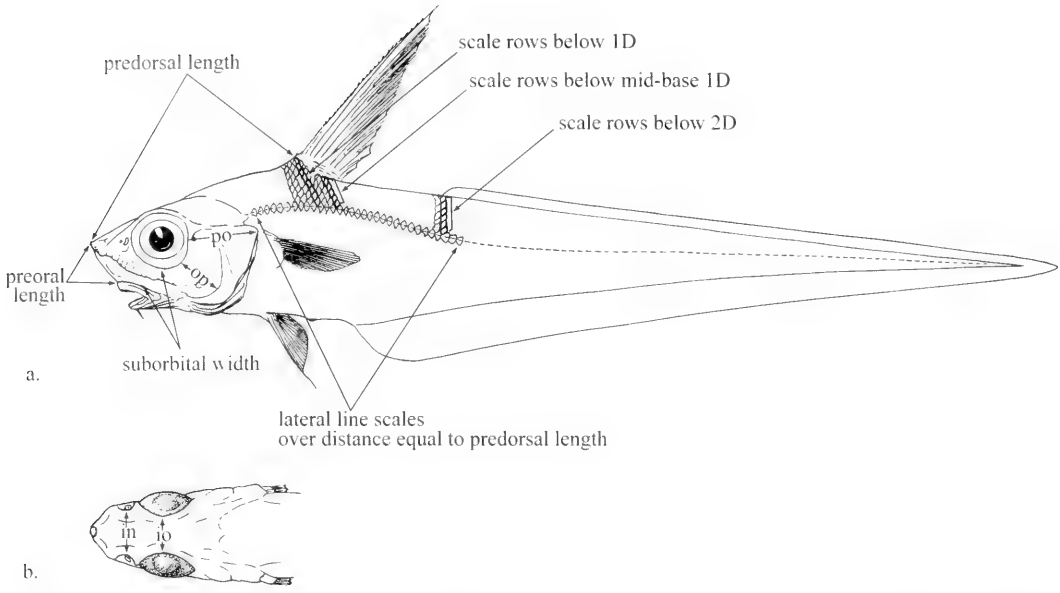

FIGURE 2. Diagrammatic illustration of typical grenadier to show method of counting scale rows and measuring predorsal length, preoral length, and suborbital width; (a) lateral view; (b) dorsal view of head. Abbreviations: *in*, internasal width, *io*, interorbital width, *po*, postorbital length, *op*, opercle to preopercle distance, 1D, first dorsal fin, 2D, second dorsal fin.

RESULTS

***Kapala* Surveys**. Prior to 1970, little was known about the extent and productivity of trawl grounds along the NSW slope. Between 1971 and 1981 exploratory trawling and resource assessment surveys determined the extent of upper-slope trawling grounds and the nature of demersal prawn and fish stocks on those grounds (Gorman and Graham 1975; Graham and Gorman 1985; Andrew et al. 1997). Off northern NSW only two relatively small areas of trawlable seabed were found, one off the Clarence River and the other off the NSW-Queensland border. Apart from a single tow in 740 m off Danger Point, all trawls north of latitude 31°30′S were shallower than 600 m. Because catch rates of commercial fishes were relatively low during early surveys, there was no trawling by *Kapala* in any slope depths off northern NSW after 1978. At present, commercial trawlers occasionally fish for royal red prawns (*Haliporoides sibogae*) and deepwater slipper lobsters (*Ibacus* spp.) in 200–500 m on the Clarence River ground.

In contrast, relatively large areas of trawlable ground with commercial fish stocks were found on the upper-slope off central and southern NSW. A significant trawl fishery for both deep-water fishes and prawns developed during the late 1970s (Tilzey 1994), and today about 40 trawlers continue to fish these grounds. Consequently the majority of *Kapala* upper-slope trawling was done south of Port Stephens, particularly on grounds off Sydney, Ulladulla, and Eden-Gabo Island. This included the final study by *Kapala* before her decommissioning in 1996–97, which was a repeat stock-assessment survey of the upper-slope south of Newcastle (Graham et al. 1997, 2001).

Mid-slope trawl grounds (700–1200 m) were charted in detail by *Kapala* between 1983 and 1989 (Graham 1990). Trawlable seabed on the mid-slope was more restricted in area than on the upper-slope, and very little trawl ground was found in depths below 1000 m. Most fishable ground was located between latitudes 31°40′S and 36°00′S, and consequently, almost all mid-slope stations were in this area. A small number of tows were also made southeast of Gabo Island (37°40′S). No large

stocks of commercial fish were found, but commercial trawlers occasionally target orange roughy (*Hoplostethus atlanticus* Collett, 1889), oreo dories (family Oreosomatidae), and edible dogsharks (family Squalidae) in mid-slope depths off NSW.

Outer shelf grounds (100–200 m) were surveyed off northern NSW in 1978, and between Port Stephens and Gabo Island in 1993–94 (Graham et al. 1995, 1996).

***Kapala* Grenadier Data**. Table 1 shows the distribution by depth and latitude of *Kapala* survey trawls on the NSW outer shelf and slope between 1976 and 1997. For each of these trawls a list of fishes was compiled, and from these data, abundance and distributional information for NSW grenadiers were derived (see species descriptions for details). Figure 1 shows the locations of all *Kapala* stations from which grenadiers were collected for AMS; station numbers, location and depths for these are listed in Appendix 1.

The depth and geographic ranges derived from *Kapala* catches were influenced by the distribution of stations, which, as discussed above, reflected the lack of mid-slope trawling off northern NSW. As Table 1 shows, most trawling was done on the commercially productive grounds off central and southern NSW, the maximum depth trawled was about 1200 m, and no depths greater than 740 m were sampled north of Crowdy Head (31°45′S). The style of trawl used during the various surveys may have also influenced the data. About 75% of upper-slope trawls and 56% of mid-slope trawls were done with large-meshed fish nets, which reduced the likely capture of small specimens. The capture rate by *Kapala* may therefore understate the true abundance of some species of small adult size.

During the period that detailed catch data were recorded (1976–97), grenadiers were caught in 1072 *Kapala* trawls over a depth range of 130–1240 m. Grenadiers were present in about 10% of outer-shelf tows, about half of all tows between 200 and 300 m, and in almost every trawl deeper than 300 m. The number of species caught at each station was related to the trawl gear and depth fished (Fig. 3). Nets with 45 mm codend mesh caught, on average, two more species per station than those with 90 mm mesh, and the mean number of species per trawl increased almost linearly with depth (see Appendix 2 for data). The data also suggest that the grenadier fauna off NSW is relatively rich in spe-

TABLE 1. Distribution by latitude and depth of FRV *Kapala* demersal stations over 100 m trawled between 1976 and 1997. New South Wales distribution and abundance were derived from catches at these stations.

	Depth (m)											
Latitude (°S)	100–199	200–299	300–399	400–499	500–599	600–699	700–799	800–899	900–999	1000–1099	1100–1200	Total
27	0	1	1	0	1	0	0	0	0	0	0	3
28	22	3	3	5	2	0	1	0	0	0	0	36
29	14	7	9	13	4	0	0	0	0	0	0	47
30	11	7	1	0	0	0	0	0	0	0	0	19
31	6	2	1	0	0	0	0	1	1	1	0	12
32	94	8	10	13	9	1	4	10	14	31	0	194
33	104	45	68	96	34	14	15	22	30	23	6	457
34	102	10	13	44	10	7	7	8	18	12	4	235
35	79	53	64	54	33	10	4	9	24	15	3	348
36	71	9	9	6	0	0	0	0	0	0	0	95
37	75	42	68	45	22	6	1	3	3	2	0	267
38	1	4	10	10	6	3	1	0	1	1	0	37
Total	579	191	257	286	121	41	33	53	91	85	13	1750

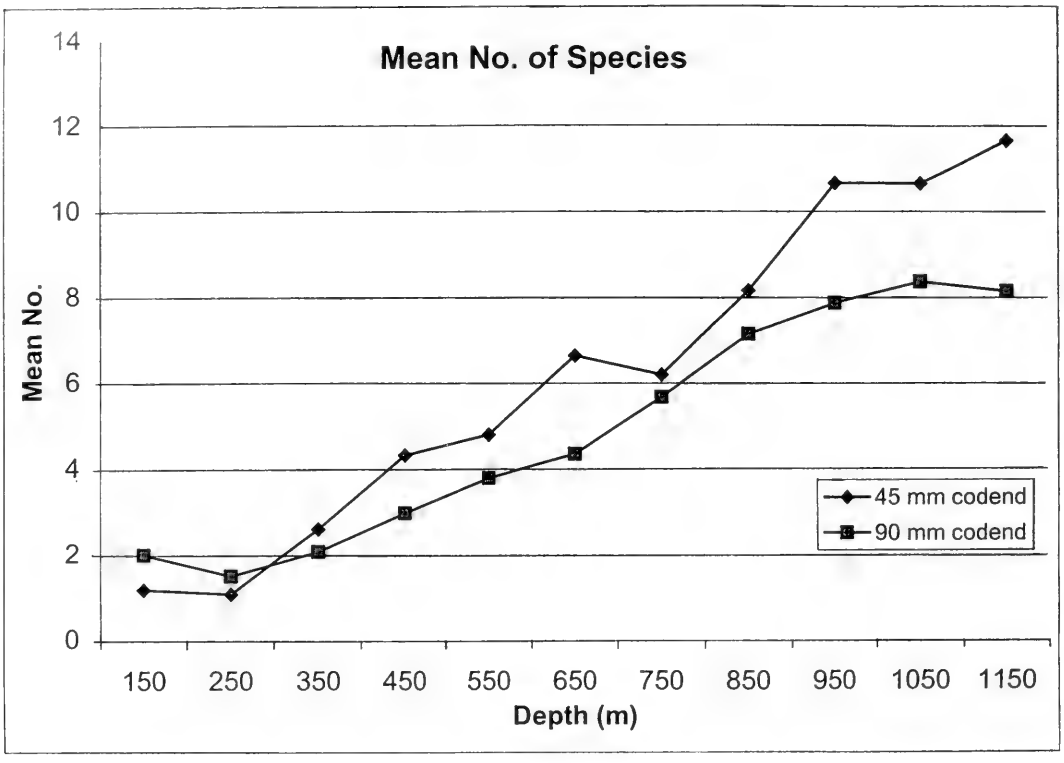

FIGURE 3. Graph showing influence of depth and mesh size to mean number of grenadier species captured off New South Wales by *Kapala*.

cies at depths beyond those sampled by *Kapala*. Apart from a small number of ORV *Franklin* stations, the lower slope and extensive abyssal seabed off NSW is largely unsampled.

Figures 4 and 5 summarize the depth and geographical ranges for each of the 55 species caught by *Kapala*. In Figure 4, the 53 demersal species are ordered according to their minimum depth of capture; those recorded on more than five occasions are divided into "upper-slope" and "mid-slope" groups, and rarely caught species are listed beneath. The same species, ordered by their latitudinal ranges, are shown in Figure 5; the bathypelagic species *Cynomacrurus piriei* and *Odontomacrurus murrayi* are included in this figure. The depth range of the upper slope is arbitrarily defined as 200–700 m and the mid slope as 700–1300 m. Figure 4 shows that while some species fit neatly within these depth categories, many show some overlap, and for those taken in the deepest trawls (>1100 m), no maximum depth range can be defined. There is an overall pattern of gradually increasing depth ranges, but within this a number of depth groupings can be discerned.

Ten species are characteristic of the upper slope. Although the depth ranges of six of these extended to about 800 m or more, each was most abundant in depths less than 700 m. The two species with the shallowest depth ranges, *Caelorinchus mirus* and *C. australis*, were also caught in outer-shelf depths; either or both species were present in about 10% of the 579 outer-shelf trawls. *Lepidorhynchus denticulatus* was the most abundant upper-slope species and also exhibited the greatest depth range (230–1080 m) of any NSW grenadier. Trends in geographic range are also evident for several upper-slope species (Fig. 4). The ranges of three species (*Lucigadus microlepis*, *Ventrifossa nigrodorsalis*, and *Hymenocephalus longibarbis*) with known tropical distributions extended to central or southern NSW; the latter two were caught by *Kapala* as far south as Jervis Bay and Ulladulla,

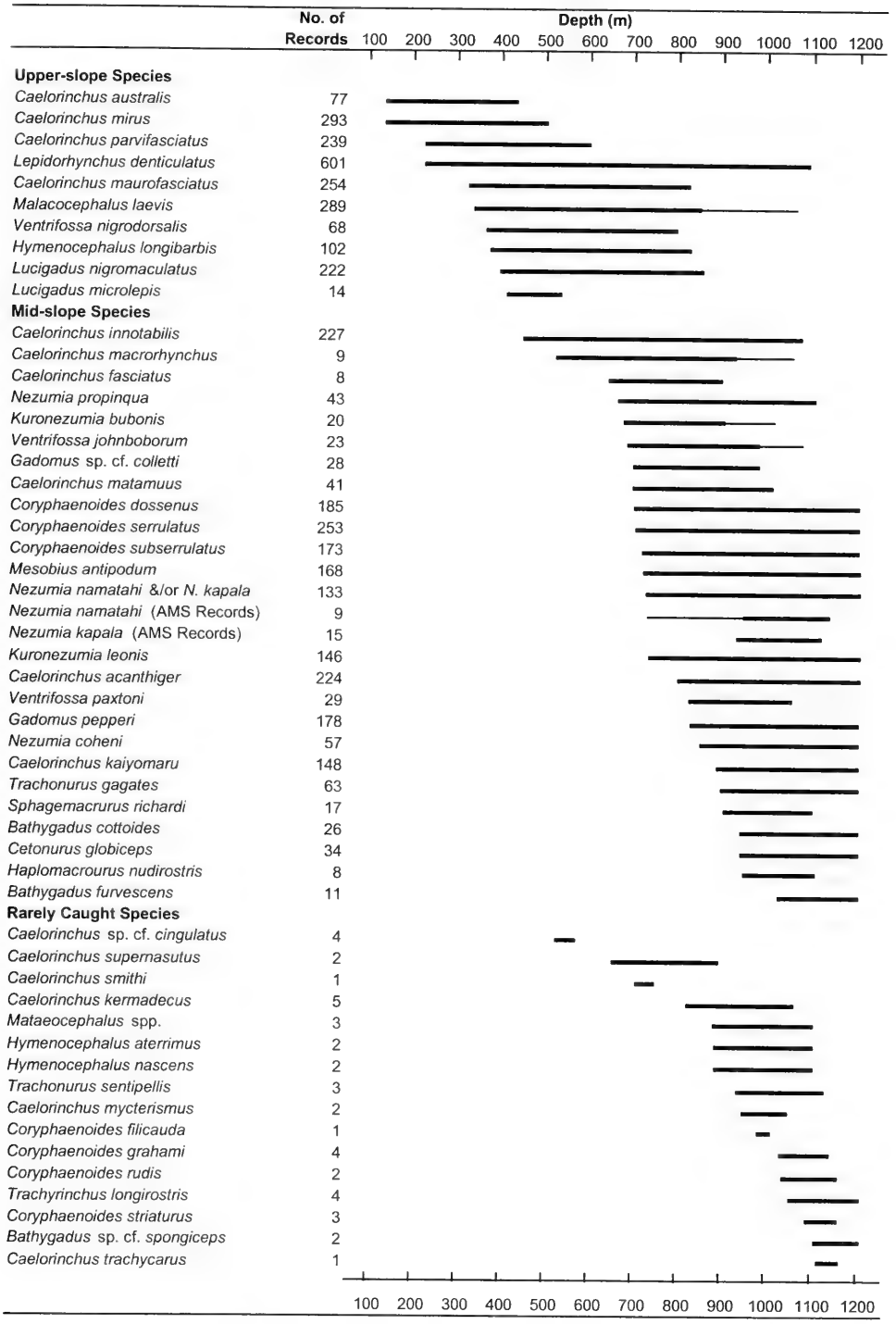

FIGURE 4. Depth distributions for NSW species collected by *Kapala* (thin line represents range or range extension by 1 or 2 observations only).

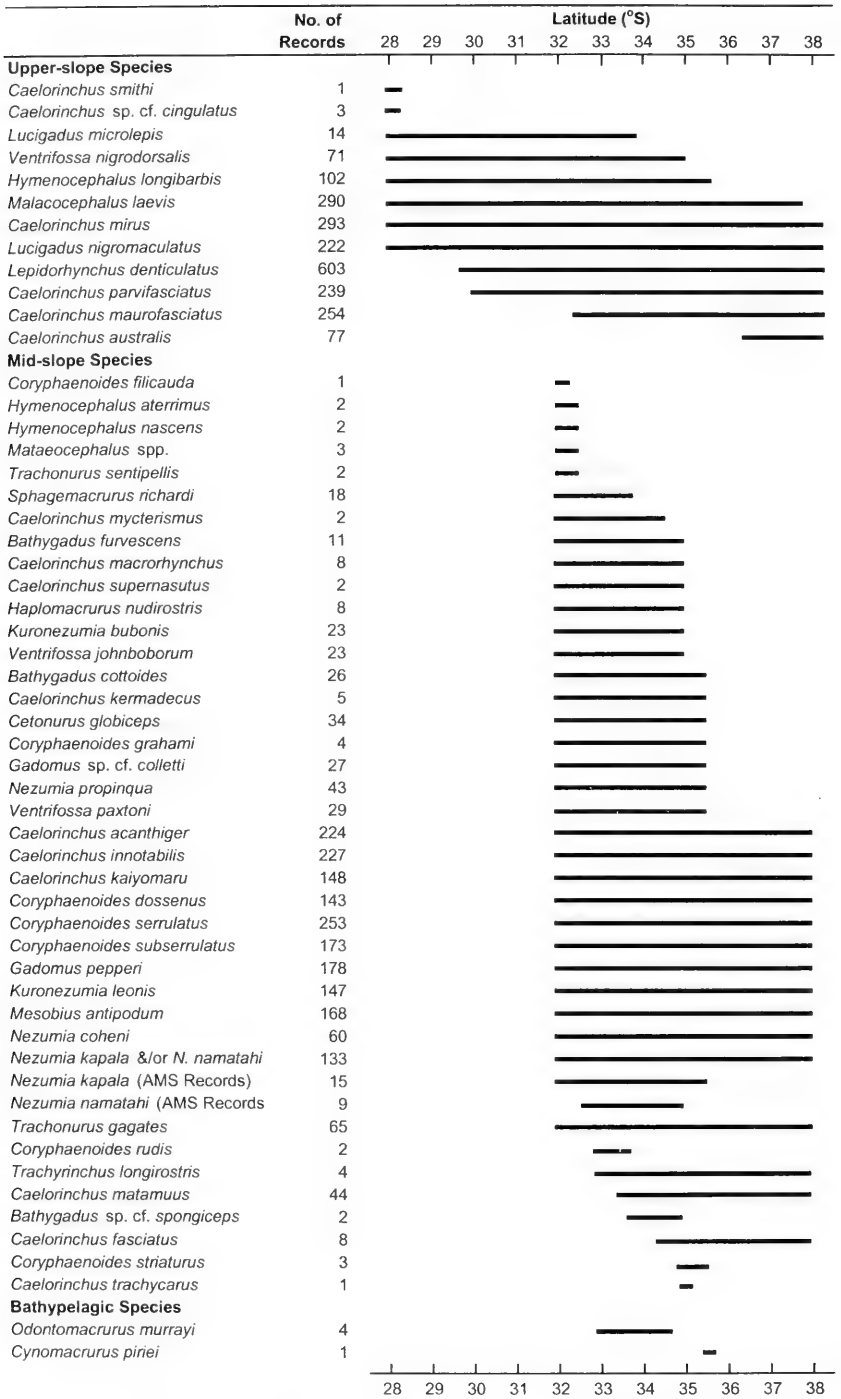

FIGURE 5. Geographical distributions for NSW species collected by *Kapala*.

although recently both were collected (by Graham) further south off Bermagui (36°20′S). Four southern species showed limits to their northern distributions within NSW: *C. parvifasciatus* and *Lepidorhynchus denticulatus* did not extend north of the Clarence River, *C. maurofasciatus* was only caught south of Port Stephens, whereas *C. australis* was restricted to waters south of Batemans Bay.

The depth range of *C. innotabilis* (450–1075 m) spanned both the upper and middle slopes, but the species was most abundant between 600 and 900 m. *Caelorinchus innotabilis* can be included in a group that mainly inhabits the shallower mid-slope depths. This group also includes *Caelorinchus macrorhynchus*, *C. fasciatus*, *C. matamuus*, *Gadomus* sp. cf. *colletti*, *Kuronezumia bubonis*, *Nezumia propinqua,* and *Ventrifossa johnboborum*. They were mostly caught shallower than about 1000 m and mainly between 700 and 900 m, and although all showed relatively extensive geographic ranges, none was abundant in any part of their NSW range. Four of these species are also found in tropical waters; of these, *C. macrorhynchus*, *K. bubonis,* and *V. johnboborum* were caught by *Kapala* south to Jervis Bay, and *N. propinqua* to about Batemans Bay. A juvenile *C. macrorhynchus* was recently collected (by Graham) further south near Montague Island. Two southern species, *C. fasciatus* and *C. matamuus*, were taken as far north as Broken Bay.

Eighteen species (with eight or more captures) were found only in depths greater than 700 m. *Haplomacrourus nudirostris*, *Sphagemacrurus richardi,* and *Ventrifossa paxtoni* are species previously reported from more tropical waters than NSW (Iwamoto and Merrett 1997) and were caught by *Kapala* mostly north of Sydney and only between 800 and 1100 m. The full depth ranges of the remaining species were probably greater than those shown by *Kapala* catches. Six species, *Coryphaenoides dossenus*, *C. serrulatus*, *C. subserrulatus*, *Kuronezumia leonis*, *Mesobius antipodum,* and *Nezumia namatahi*, were caught across the full mid-slope depth range (about 700–1200 m) and on all grounds between Crowdy Head and Gabo Island. Another five species also caught between Crowdy Head and Gabo Island but with greater minimum depths (800–900 m) were *Caelorinchus acanthiger*, *C. kaiyomaru*, *Gadomus pepperi*, *Nezumia coheni*, and *Trachonurus gagates*; *N. kapala* is also likely to be in this group (based on AMS collection; see species description). These 12 species have generally southern distributions, being found around the south coast of Australia and many also off New Zealand. The last three mid-slope species on the list, *Bathygadus cottoides*, *B. furvescens,* and *Cetonurus globiceps,* were mostly caught deeper than 1000 m and are possibly more abundant at depths greater than trawled by *Kapala*.

Species rarely caught by *Kapala* may be put in one or other of the groups discussed above, but there are too few observations to be definitive. Most of these species appear to have been caught at the fringe of either their geographic or depth range. Eight species, *Caelorinchus cingulatus*, *C. kermadecus*, *C. smithi*, *Hymenocephalus aterrimus*, *H. nascens*, *Mataeocephalus* sp., *M. acipenserinus,* and *Trachonurus sentipellis*, are more commonly found in tropical waters (Iwamoto and Merrett 1997). *Kapala* captures of these species were from the most northern stations, although the small size of *Hymenocephalus* spp. and *Mataeocephalus* spp. may have also contributed to their relatively low number of captures. In contrast, *Cynomacrurus piriei,* which was caught once by *Kapala* off the NSW south coast, is primarily a Southern Ocean species (Iwamoto 1990). McMillan and Paulin (1993) reported that *Caelorinchus mycterismus* and *C. supernasutus* are relatively common around northern New Zealand and are also recorded from the Wanganella Bank to the northwest of the North Island. The *Kapala* captures are the only confirmed specimens from the western Tasman Sea. The few specimens of *Bathygadus* sp. cf. *spongiceps*, *Caelorinchus trachycarus*, *Coryphaenoides filicauda*, *C. grahami*, *C. rudis*, *C. striaturus*, and *Trachyrincus longirostris* were caught only in trawls deeper than 1000 m and are possibly more abundant at depths greater than those sampled by *Kapala*.

TAXONOMY

We use grenadier as a collective term for four distinct groups of gadiform fishes, each of which has at one time or another been considered as a separate family. In fact, the bathygadids have been placed in a separate suborder (Gadoidea) from the others (Macrouroidea) (Howes 1989). The problems of relationships have yet to be adequately resolved, so for this paper we have chosen to take a conservative approach as used by Iwamoto and Merrett (1997). It should be noted that the long-tailed hakes (*Macrouronus* spp., Merlucciidae) are also called grenadiers. The southern Australian species, *M. novaezealandia*, is known as blue grenadier (Last et al. 1983; Gomon et al. 1994). All grenadiers have a long, tapered tail with long dorsal and anal fins that meet posteriorly without a noticeable caudal fin, and the anal fin lacks an elevated lobe. The trachyrincines are reported to have a caudal fin, but it is so rudimentary that examination under magnification is usually necessary to observe its presence. One often finds specimens with what appears to be a sizable caudal fin, but that structure is a result of loss of the tail tip and an overgrowth of the anal and dorsal fin rays. Grenadiers can be distinguished from other deep-sea fishes that have a long tapered tail by a combination of the lack of a distinct caudal fin, one or two dorsal fins, a single, long, low anal fin lacking lobes or dips in its profile, pelvic fins present (in all but *Macrouroides inflaticeps*), well separated, and consisting of five to as many as 18 rays, and no teeth on roof of mouth or on tongue.

KEY TO THE FAMILIES AND SUBFAMILIES OF GRENADIERS FROM NEW SOUTH WALES

1a. A single long-based, low dorsal fin; head enormous, bulbous and spongy; eyes tiny, more than 10 in head length (Fig. 6) . . . . . [Macrouridae, subfam. Macrouroidinae—not yet found off NSW but can be expected]
1b. Two dorsal fins; head variously shaped, not especially huge and bulbous; eyes less than 10 in head length 2

2a. First and second dorsal fins separated by a distinct gap (Fig. 7a); gill rakers all short, tubercular or tablike (Fig. 8a); opening of first gill slit restricted by membrane across upper and lower arms of gill arch (Fig. 9) . . . . . Macrouridae, subfam. Macrourinae (Fig. 10)
2b. First and second dorsal fins closely approximated, without a distinct gap (Fig. 7b); gill rakers slender, lathlike (Fig. 8b); opening of first gill slit unrestricted by membrane. 3

3a. Mouth subterminal to inferior, a long, stout, sharp snout; scales covered with spinules; series of sharply spined scutes present along bases of dorsal and anal fins (Fig. 11) . . . . . Macrouridae, subfam. Trachyrincinae
3b. Mouth essentially terminal, snout rounded not protruding (Fig. 12); scales all smooth; no scutes on body . Bathygadidae

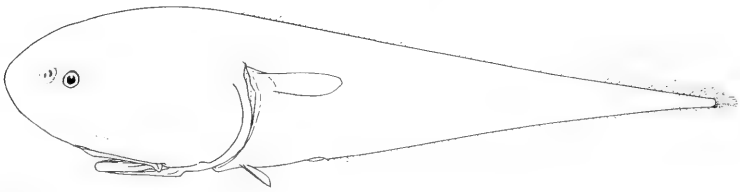

FIGURE 6. Diagrammatic illustration of a Macrouroidinae (*Squalogadus modificatus*).

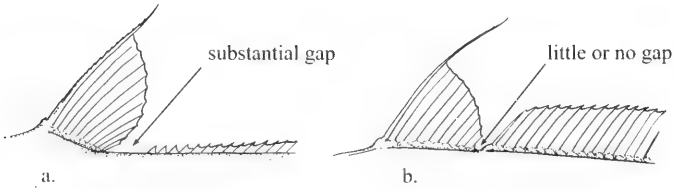

FIGURE 7. (a) First and second dorsal fins separated by a distinct gap; (b) first and second dorsal fins closely approximated.

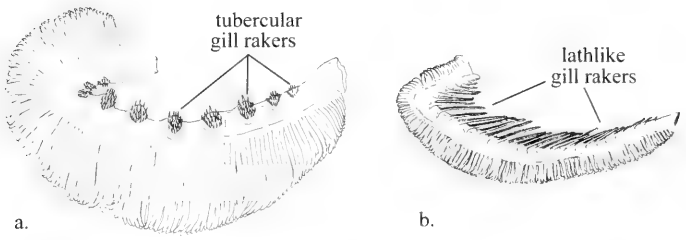

FIGURE 8. (a) Gill rakers on outer arch short and tubercular; (b) gill rakers long and slender.

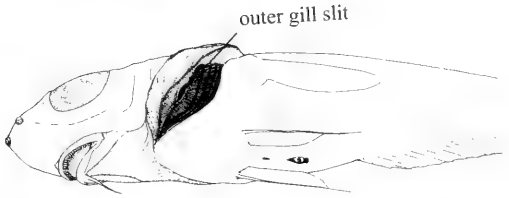

FIGURE 9. Opening of first (outermost) gill slit restricted by membranes across upper and lower arms of gill arch.

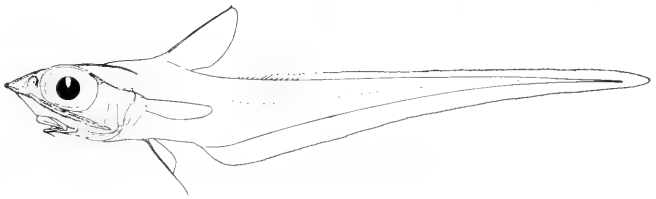

FIGURE 10. Diagrammatic illustration of a Macrourinae (*Caelorinchus* sp.).

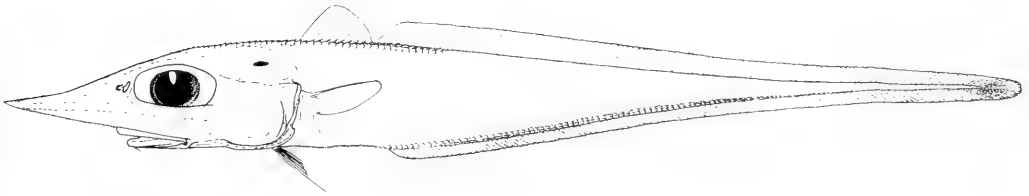

FIGURE 11. Diagrammatic illustration of a Trachyrincinae (*Trachyrincus sp.*).

FIGURE 12. Diagrammatic illustration of a Bathygadidae (*Bathygadus* sp.).

FAMILY BATHYGADIDAE

DISTINGUISHING FEATURES. — Two dorsal fins, the second beginning immediately behind first without a pronounced gap. Outer gill rakers on first arch long, lathlike, 20 or more total. Branchiostegal rays 7. No membrane restricting first gill slit. Pelvic fin rays 8–10; first dorsal fin with smooth, flexible spinous ray. No spinules on scales. Large terminal mouth and no protruding snout.

REMARKS. — Only two genera are recognized, *Bathygadus* and *Gadomus*, with about 35 nominal species; the taxonomy of the group is still not fully resolved. Members of the family are found in tropical to temperate waters, and the family is widely distributed in the Atlantic, Indian, and Pacific oceans, but notably absent (as are many macrourid genera) in the eastern North Pacific. Bathygadids are abundant throughout the Indian Ocean and the western South Pacific, but their occurrence and abundance in the central and eastern South Pacific is uncertain because of the lack of sampling in those regions (aside from the Nazca and Sala y Gomez ridges in the southeastern Pacific; see Sazonov and Iwamoto 1992). Contrary to Howes and Crimmen's (1990:201) statement, the family is not found in the Southern Ocean as it is usually defined (see for example, Gon and Heemstra 1990), as the Kermadec Islands and Lord Howe Rise, from which they cite occurrences of the family, have never been considered part of the Southern Ocean.

REFERENCES. — Gilbert and Hubbs (1920); Howes and Crimmen (1990); Iwamoto (1990).

KEY TO GENERA AND SPECIES OF BATHYGADIDS FROM NEW SOUTH WALES

1a. Chin barbel well developed; ground color of body cream to light brown; first dorsal, pectoral, and pelvic fins with stout, greatly produced rays (Fig. 13) . . . . . (*Gadomus*) 2
1b. Chin barbel absent; ground color of body dark, usually blackish; rays of first dorsal, pectoral, and pelvic fins weak, anterior ray of fins if produced, distally hair thin (Fig. 14) . . . . . (*Bathygadus*) 3

2a. Outer gill rakers 24–25 total, longest about length of longest gill filaments; chin barbel about 3 times orbit diameter; mouth pale; all fins black; pyloric caeca short, more than 100 . . . . . *Gadomus* sp. cf. *colletti*
2b. Outer gill rakers 28–31 total, longest about twice length of gill filaments; chin barbel about 1–2 times orbit diameter; mouth black; fins dark but not intensely black; pyloric caeca long, about 75 . . . . . *Gadomus pepperi*

3a. Head broad, interorbital width 30–40% (Fig. 15a); orbit diameter 16–22%; paired fins dusky to black; flesh soft, head bones weak 4
3b. Head narrow, compressed, interorbital width 26–30% (Fig. 15b); orbit diameter 21–23%; paired fins black; flesh firm, head bones rather strong . . . . . *B. furvescens*

4a. Pyloric caeca 8–12; P i10–i15 (usually i12–i14); length longest gill rakers 14–20% HL; suborbital width 16–19% HL; small adult size, <30 cm . . . . . *B. cottoides*
4b. Pyloric caeca 15–28, usually 20–28; P i14–i18; length longest gill rakers 7–16% HL; suborbital width 12–16% HL; large adult size, >46 cm . . . . . *B.* sp. cf. *spongiceps*

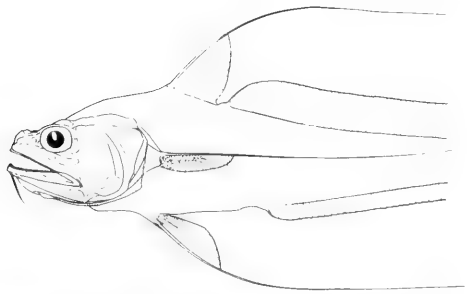

FIGURE 13. Diagrammatic illustration of a *Gadomus* sp.

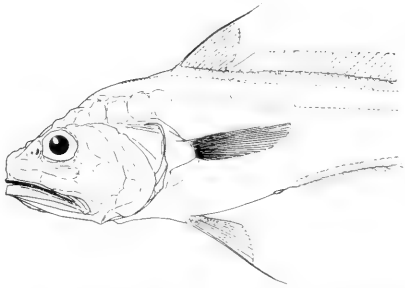

FIGURE 14. Diagrammatic illustration of a *Bathygadus* sp.

Genus *Bathygadus*

DISTINGUISHING FEATURES. — Distinguished from *Gadomus* by absence of chin barbel, more fragile head bones and head covering, generally darker color (usually mostly blackish), absence of extremely long, well-developed rays in dorsal and pectoral fins.

REMARKS. — Three species known from NSW, each widely distributed in parts of the Indian and Pacific oceans; two species found in other parts of Australia.

REFERENCES. — Gilbert and Hubbs (1920); Howes and Crimmen (1990).

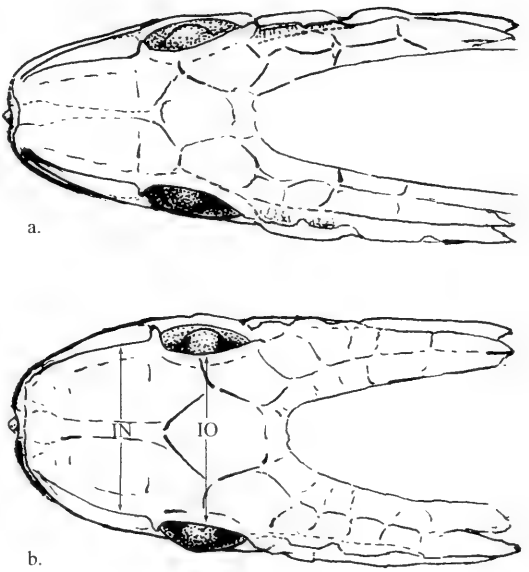

FIGURE 15. Comparison of internasal width (IN) and interorbital space (IO) in (a) *Bathygadus furvescens* and (b) *Bathygadus* sp. cf. *spongiceps*.

Bathygadus cottoides Günther, 1878
Fig. 16

DISTINGUISHING FEATURES. — D II,8–10, P i10–i14, rarely i15, V 9 (rarely 8 or 10); outer GR-I (4–6)+(19–21), total 25–28, GR-II (outer) 17–20 total; pyloric caeca 8–12. Measurements in percent HL: snout length 30–36; internasal width 31–35; interorbital width 31–40; orbit diameter 16–21; suborbital width 16–19; distance orbit to angle of preopercle about 49–59 (sometimes less); upper jaw length 49–59; height ascending premaxillary process 13–16; vent to anal fin origin 9–29; length pectoral fin 41–86; length pelvic fin 49–66; length outer gill raker 14–20. Outer pelvic ray in some specimens moderately prolonged, but most others lack produced rays; pectoral fin rays not extending beyond anus. Teeth bands relatively narrow, 7 or 8 teeth wide at broadest part of premaxillary band, 4 or 5 wide in broadest part of dentary band. Fin rays dark dusky to black. Flesh and head bones rather soft and weak.

SIZE. — Maximum size about 30 cm.

DISTRIBUTION. — Australia (NSW, Vic., Tas., SA, WA), New Zealand and southern Africa, in depths of about 1000 m to more than 1500 m.

NSW CAPTURES. — Taken by *Kapala* between Crowdy Head and Batemans Bay in depths greater than 950 m. One specimen (AMS I.29318-001) captured in 1325 m by ORV *Franklin* near Lord Howe Island. *Kapala* captured 56 specimens in 26 tows (or 14% of *Kapala* tows deeper than 900 m). Because of its small adult size (most specimens less than 20 cm), *B. cottoides* is probably more abundant than its trawl capture rate suggests.

REMARKS. — This species can be confused with small individuals of *B. furvescens*, but the lower counts of pectoral fin rays and pyloric caeca, the wider head, and the smaller orbit of *B. cottoides* are characters that differentiate the two species.

REFERENCE SPECIMENS. — AMS I.24978-005 (3 spec.); K84-20-04. AMS I.25095-004 (1 spec.); K84-20-05. AMS I.26000-010 (1 spec.); K86-01-08. AMS I.27638-003 (1 spec.); K88-11-01. AMS I.27717-001 (1 spec.); K88-04-08. AMS I.29310-001 (1 spec.); ORV *Franklin* 28°44.08′S, 161°54.59′E; 1325 m; 4 May 1989. AMS I.29745-007 (1 spec.); K89-18-02. AMS I.29801-002 (1 spec.); K89-08-02. AMS I.39052-002 (3 juveniles); K89-18-04.

REFERENCES. — Iwamoto and Merrett (1997)(in part); Merrett and Iwamoto (2000).

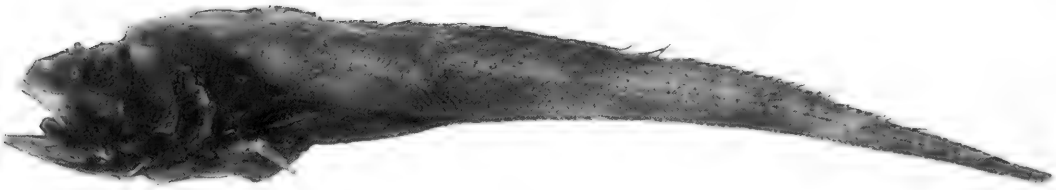

FIGURE 16. *Bathygadus cottoides* Günther, 1878. AMS I.24978-005. From *Kapala* stn K84-20-04, off Broken Bay, NSW, in 1070-1125 m.

***Bathygadus furvescens* Alcock, 1894**
Fig. 17

DISTINGUISHING FEATURES. — Holotype data in square brackets [ ]. D II,8–9 [10], P i15–i19 [i16], V 8–9 [8]; GR-I (outer/inner) (5–6)+(18–20)[6+18]/(3–4)+(15–16)[3+16], totals 23–26/18–19, GR-II 2+(14–15)[2+15]/(2–3)+(14–16)[2+15], totals 16–17/17–18; pyloric caeca 20–22[20]. Measurements (in percent HL): snout length [26] 28–30; internasal width 24; interorbital width [26] 29–30; orbit diameter [21] 21–23; suborbital width 14–15; postorbital length [51] 51–52; distance orbit to preopercle [48] 48–50; length upper jaw [57] 56–59; length pectoral fin [61] 71–81; length pelvic fin 67–83; length longest gill raker 14–15. Fins well developed; pectoral and pelvic fins long, extending to or beyond origin of anal fin; pelvic fin with distally filamentous elongated outer ray. Flesh and head bones relatively stout and more like that of *Gadomus*. Teeth tiny, in broad villiform band in both jaws, premaxillary band about 10 to 12 teeth at widest point, dentary band about 7 or 8 teeth at widest. Paired fins black, median fins black to dark dusky.

SIZE. — To approximately 55 cm.

DISTRIBUTION. — Known only from the holotype taken off the Maldives in 1315 m and the current specimens from NSW and Tasman Sea, but can be expected in other parts of the Indian Ocean and western Pacific. In addition to *Kapala* material, AMS specimen (I.29338-002) was captured in 1050 m on the Lord Howe Rise to the east of the Australian Fishing Zone.

NSW CAPTURES. — *Kapala* caught 14 specimens of *B. furvescens* at 11 stations between Crowdy Head and Jervis Bay, in depths between 1000 and 1240 m. It was present in only 11% of all *Kapala* tows deeper than 1000 m, but is possibly more abundant at greater depths.

REMARKS. — These NSW specimen agree rather closely with the holotype, for which count and measurement data in the Distinguishing Features section were provided by Yuri I. Sazonov (ZMMGU) and Yuri N. Shcherbachev (IOAN). The snout length, interorbital width, and pectoral fin length in the holotype were slightly shorter than in the NSW specimens examined, and the count of first dorsal fin rays was high. Alcock (1894:14) gave the pyloric caeca count as 20 (Sazonov and Shcherbachev counted only 18). These data fall well within the expected range of variation. The pectoral fin length in the holotype may have been longer in the fresh specimen than when examined by Sazonov and Shcherbachev. Alcock (*ibid.*) stated that the fin "... tips reach beyond the origin of the anal" and "the length ... is not quite equal to that of the postrostral portion of the head."

Gilbert and Hubbs (1920:388–390) recorded *B. furvescens* from Indonesia and the Philippines. Howes and Crimmen (1990:195) erroneously referred these to *B. cottoides* (see Iwamoto and Merrett 1997:479 for comments on Howes and Crimmen's treatment of *B. furvescens*). Our examination of three of the five specimens (CAS-SU 25442, CAS-SU 25443, CAS-SU 25444) suggested that Gilbert and Hubbs may have had a species different from *B. furvescens*. The three specimens were small and in poor shape when examined, however, and certain of our measurements may not have been entirely accurate. Notably, all three had 15 pyloric caeca, although Gilbert and Hubbs recorded 20 in one of

five specimens (they did not state which one). Additional material from the general region of the Philippines and Indonesia must be examined to properly determine which species actually occur there.

REFERENCE SPECIMENS. — AMS I.24355-016 (1 spec.); K83-18-02. AMS I.25273-003 (1 spec.); K84-11-09. AMS I.26001-016 (2 spec.); K86-01-09. AMS I.28070-002 (1 spec.); K88-11-02. AMS I.28372-002 (1 spec.); K88-08-05. AMS I.28712-002 (1 spec.); K88-10-02. AMS I.29338-002 (1 spec.); ORV *Franklin* stn FR0580-25, 28°05.76′S, 163°06.04′E; 1051 m; 5 May 1989. AMS I.29812-002 (1 spec.); K89-15-02. AMS I.30738-003 (1 spec.); K89-12-02.

REFERENCE. — Alcock (1894).

Bathygadus sp. cf. *spongiceps* Gilbert and Hubbs, 1920

Fig. 18

DISTINGUISHING FEATURES. — D II,8–10, P i14–i18, V 9 (rarely 8 or 10); GR-I (outer) (5–6)+19–20, total 25–26, GR-II (outer) 17–19; pyloric caeca 15–28, usually 20–28. Measurements (in percent HL): snout length 30–33; internasal width 31–34; interorbital width 32–39; orbit diameter 16–22; suborbital width (bony) 12–16; postorbital length 52–55; distance orbit to preopercle 48–53; length upper jaw 54–59; length pectoral fin 47–62; length pelvic fin 46–71; length outer gill raker 7–16. Outer pelvic ray in some specimens moderately prolonged, but most lack produced rays; pectoral fin not extending beyond anus. Teeth bands relatively narrow to moderately broad, 7–12 teeth wide at broadest part of premaxillary band, 4–8 wide in broadest part of dentary band. Fin rays dusky to dark, but generally not black. Flesh and head bones rather soft and weak.

SIZE. — To approximately 50 cm.

DISTRIBUTION. — From most of the southwestern Pacific, New Zealand, Australia (NSW, WA), Indonesia, and the Philippines. Depth range about 900–1500 m.

NSW CAPTURES. — A single specimen taken at each of the two deepest *Kapala* tows (1130–1240 m), off Sydney and Jervis Bay; possibly more abundant at greater depths.

REMARKS. — Iwamoto and Williams (1999) found color differences in their material of *B. spongiceps* from Western Australia, with some specimens considerably blacker than others, but they found no other characters that would suggest specific differences. Merrett and Iwamoto (2000) examined specimens from the New Caledonian region that appeared to be identical to *B. spongiceps* except for slight differences in the dentition of the lower jaw and counts of pyloric caeca. They called their specimens *B.* sp. cf. *spongiceps*. We consider our NSW specimens as identical to the New Caledonian species and have therefore followed Merrett and Iwamoto's designation. More specimens of *B. spongiceps* from the type locality must be examined and compared with specimens from other areas.

REFERENCE SPECIMENS. — AMS I.26001-005 (1 spec.); K86-01-09. AMS I.30394-03 (1 spec.); K89-16-02.

REFERENCES. — Iwamoto and Merrett (1997)[in part; most specimens *B. cottoides*]; Iwamoto and Williams (1999); Merrett and Iwamoto (2000).

Genus *Gadomus*

DISTINGUISHING FEATURES. — *Gadomus* and *Bathygadus* specimens are readily separated by the former having a firmer body, stronger head bones and fin rays, and paler overall color of body. Almost all species of *Gadomus* have a long chin barbel, although two species have small or rudimentary ones, and most have greatly elongated rays in one or more fins. Teeth are generally finer and in broader bands in *Gadomus*.

REMARKS. — The taxonomy of the genus in the western Pacific and Indian Ocean is yet to be adequately resolved. Howes and Crimmen (1990) distinguished two groups based on gill raker counts.

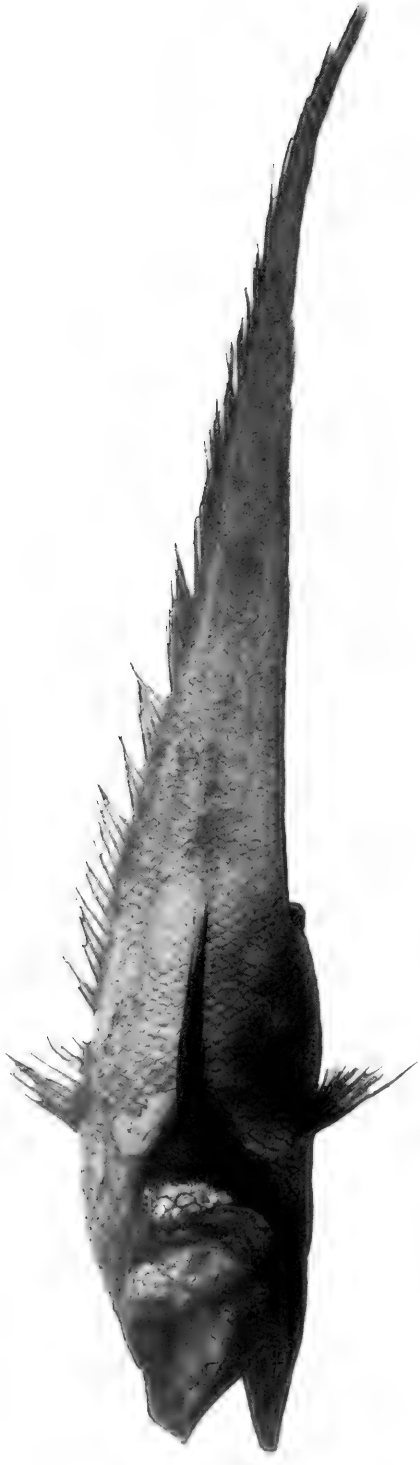

FIGURE 17. *Bathygadus furvescens* Alcock, 1894. AMS I.25273-003. From *Kapala* stn K84-11-09, east of Nowra, NSW, in 1161–1207 m.

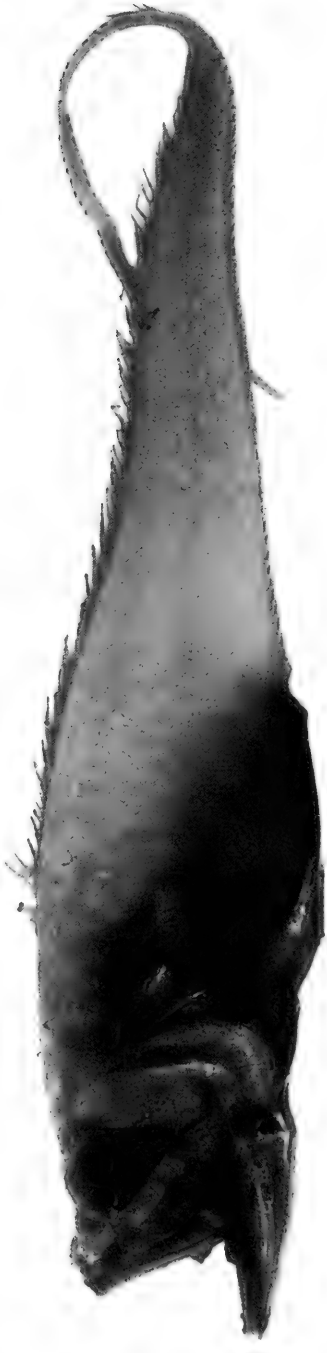

FIGURE 18. *Bathygadus* sp. cf. *spongiceps* Gilbert and Hubbs, 1920. AMS I.26001-005. From *Kapala* stn K86-01-09, off Broken Bay, NSW, in 1116–1207 m.

One of the New South Wales species falls in the group with low counts, the other (*G. pepperi*) in the high-count group. Iwamoto and Williams (1999) provide a full account of both species.

***Gadomus* sp. cf. *colletti* Jordan and Gilbert, 1904**
Fig. 19

DISTINGUISHING FEATURES. — D II,10; P i16–i21; V 8; outer gill rakers short, about length of gill filaments, (4–5)+(19–21), 24–25 total; pyloric caeca small, very numerous, more than 100. Barbel thick, long, about 3 times diameter of orbit; gums and lower branchiostegal membrane pale; all fins black; elongated dorsal ray less than twice head length, an extremely long upper pectoral ray, outer pelvic ray about equal to or less than head length.

SIZE. — To 30 cm.

DISTRIBUTION. — So far known only from Australia (NSW, WA), in 500–1150 m.

NSW CAPTURES. — Caught in a relatively narrow depth range of 690–975 m between Crowdy Head and Batemans Bay, with most taken north of Sydney. Of the 65 specimens from 27 *Kapala* stations (15% of tows in 700–1000 m), 30 specimens were from two tows off Port Stephens; all other stations yielded fewer than five specimens per tow.

REMARKS. — Distinguished from *G. pepperi* by its lower gill raker count, shorter rakers on the first gill arch, generally shorter elongated fin rays, and its pale mouth and tongue. Iwamoto and Williams (1999) discuss their reluctance to identify this species as *G. colletti*, which is described as having a blackish buccal cavity, in contrast to the distinctly pale buccal cavity in the Australian specimens.

REFERENCE SPECIMENS. — AMS I.29813-006 (1 spec.); K89-06-05. AMS I.24979-011 (1 spec.); K84-16-04. AMS I.19862-006 (1 spec.); K76-23-01. AMS I.24659-001 (1 spec.); K84-06-04. Others listed in Iwamoto and Williams (1999).

REFERENCE. — Iwamoto and Williams (1999).

FIGURE 19. *Gadomus* sp. cf. *colletti* Jordan and Gilbert, 1904. AMS I.24659-001. From *Kapala* stn K84-06-04, off Broken Bay, NSW, in 914–933 m.

***Gadomus pepperi* Iwamoto and Williams, 1999**
Fig. 20

DISTINGUISHING FEATURES. — 1D II,9; P i14–i18 (rarely i20); V 8; outer gill rakers long, twice length of gill filaments, (5–6)+(22–25), total 28–31; pyloric caeca about 75 long, slender. Barbel slender, length about one to two times orbit diameter; interorbital width 18–23% of HL; mouth all black; gular membrane pale, branchiostegal membrane blackish, lips dark; fins dark but not intensely black, tail tip dusky; first dorsal, pectoral, and pelvic fins with a prolonged ray generally exceeding twice head length.

SIZE. — To 40 cm.

DISTRIBUTION. — Australia (Qld, NSW, west to WA), in 800–1500 m.

NSW CAPTURES. — Relatively common between Crowdy Head and Gabo Island in 825–1200 m. Recorded from 178 *Kapala* stations (including 94% of all tows deeper than 900 m); usually more than 10 specimens per tow.

REMARKS. — Distinguished from *G.* sp. cf. *colletti* by its higher gill raker counts, fewer pyloric caeca, shorter barbel, dark mouth, pale gular membrane, longer fin rays, and less intensely black fins.

REFERENCE SPECIMENS. — AMS I.24059-002 and I.24059-020 (7 spec.); K83-09-02. Others listed in Iwamoto and Williams (1999).

REFERENCE. — Iwamoto and Williams (1999).

Family Macrouridae

DISTINGUISHING FEATURES. — The most noticeable feature that separates this family from the bathygadids is the protruding snout (the nasal bones have an anteriorly directed medial process that is lacking in the bathygadids). Exceptions to this are *Haplomacrourus nudirostris* and *Kuronezumia spp.*, which may lack a protruding snout in adults, but unlike bathygadids they have small mouths. In addition, almost all macrourids have spinules on the scales. The exceptions are some species of *Hymenocephalus*, which may have lost the spinules secondarily.

REMARKS. — This large family contains about 300 species, many of which have yet to be described. Three subfamilies are generally recognized, although each may warrant full family status. Subfamily Macrourinae contains most of the 300 plus species in about 30 genera; Trachyrincinae has about seven species in two genera; and Macrouroidinae has only two species in two genera.

REFERENCES. — Okamura (1970, 1989); Marshall (1973).

SUBFAMILY MACROURINAE

DISTINGUISHING FEATURES. — First dorsal fin high, the segmented rays preceded by one rudimentary or spikelike spinous ray closely adpressed to a long spinous ray; first dorsal fin separated from second dorsal by a distinct gap; anal fin rays much better developed (usually longer and stouter) than those of second dorsal fin in almost all species. Branchiostegal rays 6–7 (rarely 8). Gill rakers short, usually tubercular; the outer gill arch closely attached to gill cover by membrane, greatly reducing size of outermost gill slit.

FIGURE 20. *Gadomus pepperi* Iwamoto and Williams, 1999. AMS I.24059-002. From *Kapala* stn K83-09-02, east of Broken Bay, NSW, in 933–969 m.

KEY TO GENERA AND SOME SPECIES OF MACROURINAE FROM NEW SOUTH WALES

(Adapted from Iwamoto and Williams 1999. Species in square brackets are not yet recorded from NSW but can be expected.)

1a. Second spinous ray of first dorsal fin smooth (Fig. 21a). 2
1b. Second spinous ray of first dorsal fin serrated along leading edge (weakly or much reduced in some) (Fig. 21b) 9

2a. Snout stoutly supported and pointed; a continuous suborbital ridge of coarsely spined scales extending from snout tip to preopercle angle, terminating in a sharp point . . . . . *Caelorinchus* (Fig. 22)
2b. Snout strongly to weakly supported, rounded to pointed; suborbital ridge, if present, not continuous from snout tip to angle of preopercle and not terminating in a sharp point 3

3a. Broad areas of fine, parallel black lines (ventral striae) overlying silvery ground on ventral surfaces of chest, shoulder girdle, along each side of isthmus, and belly (Fig. 23, 24) 4
3b. No ventral striae 5

4a. Ventral striae extend alongside anterior half or more of anal fin base; 6 branchiostegal rays; no lenslike light organ on chest; attains more than 50 cm TL . . . . . *Lepidorhynchus denticulatus* (Fig. 23)
4b. Ventral striae rarely extend posterior to anus; 7 branchiostegal rays; a small lens of light organ on chest; adults small, usually less than 23 cm TL. . . . . *Hymenocephalus* (Fig. 24)

5a. Lower jaw with large, widely spaced, fanglike teeth in one row 6
5b. Lower jaw with rather small teeth in more than one row 8

6a. Head pores small; grooved lateral line complete to end of tail; chin barbel present; 7 branchiostegal rays . . . . . *Malacocephalus laevis* (Fig. 25)
6b. Large open pores on head; grooved lateral line interrupted posterior to first dorsal fin; no chin barbel; 6 branchiostegal rays 7

7a. Anus removed from anal fin, usually about midway between pelvic fin and anal fin, preceded by a small black fossa of light organ between pelvic fins; grooved lateral line single, short, terminating at vertical behind first dorsal fin; abdomen short, distance isthmus to anus less than half head length . . . . . *Odontomacrurus murrayi* (Fig. 26)

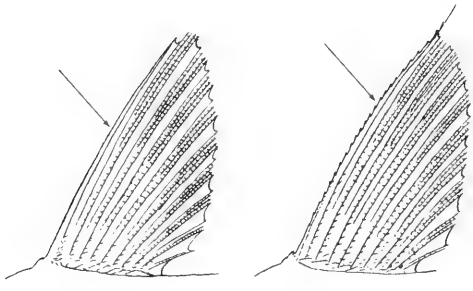

FIGURE 21. Leading edge of second spinous ray of first dorsal fin smooth (a) and serrated (b).

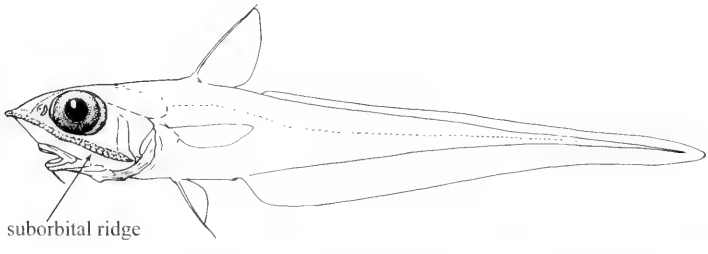

FIGURE 22. Suborbital ridge in *Caelorinchus* extending from snout tip to preopercle angle, terminating in a sharp point.

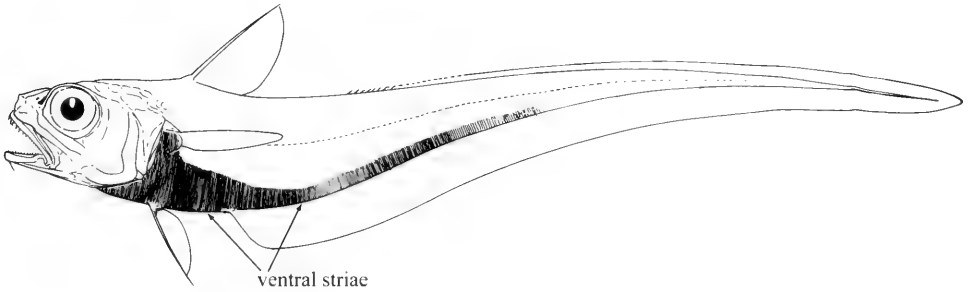

FIGURE 23. Ventral striae in *Lepidorhynchus denticulatus*.

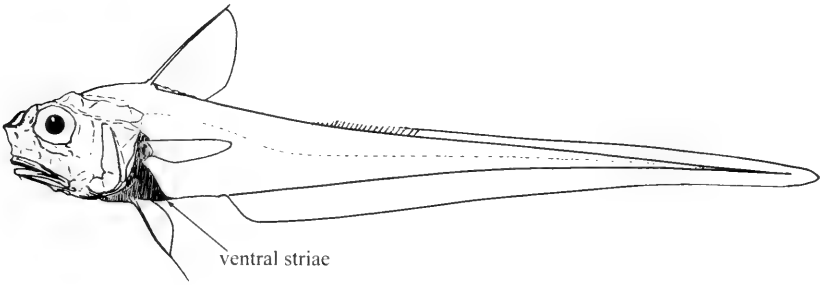

FIGURE 24. Ventral striae in *Hymenocephalus* sp.

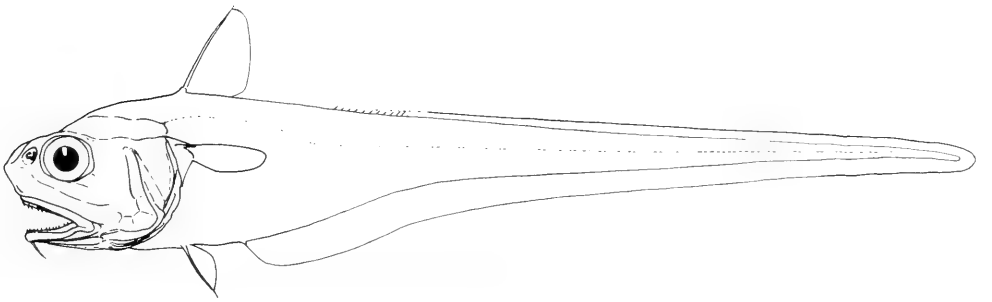

FIGURE 25. Diagrammatic illustration of a *Malacocephalus* sp.

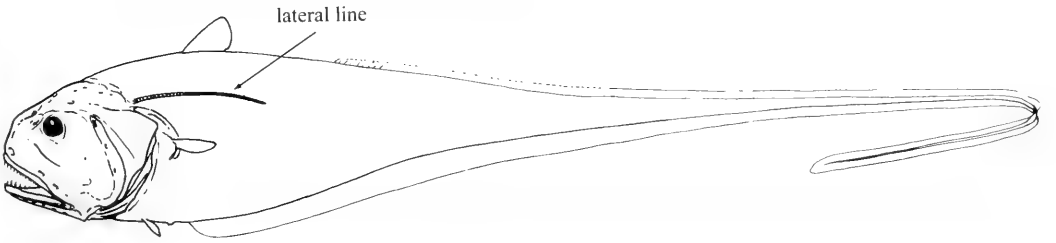

FIGURE 26. Diagrammatic illustration of an *Odontomacrurus murrayi* showing position of anus and short lateral line.

7b. Anus immediately before anal fin, no fossa of light organ; grooved lateral line prominent, in two parts, an anterior dorsolateral section and a posterior midlateral section; abdomen long, distance isthmus to anus more than three-fourths of head length . . . . . *Cynomacrurus piriei* (Fig. 27)

8a. Pelvic rays 6–7 . . . . . *Trachonurus* (Fig. 28)
8b. Pelvic rays 9–12 . . . . . [*Ventrifossa sazonovi*]

9a. Head massive, globose, soft; scales along base of second dorsal fin enlarged 10
9b. Head not especially massive or globose; no enlarged scales along base of second dorsal fin 11

10a. Base of pelvic fin posterior to vertical through origins of first dorsal and pectoral fins; interorbital width 31–34% HL . . . . . [*Cetonurichthys subinflatus*]
10b. Base of pelvic fin about at or anterior to vertical through origin of first dorsal and pectoral fins; interorbital width 36–48% HL (Fig. 29). . . . . *Cetonurus globiceps*

11a. Scales of head elongated, with spinules longitudinally aligned to give striated pattern to head surfaces; chin barbel absent. . . . . *Mesobius* (Fig. 30)
11b. Head scales not elongated, no striated pattern to head surfaces; chin barbel present 12

12a. Snout rounded, not protruding beyond mouth in adults, naked; scales on head and front of body without spinules or ridges; maxilla reaches only to vertical through front of orbit in adults (more posteriorly in juveniles); second spinous ray of first dorsal fin notably large and laterally compressed, heavily serrated. . *Haplomacrourus nudirostris* (Fig. 31)
12b. Snout angular, protruding beyond mouth, completely naked to variously covered with scales; almost all scales covered with spinules or low ridges; maxilla usually extends well posterior to front of orbit (except in some species of *Sphagemacrurus* and *Lucigadus*); spinous second ray of first dorsal fin not greatly compressed laterally, sparsely to densely serrated or smooth along leading edge. 13

13a. Branchiostegal rays 6 14
13b. Branchiostegal rays 7 15

14a. Anus at or close to anal fin origin; no light organ . . . . . *Coryphaenoides*
14b. Anus removed from anal fin; small light organ present (Fig. 32) . . . . . *Mataeocephalus* sp.

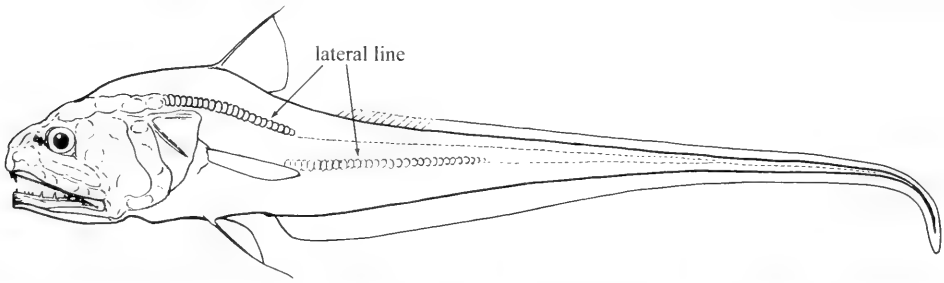

FIGURE 27. Diagrammatic illustration of a *Cynomacrurus piriei* showing position of anus and lateral line in two parts.

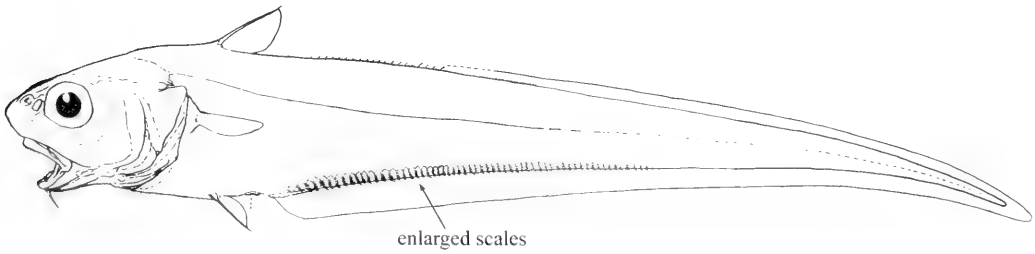

FIGURE 28. Diagrammatic illustration of a *Trachonurus* showing enlarged scales along base of anal fin.

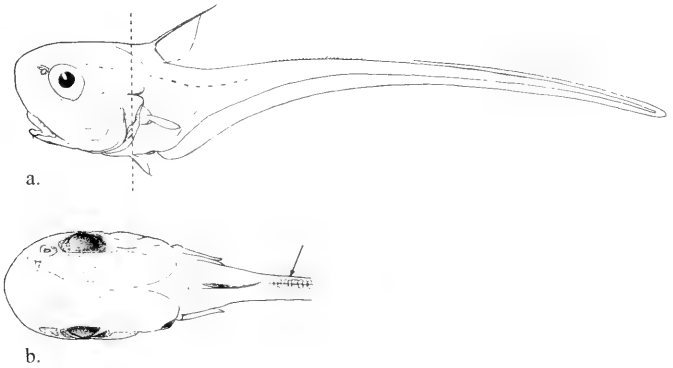

FIGURE 29. Diagrammatic illustration of a *Cetonurus* sp. (a) Lateral view showing relative positions of pelvic, pectoral, and first dorsal fins. (b) Dorsal view of head; arrow points to enlarged scales along anterior part of second dorsal fin.

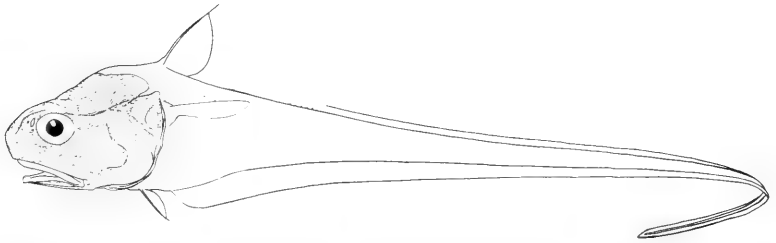

FIGURE 30. Diagrammatic illustration of a *Mesobius* sp. showing striated pattern of spinulation on head.

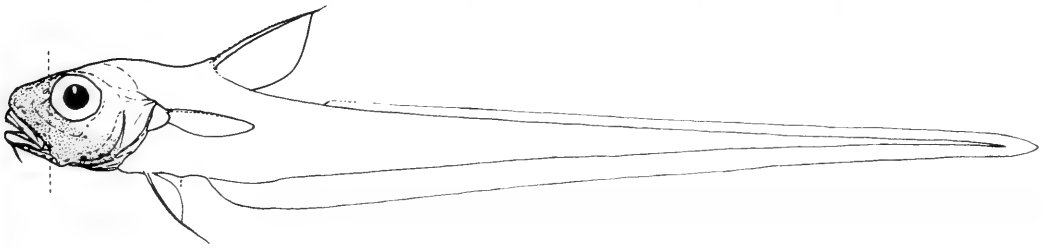

FIGURE 31. Diagrammatic illustration of a *Haplomacrourus nudirostris* showing extensive naked areas on head (stippled) and forward position of mouth.

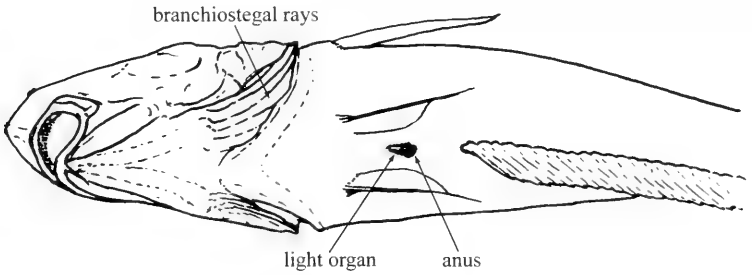

FIGURE 32. Diagrammatic ventrolateral view of *Mataeocephalus* sp. with six branchiostegal rays: anus far removed from anal fin origin and small light organ before anus.

15a. Snout mostly naked dorsally and ventrally without terminal and lateral tubercular scales 16
15b. Snout variously naked, but usually no extensive naked area dorsally; tubercular scales present at terminal and lateral tips of snout 18

16a. Olfactory organ huge, length of posterior nostril about one-half diameter of orbit . . . [*Macrosmia phalacra*] (Fig. 33)
16b. Olfactory organ normal, posterior nostril much less than half diameter of orbit 17

17a. Origin of anal fin below first dorsal fin; anus usually closer to pelvic fin than to anal fin. . . . . [*Kumba*] (Fig. 34)
17b. Origin of anal fin well posterior to vertical through hind margin of first dorsal fin; anus immediately before anal fin . . . . . *Asthenomacrurus victoris* (Fig. 35)

18a. A double row of stout, modified scales under orbit forming a stout shelf and usually a sharp, rough ridge (Fig. 36) . 19
18b. Scales under orbit all small, forming smooth, rounded surface 21

19a. Anus closer to pelvic fin insertions than to anal fin origin (Fig. 37a) . . . . . *Nezumia*
19b. Anus closer to anal fin than to pelvic fin (Fig. 37b). 20

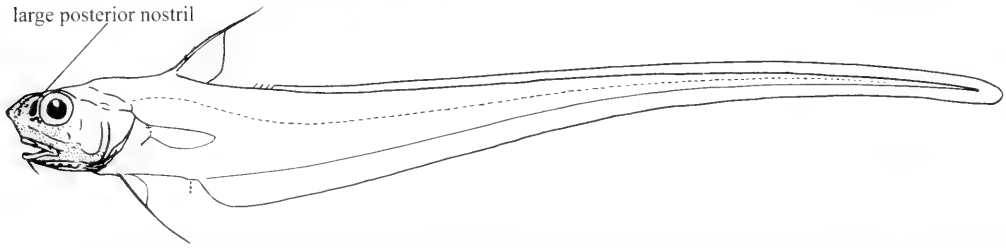

FIGURE 33. Diagrammatic illustration of a *Macrosmia phalacra* showing extensive naked areas (stippled) on head and large posterior nostril.

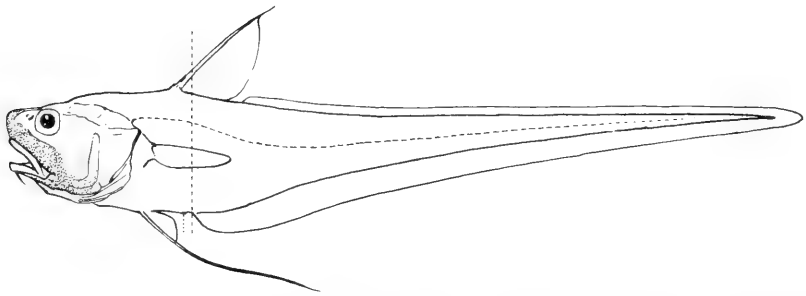

FIGURE 34. Diagrammatic illustration of a *Kumba* sp. showing extensive naked areas (stippled) on head and position of anal fin origin relative to first dorsal fin.

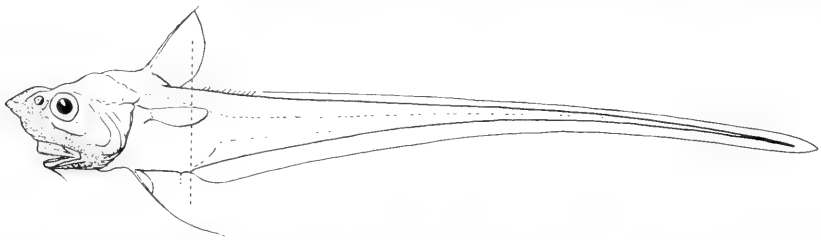

FIGURE 35. Diagrammatic illustration of *Asthenomacrurus victoris* showing extensive naked areas (stippled) on head and position of anal fin origin relative to first dorsal fin.

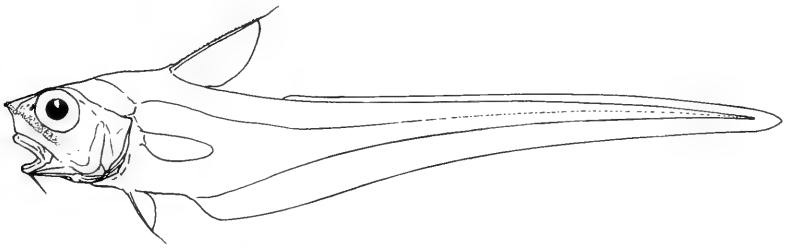

FIGURE 36. Diagrammatic illustration of a *Nezumia* sp.

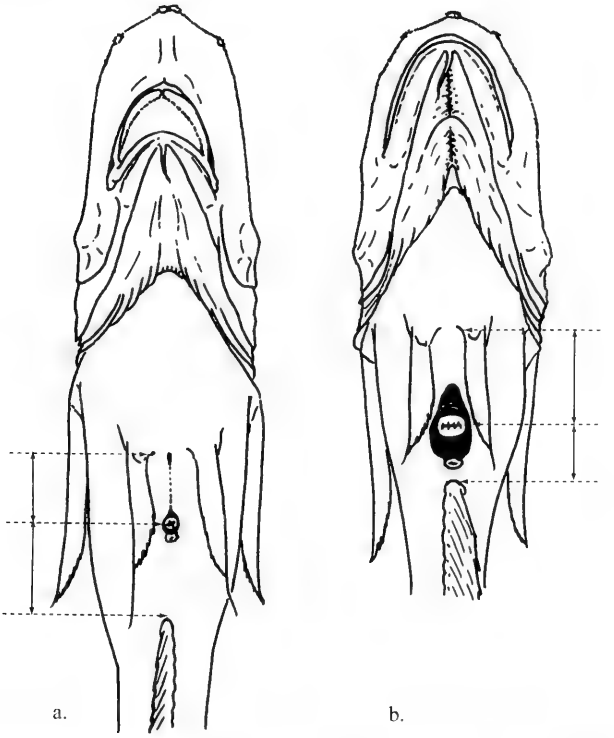

FIGURE 37. Diagrammatic ventral views of (a) *Nezumia* and (b) *Sphagemacrurus* showing positions of anus and relative sizes of periproct region.

20a. Snout short, high, scarcely protruding beyond steeply oblique mouth; pelvic fin anteriorly placed, about under preopercle; anal fin origin about under first dorsal fin origin . . . . . *Sphagemacrurus* (Fig. 38)
20b. Snout long, protruding well beyond slightly oblique mouth; pelvic fin origin below or behind opercle, anal fin origin below or behind vertical through posterior margin of first dorsal fin . . . . . *Mataeocephalus* (Fig. 39)

21a. Outer gill rakers of second arch 13–18; no scales on gular and branchiostegal membranes . . . . *Ventrifossa* (Fig. 40)
21b. Outer gill rakers of second arch 12 or fewer; small scales sometimes present on gular or branchiostegal membranes 22

22a. Prominent fin markings (black blotches or streaks) in most species; spinules on body scales aligned in more or less parallel rows; adult size less than 30 cm TL in most species. . . . . *Lucigadus* (Fig. 41)
22b. Fins lacking prominent markings; spinules on body scales in irregularly quincunx to somewhat divergent rows; adult size greater than 30 cm TL . . . . . *Kuronezumia* (Fig. 42)

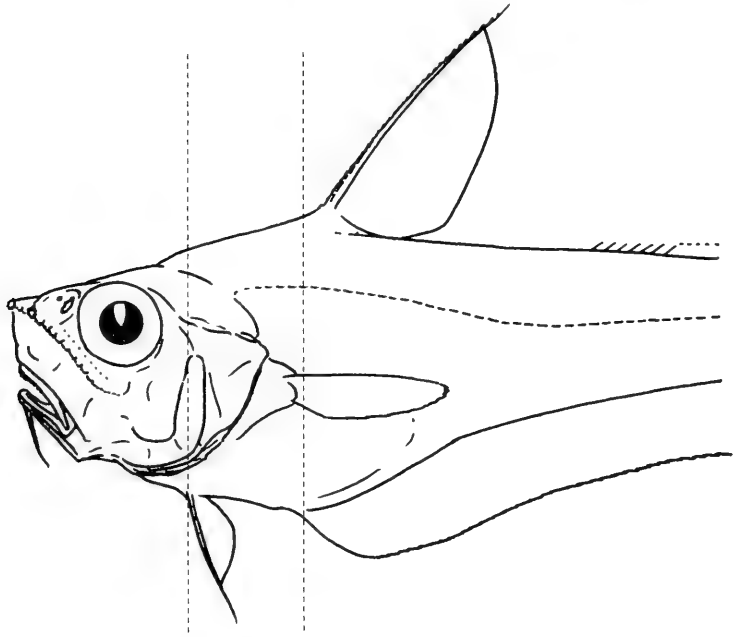

FIGURE 38. Diagrammatic illustration of a *Sphagemacrurus* sp. showing oblique mouth and relative positions of pelvic fin and anal fin origin.

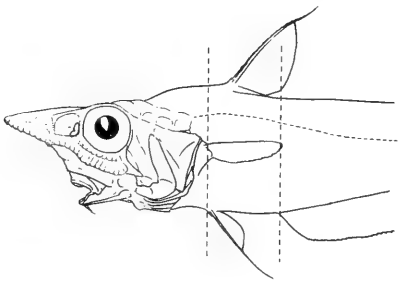

FIGURE 39. Diagrammatic illustration of a *Mataeocephalus* sp. showing thick, coarse scales along suborbital and relative positions of pelvic fin and anal fin origin.

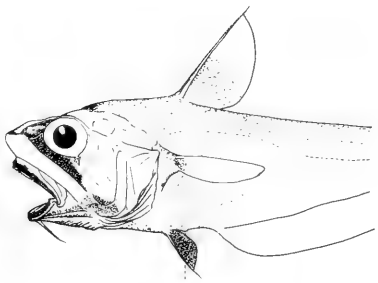

FIGURE 40. Diagrammatic illustration of a *Ventrifossa* sp.

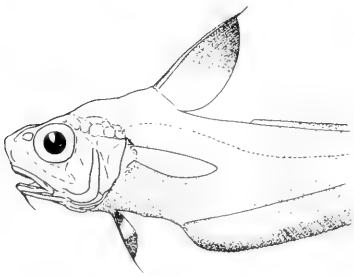

FIGURE 41. Diagrammatic illustration of *Lucigadus microlepis*.

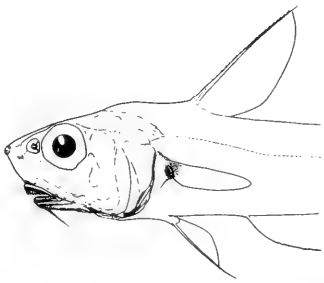

FIGURE 42. Diagrammatic illustration of *Kuronezumia leonis*.

Genus *Asthenomacrurus*

DISTINGUISHING FEATURES. — Anus immediately in front of anal fin. Pelvic fin slightly in advance of vertical through pectoral fin base. Head bones weak, no coarse scaly ridges on head; snout almost entirely naked. Long spinous ray of first dorsal fin with few weak serrations along leading edge. Seven branchiostegal rays. Light organ poorly developed or apparently absent. Species small, probably less than 25 cm.

REMARKS. — The genus is enigmatic and may eventually be considered the same as *Pseudonezumia* Okamura, 1970. Only two species of small adult size, *A. victoris,* here reported, and *A. fragilis* (Garman, 1899) from the eastern central Pacific. Specimens identified as *Paracetonurus* sp. by Iwamoto (1986) are probably of this genus.

REFERENCE. — Sazonov and Shcherbachev (1982b).

Asthenomacrurus victoris Sazonov and Shcherbachev, 1982

Fig. 35

DISTINGUISHING FEATURES. — As for genus, with V7 or 8; outer GR-I 13–14.

SIZE. — Probably less than 25 cm.

DISTRIBUTION. — Indian Ocean, off Japan, and Australia (NSW, WA), in about 1650–3500 m.

NSW CAPTURES. — Two specimens were taken in 1650–1900 m off Nowra by the *ORV Franklin.*

REMARKS. — The species was originally described from three specimens, one of which was from about 200 n. mi. west of Freemantle (WA). The two NMV specimens are the shallowest captures and the first record of the species from the Pacific coast of Australia.

REFERENCE SPECIMENS. — NMV A7000 (220 mm TL) and NMV A7001 (154 mm TL; 67 km ene of Nowra (34°41.97′S, 152°22.44′E); 1896–1642 m; ORV *Franklin* stn CSIRO FR9/88, Slope 59, 22 Oct. 1988.

REFERENCE. — Sazonov and Shcherbachev (1982b).

Genus *Caelorinchus*

DISTINGUISHING FEATURES. — Branchiostegal rays 6. A stout ridge formed of modified scales extending from tip of snout to angle of preopercle, terminating posteriorly in a sharp point; other head ridges stout in most species. Spinous ray of first dorsal fin smooth along leading edge. Pelvic fin rays almost invariably 7. A ventral light organ with a black fossa either on belly or on chest in most species. No gill rakers on outer side of first arch; rakers on inner side of arch tubercular, 10 or fewer total (except in *C. matamuus,* with as many as 12). Chin barbel present.

REMARKS. — This is the most speciose genus of grenadiers with more than 100 known and more awaiting description. The genus is best represented in tropical and subtropical waters, but is also numerous in certain temperate waters such as off New Zealand, where 21 species have been recorded. We have found 16 species of *Caelorinchus* off New South Wales. Most of these are widespread in the southern part of the continent, with other species more representative of the subtropical-tropical Queensland fauna.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto (1990); McMillan and Paulin (1993); Iwamoto and Williams (1999).

KEY TO THE SPECIES OF *CAELORINCHUS* OF NEW SOUTH WALES

1a. Underside of snout naked 2
1b. Underside of snout fully scaled 8

2a. A prominent black fossa of light organ on midline of chest or belly (Fig. 43) 3
2b. No fossa on chest or belly 7

3a. Rays of second dorsal fin long, about equal to opposite rays of anal fin; black fossa of light organ on chest . . . . . *C.* sp. cf. *cingulatus* (Fig. 44)
3b. Rays of second dorsal fin short, much shorter than opposite rays of anal fin; black fossa of light organ on belly 4

4a. A small but prominent black spot at base of pectoral fin; pelvic fin with large black blotch in middle of fin; light organ large, extending anteriorly to or beyond transverse line connecting origins of pelvic fins (Fig. 45) . . . . . *C. mirus*
4b. No spot at base of pectoral fin; pelvic fins lacking large black blotch; light organ extends forward no further than to line connecting insertions of pelvic fins 5

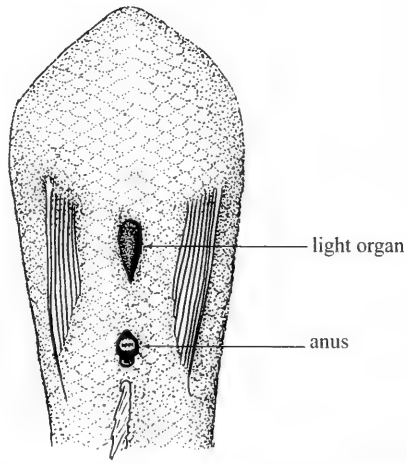

FIGURE 43. Ventral view of trunk of a *Caelorinchus* showing large anterior dermal window of light organ between pelvic fins.

5a. Dorsally behind leading edge of snout with usually clear naked area on each side of midline (Fig. 46); saddles usually absent on trunk, but faintly present on tail; pale interspaces between saddles spotlike in dorsal view (Fig. 47) . . . . . *C. parvifasciatus*
5b. Dorsally behind leading edge of snout densely covered with scales, lacking clear naked areas; saddles prominent on trunk and tail, interspaces not spotlike in dorsal view 6

6a. First dorsal and anal fins black or very dark to base, without prominent pale areas (Fig. 48); body scales relatively deciduous; pyloric caeca 12–23 (Fig. 49) . . . . . *C. fasciatus*
6b. Base of first dorsal fin distinctly pale, anal fin with a prominent black stripe posteriorly (Fig. 50); body scales relatively adherent; pyloric caeca 18–34 (usually 22–32). . . . . *C. maurofasciatus*

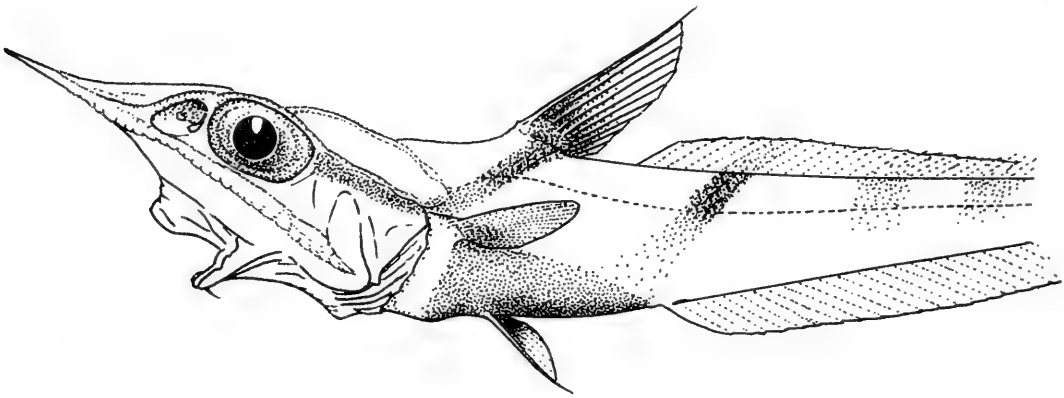

FIGURE 44. Diagrammatic illustration of *Caelorinchus* sp. cf. *cingulatus* showing pigmentation pattern and high second dorsal fin.

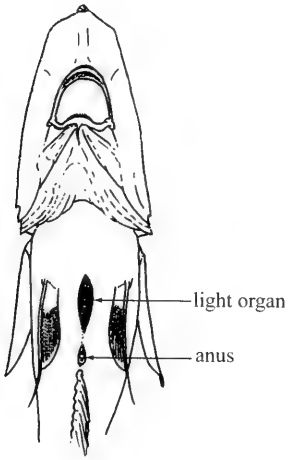

FIGURE 45. Ventral view of a *Caelorinchus mirus* showing large anterior dermal window of light organ and prominent black spot on pelvic fins.

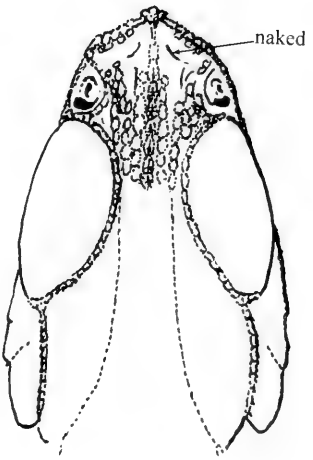

FIGURE 46. Dorsal view of snout of *Caelorinchus parvifasciatus* showing naked areas behind leading edge.

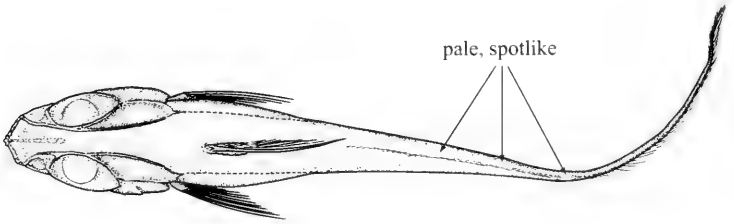

FIGURE 47. Diagrammatic dorsal view of *Caelorinchus parvifasciatus* showing pale spotlike interspaces between saddle marks on tail.

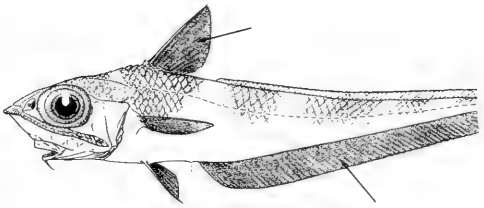

FIGURE 48. Diagrammatic illustration of *Caelorinchus fasciatus* showing banding pattern and pigmentation of first dorsal and anal fins.

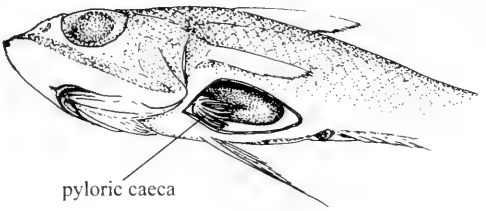

FIGURE 49. Ventrolateral view of a *Caelorinchus* showing cut-away of left abdominal wall exposing stomach and pyloric caeca.

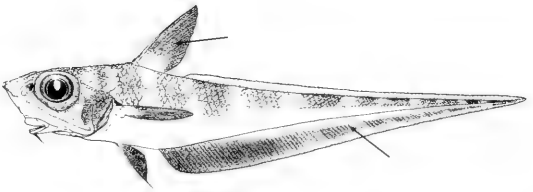

FIGURE 50. Diagrammatic illustration of *Caelorinchus maurofasciatus* showing banding pattern and pigmentation on first dorsal and anal fins.

7a. Trunk completely encircled with broad bluish band (Fig. 51); pyloric caeca 10–14; anterolateral margin of snout incompletely supported by bone (Fig. 52) . . . . . *C. kaiyomaru*
7b. Trunk not encircled by bluish band; pyloric caeca 7–9; anterolateral margin of snout completely supported by bone . . . . . *C. innotabilis*

8a. Body with about 8–10 pale longitudinal stripes; light organ relatively large, extending forward to about midpoint between pelvic and anal fin bases . . . . . *C. australis*
8b. Body lacking longitudinal stripes; light organ small, usually not extending to midpoint between anal and pelvic fins . 9

9a. Anterior one-half to one-third of anal fin black, remainder pale; trunk completely encircled by dark band; orbit equal to or longer than snout length . . . . . *C. matamuus* (Fig. 53)
9b. No sharp contrast in anal fin pigmentation; trunk not encircled by dark band; orbit diameter much shorter than snout length 10

10a. Anterolateral snout margin completely supported by bone; spinule rows on body scales 3–8, widely divergent (Fig. 54a). 11
10b. Anterolateral snout margin incompletely supported by bone; spinule rows on body scales 3–13, more or less parallel (Fig. 54b) 13

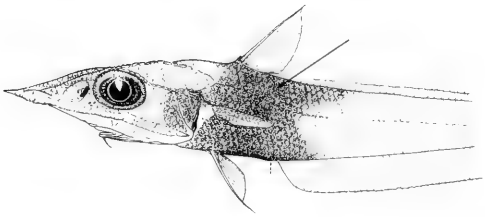

FIGURE 51. Diagrammatic illustration of *Caelorinchus kaiyomaru* showing broad dark band encircling trunk.

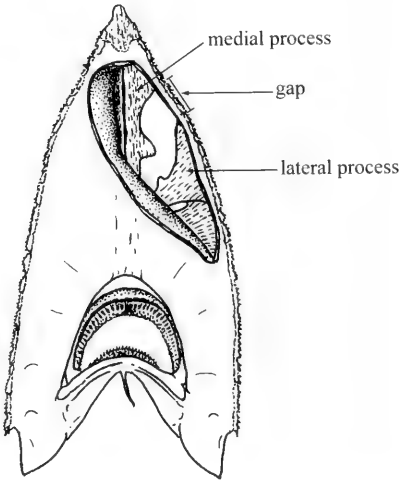

FIGURE 52. Diagrammatic ventral view of head of a *Caelorinchus* sp. showing partial cut-away of ventral snout surface to expose lateral and medial processes of nasal bone (a wide gap between processes).

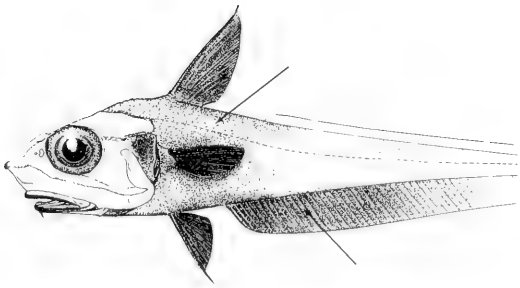

FIGURE 53. Diagrammatic illustration of *Caelorinchus matamuus* showing broad dark band encircling trunk and black anterior portion of anal fin.

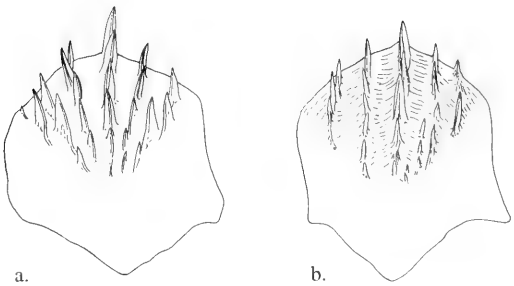

FIGURE 54. Diagrammatic illustrations of *Caelorinchus* body scales taken from region below anterior end of second dorsal fin. (a) *C. smithi*—spinule rows widely divergent, (b) *C. mycterismus*—spinule rows more or less parallel.

11a. Snout length in adults 1.5–1.7 times orbit diameter (1.7–2.0 in young); GR-II (total inner) 6–7; scale rows below origin of first dorsal fin 5–6 . . . . . *C. smithi*
11b. Snout length 1.7–2.5 times orbit diameter; GR-II (total inner) 8–10; scale rows below origin of first dorsal fin 6–8 . 12

12a. GR-I 8 total; scales rows below origin of first dorsal fin 6–7, lateral line scales over a distance equal to predorsal length 38–44; orbit diameter 1.27–1.44 into postorbital length . . . . . *C. macrorhynchus*
12b. GR-I 9–10 total; scales rows below origin of first dorsal fin 8, lateral line scales over a distance equal to predorsal length 53–55; orbit diameter 0.97–1.08 into postorbital length . . . . . *C. supernasutus*

13a. Scale rows below origin of first dorsal fin 8.0–10.0, below second dorsal fin 5.0–7.5; nasal fossa usually naked, sparsely scaled in some (Fig. 55a) . . . . . *C. acanthiger*
13b. Scale rows below origin of first dorsal fin 4.0–7.0, below second dorsal fin 3.5–7.0; nasal fossa naked or scaled ventrally (Fig. 55b) 14

14a. Scales on head ridges notably coarse and sharply spined; 5–13 parallel rows of spinules on body scales (Fig. 56a); overall color dark grayish with violet tinge; fins all blackish . . . . . *C. trachycarus*
14b. Scales on head not especially coarse; 4–9 more or less parallel rows of spinules on body scales (Fig. 56b); overall color tawny to grayish brown, not tinged with violet; fins dusky to blackish 15

15a. Snout 1.9–2.2 into HL; anal fin dusky except pale near posterior tip; snout slightly upturned (Fig. 57a) *C. mycterismus*
15b. Snout 2.4–2.6 into HL; anal fin dusky to blackish overall; snout lacking upturned tip (Fig. 57b) . . . . *C. kermadecus*

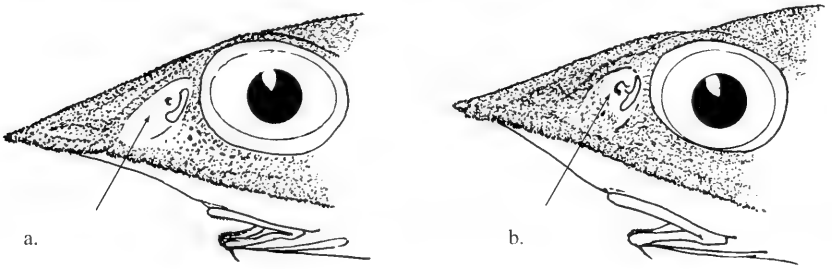

FIGURE 55. Nasal fossa in *Caelorinchus* spp. showing (a) fossa surface naked and (b) fossa surface scaled ventrally.

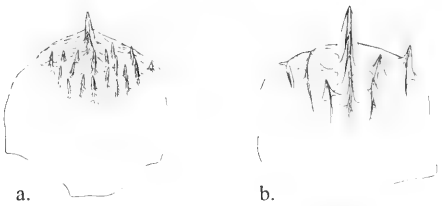

FIGURE 56. Scales from region below anterior end of second dorsal fin of (a) *Caelorinchus trachycarus* and (b) *C. kermadecus*.

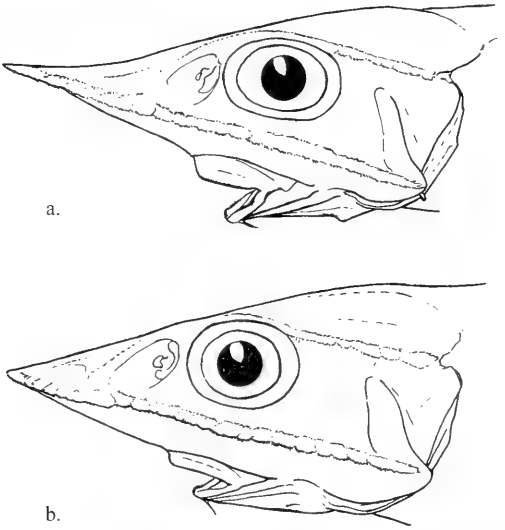

FIGURE 57. Lateral view of snout of (a) *Caelorinchus mycterismus* showing upturned tip and (b) *C. kermadecus* with straight tip.

***Caelorinchus acanthiger* Barnard, 1925**
Fig. 58

DISTINGUISHING FEATURES. — 1D II,8–9; P i17–i19; V 7; GR-I 8–9 total; scales below 1D 8–10, below 2D 5–7.5, lat.l. about 33–49; pyloric caeca 9–12. Snout about 2/5ths of head length, with straight to slightly concave dorsal profile; anterolateral margin incompletely supported by bone. Underside of head covered with small scales; nasal fossa usually entirely naked; body scales with 3–5 parallel spinules rows, middle row longest, other rows usually much shorter. Small black fossa immediately anterior to anus.

SIZE. — To 50 cm.

DISTRIBUTION. — Southern Africa, southern Australia (NSW, Vic., Tas., SA, WA), and New Zealand in mid-slope depths of about 800 m to at least 1200 m.

NSW CAPTURES. — Relatively abundant between Crowdy Head and Gabo Island in 790–1200 m. *Caelorinchus acanthiger* was recorded from 224 *Kapala* stations, including 66% of tows in 800–900 m and all tows deeper than 900 m. Between 10 and 50 specimens were captured in most trawls.

REMARKS. — Among grenadiers, *C. acanthiger* is second only to *Coryphaenoides serrulatus* in abundance in mid-slope depths off NSW. The species is distinguished from two similar species, *C. kermadecus* and *C. mycterismus*, by its higher scale-row counts below the first dorsal fin and by the absence of scales on the nasal fossa (present ventrally in other two species). *C. mycterismus* also has a noticeably longer snout. *C. trachycarus* has much more spiny scales, especially on head ridges, more spinule rows on body scales, a darker overall color, black fins, and fewer scale rows below the first dorsal fin. *C. macrorhynchus, C. smithi*, and *C. supernasutus* have the anterolateral snout margins completely supported by bone.

REFERENCE SPECIMENS. — AMS I.19860-017 (1 spec.); K76-24-03. AMS I.20068-010 (5 spec.); K77-23-13. AMS I.20098-023 (1 spec.); K77-23-07. AMS I.20099-018 (3 spec.); K77-23-12. AMS I.21722-002 (1 spec.); K79-20-13. AMS I.21724-011 (1 spec.); K79-20-15. AMS I.24037-012 (6 spec.); K78-26-16. AMS I.24054-004 (1 spec.); K83-06-02. AMS I.24056-007 (2 spec.); K83-08-02. AMS I.24059-007 (1 spec.); K83-09-02. AMS I.24060-007 (1 spec.); K83-09-01. AMS I.24100-001 (6 spec.); K83-07-11. AMS I.24157-006 (1 spec.); K83-12-04. AMS I.25273-007 (1 spec.); K84-11-09. AMS I.28475-002 (1 spec.); K88-04-06. AMS I.28745-004 (1 spec.); K88-04-06. AMS I.28749-002 (2 spec.) and AMS I.28749-003 (1 spec.); K88-17-03. AMS I.29798-011 (4 spec.); K89-12-04. AMS I.29807-002 (1 spec.); K89-07-05.

REFERENCES. — Trunov (as *C. pseudoparallelus*) (1983); Gomon et al. (1994); Iwamoto and Anderson (1994); Iwamoto and Williams (1999).

***Caelorinchus australis* (Richardson, 1839)**
Fig. 59

DISTINGUISHING FEATURES. — 1D II, 9–11; P i13–i18; V 7; GR-I 7–9 total; scales below 1D 3.5–5.5, below 2D 3.5–4.5, lat.l. about 24–32; pyloric caeca 31–34. Snout about one-third of head length; anterolateral margin incompletely supported by bone. Underside of head covered with small scales; nasal fossa with small scales over ventral surfaces; body scales with as many as 20 parallel rows of short, small spinules. Large black fossa of light organ extends forward from anus about halfway to pelvic fin insertions. About 8–10 pale longitudinal stripes on dorsolateral aspects of body; first dorsal fin black on distal half; anal fin dusky to blackish along distal margin, mostly blackish posteriorly. (Adapted from Arai and McMillan 1982)

SIZE. — To at least 55 cm.

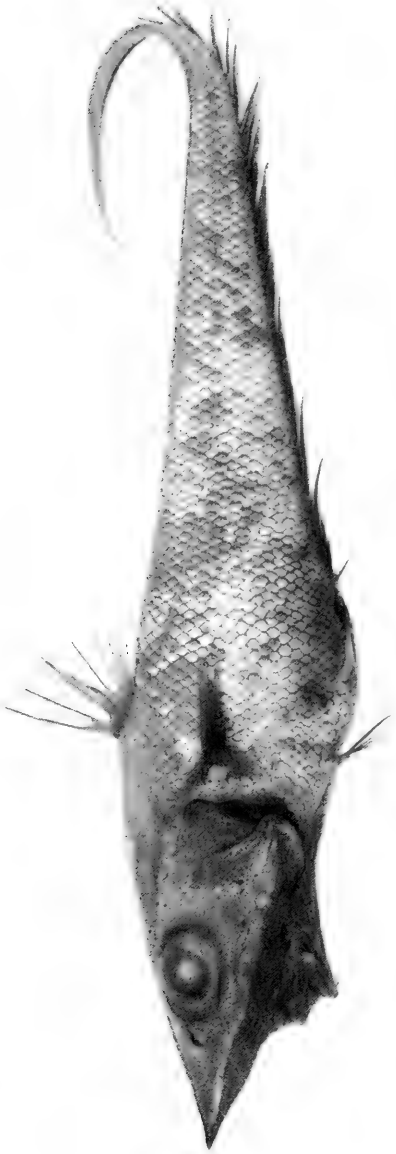

FIGURE 58. *Caelorinchus acanthiger* Barnard, 1925. AMS I.25273-007. From *Kapala* stn K84-11-09, east of Nowra, NSW, in 1161–1207 m.

FIGURE 59. *Caelorinchus australis* (Richardson, 1839). AMS I.29385-002. From *Kapala* stn K89-03-15, southeast of Gabo I., Vic., in 152–159 m.

DISTRIBUTION. — Southeastern Australia (NSW, Vic., Tas., SA) on shelf and upper slope in about 100–450 m. Off Tasmania, Last et al. (1983) stated that the species "is commonly trawled between 80 and 300 metres but on rare occasions has been collected in shallow coastal waters."

NSW CAPTURES. — Caught by *Kapala* only south of Batemans Bay in depths of 130–440 m. Moderately abundant, *C. australis* was caught in 22% of all tows in 100–400 m but was most common in 200–300 m (present in 55% of tows in that depth range). This species of relatively large adult size has no commercial value, but its numbers off southern NSW appear to have been reduced by trawling over the last 20 years. During 1976–77 it was recorded in 80% of *Kapala* tows in 200–400 m, and catches were mostly greater than 20 specimens per tow; in comparison, it was present in only 23% of 1996–97 tows, with an average of 3 per tow.

REMARKS. — The species name was previously applied to a common grenadier of New Zealand waters until Arai and McMillan (1982) determined that *C. australis* was confined to southeastern Australia. The New Zealand species for which the name was being applied is endemic and was undescribed until Arai and McMillan named it. Note that fig. 21.12 in Last et al. (1983) is of *C. biclinozonalis*.

REFERENCE SPECIMENS. — AMS I.29385-002 (2 spec.); K89-03-15.

REFERENCES. — Arai and McMillan (1982); Last et al. (1983); Gomon et al. (1994)

Caelorinchus sp. cf. *cingulatus* Gilbert and Hubbs, 1920
Fig. 60

DISTINGUISHING FEATURES. — 1D II, 8–9; P i16–i19; V 7; GR-I 6–8 total; scales below 1D 5–7, below 2D 4.5–6.0, lat.l. about 30–40. Snout two-fifths to one-half of head length; anterolateral margin incompletely supported by bone. Underside of head naked; nasal fossa naked or sparsely scaled; body scales with short, spikelike, recumbent spinules in 7–15 parallel to slightly divergent rows. Light organ extends forward from anus to chest, dilated at each end, anteriorly with a shallow, scaled fossa. Rays of second dorsal fin about as high as opposites of anal fin; interspace between first and second dorsal fins short, usually less than length base of first dorsal. A saddle extending from base of first dorsal to base of pectoral fin; a second faint saddle usually visible below origin of second dorsal fin; a darker third saddle below 9th–12th rays of second dorsal extending anteroventrally and leveling off midlaterally; faint saddles posteriorly on body, but usually not extending ventrally below lateral line; first dorsal with a dark midlateral band.

SIZE. — To about 30 cm.

DISTRIBUTION. — New Caledonia, and ne. Australia (Qld, NSW). Depth range about 250–550 m.

NSW CAPTURES. — Five specimens collected by *Kapala* from three stations in 550 m off the Qld-NSW border (about 28°S).

REMARKS. — Iwamoto and Merrett (1997) first reported this species as *C. cingulatus* from specimens collected in the New Caledonian region. In their subsequent study (Merrett and Iwamoto 2000), they realized that their specimens, though closely similar, did not entirely agree with descriptions of *C. cingulatus* Gilbert and Hubbs, 1920, especially in regards to certain body markings, but they did not describe it as new. The species is readily distinguished from other NSW members of the genus by the combination of its distinctive pattern of saddles; moderately prolonged spinous first dorsal ray, high second dorsal, the rays about equal in length to opposites of anal fin; and relatively long span between the isthmus and anal fin origin.

REFERENCE SPECIMENS. — AMS I.20518-012 (2 spec.); K78-09-05. AMS I.20459-014 (3 spec.) and I.20459-019 (1 spec.); K78-17-10. AMS I.20651-014 (1 spec.); K78-23-09.

REFERENCES. — Iwamoto and Merrett (1997); Merrett and Iwamoto (2000).

***Caelorinchus fasciatus* (Günther, 1878)**
Fig. 61

DISTINGUISHING FEATURES. — 1D II,9–10; P i14–i18; V 7; GR-I 8–9 total; scales below 1D 3.5–5.0, below 2D 3.5–4.5, lat.l. about 21–29; pyloric caeca 12–23. Snout 18–33% of head length, much shorter than huge orbit, which is about two-fifths or more of head length; anterolateral margin of snout incompletely supported by bone. Underside of head naked; dorsal surface of snout lacking clear scaleless areas; nasal fossa with small scales over ventral surfaces. Body scales large, rather deciduous, exposed fields covered with 7–12 parallel rows of spinules. Narrow fossa of light organ extends forward from anus about halfway to pelvic-fin insertions. A series of 8–12 dark saddle marks on body beginning on nape. First dorsal fin black on distal half or more; anal fin dusky to blackish along distal margin, mostly blackish posteriorly.

SIZE. — To at least 35 cm.

DISTRIBUTION. — Southeastern Australia (NSW, e. Vic.), New Zealand, and South America. Depth range off NSW about 600–1000 m, much more restricted than the 200–1000 m off New Zealand (P. McMillan, pers. commun. with Graham). Off Chile and Argentina, Iwamoto (unpublished records) has verified records only from much shallower depths of about 75–450 m.

NSW CAPTURES. — Uncommon off NSW; 19 specimens captured in eight tows by *Kapala* in 630–960 m, from just south of Sydney (34°15′S) to Gabo Island (37°40′S).

REMARKS. — It is likely that the *Kapala* specimens treated here are the only Australian records definitely referable to *C. fasciatus*. Australian records of *C. fasciatus* in the literature prior to about 1990 most probably relate to *C. maurofasciatus* or *C. parvifasciatus* (e.g., Last et al. 1983; Munro 1957). In addition to NSW, Vic. and Tas., Last et al. (1983: 240) reported *C. fasciatus* from WA and SA, but Iwamoto and Williams (1999) found no specimens to verify those records. The species was not treated in *The fishes of Australia's south coast* (Gomon et al. 1994). Records of *C. fasciatus* off southern Africa were based on different species (see Iwamoto and Anderson 1994).

Caelorinchus fasciatus and *C. maurofasciatus* are closely similar and difficult to differentiate. Characters that appear to separate the two species include the presence in *C. fasciatus* of one or two large, thick, somewhat elevated scales on the median line of the nape two to four scales forward of the first dorsal fin. The pyloric caeca count also differs: 12–23 (x = 16.6) in *C. fasciatus* (data from McMillan and Paulin 1993), compared with 18–34 in *C. maurofasciatus* (McMillan and Paulin [1993] gave 22–32, x = 27.6). Compared to *C. maurofasciatus*, the overall body color of *C. fasciatus*, including banding, is duller, the anal fin lacks a dark stripe, the first dorsal fin is uniformly dusky to blackish, and the scales are more deciduous.

REFERENCE SPECIMENS. — AMS I.24774-001 (3 spec.); K84-08-05. AMS I.26998-003 (1 spec.); K87-14-02. AMS I.32431-002 (1 spec.); K89-07-04.

REFERENCES. — Last et al. (1983); McMillan and Paulin (1993).

***Caelorinchus innotabilis* McCulloch, 1907**
Fig. 62

DISTINGUISHING FEATURES. — 1D II,9–10; P i16–i19 V 7; GR-I 6–8 total; scales below 1D 6–7, below 2D 6.0–7.5, lat.l. about 32–40; pyloric caeca 7–9. Snout slender and sharp, two-fifths or more of HL, much longer than orbit diameter, which is about one-third of HL; anterolateral margin sharp, completely supported by bone. Underside of head naked anteriorly, but some small, nonimbricate scales in small patches above and behind mouth; nasal fossa naked; body scales with 9–13 parallel rows of short, slender spinules. Light organ externally inconspicuous, not generally visible without dissection, relatively short, extending forward from anus to level of pelvic fin insertions; anus re-

FIGURE 60. *Caelorinchus* sp. cf. *cingulatus*. AMS I.20459-019. From *Kapala* stn K78-17-10, off Danger Pt, NSW-Qld border, in 549 m.

FIGURE 61. *Caelorinchus fasciatus* (Günther, 1887). AMS I.24774-001. From *Kapala* stn K84-08-05, off Batemans Bay in 805–850 m.

moved from anal fin origin by 2 or 3 scale rows. No distinct markings on body or fins; second dorsal fin rays about as long anteriorly as anal fin rays.

SIZE. — To about 35 cm.

DISTRIBUTION. — Southern Australia (NSW, Vic., Tas., SA. WA) and New Zealand.

NSW CAPTURES. — Captured by *Kapala* between Crowdy Head and Gabo Island in 450–1075 m. Recorded from 227 tows (about half of all tows between 500 and 1100 m), with greatest abundance in 700–900 m (in 93% of tows at that depth range). Frequently more than 50/tow in trawls with small-meshed codends.

REMARKS. — This is a plain fish with no distinguishing pigment pattern, an almost-cylindrical body, and a sharp suborbital ridge that is completely supported by bone along the leading edge of the snout. These features separate *C. innotabilis* from most other NSW members of the genus (*C. smithi* and *C. macrorhynchus* also have complete support of the leading snout margin). *Caelorinchus innotabilis* might be confused with *C. kaiyomaru*, but the dark, broad band girdling the trunk in *C. kaiyomaru* is distinguishing.

REFERENCE SPECIMENS. — AMS I.7893 (holotype, 138 mm TL); off Sydney, 800 fm [1463 m; but see note in Historical Perspective]; *Woy Woy*. AMS I.15973-010 (1 spec.); K71-07-03. AMS I.15976-001 (1 spec.); K71-09-01. AMS I.16589-003 (1 spec.); K72-05-05. AMS I.18726-027 (5 spec.); K75-01-02. AMS I.18770-009 (2 spec.); K75-02-08. AMS I.18838-010 (1 spec.); K75-05-03. AMS I.18839-001 (28 spec.) and AMS I.18839-037 (25 spec.); K75-05-04. AMS I.19198-002 (2 spec.); K76-05-04. AMS I.19202-002 (1 spec.); K76-06-03. AMS I.19859-002 (10 spec.); K76-24-04. AMS I.19860-009 (1 spec.); K76-24-03. AMS I.19862-008 (2 spec.); K76-23-01. AMS I.20098-011 (2 spec.); K77-23-07. AMS I.20452-015 (1 spec.); K75-05-05. AMS I.21722-008 (3 spec.); K79-20-13. AMS I.21724-013 (1 spec.); K79-20-15. AMS I.21806-001 (3 spec.); K77-07-10. AMS I.23885-014 (1 spec.); K78-27-05. AMS I.24055-006 (2 spec.); K83-08-01. AMS I.24056-005 (6 spec.); K83-08-02. AMS I.24059-008 (4 spec.); K83-09-02. AMS I.24060-005 (1 spec.), I.24060-008 (3 spec.), and I.24060-016 (2 spec.); K83-09-01. AMS I.29756-005 (1 spec.); K89-15-04. QM I.23010 (1 spec.); e. of Terrigal, NSW, in 446 fm; Oct. 1978.

REFERENCES. — Gomon et al. (1994); Last et al. (1983); Iwamoto and Williams (1999).

***Caelorinchus kaiyomaru* Arai and Iwamoto, 1979**
Fig. 63

DISTINGUISHING FEATURES. — 1D II,7–10; P i16–i20, V 7; GR-I 6–9 total; scales below 1D 5–8, below 2D 5.0–6.5, lat.l. about 31–41, usually 35–40; pyloric caeca 10–14. Snout slender and sharp, two-fifths to almost half of head length, much longer than orbit diameter (25–30% of HL); anterolateral margin incompletely supported by bone. Underside of head naked or with 1 or 2 isolated scales above posterior end of mouth; nasal fossa naked; body scales with 8–10 parallel or slightly divergent rows of small spinules. Light organ short, seen only as a small blackish area before anus; anus removed from anal fin origin by 1 or 2 scale rows. Entire trunk encircled by broad dark, bluish band; blackish orbital ring.

SIZE. — To 40 cm.

DISTRIBUTION. — Australia (NSW, Vic., Tas.), New Zealand, South Atlantic off Falkland Is., in about 845–1150 m.

NSW CAPTURES. — Caught by *Kapala* in 880–1150 m on all grounds south of Crowdy Head. Relatively common in mid-slope depths and recorded from 148 stations (present in 76% of all tows between 900 and 1100 m), frequently more than 10 specimens per tow.

REMARKS. — This slender species is readily recognized by the prominent dark blue color completely encircling the trunk. In NSW *Caelorinchus* species, this character is found only in *C. matamuus*, a large-sized, heavy-bodied species.

FIGURE 62. *Caelorinchus innotabilis* McCulloch, 1907. From *Kapala* stn K86-01-07 off Sydney in 819–889 m.

FIGURE 63. *Caelorinchus kaiyomaru* Arai and Iwamoto, 1979. AMS I.24060-012. From *Kapala* stn K83-09-01, east of Sydney in 942–950 m.

REFERENCE SPECIMENS. — AMS I.24055-002 (1 spec.); K83-08-01. AMS I.24059-005 (7 spec.); K83-09-02. AMS I.24060-012 (3 spec.), I.24060-015 (2 spec.); K83-09-01. AMS I.24150-007 (1 spec.); K83-13-01. AMS I.24157-005 (1 spec.); K83-12-04. AMS I.24173-008 (3 spec.); K83-14-06. AMS I.24355-009 (2 spec.); K83-18-02. AMS I.24356-001 (1 spec.); K83-14-05. AMS I.24462-002 (1 spec.); K83-15-02. AMS I.24565-001 (1 spec.); K83-14-03. AMS I.24980-005 (4 spec.); K84-16-15. AMS I.29737-005 (1 spec.); K89-19-01.

REFERENCES. — Arai and Iwamoto (1979); Gomon et al. (1994).

***Caelorinchus kermadecus* Jordan and Gilbert, 1904**

Fig. 64

DISTINGUISHING FEATURES. — 1D II,7–9; P i16–i19; V 7; GR-I 7–9 total; scales below 1D 4.5–6.0, below 2D 4.5–6.0, lat.l. about 32–38; pyloric caeca 10–12. Snout 2.4–2.6 into head length in adults (longer in smaller specimens); anterolateral margin incompletely supported by bone. Underside of head covered with small scales; nasal fossa finely scaled ventrally; body scales with 4–7 more-or-less parallel rows of broadly triangular spinules, middle row largest. Light organ short, not externally visible. Overall color grayish brown; all fins dusky to blackish; mouth dark gray to blackish; area around anus bluish, but color not extending to bases of pelvic fins.

SIZE. — To about 60 cm.

DISTRIBUTION. — Kermadec Is., New Zealand, s. of New Caledonia, and Australia (NSW), in about 800–1150 m.

NSW CAPTURES. — Only seven specimens taken at five *Kapala* stations between Crowdy Head and Batemans Bay.

REMARKS. — The *Kapala* specimens are the only Australian records of this species, but it can be expected off Queensland. *Caelorinchus kermadecus* is most similar to *C. acanthiger*, differing principally in squamation features. Body scales are larger (fewer scale rows below the dorsal fins) than in *C. acanthiger*, and the nasal fossa is scaled ventrally (naked in *C. acanthiger*).

REFERENCE SPECIMENS. — AMS I.24991-003 (1 spec.); K84-16-05. AMS I.28100-001 (1 spec.); K88-08-06. AMS I.29750-001 (1 spec.), AMS I.29750-004 (1 spec.), and AMS I.29750-005 (1 spec.); K89-17-04. AMS I.29798-013 (1 spec.); K89-12-04. AMS I.29807-003 (1 spec.); K89-07-05.

REFERENCES. — McMillan and Paulin (1993); Iwamoto and Merrett (1997).

***Caelorinchus macrorhynchus* Smith and Radcliffe, 1912**

Fig. 65

DISTINGUISHING FEATURES. — 1D II,8–9; P i16–19; V 7; GR-I 8–10 total; scales below 1D 6–7, below 2D 5.5, lat.l. about 38–44. Snout length 47–50% HL; interorbital width 19–20%; suborbital width 11–12% HL; postorbital length (30–31%); length orbit to angle of preopercle (32–34%); upper jaw length (24–25%), outer gill slit length 11–13%; and barbel length (8–9%). Snout narrow, sharply pointed, about one-half of head length; anterolateral margin completely supported by bone. Underside of head covered with small scales; nasal fossa mostly covered with small scales; body scales with 5–8 divergent rows of broad-based spinules. Light organ small, a black streak extends forward from ventral fossa to midway between anus and pelvic fin base. Overall color swarthy to black; mouth and fins blackish.

SIZE. — To about 50 cm.

DISTRIBUTION. — Philippines, Indonesia, and Australia (Qld, NSW, WA), in about 500–1100 m.

NSW CAPTURES. — Uncommon; taken only six times (7 specimens) by *Kapala* between Newcastle (33°S) and Jervis Bay (35°S), in 550–950 m. One AMS specimen (I.26806-003) was collected

FIGURE 64. *Caelorinchus kermadecus* Jordan and Gilbert, 1904. AMS I.28100-001. From *Kapala* stn K88-08-06, east of Tuncurry, NSW, in 1024–1079 m.

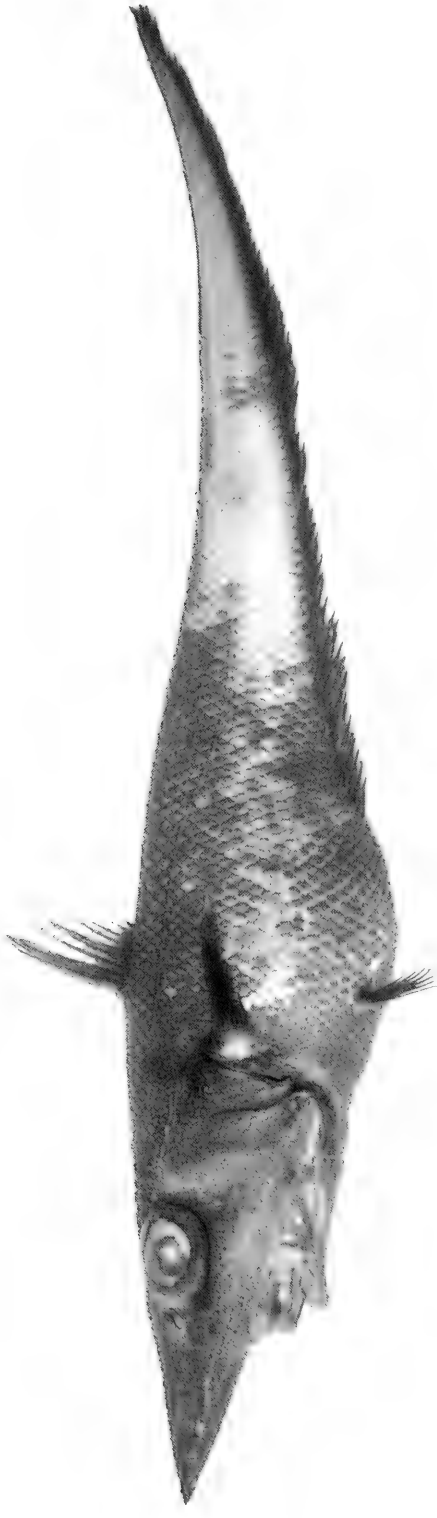

FIGURE 65. *Caelorinchus macrorhynchus* Smith and Radcliffe, 1912. AMS I.24778-001. From *Kapala* stn K84-08-02, east of Nowra, NSW, in 814–850 m.

by a commercial trawler in 550 m off Port Stephens. A juvenile (CAS 214042, 145+ mm TL) was collected recently off Montague I. (36°12′S) in 500 m.

REMARKS. — A notably long snout, dark color, and divergent spinule rows distinguish *Caelorinchus macrorhynchus* from most other NSW members of the genus. The species resembles *C. supernasutus* in its notably long snout, small orbits, and small ventral light organ. *Caelorinchus supernasutus*, however, has smaller scales (8 rows below 1D origin, 5.5 below mid-base of 1D, and 53–55 lateral line scales over a distance equal to predorsal length), and shorter measurements of suborbital (9–10% HL), postorbital (24–25%), orbit to angle of preopercle (26%), upper jaw (20–21%), and barbel (4–6%). One specimen (AMS I.29601-001) listed under this species has a noticeably short (1.5 times orbit) broad snout, very unlike that in most other specimens examined, and more like that in *C. smithi*. However, scale features distinguish that specimen from *C. smithi*, and other characters appear to be the same as those of *C. macrorhynchus*. Because of the short snout in the specimen, it will not key out properly in the key to species. More specimens are needed to adequately delimit the range of variation in snout length and shape in *C. macrorhynchus*.

REFERENCE SPECIMENS. — AMS I.21722-007 (1 spec.); K79-20-13. AMS I.24625-005 (1 spec.); K84-06-06. AMS I.24778-001 (2 spec.); K84-08-02. AMS I.26806-003 (1 spec.); FV *Vincenzann*; e. of Port Stephens, 550 m; 25 Oct. 1986. AMS I.29600-001 (1 spec.); K87-24-01. AMS I.29601-001 (1 spec.); K88-08-08. AMS I.29825-001 (1 spec.); K89-09-09. CAS 214042 (1 spec.); FV *Shelley H*, off Montague I. (36°12′S, 150°24′E); 490-525 m; 1 Mar. 2000.

REFERENCES. — Radcliffe (1912); Iwamoto and Williams (1999).

***Caelorinchus matamuus* (McCann and McKnight, 1980)**
Fig. 66

DISTINGUISHING FEATURES. — 1D II,8–10; P i16–i19; V 7; GR-I 12–13 total; scales below 1D 7–10, below 2D 7–9; pyloric caeca 18–29. Snout bluntly conical, anterolateral margin not completely supported by bone; mouth large, upper jaw extends to below middle of orbit; orbit about one-third of HL. Underside of head scaled; head ridges stout but not especially spiny; nasal fossa covered with scattered small scales; body scales with 8–11 slightly divergent rows of low spinules. Light organ small, immediately before anus, not externally visible. Trunk completely encircled by a broad, blue-black band; anterior half to one-third of anal fin black, remainder pale.

SIZE. — To about 65 cm.

DISTRIBUTION. — Southeastern Atlantic to southern Africa, across Indian Ocean to southern coast of Australia (NSW, Vic., Tas., SA, WA), and New Zealand, in about 650–1100 m.

NSW CAPTURES. — Caught frequently in small numbers by *Kapala* in depths between 690 and 1010 m on all grounds south of Broken Bay (33°25′S). Overall, about 200 specimens captured in 44 *Kapala* trawls; most frequently caught in 700–900 m, where it was recorded in 44% of all tows in that depth range.

REMARKS. — *Caelorinchus matamuus* is a distinctive, widespread species of the Southern Ocean having a geographical distribution similar to that of *C. acanthiger*. The large size, broad bulky head, blunt snout, prominent blackish trunk band, and black anterior part of anal fin immediately identify the species.

REFERENCE SPECIMENS. — AMS I.18726-024 (2 spec.); K75-01-02. AMS I.19860-012 (1 spec.); K76-24-03. AMS I.20099-005 (1 spec.), I.20099-009 (1 spec.), I.20099-017 (1 spec.); K77-23-12. AMS I.20485-015 (1 spec.); K77-23-06. AMS I.23885-005 (1 spec.); K78-27-05. AMS I.24054-002 (3 spec.); K83-06-02. AMS I. 24157-007 (1 spec.); K83-12-04. AMS I.24613-006 (1 spec.); K75-05-05.

REFERENCES. — McCann and McKnight (as *Mahia matamua*) (1980); Sazonov and Shcherbachev (1982a); Last et al. (1983); Iwamoto and Williams (1999).

***Caelorinchus maurofasciatus* McMillan and Paulin, 1993**
Fig. 67

DISTINGUISHING FEATURES. — 1D II,9–10; P i15–i19; V 7; GR-I 7–9 total; scales below 1D 4.5–6.0, below 2D 4–5, lat.l. about 22–31; pyloric caeca 18–34. Snout about one-third or less of head length, much less than huge orbit; anterolateral snout margin incompletely supported by bone. Underside of head naked; nasal fossa partially scaled; no broad naked areas above leading edge of snout; body scales with 11 or more rows of short, small spinules. Slender fossa of light organ between pelvic and anal fins. About 9–11 prominent saddle marks, the first beginning forward on nape and ending below anterior portion of first dorsal fin, the second saddle beginning under posterior end of first dorsal fin and ending two scale rows behind origin of second dorsal fin; most fins dark distally; first dorsal fin blackish distally, with paler base; anal fin with dark stripe; mouth dark.

SIZE. — To at least 50 cm.

DISTRIBUTION. — Southern Australia (NSW, Vic., Tas., SA, WA) and New Zealand, in about 300–900 m.

NSW CAPTURES. — Absent off northern NSW, but recorded south of about 32°20′S in 320–820 m. Very abundant on upper slope, particularly in 400–700 m. During 1996–97, *C. maurofasciatus* was caught in 74 *Kapala* tows in 400–650 m (94% of all tows in that depth range) between Sydney and Gabo Island, with an average catch of 57/tow.

REMARKS. — *Caelorinchus maurofasciatus* is most similar to *C. fasciatus*, with which it has been confused (see description of that species for comparison). The prominent black saddle markings and the black stripe along the anal fin distinguish the species from similar NSW members of the genus.

REFERENCE SPECIMENS. — AMS I.15970-005 (1 spec.); K71-06-04. AMS I.18839-014 (10 spec.), AMS I.18839-016 (8 spec.); K75-05-04. AMS I.19197-001 (1 spec.); K76-04-03. AMS I.23470-006 (5 spec.); K82-17-01. AMS I.23862-001 (10 spec.); K81-18-05. AMS I.24854-003 (1 spec.); K84-14-01. AMS I.28713-001 (1 spec.); K84-13-03. NMV A2460 (1 spec.); K81-17-03.

REFERENCES. — McMillan and Paulin (1993); McMillan *in* Gomon et al. (as *Caelorinchus* sp. 1, the "false banded whiptail") (1994); Iwamoto and Williams (1999).

***Caelorinchus mirus* McCulloch, 1926**
Fig. 68

DISTINGUISHING FEATURES. — 1D II,9–10; P i17–i19; V 7; GR-I 7–8 total; scales below 1D 5.0–5.5, below 2D 4.0–5.5, lat.l. about 23–26; pyloric caeca about 40. Snout less than one-third of head length, much less than large orbit; anterolateral snout margin incompletely supported by bone. Underside of snout and suborbital anteriorly naked, lower jaw and preopercle scaled; nasal fossa and lunate areas above leading edge of snout naked; body scales with 9–20 rows of small spinules. Naked fossa of light organ large, extends to origin of pelvic fin. No saddle markings except in juveniles (<100 mm TL) with banding pattern; pectoral fin with small black spot at ventral corner, pelvic fin with black blotch; other fins dusky to pale, but anal fin with blackish distal margin posteriorly.

SIZE. — To about 30 cm.

DISTRIBUTION. — Australia (Qld, NSW, e. Vic., WA) in about 100–500 m.

NSW CAPTURES. — One of the most abundant species of genus and found along entire coast of NSW in depths between 110 and 500 m. Recorded from 293 *Kapala* stations, with most tows at depths between 200 and 400 m. Despite the large codend mesh (90 mm) used during 1996–97 surveys, *C. mirus* was caught in 43 tows between 200 and 350 m (65% of all tows in that depth range), with a mean catch of 153/hour tow; some individual catches were in excess of 1000 fish. *Caelorinchus mirus* is one of only two NSW grenadiers (also *C. australis*) inhabiting outer shelf depths as well as the slope. It is

FIGURE 66. *Caelorinchus matamuus* (McCann and McKnight, 1980). From *Kapala* stn K83-09-04, east of Nowra, NSW, in 951–978 m.

FIGURE 67. *Caelorinchus maurofasciatus* McMillan and Paulin, 1993. From *Kapala* stn K82-14-16, southeast of Gabo I., Vic., in 730 m.

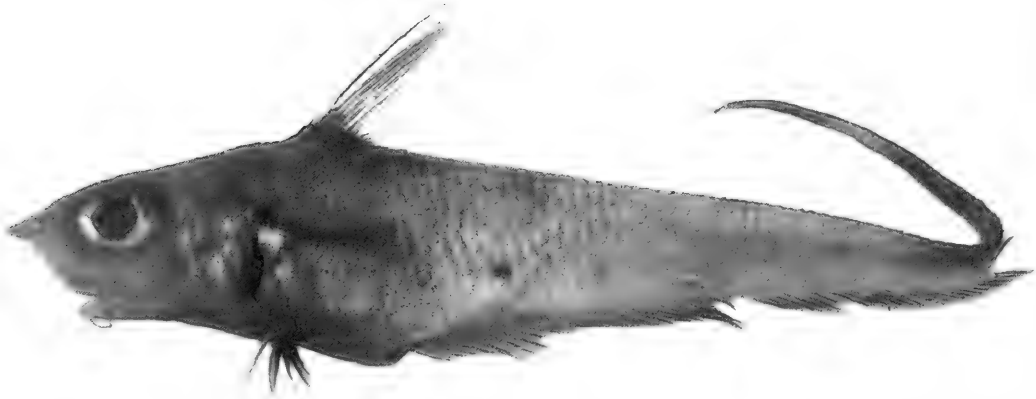

FIGURE 68. *Caelorinchus mirus* McCulloch, 1926. AMS I.26221-002. From *Kapala* stn K85-20-10, off Port Stephens, NSW, in 154–157 m.

caught at night by prawn trawlers off northern NSW in depths as shallow as 110 m (K. Graham, pers. observ.).

REMARKS. — *Caelorinchus mirus* is endemic to Australia. It has been erroneously recorded off New Zealand, but McMillan and Paulin (1993) have determined that it does not exist there. There are no confirmed records of *C. mirus* from Tas., western Vic., or SA. This apparent disjunct distribution between the east coast and WA (including the Great Australian Bight) is similar to those of *Gadomus* sp. cf. *colletti* (see above) and a number of endemic Australian sharks and rays (see Last and Stevens 1994).

REFERENCE SPECIMENS. — AMS I.19205-004 (4 spec.); K76-07-01. AMS I.21793-010 (2 spec.); K78-17-11. AMS I.23993-008 (2 spec.); K78-17-14. AMS I.25932-006 (1 spec.); K85-21-06. AMS I.26221-002 (3 spec.); K85-20-10. Others listed in Iwamoto and Williams (1999).

REFERENCES. — McMillan and Paulin (1993); McMillan *in* Gomon et al. (1994); Iwamoto and Williams (1999).

Caelorinchus mycterismus McMillan and Paulin, 1993
Fig. 69

DISTINGUISHING FEATURES. — 1D II,7–9; P i16–i19; V 7; GR-I 6–8 total; scales below 1D 4–5, below 2D 5–7; pyloric caeca 8–11. Snout 1.9–2.2 into head length in adults (longer in smaller specimens), upturned anteriorly; anterolateral margin incompletely supported by bone. Underside of head covered with small scales; nasal fossa finely scaled; body scales with 4–9 parallel to slightly divergent rows of triangular spinules, middle row highest and longest, lateral rows lower and shorter. Light organ short; no black, lens-like fossa. Overall color in alcohol tawny to brownish; all fins dusky except posterior part of anal fin pale; mouth dark; area around anus bluish.

SIZE. — To about 50 cm.

DISTRIBUTION. — New Zealand, s. of New Caledonia (on Norfolk Ridge), and Australia (NSW, possibly WA) in about 850–1150 m.

NSW CAPTURES. — Two juveniles, one taken east of Crowdy Head in 1050 m, the other off Nowra in 950–978 m.

REMARKS. — New South Wales is probably outside its normal range, but the species may be expected off Qld. Two juveniles of less than 25 cm TL were tentatively recorded by Iwamoto and Williams (1999) from the North-West Shelf off WA. *C. mycterismus* bears close resemblance to several

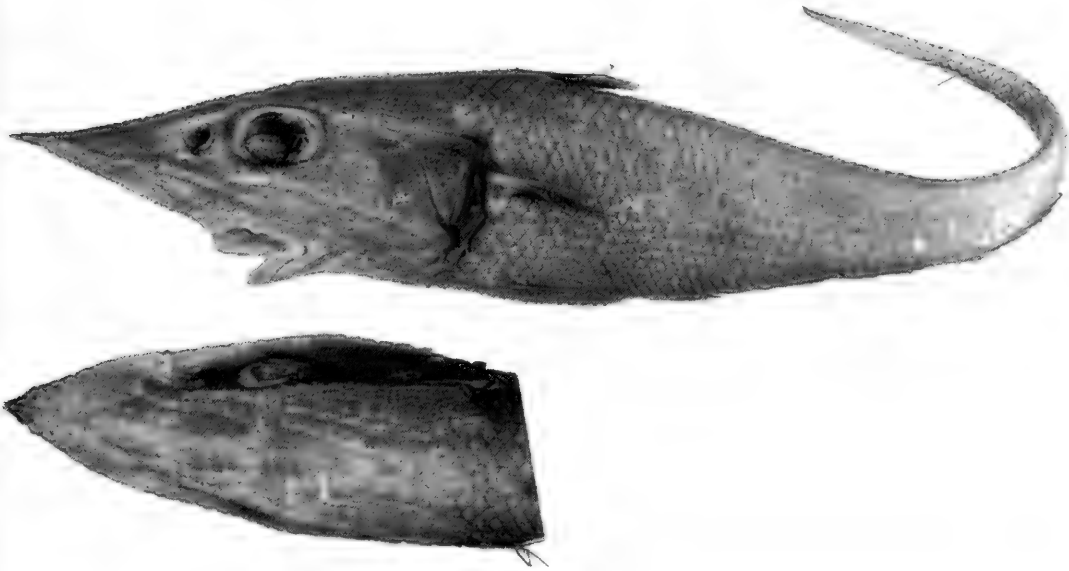

FIGURE 69. *Caelorinchus mycterismus* McMillan and Paulin, 1993. AMS I.24057-004. From *Kapala* stn K83-09-04, east of Nowra, NSW, in 951–978 m.

other members of the genus from the southwestern Pacific, including *C. acanthiger, C. trachycarus,* and *C. kermadecus.* The first two are immediately distinguished by their naked nasal fossae (among other characters). The longer snout with slightly upturned tip and the pale posterior end of the anal fin generally suffice to distinguish *C. mycterismus* from *C. kermadecus.*

REFERENCE SPECIMENS. — AMS I.24057-004 (1 spec.); K83-09-04. AMS I.29750-007 (1 spec.); K89-17-04.

REFERENCES. — McMillan and Paulin (1993); Iwamoto and Williams (1999).

***Caelorinchus parvifasciatus* McMillan and Paulin, 1993**
Fig. 70

DISTINGUISHING FEATURES. — 1D II,9–12 (usually 10); P i17–i20; V. 7; GR-I 7–8 total; scales 1D 5–6, 2D 4.5–5.5, lat.l. 26–28; pyloric caeca 19–26. Snout short, broad, blunt; anterolateral margins incompletely supported by bone; orbit longer than snout length. Naked fossa of light organ extends forward close to line connecting pelvic fin insertions. Underside of head naked or with 1–3 small scales above angle of lower jaw; broad, naked, translucent areas dorsally behind leading edges of snout; nasal fossa naked. Seven or eight faint, sometimes almost obscure, saddles posteriorly on body, more pronounced posteriorly; narrow pale bands occupying one or two scale rows at dorsomedial line separating saddle marks, pale areas often with appearance of white dorsal spots; mouth and gill cavities dark.

DISTRIBUTION. — Southeastern Australia (NSW, Vic., Tas.) and New Zealand.

NSW CAPTURES. — Commonly captured by *Kapala* between Crowdy Head and eastern Bass Strait in depths of 220–600 m; a single record off the Clarence River. This species of relatively small size is possibly the most abundant *Caelorinchus* off central and southern NSW and was recorded from more than 250 *Kapala* upper-slope stations. During the 1996–97 *Kapala* survey, 95 trawls (75% of total) in 250–550 m averaged almost 200 *C. parvifasciatus* per tow, despite the 90 mm codend mesh.

SIZE. — To about 30 cm.

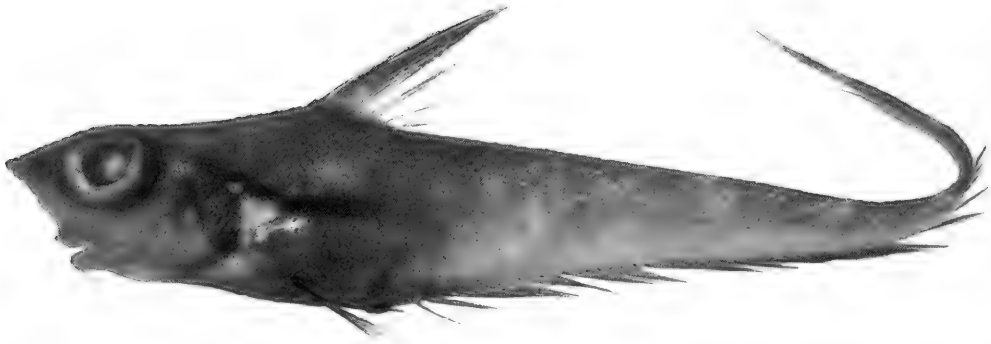

FIGURE 70. *Caelorinchus parvifasciatus* McMillan and Paulin, 1993. AMS I.26240-001. From *Kapala* stn K85-17-02, east of Broken Bay, NSW, in 421–457 m.

REMARKS. — Our Australian specimens agreed in most respects with the New Zealand type-specimens (see McMillan and Paulin, 1993, from which we gleaned the following comparative data). We noted some differences in the ranges of certain measurements and in the count of pectoral fin rays (i17–i20 in Australia cf. i15–i18 in types); snout length 27–31% of HL cf. 29–34%; preoral length 26–34% cf. 21–35%; orbit diameter 44–49% cf. 31–46%; suborbital width 16–18% cf. 13–16%; upper jaw length 26–33% cf. 20–30%; and barbel length 9–14% cf. 5–11%. The anterior dermal window of the light organ was generally larger in New Zealand specimens, but there was overlap in the proportional measurements of that length. Our specimens were also darker than described for the species, especially the fins. The first dorsal fin is dark, almost blackish with a pale base, compared with dusky in the type-specimens; the pectoral fins are dark dusky to blackish, compared with pale; the pelvic fins are blackish with the outer ray distally white, compared with "dusky blackish"; and the anal is blackish overall, paler posteriorly, compared with "pale with a dusting of melanophores diffuse anteriorly." Finally, our specimens completely lacked the one to three small scales on the ventral surface of the head above the articulation of the lower jaws, and the count of pyloric caeca in 31 of our specimens ranged somewhat lower than that given in the original description (19–26, $x = 21.8$, compared with 22–28, $x = 25.3$).

Caelorinchus parvifasciatus closely resembles *C. mirus,* but its relatively small light organ distinguishes it from that species. It differs from *C. fasciatus* and *C. maurofasciatus* in having less prominent saddle marks, spotlike pale markings along the dorsal midline of the tail, and broad naked areas behind the leading edge of the snout. The last two species also attain a much larger size than does *C. parvifasciatus.*

A NSW specimen of *C. parvifasciatus* (AMS I.15975-036) was misidentified by Iwamoto and Williams (1999:128) as *C. amydrozosterus*. That species has a different banding pattern without spotlike pale interspaces, a slightly larger dermal window of the light organ, and fewer pyloric caeca. *Caelorinchus amydrozosterus* has yet to be recorded from the Australian east coast, although it is commonly caught with *C. parvifasciatus* off Portland, western Victoria (K. Graham, pers. observ.).

REFERENCE SPECIMENS. — AMS I.15968-013 (5 spec.); K71-05-04. AMS I.15970-027 (4 spec.); K71-06-04. AMS I.15973-008 (3 spec.); K71-07-03. AMS I.15994-007 (35 spec.); K71-13-02. AMS I.16565-003 (1 spec.); K72-04-01. AMS I.18774-001 (1 spec.); K75-03-02. AMS I.18838-017 (19 spec.); K75-05-03. AMS I.18839-054 (1 spec.); K75-05-04. AMS I.19205-003 (4 spec.); K76-07-01. AMS I.20301-006 (1 spec.); K77-13-12. AMS I.24127-001 (1 spec.); K75-05-02. AMS I.26240-001 (1 spec.); K85-17-02.

REFERENCES. — McMillan and Paulin (1993); McMillan *in* Gomon et al. (as *Caelorinchus* sp. 3, "little whiptail") (1994).

***Caelorinchus smithi* Gilbert and Hubbs, 1920**
Fig. 71

DISTINGUISHING FEATURES. — 1D II,8–10; i15–i19; V 7; GR-I 7–8 total; scales below 1D 5.0–6.0, below 2D 4.5–6.0, lat.l. about 29–37; pyloric caeca 19–26. Snout 1.9–2.4 into head length; anterolateral margin completely supported by bone. Underside of head covered with small scales; nasal fossa finely scaled anteriorly and ventrally to almost naked; body scales with 3–7 divergent rows of stout, triangular spinules, middle row strongest, with 4–6 spinules; all rows complete to edge of scale. Light organ short, externally visible as short black fossa before anus. Overall color dark brown to swarthy; all fins blackish; mouth blackish; belly region bluish.

SIZE. — To about 35 cm.

DISTRIBUTION. — Philippines to Indonesia and Australia (Qld, NSW, NT), in about 400–750 m.

NSW CAPTURES. — Only one specimen caught by *Kapala* in 740 m off Qld-NSW border.

REMARKS. — *Caelorinchus smithi* is a tropical species and may be confused in NSW waters only with *C. macrorhynchus*, which has a longer snout (about 2 in HL cf. 2.0–2.3 in *C. smithi*), smaller orbit (4–5 in HL cf. 3.5–4.2), and somewhat more gill rakers on first arch (8–10 cf. 7–8).

REFERENCE SPECIMEN: AMS I.21795-012 (1 spec.); K78-23-08.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto and Williams (1999).

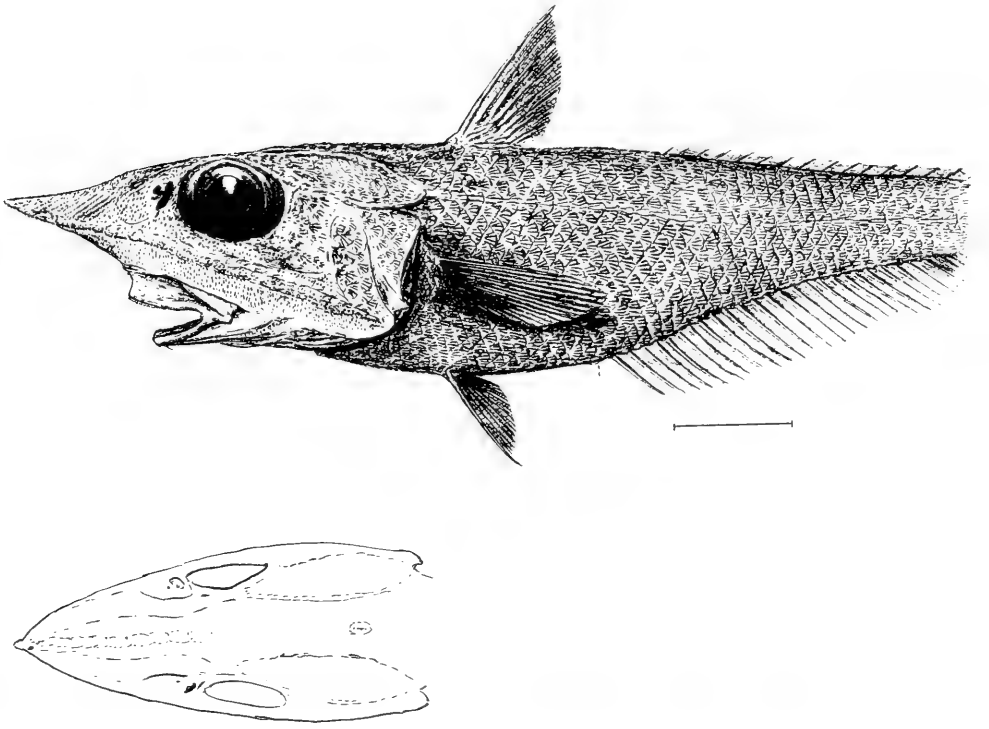

FIGURE 71. *Caelorinchus smithi* Gilbert and Hubbs, 1920 (from Iwamoto and Williams 1999:fig. 22).

Caelorinchus supernasutus **McMillan and Paulin, 1993**
Fig. 72

DISTINGUISHING FEATURES. — 1D II,9; P i18–19; V 7; GR-I 9–10 total; scales below 1D 8, below 2D 6.5, lat.l. about 53–55. Snout length 52–54% HL; interorbital width 17–18%; suborbital width 10–11% HL; postorbital length (24–25%); length orbit to angle of preopercle (26%); upper jaw length (20–21%), outer gill slit length 9%; and barbel length (4–6%). Snout long, narrow, tipped with a broad, flat diamond-shaped scute; length about one-half of head length; anterolateral margin completely supported by bone. Underside of head covered with small scales; nasal fossa mostly covered with small scales; body scales with 5–8 divergent rows of broad-based spinules. Light organ small but externally visible with black dermal window before anus. Overall color darker dorsally and blackish over abdomen and gill covers; lips, gums, mouth lining dark; ridge of median nasal bone dark; first dorsal fin blackish, other fins pale to dusky.

SIZE. — To about 64 cm.

DISTRIBUTION. — Australia (NSW) and New Zealand, in about 500–900 m.

NSW CAPTURES. — Taken twice by *Kapala,* off Crowdy Head and Nowra, in 500–900 m.

REMARKS. — The small size and few captures suggest that NSW is outside the normal range of this primarily New Zealand species. In having a long snout, small orbit, and small dermal window of the light organ immediately before the anus, *Caelorinchus supernasutus* most closely resembles *C. macrorhynchus* (the two species are compared in the description of *C. macrorhynchus*). Our two NSW specimens of *C. supernasutus* are juveniles of 162 and 280 mm TL; they were not compared with the much larger (418–635 mm TL) paratypes from New Zealand. Specimens of comparable size from the two areas should be compared to verify our identification.

REFERENCE SPECIMENS. — AMS I.27609-001 (1 spec.); K87-23-02. AMS I.29738-001 (1 spec.); K87-24-05.

REFERENCE. — McMillan and Paulin (1993).

Caelorinchus trachycarus **Iwamoto, McMillan, and Shcherbachev, 1999**
Fig. 73

DISTINGUISHING FEATURES. — 1D II,7–9; P i15–i18; V 7; GR-I 7–9 total; scales below 1D 4.5–7.0, below 2D 3.5–6.0, lat.l. about 28–37; pyloric caeca 7–9. Snout about 2.0–2.5 of head length, with straight to slightly concave dorsal profile; anterolateral margin incompletely supported by bone. Underside of head scaled; nasal fossa naked to suborbital ridge; head ridges especially spiny and coarse; body scales with 5–13 parallel spinules rows, middle row longest and highest, other rows usually much shorter and lower. Light organ small, not externally visible.

SIZE. — To about 50 cm.

DISTRIBUTION. — Southern Australia (NSW, Vic., Tas., SA, WA), New Zealand, and Norfolk Ridge s. of New Caledonia, in 622–1730 m.

NSW CAPTURE: Only one confirmed specimen from off Jervis Bay in 1130 m.

REMARKS. — *Caelorinchus trachycarus* is relatively more abundant in deeper, more southern waters of New Zealand and Australia, especially in the Great Australian Bight. Almost all reported captures were from depths greater than 1000 m. It is likely to be confused with the common *C. acanthiger,* which has smaller scales, more spinules rows on body scales, weaker spines on head ridges, paler body and fin color, and absence of a violet tinge to the body.

REFERENCE SPECIMEN: AMS I.28475-004 (1 spec.); K88-04-06.

REFERENCES. — Iwamoto et al. (1999); Iwamoto and Williams (1999).

FIGURE 72. *Caelorinchus supernasutus* McMillan and Paulin, 1993. AMS I.29738-001 (280 mm TL). From *Kapala* stn K87-24-05.

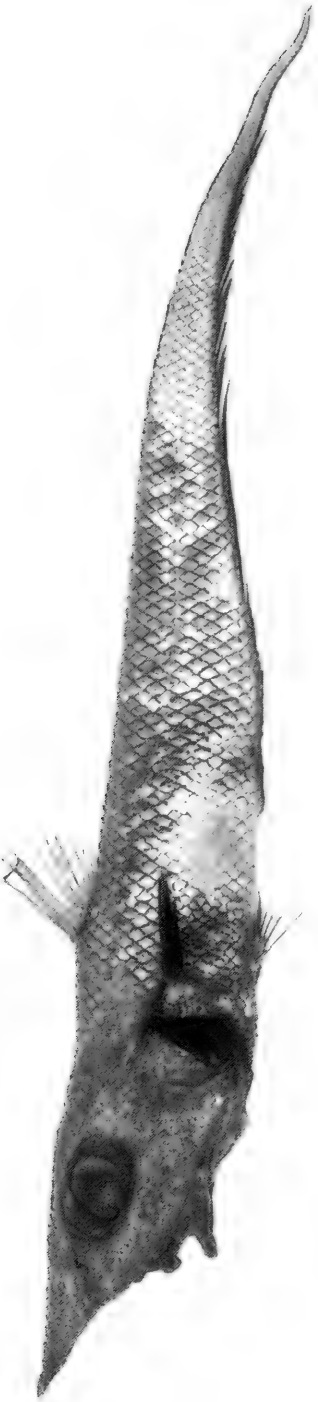

FIGURE 73. *Caelorinchus trachycarus* Iwamoto, McMillan and Shcherbachev, 1999. AMS I.28475-004. From *Kapala* stn K88-04-06, off Jervis Bay, NSW, in 1130 m.

Genus *Cetonurus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Head massive, globose, with capacious, fluid-filled chambers; head ridges lacking thick modified scales. First dorsal fin short, high, with steep base; slightly prolonged spinous ray serrated along leading edge. Anus surrounded by broad, circular naked area, the anterior edge of which extends most of distance between anal and pelvic fins. Scales small, densely covered with short, erect spinules; head entirely scaled, including branchiostegal membranes and usually gular membrane. Grooved lateral line interrupted, not continuous; scales along, and anterior to, second dorsal fin base enlarged, usually with enlarged spinules.

REMARKS. — Two widespread species: *C. globiceps,* the only species found in NSW, and *C. crassiceps* (Günther, 1878).

REFERENCE. — Sazonov and Shcherbachev (1985).

Cetonurus globiceps (Vaillant *in* Filhol, 1884)
Fig. 74

DISTINGUISHING FEATURES. — 1D II,7–11, usually 9–10; P i15–i19; V 8–11, usually 9–10; GR-I 10–14; pyloric caeca 7–11. Orbit diameter 24–32% of HL; interorbital width 36–48%.

SIZE. — To about 40 cm.

DISTRIBUTION. — Widespread in central Atlantic, southern Africa, Indian Ocean, Australia (NSW, Vic., SA, WA), New Zealand, and Japan.

NSW CAPTURES. — Caught by *Kapala* between Crowdy Head and Batemans Bay in 940–1200 m. A total of 99 specimens was caught in 34 tows (19% of all tows deeper than 900 m).

REMARKS. — Sazonov and Shcherbachev (1985) provided important information on the two species of the genus. *Cetonurus globiceps* can be distinguished from *C. crassiceps* by the former having a larger orbit, narrower interorbital, and somewhat more scale rows below first dorsal fin (13–19 vs. 11–14).

REFERENCE SPECIMENS. — AMS I.24057-002 (1 spec.); K83-09-04. AMS I.24187-001 (1 spec.); K83-14-02. AMS I.24355-006 (3 spec.) and AMS I.24355-011 (3 spec.); K83-18-02. AMS I.24624-002 (1 spec.); K84-04-10. AMS I.25273-002 (6 spec.); K84-11-09. AMS I.29605-005 (2 spec.); K89-09-07.

REFERENCES. — Sazonov and Shcherbachev (1985); Gomon et al. (1994); Paxton et al. (1989) as *C. crassiceps*.

FIGURE 74. *Cetonurus globiceps* (Vaillant *in* Filhol, 1884). AMS I.24057-005. From *Kapala* stn K83-09-04, east of Nowra, NSW, in 951–978 m.

Genus *Coryphaenoides*

DISTINGUISHING FEATURES. — Branchiostegal rays 6. Anus at or close to anal fin origin; no associated light organ. Spinous second ray of first dorsal fin serrated along leading edge (sometimes rudimentary or lost). Rays of second dorsal fin much shorter than opposite rays of anal fin. Outer gill rakers present (sometimes rudimentary) on first gill arch.

REMARKS. — The members of this genus are mostly found at mid-slope to lower-slope depths, but a few range down to abyssal levels. The genus is represented in all ocean basins, from polar to equatorial seas. Of the more than 60 species found worldwide, 11 were captured off NSW, with *Coryphaenoides serrulatus* one of the most abundant of all grenadiers. In contrast, the deepest-living *Coryphaenoides* species were represented by only one or a few specimens, probably reflecting the paucity of sampling in depths greater than 1200 m.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto (1990); Iwamoto and Shcherbachev (1991). Shcherbachev and Iwamoto (1995).

KEY TO THE SPECIES OF *CORYPHAENOIDES* FROM NSW

1a. Pelvic fin rays 7, rarely 6 or 8; spinules on body scales lanceolate 2
1b. Pelvic fin rays 8 or more; spinules on body scales needlelike. 3

2a. Chin barbel rudimentary; a greatly elongated ray in pectoral fin; inner gill rakers on first arch 16–19 . *C. subserrulatus*
2b. Chin barbel well developed, 20–30% of head length; no elongated ray in pectoral fin; inner gill rakers on first arch 11–15. . . . . *C. serrulatus*

3a. Snout completely scaled or naked surfaces confined to midventral swath and along ventral snout margin 4
3b. Snout entirely or almost entirely naked ventrally (and often on dorsal surface) 7

4a. Outer gill slit greatly restricted, 4–9% of head length; inner rakers on first gill arch 9 or 10 total . . . . . *C. rudis*
4b. Outer gill slit 14% of head length or greater; inner rakers on first gill arch 11 or more total. 5

5a. Pelvic fin rays 8, rarely 7 or 9 . . . . . *C. dossenus*
5b. Pelvic fin rays 11 or 12 6

6a. Preopercle with 4 spikelike struts (Fig. 75); head about 6 times into total length; teeth rather small and weak, somewhat deciduous. . . . . *C. grahami*
6b. Preopercle lacking spikelike struts; head about 5.5 times into total length; teeth strong, tightly attached . . *C. striaturus*

7a. Chin barbel less than 5% of head length, usually a mere stump; pelvic fin rays 8, rarely 9; inner gill rakers on outer arch 16–19. . . . . *C. mcmillani*
7b. Chin barbel 5% of head length or longer; pelvic fin rays 9–12; inner gill rakers on outer arch 9–16 8

8a. Inner gill rakers on outer arch 14–16; chin barbel 23–26% of head length; outer gill slit 20–22% of head length · *C. murrayi*
8b. Inner gill rakers on outer arch 9–13; chin barbel 4–16% of head length; outer gill slit 12–19% of head length· 9

9a. Long spinous ray of first dorsal fin with numerous serrations along leading edge; outer gill rakers on first arch 6–13· 10
9b. Long spinous ray of first dorsal fin with few or no serrations along leading edge; outer gill rakers on first arch 3–6 · · · · · · · · · · · · · · · · · · · *C. filicauda*

10a. Snout distinctly pointed in lateral view, protruding beyond mouth a distance about equal to half orbit diameter; chin barbel 9–16% of head length · · *C. carapinus*
10b. Snout blunt, scarcely protruding beyond mouth, ventral profile steep; chin barbel short, 5–9% of head length · · · · · · · · · · · · · · · · · *C.* sp. cf. *fernandezianus*

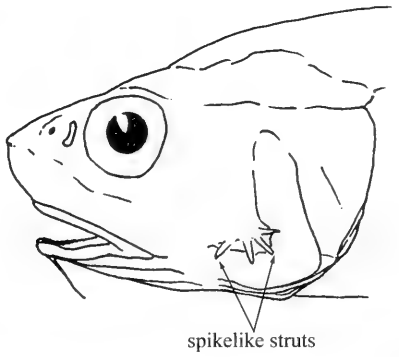

FIGURE 75. Preopercle of *Coryphaenoides grahami* showing spikelike struts.

***Coryphaenoides carapinus* (Goode and Bean, 1883)**
Fig. 76

DISTINGUISHING FEATURES. — 1D II,8–9; P i16–i20; V 9–10; GR-I (total, outer/inner series) 6–9/11–13; pyloric caeca 6–9. Snout length 33–37% of HL; orbit diameter 17–21%; interorbital width 34–39%; suborbital width 12–16%; upper jaw length 35–40%. Head about 5–6 in TL; chin barbel short, thin, 9–13% of HL. Dentition in upper jaw three or four teeth across at widest portion, outer series slightly enlarged; teeth in lower jaw in one row except at symphysis in about two rows. Outer gill rakers of first arch short, flaplike. Head lacking stout ridges of modified scales; leading edge of snout with row of small, deciduous, tubercular scales; snout otherwise naked. Body scales large, deciduous; spinules on exposed field reduced or lacking. Long spinous ray of first dorsal fin with numerous short, reclined spinules along leading edge. Pectoral fin relatively long, about 50–70% HL. Outer pelvic ray slightly produced, its length 50–80% HL. Color in alcohol overall gray to brownish, somewhat darker on head; blackish over operculum, gill membranes, and jaws; fins pale except for blackish spinous ray of first dorsal, uppermost ray of pectoral, and outer ray of pelvic.

SIZE. — To about 40 cm.

DISTRIBUTION. — Worldwide at bathyal depths; recorded around southern Australia (NSW, Vic., Tas., SA, WA) in 1000–3000 m, but range to 4900 m in eastern North Atlantic.

NSW CAPTURES. — A single NSW record (6 specimens) by ORV *Franklin* off Nowra in 1600–1900 m.

REMARKS. — Probably occurs too deep to have been sampled by *Kapala*. The description above for *Coryphaenoides carapinus* is based on Australian specimens only. Specimens from other areas differ from Australian specimens in certain counts and measurements, and we are uncertain if these differences are indicative of separate taxa or populations.

REFERENCE SPECIMENS. — NMV A7003 (6 spec., 85–254 mm TL); 67 km off Nowra, NSW, 34°41.97′S, 151°22.44′E, in 1896–1642 m; ORV *Franklin* stn CSIRO FR9/88, Slope 59; 22 Oct 1988.

REFERENCES. — Marshall and Iwamoto (1973); Haedrich and Polloni (1976).

***Coryphaenoides dossenus* McMillan, 1999**
Fig. 77

DISTINGUISHING FEATURES. — 1D II,9–10; P i17–i21; V 8 (rarely 7 or 9); GR-I (total, outer/inner series) 7–9/11–13, GR–II 9–12/11–13; scales below 1D 9.5–11, below 2D 7–12, lat.l. 38–48; pyloric caeca 10–18. Snout length 25–29% HL; orbit diameter 19–23%; interorbital width 16–20%; suborbital width 9–13; upper jaw length 40–45%. Head long, shallow, its width about half its length,

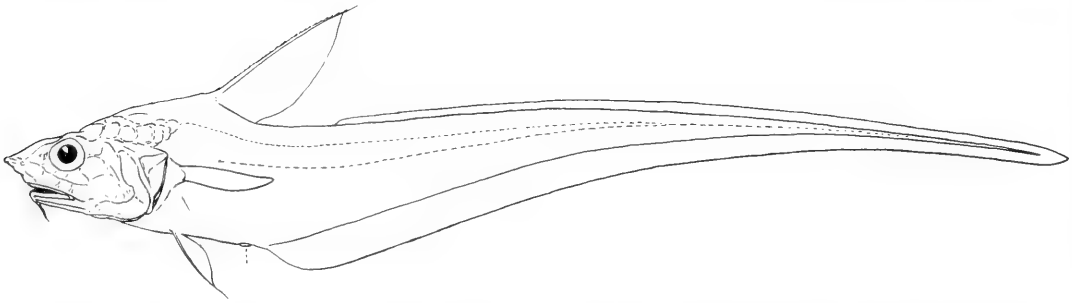

FIGURE 76. *Coryphaenoides carapinus* (Goode and Bean, 1883). CAS 58671, from eastern Indian Ocean, about 300 n.mi. w. of Perth, Western Australia.

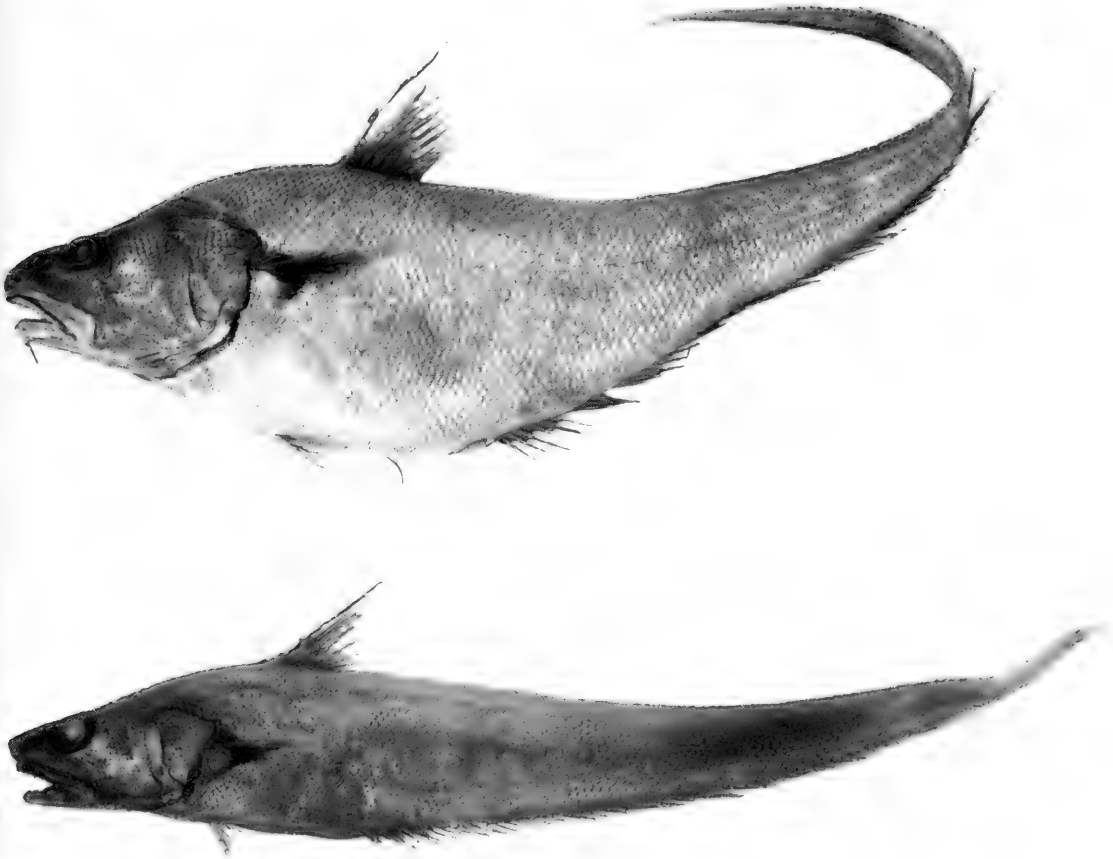

FIGURE 77. *Coryphaenoides dossenus* McMillan, 1999. (a) Female, AMS I.24658-001, from *Kapala* stn K84-08-03, east of Nowra, NSW, in 869–924 m; (b) male, AMS I.26245-015, from *Kapala* stn K86-01-07, off Sydney, NSW, in 819–899 m.

about 4.2–5.6 in TL (in females, more in males); snout low, blunt, barely protruding; chin barbel well developed, its length 21–34% HL. Upper jaw teeth in broad band, with outer series enlarged and widely spaced; lower jaw teeth in 3 or 4 irregular rows laterally. Gill rakers somewhat tablike. Head ridges not especially prominent and not reinforced by enlarged, thickened scales; underside of snout mostly covered with small scales, although narrow ventral margin naked; body scales rather large, with numerous subparallel to slightly convergent rows of small, needlelike spinules. Tip of outer pelvic ray barely or not reaching anal fin origin. Color in alcohol variable from light brown to swarthy overall, fins dusky to blackish, mouth and gill cavities dark.

SIZE. — Males to about 50 cm; females to more than 85 cm.

DISTRIBUTION. — Widespread around New Zealand, New Caledonia and the Coral Sea, Australia (Qld, NSW, Vic., Tas., SA, WA) and in the Indian Ocean; also in the southeastern Atlantic from South Africa north to the Gulf of Guinea. Depth range from about 700 to 1600 m, but most commonly around 900–1200 m.

NSW CAPTURES. — Captured frequently but in small numbers on all mid-slope grounds between Crowdy Head and Gabo Island in depths from 695 to 1200 m. It was present in 143 *Kapala* trawls including 51% of those deeper than 700 m; average catch about 3 per tow.

REMARKS. — Females (Fig. 77a) are more robust and attain a much larger size than males (Fig. 77b); larger individuals generally have a well-marked humped nape. Specimens of *C. dossenus* are

unlikely to be mistaken for other members of the genus owing to the combination of low, scarcely protruding snout, large mouth, large size, few pelvic fin rays, relatively high number of gill rakers, and long barbel.

REFERENCE SPECIMENS. — AMS I.17866-007 (1 female); K72-07-01. AMS I.17867-007 (2 females); K72-07-04. AMS I.18726-026 (1 female); K75-01-02. AMS I.19859-012 (1 female); K76-24-04. AMS I. 20477-002 (1 female); K77-23-10. AMS I.20485-006 (1 female), AMS I.20485-011 (1 female); K77-23-06. AMS I.21724-003 (7 males), AMS I.21724-006 (1 male); K79-20-15. AMS I. 24037-006 (3 females); K78-26-16. AMS I.24055-012 (1 female); K83-08-01. AMS I.24056-004 (2 females); K83-08-02. AMS I.24059-016 (2 females); K83-09-02. AMS I.24173-015 (1 female); K82-14-06. AMS I.24613-005 (1 female), AMS I.24613-007 (3 females); K75-05-05. AMS I.24624-001 (3 males), AMS I.24624-006 (2 females); K84-04-10. AMS I.24658-002 (1 female); K84-08-03. AMS I.24771-002 (1 female); K84-10-08. AMS I.24980-006 (1 female); K84-16-15. AMS I.24981-003 (2 females); K84-17-04. AMS I.24992-002 (2 females); K84-11-07. AMS I.25273-005 (1 female); K84-11-09. AMS I.25415-001 (1 female); K84-04-11. AMS I.25933-005 (1 female); K79-20-06. AMS I.26245-003 (2 females) and I.265245-015 (1 male); K86-01-07. AMS I.28717-003 (1 female); K88-10-04. NMV A6842 (2 spec.); 56 km off Nowra, NSW, 34°44.0′S, 151°14.5′E, in 817-1009 m; ORV *Franklin* stn CSIRO FR9/88, Slope 58; 22 Oct 1988.

REFERENCES. — McMillan *in* Gomon et al. (1994); Shcherbachev and Iwamoto (1995); McMillan (1999).

***Coryphaenoides* sp. cf. *fernandezianus* (Günther, 1887)**
Fig. 78

DISTINGUISHING FEATURES. — 1D II,8; P i17; V 9–10; GR-I (total, outer/inner series) 10–11/11–12. Snout length 27–36% of HL; preoral length 16–18% of HL; orbit diameter 18–20%; interorbital width 31–37%; suborbital width 15–16%; upper jaw length 40–41%. Head about 5 in TL; chin barbel short, thin, 5–9% of HL. Dentition in upper jaw in two series; teeth in lower jaw in one row. Outer gill rakers of first arch short, flaplike. Head lacking stout ridges of modified scales; few small, deciduous scales on suborbital and lower jaw, snout naked ventrally and along anterior part of dorsal surface. Body scales deciduous; spinules on exposed field reduced or lacking. Long spinous ray of first dorsal fin with numerous short, reclined spinules along leading edge. Outer pelvic ray slightly produced, its length about 70% HL. Color in alcohol overall dark brownish, somewhat darker on head; blackish over operculum, gill membranes, and jaws; fins dark.

SIZE. — To at least 16 cm.

DISTRIBUTION. — Australia (NSW and Lord Howe Rise) in 1600–2500 m.

NSW CAPTURES. — Two juveniles captured by ORV *Franklin,* one off Nowra in about 1800 m, the other on the Lord Howe Rise in 2450 m.

REMARKS. — We are uncertain of the identity of these two small specimens, but many of their characters are similar to those of *C. fernandezianus* (Günther, 1887), a species known only from the holotype taken off Juan Fernandez Island off the west coast of Chile. Our two specimens differ sufficiently from one another that they may represent separate species. The Nowra specimen has a longer snout (36% of HL vs. 27% in the Lord Howe Rise specimen), broader interorbital (37% of HL vs. 31%), shorter orbit to preopercle distance (48% HL vs. 54%), and fewer pelvic fin rays (9 vs. 10). More specimens are needed to resolve the identification questions.

REFERENCE SPECIMENS. — AMS I.29316-005 (1 spec.); Lord Howe Rise, 29°42.06′S, 159°48.31′E; 2450 m; ORV *Franklin*, 3 May 1989. NMV A7002 (1 spec.); 67 km off Nowra, 34°41.97′S, 151°22.44′E, 1896-1642 m; ORV *Franklin*, Slope 59, stn FR 9/88, 22 Oct. 1988.

REFERENCES. — Günther (1887); Iwamoto and Sazonov (1988).

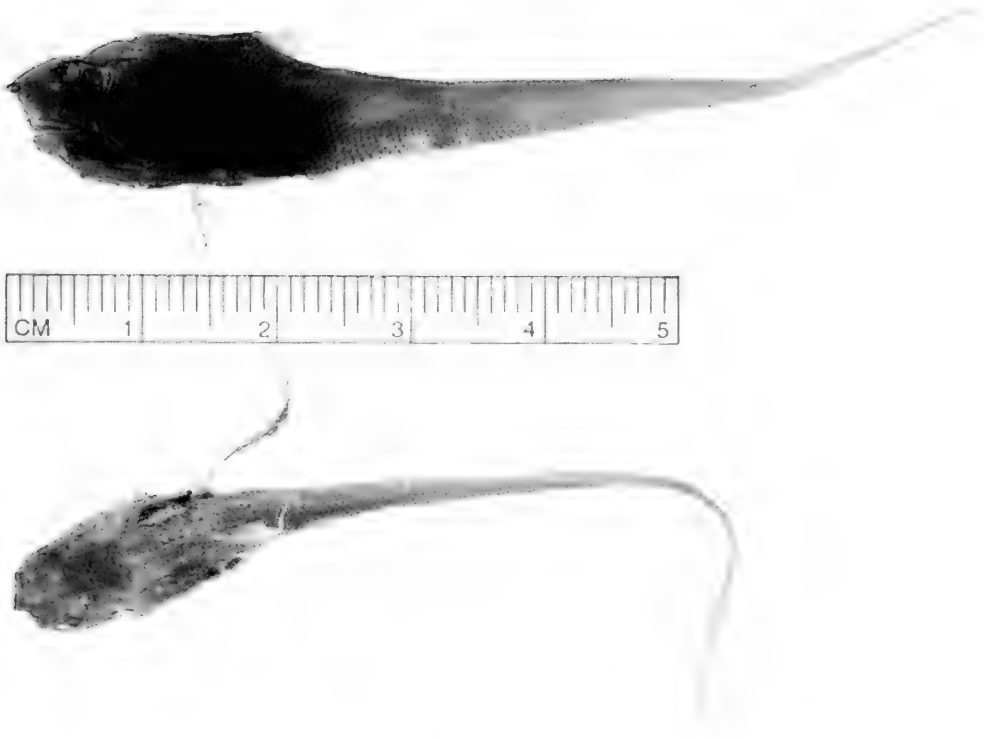

FIGURE 78. *Coryphaenoides* sp. cf. *fernandezianus*. AMS I.29316-001. From ORV *Franklin* stn off Lord Howe Island, in 2450 m.

Coryphaenoides filicauda Günther, 1878

Fig. 79

DISTINGUISHING FEATURES. — 1D II,8–10; P i16–i19; V 9–10; GR-I (total, outer/inner series) 3–6/9–10; pyloric caeca 6–8. Snout length 33–38% of HL; orbit diameter 16–18%; interorbital width 30–33%; suborbital width 12–17%; upper jaw length 33–37%. Head about 5–6 in TL; chin barbel short, thin, 4–12% of HL. Upper jaw teeth in narrow band, with slightly enlarged outer series; lower jaw teeth in narrow band tapering to one row posteriorly. Outer gill rakers of first arch few, weakly de-

FIGURE 79. *Coryphaenoides filicauda* Günther, 1878. AMS I.27643-004. From *Kapala* stn K88-12-02, southeast of Crowdy Head, NSW, in 990–1020 m.

veloped. Head lacking stout ridges of modified scales; tip and lateral angles of snout armed with small tubercular scales with upturned spinules; snout otherwise naked. Body scales large, deciduous; spinules on exposed field reduced or lacking. Long spinous ray of first dorsal fin with few or no spinules along leading edge. Pectoral fin relatively long, 50–70% HL; rays fine, none thickened or notably prolonged beyond others. Outer pelvic ray slightly produced, its length 40–60% HL. Color in alcohol overall pale to brownish, flesh translucent over anal pterygiophores; blackish over abdomen, operculum, and somewhat dusky on underside of head; fins pale except for blackish spinous ray of first dorsal, uppermost ray of pectoral, and outer ray of pelvic.

SIZE. — To about 41 cm.

DISTRIBUTION. — High latitudes of southern hemisphere; known off Australia (NSW, including Lord Howe Rise, Tas., SA); capture depths range about 1000–5100 m, but most from 3500–5000 m.

NSW CAPTURES. — A single *Kapala* specimen in 990–1020 m off Crowdy Head and three *Franklin* specimens from 2450 m on the Lord Howe Rise.

REMARKS. — *Coryphaenoides filicauda* is primarily an abyssal species, and the *Kapala* capture at mid-slope depths off NSW is the shallowest record for the species. The three juveniles (17.5–20.1 mm HL) from the Lord Howe Rise differed from others examined (including from other areas) in a number of features, including slightly more gill rakers on first arch (6–8 outer rakers; 11 inner rakers), somewhat longer snout (30–37% HL), wider interorbital (32–29% HL), longer upper jaw (38–39% HL), and longer barbel (12–13% HL). We are uncertain whether these differences reflect ontogenetic change or different taxa. A closely related species, *C. carapinus*, can be distinguished from *C. filicauda* by its well-serrated leading edge of the spinous dorsal ray, longer barbel (9–15% HL), more numerous and better-developed gill rakers (GR-I 6–10/9–13), and more adherent, more heavily spinulated scales.

REFERENCE SPECIMENS. — AMS I.27643-004 (1 spec.); K88-12-02. AMS I.29316-004 (3 spec.); Lord Howe Rise, 29°42.06′S, 159°48.13′E; 2450 m; ORV *Franklin* stn FR0589-17; 3 May 1989.

REFERENCES. — Iwamoto and Sazonov (1988); Gon and Heemstra (1990).

Coryphaenoides grahami Iwamoto and Shcherbachev, 1991
Fig. 80

DISTINGUISHING FEATURES. — 1D II,8–9; P i19–i23; V 12; GR-I (total, outer/inner series) 8–10/11–14; scales below 1D 7.5–9.0, below 2D 8.0–9.5, lat.l about 26–31; pyloric caeca about 10. Snout length 25–29% of HL; orbit diameter 21–23%; interorbital width 28–31%; suborbital width 11–14%; upper jaw length 39–42%; barbel length 13–23%. Head about 6 in TL; preopercle with 4 spikelike struts. Teeth small, weak, somewhat deciduous, in single row in lower jaw. Head lacking

FIGURE 80. *Coryphaenoides grahami* Iwamoto and Shcherbachev, 1991. AMS I.29798-010. From *Kapala* stn K89-12-04, off Tuncurry, NSW, in 1033–1079 m.

stout ridges of large, modified scales and large tubercular scale at snout tip; underside of head (except gill membranes) entirely scaled; body scales deciduous, about 8–10 parallel rows of small spinules. Color fresh ivory white with silvery sheen; in alcohol overall dark gray to brown, blackish over ventral surfaces and lips, mouth, gill membranes, gill chamber, and most fins.

SIZE. — To about 40 cm.

DISTRIBUTION. — South Atlantic off South Africa, southern Indian Ocean, eastern Australia (NSW), in about 1050–1300 m.

NSW CAPTURES. — Six specimens collected at four *Kapala* stations between Crowdy Head and Jervis Bay in 1040–1140 m.

REMARKS. — *Coryphaenoides grahami* has not been collected from any other Australian state. It is likely to be mistaken only for *C. striaturus,* which is similar in shape, and shares many counts, measurements, and scale features. *Coryphaenoides grahami* is, however, darker overall and has a broader interorbital, smaller, weaker teeth, and spikelike processes on the preopercle.

REFERENCE SPECIMENS. — AMS I.29737-002 (paratype), and I.29737-004 (2 spec.); K89-19-01. AMS I.29742-003 (paratype); K89-17-07. AMS I.29745-005 (paratype); K89-18-02. AMS I.29798-010 (paratype); K89-12-04.

REFERENCE. — Iwamoto and Shcherbachev (1991).

***Coryphaenoides mcmillani* Iwamoto and Shcherbachev, 1991**
Fig. 81

DISTINGUISHING FEATURES. — 1D II,9–11; P i17–i20; V 8–9; GR-I (total, outer/inner series) 11–16/16–19; scales below 1D 7.5–9.0, below 2D 6.5–9.5, lat.l about 31–34; pyloric caeca about 9–10. Snout length 28–31% of HL; orbit diameter 27–31%; interorbital width 26–30%; suborbital width 11–12%; upper jaw length 46–50%. Head about 4.5–6 in TL; sensory pores prominent; chin barbel rudimentary, stumplike. Upper jaw teeth in narrow band, with slightly enlarged outer series; lower jaw teeth in single row. Outer gill rakers of first arch relatively long and flat, triangular to saber-shaped. Head lacking stout ridges of large, modified scales; snout naked except for small tubercular scale at tip and lateral angles; body scales deciduous, about 8–10 parallel rows of slender, conical spinules. Pectoral fin relatively long, 70–90% HL, but rays fine, none thickened or notably prolonged beyond others. Outer pelvic ray elongated, its length 70–90% HL. Color in alcohol overall swarthy, blackish over abdomen behind pelvic fins; operculum and most head membranes black; fins blackish to dusky.

SIZE. — To about 35 cm.

DISTRIBUTION. — New Zealand, Australia (NSW, Tas., SA), southern Indian Ocean, southern Africa, South Atlantic off Whale Ridge, in 950–1400 m.

NSW CAPTURES. — Captured once by ORV *Franklin* off Nowra in 817–1009 m.

REMARKS. — *Coryphaenoides mcmillani* was not collected by *Kapala* despite the holotype coming from an area and depth extensively trawled. It is either very rare off NSW or was misidentified in the field as *C. subserrulatus*, which was commonly recorded from the type area. *C. mcmillani* is distinguished from the similar *C. subserrulatus* by having more pelvic fin rays and shorter pectoral and pelvic fins.

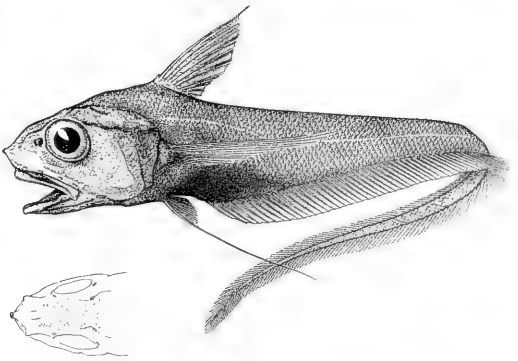

FIGURE 81. *Coryphaenoides mcmillani* Iwamoto and Shcherbachev, 1991 (from original illustration of holotype).

REFERENCE SPECIMEN: NMV A6794 (holotype); NSW, 56 km off Nowra, 34°44′S, 151°14.3′E, in 1009–817 m; ORV *Franklin* stn CSIRO FR5/86, Slope 9.

REFERENCE. — Iwamoto and Shcherbachev (1991).

***Coryphaenoides murrayi* Günther, 1878**
Fig. 82

DISTINGUISHING FEATURES. — 1D II,8–10; P i18–i20; V 10–12(usually 12); GR-I (total, outer/inner series) 9–11/14–16; scales below 1D 9–11, below 2D 9–11, lat.l about 33; pyloric caeca about 9–10. Snout length 28–30% of HL; orbit diameter 20–23%; interorbital width 28–34%; suborbital width 13–17%; upper jaw length 42–45%. Head broad, width about two-thirds its length; chin barbel slender, about equal to or longer than orbit. Upper jaw teeth in broad band, with outer series slightly enlarged; lower jaw teeth in one row. Head lacking ridges of large, stout, modified scales; a row of small scales along leading edge of snout; snout naked on underside, with broad naked areas on dorsal surface behind leading edge; body scales rather deciduous, about 5–8 parallel rows of weak, slender, conical spinules. Color in alcohol overall dark brownish to swarthy.

SIZE. — To at least 37 cm.

DISTRIBUTION. — Western Indian Ocean to southeastern Australia (NSW, Vic.), New Zealand, and Fiji, in depths of 1196–2350 m.

NSW CAPTURE. — Taken once by ORV *Franklin* off Nowra in 1896–1642 m.

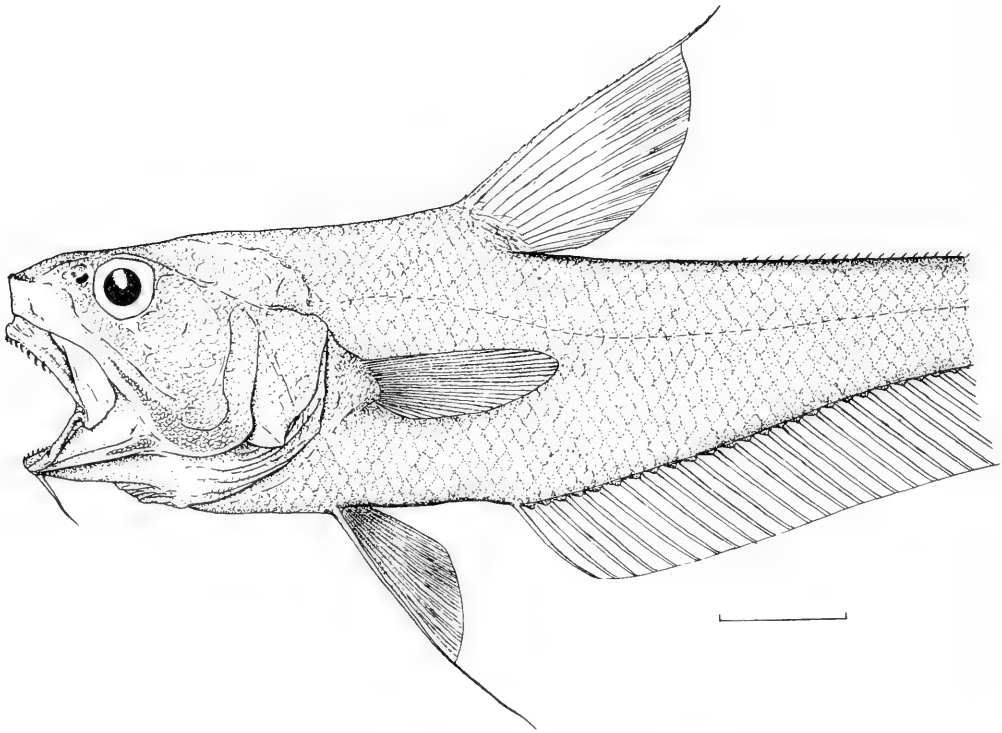

FIGURE 82. *Coryphaenoides murrayi* Günther, 1878. Holotype, BMNH 1887.12.7.113, *Challenger* stn 168, off New Zealand, in 2012 m. Fins and scales reconstructed.

REMARKS. — This is a species of lower-slope depths known mostly from captures off New Zealand. The only Australian specimens are from off NSW and eastern Victoria.

REFERENCE SPECIMENS. — NMV A7004 (1 spec.); 67 km off Nowra, NSW, 34°41.97′S, 151°22.44′E, in 1896–1642 m; ORV *Franklin* stn CSIRO FR9/88, Slope 59, 22 Oct 1988. NMV A6793 (1 spec.); 85 km s. of Pt. Hicks, 38°31.4′S, 149°21.1′E, in 1986–1360 m.

REFERENCE. — Iwamoto and Shcherbachev (1991).

***Coryphaenoides rudis* Günther, 1878**
Fig. 83

DISTINGUISHING FEATURES. — 1D II,9–11; P i16–i21; V 8–11 (usually 9 or 10, rarely 8 or 11); GR-II (total, outer/inner series) 7–10/9–10; scales below 1D 9, below 2D 6.5, lat.l about 37; pyloric caeca about 14. Head broad, width about two-thirds its length; snout low, scarcely protruding in large adults, length about 23–29% HL; orbit small, 16–26% HL; interorbital width 26–30% HL; mouth large, upper jaw extending to below posterior margin of orbit, 37–43% HL; chin barbel slender, 10–23% HL. Upper jaw teeth in moderately broad band, with outer series enlarged; lower jaw teeth in 1–3 irregular rows. Head lacking ridges of large, stout, modified scales; snout completely scaled; body scales with small spinules. Color in alcohol overall brownish to brownish gray.

SIZE. — One of the largest known grenadiers, attaining at least 120 cm in TL. The two NSW specimens measured 71 and 95 cm in length.

DISTRIBUTION. — Broadly distributed in central and western Pacific, Indian Ocean, and middle to low latitudes in the Atlantic, in depths of 1,000–2,400 m. Recorded from Australia off NSW and WA.

NSW CAPTURES. — Only two specimens caught by *Kapala*, one in 1050 m off Newcastle, the second in 1150 m off Sydney.

REMARKS. — Juveniles of this large species have a more protruding snout and proportionately larger orbits than do the adults, which affects the relative dimensions of the interorbital, suborbital, and postorbital. *Coryphaenoides rudis* is a large, widely distributed species originally described from the Kermadec Islands, but subsequently recorded from other areas under the names *C. paradoxus* and *C. macrocephalus*, as well as *C. rudis*. It appears to be rare wherever found.

REFERENCE SPECIMENS. — AMS I.28477-001 (1 spec.); K88-16-04; AMS I.29340-001 (1 spec.); K89-13-02.

REFERENCES. — Sazonov and Iwamoto (1992); Shcherbachev and Iwamoto (1995); Iwamoto and Williams (1999).

***Coryphaenoides serrulatus* Günther, 1878**
Fig. 84

DISTINGUISHING FEATURES. — 1D II,8–11; P i18–i22; V 7 (rarely 6 or 8); GR-I (total, outer/inner series) 7–10/11–15, GR-II 10–14/10–14; scales below 1D 8–10, below 2D 6.5–8.5, lat.l 35–40; pyloric caeca 16–19. Snout length 27–30% HL; orbit diameter 30–33%; interorbital width 18–24%; suborbital width 11–14%; upper jaw length 39–44%. Head short and compressed, about 6 times in TL; chin barbel well developed, length 20–30% HL. Upper jaw teeth in relatively narrow band, with outer series enlarged; lower jaw teeth in one row. Gill rakers rather numerous, the outer rakers somewhat tablike. Suborbital ridge with row of stout, coarsely thickened scales; tip and lateral angles of snout with large, tubercular scales, snout otherwise uniformly covered with small scales; body scales rather large, covered with lanceolate spinules. Outer pelvic ray 50–80% HL, extending to anal origin or slightly beyond. Color in alcohol overall brownish, darker over abdomen and gill covers with bluish to blackish.

FIGURE 83. *Coryphaenoides rudis* Günther, 1878. AMS I.28477-001. From *Kapala* stn K89-13-02, off Sydney, NSW, in 1116–1170 m.

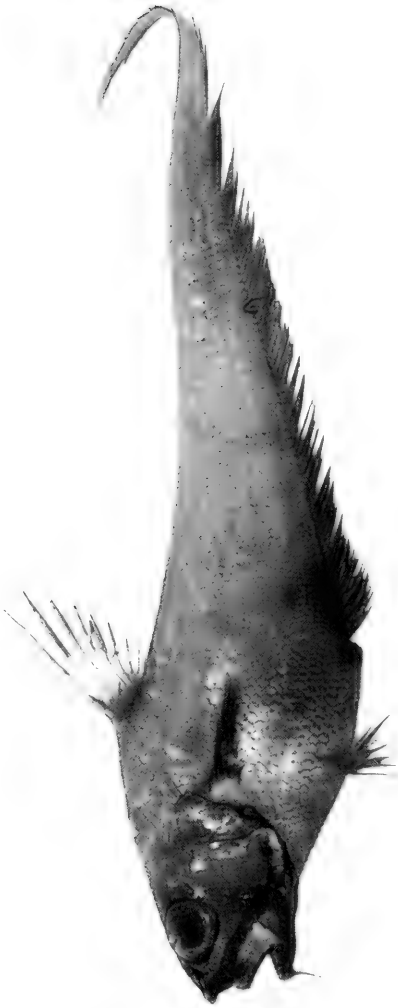

FIGURE 84. *Coryphaenoides serrulatus* Günther, 1878. AMS I.24172-006. From *Kapala* stn K83-14-01, off Ulladulla, NSW, in 978–1024 m.

SIZE. — To about 45 cm.

DISTRIBUTION. — New Zealand and Australia (NSW, Vic., Tas., SA, WA), in 550–1200 m.

NSW CAPTURES. — Caught on all mid-slope grounds south of Crowdy Head in 690–1200 m. The most abundant grenadier in *Kapala* mid-slope catches. Recorded from 253 stations and present in all but 5 trawls in depths between 800 and 1200 m. Average catch about 40 per tow.

REMARKS. — Two subspecies of this widely distributed species of the southern hemisphere were recognized by Iwamoto and Shcherbachev (1991), with *Coryphaenoides s. serrulatus* occurring off New Zealand and southern Australian waters and *C. s. oceanus* found in oceanic waters of the Indian Ocean. The latter subspecies differs from the former in having a longer outer pelvic ray that extends beyond the base of the 10th anal ray, as well as several differences in proportional measurements.

REFERENCE SPECIMENS. — AMS I.18726-025 (3 spec.); K75-01-02. AMS I.19859-001 (13 spec.); K76-24-04. AMS I.19860-006 (8 spec.); K76-24-03. AMS I.19862-004 (5 spec.); K76-23-01. AMS I.20096-007 (8 spec.); K77-22-06. AMS I.20098-006 (3 spec.); K77-23-07. AMS I.20484-002 (1 spec.); K77-21-01. AMS I.20485-007 (3 spec.); K77-23-06. AMS I.23885-015 (1 spec.); K78-27-05. AMS I.24037-004 (6 spec.); K78-26-16. AMS I.24054-013 (1 spec.); K83-06-02. AMS I.24055-009 (1 spec.); K83-08-01. AMS I.24172-006 (1 spec.); K83-14-01. AMS I.24613-001 (8 spec.); K75-05-05. AMS I.25933-006 (1 spec.); K79-20-06. NMV A17 (1 spec.) and NMV A9077 (2 spec.); 56 km off Nowra; 1009-817 m; ORV *Franklin* stn CSIRO FR5/86, Slope 9. NMV A5783 (1 spec.), off Nowra; 1100 m; ORV *Franklin* stn CSIRO FR9/88, Slope 58.

REFERENCES. — Last et al. (1983); Iwamoto and Shcherbachev (1991); McMillan *in* Gomon et al. (1994); Iwamoto and Williams (1999).

***Coryphaenoides striaturus* Barnard, 1925**
Fig. 85

DISTINGUISHING FEATURES. — 1D II,8–10; P i18–i24; V 11–12; GR-I (total, outer/inner series) 7–11/12–16, GR-II 11–14/11–15; scales below 1D 7.5–10, below 2D 8–9, lat.l 30–36; pyloric caeca 9–12. Snout length 26–30% HL; orbit diameter 18–24%; interorbital width 23–30%; suborbital width 11–15%; upper jaw length 38–46%. Head robust, its width about equal to postorbital length, about 5.5 in TL; chin barbel well developed, length 18–26% HL. Upper jaw teeth in band, with outer series enlarged; lower jaw teeth in one row. Gill rakers somewhat tablike. Head ridges prominent but not reinforced by thickened scales; underside of snout covered with small scales; body scales rather large, with 9–11 parallel rows of small, needlelike spinules. Outer pelvic ray extends beyond anal fin origin,

FIGURE 85. *Coryphaenoides striaturus* Barnard, 1925. AMS I.29737-007. From *Kapala* stn K89-19-01, off Ulladulla, NSW, in 1116–1134 m.

usually to base of 6th–11th ray. Color in alcohol overall dark brown to swarthy, darker on underside of head and gill covers.

SIZE. — To about 55 cm.

DISTRIBUTION. — New Zealand, Australia (Qld, NSW, Vic., Tas., SA, WA), to the southeastern Atlantic off southern Africa, in depths of about 800 to 2000 m; most often taken in 1000–1400 m. Generally confined to cooler, temperate waters off southern coasts, although two AMS specimens were taken on the Lord Howe Rise off southern Qld and northern NSW.

NSW CAPTURES. — Collected from only three *Kapala* stations (5 specimens) south of 34°50′S in about 1100 m depth. A fourth NSW specimen was collected by ORV *Franklin* on the Lord Howe Rise in 1590 m.

REMARKS. — *Coryphaenoides striaturus* is normally an abundant species throughout its range, but off NSW it may be more common in depths greater than those trawled by *Kapala*. The uniformly and completely scaled snout, the pelvic fin ray count, and the highly arched nape help to distinguish this species from other Australian members of the subgenus *Chalinura*. The sympatric species *C. grahami* is closely similar but can be differentiated by its spikelike ridges of the preopercle, darker overall color, and less arched nape. Also, *C. striaturus* is a stouter, firmer-fleshed fish than is *C. grahami*.

REFERENCE SPECIMENS. — AMS I.24992-004 (2 spec.); K84-11-07. AMS I.29737-007 (2 spec.); K89-19-01. AMS I.29745-002 (1 spec.) and AMS I.29745-003 (1 spec.); K89-18-02. AMS I.29315-002 (1 spec.); Lord Howe Rise, 29°10.29′S, 160°29.78′E; 1590 m; 4 May 1989; ORV *Franklin* stn FR0589-21. AMS I.29339-001 (1 spec.); Lord Howe Rise, 27°39.8′S, 161°46.38′E; 1423 m; 1989; ORV *Franklin* stn FR0589-31.

REFERENCES. — Iwamoto and Shcherbachev (1991); Iwamoto and Williams (1999).

Coryphaenoides subserrulatus **Makushok, 1976**
Fig. 86

DISTINGUISHING FEATURES. — 1D II,9–11; P i13–i18; V 7; GR-I (total, outer/inner series)10–14/16–19, GR-II 16–18/14–17; scales below 1D 8–9, below 2D 6.5–8.5, lat.l 29–37; pyloric caeca 12–14. Snout length 25–29% HL; orbit diameter 30–34%; interorbital width 20–25%; suborbital width 7–10%; upper jaw length 44–49%. Head short and laterally compressed, more than 6 times

FIGURE 86. *Coryphaenoides subserrulatus* Makushok, 1967. AMS I.24054-006. From *Kapala* stn K83-06-02, off Wollongong, NSW, in 869–878 m.

in TL; chin barbel rudimentary. Upper jaw teeth in relatively narrow band, with outer series slightly enlarged; lower jaw teeth in one row. Gill rakers numerous for genus, the outer rakers on first arch somewhat tablike. Suborbital shelf narrow, with row of stout, coarsely thickened scales; tip and lateral angles of snout with large, tubercular scales, snout otherwise mostly naked ventrally and partly dorsally; body scales rather large, covered with lanceolate spinules. Uppermost developed pectoral fin ray stouter than other rays of fin and greatly elongated, 115–214% HL. Outer pelvic ray elongated, 158–221% HL, extending far beyond anal fin origin. Color in alcohol overall light to medium brown, darker over abdomen, gill covers bluish to blackish.

SIZE. — To 37 cm.

DISTRIBUTION. — Widely distributed off southeastern Australia (NSW, Vic., Tas.), New Zealand, Chile, and in the South Atlantic off Argentina and on the Agulhas Plateau. Depth range about 700–1200 m, but one capture off Chile at 470–440 m.

NSW CAPTURES. — Commonly caught on all grounds south of Crowdy Head in 720–1200 m. Recorded from 173 *Kapala* stations including 70% of stations deeper than 800 m; average catch about 10 per trawl.

REMARKS. — *Coryphaenoides subserrulatus* differs from the closely similar *C. mcmillani* in the relatively thick, greatly elongated uppermost pectoral fin ray (no prolonged ray in *C. mcmillani*), fewer pelvic fin rays (7 cf. 8 or 9), and lanceolate scale spinules (cf. needlelike, in parallel rows).

REFERENCE SPECIMENS. — AMS I.20068-005 (1 spec.); K77-23-13. AMS I.24037-003 (7 spec.); K78-26-16. AMS I.24054-006 (5 spec.); K83-06-02. AMS I.24055-004 (1 spec); K83-08-01.

REFERENCES. — Makushok (1967); McCann and McKnight (1980) (as *Coryphaenoides quadripennatus*); Iwamoto and Shcherbachev (1991).

Genus *Cynomacrurus*

DISTINGUISHING FEATURES. — Branchiostegal rays 6. Mouth large, upper jaw extending well past orbit. Anus located immediately before anal fin origin; no light organ. Swim bladder very small. Sensory pores large, prominent; orbit small, more than 5 in head length. One or more pairs of large fanglike teeth in upper jaw; lower jaw with single row of 4 to 11 fanglike teeth. Lateral line broken into two main segments, anterodorsal segment ending somewhat behind first dorsal fin, second segment midlateral, beginning below end of first segment.

REMARKS. — Monotypic genus; bathypelagic in Southern Ocean.

REFERENCES. — Dollo (1909); Marshall (1964); Iwamoto *in* Gon and Heemstra (1990).

Cynomacrurus piriei Dollo, 1909

Fig. 87

DISTINGUISHING FEATURES. — 1D II,8–9; P i13–i16; V 7–8; GR-I (outer/inner) 8 or 9 total/14–16 total; scale rows below 1D about 7; pyloric caeca 9 or 10. Head about 5 times in total length; snout not protruding. Extensive naked areas on head. Barbel absent. Spinous second ray of first dorsal fin smooth.

SIZE. — To about 46 cm.

DISTRIBUTION. — Southern Ocean, Australia (NSW), and New Zealand (*fide* Peter McMillan).

NSW CAPTURE: One specimen (the only Australian record) captured by *Kapala* off Ulladulla (35°30′S) when trawling in 1030–1070 m. It may have been captured in midwater when hauling the trawl.

REMARKS. — The species is abundant at bathypelagic depths of the Southern Ocean.

REFERENCE SPECIMEN: AMS I.24424-005 (1 spec.); K83-19-02.

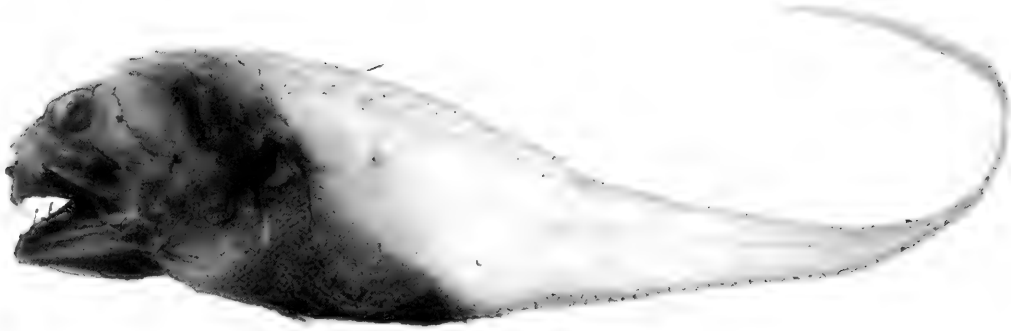

FIGURE 87. *Cynomacrurus piriei* Dollo, 1900. AMS I.24424-005. From *Kapala* stn K83-19-02, off Ulladulla, NSW, in 1079–1116 m.

Genus *Haplomacrourus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Head laterally compressed, snout rounded in profile; in larger specimens (>30 cm TL) upper jaws fall short of vertical through anterior margin of orbit and snout not protruding beyond mouth. Snout and ventral parts of head naked; scales small, those on head and anterior part of body lacking spinules. Anus about midway between anal and pelvic fins; a small dermal window of light organ between bases of pelvic fins. Spinous dorsal ray stout, flattened laterally, recurved and finely serrated along leading edge.

REMARKS. — A peculiar monotypic species of uncertain relationships.

REFERENCES. — Trunov (1980); Iwamoto and Merrett (1997).

Haplomacrourus nudirostris Trunov, 1980
Fig. 88

DISTINGUISHING FEATURES. — 1D II,9–10; P i25–i28; V 8–9; scales small, 15–18 below 1D, 15–17 below 2D; pyloric caeca about 30.

SIZE. — To about 60 cm.

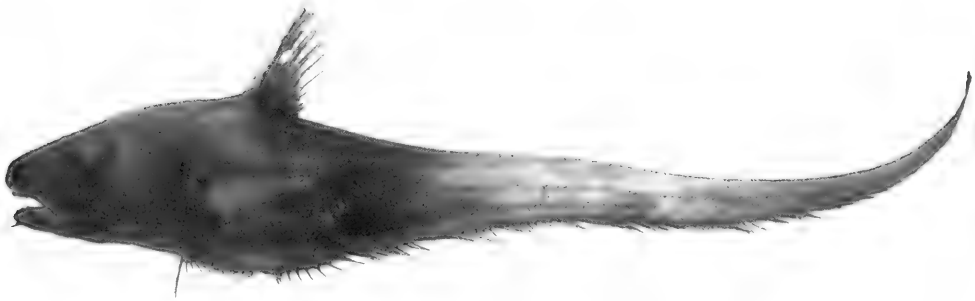

FIGURE 88. *Haplomacrourus nudirostris* Trunov, 1980. AMS I.26247-004. From *Kapala* stn K85-21-04, east of Broken Bay, NSW, in 1024–1052 m.

DISTRIBUTION. — Southeastern Atlantic off Africa through Indian Ocean to Australia (NSW) and New Zealand, north to New Caledonia, in about 800–1600 m.

NSW CAPTURES. — Caught at eight stations (9 specimens) between Crowdy Head and Jervis Bay in 950–1100 m.

REMARKS. — All *Kapala* specimens were small (174–280 mm TL), overall bluish black (trunk blackish), with a rounded snout profile, and jaws extending posterior to a vertical through the anterior margin of the orbit. The small numbers and absence of large adults in *Kapala* catches suggests that *Haplomacrourus* more commonly inhabits depths greater than those fished, or the adults are avoiding the net, or that NSW is marginal to its normal distribution.

REFERENCE SPECIMENS. — AMS I.24057-005 (2 spec.); K83-09-04. AMS I.24993-001 (1 spec.); K84-16-14. AMS I.26247-004 (1 spec.); K85-21-04. AMS I.29752-001 (1 spec.); K89-17-08. AMS I.29754-004 (1 spec.); K89-17-03. AMS I.29797-002 (1 spec.); K89-12-05. AMS I.29799-001 (1 spec.); K89-06-02. AMS I.40272-004 (1 spec.); K80-20-05.

Genus *Hymenocephalus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Head bones weakly ossified, head covering membranous, transparent. Spinous ray of first dorsal fin usually smooth (weakly serrated in subgenus *Hymenogadus*, species of which may occur off NSW but have yet to be recorded). Anus immediately before anal fin origin, without broad black naked perianal margin. Two lens-like structures of light organ, one on chest, the other immediately before anus; luminescent tissue, consisting of fine black striations between silver ground, cover parts of abdomen, chest, shoulder girdle and isthmus between gill membranes. Gill rakers tubercular, inner rakers of first arch usually more than 18. Most species small, usually < 20 cm TL. Color blackish, with silvery cover over most of head and ventral surfaces of body; but some species almost entirely black.

REMARKS. — Only three species of this widespread genus were identified from *Kapala* catches, but others could be expected off northern NSW, especially those species reported from New Caledonia by Iwamoto and Merrett (1997).

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto and Merrett (1997).

KEY TO THE SPECIES OF *HYMENOCEPHALUS* IN NEW SOUTH WALES

1a. Chin barbel long, well developed; pelvic fin rays 8 . . . . . *H. longibarbis*
1b. Chin barbel absent or rudimentary; pelvic fin rays 11–14. 2

2a. Orbits small, 3.6–4.5 times into HL; midlateral dark stripe faint or inconspicuous; body rather uniformly dark, fading posteriorly; suborbital broad, 1.0–1.6 into orbit . . . . . *H. aterrimus*
2b. Orbits large, 3.2 or less times in HL; distinct midlateral dark stripe present extending to end of tail; suborbital 2–3 into orbit . . . . . *H. nascens*

Hymenocephalus aterrimus Gilbert, 1905
Fig. 89

DISTINGUISHING FEATURES. — V 12–14; total GR-I (outer/inner) 14–20/22–27. Chin barbel absent. Suborbital region broad, width 17–22% HL; interorbital broad, width 36–39% HL; orbit small, diameter 22–28% HL. Color uniformly black to dark brown in preserved specimens, generally paler on tail.

SIZE. — To about 19 cm.

DISTRIBUTION. — Widespread in warm waters of Indian, Atlantic, and Pacific oceans, including Australia (NSW). Questionably recorded from the southeastern Pacific off Sala-y-Gomez and Nazca ridges (Sazonov and Iwamoto 1992), but otherwise not present in tropical eastern Pacific.

FIGURE 89. *Hymenocephalus aterrimus* Gilbert, 1905. AMS I.29753-001. From *Kapala* stn K89-17-06, east of Crowdy Head, NSW, in 878–933 m.

NSW CAPTURES. — Collected twice in 820–830 m off Crowdy Head at the northern end of the mid-slope trawling ground.

REMARKS. — The NSW specimens are the only Australian records, but *H. aterrimus* can be expected off Queensland. Its small size and more tropical distribution could account for its rarity in *Kapala* trawls. This species deserves closer scrutiny, as specimens recorded from widely separated areas under the name may represent more than one species.

REFERENCE SPECIMENS. — AMS I.29742-001 (1 spec.); K89-17-09. AMS I.30304-006 (3 spec.); K89-17-06.

REFERENCES. — Gilbert (1905); Sazonov and Iwamoto (1992); Iwamoto and Merrett (1997).

***Hymenocephalus longibarbis* (Günther, 1887)**
Fig. 90

DISTINGUISHING FEATURES. — V 8; total GR-I (outer/inner) 12–16/19–22. Chin barbel well developed, its length 38–58% HL. Body long and slender, head rather shallow, suborbital region narrow, its width 8–10% HL, interorbital width 16–23% HL, orbit large, diameter 32–41% HL. Color when fresh overall silvery, with grayish dorsally and blackish ventrally on trunk and over gill membranes; in alcohol silvery color often lost, lateral stripe somewhat diffuse in larger specimens but prominent on trunk in smaller specimens. Ventral surfaces of tail lacking pigmentation.

DISTRIBUTION. — Fiji, New Caledonia region, Australia (Qld, NSW, possibly WA), and possibly Indonesia.

NSW CAPTURES. — Collected by *Kapala* between southern Queensland (27°50′S) and Ulladulla (35°30′S) in 360–820 m. Recently collected in small numbers southeast of Bermagui (36°30′S)(AMS I.40289-002). Recorded from 102 *Kapala* stations with its greatest abundance in 400–600 m off central and northern NSW. Because of its small size, few were collected in fish trawls fitted with 90 mm mesh codends (caught in only 6% of fish trawls in 400–600 m). In contrast, *H. longibarbis* was recorded from 62% of prawn trawl stations in 400–600 m (45 mm mesh nets). Tows with prawn trawls frequently captured 25–50 specimens.

FIGURE 90. *Hymenocephalus longibarbis* Günther, 1877. From *Kapala* stn K83-01-08 off Sydney, NSW, in 490–570 m.

REMARKS. — *Hymenocephalus longibarbis* is abundant off Queensland, and Iwamoto and Williams (1999) also recorded the species from two captures on the North West Shelf off WA. Their specimens had notably different proportional measurements of the orbit diameter, interorbital width, and suborbital width, which led them to suggest that they might represent another species.

REFERENCE SPECIMENS. — AMS I.20071-041 (1 spec.); K77-19-05. AMS I.20118-034 (11 spec.); K77-13-10. AMS I.20301-024 (3 spec.); K77-13-12. AMS I.20518-005 (4 spec.), AMS I.20518-013 (1 spec.); K78-09-05. AMS I.21669-003 (3 spec.); K77-16-16. AMS I.21795-006 (3 spec.); K78-23-08. AMS I.21805-001 (2 spec.); K77-23-09. AMS I.21806-003 (1 spec.); K77-07-10. AMS I.23486-001 (1 spec.); K82-24-02. AMS I.24619-006 (1 spec.); K81-17-03. AMS I.24850-001 (3 spec.); K84-15-01. AMS I.24852-010 (1 spec.); K84-15-03. AMS I.29535-002 (7 spec.); K79-15-01. AMS I.30407-004 (3 spec.); K78-01-01. AMS I.40289-002 (3 spec.); FV *Shelley H*; 36°30′S, 150°21′E; 390-558 m; off Bermagui, NSW; 18 April 2000. AMS I.40292-002 (3 spec.); FV *Shelley H*; 36°26′S, 150°21′E; 428-468 m; off Bermagui, NSW; 2 May 2000.

REFERENCES. — Paxton et al. (1989)(as *H. longiceps,* in part); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Hymenocephalus nascens Gilbert and Hubbs, 1920
Fig. 91

DISTINGUISHING FEATURES. — V 11–13, usually 11 or 12; total GR-I (outer/inner) 16–20/22–27. Chin barbel absent. Snout conically pointed in lateral view, projecting well beyond mouth. Suborbital region narrow, width 12–16% HL, interorbital width 1.0–1.4 into orbit, width 27–35% HL, orbit large, diameter 31–38% HL. Color mostly silvery ventrally on head and body; in preservative, a prominent dark lateral stripe present (silvery when fresh). (After Iwamoto and Merrett, 1997.)

SIZE. — To about 16 cm.

DISTRIBUTION. — Widespread in tropical western Pacific through Philippines, Indonesia, and northern Australia (Qld, NSW, WA) in depths of about 350–800 m.

NSW CAPTURES. — Captured only twice by *Kapala,* in 820–930 m off Crowdy Head (at same stations as *H. aterrimus*).

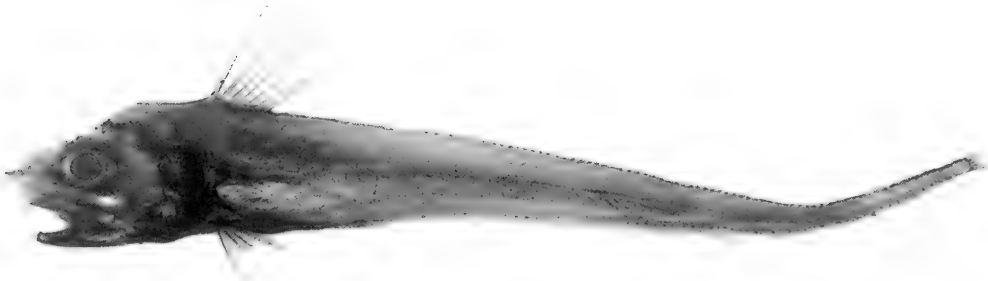

FIGURE 91. *Hymenocephalus nascens* Gilbert and Hubbs, 1920. AMS I.29753-012. From *Kapala* stn K89-17-06, east of Crowdy Head, NSW, in 878–933 m.

REMARKS. — As with *H. aterrimus*, this species is marginal to NSW, having its main distribution in warmer tropical waters; it is abundant in the New Caledonian region. Its small size also made it unlikely to be captured in *Kapala's* trawls.

REFERENCE SPECIMENS. — AMS I.29753-012 (1 spec.); K89-17-06. AMS I.30304-005 (1 spec.); K89-17-09.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Genus *Kuronezumia*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Anus situated in an oval to teardrop-shaped (periproct) area between pelvic fin base and anal fin origin, usually closer to former; a small shallow black pit representing dermal window of light organ anterior to periproct and between pelvic fin bases. Body deep, laterally compressed, depth 90–110% HL. Head usually much deeper than wide; almost completely and uniformly covered with small spinulated scales, including those over broad, flat suborbital region; snout somewhat rounded or bluntly protruding; mouth moderate in size, upper jaw 30–44% HL. Second spinous ray of first dorsal fin serrated along leading edge. Teeth in broad bands in both jaws. Gill rakers on outer side of second arch 8–11 total. Color light gray to brown to swarthy, but lacking bluish or violet.

REMARKS. — Five species of this genus are currently recognized, with two represented in NSW. Members of the genus are similar to some species of *Nezumia*, especially in terms of their overall physiognomy, but they can be distinguished by their almost entirely scaled head and the absence of a well-developed double row of enlarged, thickened scales along the suborbital ridge.

REFERENCES. — Iwamoto (1974); Shcherbachev et al. (1992)

KEY TO THE SPECIES OF *KURONEZUMIA* IN NEW SOUTH WALES

1a. Pelvic fin rays 11–13; snout rounded, not terminating in a large tubercular scale; upper jaw length 35–44% HL; scales rows between origin of second dorsal fin and lateral line 12–15 . . . . . *K. bubonis*

1b. Pelvic fin rays 8–9, rarely 10; snout bluntly pointed, terminating in a large tubercular scale; upper jaw length 28–35% HL; scales between origin of second dorsal fin and lateral line 11–12 . . . . . *K. leonis*

Kuronezumia bubonis (Iwamoto, 1974)

Fig. 92

DISTINGUISHING FEATURES. — D II,10–12; P i21–i25; V 11–13; total GR-I (outer/inner) 6–8/8–11 total; scale rows below 1D about 14–21; pyloric caeca 35–39. Snout length 26–32% of HL, orbit diameter 23–31%, interorbital width 23–26%, height of first dorsal fin about 90%. Snout

FIGURE 92. *Kuronezumia bubonis* (Iwamoto, 1974). AMS I.24645-004. From *Kapala* stn K84-06-03, off Broken Bay, NSW, in 777–823 m.

rounded, scarcely protruding beyond mouth, not tipped with an enlarged spiny scute. A large, scaly, tubercular swelling between pelvic fin bases.

SIZE. — To more than 73 cm.

DISTRIBUTION. — Known from the western Atlantic, Hawaii, South China Sea, southern Indian Ocean, New Zealand, and eastern Australia (NSW) in depths of around 600 to about 1100 m.

NSW CAPTURES. — Uncommon; 31 specimens caught at 23 *Kapala* stations on grounds between Crowdy Head and Jervis Bay in 670–1010 m. Within its main depth range (700–900 m), *K. bubonis* was recorded in 21% of trawls.

REMARKS. — So far only reported in Australian waters from NSW; the record by Paxton et al. (1989) off Cape Everard, Vic., was a misidentification of *K. leonis*. It is somewhat peculiar that the only *Kuronezumia* collected off Western Australia by Iwamoto and Williams (1999) was a related species, *K. pallida* (Sazonov and Iwamoto, 1992), a species previously known only from the southeastern Pacific. The *Kuronezumia* specimens recorded from the Indian Ocean by Shcherbachev (1987) should be re-examined in this light.

REFERENCE SPECIMENS. — AMS I.17316-008 (1 spec.); K72-07-15. AMS I.17859-002 (2 spec.); K72-06-06. AMS I.17867-008 (2 spec.); K72-07-04. AMS I.18726-020 (1 spec.), AMS I.18726-021 (1 spec.); K75-01-02. AMS I.19860-015 (1 spec.); K76-24-03. AMS I.21722-001 (1 spec.); K79-20-13. AMS I.24054-001 (2 spec.); K83-06-02. AMS I.24101-010 (1 spec.); K83-06-01. AMS I.24645-004 (1 spec.); K84-06-03. AMS I.24991-002 (2 spec.); K84-16-05.

REFERENCES. — Iwamoto (1974); Shcherbachev et al. (1992).

Kuronezumia leonis (Barnard, 1925)

Fig. 93

DISTINGUISHING FEATURES. — D II,9–10; P i19–i26; V 8–10; total GR-I (outer/inner) 8–11/7–12; scale rows below 1D 17–20; pyloric caeca 14–18. Snout length 27–34% HL, orbit diameter 27–35%, interorbital width 22–30%, height first dorsal fin about 70–90%. Snout bluntly pointed, tipped with an enlarged, buttonlike spiny scute.

SIZE. — To about 50 cm.

FIGURE 93. *Kuronezumia leonis* (Barnard, 1925). AMS I.28071-001. From *Kapala* stn K88-04-09, off Broken Bay, NSW, in 905–969 m.

DISTRIBUTION. — South Atlantic, southern Indian Ocean, Australia (NSW, Vic., Tas., WA), and New Zealand, in depths of around 700–1100 m.

NSW CAPTURES. — Caught on all mid-slope grounds south of Crowdy Head in 730–1180 m. The species was common but never taken in large numbers; it was recorded from 147 *Kapala* stations (61% of trawls deeper than 800 m) with an average of four specimens per tow.

REMARKS. — *Kuronezumia leonis* was taken on three occasions with its congener *K. bubonis*, but that species has a generally shallower depth range and is much less common.

REFERENCE SPECIMENS. — AMS I.18726-017 (1 spec.); K75-01-02. AMS I. 19860-010 (1 spec.); K76-24-03. AMS I.20068-011 (4 spec.); K77-23-13. AMS I.20096-008 (1 spec.); K77-22-06. AMS I.20098-005 (4 spec.), AMS I.20098-017 (1 spec.), AMS I.20098-024 (1 spec.); K77-23-07. AMS I.20099-008 (1 spec.), AMS I.20099-019 (2 spec.); K77-23-12. AMS I.24054-005 (3 spec.), AMS I.24054-011 (1 spec.), AMS I.24054-018 (1 spec.); K83-06-02. AMS I.24056-002 (2 spec.); K83-08-02. AMS I.24060-013 (2 spec.); K83-09-01. AMS I.24157-003 (1 spec.); K83-12-04. AMS I.24356-004 (1 spec.), AMS I.24356-006 (1 spec.); K83-14-05. AMS I.24462-004 (1 spec.); K83-15-02. AMS I.25933-001 (2 spec.), AMS I.25933-003 (4 spec.); K79-20-06. AMS I.27637-003 (1 spec.); K88-14-04. AMS I.28071-001 (1 spec.); K88-04-09.

REFERENCES. — Iwamoto (1986); Shcherbachev et al. (1992); Iwamoto and Williams (1999).

Genus *Lepidorhynchus*

DISTINGUISHING FEATURES. — Branchiostegal rays 6. Anus immediately before anal fin. Head and body laterally compressed, much deeper than wide; head covering thin, somewhat transparent. Snout scarcely or not protruding. Mouth large, premaxillary extends to hind one-third of orbit. Small teeth in narrow band in upper jaw with outer row of widely spaced canines; lower jaw teeth in one row, teeth larger laterally. Scales thin, deciduous, covered with short needlelike spinules, none thickened or enlarged. Spinous dorsal fin ray smooth along leading edge. Light-producing tissue appearing as fine black striations cover broad areas ventrally on trunk forward to isthmus and dorsally onto pectoral girdle to pectoral base, over abdomen, and above anterior part of anal fin; a small naked fossa of light organ adjacent to anus. Color overall silvery; dorsum grayish green; gill membranes, lower jaw, and abdomen black.

REMARKS. — Monotypic. Relationships of the genus are obscure, but there are some resemblances to *Hymenocephalus*, especially in regards to the nature of the luminescent tissue on the body.

REFERENCES. — McCulloch (1926); McCann and McKnight (1980); Gomon et al. (1994).

***Lepidorhynchus denticulatus* Richardson, 1846**
Fig. 94

DISTINGUISHING FEATURES. — 1D II,10–11; P i16–i18; V 8–9; total GR-I (outer/inner) about 9/16–19. Orbit large, diameter about 30–40% HL, much greater than interorbital space. Chin barbel small.

SIZE. — To about 55 cm.

DISTRIBUTION. — Southern Australia (NSW, Vic., Tas., SA, WA), New Zealand, Kermadec Islands, in depths less than 100 to more than 1000 m, but most frequent at 300–700 m.

NSW CAPTURES. — Probably the most abundant grenadier off NSW. Captured by *Kapala* in 603 trawls on all slope grounds south of the Clarence River (29°40′S) in 230–1080 m, the greatest depth range recorded for any NSW grenadier (apart from some bathyal species). It was most abundant between 300 and 900 m, where it was captured at over 70% of stations. In the 1996–97 survey using nets with 90 mm codend mesh, the species was caught in 117 of 165 tows between 220 and 630 m, and the mean catch was 164 per one-hour tow.

REMARKS. — This species is the most common grenadier off southeastern Australia. Juveniles are found mostly between 200 and 600 m, and adults usually in depths greater than 500 m. Last et al. (1983) reported that off Tasmania it is "frequently caught by the tonne as a large part of the bycatch of trawlers," and it "appears to be an important prey item for the economically important blue grenadier [*Macruronus novaezelandiae*]." Although of no market value at present, the species is frequently used as tuna longline bait.

REFERENCE SPECIMENS. — AMS I.15969-001 (2 spec.); K71-05-06. AMS I.18838-008 (14 spec.); K75-05-03. AMS I. 21724-021 (2 spec.); K79-20-15. AMS I.24619-009 (4 spec.); K88-17-03.

REFERENCES. — McCann and McKnight (1980); McMillan *in* Gomon et al. (1994).

Genus *Lucigadus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Anus removed from anal fin, closer to pelvic fin bases. Light organ well developed, two dermal windows, one immediately before anus, the second between bases of pelvic fins. Head smoothly rounded, without sharp or coarsely scaled ridges; snout rounded. Ventral region of body appearing to have swung far forward so that gill membranes

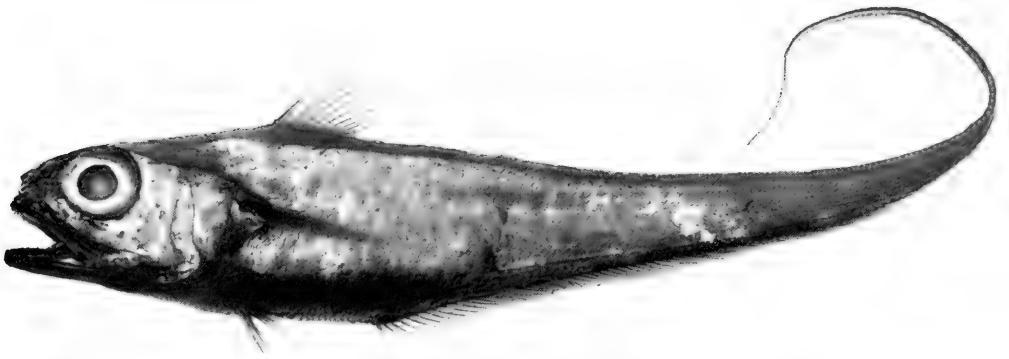

FIGURE 94. *Lepidorhynchus denticulatus* Richardson, 1846. From *Kapala* stn K83-01-08 off Sydney, NSW, in 490–570 m.

unite below orbits, pelvic fin origin below opercle, anal fin origin under first dorsal fin. Suborbital shelf covered with several rows of small scales, no sharp ridge of modified scales. Underside of snout all or mostly scaled. Spinous ray of first dorsal fin serrated along leading edge. Teeth in both jaws small, in tapered bands; premaxillary band not reaching beyond posterior edge of maxillary process. Scale spinules aligned in parallel rows. (From Iwamoto and Merrett 1997.)

REMARKS. — This genus is close to *Ventrifossa* and *Malacocephalus* and was formerly included in the former as a subgenus. The high, bluntly rounded snout, the short trunk with only 10 or 11 trunk vertebrae, the forward position of the ventral parts of the trunk, the shorter band of premaxillary teeth, the characteristic arrangement of spinule rows on the scales, and the frequent presence of scales on the branchiostegal membrane, in combination distinguish members of the genus from those of *Ventrifossa*. *Malacocephalus* species are readily distinguished by the longer jaws beset with larger teeth in fewer, longer rows.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto and Merrett (1997).

***Lucigadus microlepis* (Günther, 1878)**
Fig. 95

DISTINGUISHING FEATURES. — 1D II,10–12; P i20–i25; V 11–13; total GR-I (outer/inner) 8–10/11–12; scales below 2D 8.5–10.5. Snout length 24–31% HL, interorbital width 25–33%, orbit diameter 32–42%; suborbital width 12–16%; upper jaw length 34–40%; barbel length 18–30%; height 1D 102–128. A prominent black blotch at tip of first dorsal fin; body with banded pattern, the anal fin with distinct black margins under darkly banded areas; few or no scales on branchiostegal and gular membranes.

SIZE. — To about 20 cm.

DISTRIBUTION. — Western South Pacific from Wallis and Futuna islands, Fiji, New Caledonia, Norfolk Ridge, eastern Australia (Qld, NSW), and Arafura and Madura seas. Depth range about 200–700 m.

NSW CAPTURES. — The *Kapala* captured the species at 14 stations (36 specimens) on grounds north of Sydney in the relatively narrow depth range of 410 to 540 m. The small adult size of the species made capture in large-meshed trawls unlikely, and in fact, all records were from stations using prawn trawls. The species was taken from 17% of prawn trawls north of Sydney at 400–600 m depth.

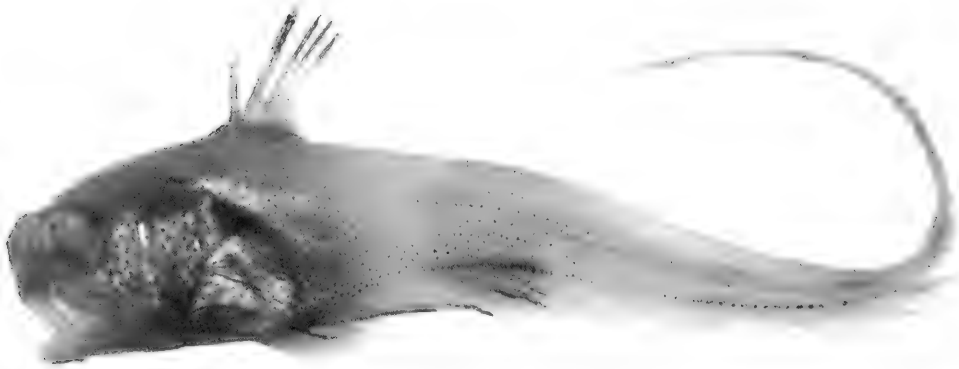

FIGURE 95. *Lucigadus microlepis* (Günther, 1878). AMS I.25932-007. From *Kapala* stn K85-21-06, off Sydney, NSW, in 439–466 m.

The overall low capture rate by *Kapala* suggests that NSW is marginal to its normal tropical distribution.

REMARKS. — *Lucigadus microlepis* is readily distinguished from *L. nigromaculatus* by its banded body pattern, the head peppered with large melanophores, the location of the black dorsal fin blotch (to distal tip, compared to below distal tip in *L. nigromaculatus*), and its somewhat fewer pelvic fin rays (11–13 cf. 13–15).

REFERENCE SPECIMENS. — AMS I.20435-015 (1 spec.); K78-16-07. AMS I.21725-003 (1 spec.); K80-05-01. AMS I. 23689-002 (1 spec.); K78-17-07. AMS I.24850-002 (7 spec.); K84-15-01. AMS I.25932-007 (1 spec.); K85-21-06. AMS I.26394-001 (2 spec.); K86-01-05. AMS I.26446-008 (2 spec.); K85-17-02. AMS I.26453-004 (1 spec.); K86-10-07. AMS I.26756-005 (1 spec.); K86-10-14. AMS I.26932-004 (1 spec.); K79-15-03.

REFERENCES. — Paxton et al. (1989)(as *Ventrifossa fasciata*); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

***Lucigadus nigromaculatus* (McCulloch, 1907)**
Fig. 96

DISTINGUISHING FEATURES. — 1D II,10–11; P i18–i22; V 13–15; total GR-I (outer/inner) 9–11/12–16; scales below 2D 10–12. Snout length 25–30% HL, interorbital width 20–26%, orbit diameter 40–47%; suborbital width 12–18%, upper jaw length 39–45%; barbel length 18–26%; height 1D 101–134%. A prominent black blotch across anterior half to two-thirds of first dorsal fin; anterior margin of anal fin blackish. Scale patches present on lowermost branchiostegal rays.

SIZE. — To about 35 cm.

DISTRIBUTION. — Southeastern Australia (southern Qld, NSW, Vic., Tas.), New Zealand, and off Chile. Depth range about 200–1460 m, but most often taken at 400–800 m.

NSW CAPTURES. — Recorded from 222 *Kapala* stations along the entire NSW coast in depths between 380 and 850 m. In the 1996–97 survey, *L. nigromaculatus* was caught in 70% of tows in 440–630 m, with a mean catch of 15 per one-hour tow; most trawls took less than 20 specimens, but 150 were caught in a single tow in 500 m off Ulladulla.

REMARKS. — This species is captured frequently throughout its normal distribution range but seldom in great abundance. Mesh size may be a factor in its reported low abundance in commercial trawls, as the species is relatively small as an adult.

FIGURE 96. *Lucigadus nigromaculatus* McCulloch, 1907. From *Kapala* stn K84-18-03, off Nowra, NSW, in 732–750 m.

REFERENCE SPECIMENS. — AMS I.15974-008 (4 spec.); K71-08-03. AMS I.15975-032 (4 spec.); K71-08-05. AMS I.15987-001 (4 spec.); K71-11-09. AMS I.15995-011 (2 spec.); K71-13-06. AMS I.16577-009 (1 spec.); K72-04-02. AMS I.18838-035 (1 spec.); K75-05-03. AMS I.18839-005 (23 spec.), AMS I.18839-012 (4 spec.); K75-05-04. AMS I.19076-003 (1 spec.); K75-05-08. AMS I.19198-003 (3 spec.); K76-05-04. AMS I.20118-003 (2 spec.); K77-13-10. AMS I.20484-004 (3 spec.); K77-21-01. AMS I.21669-007 (1 spec.); K77-16-16. AMS I.21806-005 (2 spec.); K77-07-10. AMS I.24851-004 (1 spec.); K84-17-03. AMS I.24852-003 (1 spec.); K84-15-03. AMS I.26002-001 (1 spec.); K86-01-06. AMS I.26245-013 (1 spec.); K86-01-07.

REFERENCES. — Paxton et al. (1989)(as *Ventrifossa nigromaculata*); McMillan *in* Gomon et al. (1994).

Genus *Malacocephalus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Anus removed from anal fin, closer to pelvic fin bases. Head laterally compressed; snout rounded, without coarse, thickened scales. Head surfaces uniformly scaled, no sharp ridge of modified scales, no naked areas; branchiostegal rays scaled. Spinous ray of first dorsal fin smooth or serrated along leading edge. Light organ well developed, two dermal windows, one immediately before anus, the second (large and somewhat bean-shaped) between bases of pelvic fins. Teeth in upper jaw in two rows to narrow band, outer series enlarged; lower jaw with a single row of wide-spaced, enlarged, canine-like teeth. Scales of body densely covered with small fine scales giving velvety surface. Pyloric caeca numerous, 50–100. Color light gray to swarthy, often with silvery flanks.

REMARKS. — There are seven named species, but the number of valid species is uncertain. Three Pacific species (*M. hawaiiensis, M. luzonensis, M. nipponensis*) are so closely similar to *M. laevis* that the four may eventually prove to be the same, in which case *M. laevis* has priority as the oldest name.

REFERENCES. — Iwamoto (1990); Sazonov and Iwamoto (1992).

Malacocephalus laevis (Lowe, 1843)
Fig. 97

DISTINGUISHING FEATURES. — 1D II,9–13; P i15–i21 (usually i17–i19); V 9; total GR-I (outer/inner) 0–8–11/11–14; scales below 2D 8.5–11.5. Snout length 26–31% HL, interorbital width 28–33%, orbit diameter 30–37%; suborbital width 10–13%, upper jaw length 44–50%; barbel length

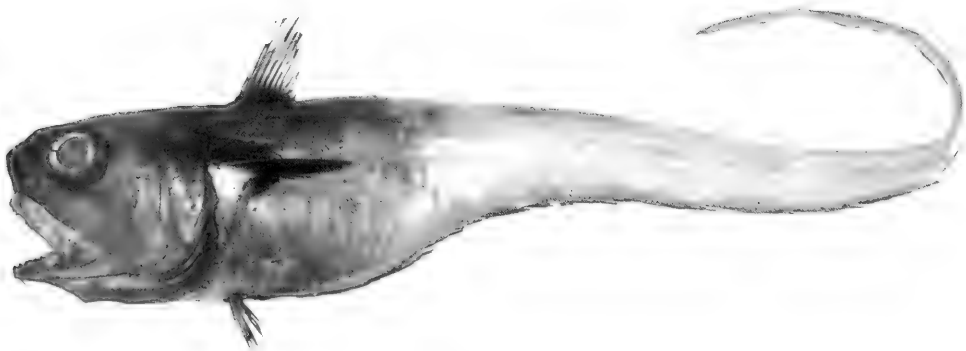

FIGURE 97. *Malacocephalus laevis* (Lowe, 1843). From *Kapala* stn K83-01-08, off Sydney, NSW, in 490–570 m.

16–23%; height 1D about 60–70%. Two rows of teeth in upper jaw. Spinous ray of first dorsal fin smooth.

SIZE. — To more than 65 cm.

DISTRIBUTION. — Widespread in tropical to temperate waters throughout Atlantic and Indian oceans, and probably into Pacific (but greatly restricted in eastern Pacific). Depths approximately 200–1000 m, but most commonly in about 300–700 m. Known off Australia (Qld, NSW, ne. Vic., WA).

NSW CAPTURES. — Captured by *Kapala* on all grounds between the Qld-NSW border and Batemans Bay (35°42′S); single specimens were also caught in three trawls off ne. Vic. (37°37′–38°02′S). All stations but two were in 330–800 m; the two other records were in 1030–1080 m. Regularly taken in moderate numbers on the upper slope off NSW. *Malacocephalus laevis* was recorded 290 times by the *Kapala*; north of Jervis Bay, it was present in 78% of all trawls in 400–800m. Overall, the average catch was about 10 specimens per trawl, although some tows caught in excess of 100.

REMARKS. — *Malacocephalus laevis* is a well-known, apparently worldwide species with a mainly tropical and subtropical distribution. It appears to be found only in relatively warm waters around Australia. Off NSW few were caught south of 35°00′S, and it appears to be absent in Tasmanian and most of southern Australian waters. Off WA the species is reported from the western Great Australian Bight off Eucla (128°E) and to the north off Shark Bay.

REFERENCE SPECIMENS. — AMS I.15970-009 (1 spec.); K71-06-04. AMS I.15973-009 (1 spec.); K71-07-03. AMS I.18838-036 (6 spec.); K75-05-03. AMS I.18839-008 (6 spec.), AMS I.18839-023 (4 spec.); K75-05-04. AMS I.19085-001 (1 spec.); K75-07-03. AMS I.20099-004 (1 spec.); K77-23-12. AMS I.20118-032 (2 spec.); K77-13-10. AMS I.20459-029 (2 spec.); K78-17-10. AMS I.28189-003 (1 spec.); K87-24-03. AMS I.29812-003 (1 spec.); K89-15-02.

REFERENCES. — Last et al. (1983); McMillan *in* Gomon et al. (1994); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Genus *Mataeocephalus*

DISTINGUISHING FEATURES. — Branchiostegal rays 6 or 7. Snout relatively long, somewhat flattened, tipped with two tubercular scales; a series of coarse, modified scales along, and a naked groove dorsally on each side behind, the leading edge. Mouth small, inferior, upper jaw length less than one-third of HL. Outer gill rakers on first arch 0–5. Spinous ray of first dorsal fin slightly prolonged, serrated along leading edge. Teeth on premaxillary in broad, short, truncated to slightly tapered band. Periproct far removed from origin of anal fin. Scale spinules short, needlelike to lanceolate, in numerous, more-or-less parallel rows.

REMARKS. — Two species in NSW, including an undescribed species that is problematically placed in *Mataeocephalus*. The genus is in need of revision and the characters in the generic diagnosis apply only to the two NSW species. Species of the genus are usually caught in more tropical waters. It is likely that central NSW is at the southern end of their normal distribution, as the two NSW species (six specimens in total) were caught north of Newcastle. The small size of the two species also makes capture by commercial-sized trawls difficult.

REFERENCES. — Iwamoto (1990); Iwamoto and Merrett (1997).

KEY TO THE SPECIES OF *MATAEOCEPHALUS* FROM NEW SOUTH WALES

1a. Underside of snout mostly scaled; pelvic fin rays 7 (rarely 8); teeth in broadly tapered bands extending at least to middle of jaws; branchiostegal rays 6 . . . . . *Mataeocephalus* sp.

1b. Underside of snout almost entirely naked; pelvic fin rays 8–9; teeth in broad, short bands confined to front of mouth; branchiostegal rays 7 . . . . . *M. acipenserinus*

FIGURE 98. *Mataeocephalus acipenserinus* (Gilbert and Cramer, 1897). AMS I.29753-009. From *Kapala* stn K89-17-06, east of Crowdy Head, NSW, in 878–933 m.

Mataeocephalus acipenserinus (Gilbert and Cramer, 1897)
Fig. 98

DISTINGUISHING FEATURES. — 1D II,8–10, spinous ray of 1D serrated along leading edge; P i19–i25; V 8–9; total inner GR-I 6–8; scales below 2D 8–9, lat.l. about 40–42; pyloric caeca 13–19; branchiostegal rays 7. Snout long, prominently protruding, length 39–44% HL; orbit diameter 29–34%; interorbital width 20–23%; mouth small, inferior, upper jaw length 20–28%; height 1D 50–63%. Underside of head naked except along front edge of snout; body scales with 4–6 parallel rows of short conical spinules. Periproct oval to pear-shaped, situated midway between pelvic fin and anal fin; small fossa of light organ anterior to anus. Overall color swarthy to pale brownish, darker (bluish to violet) over abdomen; fins blackish to dusky.

SIZE. — To about 25 cm.

DISTRIBUTION. — Widespread in Pacific and Indian oceans, including Australia (NSW, WA), in depths of about 600–900 m.

NSW CAPTURES. — Captured twice (five specimens) near Crowdy Head at somewhat greater depths (823–933 m) than previously reported for the species.

REMARKS. — See Sazonov and Iwamoto (1992) for a detailed description and discussion of related taxa.

REFERENCE SPECIMENS. — AMS I.29753-009 (4 spec.); K89-17-06. AMS I.30304-007 (1 spec.); K89-17-09.

REFERENCES. — Sazonov and Iwamoto (1992); Iwamoto and Merrett (1997).

Mataeocephalus sp.
Fig. 99

DISTINGUISHING FEATURES. — 1D II,8–10; i17–i20; V 7 (rarely 6); total inner GR-I 7–8; scales below 2D 5.5–7.5, lat.l. 31–35; pyloric caeca 16–18; branchiostegal rays 6. Snout of moderate length, protruding, 32–36% HL; orbit diameter 24–29%; interorbital width 21–24%; mouth small, inferior, upper jaw length 26–29%; height 1D 94–114%. Underside of head mostly scaled except for naked median swath under snout; body scales covered with dense rows of lanceolate spinules. Periproct small, anus closer to pelvic fin insertions than to anal fin origin. Few or no denticulations on spinous ray of first dorsal fin.

SIZE. — To at least 21 cm.

FIGURE 99. *Mataeocephalus* sp. AMS I.29804-002. From *Kapala* stn K89-09-01, off Newcastle, NSW, in 896–960 m.

DISTRIBUTION. — Southwestern Pacific off New Caledonia and adjacent waters, and Australia (Qld, NSW, WA), in depths of about 400 to almost 1000 m.

NSW CAPTURES. — Captured only once by *Kapala*, off Newcastle in 896–960 m.

REMARKS. — The six branchiostegal rays in this species set it apart from all other members of this tribe (Malacocephalini). This species probably should be included in the genus *Hyomacrurus* Gilbert and Hubbs, 1920. It awaits description by our Russian colleagues, Y. I. Sazonov and Y. N. Shcherbachev.

REFERENCE SPECIMEN: AMS I.29804-002 (1 spec.); K89-09-01.

REFERENCES. — Iwamoto and Merrett (1997); Iwamoto and Williams (1999)

Genus *Mesobius*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Anus situated in a broad oval periproct area immediately anterior to anal fin. Body relatively deep, laterally compressed. Head smoothly rounded, much deeper than wide, entirely covered with elongated scales with spinules aligned in 1–3 discrete longitudinal rows giving striated appearance to surface. Snout broadly rounded in lateral view; no stout or sharp ridges on head. Chin barbel absent. Overall color of body and fins black, tail somewhat paler.

REMARKS. — Two species, each sometimes taken in bathypelagic waters; only one species known from NSW.

REFERENCES. — Hubbs and Iwamoto (1977); Arai (1979); Shcherbachev et al. (1979).

Mesobius antipodum Hubbs and Iwamoto, 1977
Fig. 100

DISTINGUISHING FEATURES. — 1D II,9–10; P i13–i14; V 6–7; total GR-I (outer/inner) 7–10/13, GR-II 13–14/12–16; scales below 2D 9.5–10.5. Snout length 30–31% HL; orbit diameter 26–30%; interorbital width 33–34%; suborbital width 14–16%; postorbital length 48–49%; upper jaw length 44–47%. Posttemporal region extending posterior to vertical through origin of pectoral fin base.

SIZE. — To 67 cm.

DISTRIBUTION. — Southern hemisphere, from South Atlantic off South Africa, through southern part of Indian Ocean, southern coast of Australia (NSW, Vic., Tas., WA), to New Zealand, in 700–1300 m.

NSW CAPTURES. — Caught by *Kapala* on all mid-slope grounds south of Crowdy Head in 720–1200 m. Relatively common. *Mesobius antipodum* was recorded from 168 *Kapala* stations (including 69% of all trawls deeper than 800 m). The average catch was about eight specimens, although many trawls yielded more than 25 specimens.

FIGURE 100. *Mesobius antipodum* Hubbs and Iwamoto, 1977. AMS I.25095-007. From *Kapala* stn K84-20-05, off Broken Bay, NSW, in 1170–1207 m.

REMARKS. — Shcherbachev et al. (1979) recorded *Mesobius berryi* Hubbs and Iwamoto, 1977, the only congener of *M. antipodum*, from the Indian Ocean but not from off Australia. Those authors provided a good comparison of the two species. Recently, Iwamoto and Williams (1999) reported one specimen of *M. berryi* collected west of Cape Freycinet, Western Australia, in 1225–1240 m.

REFERENCE SPECIMENS. — AMS I.20068-028 (1 spec.); K77-23-13. AMS I.20098-004 (1 spec.); K77-23-07. AMS I.20485-003 (3 spec.); K77-23-06. AMS 25095-007 (1 spec.); K84-20-05. AMS I.25290-011 (4 spec.); K84-20-03. AMS I.25933-002 (1 spec.); K79-20-06.

REFERENCES. — McMillan *in* Gomon et al. (1994); Iwamoto and Williams (1999).

Genus *Nezumia*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Snout pointed, slightly to extensively protruding, tipped with paired, sometimes joined, thick tubercular scales. Chin barbel well developed. Spinous ray of first dorsal fin serrated along leading edge. Anus closer to pelvic fin insertions than to anal fin origin; periproct teardrop-shaped, a narrow connection to small dermal window of light organ situated between pelvic fins. Underside of snout usually with naked area; suborbital shelf formed of two rows of stout, coarsely modified scales. Teeth small, in band in both jaws, teeth in premaxillary not reaching beyond posterior edge of maxillary process. Pyloric caeca usually not branched with fewer than about 30 distal tips.

REMARKS. — More than 40 species known, but only four were found in NSW waters. In contrast, seven were recorded from Western Australia by Iwamoto and Williams (1999). Several species previously classified under *Nezumia* (e.g., Iwamoto 1990) have been subsequently removed to other genera, especially *Kumba* and *Kuronezumia*.

REFERENCES. — Iwamoto (1990); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

KEY TO THE SPECIES OF *NEZUMIA* FROM NEW SOUTH WALES

1a. Pelvic fin rays 13–17; first dorsal fin pale or lightly dusky with a prominent black tip . . . . . *N. propinqua*
1b. Pelvic fin rays 9–12; first dorsal fin dusky to black, without a prominent black tip. 2

2a. Dermal window of light organ about on line with pelvic fin insertions (Fig. 101a); dorsum rather uniformly pigmented, although area above abdomen often slightly darker · *N. coheni*

2b. Dermal window of light organ well posterior to line connecting pelvic fin insertions (Fig. 101b); dorsal aspects of trunk darker than comparable areas on tail, forming complete dark band around trunk · · · · · · · · · · · 3

3a. Pelvic fin rays 9–10; sensory pores on underside of head prominent · · · · · · · · · · · · · · · · · · *N. namatahi*

3b. Pelvic fin rays 11–12; sensory pores on underside of head small · · · · · · · · · · · · · · · · · · · *N. kapala*

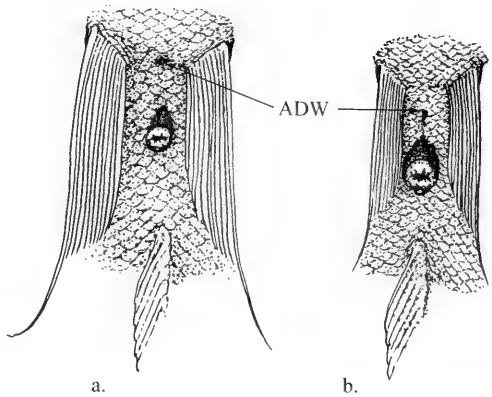

FIGURE 101. Ventral view of belly of *Nezumia* spp. showing position of anterior dermal window (ADW) of light organ in (a) *N. coheni* and (b) *N. namatahi*.

Nezumia coheni Iwamoto and Merrett, 1997
Fig. 102

DISTINGUISHING FEATURES. — 1D II,9–10; i20–i22; V 11 (rarely 10 or 12); total GR-I (outer/inner) 6–9/9–11, GR-II 8–10/10–11; scales below 1D 7–10, below 2D 7.0–8.5, lat.l. 34–40. Snout moderately protruding, length 30–34% HL; orbit diameter 29–34%; interorbital width 20–26%; distance orbit to angle of preopercle 38–44%; postorbital length 39–45%; upper jaw length 30–34%; height 1D about 80–95%. Underside of head mostly scaled except for naked median swath under snout; body scales covered with dense rows of lanceolate spinules. Periproct small, anus closer to pelvic fin insertion than to anal fin origin; ADW about on line connecting insertions of pelvic fins. Dark band encircling trunk faint or lacking.

SIZE. — To more than 40 cm.

DISTRIBUTION. — Australia (NSW, Vic., SA), New Caledonia, and the Kermadec Is., in 710–1032 m.

NSW CAPTURES. — Recorded from 60 *Kapala* stations on all mid-slope grounds south of Crowdy Head in 850–1200 m. *Nezumia coheni* was rare in catches south of Sydney, but two specimens taken at one station in 1050 m off Gabo Island (37°40′S). Between Crowdy Head and Sydney, the species was present in more than 40% of all trawls deeper than 900 m, with up to nine specimens per trawl.

FIGURE 102. *Nezumia coheni* Iwamoto and Merrett, 1997. AMS I.24181-003. From *Kapala* stn K83-13-02, east of Newcastle, NSW, in 960–988 m.

REMARKS. — On first inspection, *N. coheni* can easily be confused with the closely similar *N. kapala* and *N. namatahi,* but those species have a prominent dark band completely encircling the trunk. *Nezumia namatahi* has 9 or 10 pelvic fin rays, in contrast to the predominantly 11 of *N. coheni,* and the anterior dermal window is well posterior to a line connecting the insertions of the pelvic fins. *Nezumia kapala* has a somewhat shorter orbit to angle of preopercle distance (34–39% HL) than does *N. coheni,* and its anterior dermal window is about on or (usually) well posterior to a line connecting the insertions of the pelvic fins. All three species were captured together in a number of *Kapala* trawls; of the 60 stations with *N. coheni*, 44 also contained *N. kapala* and/or *N. namatahi.*

REFERENCE SPECIMENS. — AMS I.21724-026 (2 paratypes); K79-20-15. AMS I.24057-007 (2 spec.) and AMS I.24057-008 (2 spec.); K83-09-04. AMS I.24173-006 (1 paratype); K83-14-06. AMS I.24181-003 (1 spec.); K83-13-02. AMS I.24355-005 (1 spec.); K83-18-02. AMS I.24357-002 (2 spec.); K83-18-01. AMS I.24993-007 (4 paratypes); K84-16-14. AMS I.25127-002 (1 paratype); K84-18-03. AMS I.25264-003 (3 paratypes); K84-19-04. AMS I.25266-000 (2 spec.); K84-22-02. AMS I.25290-006 (1 spec.); K84-20-03. AMS I.26247-005 (6 spec.); K85-21-04. AMS I.29340-007 (4 paratypes); K89-13-02. AMS I.29741-004 (1 paratype); K87-25-06. AMS I.29754-002 (1 paratype); K89-17-03. AMS I.29761-004 (1 spec.); K89-19-02. AMS I.29823-013 (2 paratypes); K89-13-01. AMS I.29827-003 (4 spec.); K89-15-01.

REFERENCES. — Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

***Nezumia kapala* Iwamoto and Williams, 1999**
Fig. 103

DISTINGUISHING FEATURES. — 1D II,8–11; i18–i22; V 11–12; total GR-I (outer/inner) 6–9/8–10, GR-II 8–9/8–11; scales below 1D 8–12, below 2D 7.5–9.5, lat.l. 33–38. Snout moderately protruding, length 27–34% HL; orbit diameter 29–33%; interorbital width 18–25%; distance orbit to angle of preopercle 34–39%; postorbital length 40–45%; upper jaw length 26–31%; height 1D about 86–109%. Underside of head mostly scaled except for naked median swath under snout; body scales covered with dense rows of lanceolate spinules. Periproct small, anus closer to pelvic fin insertions than to anal fin origin; anterior dermal window about on, or usually well behind, line connecting insertions of pelvic fins. A prominent dark band encircling trunk.

SIZE. — To about 41 cm.

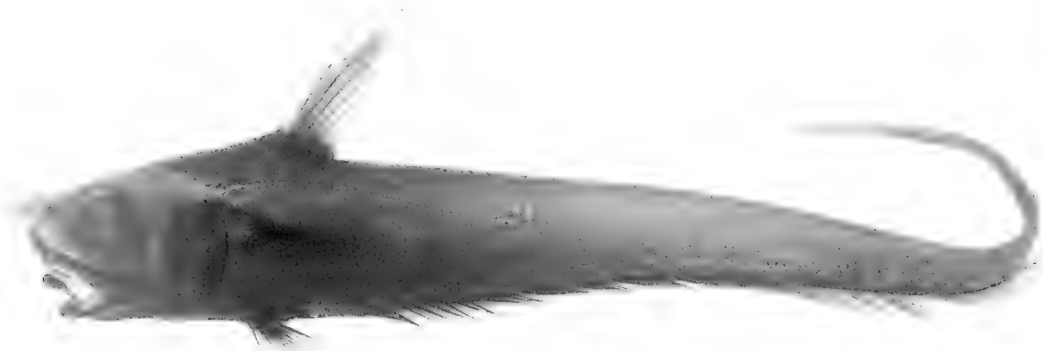

FIGURE 103. *Nezumia kapala* Iwamoto and Williams, 1999. AMS I.24178-003. From *Kapala* stn K83-14-08, off Broken Bay, NSW, in 978–1006 m.

DISTRIBUTION. — Australia (NSW, Tas., WA) in 842–1243 m. Can be expected off Vic. and SA.

NSW CAPTURES. — *Nezumia kapala* was not distinguished from *N. namatahi* in *Kapala* field records. Based on 15 AMS registrations, *N. kapala* was caught by *Kapala* between 32°01′S (Crowdy Head) and 35°30′S (se. of Ulladulla) in 930–1100 m. Either or both species were caught in 135 *Kapala* stations between Crowdy Head and Gabo Island; most catches were between 4 and 8 specimens.

REMARKS. — *Nezumia kapala* and *N. namatahi* are very similar in overall appearance, and as they are often caught together, they are susceptible to being confused with one another. The pelvic ray counts, however, readily distinguish the species (11 or 12 in *N. kapala*, 9 or 10 in *N. namatahi*). *Nezumia namatahi* also has more broadly lanceolate to shield-shaped scale spinules and larger sensory pores under the head. Specimens of *N. namatahi* and *N. kapala* in AMS were collected without knowledge of their distinction. Subsequently, both species were found together in five of the stations represented in the collection. This suggests that there is a high probability that both species, recorded as "*N. namatahi*," were present in a significant proportion of the 135 *Kapala* stations

REFERENCE SPECIMENS. — AMS 21724-005 (1 paratype); K79-20-15. AMS I.24057-001 (4 paratypes); K83-09-04. AMS I.24059-006 (4 paratypes), AMS I.24059-021 (2 spec.); K83-09-02. AMS I.24060-023 (1 paratype); K83-09-01. CAS 200228, formerly AMS I.24150-006 (1 paratype); K83-13-01. AMS I.24173-009 (1 spec.); AMS I.24173-010 (1 spec.); AMS I.24173-012 (1 spec.); K83-14-06. AMS I.24178-003 (1 spec.); K83-14-08. AMS I.24993-008 (holotype), AMS I.24993-010 (1 paratype); K84-16-14. AMS I.25127-006 (1 spec.); K84-18-03. AMS I.25264-002 (4 paratypes); K84-19-04. AMS I.25266-008 (2 paratypes); K84-22-02. AMS I.29741-005 (1 spec.); K87-25-06. AMS I.29754-007 (1 spec.); K89-17-03. AMS I.29761-002 (1 spec.); K89-19-02. AMS I.29797-006 (2 spec.); K89-12-05. AMS I.29827-004 (3 spec.); K89-15-01.

REFERENCES. — McMillan *in* Gomon et al. 1994; "darknose whiptail," in part; Iwamoto and Williams (1999).

***Nezumia namatahi* McCann and McKnight, 1980**
Fig. 104

DISTINGUISHING FEATURES. — 1D II,9–10, rarely 11; i18–i21; V 9–10, usually 10; total GR-I (outer/inner) 5–8/7–9, GR-II 7–9/8–10; scales below 1D 8–11, usually 9–10, below 2D 7.5–9.5, lat.l. 32–38; pyloric caeca about 21–22. Snout length 29–33% HL; orbit diameter 32–38%; interorbital width 19–24%; distance orbit to angle of preopercle 33–37%; postorbital length 37–43%; upper jaw length 24–30%; barbel length 14–30%; height 1D about 90–121%. Underside of snout broadly naked, sensory pores on head prominent; body scales covered with broadly lanceolate to shield-shaped spinules in parallel to slightly convergent rows. Periproct small, anus closer to pelvic fin insertions than to anal fin origin; ADW usually well behind line connecting insertions of pelvic fins. A prominent dark band encircling trunk.

SIZE. — To at least 36 cm.

DISTRIBUTION. — Australia (NSW, Tas., Vic.?, to 138°E in SA) and New Zealand, in 700–1170 m.

NSW CAPTURES. — Based on 10 AMS registrations, the species was caught between 32°28′S (ne. of Port Stephens) and 34°55′S (Jervis Bay) in 730–1150 m. (See NSW Captures section for *N. kapala* for discussion of both species.)

REMARKS. — *Nezumia toi* McCann and McKnight, 1980 is a synonym of this species and was based on an immature specimen in rather poor condition. (See Remarks section for *N. kapala* for discussion of both species.)

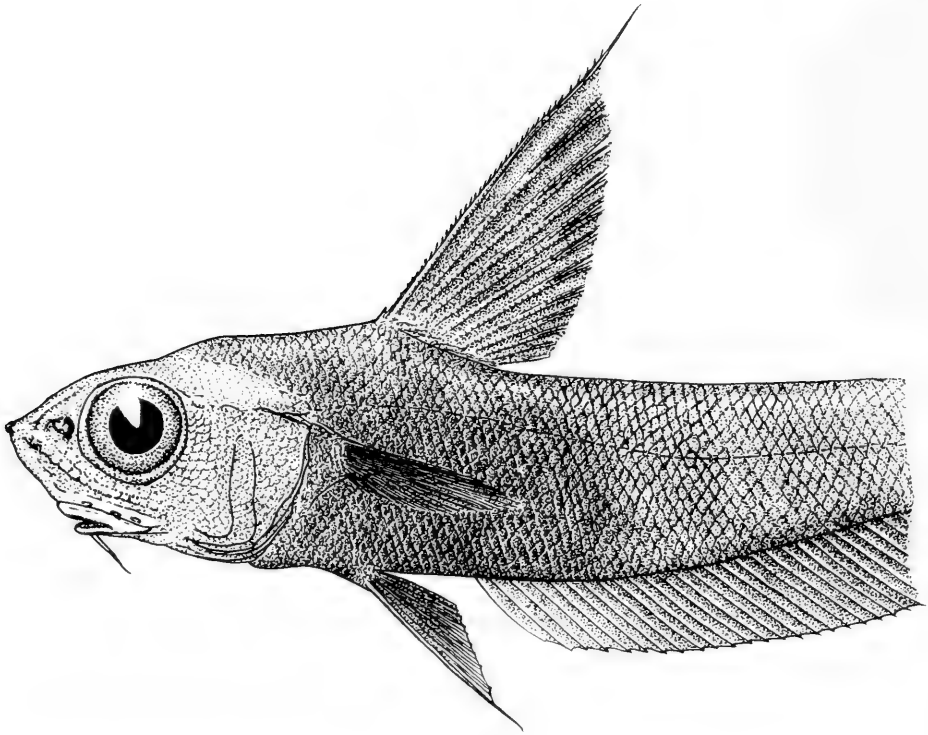

FIGURE 104. *Nezumia namatahi* McCann and McKnight, 1980.

REFERENCE SPECIMENS. — AMS 21724-002 (3 spec.); K79-20-15. AMS I.23460-001 (1 spec.); stn NZOI U-222; ne. of Newcastle, 32°49′S, 152°49′E; 1040-1075 m; 9 Oct. 1982. AMS I.24057-009 (1 spec.); K83-09-04. AMS I.24059-010 (1 spec.), AMS I.24059-022 (1 spec.); K83-09-02. AMS I.24060-017 (1 spec.); K83-09-01. AMS I.24980-004 (3 spec.); K84-16-15. AMS I. 25290-010 (1 spec.); K84-20-03. AMS I.29340—006 (2 spec.); K89-13-02. AMS I.29754-005 (1 spec.); K89-17-03. AMS I.29823-014 (1 spec.); K89-13-01.

REFERENCES. — McCann and McKnight (1980); Iwamoto and Williams (1999).

***Nezumia propinqua* (Gilbert and Cramer, 1897)**
Fig. 105

DISTINGUISHING FEATURES. — 1D II,10–12; i19–i22; V 13–17; total GR-I (outer/inner) 8–10/8–10, GR-II 7–9/9–10; scales below 1D 10–13, below 2D 8.5–10, lat.l. 36–42; pyloric caeca about 21–28. Snout length 29–34% HL; orbit diameter 30–34%; interorbital width 20–25%; distance orbit to angle of preopercle 30–39%; postorbital length 41–45%; upper jaw length 31–35%; barbel length 15–23%; height 1D about 97–113%. Underside of snout, suborbital, and lower jaw naked, sensory pores on naked areas small but prominent; body scales covered with spinules in 10–12 parallel to slightly convergent rows. Periproct large, situated about midway between pelvic fin insertions and anal fin origin; ADW slightly in advance of line connecting insertions of pelvic fins. First dorsal fin with prominent black tip; no dark band encircling trunk. (After Iwamoto and Williams 1999.)

SIZE. — To about 25 cm.

FIGURE 105. *Nezumia propinqua* (Gilbert and Cramer, 1897). AMS I.27722-002. From *Kapala* stn K88-08-09, east of Newcastle, NSW, in 704–750 m.

DISTRIBUTION. — Widespread in tropical waters of Pacific and Indian oceans, including Australia (Qld, NSW, WA). Capture depths about 400–1100 m.

NSW CAPTURES. — Recorded from 43 mid-slope stations (85 specimens) between Crowdy Head and Batemans Bay in 660–1100 m. Most captures were north of Sydney in 800–900 m; 38 of the 43 stations were with small-meshed nets, suggesting that the small *N. propinqua* was seldom retained in the larger-meshed trawls.

REMARKS. — There is some uncertainty as to the status of this and two closely similar species, *N. condylura* (Jordan and Gilbert, 1904) and *N. evides* (Gilbert and Hubbs, 1920). Iwamoto and Williams (1999) and Sazonov and Iwamoto (1992) briefly discuss the problems.

REFERENCE SPECIMENS. — AMS I.19859-009 (3 spec.); K76-24-04. AMS I.19860-018 (8 spec.); K76-24-03. AMS I.20484-003 (1 spec.); K77-21-01. AMS I.20485-005 (1 spec.); K77-23-06. AMS I.23710-002 (1 spec.); K79-20-04. AMS I.24037-005 (1 spec.); K78-26-16. AMS I.24613-003 (2 spec.); K75-05-05. AMS I.24979-001 (2 spec.); K84-16-04. AMS I.24980-002 (5 spec.); K84-16-15. AMS I.24981-001 (1 spec.); K84-17-04. AMS I.24989-002 (1 spec.); K84-17-01. AMS I.24990-002 (1 spec.); K84-16-13. AMS I.26000-003 (1 spec.); K86-01-08. AMS I.26002-003 (1 spec.); K86-01-06. AMS I.26245-014 (1 spec.); K86-01-07. AMS I.27722-002 (1 spec.); K88-08-09. AMS I.29591-002 (1 spec.); K88-12-03. AMS I.29601-002 (1 spec.); K88-08-08. AMS I.29743-001 (2 spec.); K89-20-01. AMS I.29749-001 (1 spec.); K89-17-02. AMS I.29753-004 (1 spec.); K89-17-06. AMS I.29754-006 (1 spec.); K89-17-03. AMS I.29757-001 (3 spec.); K89-15-03. AMS I.29762-006 (1 spec.); K89-12-03. AMS I.29797-007 (2 spec.); K89-12-05. AMS I.29803-002 (1 spec.); K89-07-01. AMS I.29805-002 (1 spec.); K87-24-04. AMS I.29811-004 (1 spec.); K89-08-01. AMS I.29823-004 (5 spec.); K89-13-01. AMS I.30304-002 (1 spec.); K89-17-09.

REFERENCE. — Sazonov and Iwamoto (1992); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Genus *Odontomacrurus*

DISTINGUISHING FEATURES. — Branchiostegal rays 6. Long spinous ray of first dorsal fin smooth along leading edge. Mouth large, jaws armed with fanglike teeth in one row. Chin barbel absent. Anus midway between pelvic fin insertions and anal fin origin, preceded by a small fossa of light organ. Large, prominent sensory pores on head. Lateral line in two parts, anterior section short, dorsolateral, ending below hind margin of first dorsal fin.Swim bladder very small. Color overall black to swarthy.

REMARKS. — One widespread bathypelagic species. Known only from tropical and subtropical waters.

REFERENCES. — Norman (1939); Marshall (1964).

***Odontomacrurus murrayi* Norman, 1939**
Fig. 106

DISTINGUISHING FEATURES. — As for genus.

SIZE. — To about 55 cm.

DISTRIBUTION. — Widely distributed in Atlantic and Indian oceans; in western Pacific previously recorded only from South China Sea, but now known from off southeastern Australia (NSW, Tas.).

NSW CAPTURES. — Specimens were caught by *Kapala* in each of four midwater trawl stations between Port Stephens and Wollongong. Capture depths were 0–900 m in oceanic waters deeper than 2000 m.

REMARKS. — This species and *Cynomacrurus piriei* are among the few strictly bathypelagic species of grenadier. *Cynomacrurus* differs in having the anus immediately before the anal fin and a posterior midlateral section of the lateral line, and in lacking an abdominal fossa of the light organ. *Odontomacrurus murrayi* is a broadly distributed species but rarely captured, probably because large midwater trawls are seldom towed in oceanic waters (the *Kapala* specimens were taken when trawling for bathypelagic and mesopelagic fishes for AMS).

REFERENCE SPECIMENS. — AMS I.20064-023 (1 spec.); K77-18-01. AMS I.20314-047 (1 spec.); K77-24-10. AMS I.20315-050 (1 spec.); K77-24-11. AMS I.21369-004 (1 spec.); K79-19-07.

REFERENCES. — Norman (1939); Marshall (1964); Iwamoto (1970).

Genus *Sphagemacrurus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Snout blunt, upturned, tip and lateral angles armed with spiny tubercular scales. Mouth cleft moderately to steeply oblique. Chin barbel present. Spinous ray of first dorsal fin serrated along leading edge. Ventral aspects of body shifted forward so that pelvic fin origin usually under opercle, anal fin origin under first dorsal fin, gill membranes united under preopercle. Broad, naked periproct region abutting anal fin origin; small fossa of light organ between pelvic fins but well posterior to pelvic fin base. Underside of snout variously naked; sub-

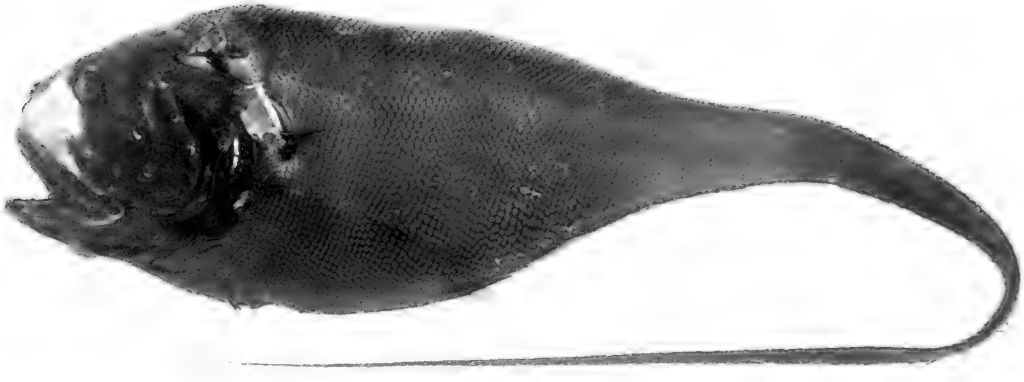

FIGURE 106. *Odontomacrurus murrayi* Norman, 1939. AMS I.20064-023. From *Kapala* stn K77-18-01, midwater trawl in 0–900 m, 42 n. mi. ese. of Sydney, NSW.

orbital shelf formed by two rows of stout, coarsely modified scales. Body scales covered with several rows of short, slender, conical spinules in parallel to slightly divergent rows. Teeth small, in narrow to moderately wide band in both jaws, teeth in premaxillary not reaching beyond posterior edge of maxillary process. Pyloric caeca usually less than 30.

REMARKS. — Six species recognized, but only one presently known from NSW. *Sphagemacrurus pumiliceps* (Alcock, 1894) could be expected, as the species is known from Qld, WA, New Caledonia, and other areas in the Indian and Pacific oceans.

REFERENCES. — Weber and de Beaufort (1929); Iwamoto (1990); Iwamoto and Williams (1999).

***Sphagemacrurus richardi* (Weber, 1913)**
Fig. 107

DISTINGUISHING FEATURES. — 1D II,9–11; i17–i20; V 8–11; total GR-I (outer/inner) 9–12/11–13, GR-II 9–11/11–13; scales below 1D 11–14, below 2D 8.5–9.5, lat.l. 37–43; pyloric caeca about 10. Snout length 30–37% HL; internasal width 28–33%; interorbital width 28–32%; orbit diameter 31–36%; distance orbit to angle of preopercle 39–44%; postorbital length 36–41%; upper jaw length 35–40%; barbel length 13–16%; height 1D about 85–100%; distance outer pelvic ray to anal fin origin about 30–40%. Body scales covered with short, fine spinules in 7–9 parallel rows. Periproct large, immediately before anal fin origin and spanning about half distance to pelvic fin insertion; ADW extending forward from periproct. Head relatively pale along sides, eye ring prominent; trunk and tail darker; abdomen and chest dark with violet hue; first dorsal, pectoral, and anal fins dusky, pelvic fin blackish.

SIZE. — To about 23 cm.

DISTRIBUTION. — Indonesia and Australia (NSW).

NSW CAPTURES. — Uncommon in *Kapala* catches; caught on 18 occasions (56 specimens) north of Sydney at 880–1100 m depth. A species of small adult size, most were caught in trawls with small-meshed codends and were probably more abundant than their capture rate suggests.

REMARKS. — The species appears to be closely similar to *S. decimalis* (Gilbert and Hubbs, 1920) from the Philippines, but that species has a lower gill raker count (about 7 on lower limb of first arch). *Sphagemacrurus pumiliceps* (Alcock, 1894) has somewhat higher pelvic fin ray counts (11–14), a longer barbel (16–22% HL), and narrower interorbital (23–26% HL).

REFERENCE SPECIMENS. — AMS I.26000-002 (1 spec.); K86-01-08. AMS I.26247-001 (1 spec.); K85-21-04. AMS I.27720-001 (1 spec.); K88-08-04. AMS I.27721-001 (3 spec.); K88-08-07. AMS I.28900-001 (3 spec.); K88-17-06. AMS I.28988-002 (5 spec.); K89-09-03. AMS I.29298-001

FIGURE 107. *Sphagemacrurus richardi* (Weber, 1913). AMS I.27721-001. From *Kapala* stn K88-08-07, east of Newcastle, NSW, in 1006–1079 m.

(4 spec.); K88-20-03. AMS I.29605-006 (5 spec.); K89-09-07. AMS I.29750-002 (6 spec.); K89-17-04. AMS I.29753-011 (2 spec.); K89-17-06. AMS I.29799-002 (6 spec.) and I.29799-007 (7 spec.); K89-06-02. AMS I.29809-001 (6 spec.); K88-20-01. AMS I.29823-012 (1 spec.); K89-13-01. AMS I.29827-005 (8 spec.); K89-15-01.

REFERENCES. — Weber (1913); Weber and de Beaufort (1929); Iwamoto (1990).

Genus *Trachonurus*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Snout rounded, lacking a prominently protruding terminal tubercle. Chin barbel present. Broad, naked black periproct region extending most of (relatively short) distance between pelvic and anal fins. Spinous ray of first dorsal fin flexible, smooth along leading edge. Origin of pelvic fin usually behind pectoral fin base. Head almost fully scaled except for patches or single scales on branchiostegal and gular membranes in some species; suborbital vertical in most, with smoothly rounded contours, lacking sharp or coarsely scaled ridges. Body scales covered with short, conical spinules in somewhat quincunx pattern. Teeth in narrow band in upper jaw with outer series usually somewhat enlarged, teeth in lower jaw in 2 or 3 rows or narrow band. Pyloric caeca usually less than 15. Color overall black or brown or gray.

REMARKS. — At least six species, two of which are recorded from NSW. Iwamoto and Williams (1999) were uncertain as to the identification of one specimen (AMS I.27718-010) from southern NSW off Ulladulla. Its characters did not agree well with the characters of *T. sentipellis* and may represent another species. The key provided below is adapted from Iwamoto and Williams (1999:212), but does not include *T. yiwardaus* Iwamoto and Williams, 1999, a species so far known only from WA and SA.

REFERENCES. — Iwamoto and McMillan (1997); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

KEY TO THE SPECIES OF *TRACHONURUS* FROM NEW SOUTH WALES

1a. Grooved lateral line present; body scales large, 8 or 9 rows between pelvic fin base and gill cover (Fig. 108a) . . . . . *T. sentipellis*

1b. Grooved lateral line absent; body scales relatively small, 10–14 rows between pelvic fin base and gill cover (Fig. 108b) . . . . . *T. gagates*

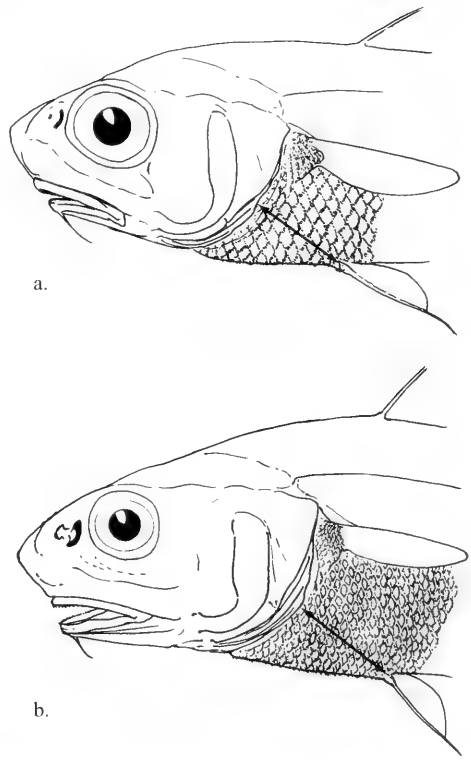

FIGURE 108. Diagrammatic lateral views of *Trachonurus* spp. showing method of counting scale rows between pelvic fin base and gill cover in (a) *T. sentipellis* and (b) *T. gagates*.

Trachonurus gagates Iwamoto and McMillan, 1997

Fig. 109

DISTINGUISHING FEATURES. — Grooved lateral line absent. Chin barbel short, length 4–8% of HL. Scale rows between pelvic fin and gill cover 10–14. Color uniformly black to dark brown.

SIZE. — To about 48 cm.

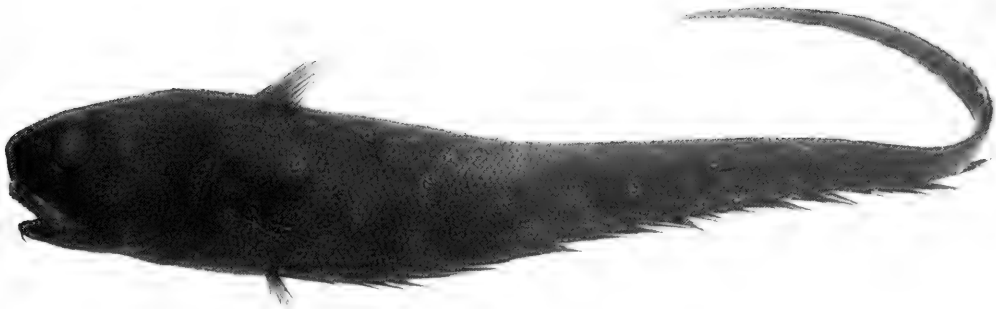

FIGURE 109. *Trachonurus gagates* Iwamoto, McMillan, 1997. AMS I.24059-009. From *Kapala* stn K83-09-02, east of Broken Bay, NSW, in 933–969 m.

DISTRIBUTION. — Australia (Qld, NSW, Vic., Tas., SA, WA) and New Zealand, in 435–1200 m.

NSW CAPTURES. — Recorded in 65 *Kapala* stations from Crowdy Head to se. of Gabo Island; depth range 890–1200 m. An average of two specimens was caught in the 65 stations; most were caught deeper than 1000 m where 47% of trawls contained *T. gagates*.

REMARKS. — This relatively large, dark species with small body scales is readily distinguished from its congeners by the absence of a grooved lateral line. One specimen (AMS I.20307-067) was taken by midwater trawl in oceanic waters.

REFERENCE SPECIMENS. — AMS I.20307-067 (1 spec.); K77-24-03). AMS I.24059-009 (holotype); K83-09-02. AMS I.24157-002 (1 spec.); K83-12-04. AMS I.24173-007 (3 spec.) and AMS I.24173-011 (7 spec.); K83-14-06. AMS I.24178-004 (1 spec.); K83-14-08. AMS I.24355-001 (1 spec.); K83-18-02. AMS I.24356-005 (3 spec.) and AMS I.24356-007 (1 spec.); K83-14-05. AMS I.24357-001 (1 spec.); K83-18-01. AMS I.24451-002 (2 spec.); K83-14-09. AMS I.24625-003 (3 spec.); K84-06-06.

REFERENCES. — Paxton et al. (1989)(as *T. villosus*); Iwamoto and McMillan (1997).

Trachonurus sentipellis Gilbert and Cramer, 1897
Fig. 110

DISTINGUISHING FEATURES. — Grooved lateral line present. Body scales relatively large, coarsely covered with stout, erect spinules, 26–34 lat.l. scales over distance equal to predorsal length, 4–7 scale rows below midbase of first dorsal fin, 5–7 below origin of second dorsal; 8 or 9 between

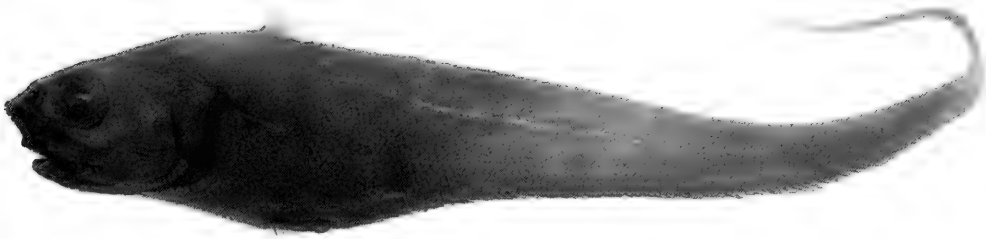

FIGURE 110. *Trachonurus sentipellis* (Gilbert and Cramer, 1897). AMS I.28100-003. From *Kapala* stn K88-08-06, east of Tuncurry, NSW, in 1024–1079 m.

pelvic fin base and gill cover. Small scale patch or none on gular membrane, few or no scales on branchiostegal rays. Teeth in both jaws small, outer premaxillary series scarcely enlarged. Chin barbel moderate, 9–14% of HL. Total GR-II (outer) 10–14. Pyloric caeca short, thick, 9–13. Color uniformly black to dark brown.

SIZE. — To 31+ cm.

DISTRIBUTION. — Hawaiian Is., Australia (NSW, WA), and New Caledonia, in 500–1136 m.

NSW CAPTURES. — Three specimens taken by *Kapala* in 940–1130 m off Crowdy Head at the northern end of the mid-slope grounds.

REMARKS. — Iwamoto and Williams (1999) listed four specimens as uncertain variants of this species. The four showed differences in scale distribution and spinulation, gill-raker and scale-row counts, and some proportional measurements, compared with their other specimens, indicating the possibility of more than one species being involved. One of the uncertain variants was from NSW (AMS I.27718-010, off Ulladulla in 1150 m).

REFERENCE SPECIMENS. — AMS I.24462-003 (1 spec.); K83-15-02. AMS I.28100-003 (1 spec.); K88-08-06. AMS I.29808-001 (1 spec.); K89-06-04.

REFERENCES. — Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Genus *Ventrifossa*

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Snout moderately pointed to bluntly rounded, lacking thickened tubercular scales at lateral angles and (in most species) tip of snout. Chin barbel well developed. Spinous ray of first dorsal fin finely serrated along leading edge in NSW species. Anus closer to pelvic fin insertions than to anal fin origin; periproct teardrop-shaped, a narrow connection to small dermal window of light organ situated between pelvic fins. Underside of snout fully and uniformly scaled; suborbital ridge rounded, without coarsely modified scales. Teeth in bands in both jaws, outer premaxillary teeth enlarged, with tooth band extending beyond posterior edge of maxillary process. Pyloric caeca more than 30. Color often silvery along sides of head and body; lips usually black; leading edge of snout, suborbital shelf, and dorsal snout ridges in most species dark, or terminal snout scute blackish.

REMARKS. — More than 25 species. Only three species recorded from NSW waters, although seven are known from Western Australia (Iwamoto and Williams 1999).

REFERENCES. — Iwamoto (1990); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

KEY TO THE SPECIES OF *VENTRIFOSSA* FROM NEW SOUTH WALES

1a. A tubercular scale at tip of snout; suborbital shelf narrowly constricted anteriorly; lateral line scales over distance equal to predorsal length of head 64–75 . . . . . *V. johnboborum*
1b. No tubercular scale at tip of snout; suborbital shelf not especially constricted anteriorly; lateral line scales over distance equal to predorsal length of head less than 51 2

2a. A prominent blotch or dark streak across first dorsal fin; pelvic fin rays 8 or 9, usually 8 . . . *Ventrifossa nigrodorsalis*
2b. First dorsal fin dark overall, without blotch or streak; pelvic fin rays 9 or 10, usually 9 . . . . . *V. paxtoni*

Ventrifossa johnboborum Iwamoto, 1982
Fig. 111

DISTINGUISHING FEATURES. — 1D II,9–11; i17–i23; V 8–9; total GR-I (outer/inner) 9–12/13–15, GR-II 12–15/12–14; scales below 1D about 12–16, below 2D about 9–12, lat.l. 64–75. Snout moderately protruding, length 28–31% HL; orbit diameter 29–35%; interorbital width 25–30%; distance orbit to angle of preopercle 41–44%; postorbital length 41–44%; upper jaw length 36–41%; barbel length 7–13 (18)%; height 1D about 54–68%. Suborbital shelf extremely narrow an-

FIGURE 111. *Ventrifossa johnboborum* Iwamoto, 1982. AMS I.25126-001. From *Kapala* stn K84-18-06, east of Sydney, NSW, in 914–924 m.

teriorly, but broadening posteriorly. Body scales small, densely covered with small needlelike spinules. Spinous second ray of first dorsal fin with finely serrated leading edge. Tip of snout (and sometimes leading edge) blackish or dark dusky, other head ridges not marked. Lining of mouth dark.

SIZE. — To about 48 cm.

DISTRIBUTION. — Western Indian Ocean, east to Australia (Qld, NSW, WA) and New Caledonia, north to Philippines and South China Sea, and in the southeastern Pacific at Sala-y-Gomez Ridge. Depth range about 400–1100 m.

NSW CAPTURES. — Recorded from 23 *Kapala* stations (88 specimens) between Crowdy Head and Ulladulla, all but one station north of Sydney. Depth range 680–980 m, plus a single capture in 1070 m. Not commonly caught, *V. johnbororum was* present in only 20 of the 98 trawls in 700–1000 m north of Sydney. Most trawls caught less than five specimens, but 25 were taken in one station off Port Stephens.

REMARKS. — The northerly NSW distribution conforms to the generally tropical occurrence of the species. However, the NSW capture depths were somewhat greater than previously reported (412–855 m). Some questions remain as to the taxonomic status of the various populations of this apparently widespread species. *Ventrifossa fusca* Okamura, 1982 from the Kyushu-Palau Ridge and *V. misakia* Jordan and Gilbert, 1904 from Japan are closely related to this species, and the three compose the subgenus *Sokodara*.

REFERENCE SPECIMENS. — AMS I.19860-014 (1 spec.); K76-24-03. AMS I.25126-001 (1 spec.); K84-18-06. AMS I.27647-003 (1 spec.); K87-16-02. AMS I.28189-004 (1 spec.); K87-24-03. AMS I.29746-003 (2 spec.); K88-21-03. AMS I. 29747-004 (3 spec.); K88-21-02. AMS I.29749-007 (1 spec.); K89-17-02. AMS I.29756-003 (3 spec.); K89-15-04. AMS I.29762-005 (3 spec.); K89-12-03. AMS I.29806-001 (1 spec.); K89-09-06. AMS I.29811-002 (1 spec.); K89-08-01. AMS I.29813-007 (1 spec.); K89-06-05. AMS I.30737-002 (4 spec.); K87-24-02.

REFERENCES. — Sazonov and Iwamoto (1992); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

Ventrifossa nigrodorsalis Gilbert and Hubbs, 1920

Fig. 112

DISTINGUISHING FEATURES. — 1D II,9–11; i18–i23; V 8–9 (usually 8); total GR-I outer/inner) 8–12/13–16, GR-II 13–15/12–14; scales below 1D about 7–10, below 2D 7.5–10, lat.l. 39–42. Snout slightly protruding, length 26–33% HL; orbit diameter 29–35%; interorbital width 24–30%; distance

FIGURE 112. *Ventrifossa nigrodorsalis* Gilbert and Hubbs, 1920. From *Kapala* stn K83-01-08, off Sydney, NSW, in 490–570 m.

orbit to angle of preopercle 38–45%; postorbital length 40–46%; upper jaw length 37–45%; barbel length 16–27%; height 1D about 64–96%. Suborbital shelf uniformly broad. Body scales thin, rather deciduous, covered with small conical spinules in quincunx pattern. Spinous second ray of first dorsal fin with finely serrated leading edge. Dorsal surfaces of trunk and tail dark, contrasting with silvery (when fresh) or pale (when preserved) ventral body surfaces. Prominent black blotch or streak across anterior portion of first dorsal fin. Leading edge of snout, supranasal ridge (but not median nasal ridge), and suborbital shelf blackish.

SIZE. — To about 30 cm.

DISTRIBUTION. — Widespread in the western Pacific, from the Philippines, South China Sea, and Indonesia south to New Caledonia and Australia (Qld, NSW, WA). Depth range about 300–800 m.

NSW CAPTURES. — Relatively common in upper slope depths off central and northern NSW, particularly in 500–700 m. Captured by *Kapala* in 71 trawls on all grounds between the Qld-NSW border and Jervis Bay (35°00′S) in 360–790 m. Recently collected south of Bermagui to 36°46′S. Between 10 and 20 specimens were caught at most *Kapala* stations with small-meshed nets. Because of its small size, few were caught with large-meshed trawls.

REMARKS. — An apparently widespread, highly variable species deserving further study (see Iwamoto and Williams 1999).

REFERENCE SPECIMENS. — AMS I.15987-014 (1 spec.); K71-11-09. AMS I.18839-013 (1 spec.); K75-05-04. AMS I.20301-025 (1 spec.); K77-13-12. AMS I.20459-015 (17 spec.) and I.20459-027 (4 spec.); K78-17-10. AMS I.20518-008 (20 spec.) and I.20518-018 (2 spec.); K78-09-05. AMS I.21669-004 (3 spec.); K77-16-16. AMS I.21805-002 (25 spec.); K77-23-09. AMS I.21806-002 (3 spec.); K77-07-10. AMS I.23710-001 (4 spec.); K79-20-04. AMS I.24852-009 (1 spec.); K84-15-03. AMS I.29535-005 (1 spec.); K79-15-01. CAS 214043 (6 spec.); off Bermagui (36°46′S, 150°21′E); 530-549 m; FV *Shelley H*, 15 Feb. 2000. CAS 214044 (6 spec.); off Bermagui (36°12′S, 150°24′E); 421 m; FV *Shelley H*, 1 Mar. 2000.

REFERENCES. — Gilbert and Hubbs (1920); Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

***Ventrifossa paxtoni* Iwamoto and Williams, 1999**
Fig. 113

DISTINGUISHING FEATURES. — 1D II,9–11; i20–i25; V 9–10 (usually 9); total GR-I outer/inner) 10–13/15–18, GR-II 14–18/15–18; scales below 1D about 8–12, below 2D 7.5–9.0, lat.l. 37–50. Snout rather blunt, length 24–31% HL; orbit diameter 27–38%; interorbital width 24–30%; distance orbit to angle of preopercle 42–48%; postorbital length 43–53%; upper jaw length 43–50%; barbel length 24–38%; height 1D about 63–73%. Suborbital shelf uniformly broad. Body scales covered with small conical spinules in subparallel rows. Spinous second ray of first dorsal fin with finely serrated leading edge. Color overall swarthy, especially dark over head, chest and abdomen. Fins all black or blackish. Leading edge of snout, lateral nasal ridges, and suborbital shelf black, median nasal ridge dusky to blackish.

SIZE. — To about 43 cm.

DISTRIBUTION. — Australia (Qld, NSW, WA) and the New Caledonian region, in about 800–1100 m.

NSW CAPTURES. — Captured at 27 *Kapala* stations between Crowdy Head and Sydney, with additional single captures off Nowra and Ulladulla; depth range 825–1050 m. Caught in about 20% of all trawls in 800–1100 m north of Sydney. Overall average catch about four per trawl, with highest catch numbers at stations north of Newcastle (up to 25 specimens).

REMARKS. — *Ventrifossa paxtoni* is a dark, blunt-snouted species similar to *V. macropogon*, a widespread species from the western North Atlantic, Western Australia, and New Caledonia. *Ventrifossa paxtoni*, however, has a somewhat shorter, thinner barbel, fainter median nasal streak, and higher gill raker counts. *Ventrifossa saikaiensis* Okamura, 1984 is also closely similar but has somewhat lower counts of pelvic fin rays (8 or 9), slightly higher counts of outer gill rakers (12–15), and lacks darkly marked head ridges, including the leading edge of the snout.

REFERENCE SPECIMENS. — AMS I.20099-006 (2 spec.); K77-23-12. AMS I.24150-004 (1 spec.); K83-13-01. AMS I.24990-001 (1 paratype); K84-16-13. AMS I.26981-005 (5 paratypes); K87-02-01. AMS I.27647-002 (holotype) and AMS I.27647-004 (1 paratype); K87-16-02. AMS I.28189-005 (2 paratypes); K87-24-03. AMS I.29753-008 (4 paratypes); K87-17-06. AMS I.29797-005 (4 spec.); K89-12-05. AMS I.29805-001 (1 paratype); K87-24-04. AMS I.30737-001 (4 spec.); K87-24-02.

REFERENCES. — Iwamoto and Merrett (1997); Iwamoto and Williams (1999).

FIGURE 113. *Ventrifossa paxtoni* Iwamoto and Williams, 1999. AMS I.24150-004. From *Kapala* stn K83-13-01, from off Broken Bay, NSW, in 988–1015 m.

SUBFAMILY TRACHYRINCINAE

DISTINGUISHING FEATURES. — Branchiostegal rays 7. Outer gill slit wide and free, not restricted by folds of skin connecting upper and lower limbs of gill arch. Dorsal fins two, closely approximated, the first short-based and armed with a flexible leading spinous ray; the second long and continuous to end of tail. Anal fin long, height usually somewhat lower and length slightly shorter than second dorsal fin. A rudimentary caudal fin sometimes developed. Heavy scutelike scales forming long ridges along dorsal and ventral margins lateral to median fins. No light organ.

REMARKS. — Two genera, *Idiolophorhynchus* (monotypic) and *Trachyrincus* (with six species, one of which is found off NSW). *Idiolophorhynchus* has leathery head ridges and scales that have low, flattened, or no spinules on exposed fields; a midlateral row of enlarged scutes on trunk; pelvic fin rays 3 or 4; no chin barbel; and no posttemporal pit. The single species, *I. andriashevi* Sazonov, 1981, may occur off NSW at depths greater than trawled by the *Kapala*.

REFERENCES. — Iwamoto (1990); McMillan (1995).

Genus *Trachyrincus*

DISTINGUISHING FEATURES. — V 6 or 7. Snout strongly supported and pointed. A sensory pit in temporal region of head. Small chin barbel present. Scales on head and body covered with stout spinules. Pyloric caeca bifid.

REFERENCE. — McMillan (1995).

Trachyrincus longirostris (Günther, 1878)

Fig. 114

DISTINGUISHING FEATURES. — Snout long, 41–46% of HL, ventral length 34–39%; upper jaw length 25–28%; pyloric caeca 35–62. Color pale brownish to grayish.

SIZE. — To about 50 cm.

DISTRIBUTION. — Australia (NSW, Vic.), New Zealand, and southern Africa, in about 1100–1400 m.

NSW CAPTURES. — Caught at four *Kapala* stations (five specimens) off Port Stephens, Broken Bay (2) and Gabo Island in 1050–1200 m. Possibly more abundant in depths greater than 1200 m.

REMARKS. — *Trachyrincus aphyodes* McMillan, 1995 from New Zealand waters is closely similar to *T. longirostris*, but may be distinguished by its more numerous pyloric caeca (119–211), somewhat longer upper jaw (29–34% of HL), and shorter ventral snout length (26–34%). *Trachyrincus longirostris* is a smaller species, attaining about 50 cm, compared with 96 cm in *T. aphyodes*.

REFERENCE SPECIMENS. — AMS I.24644-003 (2 spec.); K84-06-07. AMS I.25266-004 (1 spec.); K84-22-02. AMS I.28749-004 (1 spec.); K88-17-03. AMS I.29812-001 (1 spec.); K89-15-02.

REFERENCES. — McMillan *in* Gomon et al. (1994); McMillan (1995).

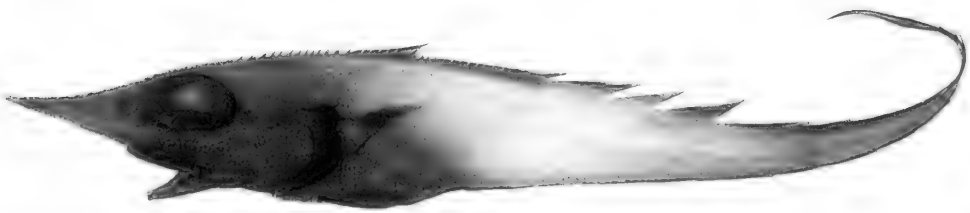

FIGURE 114. *Trachyrincus longirostris* (Günther, 1878). AMS I.25266-004. From *Kapala* stn K84-22-02, off Gabo Island, Vic., in 1052–1079 m.

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APPENDIX 1. Data for FRV *Kapala* stations cited in text. (Locations are approximate midpoints of trawls: latitude °S, longitude °E; * bottom depth for midwater trawl stations.)

Station	AMS Reg. No.	Date	Location	Depth (m)
K71-05-03	15967	6-IV-71	33°42', 151°52'	270-280
K71-05-04	15968	6-IV-71	33°42', 151°50'	366-366
K71-05-06	15969	7-IV-71	33°48', 151°47'	357-366
K71-06-04	15970	15-IV-71	33°46', 151°52'	503-503
K71-07-03	15973	21-IV-71	33°35', 151°59'	375-384
K71-08-03	15974	28-IV-71	32°52', 152°39'	366-375
K71-08-05	15975	29-IV-71	33°14', 152°21'	549-567
K71-09-01	15976	7-V-71	32°48', 152°44'	585-595
K71-11-09	15987	8-VII-71	34°59', 151°07'	366-366
K71-13-02	15994	30-VII-71	37°42', 150°15'	402-408
K71-13-06	15995	2-VIII-71	35°27', 150°49'	549-549
K72-04-01	16565	19-IX-72	33°45', 151°49'	457-457
K72-04-02	16577	19-IX-72	33°38', 151°55'	457-457
K72-05-05	16589	4-X-72	33°44', 151°53'	549-600
K72-06-05	17859	23-X-72	33°48', 151°47'	400-405
K72-07-01	17866	6-XI-72	33°57', 151°45'	729-730
K72-07-04	17867	9-XI-72	33°42', 151°56'	729-730
K72-07-15	17316	7-XII-72	33°50', 151°52'	770-780
K75-01-02	18726	2-IV-75	33°36', 151°59'	784-795
K75-02-08	18770	4-VI-75	34°57', 151°10'	732-805
K75-03-02	18774	11-VII-75	37°42', 150°13'	402-421
K75-05-02	24127	8-VIII-75	34°17', 151°26'	402-411
K75-05-03	18838	18-VIII-75	33°04', 152°33'	448-466
K75-05-04	18839	19-VIII-75	33°27', 152°05'	622-658
K75-05-05	20452	19-VIII-75	33°35'; 152°02'	805-841
K75-05-05	24613	19-VIII-75	33°35', 152°02'	805-841
K75-05-08	19076	21-VIII-75	34°30', 151°18'	494-512
K75-07-03	19085	16-IX-75	32°24', 152°59'	450-460
K76-04-03	19197	30-IV-76	33°46', 151°50'	485-494
K76-05-04	19198	4-V-76	33°45', 151°51'	604-604
K76-06-03	19202	11-V-76	33°12', 152°23'	600-604
K76-07-01	19205	26-V-76	33°30', 151°58'	375-384
K76-23-01	19862	13-XII-76	34°24', 151°25'	732-768
K76-24-03	19860	20-XII-76	33°33', 152°02'	823-823
K76-24-04	19859	21-XII-76	33°29', 152°06'	823-823
K77-07-10	21806	26-VI-77	33°30', 152°05'	604-604
K77-13-10	20118	23-VIII-77	29°52', 153°43'	503-512
K77-13-12	20301	23-VIII-77	29°53', 153°42'	503-503
K77-16-16	21669	28-IX-77	33°33', 152°02'	604-604
K77-18-01	20064	26-X-77	34°11', 152°03'	*2200-2380
K77-19-05	20071	3-XI-77	34°38', 151°16'	*2750-2930
K77-21-01	20484	21-XI-77	34°32', 151°20'	695-695
K77-22-03	20097	29-XI-77	37°41', 150°18'	732-732
K77-22-06	20096	30-XI-77	37°40', 150°20'	823-823
K77-23-06	20485	6-XII-77	33°38', 151°56'	713-732
K77-23-07	20098	6-XII-77	33°32', 152°03'	914-914
K77-23-09	21805	7-XII-77	33°09', 152°25'	585-594
K77-23-10	20477	7-XII-77	33°10', 152°24'	732-732
K77-23-12	20099	8-XII-77	33°34', 152°01'	823-823
K77-23-13	20068	8-XII-77	33°26', 152°10'	878-896
K77-24-03	20307	13-XII-77	33°21', 152°26'	*1830-2750
K77-24-10	20314	14-XII-77	33°32', 152°35'	*3660-3840
K77-24-11	20315	14-XII-77	34°09', 152°01'	*2470-2560
K78-01-01	30407	22-III-78	33°42', 151°51'	448-457
K78-09-05	20518	2-VI-78	28°02', 153°59'	549-549
K78-16-07	20435	2-VIII-78	29°47', 153°44'	421-439

Station	AMS Reg. No.	Date	Location	Depth (m)
K78-17-07	23689	16-VIII-78	28°00', 153°58'	411-411
K78-17-10	20459	17-VIII-78	28°01', 154°00'	549-549
K78-17-11	21793	17-VIII-78	28°03', 153°58'	411-411
K78-17-14	23993	17-VIII-78	28°17', 153°53'	174-201
K78-23-08	21795	6-XI-78	28°03', 154°04'	732-741
K78-23-09	20651	6-XI-78	27°56', 154°03'	549-549
K78-26-16	24037	7-XII-78	33°47', 151°55'	823-850
K78-27-05	23885	12-XII-78	34°55', 151°13'	801-827
K79-15-01	29535	2-X-79	33°48', 151°49'	439-439
K79-15-03	26932	3-X-79	33°31', 152°02'	402-402
K79-19-07	21369	28-XI-79	32°55', 153°02'	*3600-3700
K79-20-04	23710	4-XII-79	33°34', 152°04'	713-732
K79-20-06	25933	4-XII-79	33°36', 152°06'	914-933
K79-20-13	21722	6-XII-79	33°32', 152°06'	823-823
K79-20-15	21724	6-XII-79	33°37', 152°06'	1005-1010
K80-05-01	21725	13-V-80	33°42', 151°52'	439-550
K80-20-05	40274	9-XII-80	33°37', 152°03'	960-988
K81-17-03	24619	9-IX-81	33°46', 151°49'	439-475
K81-18-05	23862	15-IX-81	34°40', 151°15'	520-530
K82-17-01	23470	12-X-82	33°43', 151°53'	475-494
K82-24-02	23486	20-XII-82	33°47', 151°49'	457-475
K83-06-01	24101	25-VII-83	33°45', 151°55'	805-841
K83-06-02	24054	26-VII-83	34°36', 151°19'	869-878
K83-07-11	24100	10-VIII-83	33°04', 152°34'	960-997
K83-08-01	24055	18-VIII-83	33°45', 151°59'	933-942
K83-08-02	24056	18-VIII-83	33°37', 152°04'	860-896
K83-09-01	24060	22-VIII-83	33°47', 151°58'	942-960
K83-09-02	24059	23-VIII-83	33°30', 152°10'	933-969
K83-09-04	24057	24-VIII-83	34°53', 151°14'	951-978
K83-12-04	24157	27-IX-83	38°18', 149°48'	997-1015
K83-13-01	24150	17-X-83	33°38', 152°05'	988-1015
K83-13-02	24181	18-X-83	32°57', 152°43'	960-988
K83-14-01	24172	25-X-83	35°28', 150°53'	978-1024
K83-14-02	24187	25-X-83	35°28', 150°53'	988-1024
K83-14-03	24565	25-X-83	35°28', 150°53'	1033-1042
K83-14-05	24356	26-X-83	34°53', 151°15'	1042-1061
K83-14-06	24173	26-X-83	34°54', 151°14'	1097-1116
K83-14-08	24178	27-X-83	33°37', 152°06'	978-1006
K83-14-09	24451	27-X-83	33°32', 152°10'	1042-1061
K83-15-01	24419	2-XI-83	32°08', 153°07'	910-950
K83-15-02	24462	2-XI-83	32°04', 153°08'	942-978
K83-18-01	24357	30-XI-83	34°55', 151°14'	969-1024
K83-18-02	24355	30-XI-83	34°55', 151°16'	1105-1152
K83-19-02	24424	6-XII-83	35°29', 150°53'	1033-1070
K84-04-10	24624	11-IV-84	34°57', 151°13'	1097-1134
K84-04-11	25415	11-IV-84	34°54', 151°14'	988-1024
K84-06-03	24645	1-V-84	33°29', 152°08'	777-823
K84-06-04	24659	1-V-84	33°29', 152°09'	914-933
K84-06-06	24625	2-V-84	33°30', 152°10'	1042-1106
K84-06-07	24644	2-V-84	33°29', 152°14'	1170-1198
K84-08-02	24778	22-V-84	34°54', 151°13'	814-850
K84-08-03	24658	22-V-84	34°52', 151°14'	869-924
K84-08-05	24774	23-V-84	35°38', 150°44'	805-850
K84-10-03	24771	17-VII-84	32°55', 152°46'	963-1039
K84-10-06	24820	18-VII-84	32°04', 153°09'	960-969
K84-10-08	24988	19-VII-84	33°41', 152°04'	1097-1134
K84-11-07	24992	1-VIII-84	35°27', 150°55'	1079-1116
K84-11-09	25273	2-VIII-84	34°53', 151°16'	1161-1207
K84-13-03	28713	24-VIII-84	36°27', 150°20'	411-457

Station	AMS Reg. No.	Date	Location	Depth (m)
K84-14-01	24854	3-IX-84	34°17', 151°27'	439-512
K84-15-01	24850	10-IX-84	33°45', 151°51'	411-439
K84-15-03	24852	11-IX-84	33°34', 152°01'	512-530
K84-16-04	24979	25-IX-84	33°34', 152°03'	722-777
K84-16-05	24991	25-IX-84	33°36', 152°03'	814-832
K84-16-13	24990	27-IX-84	33°47', 151°58'	905-924
K84-16-14	24993	27-IX-84	33°42', 152°04'	1042-1070
K84-16-15	24980	27-IX-84	33°43', 152°01'	960-997
K84-17-01	24989	3-X-84	34°15', 151°30'	668-704
K84-17-03	24851	4-X-84	34°37', 151°19'	768-786
K84-17-04	24981	4-X-84	34°36', 151°20'	860-878
K84-17-05	24860	4-X-84	34°48', 151°16'	914-969
K84-18-03	25127	10-X-84	34°48', 151°13'	732-750
K84-18-06	25126	11-X-84	33°49', 151°56'	914-924
K84-19-04	25264	16-X-84	33°35', 152°08'	1025-1244
K84-20-03	25290	1-XI-84	33°43', 152°01'	969-1006
K84-20-04	24978	1-XI-84	33°37', 152°07'	1070-1125
K84-20-05	25095	1-XI-84	33°30', 152°13'	1170-1207
K84-22-02	25266	21-XI-84	37°40', 150°21'	1052-1079
K85-17-02	26240	14-XI-85	33°36', 151°57'	421-457
K85-17-02	26446	14-XI-85	33°36', 151°57'	421-457
K85-20-10	26221	10-XII-85	32°35', 152°49'	154-157
K85-21-04	26247	19-XII-85	33°34', 152°09'	1024-1052
K85-21-06	25932	19-XII-85	33°43', 151°53'	439-466
K86-01-05	26394	11-II-86	33°29', 152°06'	454-523
K86-01-06	26002	11-II-86	33°35', 152°01'	657-662
K86-01-07	26245	11-II-86	33°42', 151°59'	819-889
K86-01-08	26000	12-II-86	33°32', 152°10'	951-1015
K86-01-09	26001	12-II-86	33°28', 152°13'	1116-1207
K86-10-07	26453	22-IV-86	33°02', 152°33'	439-512
K86-10-14	26756	23-IV-86	33°00', 152°36'	457-503
K87-02-01	26981	19-II-87	32°22', 153°01'	896-960
K87-14-02	26998	5-VIII-87	34°18', 151°30'	636-781
K87-16-02	27647	27-VIII-87	32°23', 153°03'	878-951
K87-23-02	27609	3-XII-87	34°53', 151°11'	503-658
K87-24-01	29600	7-XII-87	33°52', 151°51'	783-978
K87-24-02	30737	8-XII-87	32°56', 152°40'	832-997
K87-24-03	28189	8-XII-87	32°53', 152°46'	863-960
K87-24-04	29805	8-XII-87	32°39', 152°54'	887-951
K87-24-05	29738	9-XII-87	31°54', 153°12'	479-922
K87-25-06	29741	16-XII-87	35°28', 150°52'	933-960
K88-04-06	28475	23-III-88	34°55', 151°15'	1116-1152
K88-04-08	27717	24-III-88	33°33', 152°08'	1024-1143
K88-04-09	28071	24-III-88	33°29', 152°11'	905-969
K88-05-01	27718	29-III-88	35°30', 150°54'	1134-1189
K88-08-04	27720	4-V-88	32°04', 153°08'	1024-1079
K88-08-05	28372	4-V-88	32°06', 153°09'	1070-1106
K88-08-06	28100	4-V-88	32°08', 153°09'	1024-1079
K88-08-07	27721	5-V-88	32°56', 152°44'	1006-1079
K88-08-08	29601	5-V-88	33°05', 152°34'	896-951
K88-08-09	27722	5-V-88	33°00', 152°38'	704-750
K88-10-02	28712	17-V-88	32°50', 152°48'	1024-1061
K88-10-04	28717	17-V-88	32°52', 152°48'	1079-1097
K88-11-01	27638	14-VI-88	33°43', 152°07'	1024-1042
K88-12-02	27643	21-VI-88	32°02', 153°10'	990-1020
K88-12-03	29591	21-VI-88	31°46', 153°18'	1005-1042
K88-14-04	27637	4-VIII-88	35°30', 150°53'	988-1024
K88-16-04	29340	17-VIII-88	32°56', 152°45'	1042-1061
K88-17-03	28749	31-VIII-88	33°28', 152°14'	1143-1198

Station	AMS Reg. No.	Date	Location	Depth (m)
K88-17-06	28900	1-IX-88	33°29', 152°12'	1033-1070
K88-20-01	29809	8-XI-88	32°54', 152°47'	1070-1097
K88-20-02	29297	8-XI-88	32°50', 152°48'	1024-1097
K88-20-03	29298	8-XI-88	32°50', 152°48'	988-1033
K88-21-02	29747	3-XII-88	32°48', 152°47'	841-933
K88-21-03	29746	3-XII-88	32°40', 152°50'	713-750
K89-03-15	29385	27-II-89	38°06', 149°42'	152-159
K89-06-02	29799	11-IV-89	32°56', 152°47'	1042-1061
K89-06-04	29808	11-IV-89	32°51', 152°48'	1090-1134
K89-06-05	29813	12-IV-89	33°12', 152°23'	722-768
K89-07-01	29803	18-IV-89	35°05', 151°07'	695-768
K89-07-04	32431	19-IV-89	35°42', 150°43'	887-960
K89-07-05	29807	19-IV-89	35°41', 150°43'	1015-1042
K89-08-01	29811	9-V-89	33°43', 151°59'	805-869
K89-08-02	29801	10-V-89	33°28', 152°13'	1134-1189
K89-09-01	29804	16-V-89	33°04', 152°36'	896-960
K89-09-03	28988	16-V-89	32°51', 152°49'	1024-1061
K89-09-06	29806	17-V-89	33°30', 152°07'	732-796
K89-09-07	29605	18-V-89	33°39', 152°05'	1024-1088
K89-09-09	29825	18-V-89	33°27', 152°10'	741-768
K89-11-02	28070	8-VI-89	32°51', 152°49'	1006-1052
K89-12-02	30738	14-VI-89	32°51', 152°48'	1079-1143
K89-12-03	29762	14-VI-89	32°43', 152°49'	713-796
K89-12-04	29798	15-VI-89	32°06', 153°10'	1033-1079
K89-12-05	29797	15-VI-89	32°03', 153°09'	914-997
K89-13-01	29823	29-VI-89	32°33', 152°59'	896-969
K89-13-02	28477	30-VI-89	33°44', 152°03'	1116-1170
K89-15-01	29827	3-VIII-89	32°56', 152°45'	1024-1061
K89-15-02	29812	3-VIII-89	32°51', 152°49'	1061-1097
K89-15-03	29757	3-VIII-89	32°51', 152°48'	933-988
K89-15-04	29756	4-VIII-89	33°39', 151°59'	677-750
K89-16-02	30394	10-VIII-89	34°47', 151°18'	1134-1225
K89-17-02	29749	15-VIII-89	32°39', 152°52'	814-850
K89-17-03	29754	15-VIII-89	32°30', 153°00'	1006-1052
K89-17-04	29750	16-VIII-89	31°47', 153°18'	1024-1052
K89-17-06	29753	16-VIII-89	31°52', 153°16'	878-933
K89-17-07	29742	17-VIII-89	32°07', 153°09'	1079-1143
K89-17-08	29752	17-VIII-89	32°06', 153°09'	1024-1061
K89-17-09	30304	17-VIII-89	32°12', 153°06'	823-860
K89-18-02	29745	22-VIII-89	34°56', 151°15'	1090-1143
K89-18-04	39052	22-VIII-89	34°45', 151°16'	950-990
K89-19-01	29737	31-VIII-89	35°29', 150°55'	1116-1134
K89-19-02	29761	31-VIII-89	35°29', 150°53'	1024-1061
K89-20-01	29743	7-IX-89	33°41', 152°00'	805-869
K97-01-21	39957	29-IV-97	37°43', 150°10'	219-227
K97-01-22	39958	30-IV-97	37°39', 150°17'	543-567
K97-02-01	38576	27-V-97	35°33', 150°46'	505-549

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. J. Asiat. Soc. Bengal 63 (pt. 2)(2):115–137, pls. 6–7.

ANDREW, N. L., K. J. GRAHAM, K. E. HODGSON, AND G. N. G. GORDON. 1997. Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. NSW Fisheries Final Report Series No. 1. 210 pp.

ARAI, T. 1979. Additional information on a rare macrourid fish, *Mesobius antipodum*, from New Zealand. Japan. J. Ichthyol. 25(4):286–289, figs. 1–3, table 1.

ARAI, T. AND T. IWAMOTO. 1979. A new species of the macrourid fish genus *Coelorinchus* from off Tasmania, New Zealand, and the Falkland Islands. Japan. J. Ichthyol. 26(3):238–246.

ARAI, T. AND P. J. MCMILLAN. 1982. A new macrourid fish, *Coelorinchus biclinozonalis* from New Zealand, and redescription of *C. australis* from Australia. Japan. J. Ichthyol. 29(2):115–126.

BARNARD, K. H. 1925. Descriptions of new species of marine fishes from S. Africa. Ann. Mag. Nat. Hist., ser. 9, 15(87):498–504.

DOLLO, L. 1909. *Cynomacrurus Piriei*, Poisson abyssal nouveau recueilli par l'Expédition Antarctique Nationale Ecossaise. Note préliminaire. Proc. Roy. Soc. Edinburgh 29(4):316–326.

FILHOL, H. 1884. Explorations sous-marines—Voyage du "Talisman." Nature, Paris (558):182–186.

GARMAN, S. 1899. Report on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the US Fish Commission steamer "Albatross" during 1891, XXVI (The Fishes). Mem. Mus. Comp. Zool. Harvard Coll. 24:1–431.

GILBERT, C. H. 1905. The deep-sea fishes of the Hawaiian Islands. Pp. 575–713, figs. 230–276, pls. 66–101 *in* The aquatic resources of the Hawaiian Islands, D. S. Jordan, and B. W. Evermann, eds., Bull. U. S. Fish Comm. 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. Proc. U. S. Natl. Mus. 19:403–435.

GILBERT, C. H. AND C. L. HUBBS. 1920. The macrourid fishes of the Philippine Islands and the East Indies. U. S. Natl. Mus. Bull. 100, 1 (pt. 7):369–588, figs. 1–40.

GOMON, M. F., J. C. M. GLOVER, AND R. H. KUITER, eds. 1994. The fishes of Australia's south coast. State Print, Adelaide. 992 pp.

GON, O. AND P. C. HEEMSTRA, eds. 1990. Fishes of the Southern Ocean. J. L. B. Smith Institute of Ichthyology, Grahamstown. 462 pp., 12 pl.

GOODE, G. B. AND T. H. BEAN. 1883. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the U. S. XIX. Report on the fishes. Bull. Mus. Comp. Zool. Harvard 10(5):183–226.

GORMAN, T. B. AND K. J. GRAHAM. 1975. Deepwater prawn survey off New South Wales. Pp. 162–172 *in* Proceedings of First Aust. Nat. Prawn Sem., P. C. Young, ed. Australian Government Publishing Service, Canberra.

GRAHAM, K. J. 1990. Report for Cruises 89-06 to 89-20 on the NSW mid-slope between Crowdy Head and Batemans Bay during April-September, 1989. Kapala Cruise Report 107. NSW Fisheries, Cronulla, Australia. 22 pp.

GRAHAM, K. J., N. L. ANDREW, AND K. E. HODGSON. 2001. Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. New Zealand J. Mar. Freshwater Res. 52:549–561.

GRAHAM, K. J. AND T. B. GORMAN. 1985. New South Wales deepwater prawn fishery research and development. Pp. 231–243 *in* Second Aust. Nat. Prawn Sem., P. C. Rothlisberg, B. J. Hill and D. J. Staples, eds. NPS2, Cleveland , Australia.

GRAHAM, K. J., G. W. LIGGINS, AND J. WILDFORSTER. 1996. NSW continental shelf trawl survey results for Year 2: 1994. Kapala Cruise Report No. 115. NSW Fisheries, Cronulla, Australia. 63 pp.

GRAHAM, K. J., G. W. LIGGINS, J. WILDFORSTER, AND B. WOOD. 1995. NSW continental shelf trawl-fish survey results for Year 1: 1993. Kapala Cruise Report No. 114. NSW Fisheries, Cronulla, Australia. 52 pp.

GRAHAM, K. J., B. R WOOD, AND N. L. ANDREW. 1997. The 1996–97 survey of New South Wales upper slope trawling grounds between Sydney and Gabo island. Kapala Cruise Report No. 117. NSW Fisheries, Cronulla, Australia. 96 pp.

GÜNTHER, A. 1877. Preliminary notes on new fishes collected in Japan during the expedition of H. M. S. "Challenger." Ann. Mag. Nat. Hist., ser. 4, 20:433–447.

———. 1878. Preliminary notices of deep-sea fishes collected during the voyage of H. M. S. "Challenger." Ann. Mag. Nat. Hist., ser 5, 2:17–28.

———. 1887. Report on the deep-sea fishes collected by H. M. S. Challenger during the years 1873–76. Rep. Sci. Res. Challenger 22(pt. 57):i-lxv + 1–268, pls. 1–73.

HAEDRICH, R. L. AND P. T. POLLONI. 1976. A contribution to the life history of a small rattail fish, *Coryphaenoides carapinus*. Bull. So. Calif. Acad. Sci. 75(2):203–211.

HOWES, G. J. 1989. Phylogenetic relationships of macrouroid and gadoid fishes based on cranial myology and arthrology. Pp. 113–128 *in* Papers on the systematics of gadiform fishes, D. M. Cohen, ed. Nat. Hist. Mus. Los Angeles County, Sci. Ser. 32. 262 pp.

HOWES, G. J. AND O. A. CRIMMEN. 1990. A review of the Bathygadidae (Teleostei: Gadiformes). Bull. Br. Mus. Nat. Hist. (Zool.) 56(2):155–203.

HUBBS, C. L. AND T. IWAMOTO. 1977. A new genus (*Mesobius*), and three new bathypelagic species of Macrouridae (Pisces, Gadiformes) from the Pacific Ocean. Proc. Calif. Acad. Sci. ser. 4, 41(7):233–251.

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. Stud. Trop. Oceanogr. (4)(pt.2):316–431.

———. 1974. *Nezumia* (*Kuronezumia*) *bubonis*, a new subgenus and species of grenadier (Macrouridae: Pisces) from Hawaii and the western North Atlantic. Proc. Calif. Acad. Sci. ser. 4, 39(22):507–516.

———. 1982. *Ventrifossa johnboborum*, a new grenadier from the western Pacific (Macrouridae: Pisces). Austr. Zool. 21(pt.1):55–61.

———. T. 1986. Family No. 93: Macrouridae. Pp. 330–341 *in* Smiths' sea fishes, M. M Smith. and P. C. Heemstra, eds. Macmillan South Africa, Johannesburg.

———. 1990. Macrouridae. Pp. 90–317 *in* FAO Species Catalogue, vol. 10. Gadiform fishes of the world. An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date, D. M. Cohen, T. Inada, T. Iwamoto, and N. Scialabba. FAO, Rome.

IWAMOTO, T. AND M. E. ANDERSON. 1994. Review of the grenadiers (Teleostei: Gadiformes) of southern Africa, with descriptions of four new species. Ichthyol. Bull. J. L. B. Smith Inst. Ichthyol. (61):1–28.

IWAMOTO, T. AND P. MCMILLAN. 1997. A new grenadier, genus *Trachonurus*, from New Zealand and Australia (Macrouridae, Gadiformes, Pisces). Mem. Mus. Victoria 56(pt. 1):255–259.

IWAMOTO, T., P. MCMILLAN, AND Y. N. SHCHERBACHEV. 1999. A new grenadier, genus *Caelorinchus*, from Australia and New Zealand (Pisces, Gadiformes, Macrouridae). New Zealand J. Mar. Freshwater Res. 33(1):49–54.

IWAMOTO, T. AND N. R. MERRETT. 1997. Pisces Gadiformes: Taxonomy of grenadiers of the New Caledonian region, southwest Pacific. Pp. 473–570 *in* Résultats des Campagnes MUSORSTOM, vol. 18, A. Crosnier, ed. Mém. Mus. Natn. Hist. Nat. 176.

IWAMOTO, T. AND Y. I. SAZONOV. 1988. A review of the southeastern Pacific *Coryphaenoides* (sensu lato) (Pisces, Gadiformes, Macrouridae). Proc. Calif. Acad. Sci. 45(3):35–82, figs. 1–9.

IWAMOTO, T. AND Y. N. SHCHERBACHEV. 1991. Macrourid fishes of the subgenus *Chalinura*, genus *Coryphaenoides*, from the Indian Ocean. Proc. Calif. Acad. Sci. 47(7):207–233, figs. 1–17, tables 1–7.

IWAMOTO, T. AND A. WILLIAMS. 1999. Grenadiers (Pisces, Gadiformes) from the continental slope of western and northwestern Australia. Proc. Calif. Acad. Sci. 51(3):105–243.

JORDAN, D. S. AND C. H. GILBERT. 1904. Macrouridae. Pp. 602–621 *in* 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, D. S. Jordan and E. C. Starks. Bull. U. S. Fish Comm. 22(1902):577–630, pls. 1–8.

LAST, P. R., E. O. G. SCOTT, AND F. H. TALBOT. 1983. Fishes of Tasmania. Tasmanian Fishery Development Authority, Hobart. 563 pp.

LAST, P. R. AND J. D. STEVENS. 1994. Sharks and rays of Australia. CSIRO Australia. 513 pp., 84 pls.

LEVITON, A. E. AND R. H. GIBBS, JR. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institution resource collections in herpetology and ichthyology. Supplement No. 1: additions and corrections. Copeia 1988(1):282.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3):802–832.

LOWE, R. T. 1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841 and 1842. Proc. Zool. Soc. Lond. 11–91.

MAKUSHOK, M. 1976. The new rattail *Coryphaenoides subserrulatus* sp. n. (Macrouridae, Osteichthys) from the area south of New Zealand. Pp. 144–55 *in* Biology and distribution of tropical deep-sea fishes, N. V Parin,. ed. Trudy Inst. Okeanol. Akad. Nauk SSSR, Moscow, v. 104:1–226. [In Russian.]

MARSHALL, N. B. 1964. Bathypelagic macrourid fishes. Copeia 1964(1):86–93.

———. 1973. Family Macrouridae. Pp. 496–665 *in* Fishes of the western North Atlantic, D. M. Cohen, ed. Mem. Sears Found. Mar. Res. (1)(pt.6).

MARSHALL, N. B. AND T. IWAMOTO. 1973. Genus *Coryphaenoides*. Pp. 565–600 *in* Fishes of the western North Atlantic, D. M. Cohen, ed. Mem. Sears Found. Mar. Res. (1)(pt.6).

MCCANN, C. AND D. G. MCKNIGHT. 1980. The marine fauna of New Zealand: Macrourid fishes (Pisces: Gadida). New Zealand Oceanogr. Inst. Mem. 61:1–91.

MCCULLOCH, A. R. 1907. The results of deep sea investigations in the Tasman Sea. II. The expedition of the *Woy Woy*. Fishes and crustaceans from eight hundred fathoms. Rec. Aust. Mus. 6:345–355, 6 pls.

MCCULLOCH, A. R. 1926. Report on some fishes obtained by the F. I. S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania, South and South-western Australia. Part V. Biological results of the fishing experiments carried on by the F. I. S. "Endeavour" 1909–1914, 4(pt. 5):157–216, pls. 43–56.

MCMILLAN, P. J. 1995. Review of trachyrincine grenadier fishes (Pisces: Macrouridae) from New Zealand, with a description of a new species of *Trachyrincus*. New Zealand J. Mar. Freshw. Res. 29:83–91.

———. 1999. New grenadier fishes of the genus *Coryphaenoides* (Pisces: Macrouridae); one from off New Zealand and one widespread in the southern Indo-West Pacific and Atlantic Ocean. New Zealand J. Mar. Freshw. Res. 33:481–489.

MCMILLAN, P. J. AND C. D. PAULIN. 1993. Descriptions of nine new species of rattails of the genus *Caelorinchus* (Pisces, Macrouridae) from New Zealand. Copeia 1993(3):819–840.

MERRETT, N. R. AND T. IWAMOTO. 2000. Macrourid fishes of the New Caledonia region, Southwest Pacific Ocean; taxonomy and distribution, with ecological notes. Résultats des Campagnes MUSORSTOM, vol. 21. Mém. Mus. Natn. Hist. Nat. 184:723–781.

MUNRO, I. S. R. 1957. Handbook of Australian Fishes. No. 14. (Aust.) Fish. Newsletter 16 (8).

NORMAN, J. R. 1939. Fishes. Scientific Report of the John Murray Expedition. British Museum (N.H.), London, 7(1):1–116.

OKAMURA, O. 1970. Fauna Japonica. Macrourina (Pisces). Academic Press, Tokyo. 216 pp., 64 pls.

———. 1982. [Macrouridae] *In* Fishes of the Kyushu-Palau Ridge and Tosa Bay, O. Okamura, K. Amaoka, and F. Mitani, eds. Japan Fish Resource Conserv. Assoc., Tokyo. 435 pp.

———. 1984. [Macrouridae] *In* Fishes of the Okinawa Trough and the adjacent waters. I. The intensive research of unexploited fishery resources on continental slopes, O. Okamura and T. Kitajima, eds. Japan Fish. Resource Conserv. Assoc., Tokyo. 414 pp.

———. 1989. Relationships of the suborder Macrouroidei and related groups, with comments on Merlucciidae and *Steindachneria*. Pp. 129–142 *in* Papers on the systematics of gadiform fishes, D. M. Cohen, ed. Nat. Hist. Mus. Los Angeles County, Sci. Ser. 32. 262 pp.

PAXTON, J. R., D. F. HOESE, G. R. ALLEN, AND J. E. HANLEY. 1989. Zoological catalogue of Australia. Vol. 7, Pisces, Petromyzontidae to Carangidae. Austr. Govt. Publ. Serv., Canberra. 664 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. Proc. U. S. Natl. Mus. 43:105–140, pls. 22–31.

RICHARDSON, J. 1839. [. . . account of an interesting collection of fish formed at Port Arthur in Van Diemen's Land . . .]. Proc. Zool. Soc. London. 7:95–100.

———. 1846. Ichthyology of the voyage of H. M. S. Erebus and Terror under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839–1843. E. W. Janson, London. 139 pp, 60 pls.

SAZONOV, Y. I. 1981. *Idiolophorhynchus andriashevi* gen. et sp. n. (Osteichthyes, Macrouridae) from the Australia-New Zealand region. Zoologicheskiy Zhurnal 60, vol. 9:1357–1363.

SAZONOV, Y. I. AND T. IWAMOTO. 1992. Grenadiers (Pisces, Gadiformes) of the Nazca and Sala y Gomez ridges, southeastern Pacific. Proc. Calif. Acad. Sci. 48(2):27–95, 37 figs., 7 tables.

SAZONOV, Y. I. AND Y. N. SHCHERBACHEV. 1982a. On the taxonomic position and distribution of *Coelorinchus matamua* (McCann and McKnight)(Gadiformes, Macrouridae). Pp. 42–47 *in* Insufficiently studied fishes of the open ocean, N. V. Parin, ed. Inst. Okeanol. Akad. Nauk. SSSR, Moscow. 140 pp. [In Russian.]

———. 1982b. A preliminary review of grenadiers related to the genus *Cetonurus* Günther (Gadiformes, Macrouridae). Descriptions of new taxa related to the genera *Cetonurus* Günther and *Kumba* Marshall. [In Russian, with English summary.] Vopr. Ikhtiol. 22 (5):707–721, figs. 1–4. [also Engl. transl., J. Ichthyol. 22(5):1–15]

———. 1985. Preliminary review of grenadiers of the *Cetonurus* group (Gadiformes, Macrouridae). II. The genus *Cetonurus* Günther: taxonomic characters of the group. J. Ichthyol. 25(3):12–26, figs. 1–2, tables 1–2.

SHCHERBACHEV, Y. N. 1987. Preliminary list of thalassobathyal fishes of the tropical and subtropical waters of the Indian Ocean. Vopr. Ikhtiol. (1):3–11. [In Russian.] [English version in J. Ichthyol. 27 (2):37–46.]

SHCHERBACHEV, Y. N. AND T. IWAMOTO. 1995. Indian Ocean grenadiers of the subgenus *Coryphaenoides*, genus *Coryphaenoides* (Macrouridae, Gadiformes, Pisces). Proc. Calif. Acad. Sci. 48(14):285–314, figs. 1–8, tables 1–3.

SHCHERBACHEV, Y. N., Y. I. SAZONOV, AND T. IWAMOTO. 1992. Synopsis of the grenadier genus *Kuronezumia* (Pisces: Gadiformes: Macrouridae), with description of a new species. Proc. Calif. Acad. Sci. 48(3):97–108, figs. 1–9, table 1.

SHCHERBACHEV, Y. N., Y. I. SAZONOV, AND A. S. PIOTROVSKIY. 1979. On the discovery of *Trachonurus villosus* and species of the genus *Mesobius* (Macrouridae, Osteichthyes) in the Indian Ocean. J. Ichthyol. 19(1):16–23, figs. 1–2, tables 1–2.

SMITH, H. M., AND L. RADCLIFFE. 1912. [See RADCLIFFE, 1912]

TILZEY, R. D. J. 1994. Introduction. Pp 15–40 *in* The South East Fishery, R. D. J. Tilzey, ed. Bureau of Resource Sciences, Canberra, Australia.

TRUNOV, I. A. 1981 (1980). [A new genus and species of grenadier, *Haplomacrourus nudirostris* (Osteichthyes, Macrouridae)]. Vopr. Ikhtiol. (1980). t. 20,. 1(120):3–11. [Also published in J. Ichthyol. tome 20, 1(120):3–11.]

TRUNOV, I. A. 1983. On the characteristics of some species of the genus *Coelorinchus* (Macrouridae) from the southeastern Atlantic Ocean. Report 1. Vopr. Ikhtiol. 23(6):894–904. [In Russian.]

WEBER, M. 1913. Die Fische der SIBOGA-Expedition. Siboga Exped. 57:1–719, pls. 1–12.

WEBER, M. AND L. F. DE BEAUFORT. 1929. The fishes of the Indo-Australian Archipelago, vol. 5. E. J. Brill, Leiden. 458 pp.

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The Octandrous and Dodecandrous Species of *Topobea* (Melastomataceae) in Mexico and Central America

by

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A regional revision of the octandrous and dodecandrous species of *Topobea* is presented that recognizes 24 species in Mexico and Central America. This summary includes a key, descriptions, distributional and phenological information, discussions of useful taxonomic characters, and a brief review of what is known about the reproductive biology of *Topobea*. Rationale is given for placing nine species in synonymy. Illustrations are provided for four new species (*T. amplifolia*, *T. dimorphophylla*, and *T. gerardoana* from Costa Rica; *T. tetramera* from Panama), and for *T. multiflora*, a species erroneously reported for Costa Rica as *T. calycularis*. Representative specimens are cited to document the geographic distribution and range of variability for each species.

Resumen

Se presenta una revisión de las 24 especies de *Topobea* en México y America Central que tienen ocho y doce estambres. Este resumen incluye una clave, descripciones, información sobre distribución y fenología, y discusiones de caracteres taxonómicos muy útiles en *Topobea*. También se presentan ilustraciones para cuatro especies nuevas (*T. amplifolia*, *T. dimorphophylla*, y *T. gerardoana* de Costa Rica; *T. tetramera* de Panamá), y para *T. multiflora*, una especie erróneamente reportada para Costa Rica como *T. calycularis*. Especímenes representativos son citados para documentar la distribución geografica y el rango de variabilidad de cada especie.

Topobea, with approximately 70 species, is one of two genera comprising the neotropical tribe Blakeeae. This tribe is readily recognized by its prevailingly 6-merous axillary flowers that are individually subtended by two pairs of decussate bracts, baccate fruits, and ovoid to pyramidal seeds with a smooth testa (Almeda 1990).

Most species of *Topobea* are shrubby epiphytes of wet forest habitats; some are terrestrial shrubs, and a few attain arborescent dimensions. More than 75% of the species occur in a narrow equatorial band centered in Colombia, ranging south to Ecuador and north to Costa Rica. Another dozen or so species extend north to southern Mexico and south to Bolivia and Brazil. Because of their showy flowers, the terrestrial species, some of which are locally common, have been collected with increasing frequency in recent decades. Because so many species of *Topobea* are obligate epiphytes with very local distributions, newly discovered species have come to light with increasing frequency as the forest canopies of tropical America have received increased exploratory attention in the last two decades.

Topobea was last treated in its entirety by Cogniaux (1891) who recognized 24 species, five of which were reported for the Mesoamerican region. Subsequent regional floras (Gleason 1958; Standley 1924, 1938; Standley and Williams 1963; Winkler 1965) collectively attributed 17 species of

Topobea to Mexico and Central America, only six of which are recognized here as distinct taxa. This study of the octandrous and dodecandrous species of Mexico and Central America and my recent revision of the Central American hexandrous clade (Almeda 2000a) recognize a total of 29 species of *Topobea* for the region. Including the four new species proposed here, over half of these have been described or transferred to *Topobea* in the last 17 years.

TAXONOMIC TREATMENT

Topobea Aubl., Hist. Pl. Guiane Fr. 1:476. 1775.

TYPE: *Topobea parasitica* Aubl.

Trees, shrubs, or woody vines, often epiphytic with glabrous or variously pubescent terete to quadrate branchlets. Leaves coriaceous or chartaceous, 3–7-nerved or plinerved, often with the transverse secondary veins closely spaced, straight and parallel. Flowers 6-merous (rarely 4-merous), diplostemonous (haplostemonous in five Mesoamerican species), axillary, solitary or fascicled, typically pedunculate in the upper leaf axils and subtended by two pairs of decussate, free or partially fused, coriaceous or foliaceous bracts inserted at the base of the hypanthium. Hypanthium campanulate or suburceolate; calyx persistent, truncate or 6-lobate (4-lobate in one species). Petals white or pink, magenta or some combination of these colors, glabrous to sparsely pubescent abaxially, sometimes ciliolate at the margins. Stamens 12 or 6 (8 in one species), isomorphic and glabrous; anthers linear-oblong or subulate, uniporose or biporose with 2 dorsally-inclined apical pores that are approximate, cleft and divergent, or often confluent at anthesis; connective simple and unappendaged or thickened and modified basally at or near the filament insertion into a spur or caudiform appendage. Stigma punctiform to capitate. Ovary completely or partly inferior but varying to superior in a few species, usually 6-locular (consistently 2- or 4-locular in some species). Fruit baccate; seeds clavate to cuneate or narrowly pyriform.

Until recently, the tribe Blakeeae was thought to be constant with respect to ovary position and number of perianth parts and ovary locules (Almeda 1990, 2000a). Descriptive literature on the tribe describes it as having 6-merous flowers with 12 stamens (dodecandrous) and a 6-locular inferior ovary (Almeda 1990). This characterization still holds true for *Blakea*, which is distinguished from *Topobea* by its laterally compressed anthers that are biporose, oval, oblong, or elliptic and obtuse to rounded apically with 2 well-separated (and typically minute) apical pores (Almeda 2000b). *Topobea*, on the other hand has uniporose or biporose anthers that are linear-oblong to oblong-subulate (usually not compressed laterally) with dorsally-inclined apical pores that are commonly confluent or cleft and divergent. Most species of *Topobea* are similar to *Blakea* in having 6-merous flowers that are dodecandrous and a 6-locular ovary. This appears to be the plesiomorphic condition in the tribe. Critical study of the Mesoamerican species of *Topobea* reveals that only five species have completely inferior ovaries and a surprising number exhibit an evolutionary reduction series involving stamen and ovary locule number. The species of *Topobea* treated here fall into three groups based on stamen number. The most extraordinary one in this regard is *T. tetramera*. As its specific epithet implies it has 4-merous flowers that are octandrous (with eight stamens) and its ovary is inferior and 4-locular. The second, a hightly derived group of five species, is characterized by 6-merous flowers that are hexandrous (with 6 stamens) and an inferior ovary that is either 2- or 4-locular (Almeda 2000a). The third group consists of the remaining 23 dodecandrous species. Seventeen of these have a 6-locular ovary, five are consistently 4-locular, and one, *T. albertieae*, is prevailingly 4-locular with the occasional 3- or 5-locular ovary. Reduction in stamen number is consistently correlated with an inferior ovary position in the hexandrous and octandrous species. This kind of character correlation, however, breaks down among the dodecandrous species. The following

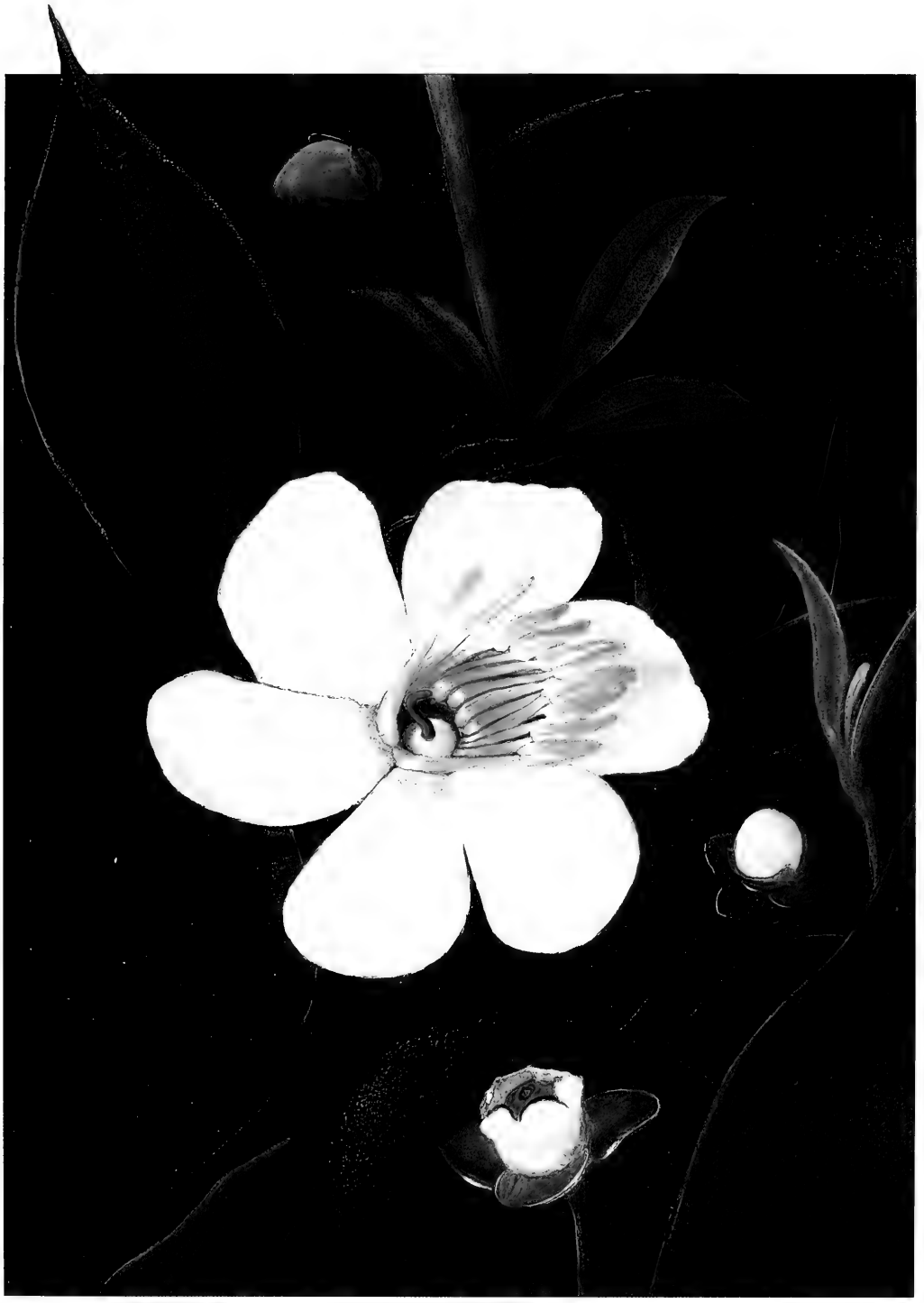

PLATE 1. *Topobea fragrantissima* Almeda. Original gouache and acrylic on hotpress illustration board by Meg Stalcup in July, 2001.

examples serve to illustrate this point: *T. aeruginosa* has 6:12:6 (petals: stamens: locules) with a completely inferior ovary; *T. brenesii* also has 6:12:6 but its ovary is wholly superior; *T. watsonii* with 6:12:6 has an ovary that is 1/3-inferior; *T. dodsonorum* has 6:12:4 and a 1/2-inferior ovary; *T. pittieri* has 6:12:4 and a 3/4-inferior. Among the dodecandrous species, the lack of correlation between ovary position and locule number provides information for identifying phenetic gaps and useful character combinations for species delimitation. It provides a challenge, however, when attempting to determine derived character states for phylogenetic reconstruction. The general assumption among students of the Melastomataceae has been that a superior ovary is plesiomorphic and an inferior ovary is apomorphic. The diversity in ovary position among the species of *Topobea* considered here is suggestive of homoplasy and leads to some intriguing questions about the forces driving this kind of character evolution.

Another character of taxonomic importance in *Topobea* is the presence of foliar domatia. Nine of the twenty-nine Mesoamerican species of *Topobea* produce specialized pit, pocket, or hair tuft chambers (acarodomatia) in the vein axils of some or all abaxial leaf surfaces. The mite-leaf domatium association is generally a mutually beneficial relationship (Walter and Proctor 1999). The domatia provide shelter and protection for eggs and moulting mites. The mites evidently benefit the plants by feeding on fungal spores and the eggs of predaceous insects.

In addition to ovary position and meristic differences in petal, stamen, and ovary locules, a number of other characters are important for the delimitation and identification of *Topobea* species. These include size, shape, and degree of fusion of floral bracts, presence or absence of lateral anther sac fusion, modifications of the anther connective into appendages, and details of the anther pores. Staminal material is essential for generic placement and for definitive identification of many species. It has been necessary to use these characters in the key that follows despite the fact that all of them are not always available on every specimen. Because of this I have also tried, where possible, to include vegetative characters which are more readily accessible.

Information on the reproductive biology of *Topobea* is available for only two species, *T. brenesii* and *T. maurofernandeziana* (including *T. durandiana* as reported in Lumer 2000). Both of these species are endemic to Mexico and/or Central America. According to Lumer (2000), these two species are self-compatible and capable of producing viable seeds without outcrossing. Lumer found that experimentally selfed flowers of *T. brenesii* produced significantly more seeds than outcrossed flowers. The showy flowers of both species offer pollen as the primary reward which attracts several species of bees despite interspecific flower differences in size and texture. The bee pollinators of *Topobea* use the same buzzing method of pollen collecting that is widespread among the melastomes and other flowering plants with poricidal anthers. Bees alight on the flowers, bend their bodies over the anther cluster, and vibrate their indirect flight muscles in a way that results in rapid evacuation of pollen from the terminal anther pores of a flower. The ejected pollen is deposited on the bee's ventral side and readily transferred to the stigma of the next flower visited (Lumer 2000). Because both species of *Topobea* studied are self-compatible, insect-mediated selfing may constitute a significant factor in effecting optimal pollination and seed set.

Key to the Octandrous and Dodecandrous Species of *Topobea*

1. Flowers 4-merous and diplostemonous (with eight stamens per flower); ovary 4-locular . . . . . *T. tetramera*

1′. Flowers 6-merous and diplostemonous (with twelve stamens per flower); ovary 4-locular or 6-locular.

  2. Outer floral bracts conspicuously decurrent on and imparting a winged aspect to the floral peduncle *T. mcphersonii*

  2′. Outer floral bracts not conspicuously decurrent on the floral peduncle.

    3. Both surfaces of mature leaf blades moderately to copiously covered with smooth ferrugineous hairs 0.5–3(–9) mm long.

      4. Mature leaves of a pair markedly unequal in size with the larger blade commonly six to twelve times the size of the smaller blade; floral peduncle 0.8–1.4 cm long; inner floral bracts fused basally for 3.5–5 mm to form a bowl-like collar; petals 0.5–0.6 0.5 cm; anthers 1.5–3 mm long . . . . . *T. dimorphophylla*

4′. Mature leaves of a pair somewhat unequal in size with the larger blade typically not more than two or three times the size of the smaller blade; floral peduncle 3.5–5.2 cm long; inner floral bracts free to the base; petals 1.6–2.3 1.4–1.7 cm; anthers 5–7.5 mm long . . . . . *T. intricata*

3′. Both surfaces of mature leaf blades not covered with ferrugineous smooth hairs.

5. Some or all mature leaf blades typically bearing domatia (pit, pocket, or hair tuft domatia) on the abaxial surface in the basal angles between the median vein and each of the two proximal lateral veins.

6. Anther sacs laterally connate for half or more of their length.

7. Mature leaf blades bearing hair tuft domatia on the abaxial surface in the angles between the median vein and each of the two proximal veins; each anther with two confluent apical pores; connective dorso-basally apendaged; ovary 6-locular.

8. Uppermost cauline nodes covered with caudate-acuminate stipuliform flaps ca. 3 mm long that envelop caducous tufts of hairs, the distal portions of each flap ± caducous with age and leaving a prominent interpetiolar ridge or corky line; outer floral bracts fused at the base for 4–6 mm; anthers 6–9 mm long . . . . . *T. multiflora*

8′. Uppermost cauline nodes not as above; outer floral bracts free from one another; anthers 4–5 mm long . . . . . *T. pluvialis*

7′. Mature leaf blades bearing perforated pit domatia on the abaxial surface in the angles between the median vein and each of the two proximal lateral veins; each anther with two separate apical pores; anther connective simple and unappendaged; ovary 4-locular . . . . . *T. parvifolia*

6′. Anther sacs completely free from one another.

9. Some or all abaxial foliar surfaces bearing hair tuft domatia that are sparsely to moderately covered with barbellate hairs in the angles formed between the median vein and the proximal pair of lateral veins.

10. Anthers 2.5 mm long, the surface granulose along the lower ventral half of the thecae; each anther with a solitary apical pore; connective prolonged dorso-basally into a deflexed caudiform appendage; ovary 6-locular. . . . . *T. lentii*

10′. Anthers 5–7 mm long, the surface smooth throughout the length of the thecae; each anther with two confluent apical pores; connective simple and unappendaged; ovary 4-locular . . . . . *T. calycularis*

9′. Some or all abaxial foliar surfaces bearing pit or pocket domatia that lack hairs of any kind.

11. Calyx consisting of a truncate flange or broadly flattened into low undulations; each anther terminating in two confluent pores. . . . . *T. laevigata*

11′. Calyx consisting of well-defined lobes; each anther terminating in a solitary pore. Principal leaves markedly dimorphic in size at each node, the larger blades broadly rounded and ± subpeltate at the base . . . . . *T. dodsonorum*

12′. Principal leaves not markedly dimorphic in size at each node, all mature blades acute to obtuse at the base.

13. Outer floral bracts 4.5–7.5 × 3-4 mm; petals 12–15 mm long; anther connective unappendaged; ovary 6-locular . . . . . *T. suaveolens*

13′. Outer floral bracts 1.2–2.5 × 1.5–2.5 mm; petals 7–8.5 mm long; anther connective prolonged dorso-basally into a ± horizontal toothlike appendage 0.5 mm long; ovary 4-locular . . . . . *T. pittieri*

5′. Mature leaf blades lacking domatia on the abaxial surface in the basal angles between the median vein and each of the two proximal lateral veins.

14. Calyx lobes 13-17 mm long, covered with a dense indument of spreading barbellate or plumose hairs.

15. Mature leaf blades dentate at least distally; anthers laterally connate for much of their length, each anther sac with 2 confluent, dorsally-inclined pores; ovary apex modified into a glandular-puberulent fluted cone and collar 7–9 mm long . . . . . *T. calophylla*

15′. Mature leaf blades entire; anthers free from one another, each anther with 2 divergent, dorsally-inclined apical pores; ovary apex glabrous and not elevated into a cone and stylar collar . . . . . *T. aeruginosa*

14′. Calyx truncate and flangelike or with triangular or depressed-triangular lobes 1-5 mm long, glabrous or if pubescent then the indument not as above.

16. Floral bracts and calyx lobes strongly undulate-recurved apically; inner floral bracts fused basally for 7–8 mm; each anther with 2 divergent, dorsally-inclined apical pores . . . . . *T. brenesii*

16′. Floral bracts and calyx lobes not strongly undulate-recurved apically; inner floral bracts free; each anther sac with 2 confluent, dorsally-inclined apical pores (if anther pores are divergent then the anther connectives are unappendaged).

17. Blades of the principal leaves broadly rounded to rounded-emarginate at the apex; abaxial foliar surfaces consistently but inconspicuously glandular-punctate . . . . . *T. albertieae*

17′. Blades of the principal leaves typically acuminate but sometimes varying to acute or caudate at the apex; abaxial foliar surfaces not glandular-punctate.

18. Anthers of a flower all free from one another.
    19. Anthers releasing pollen by a solitary apical pore.
        20. All mature leaf blades glabrous throughout, the transverse secondary veins on the abaxial surface spaced mostly 0.25 mm apart at the widest portion of the blade; ovary 4-locular. . . . . *T. fragrantissima*
        20′. Some mature leaf blades sparingly covered with a caducous indument of rusty brown subulate and conic hairs on the abaxial surface, the transverse secondary veins on the abaxial surface spaced 1-3 mm apart at the widest portion of the blade; ovary 6-locular . . . . . *T. gerardoana*
    19′. Each anther releasing pollen by two confluent apical pores.
        21. Calyx consisting of well-defined lobes.
            22. Mature leaf blades 21-25.3 × 11-14 cm; floral bracts glabrous, anther connective prolonged dorso-basally into a deflexed appendage; ovary apex elaborated into a sleeve-like distally lobulate collar 2–3 mm long . . . . . *T. amplifolia*
            22′. Mature leaf blades 9.5–15 × 5–10 cm; floral bracts moderately to sparsely covered with an indument of caducous matted hairs; anther connective unappendaged; ovary apex lacking a collar. . . . . *T. standleyi*
        21′. Calyx consisting of a truncate flange or the lobes broadly flattened into low undulations . . . . . *T. laevigata*
18′. Anthers of a flower laterally connate for half or more of their length.
    23. Anthers conspicuously granulose along at least the lower ventral half of the thecae; transverse secondary veins on the abaxial surface of mature leaf blades spaced 0.25–0.5 mm apart at the widest portion of the blade . *T.watsonii*
    23′. Anthers smooth throughout; transverse secondary veins on the abaxial surface of mature leaf blades spaced 1-4 mm apart at the widest portion of the blade.
        24. Calyx tube (fused portion of calyx below the free lobes) 6–8 mm long; filaments 7–9 mm long; anther thecae linear-oblong; ovary apex covered with a caducous ring of minute glandular hairs surrounding the stylar scar . . . . . *T. maurofernandeziana*
        24′. Calyx tube 2–4 mm long; filaments 9–12 mm long; anther thecae subulate; ovary apex elevated into a cone about 2 mm long and a shallow collar about 0.5–0.75 mm long that may disappear as the ovary enlarges on mature fruits. . . . . *T. parasitica*

1. *Topobea aeruginosa* (Standl.) L. O. Williams, Fieldiana Bot. 31:35. 1965.

Blakea aeruginosa Standl., Field Mus. Nat. Hist., Bot. Ser. 17:381. 1938.

TYPE. — HONDURAS. Comayagua: near the summit of the ridge above El Achote, 1850 m, 1 Aug. 1936, *Yuncker et al. 6267* (holotype: F!; isotypes: K!, NY!, US!).

Tree (or epiphytic shrub, fide Yuncker) 3–10 m tall. Upper cauline internodes bluntly quadrate. Uppermost internodes, vegetative buds, petioles, peduncles, and floral bracts densely covered with a ferrugineous indument of barbed or plumose hairs. Leaves coriaceous when dry, 10–23.5 × 4.5–17 cm, elliptic-oblong to elliptic-ovate, the apex short-acuminate, the base obtuse to rounded, the margin entire, 5–7-nerved, the outermost pair of primaries often concealed by revolute foliar margins when dry, the blade adaxially glabrous and glossy, abaxially covered with barbed or plumose hairs. Flowers solitary or paired in axils of upper branchlets; peduncles 1.7–3 cm long. Outer floral bracts 1.5–2.6 × 1–1.5 cm, free or fused basally for 3–5 mm, lanceolate, the apex long-attenuate; inner bracts 1.5–1.8 × 1 cm, free, ovate, the apex long-acuminate. Calyx lobes linear-oblong, 1.3–1.5 cm long. Petals 6, glabrous but caducously ciliate, 1.5–1.7 × 0.5–0.8 cm, pink, obovate, the apex rounded. Stamens 12; filaments 0.7–0.8 cm long; anthers free, 0.9–1.1 cm long, 1 mm wide, yellow, linear-oblong, each with 2 divergent, dorsally-inclined apical pores; connective elevated dorso-basally into a blunt oblong appendage 0.5–1 mm long. Ovary completely inferior, 6-locular, glabrous and not elevated into a cone or stylar collar. Style glabrous, 1.5–1.8 cm long; stigma punctiform. Mature berry 1.3–1.5 × 1–1.3 cm. Seeds 1 mm long, brown, cuneate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Local in cloud forests of Honduras and Nicaragua at 1200–1500 m. Flowering and young fruiting specimens have been collected from July through December.

REPRESENTATIVE SPECIMENS EXAMINED. — NICARAGUA. Matagalpa: camino a Aranjuez a menos de 1 km de carretera Matagalpa-Jinotega, 13°02′N, 85°55′W, 2 Jul. 1980, *Moreno 1028* (CAS); along road to La Fundadora, Cordillera Central, 22 Feb. 1963, *Williams et al. 24886* (F).

DISCUSSION. — This species is apparently known only from the type in Honduras. It is readily recognized by its rusty brown indument of plumose hairs on vegetative buds, abaxial leaf surfaces, floral peduncles, floral bracts and calyx lobes. Its free anthers are also distinctive in having two divergent apical pores.

2. *Topobea albertiae* Wurdack, Phytologia 55:146. 1984.

TYPE. — COLOMBIA. Antioquia: Fincas Montepinar and Las Palmas, Vereda Quebrada Larga, municipio Guatapé at the line with municipio San Rafael, elev. 1800 m, 4 Sep. 1982, *Albert de Escobar et al. 2278* (holotype: HUA; isotype US!)

Epiphytic shrub 2.5–3 m tall or reportedly a tree 5–12 m tall. Uppermost branchlets quadrate becoming rounded with age, the young vegetative buds and uppermost nodes covered with caducous simple hairs. Nodes on older branches becoming notably thickened with elevated interpetiolar lines or ridges. Mature leaves of a pair essentially equal or only somewhat unequal in size, glabrous adaxially but inconspicuously glandular-punctate abaxially; petioles 1–3.8 cm long; blades coriaceous, 5.7–16(–19) × 3.7–9.2(–12) cm, obovate to elliptic-obovate to elliptic, the apex rounded to rounded-emarginate, the base broadly acute to obtuse, the margin entire and sometimes revolute when dry, 5-nerved, the transverse secondary veins spaced 1–2.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of 2–4 in each leaf axil of uppermost branches; peduncles 1.1–1.5 cm long, commonly lenticellate distally. Floral bracts erect, concave and closely enveloping the hypanthium, essentially glabrous or sparsely and caducously covered with a mixture of appressed hairs 0.5–1 mm long and amorphous branlike hairs, the margin often fimbriate-ciliolate; outer bracts 8–10 × 10 mm, fused basally for 3–5 mm, ± oblong to oblate, with a mostly rounded-truncate apex that sometimes varies to bluntly acute; inner bracts 7–10 10 mm, free but imbricate, ovate to oblate, the apex ± truncate to broadly rounded. Hypanthium (at anthesis) cupulate, 4–5 × 5 mm. Calyx tube 5–6 mm long, erect and ± cylindric; calyx truncate and without evident lobes. Petals 6, glabrous and reflexed, 1.8–2.8 × 1.4–1.9 cm, pale pink or white flushed with pink, the claw typically white, obovate, the apex ± truncate-rounded, the margin caducously ciliolate. Stamens 12, the filaments 1.4–1.7 cm long, declinate, complanate, glabrous; anthers laterally connate for about half their length and forming a subparallel horizontal platform, 10–13 × 0.75–1 mm, yellow, oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into an acute appendage 2–2.5 mm long. Ovary superior or 1/2- to 1/3-inferior, (3–)4(–5)-locular, elevated into a cone 4–5 mm high but lacking a collar. Style glabrous 1.7–2 cm long, stigma punctiform. Mature berries and seeds not seen.

DISTRIBUTION AND PHENOLOGY. — Local in cloud forests of central Panama to Colombia at 100–2300 m. Collected in flower in January, February, July, and from October through December, in fruit from January through April and October through November.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Coclé: area of El Valle, 2 km E of La Mesa, N slope of Cerro Gaital, 8°38′N, 80°7′W, 16 Nov. 1983, *Churchill 3870* (CAS). Darién: Serrania del Darién, just below Cerro Mali, *Gentry et al. 16841* (DUKE). Panamá: near Cerro Jefe about 0.5–2 miles beyond road junction on the dirt road to Alto Pacora, 9°15′N, 79°30′W, 11 Jan. 1989, *Almeda et al. 6153* (CAS, PMA).

DISCUSSION. — This species is distinctive in having glandular-punctate abaxial leaf surfaces, a cylindric calyx tube that lacks well-defined calyx lobes, and anther thecae that are laterally connate for a portion of their length. The flowers are also extraordinary in producing a clove-like fragrance remi-

niscent of that encountered in some neotropical orchids that attract euglossine bees. *Topobea albertiae* is unusually variable in characters which are typically constant and diagnostic among its congeners. For example, the number of ovary locules in most specimens examined is four but some flowers have only three locules and others have as many as five. The degree of ovary fusion to the hypanthial wall is equally puzzling because the ovary is completely superior in some flowers examined and 1/2 to 1/3 inferior in other flowers.

3. *Topobea amplifolia* Almeda, sp. nov. (Fig. 1)

TYPE. — COSTA RICA. Limón: Cantón de Talamanca. Bratsi, Amubri, Alto Lari, Kivut. Afluente innominado del Río Lari, margen izquierda, 9°23′25"N, 83°04′25"W, 1200 m, 21 Mar. 1992, *Herrera 5407* (holotype, CAS!; isotypes, CR, INB!, MO!).

Arbor 6 m alta. Petioli 3–5 cm longi, lamina 21–25.3 × 11–14 cm elliptica vel elliptico-ovata apice acuminata vel acuta basi acuta vel obtusa, 5–7-nervata ad maturitatem chartacea et glabra, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore 4–5, pedunculis 1.3–2 cm longis, bracteae exteriores 0.8–1.2 × 0.7–0.9 cm ovatae vel elliptico-lanceolatae ca. 3 mm coalitae apice truncato-rotundata plerumque acuto vel cuspidato; bracteae interiores 0.9 × 1 cm omnino liberae. Hypanthium (ad torum) 0.8–0.9 longum; calycis tubus 2– 3 mm longum, lobis 3–4 mm longis. Petala alba, 1.9 × 1.3 cm oblongo-ovata vel obovata. Filamenta 6 mm longa; antherae 6 × 2 mm inter se non cohaerentes, dorsaliter biporosae; connectivum ad basim dorsaliter 1 mm descendenti armatum. Stylus 1.5 cm; ovarium 6-loculare et 2/3 inferum, collo 2–3 mm alto glabro.

Reportedly a tree 6 m tall. Uppermost branchlets with thickened interpetiolar ridges at each node, the internodes rounded-quadrate becoming rounded with age. Vegetative and very young floral buds copiously but caducously covered with an amorphous rusty brown scurfy indument. Mature leaves of a pair essentially equal or only slightly unequal in size, glabrous throughout; petioles 3–5 cm long; blades chartaceous, 21–25.3 × 11–14 cm, elliptic-ovate to elliptic, the apex acuminate to abruptly acute, the base acute to obtuse, the margin inconspicuously crenulate, 5–7-nerved, the outermost intramarginal pair commonly depressed and inconspicuous; the transverse secondary veins spaced 0.25 mm apart at the widest portion of the blade. Flowers erect to spreading, borne in clusters of four or five in each leaf axil of distal branches; peduncles 1.3–2 cm long. Floral bracts glabrous, closely enveloping the hypanthium; outer bracts 0.8–1.2 × 0.7–0.9 cm, fused basally for 3 mm, ovate varying to elliptic-lanceolate, the apex abruptly acute to cuspidate; inner bracts 0.9 × 1 cm, free, depressed-ovate to suborbicular, the apex commonly retuse and often mucronate. Hypanthium (at anthesis) campanulate, 0.8–0.9 × 0.8–0.9 cm. Calyx tube 2–3 mm long; calyx lobes (fruiting hypanthium), erect, 3–4 mm long and 3–4 mm wide basally, oblong-ovate, rounded apically and covered with callose-thickened teeth at the abaxial apex. Petals 6, glabrous, 1.9 × 1.3 cm, white, obovate, the apex rounded, entire. Stamens 12; filaments complanate and glabrous, 6 mm long; anthers free, 6 × 2 mm, reportedly yellow-brown, subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into a deflexed tooth-like appendage 1 × 0.25 mm. Ovary 2/3 inferior, 6-locular, elaborated apically into a glabrous, sleeve-like distally lobulate collar 2–3 mm long. Style glabrous, 1.5 cm long; stigma ± clavate and obliquely flattened when dry. Immature berry 0.8 × 1 cm. Seeds cuneate to narrowly obovoid, 1 mm long, brownish with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Known only from low-elevation rainforest in southeastern Costa Rica near the Panamanian border at 1200 m. The type and only known collection, which was made in March, is in flower and young fruit.

DISCUSSION. — The distinctive features of *T. amplifolia* include the closely spaced (0.25 mm) transverse secondary veins on abaxial foliar surfaces (Fig. 1B), callose-thickened teeth at the abaxial

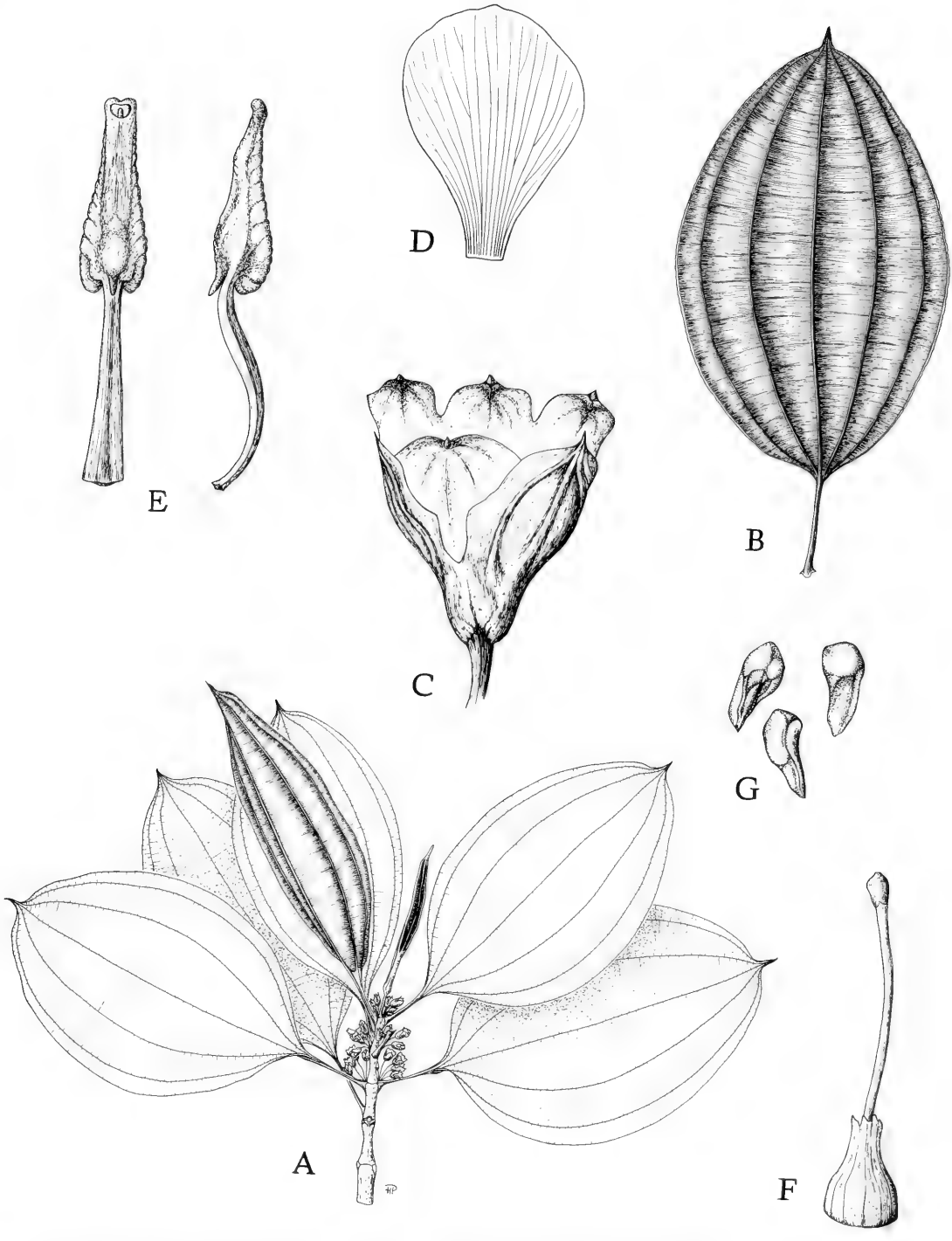

FIGURE 1. *Topobea amplifolia* Almeda. A. habit, ca. 1/5; B. representative leaf (abaxial surface, ca. 1/3; C. young fruiting hypanthium with decussate floral bracts, ca. 3; D. petals (adaxial surface), 2; E. stamens, dorsal view (left) and profile view (right), 5; F. stylar collar, style, and stigma, 3; G. seeds, 15. (A–G from *Herrera 5407*.)

apex of each calyx lobe (Fig. 1C), dorso-basally appendiculate anther connectives (Fig. 1E), and distally lobulate collar that envelops the style base (Fig. 1F). Among Mesoamerican species, it most resembles *T. multiflora* that differs in having hair tuft domatia on abaxial foliar surfaces, stipuliform nodal flaps, pink petals, and anther thecae that are laterally connate for at least half of their length. *Topobea amplifolia* is also superficially similar to *T. superba* Naudin of Colombia and *T. subscaberula* Triana of Colombia and Ecuador. The former differs by its nodal stipuliform flaps (1–2 mm long), hair tuft acarodomatia with roughened hairs 1–2.5 mm long where primary leaf veins diverge from one another abaxially, secondary transverse veins spaced 1.5–4 mm apart, and anther thecae that are laterally coherent for about half of their length. *Topobea subscaberula* differs from *T. amplifolia* in having young leaves and pedicels that are moderately but caducously puberulous with pinoid hairs 0.1–0.2 mm long, primary leaf vein divergence (abaxial) covered with roughened hairs about 1 mm long, secondary transverse veins spaced 2–2.5 mm apart, apically obtuse outer floral bracts, and an ovary apex that is elevated into a broad crateriform dome but not elaborated into a lobulate collar.

ETYMOLOGY. — The epithet *amplifolia* is derived from the Latin words *amplus*, ample or large, and *folius*, -leaved, in reference to the large leaves of this species.

4. *Topobea brenesii* Standl., Field Mus. Nat. Hist., Bot. Ser. 18:842. 1938.

TYPE. — COSTA RICA. Alajuela: La Palma de San Ramón, 1250 m, 13 Mar. 1929, *Brenes 6732* (holotype: F!; isotypes: CR!, NY!).

Epiphytic shrub 2–4 m tall. Uppermost branchlets rounded-quadrate becoming rounded with age, the uppermost internodes, young vegetative buds, pedicels, floral peduncles, floral bracts (especially abaxial surfaces), hypanthia, and calyx lobes copiously covered with a caducous mixture of elongate roughened hairs and less conspicuous stellulate or branlike hairs, the upper cauline nodes copiously setose with mostly smooth or sparingly roughened hairs. Mature leaves of a pair equal to somewhat unequal in size; petioles 0.2–0.7 cm long; blades coriaceous, 4.5–14 × 2.1–6.7 cm, obovate to elliptic, the apex rounded to obtuse or acute, the base broadly rounded to truncate, margin entire, blade 3-nerved or if 3-plinerved then the inner pair of primary veins diverging from the median vein 0.6–1 cm above the blade base (on abaxial surface), the transverse secondary veins spaced 1.5–3 mm apart at the widest portion of the blade, the blade adaxially covered with a sparse cover of elongate roughened and branlike hairs but commonly glabrous at maturity, abaxially sparsely covered with elongate roughened and branlike hairs especially on the elevated primary veins. Flowers erect, 1 to 3 in each leaf axil of distal branches; peduncles 0.2–1.3 cm long. Floral bracts closely enveloping hypanthium and strongly undulate-recurved apically; outer bracts 8–9 × 6.5–7 mm, free or fused basally for 0.5–1 mm, broadly oblong; inner bracts 9–10 × 13–14 mm, fused basally for 7–8 mm, semicircular. Hypanthium (at anthesis) campanulate, 7–8 × 7–8 mm. Calyx tube 3–4 mm long, erect and cupulate to campanulate; calyx lobes 4 × 4–6 mm, oblong and rounded at the recurved apex. Petals 6, glabrous, 1–1.5 × 0.5–1.4 cm, pale pink, obovate. Stamens 12; filaments 4–6 mm long, declinate and glabrous; anthers free, 4.5–5.5 × 1 mm, yellow, each opening by 2 divergent, dorsally-inclined pores; connective thickened dorsally and prolonged dorso-basally into a horizontally divergent or recurved knobby appendage 0.5 mm long. Ovary wholly superior, 6-locular, elevated at the glabrous apex into a lobulate rimlike collar that forms a wide circle around the stylar scar. Style glabrous, 1.2–1.4 cm long; stigma punctiform. Berry 1–1.2 × 1–1.2 cm. Seeds narrowly ovoid to cuneate, 1–1.25 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Endemic to Costa Rica where it is local and uncommon in cloud forests of the Cordillera de Tilarán and adjacent slopes southeast to the San Ramón region and east to the western slopes of Volcán Viejo in the Cordillera Central at 950–1560 m. Collected in

flower from January through April, in fruit from January through April, July, August and probably intervening months.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: Cantón de San Ramón. Los Angeles, Colonia Palmareña. Cuenca media de Río San Lorenzo, camino a la mina de yesa, 10°12′50"N, 84°35′15"W, 20 Feb. 1991, *Herrera et al. 4918* (CAS, CR, INB, MO): Cantón de San Carlos, Zapote, 31 Oct. 1938, *A. Smith 1306* (CAS, NY). Puntarenas: Cordillera de Tilarán. Selectively logged pasture known locally as the Bull Pen about 0.5–1 km downslope from Monteverde Cloud Forest Reserve Station, 29 Feb. 1992, *Almeda & Daniel 7185* (CAS, CR).

DISCUSSION. — This species is known only from the Cordillera de Tilarán south and east to the San Ramon and Volcán Viejo regions of Costa Rica. It is easily recognized by its completely superior ovary, leaf blades that are rounded to truncate basally, conspicuously appendiculate anther connectives, and undulate-recurved floral bracts and calyx lobes.

5. *Topobea calophylla* Almeda, Proc. Calif. Acad. Sci. 43:281. 1984.

TYPE. — PANAMA. Veraguas: 5 mi. W of Santa Fé on road past Escuela Agricola Alto Piedra on Pacific side of divide, elev. 800–1200 m, 18 Mar. 1973, *Croat 23000* (holotype: CAS!; isotype: MEXU!, MO!, US!).

Coarse epiphytic shrub. Upper branches rounded to subquadrate. Distal internodes, vegetative buds, peduncles, and floral bracts covered with a hirsute indument of ferrugineous barbellate hairs mostly 3–9 mm long. Mature leaves of a pair somewhat unequal in size; blades firmly chartaceous to coriaceous, 14.5–37.5 × 8.6–17.8 cm, elliptic-ovate, 5–7-nerved, the elevated transverse secondary veins spaced 4–7 mm apart at the widest portion of the blade, adaxially glabrous, abaxially moderately hirsute with barbellate hairs mostly 1–3 mm long, the apex abruptly caudate-acuminate, the base rounded to subcordate, the margin inconspicuously dentate. Flowers erect to widely spreading, paired or borne in clusters of three to four in leafy axils of distal branches; peduncles 2.8–4 cm long. Floral bracts foliaceous, entire, 2–5-nerved, free, each pair closely subtending one another or separated on the peduncle by a distance of 3–4 mm. Outer bracts 1.7–2.3 × 1.5–1.7 cm, elliptic-ovate, the apex acuminate; inner bracts 1.6–1.9 × 1.3–1.7 cm, elliptic-ovate, the apex acute to acuminate. Calyx lobes lance-triangular, 14–17 × 5–6 mm. Petals 6, glabrous, entire but sparingly glandular-ciliate, 2 × 1 cm, reportedly pink, ± spatulate, the apex acute to obtuse. Stamens 12, filaments 5 × 1.5 mm, strongly declinate; anthers laterally connate for a good portion of their length, 8 × 1.5 mm, yellow (?), linear-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally near the filament insertion into a blunt callosity. Ovary completely inferior, 6-locular, apex prolonged into a glandular-puberulent fluted cone and stylar collar mostly 7–9 mm long. Style glabrous, 11–14 × 1 mm; stigma capitellate to truncate, the actual surface appearing somewhat crateriform. Mature berry not seen.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests and cloud forests from the vicinity of Fortuna Dam to the Santa Fé region of Veraguas disjunct to Comarca de San Blas in north-central Panama at 10–1200 m. Collected in flower from February through August, in fruit during March and July.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Bocas del Toro: vicinity of Fortuna Dam, below pass on Chiriquí Grande road, 8°45′N, 82°15′W, 27 June 1986, *McPherson 9714* (CAS, MO, PMA). Comarca de San Blas: Cerro Brewster, 9°18′N, 79°16′W, 21 Apr. 1985, *de Nevers et al. 5384* (CAS, MO): Río Taindi (Taimdi of maps), 6 km above confluence with Río Mandinga, 9°25′N, 79°11′W, 5 Apr. 1986, *de Nevers & Herrera 7638* (CAS, MO, PMA). Veraguas: Distrito de Santa Fé, alrededores del Río Primer brazo de Ulaba, 8°33′N, 81°07′W, 6 Jul. 1996, *Galdames et al. 3145*

(CAS, SCZ): Boca de Concepción, in Golfo de los Mosquitos, forest near river, 8°50′N, 81°00′W, 6 Aug. 1987, *McPherson 11394* (CAS, MO, PMA).

DISCUSSION. — This large-leaved Panamanian endemic has an unusual indument of long, spreading, barbellate hairs on distal internodes, young buds, peduncles, and floral bracts. This together with the laterally connate anther thecae, and glandular-puberulent fluted ovary cone and stylar collar at the ovary apex make it a standout among Mesoamerican species. For an illustration of this species see Almeda (1984:280).

6. *Topobea calycularis* Naudin, Ann. Sci. Nat. Bot. 3, 18:149. 1852.

TYPE. — MEXICO. Chiapas: Zuluzuchiapas, *Linden 650* (holotype: P!, fragment at BR!; isotype: K!).

Epiphytic shrub or tree 2–13 m tall. Uppermost branchlets quadrate and carinate on the angles becoming rounded with age, essentially glabrous throughout, the young floral bract margins, floral buds, and calyx rim sometimes covered with a caducous furfuraceous indument of stellulate or matted fimbriate branlike hairs. Mature leaves at a node somewhat unequal in size (the larger sometimes twice the size of the opposing one); petioles 1.3–4 cm long; blades coriaceous, 4.5–17.2 × 2.1–10 cm, elliptic to elliptic-obovate, the apex abruptly acuminate, the base acute, the margin entire, 3–5-plinerved with the innermost primaries diverging from the median vein 0.4–1.5 cm above the blade base (on abaxial surface) with hair tuft acarodomatia that are sparsely to moderately covered with robust shaggy hairs (0.25–0.5 mm long) in the angles formed with the median vein, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary or in clusters of 2 to 4 in each leaf axil of distal branches; peduncles 4–9 mm long. Floral bracts ± concave and closely enveloping the hypanthium; outer bracts 3–5 × 4–5 mm, fused basally for 1.5–2 mm, rounded-triangular to ovate; inner bracts 3.5–4 × 4–5 mm, free but partly imbricate, semicircular. Hypanthium (at anthesis) campanulate, 4.5 × 4.5 mm. Calyx tube 2–3 mm long, erect and cupulate, calyx broadly flattened into low apiculate undulations 0.5 × 2 mm. Petals 6, glabrous, 1–1.3 0.3–0.6 cm, white, narrowly obovate, the margin fimbriate. Stamens 12; filaments 6–7 mm long, declinate and glabrous; anthers free, 5–7 × 0.75 mm, yellow, each with 2 confluent, dorsally-inclined pores at the apex; connective thickened dorsally, unappendaged or with a minute dorso-basal callosity. Ovary 1/3 inferior, 4-locular, apex glabrous, stylar scar evident but not elevated into a prominent cone or stylar collar. Style glabrous, 1–1.5 cm long; stigma punctiform. Berry 0.9–1.1 × 0.8–1 cm. Seeds narrowly pyriform to narrowly ovoid, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Often common in lowland and montane rainforests from Chiapas, Mexico east to Guatemala (Izabal) at 320–1625 m. Collected in flower from January through May and in November and December, in fruit from February through August, December and probably most intervening months.

REPRESENTATIVE SPECIMENS EXAMINED. — GUATEMALA. Alta Verapaz: Chapultepec Farm, 62 km beyond Cobán on Sebol road, 20 May 1964, *Contreras 4730* (CAS, LL); Pansamalá, Feb. 1887, *von Tuerckheim 1135* (DS, NY, US). Izabal: Municipio El Estor La Cumbre, al NE del Estor, 17 Jul. 1988, *Tenorio et. al. 14516* (CAS, MEXU). MEXICO. Chiapas: Municipio La Trinitaria, Lagos de Montebello National Park, 19 Nov. 1980, *Breedlove & Almeda 47572* (CAS, MEXU); Municipio of Ocosingo 70 km SW of Palenque on road to Ocosingo along the Jol Uk' um, *Breedlove & Almeda 48335* (CAS, MEXU); Municipio of Peltalcingo, slope of Ahk' ulbal Nab above Peltalcingo, *Breedlove 50462* (CAS, MEXU): Municipio of Independencia, 45–50 km E of Lagos de Montebello National Park on road to Ixcán from Santa Elena, *Breedlove & Almeda 57731* (CAS, MEXU); Municipio de Tila, pie del Cerro Acavaina, *Ton 7347* (CAS, MEXU); Municipio Margaritas, Col. Maravilla, Tenejapa, *Ton 9084* (CAS, MEXU).

DISCUSSION. — *Topobea calycularis* is distinguished by its hair tuft foliar domatia, calyx lobes that consist of low apiculate undulations, essentially unappendaged anther connectives, and its 4-locular ovary. Only one collection examined, *Tenorio et al. 14516,* CAS, lacks good development of hair tuft domatia. *Topobea laevigata* is the only other species with which *T. calycularis* might be confused. In *T. laevigata*, the domatia, when produced, are slitlike pit domatia at the abaxial margin of the leaf blade near the petiole-laminar junction, and the ovary is consistently 6-locular.

For Costa Rican specimens erroneously identified as *T. calycularis*, see the discussion under *T. multiflora*.

7. *Topobea dimorphophylla* Almeda, sp. nov. (Fig. 2)

TYPE. — COSTA RICA. Heredia: along Río Peje about 0.5 km SW of back end of Vargas property; approximately in the area where an imaginary line drawn between Magsasay (colonia penal) and Puerto Viejo de Sarapiquí would cross the Río Peje, 20 Feb. 1982, *Hammel 11217* (holotype: CAS!; isotypes: CR!, DUKE!, INB!, MO!, US!).

Frutex hemiepiphyticus. Ramuli sicut pedunculi folia inflorescentia hypanthiaque pilis 1.5–3(–9) mm longis induti. Folia in quoque pari dimorpha papyracea distanterque denticulata 3–5-plinervata. Folia maiora: lamina (5.5–)9–15.5 × 2–7.5 cm elliptica vel elliptico-ovata apice caudato-acuminata basi rotundata. Folia minora: lamina 0.9–1.7 × 0.6–1 cm ovata vel subcordata apice caudoto-acuminata basi cordata. Flores 6-meri in quoque nodo superiori singuli, pedunculis 0.8–0.9(–1.4) cm longis; bracteae exteriores omnino liberae 0.5–0.7 × 0.3–0.5 cm elliptico-ovata apice acuto; bracteae interiores 0.5–0.6 × 0.4–0.5 cm ovatae apice acuta ca. 3.5–5 mm coalitae. Calycis tubus 0.5–0.75 mm longus, lobis 0.7–0.9 × 0.2–0.3 cm. Petala 5–6 × 5 mm obovata vel subrotundata. Antherarum thecae 1.5–3 × 0.5–0.75 mm inter se non cohaerentes, dorsaliter biporosae; connectivum dorsaliter supra thecarum basim tuberculatum. Ovarium 6-loculare et onmino inferum apice glabro (cono et collo non evoluto).

Secondary hemiepiphytic shrub with main stems growing vinelike up trunks of host trees and secondary branches either drooping or horizontally spreading to 1–3 m long. Uppermost branchlets mostly terete, the older branches covered with numerous short root-like protuberances (adventitious roots?). Cauline internodes, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes copiously hirsute with rusty brown hairs mostly 1.5–3(–9) mm long. Mature leaves of a pair markedly unequal in size; blades coarsely papery when dry, the larger one at each node (5.5–)9–15.5 × 2–7.5 cm, elliptic to elliptic-ovate, the apex caudate-acuminate, the base broadly rounded, the margin denticulate (sometimes remotely so), 3-plinerved with an additional ill-defined intramarginal pair, the innermost pair of primary veins diverging from the median vein 2–3 mm above the blade base, the ± transverse secondary veins spaced 2–5 mm apart at the widest portion of the blade on the abaxial surface; petiole 5–17 mm long; the smaller blade 0.9–1.7 × 0.6–1 cm, ovate to subcordate, apex short caudate-acuminate, base cordate, margin entire, 3-nerved, the transverse secondary veins not evident on the abaxial surface; petiole barely prolonged or up to 2 mm long. Flowers erect, solitary in each axil of uppermost leaves; peduncles 0.8–0.9(–1.4) cm long. Floral bracts green and entire; outer bracts 0.5–0.7 × 0.3–0.5 cm, free, elliptic-ovate, the apex acute; inner bracts fused basally for 3.5–5 mm to form a bowl-like collar, the free lobes broadly ovate to deltoid, 0.5–0.6 × 0.4–0.5 cm. Hypanthium at anthesis 4–5 mm long to the torus and 4–5 mm in diameter. Calyx tube 0.5–0.75 mm long, ± erect at anthesis. Calyx lobes (on young fruit) deltoid at base but abruptly tapered to narrow linear upright segments 0.7–0.9 cm long and 0.2–0.3 cm wide at the base between sinuses. Petals 6, glabrous, 5–6 5 mm, translucent white, thin and translucent when dry, broadly obovate to subrotund, the apex ± rounded, the base shortly clawed, entire. Stamens 12, free and isomorphic; filaments 1.5–3 mm long,

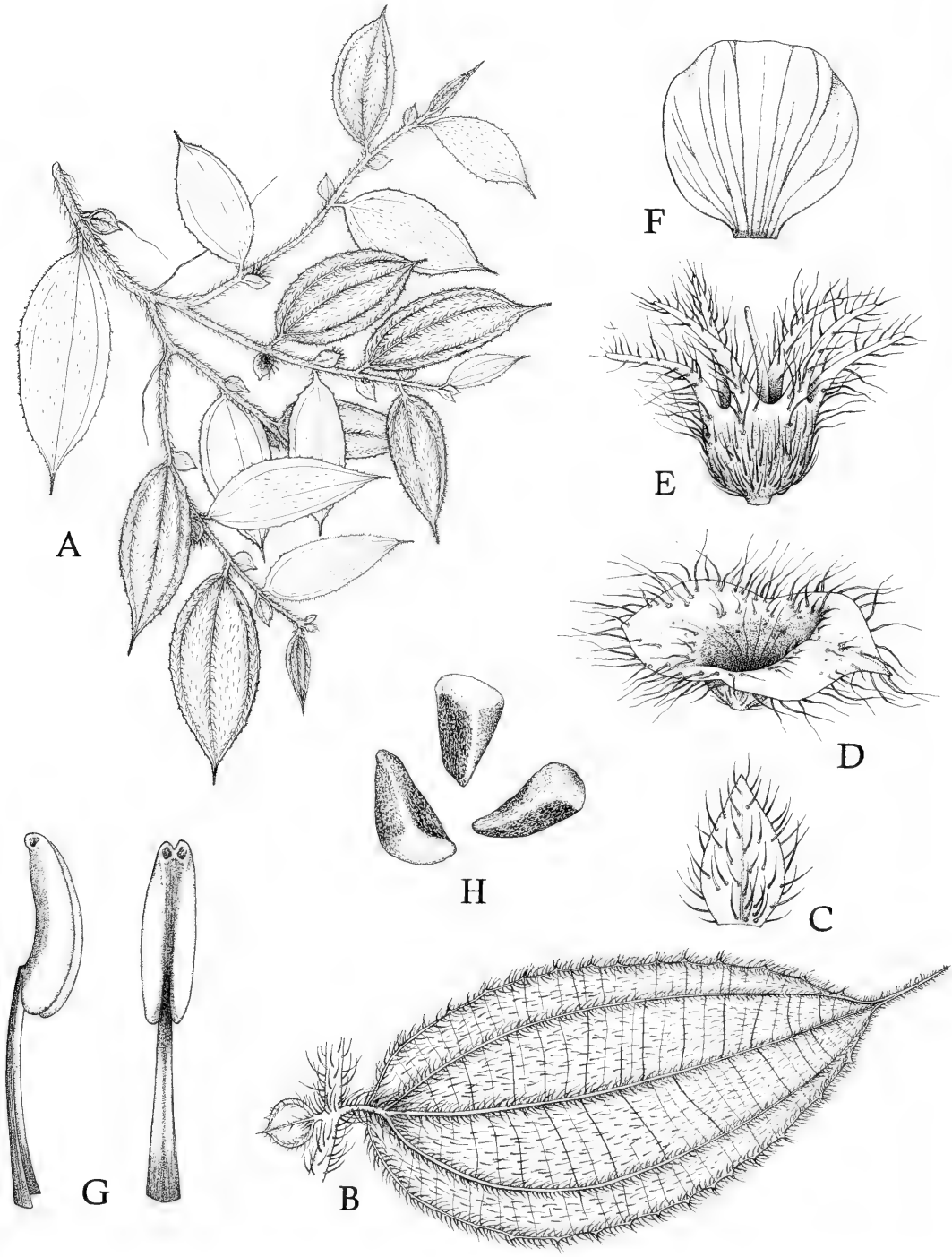

FIGURE 2. *Topobea dimorphophylla* Almeda. A. habit, 2/5; B. foliar dimorphism at a node, 2/3; C. outer floral bract, 5; D. inner floral bracts, 4; E. hypanthium (floral bracts removed). 3; F. petal (adaxial surface), ca. 5; G. stamens, profile view (left) and dorsal view (right) 12; H. seeds, 15. (A from *Gomez et al. 21127*; B from *Grayum et al. 7932*; C–G from *Hammel 11217*; H from *Hammel & Trainer 13241*.)

glabrous; anthers 1.5–3 × 0.5–0.75 mm, yellow, oblong, each with 2 confluent, dorsally-inclined pores at the apex; connective thickened dorsally and barely elevated into a blunt callose knob dorso-basally. Ovary completely inferior, 6-locular, glabrous at the apex which is barely elevated at the stylar scar. Style glabrous, declinate, 9–10 mm long; stigma punctiform. Berry red at maturity, 9–10 × 9–10 mm. Seeds 1 mm long, brown, cuneate to narrowly pyriform, testa smooth.

DISTRIBUTION AND PHENOLOGY. — Local and uncommon in the Caribbean slopes and lowlands of Costa Rica from the Puerto Viejo region south to the Cordillera de Talamanca (Limón) at 100–1000 m. Collected in flower and fruit from October through March and in June and July.

PARATYPES. — COSTA RICA. Alajuela: Reserva Biológica Monteverde Río Peñas Blancas, Laguna y Quebrada Celeste, 10°20′N, 84°41′W, 850 m, 4 Nov. 1989, *Bello 1459* (CAS); Reserva Forestal de Arenal, Quebrada San Gerardo, Río Caño Negro, 10°23′N, 84°48′W, 800 m, 18 Feb. 1990, *Bello 1909* (MO). Cartago: Valle Escondido, 720 m, 31 Mar. 1966, *Schnell 641* (CR, US). Heredia: Parque Nacional Braulio Carrillo, La Virgen, Sarapiquí, Sendero Transecto, 10°16′N, 84°05′W, 700 m, 11 Dec. 1988, *Ballestero 53* (CAS, CR, INB). Parque Nacional Braulio Carrillo, Fila Carrillo – Sendero La Botella, 400–800 m, 15 Feb. 1984, *Gomez et al. 21127* (CAS, CR); Parque Nacional Braulio Carrillo, forest between Río Peje and Río Sardinalito on Atlantic slope of Volcán Barva, 10°17.5′N, 84°05′W, 700–800 m, 14 Nov. 1986, *Grayum & Herrera 7895* (CAS, CR); Finca La Selva, OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí 100 m, 18 Jul. 1982, *Hammel & Trainer 13241* (CAS, CR, DUKE). Limón: Cantón de Talamanca, Bratsi; Alto Lari, Entre Surayo y Dapari, 50 m N de la desembocadura del Río Dapari (Pare), junto al Río Lari, 9°25′10"N, 83°03′00"W, 300 m, 25 Feb. 1992, *Aguilar & Schmidt 961* (INB, MO); Suerre, Santa Clara, 300 m, Feb. 1896 (no exact day), *Donnell-Smith 6554* (F, US); Zona Protectora Barbilla on W side of plateau separating headwaters of N fork of Río Danta from headwaters of Quebrada Barreal, Río Barbilla drainage (SE of Siquirres), 10°05′N, 83°28.5′W, 600–660 m, 11 Jan. 1987, *Grayum et al. 7932* (CAS, CR, MO); Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut. Quebrada innominada, margen derecha del Río Dapari 9°24′20"N, 83°05′35"W, 1000 m, 11 Mar. 1992, *Herrera 5294* (CAS, CR, INB, MO).

DISCUSSION. — *Topobea dimorphophylla* has leaf blades that are markedly unequal in size at each node and copiously pubescent on both surfaces (Fig. 2A). It is most like *T. intricata* which has leaf blades that are only somewhat unequal in size at each node, longer floral peduncles (3.5–5.2 cm vs. 0.8–1.4 in *T. dimorphophylla*), and free (vs. basally fused for 3.5–5 mm) floral bracts. In habit, indument details, and the pronounced foliar dimorphism at each node, *T. dimorphophylla* is also similar to *T. tetramera* which is readily separated by its 4-merous flowers, 4-locular ovary, completely free inner and outer floral bracts, and truncate anther pores.

One collection of *T. dimorphophylla*, *Donnell-Smith 6554,* was erroneously cited as a representative specimen of *Clidemia costaricensis* Cogn. & Gleason ex Gleason (Gleason 1939:126). This appears to have been an inadvertent error because this specimen, which is not mixed with *C. costaricensis,* has young fruiting hypanthia with attached floral bracts that Gleason surely would have recognized as something other than *Clidemia*.

ETYMOLOGY. — The epithet *dimorphophylla* is derived from the Latin word *dimorphus,* having two forms, and the Greek word *phyllus*, relating to leaves, in reference to the pronounced difference in leaf size at each node.

8. *Topobea dodsonorum* Wurdack, Phytologia 38:304. 1978.

TYPE. — ECUADOR. Los Ríos/Pichincha border: near La Centinela at Km 12 on road from Patricia Pilar to Flor de Mayo, Montaña de Ila, 600 m, 16 Jul.–11 Aug. 1977, *Dodson & Dodson 6752* (holotype: US!; isotype: MO, SEL).

Viny epiphytic shrub often with pendent branches 1–1.5 m long. Uppermost branchlets terete with elevated interpetiolar ridges. Upper internodes, juvenile leaves, peduncles, bracts, and calyx lobes caducously scurfy-puberulent with branlike or stellulate hairs. Mature leaves of a pair markedly dimorphic in size; blades subcoriaceous, the larger at each node 7.4–19.5 × 3.6–9.5 cm, elliptic to ovate or subcordate, the apex acuminate, the base broadly rounded and subpeltate, the margin entire, 5–7-nerved with well-developed pocket domatia formed at the point where the innermost primaries diverge from the median vein, the transverse secondary veins spaced 1–2 mm apart at the widest portion of the blade on the abaxial surface; petiole 3–5 mm long; the smaller blade 1.4–5 × 0.8–2.8 cm, narrowly elliptic, the apex acuminate, the base rounded, the margin entire, 3–5-nerved with domatia like those of the larger leaves but smaller in all dimensions and less conspicuous, the transverse secondary veins not conspicuous on the abaxial surface; petioles 0.1–1.3 mm long. Flowers erect, solitary or borne in clusters of 2 to 3 in each leaf axil of distal branches; peduncles 1–2.5 cm long. Floral bracts fused basally for 0.5–1 mm and much shorter than the hypanthium and calyx; outer bracts 2–2.5 × 2 mm, ovate; inner bracts 2 × 2 mm, oblate to semicircular. Hypanthium (at anthesis) campanulate, 4 × 3–4 mm. Calyx tube 1–1.5 mm long; calyx lobes 1–1.8 × 2 mm, triangular. Petals 6, glabrous, 5–6 × 2–3.5 mm, yellow, yellow-brown or greenish brown, oblong-obovate to subspatulate with a blunt acute apex. Stamens 12; filaments 2–3.5 mm long, declinate and glabrous; anthers free, 1.75–2 × 0.5 mm, yellow, linear-oblong to somewhat subulate, each opening by a solitary, dorsally-inclined apical pore; connective thickened dorsally and prolonged dorso-basally into a blunt appendage 0.25 mm long. Ovary 1/2-inferior, 4-locular, somewhat elevated and rounded up to the stylar scar but lacking a cone and collar. Style glabrous, 7 mm long; stigma punctiform. Berry 5–7 × 6–7 mm, greenish flushed with maroon at maturity. Seeds cuneate to narrowly pyriform, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Often locally common in rainforests and low elevation cloud forests of western and north-central Panama and eastern Ecuador at 540–1200 m. Flowering collections have been made in January, February, April, June, July and September, fruiting during these same months and in November.

REPRESENTIVE SPECIMENS EXAMINED. — PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve in Fortuna along trail to hydrological station along Rio Hornito, 8°45′N, 82°5′W, 20 Jan. 1989, *Almeda et al. 6351* (CAS, PMA). Comarca de San Blas: Cerro Brewster, 9°18′N, 79°16′W, 21 Apr. 1985, *de Nevers et al. 5459* (CAS, MO, PMA).

DISCUSSION. — The diagnostic features of *T. dodsonorum* include its pronounced foliar size dimorphism at each node, well-developed foliar pocket domatia, triangular calyx lobes, and 4-locular ovary. In his account of this species for Flora of Ecuador, Wurdack (1980) stated that domatia are lacking in the smaller leaf at each node. Although the domatia on the smaller leaf are smaller in all dimensions, I have found them to be present on all specimens examined from throughout the range of the species.

9. *Topobea fragrantissima* Almeda, Proc. Calif. Acad. Sci. 46:318. 1990.

TYPE. — PANAMA. Chiriquí: vicinity of Fortuna Dam, along trail across valley of Río Hornito, elev. 1100–1250 m, 12 Mar. 1988, *Almeda et al. 6086* (holotype: CAS!; isotypes: CR!, F!, MO!, PMA!, TEX!, US!).

Epiphytic or terrestrial shrubs or small trees 1.5–4 m tall. Distal branchlets subquadrate and glabrous with interpetiolar ridges or lines. Vegetative buds and young leaves sparingly and caducously lepidote-furfuraceous. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout, 1.5–5.5 cm long and 1.6–3 cm wide, elliptic to elliptic-obovate, the apex acuminate, the base acute, the margin entire, 3-nerved or 3-plinerved abaxially with an additional submarginal pair of inconspicuous veins, secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of upper branches; peduncles 2–3 cm long, glabrous; outer bracts 5–11 × 3–5 mm, free, elliptic or rarely varying to obovate, glabrous, apex rounded; inner bracts 4–6 × 4–5 mm, free, obovate, glabrous, apex broadly rounded. Calyx tube 1 mm long; calyx lobes 1 mm long and 1–1.5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire but sometimes roughened along interlobe sinuses, glabrous on both surfaces. Petals 6, glabrous, 1.2–1.4 × 1–1.2 cm, white flushed with pink unilaterally, obovate, apically rounded, entire. Stamens 12, free and declined to one side of the flower opposing the style; filaments 5–6 mm long; anthers 3.5–5 mm long, 1 mm wide, yellow, linear-oblong and tipped with a solitary, dorsally-inclined pore; connective modified dorso-basally into a deflexed spur 0.25 mm long. Ovary 1/2-inferior, 4-locular, glabrous at the apex but not elevated into a cone or collar. Style declinate and sigmoid, glabrous, 10–11 mm long; stigma punctiform. Berry 7–10 × 10 mm. Seeds clavate to narrowly pyriform or pyramidate, 1 mm long.

DISTRIBUTION AND PHENOLOGY. — Local and uncommon in cloud forests from the Boquete region of W Panama (Chiriquí) to the Fortuna Dam region and E to Cerro Colorado at 1000–1300 m. Flowering and fruiting material has been collected in January, March, April, and July.

REPRESENTATIVE SPECIMENS EXAMINED. — Chiriquí: Edwin Fabrega Dam and Reserve along trail to Río Hornito above Los Planes, 8°45′N, 82°15′W, 18 Jan. 1989, *Almeda et al. 6309* (CAS, MO, PMA); Monte Rey, above Boquete, 21 Jul. 1971, *Croat & Porter 15692* (CAS, MO). Chiriquí/Bocas del Toro border; windswept cloud forest off the road to Cerro Colorado, 26 Jan. 1989, *Almeda et al. 6418* (CAS, CR, DUKE, MO, PMA, US).

DISCUSSION. — The outstanding features of *T. fragrantissima* are its completely glabrous leaves with closely spaced (0.25 mm) transverse secondary veins on abaxial foliar surfaces, linear-oblong anthers with solitary pores, and 4-locular ovary. Live flowers of this species produce a pleasant perfume-like fragrance, but nothing is known about its role in attracting pollinators. For illustrations of this species see Almeda (1990:319) and Plate 1.

10. *Topobea gerardoana* Almeda, sp. nov. (Fig. 3)

TYPE. — COSTA RICA. Limón. Cordillera de Talamanca between Quebrada Kuisa and Río Lari, 09°20′25"N, 83°13′45"W, elev. 2100 m, 17 Mar. 1993, *Herrera 5914* (holotype: CAS!: isotypes: CR, INB!, MO).

Frutex epiphyticus. Petioli 1.5–3.6 cm longi; lamina 6–12.5 × 2.1–5.5 cm elliptico-obovata vel elliptica apice acuminata basi acuta, supra glabra, subtus sicut ramuli sparsiuscule pilis induti, 3–5-plinervata, nervis secundariis 1–3 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedunculis 1.3–2 cm longis; bracteae exteriores 7–8 × 5–6 mm ovatae vel elliptico-ovatae ca. 2–3 mm coalitae apice acuto vel rotundato; bracteae interiores 6–7 × 6 mm omnino liberae. Calycis tubus 0.5–0.75 mm longus, lobis 5 mm longis. Petala alba, 1–1.2 × 0.8–1 cm obovata apice mucronato. Filamenta 3–3.5 mm longa; antherae 3 × 1 mm inter se non cohaerentes, poro unico dorsaliter inclinato; connectivum ad basim dorsaliter dente 0.25 mm longo descendenti armatum. Stylus 1–1.1 cm; ovarium 6-loculare et 2/3 inferum apice glabro (cono ca. 1 mm alto).

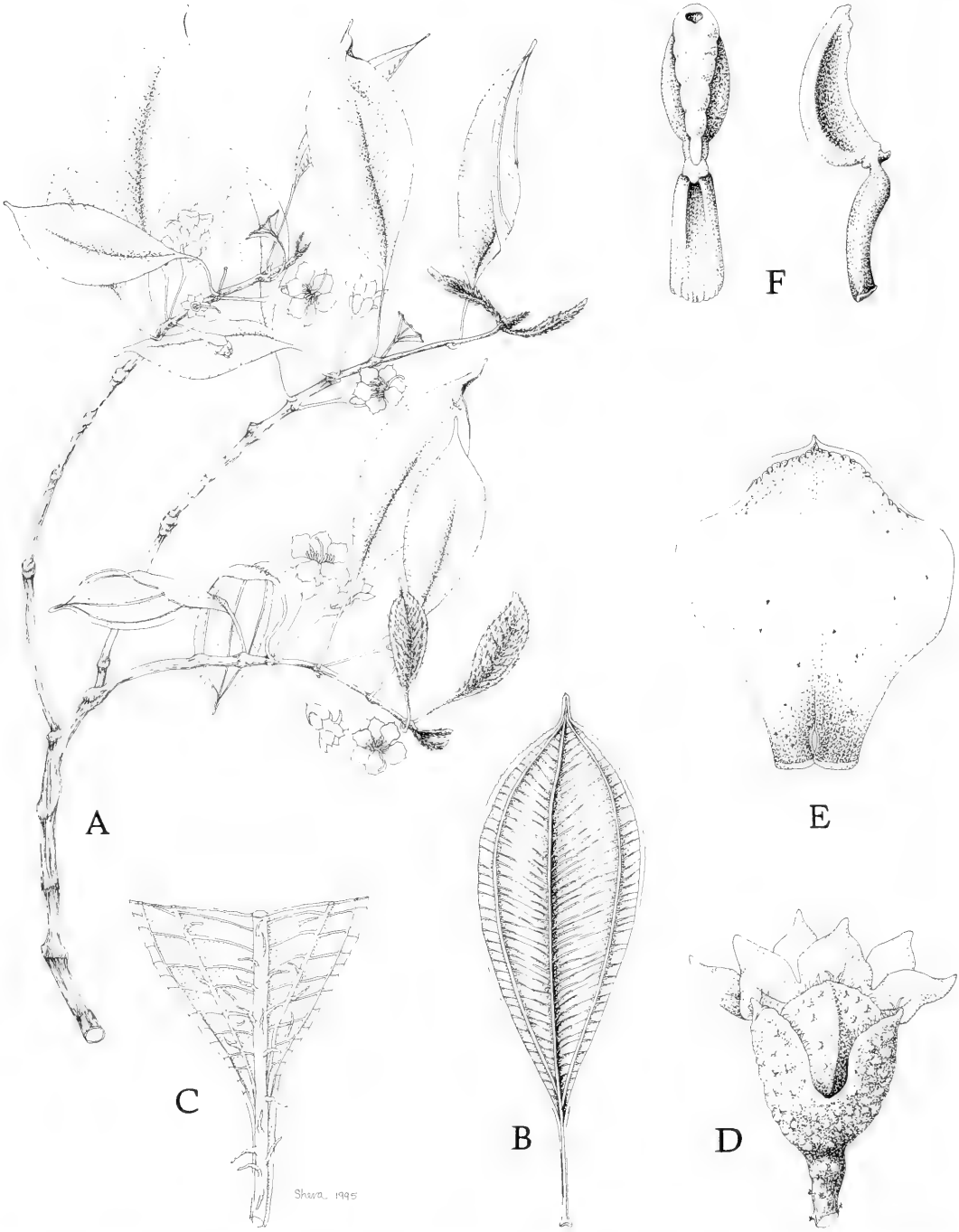

FIGURE 3. *Topobea gerardoana* Almeda. A. habit, ca. 1/3; B. representative leaf (abaxial surface), 3/5; C. enlarged leaf base (abaxial surface) showing indument detail, ca. 1; D. young fruiting hypanthium with decussate floral bracts, 3; E. petal (adaxial surface), 4; F. stamens, dorsal view (left) and profile view (right), ca. 7. (A-F from *Herrera 5914*.)

Epiphytic shrub. Uppermost internodes, vegetative buds, and abaxial surfaces of some mature leaves sparingly covered with a caducous indument of rusty brown subulate and conic hairs. Mature leaves of a pair mostly unequal in size; petioles 1.5–3.6 cm long; mature blades subcoriaceous, 6–12.5 cm long and 2.1–5.5 cm wide, elliptic-obovate to elliptic, the apex acuminate, the base acute, the margin entire to obscurely denticulate, 3–5-plinerved with the innermost pair of primary veins diverging from the median vein 1–5 mm above the blade base, the subparallel secondary veins spaced 1–3 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of uppermost branches; peduncles 1.3–2 cm long, subquadrate and lenticellate. Floral bracts entire, glabrate or sparingly covered abaxially with a lanate indument, the margins ciliate or fimbriate; outer bracts 7–8 × 5–6 mm, fused at the base for 2–3 mm, concave, ovate to elliptic-ovate, the apex bluntly acute to ± rounded; inner bracts 6–7 × 6 mm, free, oblong to oblong-ovate, the apex rounded. Hypanthium (in young fruit) suburceolate. Calyx tube 0.5–0.75 mm long; calyx lobes (in young fruit) erect, 5 mm long and 3 mm wide at the base, triangular, irregularly and sparingly covered with a caducous lanate indument on both surfaces. Petals 6, 1–1.2 × 0.8–1 cm, white, obovate, apex mucronate, entire. Stamens 12; filaments 3–3.5 × 1.5 mm, complanate, glabrous and tapering to the apex; anthers 3 mm long and 1 mm wide, free, yellow, oblong and somewhat sickle-shaped in profile view with a solitary dorsally declined apical pore; connective thickened dorsally and modified dorso-basally into an appendage 0.25 mm long or less. Ovary 2/3-inferior, 6-locular, apex glabrous and elevated into a blunt cone about 1 mm high. Style straight, glabrous, 1–1.1 cm long; stigma punctiform. Immature berry 8 × 7–8 mm. Seeds narrowly pyriform, 1 mm long, tan with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Presently known only from cloud forests in southeastern Costa Rica in a region upslope and south of the Valle de Talamanca at 1900–2100 m. The two known collections were made in March. One is in flower, the other is in young fruit.

PARATYPE. — COSTA RICA. Limón: Cantón de Talamanca. Bratsi, Amubri, Alto Lari, Kivut. Ridge between Río Lari and Río Dapari, 9°22′45"N, 83°06′15"W, 25 Mar. 1992, *Herrera 5492* (CAS, INB).

DISCUSSION. — This little-known Costa Rican endemic has well-defined triangular calyx lobes that are irregularly and sparingly covered with a caducous lanate indument (Fig. 3D), free anther thecae that are somewhat sickle-shaped in profile view with a solitary apical pore (Fig. 3F), and an anther connective that is modified dorso-basally into an appendage 0.25 mm long or less. *Topobea gerardoana* does not appear to be particularly close to any congener with single-pored anthers.

ETYMOLOGY. — This species is named for Gerardo Herrera, stellar collector of Costa Rican plants.

11. *Topobea intricata* Almeda, Brittonia 53:157. 2001.

TYPE: COSTA RICA. Cartago: Highway #224 on property of ICE hydroelectric plant (now Tapantí National Park) ca. 20–24 km E of the church in Orosí, elev. 1500–1800 m, 5 Jan. 1974, *F. Almeda et al. 2366* (holotype: CAS!; isotypes: BM!, CR!, DUKE!, INB!, MEXU!, MO!, NY!).

Epiphytic or terrestrial shrub 1–2 m tall with spreading branches to 3 m long. Uppermost branchlets rounded. Cauline internodes, vegetative buds, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes moderately to copiously hirsute with smooth ferrugineous hairs mostly 0.5–3(–6) mm long. Mature leaves of a pair typically unequal in size; blades thin and papery when dry, the larger one at each node 7.5–17.2 × 3.5–7.5 cm, the smaller one 1.8–10 × 1.7–5.4 cm, elliptic to elliptic-ovate, the apex acuminate to caudate-acuminate, the base obliquely obtuse to rounded, the margin denticulate to subentire (sometimes obscurely and remotely so), 3–5-plinerved with the innermost pair of primary veins diverging from the median vein 1–5 mm above the blade base, the transverse secondary veins spaced 2–6 mm apart at the widest portion of the blade. Flowers erect or

horizontally spreading, solitary in the axils of uppermost branches; peduncles 3.5–5.2 cm long, terete. Floral bracts green and entire; outer bracts 2.5–3.2 × 1.7–2.6 cm, free, ovate to subcordate, the apex acute to acuminate, trinerved; inner bracts 1.9–2.5 × 0.7–1 cm, the basal half closely appressed to but free from the hypanthium, narrowly elliptic-lanceolate, the apex acute to acuminate. Calyx lobes (at anthesis) linear oblong, 6–7 mm long and 1 mm wide at the ± deltoid base between sinuses. Petals 6, glabrous, 1.6–2.3 × 1.4–1.7 cm, white flushed with pink distally on the abaxial surface, thin and translucent when dry, obovate, apex rounded, base somewhat clawed, entire. Stamens 12; filaments 5–6.5 × 1 mm, declinate, complanate, glabrous; anthers free, 5–7.5 × 1 mm, yellow, oblong-subulate and incurved distally, each with 2 confluent, dorsally-inclined pores at the truncate apex; connective thickened dorso-basally into a blunt deflexed appendage 0.5–1 mm long. Ovary 1/2-inferior (at anthesis), 6-locular, glabrous at the summit which is elevated into a lobulate collar 1–1.5 mm high surrounding the style base. Style glabrous, 0.9–1.4 cm long; stigma punctiform. Berry red at maturity, 1–1.7 × 1.3–1.4 cm. Seeds mostly 1 mm long, beige, cuneate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Locally common in cloud forests of Tapantí National Park in central Costa Rica and the Fortuna region of western Panama at 1100–1800 m. Collected in flower from December through June, in fruit from March through July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Cartago: About 15 km S of Tapantí along new road on the E slope above the Río Grande de Orosí near the concrete bridge, 9°42′N, 83°47′W, 12–17 Dec. 1969, *Burger & Liesner 6810* (CAS, CR, F); Cantón de Paraíso, Parque Nacional Tapantí, Valle de Reventazón, Sendero Arboles Caidos, 09°45′00"N, 83°47′00"W, 21 July 1994, *Quesada 123* (INB). PANAMA. Bocas del Toro: Fortuna Dam area, along continental divide trail bordering Chiriquí Province, 08°45′04"N, 82°15′04"W, 10 Mar. 1988, *Almeda et al. 6048* (BM, CAS, CR, MEXU, MO, NY, PMA); 2 km W of continental divide along trail to elfin forest, 08°47′N, 82°13′W, 26 Mar. 1985, *Hampshire & Whitefoord 981* (BM, CAS). Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, 08°45′N, 82°18′W, 23 June 1994, *Croat & Zhu 76310* (CAS, MO); Fortuna Dam area, road from Gualaca to Chiriquí Grande on continental divide trail W of road, 08°45′N, 82°15′W, 18 Jan. 1986, *de Nevers & McPherson 6852* (CAS, MO); Road from Fortuna Lake to Chiriquí Grande on trail W of continental divide, 08°47′N, 82°13′W, 22 Mar. 1985, *Hampshire & Whitefoord 850* (BM); Cordillera Central, 7 Dec. 1996, *Montenegro 1585* (CAS, SCZ); Distrito Boquete, Fortuna Dam site along trail following continental divide, 8 Feb. 1985, *van der Werff & van Hardeveld 6707* (CAS, MO).

DISCUSSION. — *Topobea intricata* has a copious cover of ferrugineous hairs throughout, thin papery leaves, solitary floral peduncles, and ovate to subcordate outer floral bracts. It most closely resembles *T. dimorphophylla* in habit, pubescence details, leaf morphology, and petal color. For a comparison of these two species see the discussion under the latter. *Topobea intricata* is also superficially similar to *Blakea wilburiana* Almeda of central Panama. The latter has elliptic-lanceolate outer floral bracts, filiform to nearly acicular calyx lobes, and smaller anthers (4–5 × 1–2 mm) that are oblong and laterally compressed with ventrally-inclined (vs. dorsally-inclined) apical pores.

As noted in the protologue, what may be a regional variant or a closely related undescribed taxon, represented by *Herrera 6036* (CAS, INB) and *Herrera 2832* (CAS), has been collected on the Caribbean slopes of the Cordillera de Talamanca in southern Costa Rica. This entity, which is known from five gatherings, is similar to *T. intricata* in all details but has outer floral bracts that are uniformly elliptic and consistently smaller (1.3–1.5 × 0.8–1.5 cm). The known collections of *T. intricata* from geographically distant areas in Costa Rica and Panama are homogeneous morphologically. It is for this reason that I am reluctant to consider this distinctive population a mere variant without additional study. See Almeda (2001:158) for an illustration of this species.

12. *Topobea laevigata* (D. Don) Naudin, Ann. Sci. Nat. Bot. 3, 18:150. 1852.

Blakea laevigata D. Don, Mem. Wern. Nat. Hist. Soc. 4:327. 1823. TYPE. — MEXICO, without exact locality, *Sessé & Mociño s.n.* (BM! ex Herb. Lambert).

Epiphytic shrub or tree 5–10 m tall with a lateral spread of up to 8 m. Uppermost branchlets rounded-quadrate becoming rounded with age, essentially glabrous throughout, the young floral buds and peduncles sometimes covered with a caducous furfuraceous indument of stellulate or amorphous branlike hairs. Mature leaves of a pair equal to slightly unequal in size; petioles 0.8–3.4 cm long; blades coriaceous, 3.6–18 × 1.8–7.3 cm, elliptic to elliptic-obovate, the apex acuminate to abruptly short-acuminate, the base acute to obtuse, the margin entire, 3–5-nerved with the marginal pair of veins obscure or lacking or 3–5-plinerved with the inner pair of primary veins diverging from the median vein 4–7 mm above the blade base (on abaxial surface), commonly with some leaves bearing slitlike pit domatia at the abaxial margin of the blade near the petiole-laminar junction, the transverse secondary veins often obscure or 0.5–1 mm apart at the widest portion of the blade when visible. Flowers erect, solitary or in clusters of 2–4 in each leaf axil of distal branches; peduncles 1.2–2 cm long. Floral bracts glabrous at maturity, ± rigid, concave, and tightly enveloping the hypanthium; outer bracts 4.5–5 × 6–7 mm, fused basally for 2–4 mm or sometimes essentially free to the base, broadly deltoid to oblate or semicircular; inner bracts 4 5–6 mm, free, semicircular. Hypanthium (at anthesis) campanulate, 5–6 × 6–7 mm. Calyx tube 2.5 mm long, erect and cupulate, calyx broadly flattened into low undulations 0.5 × 3 mm. Petals 6, glabrous, 1.3 × 0.4–0.5 cm, white, narrowly obovate. Stamens 12; filaments 4–5.5 mm long, declinate, complanate, glabrous; anthers free, 4.5–5 × 1 mm, yellow, each with 2 confluent, dorsally-inclined pores at the emarginate apex; connective thickened dorsally, unappendaged or with a blunt dorso-basal callosity. Ovary 1/2-inferior, 6-locular, elevated apically into a low flangelike rim that forms a wide circle around the stylar scar. Style glabrous, 1.2–1.3 cm long; stigma punctiform. Berry 6–7 × 6 mm. Seeds ovoid to ± pyriform, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Local in montane rainforests, seasonal evergreen forests and oak-pine forests from southern Mexico (Pueblo and Veracruz, southward) to Guatemala and Belize at 300–1850 m. Flowering collections have been made in January, April, July, September, October, and December, fruiting collections have been gathered in every month except July and September.

REPRESENTATIVE SPECIMENS EXAMINED. — BELIZE. Toledo: high ridge, Jacinto Creek, Río Grande, 28 Oct 1944, *Gentle 4928* (CAS, LL). GUATEMALA. Alta Verapaz: Sebol, in potrero, 21 Apr. 1964, *Contreras 4440* (DS). Izabal: El Estor, in high forest, *Contreras 11464* (CAS). Peten: La Cumbre, top of hill in zapotal, on Pusila Road, 5 km north, *Lundell & Contreras 20228* (CAS, LL). MEXICO. Chiapas: Municipio of Berriozabal, 13 km N of Berriozabal near Pozo Turipache and Finca El Suspiro, 25 Dec. 1972, *Breedlove & Thorne 30771* (DS): Municipio of Cintalapa, between Colonia Francisco I. Madero and Colonia A. Lopez Mateos, 29 Mar. 1981, *Breedlove 50564* (CAS): Municipio of La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 19 Jan. 1982, *Breedlove & Almeda 57558* (CAS); Municipio of Ocosingo, adjacent to Laguna Ocotal Grande, 6 Feb. 1973, *Breedlove 33070* (DS): Municipio of Peltalcingo, steep slope of Ahk'ulbal Nab above Peltalcingo, 28 Mar. 1981, *Breedlove 50424* (CAS). Oaxaca: Municipio San Miguel Chimalapa. Cerro Salomon ca. 2 km en linea recta al NNO del Cerro Guayahitos, ca. 43 km en linea recta al N de San Pedro Tapantepec, 23 Dec. 1985, *Wendt et al. 5156* (CAS). Puebla: Municipio Eloxochitlan, adelante de San Miguel Eloxochitlan en camino nacia El Mirador, 12 June 1985 *Chazaro & Leach 3392* (CAS). Veracruz: Municipio Hidalgotitlan. Afluente del Río Las Cuevas, ± 5 horas a pie al S de la Laguna, 16 Apr. 1982, *Wendt et al. 3845* (CAS).

DISCUSSION. — When present in a species of *Topobea*, acarodomatia are commonly produced with consistency on most leaves of all individual plants. In *T. laevigata,* the production of domatia is inconsistent. In the specimens examined for this study, no foliar domatia were found in collections from Belize and Guatemala. Among Mexican collections studied, domatia were observed as follows: Chiapas—some leaves on 18 of 20 collections; Oaxaca—some leaves on two of five collections; Puebla—some leaves on the single collection studied; Veracruz—some leaves on three of four collections examined. For differences between *T. laevigata* and *T. calycularis* see the discussion under the latter.

13. *Topobea lentii* Almeda, Brittonia 53:160. 2001.

TYPE: COSTA RICA. Cartago: 3 km E of Cachí, beside Río Naranjo, 1300 m, 11 July 1971, *Lent 2000* (holotype: MO!; isotypes: BM!, CR!, F!, DUKE!, PMA!, US!).

Epiphytic shrub. Uppermost branchlets bluntly quadrate with elevated internodal lines or ridges but becoming rounded and coarsely striate with age. Young vegetative buds, floral peduncles, young floral bracts, hypanthia, and calyx lobes moderately covered with a caducous indument of scurfy and/or stellulate hairs. Mature leaves of a pair equal to somewhat unequal in size, essentially glabrous on both surfaces; blades coriaceous, 4.2–9.1 cm long and 1.9–4.3 cm wide, elliptic to elliptic-ovate, the apex bluntly acuminate, the base acute to obtuse, the margin entire, 5-plinerved, the innermost primaries diverging from the median vein 2–6 mm above the blade base (on abaxial surface) and forming poculate acarodomatia sparsely to moderately covered with barbellate hairs in the angles formed with the median vein, the transverse secondary veins spaced 0.25 mm apart at the widest portion of the blade. Flowers erect, 2–5 per axil in uppermost leafy branches; peduncles 5–7 mm long, lenticellate. Floral bracts free, sometimes recurved at the apex; outer bracts 3–3.5 × 2–2.5 mm, elliptic-ovate, the apex bluntly acute to rounded; inner bracts 2–2.5 × 2–2.5 mm, elliptic to elliptic-ovate, the apex rounded. Calyx tube 1.5–2 mm long, cupulate; free portions of calyx lobes 0.5–1.5 mm long and 0.5–1.5 mm wide basally between sinuses, broadly subtruncate and often apiculate, somewhat callose-thickened at the median apex abaxially. Petals 6, glabrous but sometimes fringed with inconspicuous caducous white hairs, 6–6.5 × 2–3 mm, reportedly white (fide *Lent 2000*) or pink (fide *Haber ex Bello 5174*), obovate-rhombic, the apex bluntly long-acuminate and somewhat concave. Stamens 12; filaments 3 mm long, somewhat declinate, complanate, glabrous; anthers free or laterally connate (in part), 2.5 mm long, 0.25 mm wide, pale yellow (?) and granulose along the lower ventral half of the thecae, subulate, each with a solitary, dorsally-inclined apical pore; connective thickened dorso-basally and prolonged near the filament insertion into a deflexed caudiform appendage 0.5 mm long. Ovary 1/2 inferior, 6-locular, glabrous and elevated at the apex into a lobulate collar 1 mm high that surrounds the style base. Style glabrous, 5–7 mm long; stigma punctiform. Berry 3–7 × 2.5–7 mm. Seeds 0.75–1 mm long, beige, cuneate to obovoid or narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — A rare cloud forest epiphyte known only from the vicinity of Cachí in central Costa Rica and the Río Chiquito de Tilarán in Guanacaste province at 1300–1450 m. Collected in flower in July and December, in fruit in July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Cartago: pasture on hilltop, 2 km E of Cachí, 9°49′N, 83°47′W, 16 Dec. 1972, *Lent 3118* (F, US). Guanacaste: Río Chiquito de Tilarán, Río Negro, 10°22′N, 84°52′W, 1 July 1986, *Haber ex Bello 5174* (CAS).

DISCUSSION. — Notable features of *T. lentii* are its hair tuft foliar domatia, small fruiting hypanthia, clawed obovate-rhombic petals, ventro-basally granulose anther thecae, and dorso-basal caudiform appendages on anther connectives. It most closely resembles the widespread *T. watsonii* which differs in its well-defined triangular calyx lobes, larger petals (10–16 × 4.5–7 mm), longer an-

ther thecae (6–7.5 mm) that are connate for a major portion of their length, and the absence of foliar domatia. See Almeda (2001:161) for an illustration of this species.

14. *Topobea maurofernandeziana* Cogn., DC. Monogr. Phan. 7:1193. 1891.

TYPE. — COSTA RICA. Forêts de Juan Viñas, 25 Jan. 1890, *Tonduz 1844* (holotype: BR!: isotype: CR!).

Topobea durandiana Cogn., Bull. Soc. Roy. Bot. Belgique Ser. 3, 30:268. 1892. TYPE. — COSTA RICA. Bord d'un torrent a Buenos Aires, 250 m, II. 1891, *Pittier 3789* (holotype: BR!).

Blakea intercepta Gleason, in Woodson & Schery, Ann. Missouri Bot. Gard. 28:435. 1941. TYPE. — COSTA RICA, without exact locality, 20 June 1874, *O. Kuntze s.n.* (holotype: NY!).

Terrestrial or epiphytic shrub 2–5 m tall and 3–7 m in diameter. Uppermost cauline internodes quadrate. Uppermost internodes, young vegetative and floral buds, and petioles sparsely to densely furfuraceous pubescent but glabrate with age. Leaves thick and coriaceous when dry; petioles 1.8–9 cm long; blades 11.5–23 × 7–18.5 cm, elliptic to elliptic-oblong or ovate, the apex abruptly acuminate, the base obtuse to rounded, the margin entire, 5-nerved or 5-plinerved, adaxially glabrous, sparingly furfuraceous to almost glabrous abaxially. Flowers 2–5 (rarely solitary) in each leaf axil of upper branchlets; peduncles 0.6–2.5 cm long. Inner and outer floral bracts 0.7–1.2 × 0.7–1.5 cm, essentially free, ovate to suborbicular, the apex rounded to retuse or obscurely apiculate. Calyx tube (on fruiting hypanthia) 0.6–0.8 cm long from the torus; free portions of calyx lobes 1 × 5 mm, broadly depressed-truncate with an apiculate callosity at the median apex, margin ± entire. Petals 6, glabrous, 1.7–2.5 × 1–1.3 cm, pink, obovate, the apex rounded to obliquely subtruncate. Stamens 12; filaments 7–9 mm long, declinate; anthers laterally connate, 6–9 × 1–2 mm, pink or yellow flushed with pink or red distally, linear-oblong and incurved distally, each with 2 confluent, dorsally-inclined apical pores; connective prolonged dorso-basally into a caudiform appendage 1 mm long. Ovary 1/3 inferior, 6-locular, the apex covered with a caducous ring of minute glandular hairs surrounding the stylar scar. Style glabrous, 1.2–1.5 cm long; stigma truncate to capitellate. Berry 1–1.4 × 1.3–1.5 cm. Seeds 1 mm long, beige, cuneate to clavate.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests and cloud forests, often on remnant pasture trees from southern Mexico (Guerrero and Oaxaca) disjunct to Nicaragua, Costa Rica, and Panama from sea level to 1600 m. Flowering collections have been made from September through July, fruiting collections from February through November.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: about 2–4 km N of Bijagua on road to Upala, 1 Mar. 1978, *Almeda & Nakai 4041* (CAS, CR). Cartago: about 3 km E of Cachí, 24 Jul. 1977, *Almeda et al. 3209* (CAS, CR). Guanacaste: Parque Nacional Guanacaste, Estación Cacao, Liberia, 10°55′45"N, 85°28′15"W, 2 Nov. 1990, *Chavez 339* (CAS, CR, INB, MO). Heredia: Parque Nacional Braulio Carrillo, Estación Magsasay. Sarapiquí, 10°24′10"N, 84°03′30"W, 4 Apr. 1991, *Aguilar 126* (CAS, CR, INB, MO). Limón: Parque Nacional Tortuguero, Estación Cuatro Esquinas. Laguna Tortuguero, 10°32′02"N, 83°30′26"W, 4 Jul. 1990, *Chavarria 116* (CAS, CR, INB, MO). Puntarenas: Las Cruces Tropical Botanical Garden and vicinity about 6.4 km S of San Vito de Java, 18 Mar. 1978, *Almeda et al. 4273* (CAS, CR). San José: Reserva Biológica Carara. Sitio El Chuzazo, 9°45′05"N, 84°31′50"W, 14 Feb. 1990, *Zúñiga 110* (CAS, CR, INB, MO). MEXICO. Guerrero: Sierra Madre Sur. Along road between El Paraíso and Puerto del Gallo, 6–8.7 miles NE of El Paraíso, 9 Mar. 1987, *Daniel & Bartholomew 4932* (CAS). Oaxaca: Distrito de Putla, La Cascada, 5 km al NE de La Hacienda, sobre al camino San Vicente-San Isidro, 13 Apr. 1987, *Garcia et al. 3171* (CAS). NICARAGUA. Chontales: vicinity of Finca San Pedro de Oluma, on NE flanks of Cerro Oluma, 12°18′N, 85°23′W, 22 Sep. 1983, *Nee 28328* (CAS).

Matagalpa: falda norte del Cerro Musún, frente a trocha a Wanawás, 16 May 1980, *Araquistain & Moreno 2798* (CAS). Río San Juan: near Caño Chontaleño, 20 km NE of El Castillo, 18–21 Apr. 1978, *Neill & Vincelli 3560* (CAS). Zelaya: NW de Estación Experimental El Recreo, 12°10′N, 84°18′W, 2 May 1982, *Sandino 2702* (CAS). PANAMA. Chiriquí: 15–20 km S of Volcán, road to Barrilos, 22 Dec. 1974, *Dressler 4903* (CAS).

DISCUSSION. — This is one of the most common species of *Topobea* in lowland sites of southern Central America. Like *T. watsonii*, the only notable variation in this species is in the amount and persistence of the indument on upper internodes, vegetative and floral buds, petioles and peduncles. In the protologue of *T. durandiana*, which was published shortly after *T. maurofernandeziana*, Cogniaux gives no specific differences that can be used to separate these two species. Judging from the species descriptions it appears that Cogniaux assigned those collections with furfuraceous-puberulent petioles and peduncles to *T. durandiana* whereas collections from the glabrous end of the spectrum were recognized as *T. maurofernandeziana*.

Blakea intercepta is also included here in synonymy with confidence. The holotype consists of three leaves and many young fruits. Although petals and anthers are lacking, the available material is an exact match for *T. maurofernandeziana*.

15. *Topobea mcphersonii* Almeda, Brittonia 53:163. 2001.

TYPE: PANAMA. Comarca de San Blas: San Blas boundary trail on Llano-Cartí road, 9°15′N, 79°00′W, elev. ca. 350 m, 27 Jan. 1986, *McPherson & Merello 8176* (holotype: CAS!; isotypes: BM, CR, EAP, MEXU, MO, PMA, US).

Epiphytic shrub. Uppermost branchlets bluntly quadrate becoming rounded with age. Young vegetative buds covered with an amorphous lanate indument. Mature leaves of a pair equal to slightly unequal in size, glabrous on both surfaces but glandular-punctate abaxially; petioles 0.5–1.2 cm long; blades coriaceous, 4.1–7.5 cm long and 1.7–3 cm wide, elliptic-obovate to obovate, the apex bluntly cuspidate, the base acuminate, the margin entire, 3–5-plinerved, the marginal pair of primaries inconspicuous and concealed by the revolute margins when dry, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary in leaf axils of uppermost branches; peduncles 1.2–2 cm long. Floral bracts green flushed with red, entire and glabrous throughout; outer bracts 1.6–2.1 × 1–1.6 cm, free but conspicuously decurrent on and imparting a winged aspect to the the peduncle, elliptic to elliptic-obovate, apex bluntly cuspidate to bluntly acute; inner bracts 1.1–1.5 × 0.3–0.6 cm, free, linear-oblong to narrowly obovate and distinctly cucullate, apex bluntly acute to obtuse. Calyx tube 2 mm long; free portions of calyx lobes 0.5–1 mm long and 3–4 mm wide basally between sinuses, broadly depressed-triangular, margin entire, callose-thickened at the median apex abaxially, glabrous throughout. Petals 6, glabrous, 2.1–2.7 × 1.2–1.5 cm, reportedly white-pink, thin and translucent when dry, obovate, apically rounded, entire. Stamens 12; isomorphic, filaments 5–6 mm long, declinate, complanate, glabrous; anthers laterally connate for most of their length, 3–5 mm long, 1 mm wide, yellow, linear-oblong with each anther sac opening by a separate, dorsally-inclined terminal pore; connective thickened dorsally and dilated dorso-basally into an upturned or deflexed somewhat flattened, blunt appendage ca. 0.5 × 0.25 mm. Ovary completely inferior, 6-locular, glabrous at the apex which is elevated into a blunt cone 1–3 mm high. Style and stigma not seen. Berry subglobose, 0.6–0.7 × 0.7 cm. Seeds mostly 1 mm long, beige, cuneate-clavate.

DISTRIBUTION AND PHENOLOGY. — A lowland rainforest species known only from El Llano-Cartí region of north-central Panama at 100–500 m. Collected in flower and fruit in January and February.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Comarca de San Blas: Río Nergala, 9°22′N, 79°7′W, 12 Jan. 1985, *de Nevers & Herrera 4530* (CAS, MO). Panamá: 14 km above Panamerican Highway on road from El Llano to Cartí-Tupile, 20 Feb. 1973 (fr), *Kennedy 2502* (MO, US).

DISCUSSION. — *Topobea mcphersonii* is unlike other described congeners in having floral bracts that are prominently decurrent on the floral peduncles. The inner floral bracts, which are oblong and do not tightly envelop the hypanthia, are also distinctive as are the laterally connate anther thecae with cleft or divergent pores and upturned or deflexed staminal appendages. Because of these unique features, the relationships of this species are obscure at this time. For an illustration of this species see Almeda (2001:164).

16. *Topobea multiflora* (D. Don) Triana, Trans. Linn. Soc. London 28:149. 1871. (Fig. 4)

Blakea multiflora D. Don, Mem. Wern. Nat. Hist. Soc. 4:326. 1823. (Fig. 4) TYPE. — PERU. Without exact locality: *Pavón 127-3* (holotype: K!, fragment at BR!).

Epiphytic shrub 2–4 m tall or free standing tree to 8 m tall. Uppermost branchlets quadrate becoming somewhat striate and rounded with age, the younger nodes covered with caudate-acuminate stipuliform flaps ca. 3 mm long that envelop caducous tufts of hair, the distal portions of each flap ± caducous with age and leaving a prominent interpetiolar ridge or corky line. Vegetative and young floral buds, calyx lobes (in bud), peduncles, and young pedicels moderately to sparsely covered with a caducous indument of amorphous scurfy hairs. Mature leaves of a pair essentially equal in size, glabrous on both surfaces at maturity; petioles 1.4–6 cm long; blades coriaceous, 10.3–18.5 × 6–10.4 cm, elliptic, the apex abruptly acuminate, the base acute, the margin entire, 5-nerved or 5-plinerved with the innermost primaries diverging from the median vein ca. 5 mm above the blade base (on abaxial surface) with hair tuft acarodomatia that are sparsely to moderately covered with robust shaggy hairs (0.5–2 mm long) in the angles formed with the median vein, the transverse secondary veins spaced 0.25–1.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of (1–) 2–6 in each leaf axil of distal branches; peduncles 0.3–2.1 cm long. Floral bracts essentially glabrous at maturity and closely enveloping the hypanthium; outer bracts 5–8 × 5–7 mm, fused basally for 4–6 mm, broadly ovate to suborbicular, the free distal portion bluntly acute to broadly rounded; inner bracts 7–9 × 10–11 mm, free but imbricate, obdeltoid to suborbicular, often appearing ± rounded due to the firm concave posture. Hypanthium (at anthesis) campanulate, 7–8 × 5–6 mm. Calyx tube 4–6 mm long, erect and cupulate; calyx subtruncate or barely evident as broadly oblate apiculate lobes 0.5 4–5 mm. Petals 6, glabrous, 1.1–1.8 × 0.5–1.2 cm, pink with a translucent whitish inverted V-shaped lens at the base of each petal, narrowly obovate to spatulate, the apex bluntly acute to ± rounded, margin entire but inconspicuously caducous-fimbrillate. Stamens 12; filaments 9 mm long, declinate, complanate, glabrous; anthers laterally connate for at least half their length, 6–9 × 1 mm, yellow, oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into a deflexed toothlike appendage 0.5–2.5 mm long. Ovary 1/4-inferior, 6-locular, elevated apically into a glabrous cone 3 mm high and a lobulate collar ca. 1 mm long. Style glabrous, 1.3–1.5 cm long; stigma ± truncate to somewhat expanded. Mature berry and seeds not seen.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforest habitats from central Costa Rica to Panama, Ecuador, Peru, and Bolivia from sea level to 1400 m. Flowering has been recorded from November through July; fruiting collections have been made in February and March and from May through July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: Reserva Forestal de San Ramón, 10°12′53″N, 84°36′28″W, 28 Jan. 1987, *Herrera & Solís 457* (CAS, CR, MO). Puntarenas:

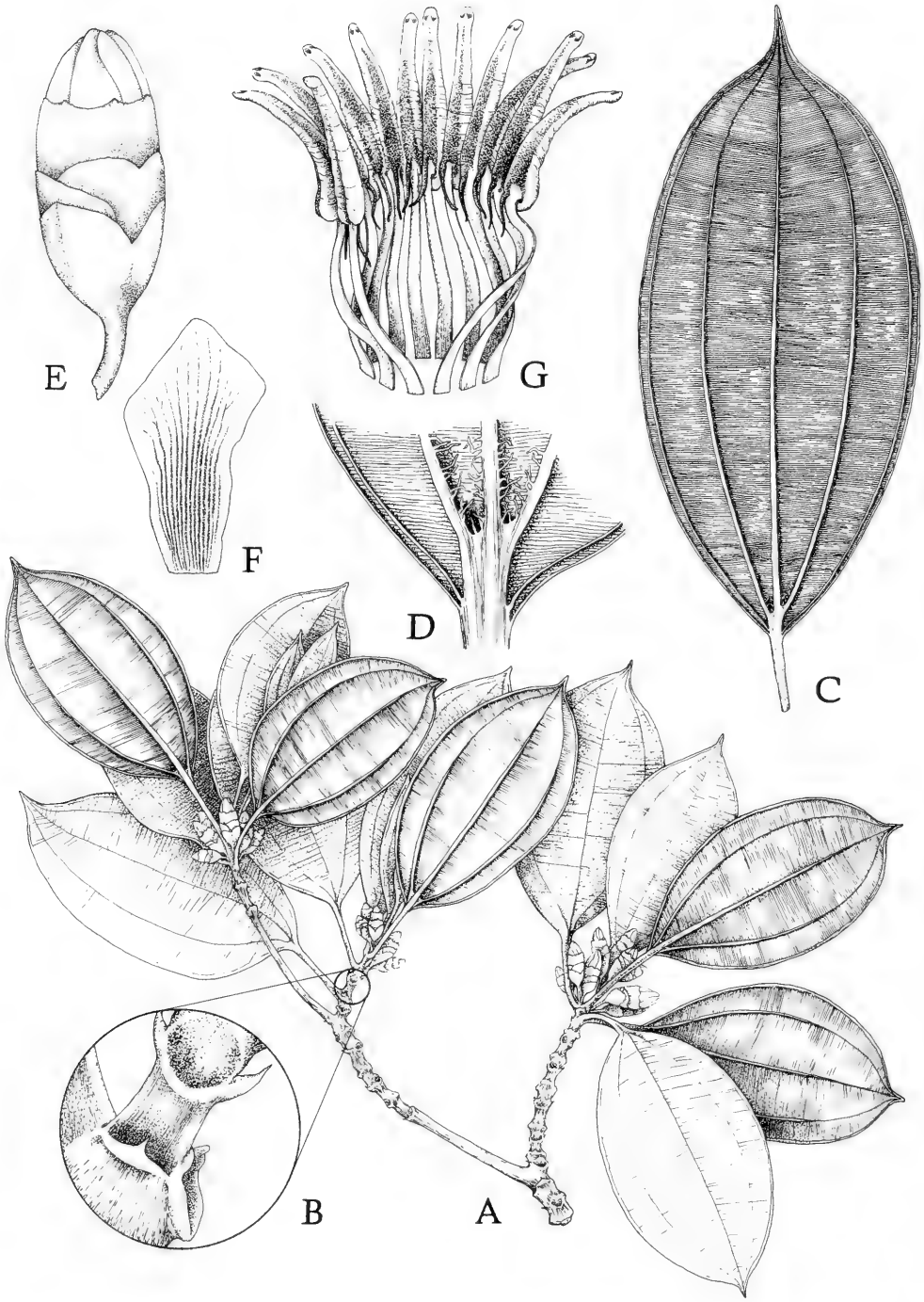

FIGURE 4. *Topobea multiflora* (D. Don) Triana. A. habit, 1/5; B. nodal enlargement showing stipuliform flaps. ca. 3; C. representative leaf (abaxial surface), ca. ½; D. enlarged leaf base (abaxial surface) showing hair tuft acarodomatia, ca. 3; E. flower bud with enveloping bracts, ca. 3; F. petal (adaxial surface), ca. 3; G. androecium, ca. 3. (A, B from *McPherson 7630*; C, D from *McPherson 15046*; E–G from *Almeda et al. 4271* and *McPherson 7964*.)

Las Cruces Tropical Botanical Garden and vicinity about 6.4 km S of San Vito de Java, 18 Mar. 1978, *Almeda et al. 4271* (CAS, CR). San José: about 13–18 km S of San Isidro del General, 5 Mar. 1978, *Almeda & Nakai 4105* (CAS, CR, INB, MBM). PANAMA. Coclé: ca. 9 km beyond the market in El Valle de Antón on a rock road to trail head to Cerro Caracoral, 16 Feb. 1996, *Almeda et al. 7600* (CAS, PMA); along Llano Grande to Coclesito road above Cascajal, near divide, 8°42′N, 80°28′W, 11 Jan. 1986, *McPherson 7964* (CAS, MO, PMA); near El Valle de Antón, 8°37′N, 80°07′W, 25 Nov. 1985, *McPherson 7630* (CAS, MO, PMA). Colón: Río Guanche, 1–4 km upstream from Portobelo Road, 10 Dec. 1973, *Gentry 8767* (MO). Darién: Alturas de Nique on the Serranía de Pirre above the Cana mining camp, 1 Mar. 1988, *Almeda & McPherson 5967* (CAS, PMA); Cana region on trail above Cana leading to ridge of Pirre massif, 7°45′N, 77°45′W, 5 May 1990, *McPherson 15046* (CAS, MO, PMA). Panamá: road past Altos de Pacora, 3–3.5 miles NE of Altos de Pacora, 11.1–11.6 miles beyond Lago Cerro Azul, 9°15′N, 79°25′W, 19 June 1988, *Croat 68669* (CAS, MO, PMA).

DISCUSSION. — This frequently collected species is recognized by a combination of characters that includes stipuliform nodal flaps on uppermost branches (Fig. 4B), hair tuft domatia on abaxial foliar surfaces (Fig. 4D), laterally connate anther thecae, and dorso-basal toothlike appendages on anther connectives (Fig. 4G). In the past, Central American collections of *T. multiflora* have been erroneously identified as *T. calycularis*. Standley (1938), for example, reported it from Costa Rica (as *T. calycularis)* based on collections from Cañas Gordas made in 1897 (*Pittier 10955* and *Pittier 11062*, both at US). It was not reported for Panama by Gleason (1958) because the species had not yet been collected in that country. *Topobea calycularis* is presently known only from Mexico (Chiapas) and adjacent Guatemala. Like *T. multiflora,* it also has hair tuft foliar domatia but it has free anther thecae that are essentially unappendaged, a 4-locular ovary, and lacks stipuliform nodal flaps.

For the most part, Central American material of *T. multiflora* has modally shorter floral peduncles (0.3–2.1 cm vs. 2–3 cm) than South American populations. Cogniaux was aware of this difference and may have intended to give formal taxonomic recognition to the Central American populations because he annotated at least one Costa Rican collection (*Pittier 10955*, BR) as *T. multiflora* var. *brevipedunculata*. The fact that this infraspecific epithet was never published also suggests that he may have changed his mind. I see no compelling reason for recognizing such an entity.

17. *Topobea parasitica* Aubl., Hist. Pl. Guiane Fr. 1:476. 1775.

TYPE. — FRENCH GUIANA. Sinnemary River, *Aublet s.n.* (holotype: BM!).

Topobea regeliana Cogn., DC. Monogr. Phan. 7:1085. 1891. TYPE. — PANAMA. Chagres, Isthmus of Panama, Mar. 1850, *Fendler 295* (holotype: LE: isotypes, BM!, BR! [2 sheets], K!, MO!, US!).

Topobea praecox Gleason, Phytologia 3:355. 1950. TYPE. — PANAMA. Coclé: El Valle de Antón, vicinity of La Mesa, *Allen 2788* (holotype: NY!; isotypes: NY![2 sheets]).

Topobea membranacea Wurdack, Brittonia 9:108. 1957. TYPE. — COLOMBIA. Antioquia: Anori-Cruces road, 11 May 1944, *Core 677* (holotype: US!; isotype: NY!).

Robust shrub or small tree 2–10 m tall, often epiphytic or rupicolous. Uppermost branchlets bluntly quadrate becoming rounded with age. Juvenile vegetative buds and uppermost nodes covered with smooth stramineous hairs and a dense cover of stellulate or scurfy hairs. Uppermost cauline internodes, petioles, peduncles, abaxial leaf surfaces (especially elevated primary veins), outer floral bracts, and calyx lobes (in bud) moderately to sparsely covered with a varying mixture of scurfy, stellulate, and roughened hairs that fall away to varying degrees with age. Mature leaves of a pair somewhat unequal in size, glabrous on the adaxial surface at maturity, sparingly covered with scurfy or stellulate hairs to nearly glabrous on the abaxial surface at maturity; petioles 1.8–9 cm long; blades membranaceous to subcoriaceous, 6.2–25.5 × 5–16 cm, elliptic varying to elliptic-ovate, the apex

abruptly short-acuminate, the base obtuse to broadly rounded but sometimes varying to acute, the margin typically entire, rarely varying to denticulate, (5–)7(–9)-nerved with secondary veins spaced 1–4 mm apart at the widest portion of the blade, or 5–7-plinerved in some plants and then the inner pair of primary veins diverging 0.5–1 cm above the blade base (on abaxial surface). Flowers erect, 1–7 per leaf axil of uppermost branches; peduncles 0.3–1.9 cm long. Floral bracts free but appressed to and commonly obscuring the hypanthium below the calyx; outer bracts 5–10 × 5–9 mm, broadly ovate to subrotund, the apex typically rounded but varying to broadly obtuse, bluntly acute, acuminate or somewhat emarginate; inner bracts 5–9 × 5–9 mm, ovate to subrotund, the apex typically broadly rounded. Hypanthium (post anthesis) campanulate, 5–8 × 6–8 mm. Calyx tube 2–4 mm long, erect and cupulate; free portions of calyx lobes 1–2 long and 3–4 mm wide basally between interlobe sinuses, triangular varying to broadly depressed-triangular to nearly undulate in fruit. Petals 6, glabrous, 1.4–2 × 0.7–1.1 cm, reportedly pink, reddish-pink, or magenta, obovate, the apex rounded to obtuse. Stamens 12; filaments 9–12 mm long, declinate, complanate, glabrous; anthers laterally connate for about ¾ their length, 7–12 × 0.75–1 mm, pale yellow to cream-colored, subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into an acute spur 1–2 mm long. Ovary superior or 1/4- to 1/5-inferior, glabrous, 6-locular, elevated apically into a cone about 2 mm high and a shallow collar ca. 0.5 mm high, the latter disappearing as the ovary cone enlarges with age on mature fruits. Style glabrous, 1.2–1.4 cm long; stigma ± truncate but not conspicuously expanded. Berry becoming red at maturity on some plants, 6–9 × 7–8 mm. Seeds 1 mm long, tan, narrowly ovoid.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests from central Costa Rica south through Panama to eastern Colombia and southeastern Venezuela, east to Surinam and French Guiana and south to the Brazilian Amazon (Amapá, Pará, Amazonas) from sea level to 1375 m. Flowering material has been collected from March through August, October and December, fruiting collections have been gathered from March through December.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: between Cataratas and San Lorenzo about 13–17 km N of La Balsa de San Ramón, 8 June 1976, *Utley & Utley 5109* (CAS, DUKE). Puntarenas: ca. 1.1 km N of Las Cruces Tropical Botanical Garden on road to San Vito, 14 July 1977, *Almeda et al. 3058* (CAS, CR). San José: Reserva Biológica Carara Estación Bijagual, 9°46′N, 84°36′W, 23 Jul. 1990, *Bello 2357* (CAS, INB, MO). PANAMA: Canal Area: Pipeline Road, approx. 15 km N of Gamboa, 8 Oct. 1982, *Schmalzel & Moreno 1100* (CAS). Chiriquí: 7.5 miles from bridge over Río Chiriquí Viejo on road to Río Sereno, 7 Apr. 1979, *Hammel et al. 6877* (CAS, MO, PMA). Coclé: La Mesa at El Valle de Antón, 6.4 km along La Mesa road from El Valle main road, 28 Apr. 1977, *Folsom & Butcher 2834* (CAS, MO). Colón: upstream from bridge over Río Guanche, 27 May 1980, *Antonio 4793* (CAS, MO). Comarca de San Blas: Río Playón Chico, 09°13.5′N, 78°15′W, 8 June 1994, *Herrera et al. 1586* (CAS, MO). Darién: S of Garachiné on W slope of Serranía Sapo, above place called Casa Vieja, 25 May 1991, *McPherson et al. 15377* (CAS, MO, PMA). Herrera: W of Las Minas, on Montoso de Chepo, vicinity of Chepo, 07°42′N, 80°51′W, 20 May 1987, *McPherson 10931* (CAS, MO, PMA). Los Santos: Los Taretos, 10 Aug. 1962, *Dwyer 2432* (MO). Panamá: El Llano-Cartí highway, about 10 km N of El Llano, 20 Apr. 1973, *Dressler 4360* (MO).

DISCUSSION. — The *T. parasitica* complex, as interpreted here, is defined by a number of consistent qualitative characters. These include floral bracts that are free to the base, anther thecae that are laterally connate for about 3/4 their length, spurlike dorso-basal anther appendages, a 6-locular ovary, and a superior or nearly superior ovary. The morphology of hair types comprising the indument is also diagnostic but indument presence and abundance vary considerably from population to population. Perhaps because of its comparatively widespread geographical distribution and elevational range, *T. parasitica* presents some puzzling variation in characters that are typically constant in other species. The most conspicuous variation involves leaf size and thickness, petiole length, number of flowers per leaf axil, peduncle length, floral bract size, calyx lobe development, hypanthial length, flower size,

and petal color. Extreme expressions for all of these characters are impressive. Previous students of the Melastomataceae who worked with geographically defined representatives of *Topobea* have seized on some of these differences in describing new taxa. When a large number of collections are examined from across the range of this species, however, it becomes clear that much of the character variation noted above is continuous or insignificant for the recognition of meaningful taxa. Gleason (1958), in his treatment of Melastomataceae for Flora of Panama, recognized *T. membranacea, T. praecox,* and *T. regeliana*, all of which I here relegate to the synonymy of *T. parasitica*, the oldest name applicable to this complex. Gleason used the name *T. praecox* for plants with triangular-ovate calyx lobes and flowers appearing when the leaves are lacking or at least not fully expanded. He described *T. membranacea* and *T. regeliana* as having calyx lobes that are almost obsolete and flowers appearing while the leaves are fully expanded. Gleason further differentiated these two species by the following couplet:

Leaves thinly coriaceous, flowers 1–2 per axil on pedicels 3–6 mm long . . . . . *T. regeliana*
Leaves membranaceous; flowers 4–6 per leaf axil on pedicels 10–15 mm long . . . . . *T. membranacea*

Unfortunately most collections attributable to this complex are in fruit, so it is difficult to critically evaluate degree of leaf maturation with flowers at anthesis. Nevertheless, the taxonomic utility of this purported correlation seems dubious. All of the other characters that Gleason used to distinguish these three taxa are too variable or exhibit much overlap. Thus the character correlations used to differentiate what he interpreted as three species make little sense when applied to the many more collections now available for study from Central America. Because of this, I see no recourse other than to recognize *T. parasitica* as a variable complex with some modally extreme character combinations that break down as sample size increases.

In his treatment of *T. parasitica* for the Flora of the Guianas, Wurdack (1993) notes that other perhaps synonymous taxa in this complex include *T. rupicola* Hoehne of Brazil and *T. floribunda* Gleason and *T. rhodantha* Uribe of Colombia. For illustrations of *T. parasitica* see Gleason (1958:246) and Wurdack (1993:299).

18. *Topobea parvifolia* (Gleason) Almeda, Proc. Calif. Acad. Sci. 46:322. 1990.

Blakea parvifolia Gleason, Phytologia 3:357. 1950. TYPE. — PANAMA. Coclé: crest of Cerro Pajita, El Valle de Antón, 1100 m, *Allen 3761* (holotype: NY!; isotype: MO!).

Tree 3–10 m tall. Uppermost branchlets glabrous, quadrisulcate but becoming rounded-quadrate with age. Young vegetative buds and floral peduncles sparingly covered with a caducous scurfy indument. Mature leaves of a pair essentially equal in size, adaxially glabrous, abaxially glandular-lepidote; petioles 0.6–1.4 cm long; blades coriaceous, 2.5–4.7 cm long and 1.4–2.6 cm wide, elliptic to obovate, the apex rounded to a blunt apiculum, the base acute to cuneate, the margin entire, 3–5-nerved with inconspicuous pustulate swellings that become perforated domatia at the abaxial blade base in the angles between the median vein and each of the two proximal lateral veins, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary in uppermost leaf axils; peduncles 1.7–3.1 cm long. Floral bracts free and entire; outer bracts 3.5 1.5–2 mm, narrowly ovate to ovate-lanceolate, apex rounded; inner bracts 3 × 1.5–2 mm, oblong, apex rounded. Calyx tube (fruiting hypanthia) 0.5–0.75 mm long, campanulate to cupulate; free portions of calyx lobes 0.75–1 mm long and 1.5–2 mm wide basally between interlobe sinuses, broadly triangular and often becoming bluntly apiculate on the most mature berries. Petals 6, obovate, glabrous with an irregular scattering of hyaline disc-shaped glands when dry, 0.7–1 × 0.5–0.6 cm, white or white flushed with pink along the margins. Stamens 12; filaments 2.5 mm long, declinate, gla-

brous; anthers oblong, laterally connate in a semicircular ring, 2–2.5 mm long, 0.5 mm wide, each anther sac opening by a separate dorsally inclined terminal pore; connective simple. Ovary 2/3-inferior, 4-locular, glabrous at the apex which is elevated into a low truncate cone that becomes increasingly rounded in fruit. Style glabrous, 6.5 mm long; stigma punctiform. Berry 6–6.5 × 6–6.5 mm. Seeds 1 mm long, beige, cuneate-clavate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Locally common in ridgetop elfin forest on Cerro Pajita, Cerro Gaital, and vicinity in central Panama at 900–1100 m. Flowering has been recorded in November and December, February, and July, fruiting collections have been made in February and July.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Coclé: Cerro Gaital, east slope and ridges leading to the summit, 24 Feb. 1988, *Almeda et al. 5898* (CAS, PMA); vicinity of La Mesa, beyond El Valle, on eastern ridge along trail to summit of Cerro Gaital, 08°37′N, 80°07′W, 13 July 1987, *McPherson 11261* (CAS, MO, PMA).

DISCUSSION. — This Panamanian endemic is known only from windswept slopes and ridges in the vicinity of El Valle de Antón. Among the species with small glabrous leaf blades and free floral bracts, *T. parvifolia* stands out by its inconspicuous pustulate swellings that become perforated domatia at the abaxial blade base in the angles between the median vein and each of the two proximal lateral veins. The anther thecae are unappendaged, laterally connate in a semicircular ring with each anther sac opening by a separate terminal pore, and the ovary is 4-locular.

19. *Topobea pittieri* Cogn., DC. Monogr. Phan. 7:1088. 1891.

TYPE. — COSTA RICA. La Palma, alt. 1550 m, 18 Dec. 1888, *Pittier 706* (holotype: BR!; isotypes: BR!, CR!).

Terrestrial or epiphytic shrub 1–4 m tall. Uppermost branchlets obscurely rounded-quadrate becoming rounded with age. Young internodes, young vegetative buds, bracts, hypanthia and calyx lobes sparsely to moderately squamulose with inconspicuous scales that may superficially appear like sessile glands. Mature leaves of a pair equal to slightly unequal in size; petioles 1.1–2.7 cm long; blades subcoriaceous, 6.5–14.5 × 2.6–7.5 cm, elliptic, the apex acuminate to caudate-acuminate, the base acute to obtuse and somewhat decurrent on the petiole, the margin obscurely undulate-crenulate, 5-plinerved with an additional inconspicuous intramarginal pair, the innermost primary veins diverging from the median vein 0.3–1 cm above the blade base (on abaxial surface) with pocket domatia formed where innermost primaries diverge from the median vein, the transverse secondary veins spaced 0.5–1.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of 2 to 5 in each leaf axil of distal branches; peduncles 1–2.5 cm long. Floral bracts free and much shorter than the hypanthium and calyx; outer bracts 1.5–2.5 × 1.5–2.5 mm, ovate to deltoid; inner bracts 1–1.5 × 1.2–1.5 mm, broadly ovate to suborbicular. Hypanthium (at anthesis) narrowly campanulate, 3–3.5 × 3–3.5 mm. Calyx tube 1 mm long; calyx lobes 0.5 2–3 mm, truncate to retuse with inframarginal teeth positioned medially on the abaxial surface. Petals 6, glabrous, 7–8.5 × 3.5–4.5 mm, white or greenish-white, oblong-ovate and acute apically. Stamens 12; filaments 2.5–3.5 mm long, declinate and glabrous; anthers free, 2.5–3 × 0.5 mm, yellow, subulate, each opening by a solitary, dorsally-inclined pore; connective thickened dorsally and prolonged dorso-basally into a ± horizontal toothlike appendage 0.5 mm long. Ovary 3/4-inferior, 4-locular, slightly elevated at the summit into a low glabrous laterally lobulate blunt cone surrounding the stylar scar. Style glabrous, 5–8 mm long, stigma punctiform. Berry 5–9 × 6–8 mm, pink-purple at maturity. Seeds narrowly ovoid to cuneate, 1 mm long, deep purple with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Locally common in very wet cloud forests from Costa Rica south to Colombia and Ecuador at 500–1800m. Flowering and fruiting specimens have been collected during every month of the year.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: about 9.7 km N of Los Angeles de San Ramón, 23 Feb. 1978, *Almeda & Nakai 3846* (CAS, CR). Cartago: Refugio Nacional de Fauna Silvestre Tapantí, 22 Mar. 1986, *Almeda et al. 5709* (CAS, CR). Heredia: 12–15 km SW of Horquetas; Finca Rara Avis, transect SE across Rara Avis boundary along Río Sardinal to S corner of property on boundary with Braulio Carrillo Park, 10°20′N, 84°02′W; 20 Apr. 1988, *Hammel et al. 16701* (CAS, CR, INB, MO). Limón: Cantón de Talamanca, Parque Nacional Cordillera de Talamanca, Río Coén, entre Ujarrás y San José Cabécar, 09°24′20, 83°13′30"W, 3 Apr. 1993, *Herrera 6194* (CAS, CR, INB, MO). San José: ca. 21 km N of San Isidro de Coronado on lower W slopes of Volcán Irazú, 5 July 1977, *Almeda et al. 2918* (CAS, CR). PANAMA. Bocas del Toro; Edwin Fabrega Dam and Reserve in Fortuna along the Continental Divide trail, 12.9 km N of Sitio de Presa offices above the dam, 08°48′04"N, 82°15′04"W, 7 Feb. 1996, *Almeda et al. 7539* (CAS, PMA). Chiriquí: Fortuna Dam area about 3.7 km S of the Sitio de Presa offices. Trail through Quebrada Alemán, 9 Feb. 1996, *Almeda et al. 7553* (CAS, PMA); Cerro Colorado, Bocas Road, 17–18 Feb. 1977, *Folsom et al. 1770* (CAS).

DISCUSSION. — This species is distinguished by the combination of pocket domatia on abaxial foliar surfaces, solitary anther pores, apically acute petals, seeds that are deep purple at maturity, and a 4-locular ovary. Cogniaux (1891), Standley (1938), and Wurdack (1980) overlooked the presence of foliar domatia in this species. He described them as "inner primaries calloused at the base beneath."

20. *Topobea pluvialis* Standl., Field Mus. Nat. Hist., Bot. Ser. 22:162. 1940.

TYPE. — PANAMA. Darién: Chepigana District, crest of Cana-Cuasi trail, 15 Mar. 1960, *Terry & Terry 1560* (holotype: F!; isotype: MO!).

Reportedly a tree 4–6 m tall or an epiphytic shrub. Uppermost branchlets quadrate becoming rounded with age and irregularly inflated into clavate-thickened formicaria just below some nodes. Young vegetative buds and young floral peduncles caducously covered with a furfuraceous indument of minute branlike hairs, otherwise glabrous throughout. Mature leaves of a pair somewhat unequal in size, glabrous on both surfaces at maturity; petioles 1.3–2.5 cm long; blades coriaceous, 10–15.5 × 3.4–7.7 cm, elliptic-oblong to elliptic-obovate, the apex caudate-acuminate, the base acute to obtuse, the margin entire, 5-plinerved with innermost primaries diverging from the median vein 3–9 mm above the blade base (on abaxial surface) and with hair tuft domatia that are sparsely covered with barbellate hairs in the angles formed with the median vein, the transverse secondary veins spaced 0.5–1.5 mm apart at the widest portion of the blade. Flowers erect, solitary or borne in clusters of 2–3 in each leaf axil of distal branches; peduncles 0.8–1.7 cm long. Floral bracts essentially glabrous at maturity; outer bracts 4–7 × 4 mm, free, ovate to elliptic-lanceolate; inner bracts 3–4 × 3–4 mm, free, depressed-ovate to suborbicular. Hypanthium cupulate, 5–6 × 6 mm. Calyx tube 2.5–3 mm long, erect; calyx with broadly depressed rounded-triangular lobes 1 × 3 mm, each of which is terminated by a tooth 0.5 mm high or the calyx often appearing nearly truncate. Petals 6, glabrous, 1–1.3 × 0.7–0.9 cm, white or pink (fide *Hartman 12381*), obovate, the apex bluntly acute to subrotund, the margin entire. Stamens 12; filaments 6–7 mm long, declinate, complanate, glabrous; anthers laterally coherent for about 2/3 of their length, 4–5 × 0.75 mm, yellow, oblong to oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective somewhat thickened dorsally and prolonged dorso-basally into a deflexed tooth-like appendage 0.5–1 mm long. Ovary 1/3-inferior, 6-locular, elevated apically in a short stipe (0.5 mm high) bearing the stylar scar but lacking a collar. Style glabrous, 1.3–1.4 cm long; stigma ± conic when expanded. Immature berry 6 × 4 mm. Seeds mostly 1 mm long, beige, the testa smooth.

DISTRIBUTION AND PHENOLOGY. — A rare and little-collected species of the rainforests of southern Panama near the Colombian frontier at 900–1650 m. Flowering collections have been made in December and February through April, fruiting collections in April, November and December.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Darién: top of ridge leading to Cerro Pirre, near Rancho Plastico, 13 Nov. 1977, *Folsom et al. 6282* (CAS, MO); SW ridge leading to Alturas de Nique, on border with Colombia, 29 Dec. 1980, *Hartman 12381* (CAS, MO, PMA); Parque Nacional Darién, Cerro Pirre, 7 Feb. 1991, *Herrera et al. 886* (CAS, MO).

DISCUSSION. — The foliar acarodomatia of *T. pluvialis* take the form of invaginated depressions on the abaxial surface but they are inflated and paired on the adaxial surface. These domatia are lacking in *T. inflata* Triana, a closely related Colombian species. This latter species also has fusiform internodal swellings (presumably inhabited by ants) that are larger and more consistently developed on uppermost internodes than in *T. pluvialis*. *Herrera et al. 1485* (CAS) from San Blas, Panama (350–480 m) could represent an outlying population of *T. pluvialis* or a closely related taxon but it is in young bud and has abaxial foliar domatia that appear to be ruptured and devoid of hairs rather than open and covered with a few barbellate hairs. Better material is needed before this entity can be identified with certainty. *Topobea pluvialis* is the only known member of the genus in Mesoamerica that produces both cauline formicaria (presumably for ants) and foliar domatia for mites.

21. *Topobea standleyi* L. O. Williams, Fieldiana, Bot. 29:583. 1963.

TYPE. — GUATEMALA. Baja Verapaz: dry rocky hills in forest of pine and oak, north of Santa Rosa, 30 Mar. 1939, *Standley 69709* (holotype: F!; isotype: NY).

Reportedly a terrestrial shrub or tree to 8 m tall. Uppermost branchlets ± terete, the very young internodes, vegetative buds, petioles on young leaves, floral peduncles, and abaxial leaf surfaces moderately furfuraceous with caducous branlike or stellulate hairs. Mature leaves of a pair somewhat unequal in size, glabrous on the adaxial surface at maturity; petioles 0.5–4 cm long; blades ± coriaceous, 9.5–15 × 5–10 cm, elliptic to elliptic-ovate, the apex abruptly acuminate, the base acute, the margin entire, 5-nerved (the outermost pair often obscure), the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in each leaf axil of upper branches; peduncles 0.7–1.2 cm long. Floral bracts moderately to sparsely covered with a lanuginose indument of caducous matted hairs at maturity; outer bracts 6–8 × 5 mm, free, ovate, typically with a keeled median vein; inner bracts 5–6 × 5 mm, free, suborbicular to obovate. Hypanthium cupulate, 0.7–0.8 × 0.7 cm (at anthesis). Calyx tube 2.5 mm long, erect; calyx lobes bluntly deltoid and ± rounded apically (often appearing like erect blunt teeth on fruiting hypanthia), 1.5–2 × 2 mm, covered with a brown lanuginose indument of woolly matted hairs. Petals 6, glabrous, 0.7–1.1 × 0.5–0.9 cm, pink and white (fide *Standley 69709*), obovate, the margin obscurely retrorse-ciliolate. Stamens 12; filaments 5 mm long, declinate, complanate, glabrous; anthers free, 5.5–7 × 1 mm, oblong, each with 2 divergent, dorsally-inclined apical pores; connective somewhat thickened dorsally but not elaborated into an appendage. Ovary 1/2-inferior, 6-locular, the apex smooth, glabrous and lacking a cone and collar. Style glabrous, 9 mm long; stigma punctiform. Berry 8 × 5 mm. Seeds 1.5 mm long, beige with a black lateral raphe and smooth testa.

DISTRIBUTION AND PHENOLOGY. — Rocky hills in pine-oak forests of Central Guatemala at 1500 m. The two known collections, which are in flower and fruit, were collected in March and April.

REPRESENTATIVE SPECIMENS EXAMINED. — GUATEMALA. Baja Verapaz: pine-oak forest on rocky hills near and above Santa Rosa, 4 Apr. 1941, *Standley 91045* (F, NY).

DISCUSSION. — This species, which has not been collected since April of 1941, appears to be a local endemic known only from the type and the one other collection cited above. It is readily recognized by its abruptly acuminate leaves, caducous lanuginose indument on hypanthia, calyx lobes, and

floral bracts, and unappendaged anthers, each of which has two divergent apical pores. For an illustration of this species see Standley and Williams (1963:520).

22. *Topobea suaveolens* Almeda, Proc. Calif. Acad. Sci. 46:323. 1990.

TYPE. — PANAMA. Veraguas: along trail to summit of Cerro Tute about ½ mile above the Escuela de Agricultura Alto Piedra near Santa Fe, 29 Jan. 1989, *Almeda et al. 6484* (holotype: CAS!; isotypes: AAU!, BM!, BR!, CR!, DUKE!, F!, MEXU!, MICH!, MO!, NY!, PMA!, TEX!, US!).

Epiphytic tree to 4 m tall, often obscuring and overtaking the crowns of host trees. Uppermost branchlets quadrate to quadrisulcate and glabrous with well-defined interpetiolar ridges or lines. Vegetative buds caducously lepidote-furfuraceous. Mature leaves of a pair equal or slightly unequal in size, glabrous throughout; blades subcoriaceous, 3.6–5.3 × 1.6–2.5 cm, elliptic, the apex acuminate to caudate-acuminate, the base acute, the margin entire, 3-plinerved with an additional inconspicuous pair of submarginal veins, transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade, pocket domatia typically formed abaxially in the angles between the median vein and the two proximal lateral veins. Flowers pendent and solitary in the leaf axils of uppermost branches; peduncles 2.3–3 cm long, glabrous. Floral bracts glabrous, entire; outer bracts 4.5–7.5 × 3–4 mm, elliptic to elliptic-ovate, apex bluntly acute to rounded; inner bracts 4–4.5 × 4 mm, ovate to suborbicular, apex broadly rounded. Calyx tube 1.5 mm long; calyx lobes 1 mm long and 4 mm wide basally, broadly ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire, glabrous throughout. Petals 6, glabrous, connivent to somewhat imbricate and bell-like when fully expanded, 1.2–1.5 × 0.9–1.1 cm, white flushed with dark pink along a broad marginal band, obovate, apically rounded, entire. Stamens 12, free and encircling the exserted style; filaments glabrous, 2.5–3.5 mm long; anthers 2.5 mm long, 1 mm wide, yellow, laterally compressed, oblong in ventral view and narrowly ovoid in profile view with a shallow dorso-basal depression at the filament insertion, tipped with a solitary, dorsally-inclined pore 0.75 mm in diameter; connective unappendaged. Ovary 1/2-inferior, 6-locular, elevated at the glabrous apex into a smooth dome 1–1.5 mm high. Style straight, glabrous, 8.5–9 mm long; stigma truncate. Berry 5–6 × 6–7 mm. Seeds narrowly and irregularly pyriform, 0.75–1 mm long.

DISTRIBUTION AND PHENOLOGY. — Known only from the cloud forests of Cerro Tute in west-central Panama at 850–1100 m. The three known collections, all of which are in flower and fruit, were collected from January through March.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Veraguas: vicinity of Cerro Tute, along trail to summit, 08°30′N, 81°07′W, 19 Mar. 1987, *McPherson 10654* (CAS, MO, PMA); near Cerro Tute-Arizona, above Santa Fe and Alto de Piedra, 8°30′N, 81°10′W, 5 Feb. 1988, *McPherson 12043* (CAS, MO, PMA).

DISCUSSION. — This little-collected Panamanian endemic appears to be restricted to the slopes of Cerro Tute. It is unusual among congeners in having sweet-smelling flowers that are pendent with free connivent anthers that form a ring around the exserted style. *Topobea suaveolens* also has distinctive laterally compressed anthers that are uniporose and narrowly ovate in profile view with a conspicuous dorso-basal depression near the filament insertion. For an illustration of this species see Almeda (1990:324).

23. *Topobea tetramera* Almeda, sp. nov. (Fig. 5)

TYPE. — PANAMA. Veraguas: headwaters of Río Caloveborita ca. 15 km past Escuela Agricola Alto Piedra above Santa Fé on the Atlantic watershed, 500 m, 16 May 1981, *Sytsma & Anderson 4758* (holotype: CAS!; isotype: MO, PMA).

Frutex epiphyticus vel terrestris. Ramuli sicut pedunculi folia inflorescentia hypanthiaque pilis 1–2 mm longis induti. Folia in quoque pari dimorpha papyracea et denticulata. Folia maiora: lamina 4.5–9.4 × 2.3–4.3 cm elliptica vel elliptico-ovata vel elliptico-obovata apice acuminata basi asymmetrice obtusa vel rotundata 5-plinervata. Folia minora: lamina 0.7–1.7 × 0.6–1 cm ovata apice acuta basi obtusa vel rotundata 3-nervata. Flores 4-meri in quoque nodo superiori singuli; pedunculis 3–4 mm longis; bracteae omnino liberae 0.7 × 0.2–0.4 cm elliptica apice acuta; bracteae interiores omnino liberae 0.9 × 0.3–0.4 cm elliptica apice acuta vel acuminata. Calycis tubus 1 mm longus, lobis 0.7 × 0.2 cm. Petala 0.8–0.9 × 0.5–0.7 cm obovata. Antherarum thecae 2 × 0.75 mm inter se non cohaerentes, dorsaliter biporosae; connectivum nec prolongatum nec appendiculatum. Ovarium 4-loculare et omnino inferum, cono glabro (collo non evoluto).

Epiphytic or terrestrial shrub to 2 m tall. Uppermost branchlets quadrate becoming rounded with age. Cauline internodes, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes moderately to copiously hirsute with rusty brown hairs mostly 1–2 mm long. Mature leaves of a pair markedly unequal in size; blades coarsely papery when dry, the larger one at each node 4.5–9.4 × 2.3–4.3 cm, elliptic varying to elliptic-ovate or elliptic-obovate, the apex abruptly acuminate, the base somewhat obliquely obtuse to rounded, the margin denticulate (sometimes obscurely so), 5-plinerved with the innermost pair of primary veins diverging from the median vein 2–5 mm above the blade base, the transverse secondary veins spaced 2–4 mm apart at the widest portion of the blade; petiole 5–7 mm long; the smaller blade 0.7–1.7 × 0.6–1 cm, ovate, apex acute, base rounded to obtuse, margin entire, 3-nerved, the transverse secondary veins not evident; petiole 2–3 mm long. Flowers erect, solitary in each axil of uppermost leaves, peduncles 3–4 mm long. Floral bracts green and entire; outer bracts 0.7 × 0.2–0.4 cm, free, narrowly elliptic, apex acute; inner bracts 0.9–1 × 0.3–0.4 cm, free, narrowly elliptic, apex acute to acuminate. Hypanthium (at anthesis) 4 mm long to the torus and 4 mm in diameter. Calyx tube 1 mm long, erect or somewhat flaring at anthesis. Calyx lobes (at anthesis) 4, deltoid at the base but abruptly tapered to narrow linear segments 0.7 cm long and 0.2 cm wide at the base between sinuses. Petals 4, glabrous, 0.8–0.9 × 0.5–0.7 cm, translucent white (fide *de Nevers et al. 5460*) or translucent pink (fide *Sytsma & Andersson 4758*), thin and translucent when dry, obovate, the apex rounded, the base broadly clawed, entire. Stamens 8, isomorphic; filaments 3–3.5 × 0.5 mm, complanate, glabrous; anthers free, 2 × 0.75 mm, yellow, narrowly ovoid, each with 2 confluent, somewhat dorsally-inclined pores at the truncate apex; connective thickened dorsally but unappendaged. Ovary completely inferior (at anthesis), 4-locular, glabrous at the summit which is elevated into a blunt cone surrounding the stylar scar. Style glabrous, 5.5–6 mm long; stigma punctiform. Berry red at maturity, 6–8 × 7–8 mm. Seeds 1 mm long, white, narrowly pyriform to cuneate, testa smooth.

DISTRIBUTION AND PHENOLOGY. — Local and evidently uncommon in low rainforests from the Fortuna region of western Panama east to Cerro Brewster in central Panama at 800–1100 m. Collected in flower in April and May, in fruit in November.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. Chiriquí: Fortuna Dam area, along Quebrada Bonito to E of road, 8°45′N, 82°13′W, 8 Feb. 1984 (sterile), *Churchill et al. 4767* (MO). Comarca de San Blas: Cerro Brewster, premontane rain forest, 9°18′N, 79°16′W, 21 Apr. 1985, *de Nevers et al. 5460* (CAS); Cerro Brewster, premontane rain forest, 9°18′N, 79°16′W, 20 Nov. 1985, *de Nevers et al. 6266* (CAS). Veraguas: 11 km from Escuela Agricola Alto de Piedra, along Río Dos Bocas, 15 Nov. 1974, *Mori & Kallunki 3092* (CAS, MO).

DISCUSSION. — This extraordinary species appears to be highly derived because of its 4-merous flowers (Fig. 5F) with eight stamens and a 4-locular ovary. The strongly dimorphic leaves at each node (Fig 5A) and the copious rusty brown hirsute pubescence on vegetative and floral parts are also characteristic. These latter features are shared with *T. dimorphophylla* which differs in having partly fused inner floral bracts, 6-merous flowers with 12 stamens, and a 6-locular ovary.

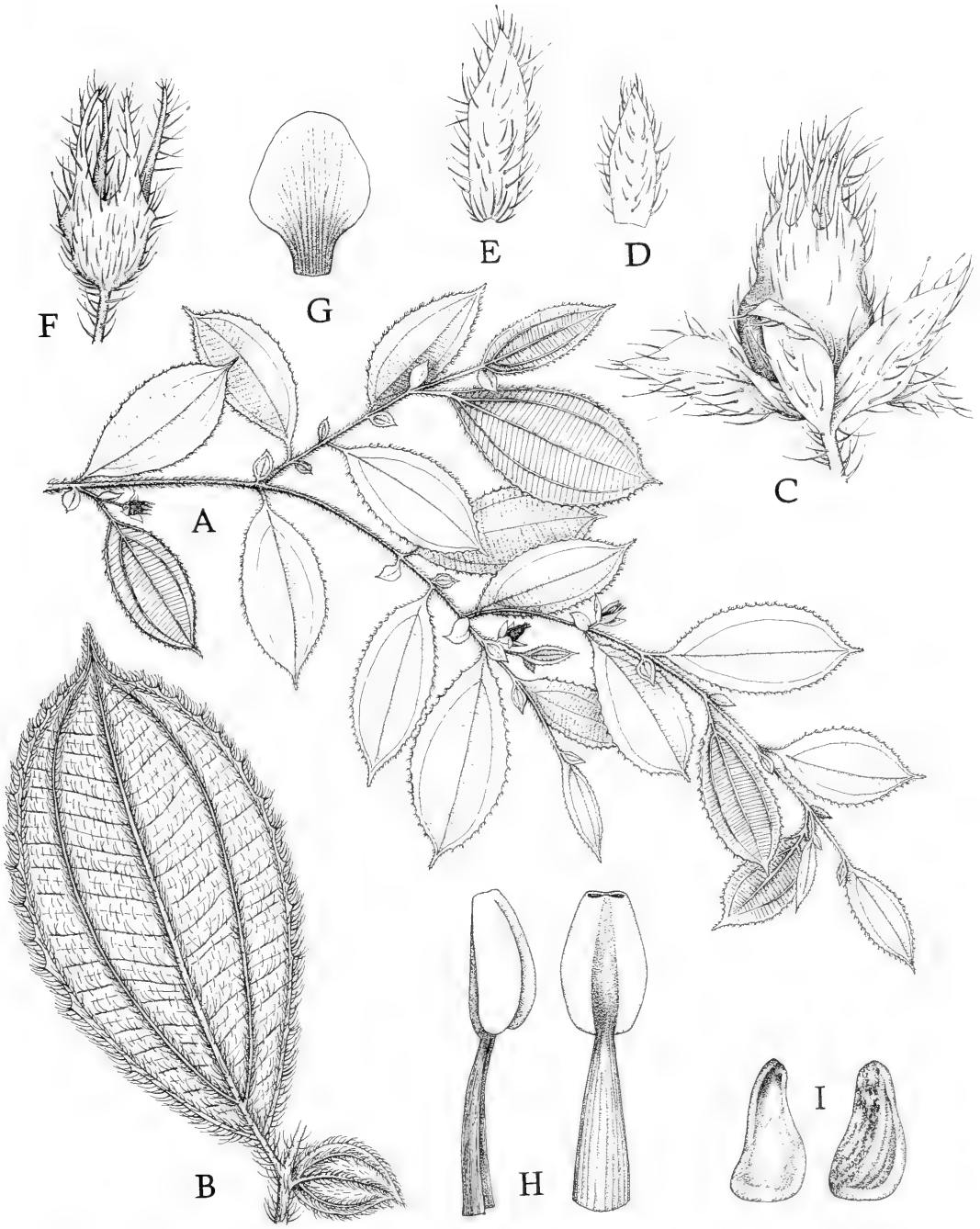

FIGURE 5. *Topobea tetramera* Almeda. A. habit, 1/5; B. foliar dimorphism at a node, ca. 1; C. fruiting hypanthium with attached decussate floral bracts, ca. 3; D. outer floral bract (adaxial surface), ca. 3; E. inner floral bract (adaxial surface), ca. 3; F. hypanthium (at anthesis) with floral bracts, petals, androecium, and style removed, ca. 3; G. petal (adaxiall surface), ca. 3; H. stamens, ¾ profile view (left) and dorsal view (right), 10; I. seeds, 20. (A, B from *Mori & Kallunki 3092*; C–I from *Sytsma & Anderson 4758*.)

ETYMOLOGY. — The epithet for this species is derived from the Greek words *tetra*, meaning four, and *merus*, referring to number of parts, in reference to the unusual 4-merous flowers and 4-locular ovary of this species.

24. *Topobea watsonii* Cogn., DC. Monogr. Phan. 7:1089. 1891.

TYPE. — GUATEMALA. Prope Chocon River, 11 Mar. 1885, *Watson 94/211* (holotype: BR!).

Topobea rosea Gleason, Publ. Carnegie Inst. Wash. 522: 536. 1940. TYPE. — BELIZE. Temash River, 13 Mar. 1936, *Schipp 1320* (holotype: NY!)

Topobea urophylla Standl., Field Mus. Nat. Hist., Bot. Ser. 22:162. 1940. TYPE. — PANAMA. Darién: Chepigana District, Río Balsa, above Tucutí, 6 Mar. 1940. *Terry & Terry 1411* (holotype: F!; isotype: MO!).

Topobea cooperi Gleason, Phytologia 3:354. 1950. TYPE. — PANAMA. Bocas del Toro: Cricamola Valley, Region of Almirante, Jan.–Mar. 1928, *Cooper 199* (holotype: NY!; isotype: F!).

Topobea allenii Standl. & L. O. Williams, Ceiba 3:216. 1953. TYPE. — COSTA RICA. Puntarenas: Esquinas Forest, region between Río Esquinas and Palmar Sur de Osa, alt. 75 m, 5 Feb. 1951, *Allen 5844* (holotype: EAP; isotypes: F!, US!).

Scandent epiphytic shrub with lax branches 3–4 m long. Uppermost branchlets bluntly quadrate but becoming rounded with age. Juvenile growth, uppermost cauline internodes, peduncles, and floral bracts moderately to densely covered with barbellate or stellulate and scurfy hairs but glabrate with age. Mature leaves of a pair equal to somewhat unequal in size, adaxially glabrous, abaxially sparsely covered with plumose or barbellate hairs (mostly on the elevated primary veins) and stellulate or branlike hairs (especially on the actual surface) varying to nearly glabrous; petioles 1–4.8 cm long; blades coriaceous, 5.5–16.5 × 3–7.7 cm, elliptic to elliptic-ovate, the apex long-acuminate to abruptly caudate, the base obtuse to rounded, margin entire, 3–5-nerved or 3–5-plinerved (sometimes with an intramarginal pair of obscure veins), the transverse secondary veins spaced 0.25–0.5 mm apart at the widest portion of the blade. Flowers erect, 1–4 per leaf axil of uppermost branches; peduncles 0.7–1.3 cm long. Floral bracts free or connate basally for 1–2 mm, elliptic to elliptic-ovate, apex acute to rounded apically; outer and inner bracts 0.6–1 × 0.4–0.8 cm. Calyx tube 3–4 mm long, campanulate; free portions of calyx lobes 2–3 mm long and 2.5–3.5 mm wide basally between interlobe sinuses, bluntly triangular with a prominently elevated callose-thickened tooth or appendage at the median apex abaxially. Petals 6, glabrous or stellulate puberulent abaxially, 10–16 × 4.5–7 mm, pink, rhombic-ovate to obovate, the apex ± acute. Stamens 12; filaments 5–7 mm long, declinate, complanate and glabrous; anthers laterally connate, 6–7.5 × 1 mm, yellow, granulose along lower ventral half of the thecae, each with 2 confluent, dorsally-inclined pores; connective prolonged dorso-basally into a deflexed caudiform appendage 0.5–1 mm long. Ovary 1/3-inferior, 6-locular, glabrous and elevated at the apex into a lobulate stylar collar 1–1.5 mm high. Style glabrous, 1.2–1.6 cm long; stigma capitellate. Berry red, 1–1.3 × 0.9–1.3 cm. Seeds 1–1.5 mm long, beige, narrowly ovoid to cuneate.

DISTRIBUTION AND PHENOLOGY. — Locally common in low rainforests and cloud forests from southern Mexico (Chiapas) and Belize south through Central America (excluding El Salvador) to Colombia from sea level to 1400 m. Flowering specimens have been collected from October through February and in May, fruiting collections from February through September.

REPRESENTATIVE SPECIMENS EXAMINED. — BELIZE. Toledo: Edwards Road beyond Columbia, on high ridge, 11 Nov. 1947, *Gentle 6316* (CAS, LL). COSTA RICA. Puntarenas: between Golfo Dulce and Río Térraba, Nov. 1947 (without exact date), *Skutch 5263* (US). GUATEMALA. Petén: Los Arcos, 2 km, E of Km 143 on Cadenas Road, 17 Dec. 1969, *Contreras 9379* (CAS, LL, US). Izabal: Río Chacón, 8 Feb. 1921, *Johnson 1237* (US). HONDURAS. Gracias a Dios: Ahuas Bila, 200 km SO de Puerto Lempira, orilla del Río Wankí, Coco o Segovia, 5–13 May 1985, *Nelson & Cruz*

9319 (CAS, TEFH). MEXICO. Chiapas: Municipio Las Margaritas, low ridges at the confluence of the Río Lacantum (Río Jataté) on the Guatemala border, 14 Mar. 1973, *Breedlove & McClintock 34103* (DS, MEXU). NICARAGUA. Jinotega: below Peñas Blancas via El Tuma, 6 May 1976, *Neill 253* (CAS, MO). Matagalpa: Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, ca. 13°14–15′N, 85°38′W, 20–21 Jan. 1982, *Stevens et al. 21282* (CAS, MO). Nueva Segovia: 10 km SE of Jalapa, 24 Dec. 1973, *Atwood et al. 6827a* (CAS, MO). Zelaya: along road from Bonanza (airstrip) through Constancia (mineshaft) to Laguna Siempreviva (dam), 23 Apr. 1978, *Stevens 8015* (CAS, MO). PANAMA. Bocas del Toro: Laguna de Chiriquí, 15 km oeste de Punta Cricamola, entrando Ensenada de Catavela, y subiendo Quebrada Nuri, 8°55′N, 81°49′W, 19 Mar. 1993, *Foster et al. 14602* (CAS, PMA). Coclé: Caribbean side of divide at El Copé, 80°35′W, 8°45′N, 4 Feb. 1983, *Hamilton & Davidse 2769* (CAS, MO, PMA). Colón: lumber road on Santa Rita east ridge, 23 Feb. 1968, *Correa & Dressler 748* (MO). Comarca de San Blas: trail from Puerto Obaldía inland towards Bongo, 24 Mar. 1985, *D'Arcy & McPherson 16142* (MO): Playón Chico, Río Ukupseni caminando por el Río Ukupseni, 09°15′N, 78°15′W, 30 Oct. 1991, *Herrera et al. 1024* (CAS, MO, PMA). Darién: Parque Nacional del Darién, ridge between N & S branches of Río Pucuro, across river from old Kuna village of Tacarcuna ca. 18 km E of Pucuro, 8°04′N, 77°16′W, 21 Oct. 1987, *Hammel et al. 16336* (CAS, MO, PMA). Panamá; along newly cut road from El Llano to Carti-Tupile, 12 miles above Pan-American highway, 13 Mar. 1973, *Croat 22899* (CAS).

DISCUSSION. — This species is defined by a number of diagnostic characters. The petals are rhombic-ovate to obovate and stellulate-puberulent abaxially (in part), the anthers are dorso-basally appendiculate, the thecae are laterally coherent for about 2/3 of their length and distinctly granulose along their lower ventral sides, and the ovary has a conspicuous fimbriate-lobulate stylar collar. This comparatively widespread species is variable in the density and persistence of the indument on cauline internodes, peduncles, and floral bracts. It is otherwise uniform in all other diagnostic features. The types of *T. allenii*, *T. cooperi*, *T. rosea*, and *T. urophylla*, taxa here relegated to synonymy, are good matches for typical *T. watsonii* in all diagnostic features. When Standley and Williams described *T. allenii* from Costa Rica they suggested a relationship with *T. urophylla* which is understandable in view of the taxonomy adopted here. Gleason also appears to have been unaware of *T. watsonii* when he described *T. rosea* from Belize because he compared it only to *T. calycularis* in the protologue. In his treatment of *Topobea* for Flora of Panama, Gleason (1958) recognized only *T. cooperi* and *T. urophylla*. His key to the genus suggests that he maintained these species based on a sparse furfuraceous indument for the former and an indument of barbellate hairs for the latter. Specimens from throughout the range of this species often have varying combinations and densities of these two indument types making Gleason's purported distinctions taxonomically insignificant.

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Literature Cited

Almeda, F. 1984. New and noteworthy additions to the Melastomataceae of Panama. Proc. Calif. Acad. Sci. 43(17):269–282.

———. 1990. New species and new combinations in *Blakea* and *Topobea* (Melastomataceae), with an historical perspective on generic limits in the tribe Blakeeae. Proc. Calif. Acad. Sci. 46(14):299–326.

———. 2000a. The hexandrous species of *Topobea* (Melastomataceae). Proc. Calif. Acad. Sci. 52(9):97–109.

———. 2000b. A synopsis of the genus *Blakea* (Melastomataceae) in Mexico and Central America. Novon 10:299–319.

———. 2001. Three new Mesoamerican species of *Topobea* (Melastomataceae). Brittonia 53(1):157–166.

Cogniaux, C. A. 1891. Mélastomacées. *In* Monographiae phanerogamarum, A. and C. de Candolle, eds. 7:1–1256. G. Masson, Paris.

Gleason, H. A. 1939. The genus *Clidemia* in Mexico and Central America. Brittonia 3:97–140.

———. 1958. Melastomataceae. *In* Flora of Panama, R. E. Woodson, Jr. and R. W. Schery, eds. Ann. Missouri Bot. Gard. 45:203–304.

Lumer, C. 2000. The reproductive biology of *Blakea* and *Topobea* (Melastomataceae). *In* Monteverde: Ecology and conservation of a tropical cloud forest, N. M. Nadkarni and N. T Wheelwright, eds. Oxford University Press, Oxford.

Standley, P. C. 1924. Melastomaceae. *In* Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23(4):1046–1074.

———. 1938. Melastomaceae. *In* Flora of Costa Rica. Field. Mus. Nat. Hist., Bot. Ser. 18(3):783–845.

Standley, P. C. and L. O. Williams. 1963. Melastomaceae. *In* Flora of Guatemala. Fieldiana, Bot. 24:407–525.

Walter, D. E. and H. C. Proctor. 1999. Mites: Ecology, evolution and behaviour. University of New South Wales Press Ltd., Sydney.

Winkler, S. 1965. Die Melastomataceae von El Salvador C. A. Bot. Jahrb. Syst. 83:331–369.

Wurdack, J. J. 1980. Melastomataceae. *In* Flora of Ecuador, G. Harling and B. Sparre, eds. 13:1–406.

———. 1993. Melastomataceae (*Topobea*). *In* Flora of the Guianas, A. R. A. Görts-van Rijn, ed. 13:9–21. Koeltz Scientific Books, Königstein.

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