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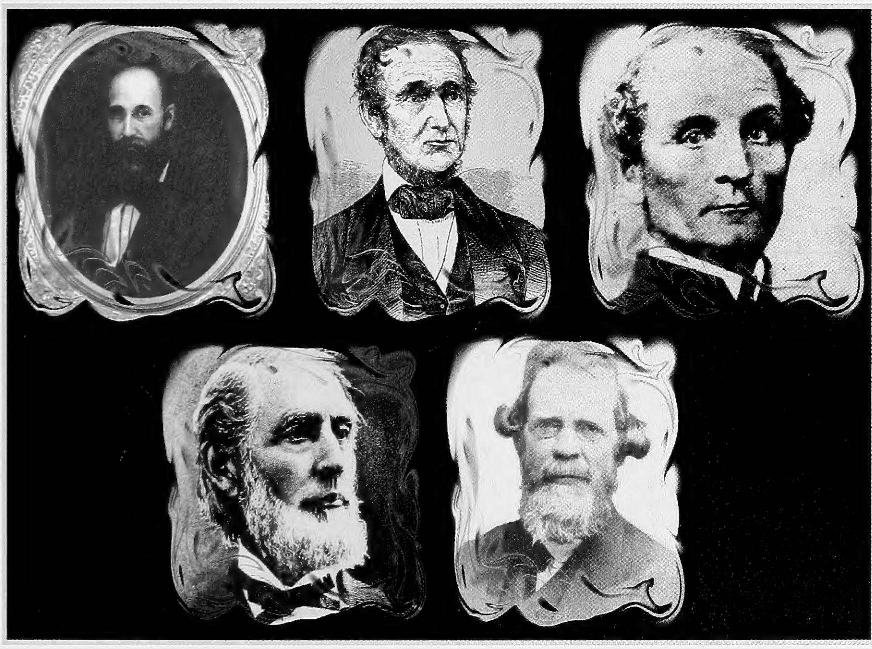

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A New Species of *Phyllodesmium* Ehrenberg, 1831 (Mollusca, Nudibranchia) from the Tropical Indo-Pacific

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This paper describes a new species of aeolidoidean nudibranch of the genus *Phyllodesmium* from the tropical Indo-Pacific. *Phyllodesmium parangatum* sp. nov. is known only from the type locality in the northern Philippines. At present, there are 16 nominal species of the genus *Phyllodesmium*, most of these described by Rudman (1981b, 1991) and Baba (1949, 1991). The most recently described species, *Phyllodesmium guamensis* (Avila et al., 1998), was named from specimens collected from Guam. *Phyllodesmium parangatum* is externally similar to *Phyllodesmium magnum* and *P. guamensis.* All three of these species have flattened cerata with curved apices and highly ramified digestive gland branches within the cerata. *Phyllodesmium parangatum* has significant internal differences that clearly distinguish it from the other two species. The presence of long radular denticles and elongate denticles on the cutting edge of the jaw are among the primary differences that differentiate this species from other members of the genus.

Rudman (1981b, 1991) provided a comprehensive account of the systematics and anatomy of species of *Phyllodesmium* (Facelinidae, Aeolidina) together with physiological and ecological aspects of the use of zooxanthellae to provide supplementary nutrition to these taxa. Variation in external color pattern, ceratal shape, digestive gland ramification, radular tooth denticulation, and anal position distinguish species within this aeolid genus. Sixteen species were identified in Rudman's (1981b, 1991) and Baba's (1949, 1991) descriptions. Only one additional species had been described since Rudman's review of the genus (Avila et al. 1998).

Recent collecting trips to the Philippine Islands have provided a wealth of material that has led to descriptions of many new doridoidean nudibranch taxa (Gosliner and S. Johnson 1994; Gosliner 1995, 1996; Gosliner and Behrens 1997, 1998a, 1998b; Gosliner and Fahey 1998; R. Johnson and Gosliner 1998; 2000; Gosliner and R. Johnson 1999; Fahey and Gosliner 1999; Elwood et al. 2000; Gosliner and Valdes 2001; Dorgan et al. 2001). Members of other opisthobranch clades have been collected but have not yet been studied systematically. Found in these collections are specimens of several undescribed species of the facelinid genus *Phyllodesmium.* The purpose of this study is to describe a new species of this genus from the tropical Indo-Pacific based on materials in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ), where type material is deposited.

Phyllodesmium parangatum Ortiz and Gosliner, sp. nov.

Figures 1–5

Material examined.— Holotype: California Academy of Sciences, CASIZ 106472, near Twin Rocks, Anilao, Batangas Province, Luzon, Philippines, 15 April, 1996, T.M. Gosliner. Paratypes: three specimens, two dissected, CASIZ 105657, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 25.3 m depth, 23 February 1995, TM.. Gosliner. One specimen dissected, CASIZ 105676, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 2.1 m depth, 27 February 1995, TM. Gosliner. One specimen, CASIZ 96325, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 13 March 1994, T.M. Gosliner.

Geographic range.— Known only from southern Luzon Island in the Philippines (present study).

Etymology.— The name of this species is derived from the Filipino words parang gatas, referring to the milky color of the living animals.

External morphology.— The body of the living specimens (Fig. 1) is elongate, extending broadly from the anterior to posterior end. The living animals range between 8–20 mm in length. Two preserved specimens examined (CASIZ 105657 and CASIZ 105676) measured 10.0 mm and 13.1mm respectively. The anterior end of the foot margin is broad and rounded, without prolonged corners of the foot, while the posterior end is somewhat blunt, rather than tapered. The elongate oral tentacles taper from the anterior edge of the head to form acutely pointed apices. The more blunt and thicker rhinophores are shorter than the oral tentacles and are smooth, but somewhat wrinkled in the distal half. This 30–40 thick cerata form a dense mass that largely covers the surface of the notum. The cerata are large and flattened in cross-section with an evenly curved apex that is acutely pointed at its tip. The more anterior cerata appear to be larger than more posterior ones.

The ceratal arrangement is complex with both single and double vertical rows inserted on distinctive ridges. There is one double row of precardiac cerata on each side of the body containing up a total of up to 14 cerata. On the right side, the genital aperture is found immediately below the precardiac double row. The renal opening is situated on the right side of the body, centered within the interhepatic space. The postcardiac cerata are arranged in vertical rows on both sides of the body. The first two postcardiac rows on the right side are separated by the anal papilla, which is located at the edge of the mantle, immediately behind the uppermost ceras of the first postcardiac row. There can be up to 15 cerata within each ceratal row. The remainder of the postcardiac cerata is arranged in clusters of double rows. There are about 6 postcardiac double rows, each one containing up to 10 cerata of various lengths.

Color.— The body color of living specimens varies only slightly between the six different individuals examined. The body wall ranges from a translucent white to an opaque milky yellow with a brownish tinge. On one of the specimens an opaque medial band of the digestive gland is visible from just behind the rhinophores to the posterior of its bluish colored body wall. The cerata often have a brownish tinge with dull white borders and apex or a milky yellow appearance with an off-white color on the upper half of their tips. The rhinophores and oral tentacles are translucent white or milky yellow in most of the specimens.

Cerata and Digestive Gland.— The cerata are flattened and smooth, terminating in a sharply curved ceratal apex. The digestive gland ducts extend throughout the cerata. Secondary branches occur perpendicular to the axis of the primary ceratal duct. Within each one of these secondary branches, tertiary branching occurs. These terminal branches extend in close proximity to

FIGURE 1. *Phyllodesmium parangatum* sp. nov. Living animal (CASIZ 105676).

the ceratal wall. Dense clusters of branches extend all along the central digestive duct and are visible through the translucent ceratal tissue (Fig. 2).

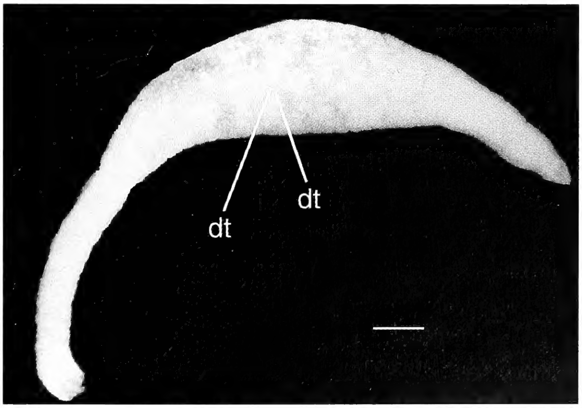

FIGURE 2. *Phyllodesmium parangatum* sp. nov. Single ceras with branching of digestive gland visible, dt = digestive gland tract. Scale bar = 0.1 mm.

BUCCAL ARMATURE.— The radular formula is 23 × 0.1.0 and 24 × 0.1.0 in two specimens examined. Each tooth consists of a narrow and somewhat short base extending to the posterior edge of the tooth in front (Figs. 3A, 4C). The central cusp is short and triangular with an acutely pointed apex. On the ventral portion of the tooth a thick rib extends from the apex of the central cusp to the posterior end of the tooth (Fig. 3B). This rib probably provides structural support for the tooth as it widens abruptly near the posterior margin of the tooth. Denticulation extends only halfway along the edge of the margin on each tooth. On each side of the radular tooth, there are 13 to 17 thin, elongate denticles with acutely pointed apices (Figs. 3C, 4D). The denticles are well-separated from each other or may be more closely spaced. The length of the denticles varies considerably. In general more basal denticles are shorter than those in closer proximity to the central cusp. The jaws (Fig. 4A) are thick and elongate, widest anteriorly. The cutting edge of the jaw plate has 8 well-separated triangular denticles that are acutely pointed distally. The lowermost denticles are more

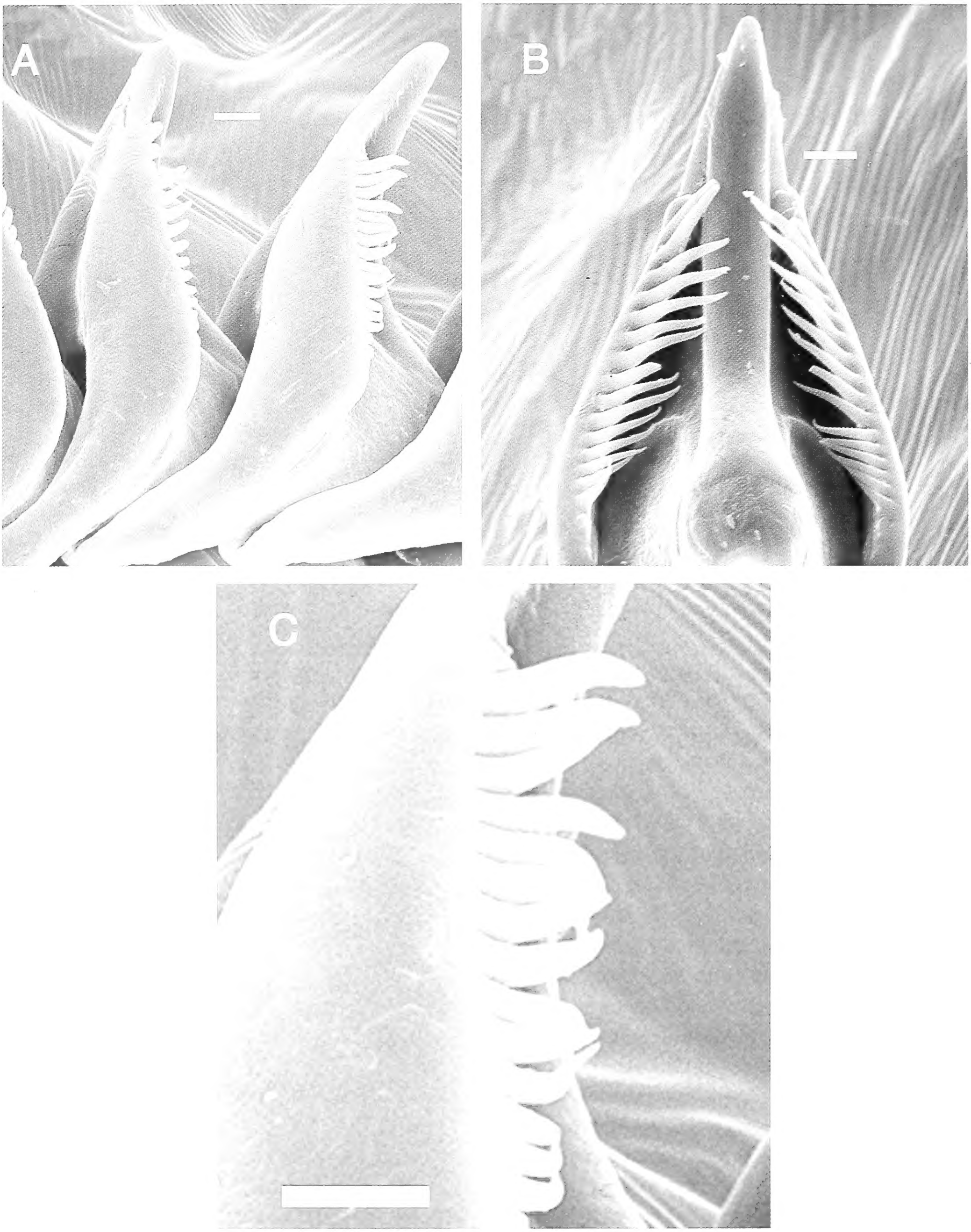

FIGURE 3. *Phyllodesmium parangatum* sp. nov. (CASIZ 105676). Scanning electron micrographs of radula. A. Lateral view of radula, scale bar = 30 µm. B. Ventral view of radular tooth, scale bar = 30 µm. C. Denticulation of masticatory margin of tooth, scale bar = 30 µm.

elongate and become successively shorter near the jaw apex (Fig. 4B).

REPRODUCTIVE SYSTEM.— The reproductive organs are arranged as a simple androdiaulic system (Fig. 5). A very long and narrow preampulla extends into a much shorter, convoluted

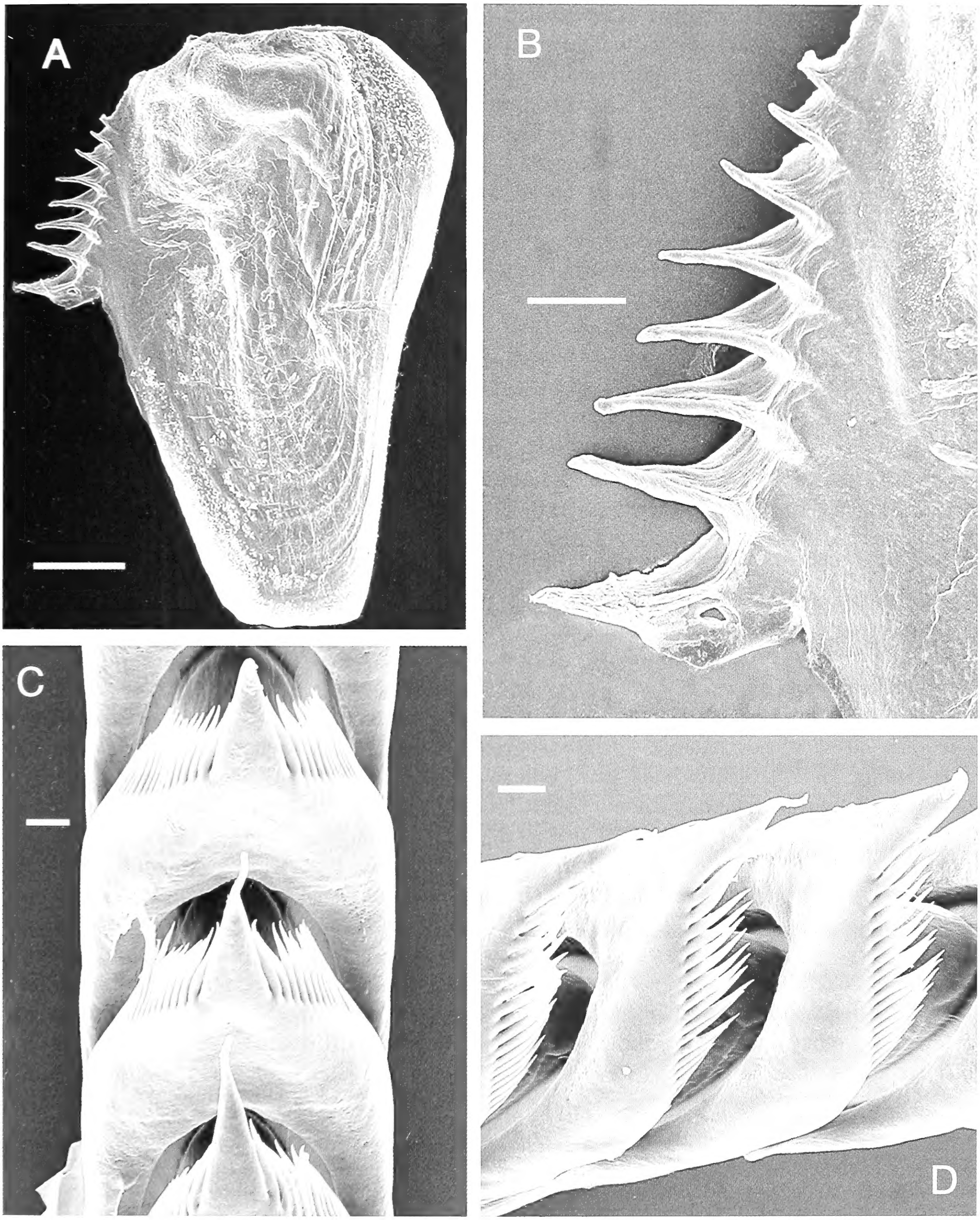

FIGURE 4. *Phyllodesmium parangatum* sp. nov. (CASIZ 105657). Scanning electron micrographs: A. Jaw, scale bar = 0.25 mm. B. Masticatory margin of jaw, scale bar = 0.08 mm. C. Dorsal view of radula, scale bar = 30 µm. D. Lateral view of radula, scale bar = 30 µm.

ampulla. The ampulla again narrows and divides into the vas deference and oviduct. The oviduct enters the female gland mass adjacent to the elongate, pyriform receptaculum seminis. The female gland mass was not fully mature in the any of the specimens dissected. The male duct is long, convolute, and massive. It extends from its division from the ampulla into the short, straight prostate, which is situated adjacent to the small, folded female gland mass. The vas deferens expands into a curved muscular duct that widens into the muscularized penial bulb. The penial bulb does not contain a distinct penial papilla and is devoid of any cuticularization or armature.

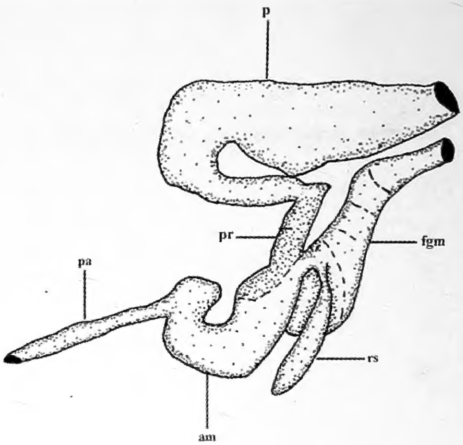

FIGURE 5. *Phyllodesmium parangatum* sp. nov. (CASIZ 105676). Reproductive system, am = ampulla, fgm = female gland mass, p = penis, pa = preampullary duct, pr = prostate, rs = receptaculum seminis. Scale = 0.5 mm.

DISCUSSION

Phyllodesmium parangatum sp. nov. is externally similar to *Phyllodesmium magnum* Rudman (1991) and *Phyllodesmium guamensis* Avila, Ballesteros, Slattery, and Paul (1998). All three species have curved ceratal apices and highly branched digestive gland tissue within the cerata. The distinctive elongate radular denticles, the large and elongate denticles on the cutting edge of the jaw, the vertical postcardiac rows along its dorsum and the position of the anal papilla (which lies at the edge of the mantle immediately behind the uppermost cerata of the first postcardiac row), distinguish *P. parangatum* from the other two species.

Phyllodesmium magnum is a larger species, reaching approximately 40mm in length. It lacks denticles on its radular teeth, has elongate rhinophores, and a smooth masticatory margin of the jaw (Rudman 1991, present study). These characteristics clearly differentiate *P. magnum* and *P. parangatum*. *Phyllodesmium guamensis* (Avila et al., 1998) may be distinguished from *P. parangatum* by its brownish grey body color, a double row of short denticles on the radular teeth, a smooth masticatory margin of the jaw.

Other species of *Phyllodesmium* have external differences that clearly distinguish them from *P. parangatum*. *Phyllodesmium iriometense* (Baba,1991) has a translucent white body more simply branched digestive gland within the cylindrical, straight cerata, postcardiac ceratal arches, an anal papilla on inside of the first postcardiac ceratal arch and tentacular anterior corners of the foot. None of these features are present in *P. parangatum*. *Phyllodesmium horridum* (Macnae, 1954) and *Phyllodesmium serratum* (Baba, 1949) have pink pigment on the cerata and a pink longitudinal medial line on the notum. They also have more simply branched digestive gland ducts and tentacular anterior corners of the foot. *Phyllodesmium opalescens* (Rudman, 1991) has opaque white medial diamonds on the notum and blue pigment on the ceratal apices, rhinophores and oral tentacles that are absent in *P. parangatum*. *Phyllodesmium opalescens* also has simple, undivided digestive gland ducts within the cerata. *Phyllodesmium pecten* (Rudman, 1981), *Phyllodesmium crypticum* (Rudman, 1981) and *Phyllodesmium hyalinum* (Ehrenberg, 1831) possess nodulose cerata and an arch rather than a double row of cerata in the first precardiac cluster.

Phyllodesmium macphersonae (Burn, 1962) possesses few ceratal clusters, cylindrical cerata and is very small in size. *Phyllodesmium longicirrum* (Bergh, 1905) also differs from *P. parangatum* by its large body size (up to 100 mm in length) by the absence of denticles on the small radular teeth, a small number of ceratal clusters and the large ceratal surface area. *Phyllodesmium kabiranum* (Baba, 1991) can be distinguished by from *P. parangatum* by radular teeth with a short cusp, flanked by short denticles, the presence of precardiac ceratal arches, nodular cerata and an anal papilla on outside of postcardiac ceratal group. *Phyllodesmium briareum* (Bergh, 1896) and *Phyllodesmium colemani* (Rudman, 1991) differ in having a narrow anterior foot, long, smooth rhinophores, smooth cutting edge of jaw and longer radular denticles.

ACKNOWLEDGMENTS

Ángel Valdés aided in preparing some specimens for scanning electron microscopy (SEM). Gary Williams and Ángel Valdés made valuable comments on several drafts of the manuscript. We thank them for their valuable comments, suggestions and support.

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Mistaken Identities: On the Discodorididae Genera *Hoplodoris* Bergh, 1880 and *Carminodoris* Bergh, 1889 (Opisthobranchia, Nudibranchia)

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The phylogenetic status of the two discodoridid genera *Hoplodoris* and *Carminodoris* has been uncertain due to the lack of distinguishing generic features and lack of complete anatomical descriptions. Recent examination of discodoridid specimens from the type localities provides further anatomical detail that allows for a comparison of the two genera. There are few morphological characters that can be used to justify two distinct genera. Analyses indicate that the genus *Carminodoris* is a junior synonym of *Hoplodoris*. *Hoplodoris desmoparypha* Bergh, 1880, *C. mauritiana* Bergh, 1891 and *C. grandiflora* (Pease, 1860) are conspecific with *H. grandiflora* having priority. *Hoplodoris novaezelandiae* (Bergh, 1904) and *H. nodulosa* (Angas, 1864) are conspecific. *Carminodoris nodulosa,* misidentified by Kay and Young, 1969 from Hawaii, and *Carminodoris bifurcata* Baba, 1993 are conspecific and quite distinct from other species of *Hoplodoris*. *Hoplodoris armata* (Baba, 1993), *H. bifurcata* (Baba, 1993), *H. estrelyado* Gosliner and Behrens, 1998, *H. grandiflora* (Pease, 1860) and *H. nodulosa* (Angas, 1864) are valid species. Additionally, *Geitodoris* is closely related to *Hoplodoris* but more basally situated than *Hoplodoris*. Important diagnostic morphological characters of *Hoplodoris* that have been inherited from a common ancestor include penial hooks and denticulate radular teeth. Two new species of *Hoplodoris* are described. *Hoplodoris flammea* sp. nov. is known from Bali, Indonesia and *Hoplodoris bramale* sp. nov. is from the Pacific coast of Costa Rica, the latter representing the first record of *Hoplodoris* from the eastern Pacific.

Numerous recent publications have dealt with the taxonomy and systematics of certain genera within the Discodorididae Bergh, 1891. These publications all agree that the systematic placement of the genera *Hoplodoris* and *Carminodoris* is problematic. The difficulty begins to a large degree with the description of each genus. For example, Bergh's original descriptions (1880, 1889 respectively) did not include details of the external morphology or coloration found on the living animals. The descriptions also did not include details of the reproductive system, particularly in the case of *Carminodoris.* For instance, there is no illustration of the female reproductive organs for this genus. Diagnostic details are also missing for *Hoplodoris,* such as the ampulla that is not illustrated.

The absence of additional specimens for comparison from either type locality or from other geographic areas has added to diagnostic difficulties. For both genera, the type species have neither been collected nor described in detail since the 1880s.

The present study has been undertaken for three reasons. First, several specimens of Discodorididae from or near the type localities of the type species of *Carminodoris* (Mauritius) and *Hoplodoris* (Palau) are in the collections of the California Academy of Sciences (designated as

CASIZ) and the Australian Museum, Sydney (designated as C). Upon examination of these specimens, it became apparent that they conform largely to the original descriptions presented by Bergh 1889, with further key anatomical details becoming obvious using more powerful microscopy. These specimens are described here and illustrated. Also, examination of recently collected specimens of *Hoplodoris* revealed two new species whose combination of morphological characters differ markedly from previously described species. These two new species are described herein.

The second reason for this study is that modern phylogenetic techniques have not been previously used to separate closely related taxa within the Discodorididae. Valdés presented the first phylogeny that included all Discodorididae although in his study, he did not include all species of each genus. In the present study, we use morphological characters derived from all described species of *Hoplodoris* and *Carminodoris* and apply the criterion of maximum parsimony to determine their systematic placement.

Finally, Valdés' recent publication (2002) of the systematics of the Cryptobranchia allows us to compare morphological characters of *Hoplodoris* and *Carminodoris* to determine which are plesiomorphic, due to common ancestry, and which may be the result of independent acquisition. In his publication, Valdés (2002) also provides further description of two additional type species of Discodorididae *Discodoris boholiensis* Bergh, 1877 and *Geitodoris planata*, that we were able to use in our analysis.

SPECIES DESCRIPTIONS

Family Discodorididae Bergh, 1891

Genus *Hoplodoris* Bergh, 1880

Type species *Hoplodoris desmoparypha* Bergh, 1880, by monotypy. = Carminodoris Bergh, 1889.
Type species *Carminodoris mauritiana* Bergh, 1891, by monotypy.

***Hoplodoris grandiflora* (Pease, 1860)**
Figs. 1–16

= *Doris grandiflora* Pease, 1860:30–31.
= *Doris grandifloriger* Abraham, 1877:206.
= *Hoplodoris desmoparypha* Bergh, 1880:51–56, pls. A–F.
= *Carminodoris mauritiana* Bergh, 1891:818–821, pl. 80, fig. 27, pl. 81, figs. 1–12.
= *Dendrodoris grandiflora* (Pease, 1860) in Pruvot-Fol, 1947:108.
Carminodoris grandiflora (Pease, 1860) in Kay & Young, 1969:185–186, fig. 12
= *Hoplodoris* sp. in Ono, 1999:114, fig. 186.

REMARKS ON SYNONYMY.— The name *Doris grandiflora* Pease, 1860 is a primary junior homonym of *Doris grandiflora* Rapp. Rapp's species is now placed in *Dendrodoris* and Pease's species is placed in *Hoplodoris*. Since these species have been considered as being in different genera after 1899, Article 23.9.5 of the International Code of Zoological Nomenclature states that these junior homonyms should not automatically be replaced. Both names have been in common usage and suppressing either would be disruptive, thus both names should be retained.

MATERIAL EXAMINED.— CASIZ 070388, one specimen, dissected, 44 mm, Saint Gilles les Bains, Reunion. Collected by T.M. Gosliner, 20 April 1989; CASIZ 073243, two specimens, dissected, 18 & 23 mm, Ile Saint Marie, Madagascar. Collected by H. Chaney, 5 April 1990; CASIZ 099336, one specimen, dissected, 30 mm, Mtwara Region, Tanzania. Collected by T.M. Gosliner, 4 November 1994; CASIZ 071866, one specimen, dissected, 44 mm, Sumilon Island, Philippines. Collected by G. Cornfield, 11 November 1987; CASIZ 109746, six specimens, two dissected, Island Reef, Ngermutideck, Palau. Collected by L. Sharon, 20 September 1996; CASIZ 068657, one specimen, 17 mm, Daphne's Reef, between Wongat and Sinub Islands, Madang, Papua New Guinea. Collected by T.M. Gosliner, 15 August, 1989; CASIZ 075106, one specimen, dissected, 54 mm, Kaneohe Bay, Oahu, Hawaii. Collected by T.M. Gosliner, 1 March 1991; CASIZ 075164, one specimen, 30 mm, Hawaii. Collected by T.M. Gosliner, 1 December 1991; CASIZ 093684, one specimen, 4 mm, Hekili Point, Maui, Hawaii. Collected by C. Pittman, 1 October 1993; CASIZ 089650, one specimen, 16 mm, Hekili Point, Maui, Hawaii. Collected by C. Pittman, 26 September 1993; CASIZ 117374, one specimen, dissected, 48 mm, Hawaii Kai Marina, Oahu, Hawaii. Collected by D. Takaoka, 17 February 1999; CASIZ 106475, one specimen, dissected, 25 mm, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 24 April 1996; CASIZ 106563, one specimen, 13 mm, Kasai Beach, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 25 April 1996; CASIZ 106435, one specimen, 10 mm. Kasai Beach, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 25 April 1996.

DISTRIBUTION.— This species is known from Hawaii (present study), from the Philippines (present study), Tanzania (present study), Palau (present study), Mauritius (Bergh 1891), Kerama Island and from Madagascar (present study).

EXTERNAL MORPHOLOGY (Fig. 1).— The preserved animals range from 23–55 mm in length. The body is oval, flat and the notum is covered with large, rounded tubercles that decrease in size towards the mantle edge. The rhinophores are closely-set and stout, with a knob-shaped lamellar region (10–15 lamellae) that terminates in a point. The low rhinophore sheaths have an irregular edge and small tubercles on the sides. The six main gill leaves are tripinnate, feathery and the tubercle-covered sheath has a scalloped edge.

The ground color of the notum is light to medium mottled brown or tan. Lateral to either side of the dorsal median on some specimens are evenly spaced clumps of darker tubercles (Fig. 1E). Some specimens have dark spots near the mantle edge (Fig. 1F) or have areas of white tubercles that appear as perpendicular rays along the mantle edge (Fig. 1D). The clumps of dark tubercles merge on some specimens into a dark ring (Fig. 1B). On the knobby tops of some tubercles, the brown coloration appears worn off and whitish coloration is visible (Fig. 1A). The gill leaves are lighter tan than the body color, with a frosted appearance on the tips. The rhinophores are also lighter tan than the body and the tips are white.

On the ventral side of some preserved specimens, dark spots are sprinkled randomly. The digitate oral tentacles have also retained some of the dark speckles, and the oral tube has dark coloration. The foot is notched at the anterior end.

BUCCAL ARMATURE.— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets (Figs. 2A–B, 3A–B, 4A, 7A, 8A–B). The radular formulae of the specimens dissected are 30 × 70.0.70 30 × 116.0.116 (CASIZ 070388), 33 × 60.0.60 (CASIZ 073243, specimen 1). 27 × 40.0.40 (CASIZ 073243, specimen 2), 30 × 60.0.60 (CASIZ 099336), 32 × 75.0.75 (CASIZ 071866), 30 × 70.0.70 (CASIZ 075106) and 26 × 41.0.41 (CASIZ 106475). The innermost lateral teeth are hamate, with no denticles visible on either edge (Figs. 3C, 4B), but some specimens have 6–7 minute denticles visible on the inner and outer edges (Figs. 5A, 8C). The middle radular teeth have a more elongate cusp, with small denticles (Figs. 2C–F) with up to 14 minute denticles (Figs. 5B–D) on the outer edge. The outer lateral teeth have small denticles (Figs. 2F, 3F, 4D, 5C, 7E) and the two or three penultimate lateral teeth are much shorter than the others, and are hamate (Figs. 2F, 3F, 4F, 5C, 6C, 7D–E, 8F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Figs. 9A, 12, 15). The ampulla is thick and tubular and lies tightly between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas

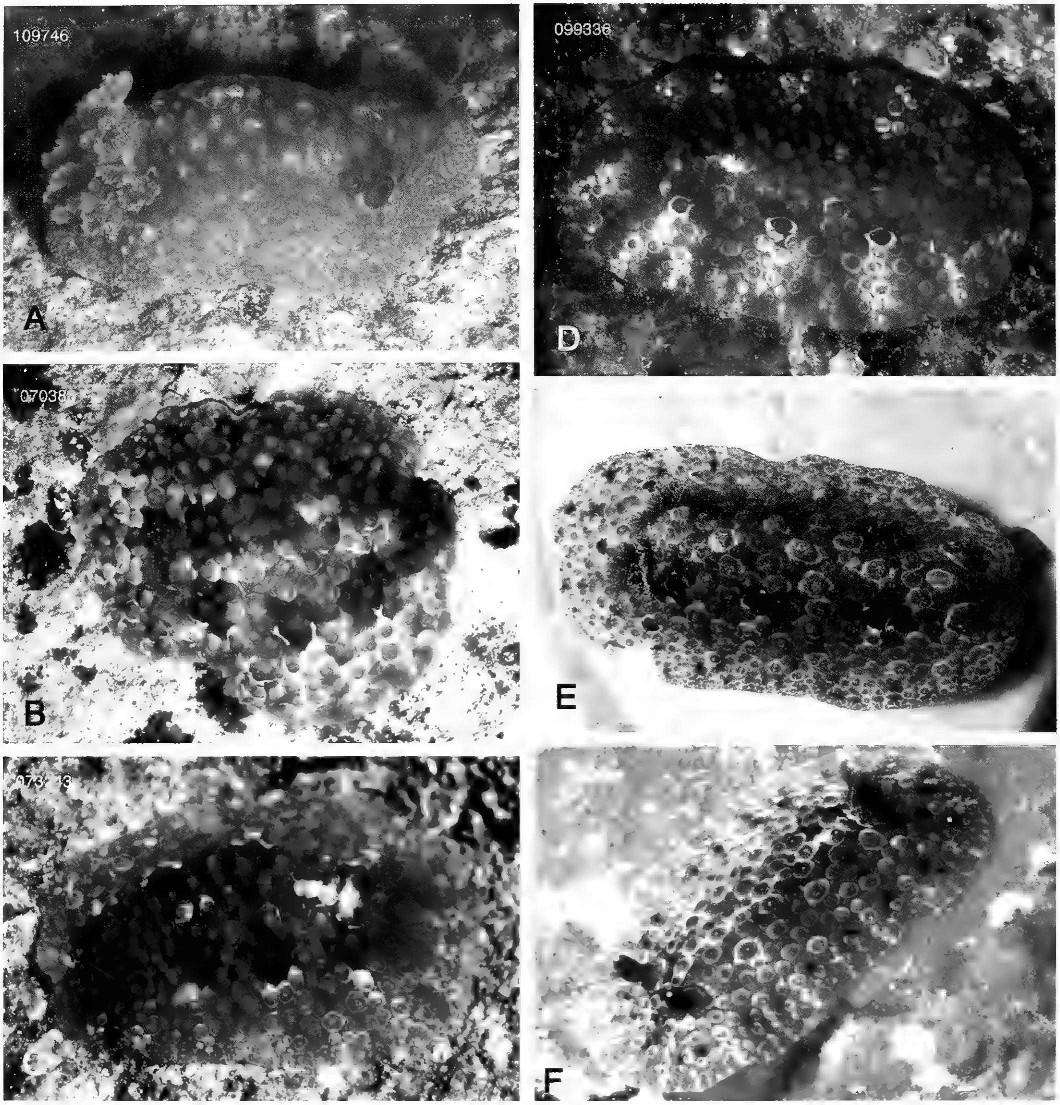


Figure 1. *Hoplodoris grandiflora*. Living animals. – A. Palau (CASIZ 109746) 40 mm. Photo taken by T.M. Gosliner. – B. Reunion (CASIZ 070388) 44 mm. Photo taken by T.M. Gosliner. – C. Madagascar (CASIZ 073243) 23 mm. Photo taken by T.M. Gosliner. – D. Tanzania (CASIZ 099336) 30 mm. Photo taken by T.M. Gosliner. – E. Hawaii (CASIZ 075106) 54 mm. Photo taken by T.M. Gosliner. – F. Hawaii (CASIZ 093684) 4 mm. Photo taken by P. Fiene.

deferens. The short oviduct enters the female gland mass. The prostate is a large mass which narrows into the long, highly convoluted, deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the vagina. The penis is armed on the inside with short, pointed thorn-like structures (Figs. 10A–D, 13A–B, 16A–B).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the duct that connects the receptaculum seminis to the bursa copulatrix. This duct is moderately short. The pyriform receptaculum seminis is nearly one-third the size of the bursa copulatrix.

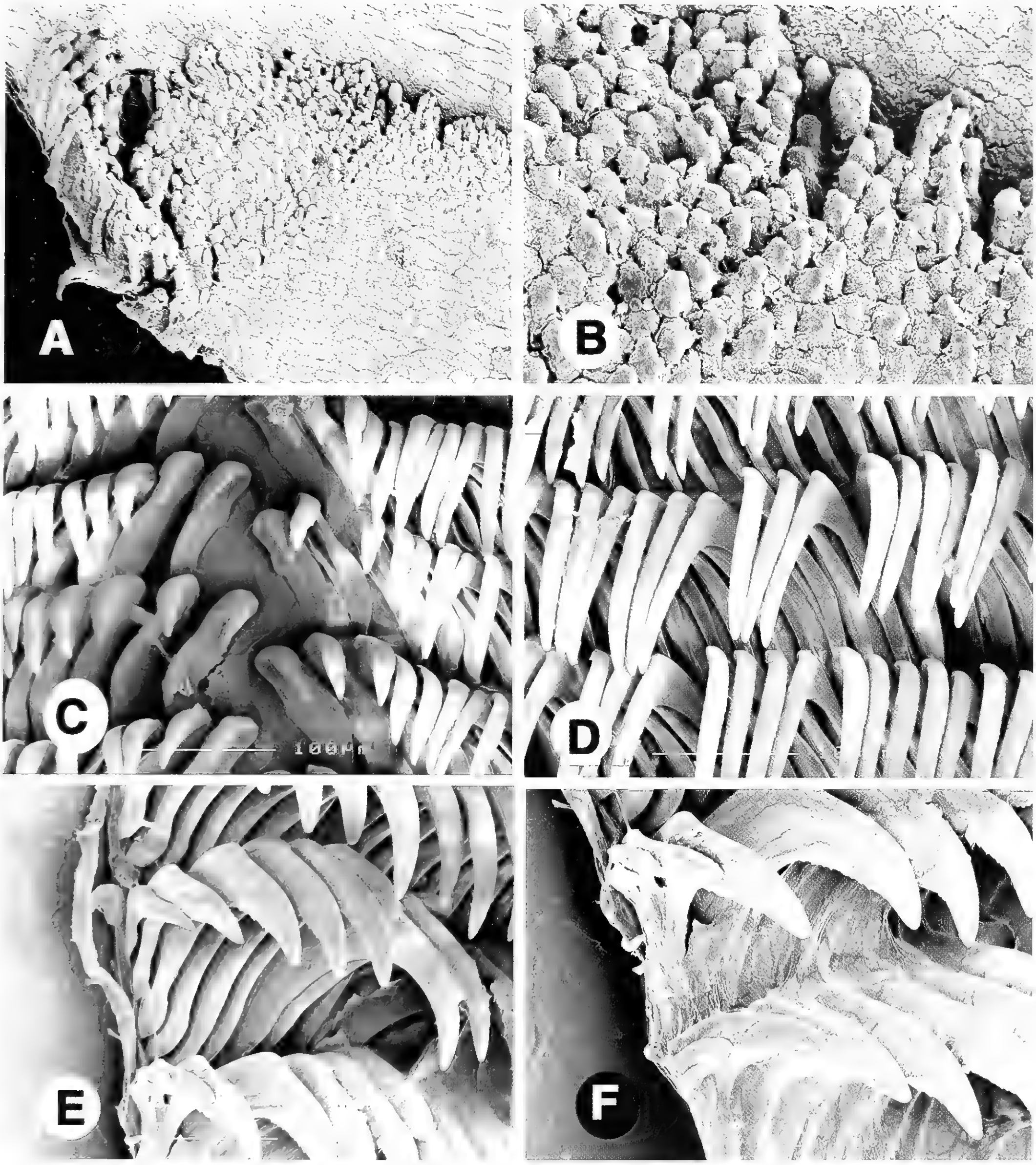


FIGURE 2. *Hoplodoris grandiflora* Palau (CASIZ 109746) radula. – A. Labial rods. Scale bar = 1 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 100 µm. – D. Middle lateral teeth. Scale bar = 100 µm. – E. Outer lateral teeth. Scale bar = 10 µm. – F. Outer lateral teeth, close-up. Scale bar = 10 µm.

The bursa is partially enveloped by the prostate. The moderately long, thin, convoluted vaginal duct emerges from the base of the bursa then widens into the vagina. The vagina is also armed with small hooks (Figs. 11, 13C, 16C–D).

At the genital atrium, is a long, tubular, blind-ended vestibular gland. This gland has a convoluted, narrow region just prior to a bulb-like terminus at the opening into the genital atrium. Inside the bulb-like terminus is a hollow stylet (Figs. 10F, 13D, 14, 16E–F).

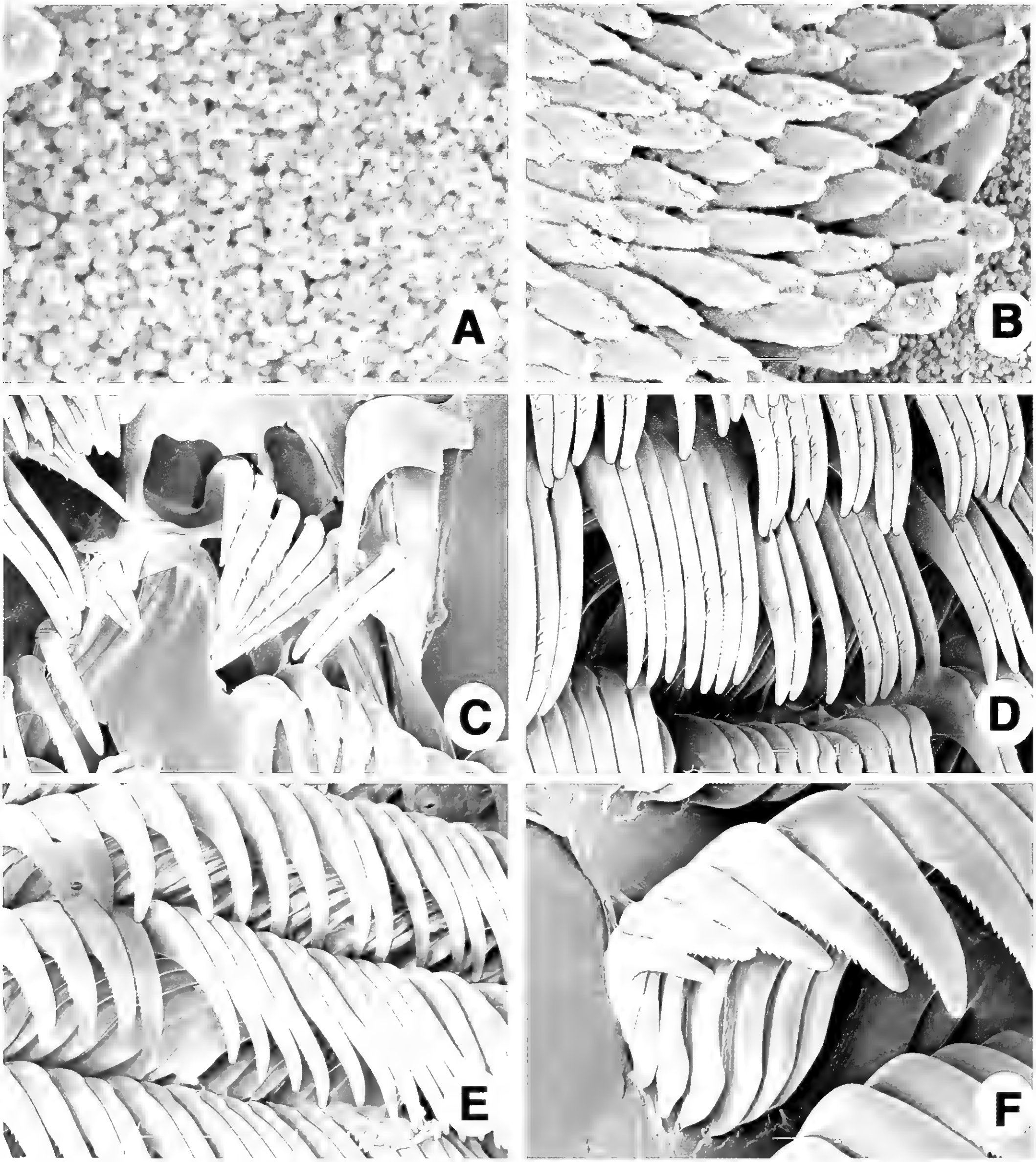


FIGURE 3. *Hoplodoris grandiflora* Reunion (CASIZ 070388) radula. Scale bar = 1µm. A. Labial rods. Scale bar = 1 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 10 µm. – D. Middle lateral teeth. Scale bar = 10 µm.– E. Middle lateral teeth. Scale bar = 100 µm. – F. Outer lateral teeth. Scale bar = 10 µm.

REMARKS.— Since Bergh's (1880) original description of *Hoplodoris*, several authors have recently described the characters that unite the genus. Thompson (1975), Miller (1991), and Valdés (2002) each provided an elaboration of Bergh's 1880 diagnostic of the genus *Hoplodoris*. Gosliner and Behrens (1998) and Miller (1991) provided further details on the anatomy of the type species *Hoplodoris desmoparypha*. Burn (1969) also used some of the generic diagnostics to place *Doris nodulosa* within the genus *Hoplodoris*.

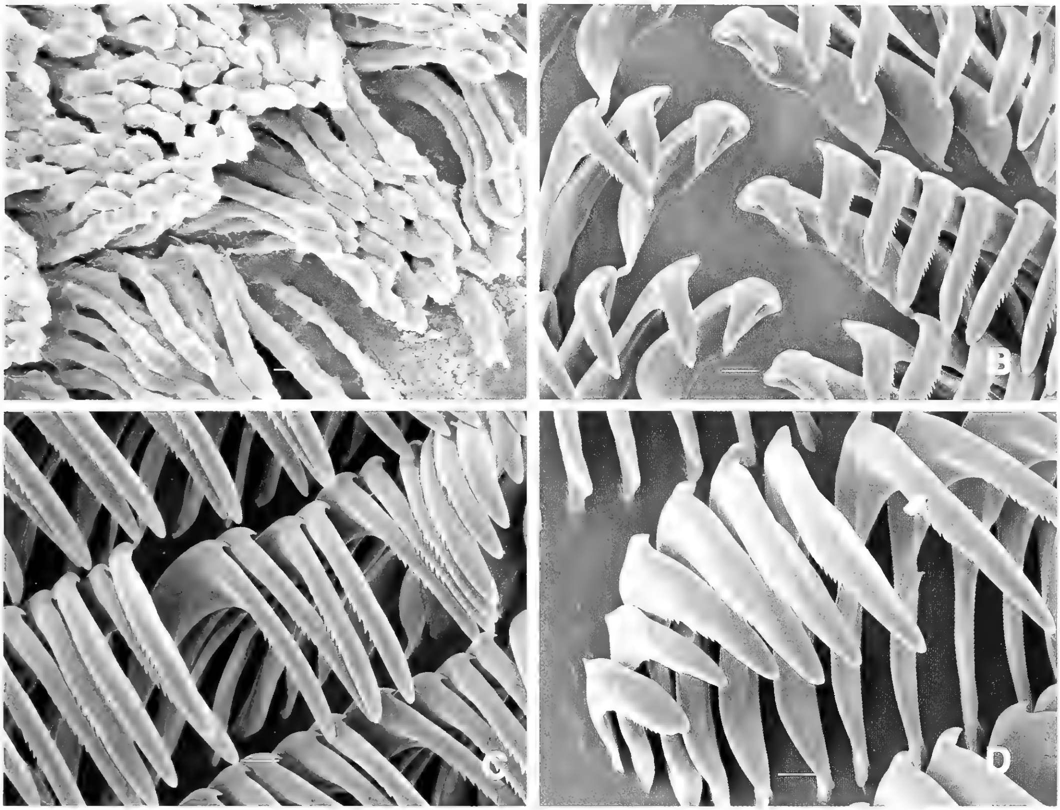


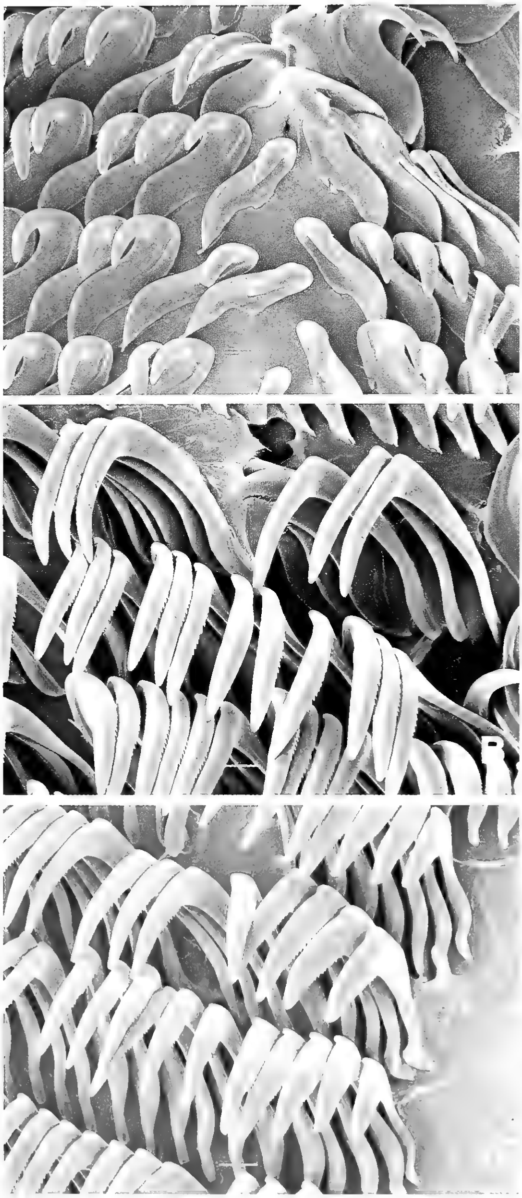
FIGURE 4. *Hoplodoris grandiflora* Philippines (CASIZ 071866) radula. – A. Labial rods. Scale bar = 10 µm. – B. Inner lateral teeth. Scale bar = 100 µm. – C. Middle lateral teeth. Scale bar = 100 µm. – D. Outer lateral teeth. Scale bar = 10 µm.

The same authors also discussed the similarities between *Hoplodoris* and the genus *Carminodoris*. In addition to these authors, Kay and Young (1969) briefly mentioned some characters of *Carminodoris* in their account of two species from Hawaii (*C. grandiflora* and *C. nodulosa*).

The difficulty in distinguishing these two genera has been primarily due to the deficiencies of the original descriptions and the absence of additional specimens of the type species since the 1880's. However, the examination of discodoridid specimens housed at the California Academy of Sciences and the Australian Museum, Sydney, that were collected from or near the type localities of *Hoplodoris* and *Carminodoris* provided further anatomical information on both genera. Recent collections of *Hoplodoris* specimens from Bali and Costa Rica also provided further insight to the varied morphology of this genus.

From our examination we are certain that our specimens from Palau do in fact represent the animals Bergh described in 1880 as *Hoplodoris desmoparypha*. They match almost all features included by Bergh in the original description. There are two primary differences we noted with our specimen. One is that some of the outer lateral teeth have very minute denticles on their outer edge, that are nearly impossible to see even with a modern compound microscope. We observed them only by high power scanning electron microscopy (SEM). The second difference is the presence of an armed vagina in our material. This feature could easily have been missed by Bergh (1880).

Our specimens from Madagascar and Tanzania match all features of Bergh's (1889) original



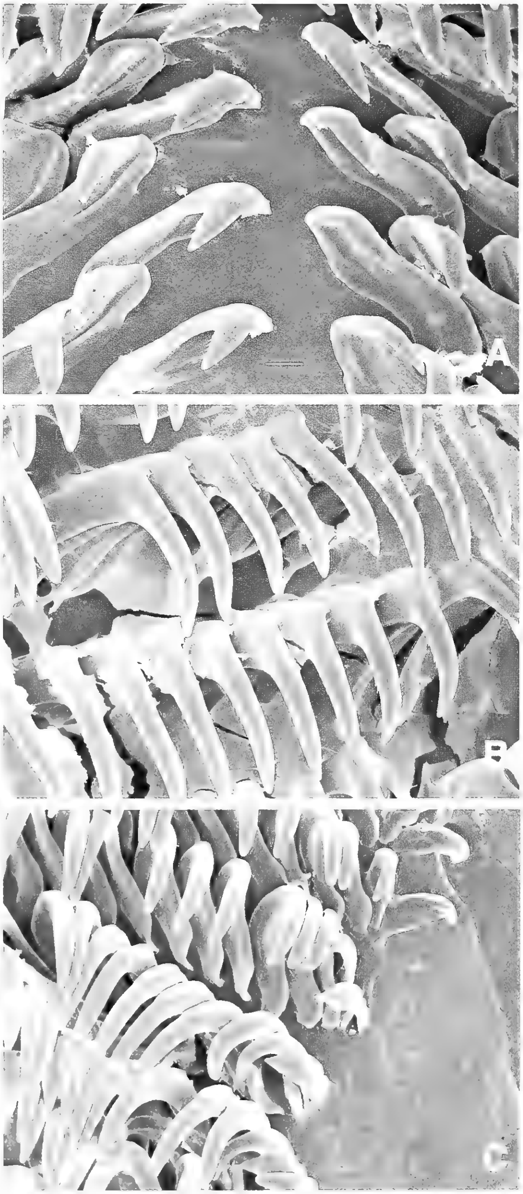


FIGURE 5 (Left). *Hoplodoris grandiflora* Madagascar (CASIZ 073243) radula. – A. Inner lateral teeth. Scale bar = 10 µm. – B. Middle lateral teeth. Scale bar = 100 µm. – C. Outer lateral teeth. Scale bar = 10 µm.

FIGURE 6 (Right). *Hoplodoris gandiflora* Philippines (CASIZ 106475) radula. – A. Inner lateral teeth. Scale bar = 100 µm. – B. Middle lateral teeth. Scale bar = 100 µm. – C. Outer lateral teeth. Scale bar = 10 µm.

description of *Carminodoris mauritiana*. Although the only drawing of the reproductive organs that Bergh provided was of the armed penis, we observed a vestibular gland that contains a spine. In Bergh's (1889) description of *C. mauritiana*, he mentioned a special gland that seemed to open near the mucus gland at the genital opening. It is likely that this "special gland" is the vestibular gland that we found in our specimens. We also observed an armed vagina that Bergh could have over-

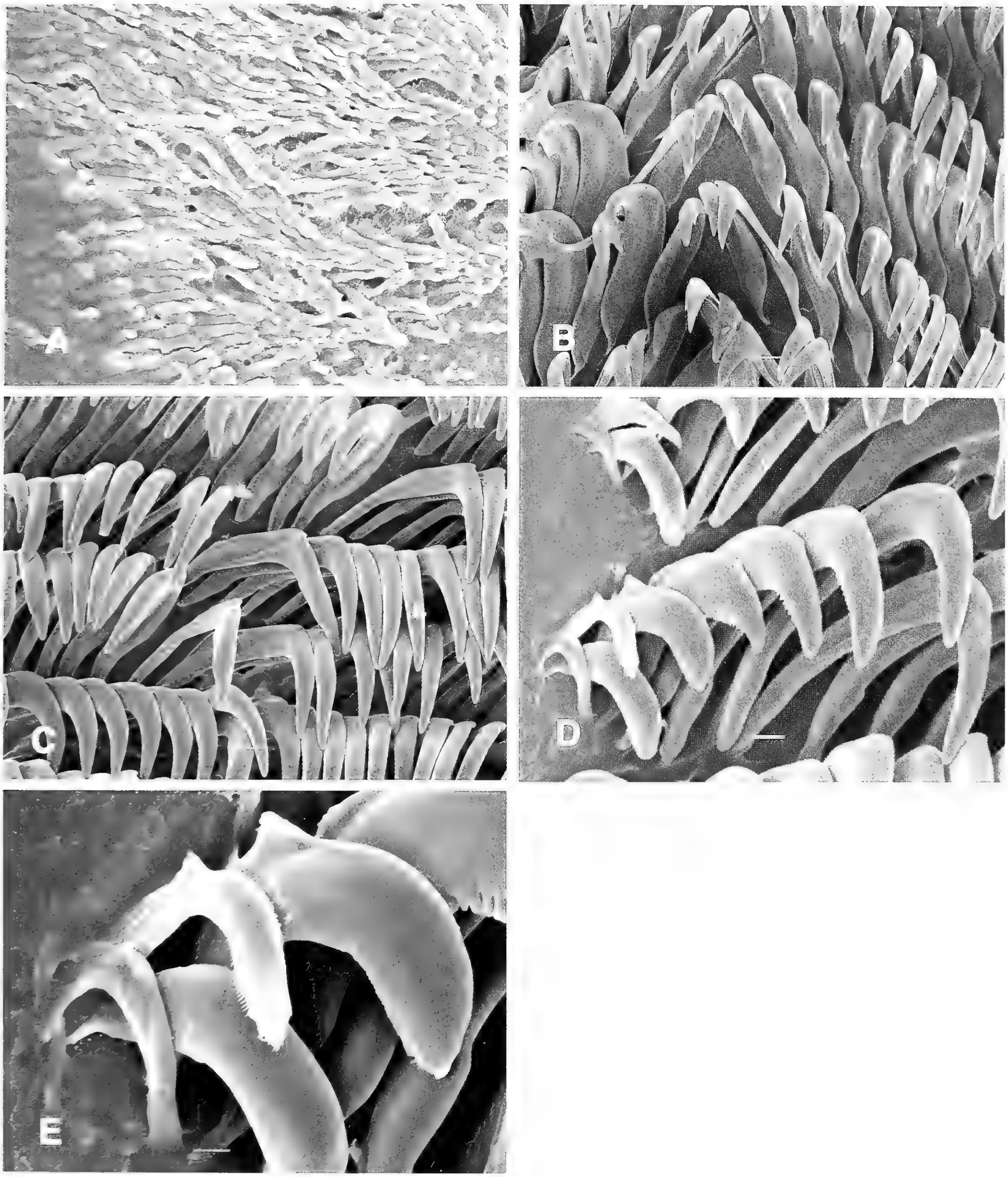


FIGURE 7. *Hoplodoris grandiflora* Hawaii (CASIZ 117374) radula. – A. Labial rods. Scale bar = 1 μm. – B. Inner lateral teeth. Scale bar = 10 μm. – C. Middle lateral teeth. Scale bar = 100 μm. – D. Outer lateral teeth. Scale bar = 10 μm. – E. Outer lateral teeth, close-up. Scale bar = 1 μm.

looked in his examination. With the addition of these probably overlooked characters, Bergh's descriptions of *Hoplodoris desmoparypha* and *Carminodoris mauritiana* are nearly identical.

In addition, the specimen we examined from Hawaii (the type locality of *Carminodoris grandiflora*) matches the description of this species by Pease and Kay and Young . These descriptions match those of Bergh's for *C. mauritiana* in all respects, when taking into consideration the armed

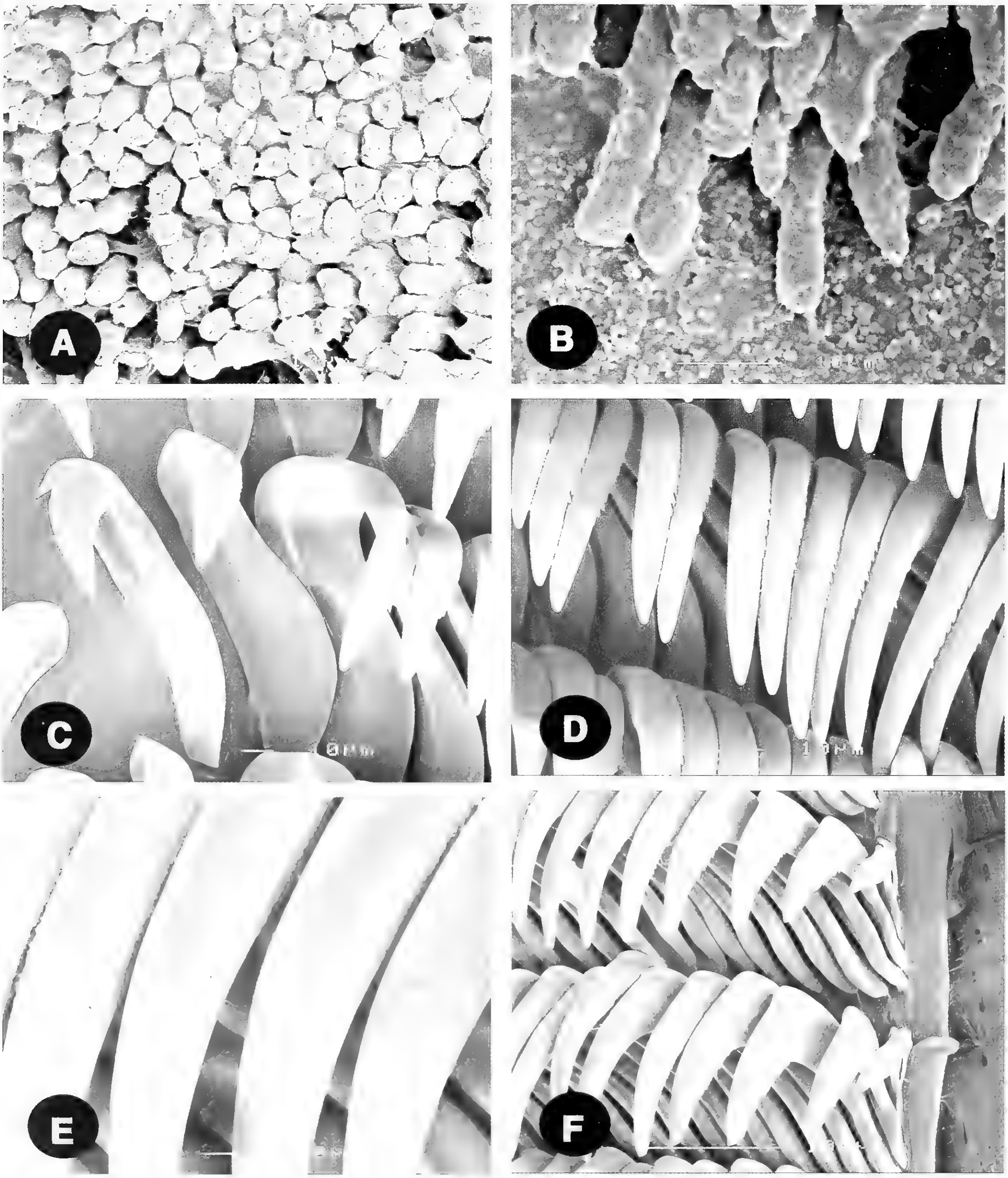


FIGURE 8. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) radula. – A. Labial rods. Scale bar = 10 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 10 µm. – D. Middle lateral teeth. Scale bar = 10 µm. – E. Middle lateral teeth, close-up. Scale bar = 10 µm. – F. Outer lateral teeth. Scale bar = 100 µm.

vagina. All three species, *Hoplodoris desmoparypha, C. mauritiana* and *C. grandiflora* appear to be the same, with the variations that we found due to our more advanced microscopic techniques. The phylogenetic analyses performed during this study also confirm that these three species remain a trichotomy when using maximum parsimony as an optimality criterion (see the following phylogenetic analysis).

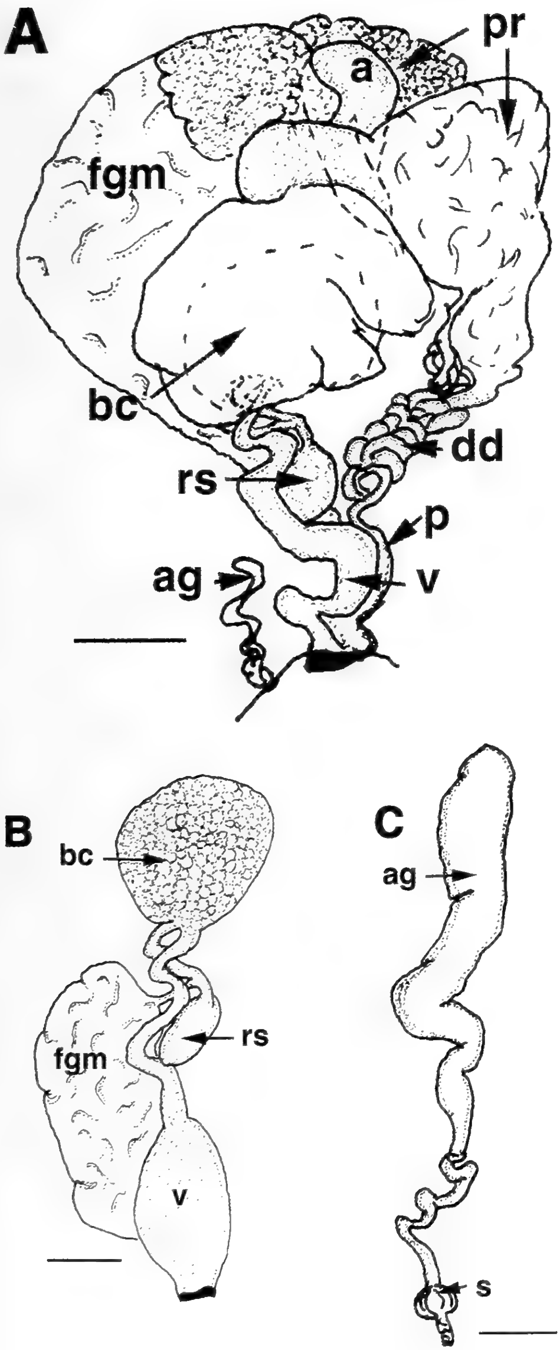


FIGURE 9. *Hoplodoris grandiflora* Palau (CASIZ 109746) reproductive system. – A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. – B. Schematic expansion of female reproductive organs. Scale bar = 0.5 mm. – C. Schematic expansion of accessory gland. Scale bar = 0.14 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina.

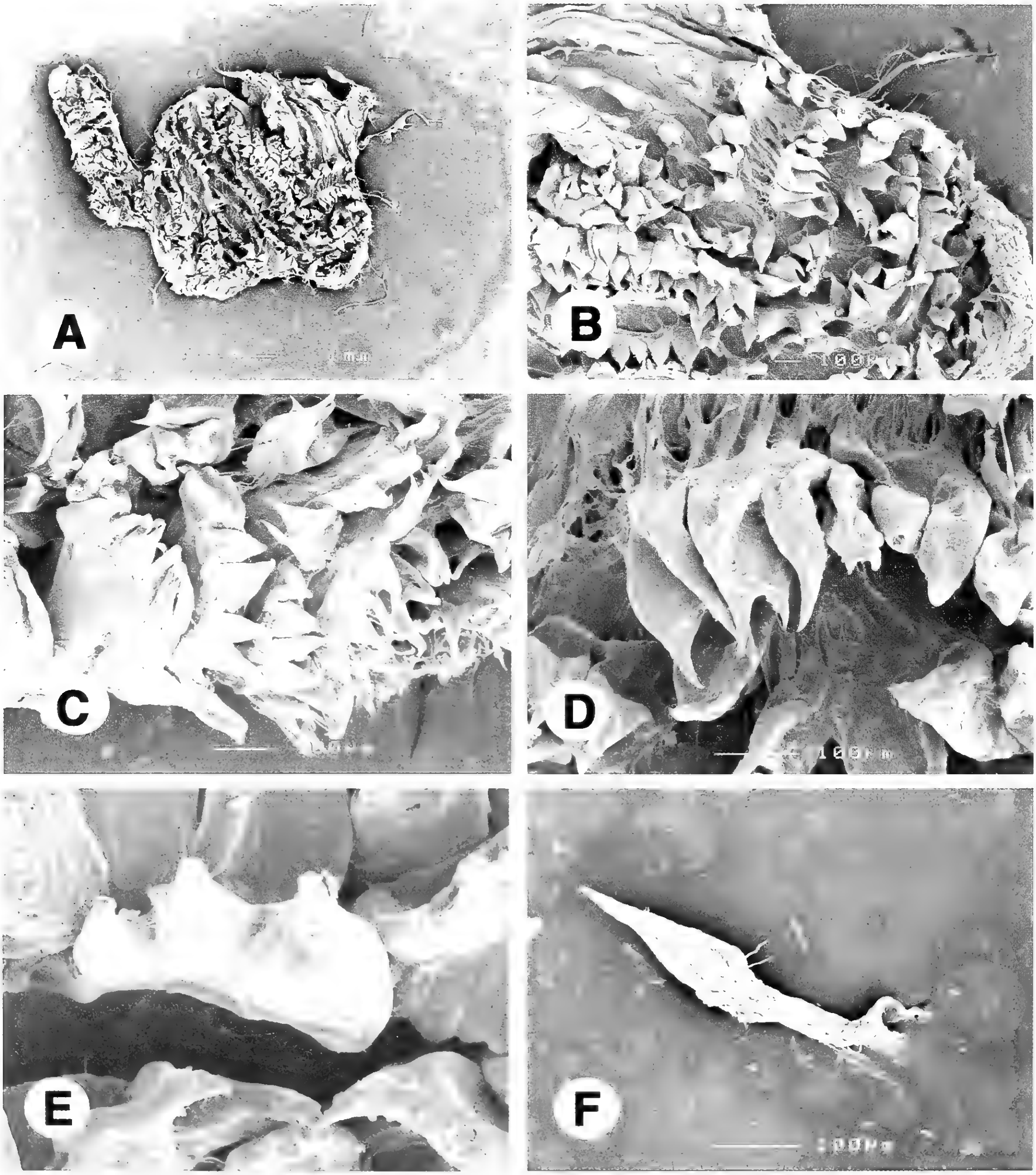


FIGURE 10. *Hoplodoris grandiflora* Palau (CASIZ 109746) detail of genital armament. – A. Entire penis dissected and opened to show armament. Scale bar = 1 mm. – B. Close-up detail of rows of spines. Scale bar = 100 µm. – C. Close-up detail of spines. Scale bar = 100 µm. – D. Close-up detail of spines. Scale bar = 100 µm. – E. Close-up detail of different form of spine. Scale bar = 10 µm. – F. Close-up detail of accessory gland stylet. Scale bar = 100 µm.

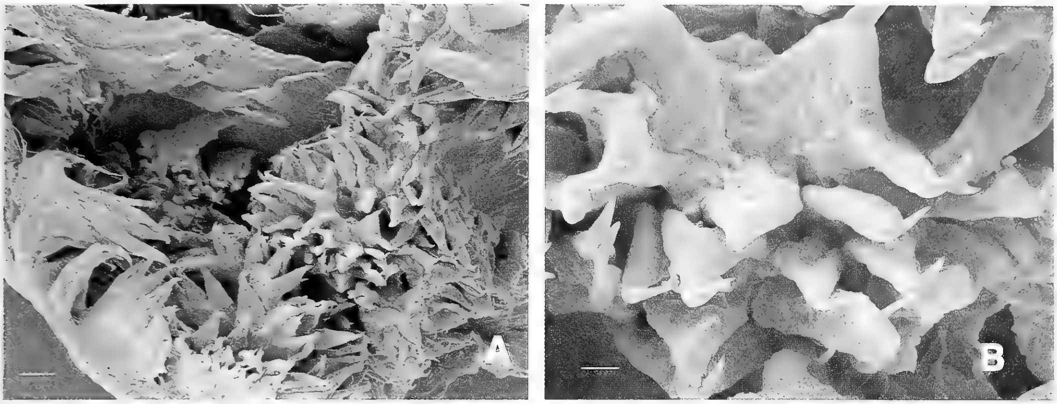


FIGURE 11. *Hoplodoris grandiflora* Palau (CASIZ 109746) detail of genital armament. –A. Vagina dissected and opened to show armament. Scale bar = 30 µm. –B. Close-up detail of rows of spines. Scale bar = 100 µm.

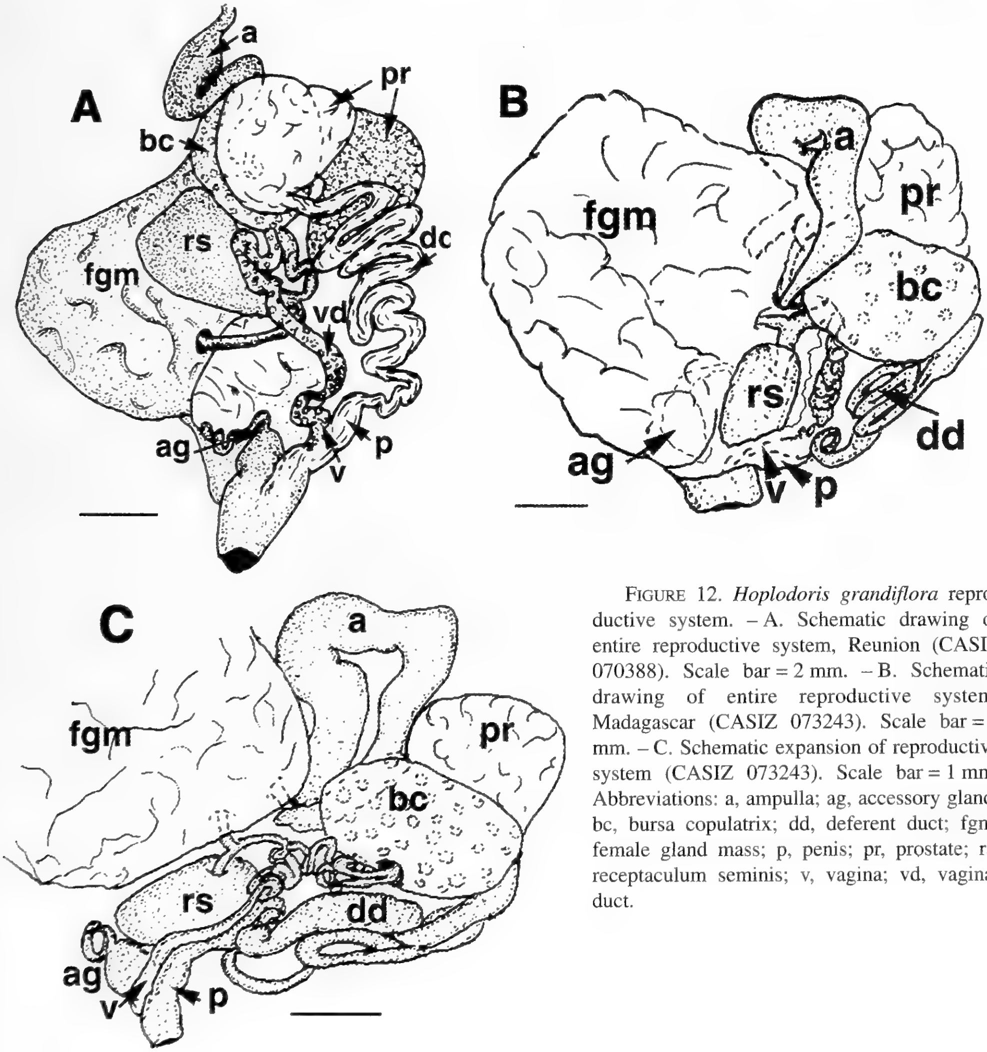


FIGURE 12. *Hoplodoris grandiflora* reproductive system. – A. Schematic drawing of entire reproductive system, Reunion (CASIZ 070388). Scale bar = 2 mm. – B. Schematic drawing of entire reproductive system, Madagascar (CASIZ 073243). Scale bar = 2 mm. – C. Schematic expansion of reproductive system (CASIZ 073243). Scale bar = 1 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, vaginal duct.

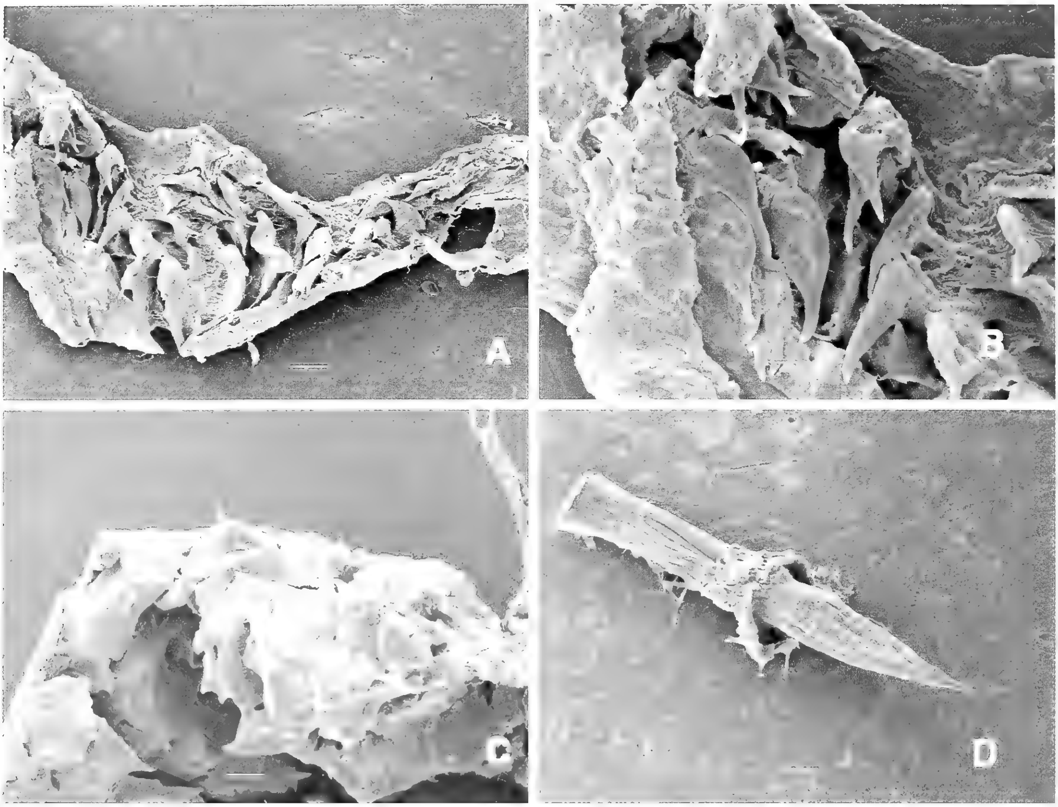


FIGURE 13. *Hoplodoris grandiflora* Madagascar (CASIZ 073243) genital armament. – A. Penis dissected and opened to show armament. Scale bar = 200 µm. – B. Close-up detail of rows of spines. Scale bar = 100 µm. – C. Vagina dissected and opened to show armament. Scale bar = 100 µm. – D. Close-up detail of accessory gland stylet. Scale bar = 100 µm.

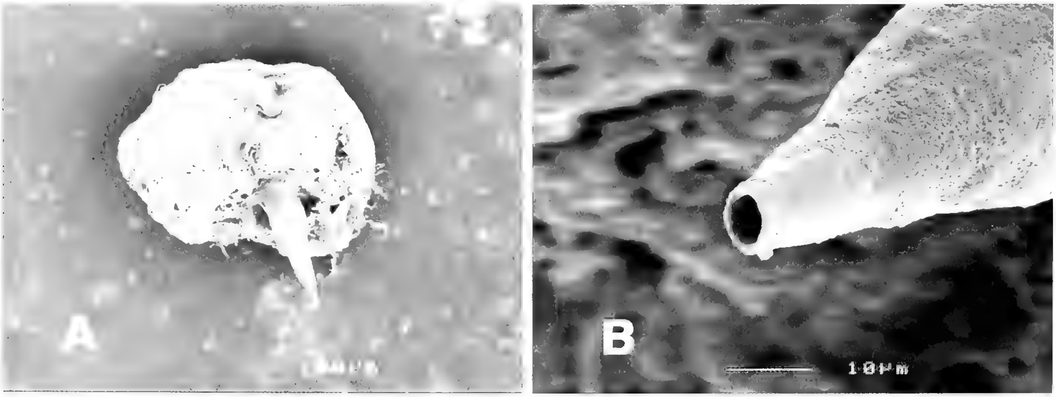


FIGURE 14. *Hoplodoris grandiflora* Reunion (CASIZ 070388) genital armature. – A. Dissected accessory gland stylet. Scale bar = 100 µm.– B. Close-up of hollow stylet. Scale bar = 10 µm.

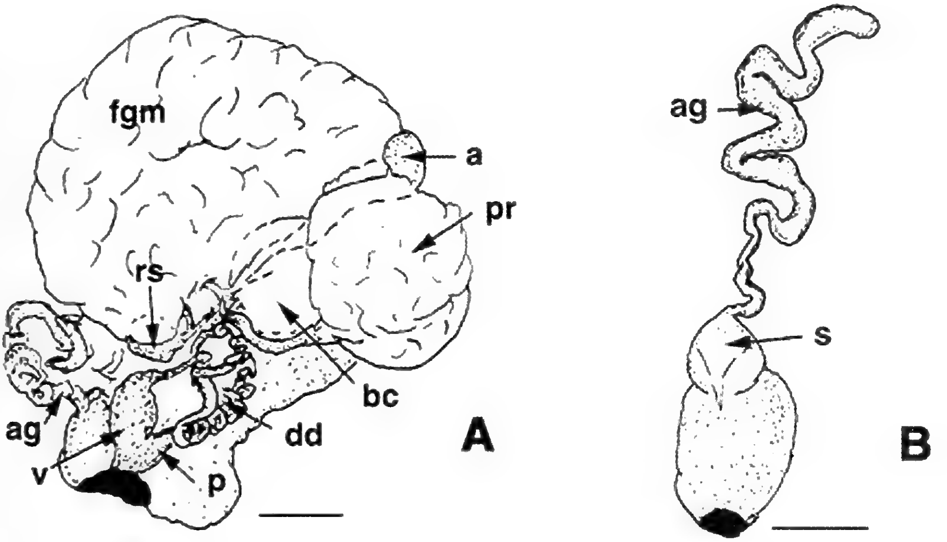


FIGURE 15. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) reproductive system. – A. Schematic drawing of entire reproductive system. Scale bar = 2 mm. – B. Schematic expansion of accessory gland. Scale bar = 0.5 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina.

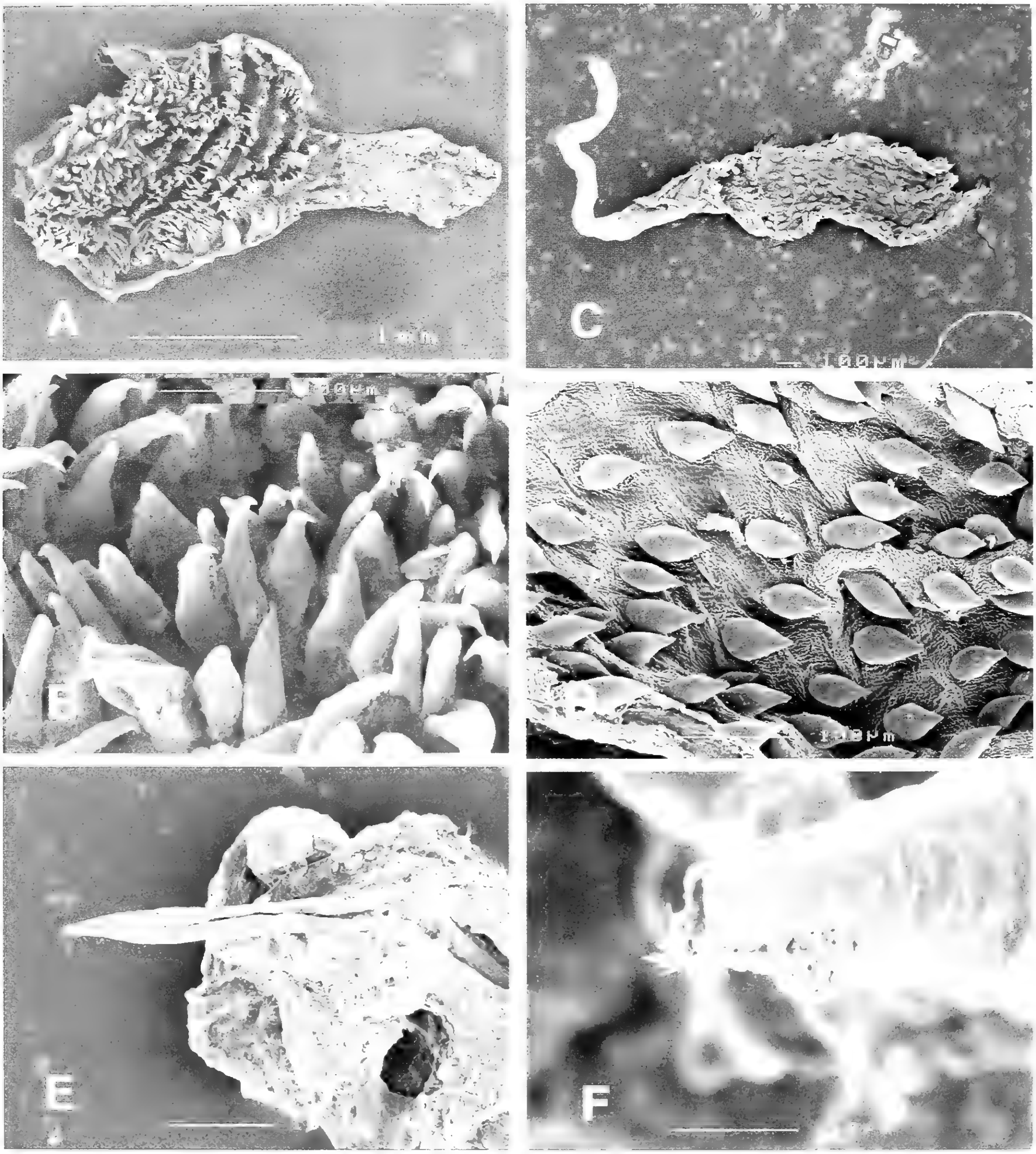


FIGURE 16. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) genital armature. –A. Entire penis dissected and opened to show armament. Scale bar = 1 mm. –B. Close-up detail of rows of hooked spikes. Scale bar = 100 µm. –C. Entire vagina dissected and opened to show armament. Scale bar = 100 µm. –D. Close-up detail of vaginal spines. Scale bar = 100 µm. –E. Accessory gland stylet. Scale bar = 100 µm. –F. Close-up detail of accessory gland hollow stylet. Scale bar = 10 µm.

Hoplodoris bifurcata (Baba, 1993)

Figs. 17A, B, 18–20

= *Carminodoris bifurcata* Baba, 1993:226–232, pls. 1, 7–10.
= *Carminodoris nodulosa* (Angas, 1864) misidentification in Kay & Young, 1969:186–187, figs. 13, 18, Ala Moana, Oahu, Hawaii.
= *H. nodulosa* (Angas, 1864) misidentification in Kay, 1979:462, fig. 148D, Oahu, Hawaii.
= *Carminodoris bifurcata* Baba, 1993 in Keiu, S., 2000:98, fig. 143.
= *H. nodulosa* (Angas, 1864) misidentification in Bertsch & Johnson, 1981:38, bottom fig., Hawaii.

Material examined.— CASIZ 070133, two specimens, one dissected, 30 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 7 May 1989; CASIZ 087898, one specimen, dissected, 35 mm, dissected, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 21 August 1992; CASIZ 079197, one specimen, 31 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 25 March 1991; CASIZ 079280, one specimen, 20 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 7 September 1989; CASIZ 110428, two specimens, one dissected, 20 mm, Arthur's Place, Calumpan Peninsula, Batangas Province, Luzon, Philippines. Collected by T.M. Gosliner, 22 April 1997; CASIZ 106562, one specimen, 10 mm, Arthur's Place, Calumpan Peninsula, Batangas Province, Philippines. Collected by T.M. Gosliner, 17 April 1996; CASIZ 116736, one specimen, 28 mm, Blowhole, Oahu, Hawaii. Collected by S. Johnson, 23 February 1980; CASIZ 116650, one specimen, 10 mm, Pupukea, Oahu, Hawaii. Collected by S. Johnson, 8 July 1985; CASIZ 071561, one specimen, dissected, 32 mm, Sand Island, Kaneohe Bay, Oahu, Hawaii. Collected by T.M. Gosliner, 10 September 1987; CASIZ 097455, two specimens, 9, 16 mm, Napili Bay, Maui. Collected by T.M. Gosliner, 6 April 1994.

Distribution.— This species is known from Hawaii (Kay and Young 1969; present study), Japan (Baba 1993), Philippines (present study) and from Okinawa (present study).

External morphology.— The living animals (Figs. 17A–B) range from 30–32 mm in length. The body is oval, flat and the notum is covered with large, round and tapered tubercles. The tubercles are mostly rounded on the dorsal median, becoming progressively more tapered around the median. The tubercles closest to the mantle edge are much smaller than the others. The coloration of the living animal is complex, and variegated. The ground color is light to medium gray, with mottled shades of darker grays and reddish-browns scattered over the mantle. There is a central dorsum, red-brown band of color, with all tubercles having the same coloration. On the tubercles towards the mantle edge, there is a white ring at the base followed by a red-brown or tan ring, and a white tip on some tubercles. Sprinkled randomly among the tubercles are tiny, dark brown or black spots. The long, tapered rhinophores have a light tan, short stalk with a darker tan, long lamellar portion (approximately 20 lamellae) that angles posteriorly and terminates with a white tip. The six posteriorly projecting gill leaves are tripinnate and feathery and the anterior leaves are light tan with whitish flecks of color, while the posterior leaves are red-brown. The rhinophore and gill sheaths are moderately tall and have tuberculate, irregular edges.

The ventral side of some preserved specimens has retained only a few randomly sprinkled dark spots. The long, pointed oral tentacles have not retained any color, and the foot is anteriorly notched.

Buccal armature (Fig. 18).— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly-tipped jaw rodlets (Figs. 18A–B). The radular formula of the specimen dissected is: 25 × 31.0.31 (CASIZ 070133). The innermost lateral tooth is hamate, bifid, with tiny finger-like projections on the inner

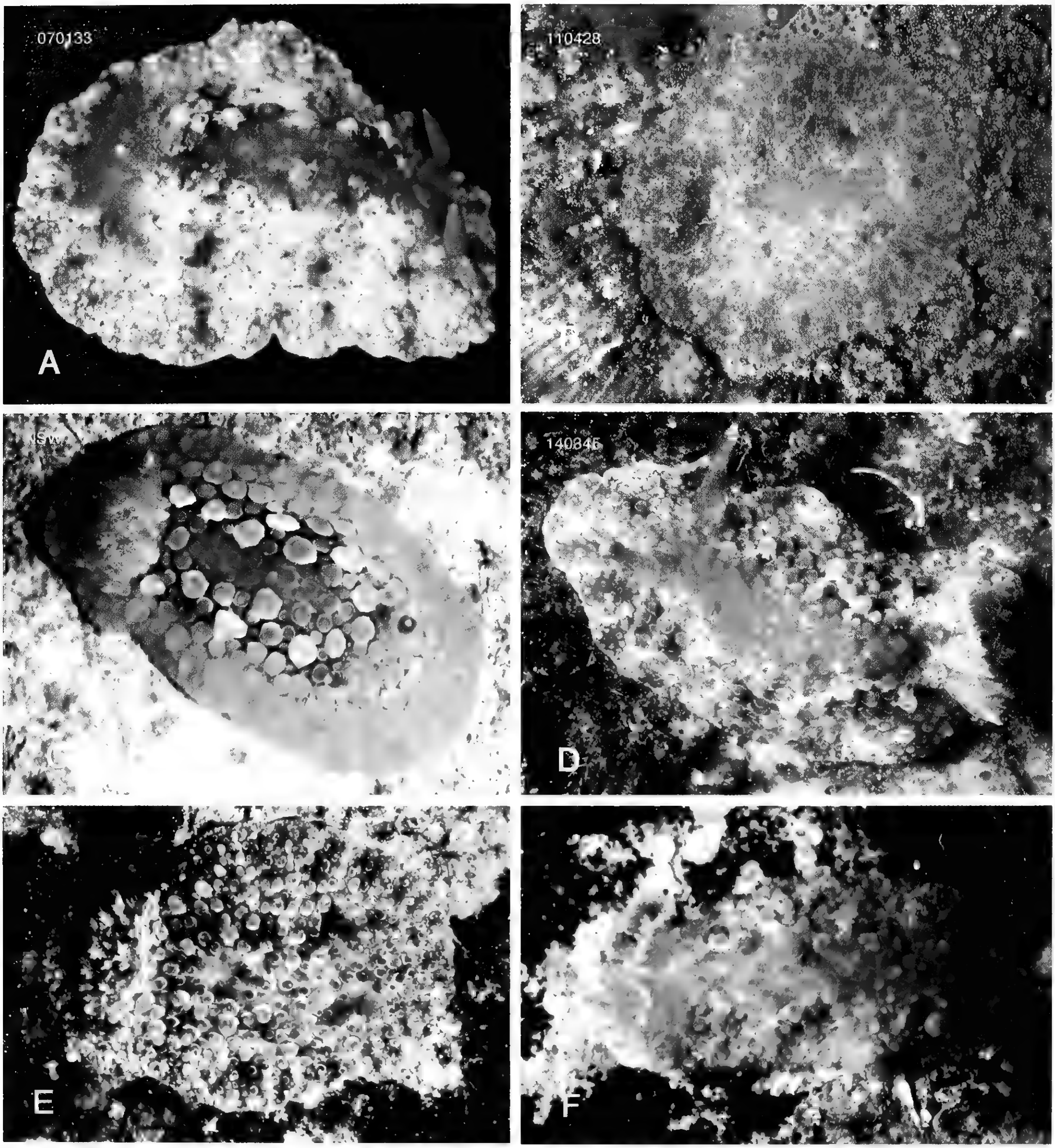


FIGURE 17. *Hoplodoris* spp. Living animals. – A. *Hoplodoris bifurcata*. (CASIZ 070133) (Okinawa) 32 mm. Photo taken by R.F. Bolland. – B. *Hoplodoris bifurcata* (CASIZ 110428) (Philippines) 20 mm. Photo taken by T.M. Gosliner. – C. *Hoplodoris nodulosa*. (New South Wales) (no length available). Photo taken by T.M. Gosliner. – D. *Hoplodoris flammea* (CASIZ 140345) (Bali) 24 mm. Photo taken by T.M. Gosliner. – E. *Hoplodoris bramale* (INB) (Costa Rica) 25 mm. Photo taken by T.M. Gosliner. – F. *Hoplodoris bramale* (INB) (Costa Rica) 18 mm. Photo taken by T.M. Gosliner.

edge and with about 5–8 minute denticles visible on the outer edge (Figs. 18C–D). The middle radular teeth have a more elongate cusp, also with 5–8 minute denticles (Fig. 18E). The two to three outermost lateral teeth are much shorter than the middle or inner teeth, are flat plates, and are denticulate (Fig. 18F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Figs. 19A–B). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla nar-

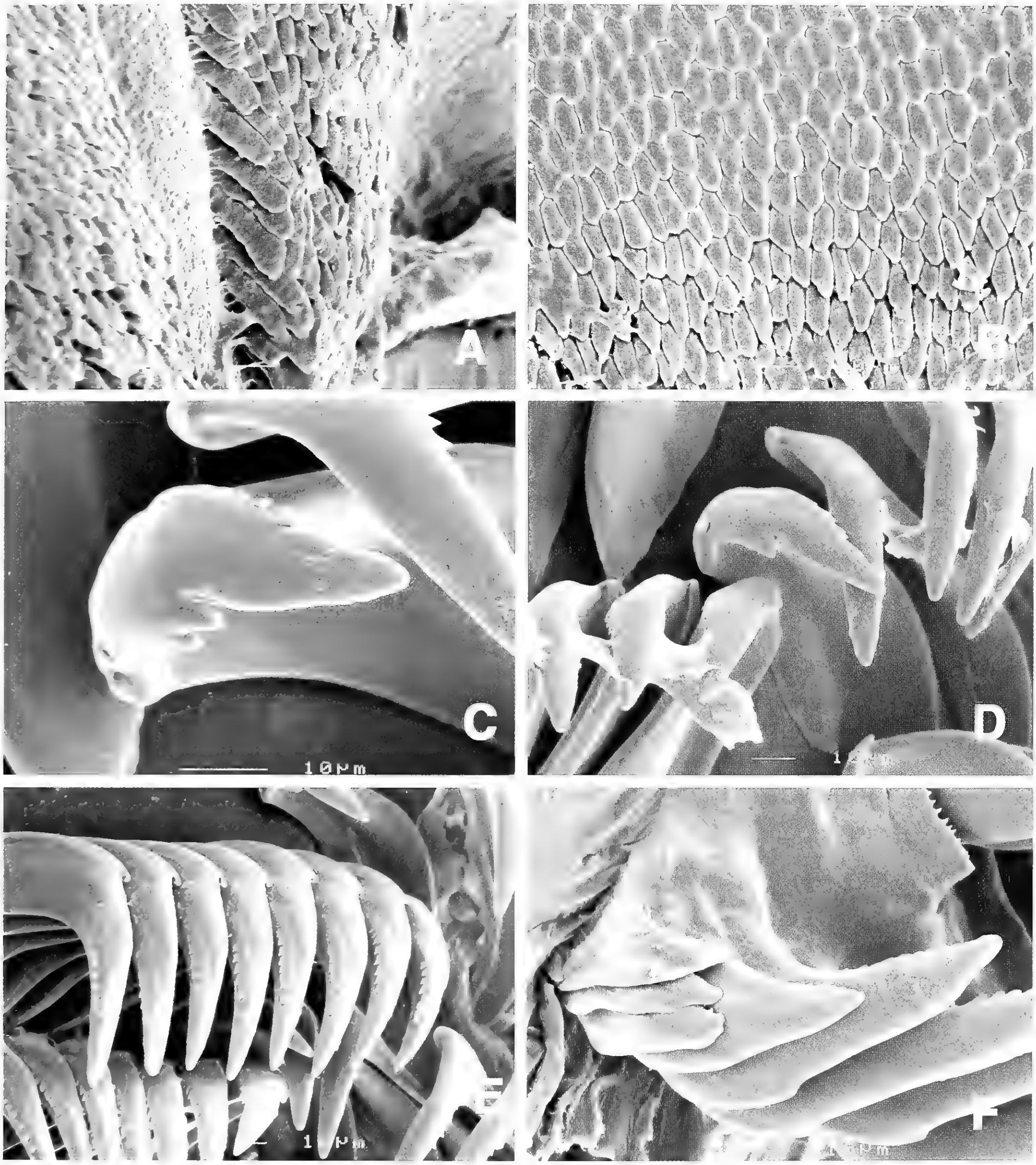


FIGURE 18. *Hoplodoris bifurcata* Okinawa (CASIZ 070133) radula. – A. Labial rods. Scale bar = 10 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth, close-up. Scale bar = 10 µm. – D. Inner lateral teeth. Scale bar = 10 µm. – E. Middle lateral teeth. Scale bar = 10 µm. – F. Outer lateral teeth. Scale bar = 10 µm.

rows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The large prostate mass narrows into a long, looped deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the longer, narrower vagina. The penis is sparsely armed on the inside with short, thorn-like structures (Fig. 20A).

The short uterine duct emerges from the female gland mass and joins the receptaculum sem-

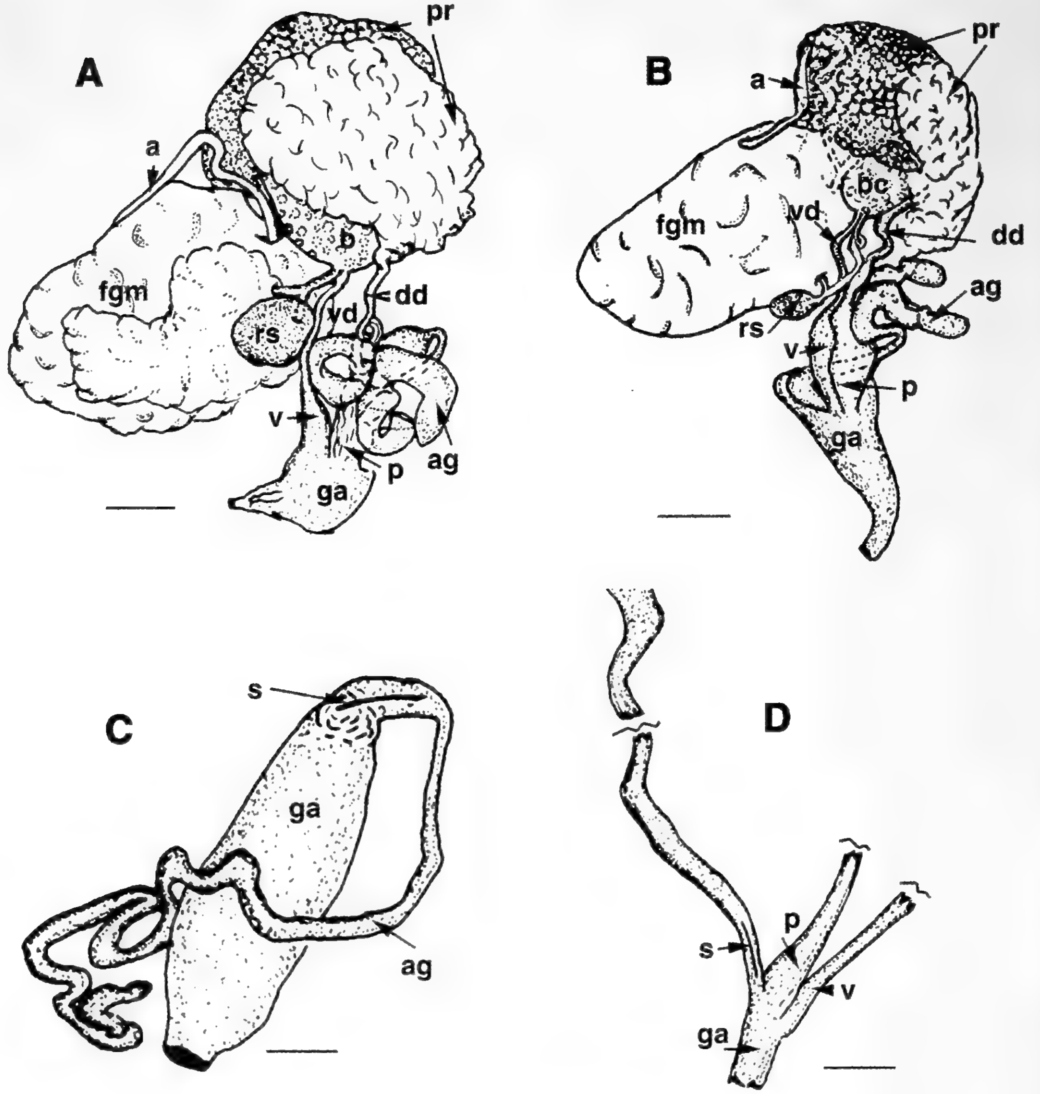


FIGURE 19. *Hoplodoris bifurcata* (CASIZ 070133)(CASIZ 087898) reproductive system. – A. Schematic drawing of entire reproductive system, Okinawa (CASIZ 070133). Scale bar = 1 mm. – B. Schematic drawing of entire reproductive system, Okinawa (CASIZ 087898). Scale bar = 1 mm. – C. Schematic expansion of CASIZ 070133. Scale bar = 0.5 mm. – D. Schematic expansion of CASIZ 087898. Scale bar = 0.5 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina; vd, vaginal duct.

inis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is much smaller than the bursa copulatrix, which is nearly the same size as the prostate. The bursa lies against the female gland mass and is partially encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

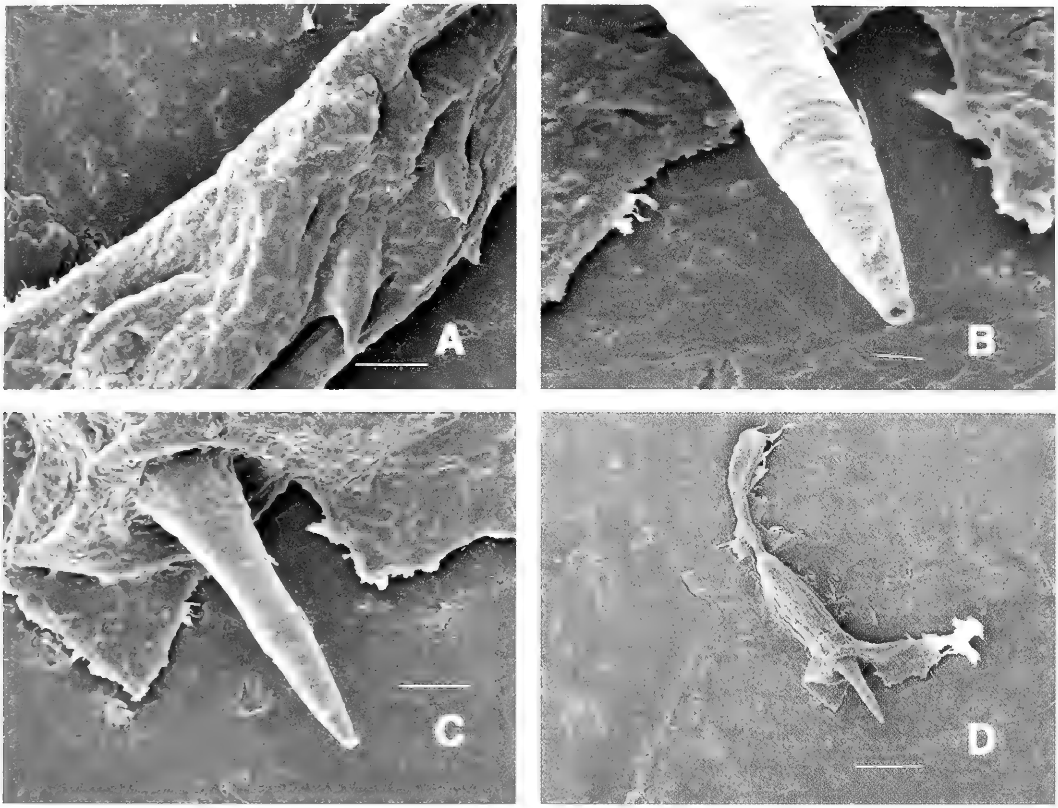


FIGURE 20. *Hoplodoris bifurcata* Hawaii (CASIZ 087898) genital armature. – A. Penial spines, close-up. Scale bar = 10 μm. – B. Accessory gland stylet, close-up showing hollow tip. Scale bar = 10 μm. – C. Accessory gland stylet, close-up. Scale bar = 100 μm. – D. Entire accessory gland stylet. Scale bar = 100 μm.

Alongside the vagina, at the genital atrium, is a large, bulbous vestibular gland. This gland has a convoluted, blind-ended, narrow duct terminating near the female gland mass (Figs. 19C–D). Inside the duct, near the junction of the muscular portion of the gland is a hollow stylet (Figs. 20B–D).

REMARKS.— Kay and Young (1969) described the anatomy of specimens they identified as *Carminodoris nodulosa* from Hawaii, but reported no armament on the penis, the vagina or in the vestibular gland. These structures were difficult to see in our examination of specimens from Hawaii and Okinawa. But the descriptions of the external morphology, the coloration and the radular features provided by Kay and Young are nearly identical to Baba's (1993) descriptions of *Carminodoris bifurcata* from Okinawa and differ from those of *C. nodulosa* from Australia and New Zealand.

Our specimens from Okinawa and Japan match Baba's original description of the external morphology and radula of *Carminodoris bifurcata.* However, Baba did not mention the presence of a vestibular gland armed with a stylet, nor did he provide a drawing of the entire reproductive system of this species.

From our examination of the specimens from Okinawa and Japan, it appears that Kay and Young's (1969) *Carminodoris nodulosa* from Hawaii and *Carminodoris bifurcata* are conspecific but quite distinct from other *Hoplodoris* species.

Debelius (1998) illustrated specimens of *Hoplodoris nodulosa* from Vietnam and Western Australia, but based on color pattern, these are *Hoplodoris estrelyado* Gosliner and Behrens, 1998.

Regarding *Hoplodoris estrelyado*, from our examination of *Hoplodoris* specimens, we can confirm that *H. estrelyado* is the only species of *Hoplodoris* that lacks both penial and vaginal armament. However, *Hoplodoris estrelyado* has one accessory gland stylet, as do all other species of *Hoplodoris* except *H. nodulosa* and *H. bramale*.

Hoplodoris nodulosa (Angas, 1864)

Figs. 17C, 21–23

= *Doris nodulosa* Angas, 1864.
= *Doris pustulosa* Abraham, 1877.
= *Homiodoris novaezelandiae* Bergh, 1904.
= *Doris novae-zelaniae* Suter, 1913:564.
= *Homoiodoris novaezelandiae* Powell, 1946:90, Powell, 1979:286.
= *Staurodoris pustulata* (Abraham, 1877) in Allan, 1950.
= *Hoplodoris nodulosa* (Angas, 1864) in Thompson, 1975:491–492, figs. 1e, 3.
= *Hoplodoris nodulosa* (Angas, 1864) in Willan & Coleman, 1984:33, fig. 92.
= *Hoplodoris novaezelandiae* (Bergh, 1904) in Miller, 1991:295–303.
= *Hoplodoris nodulosa* (Angas, 1864) in Wells & Bryce, 1993:104, fig. 125.

Material Examined.— C133935, one specimen, dissected, 26 mm, White Horse Point, Balmain, Sydney, Australia. Collected by I. Loch, 20 June 1982; C135412, two specimens, 15 and 23 mm, Sandy Beach, Coffs Harbour, New South Wales, Australia. Collected by G. Avern, 20 May 1982.

Distribution.— This species is known from Eastern Australia (Angas 1864; Abraham 1877; Allan 1950; Thompson 1975; Willan and Coleman 1984; present study), from Western Australia (Wells and Bryce 1993) and from New Zealand (Bergh 1904; Powell 1946, 1979; Miller 1991).

External morphology.— The body of the living animal (Fig. 17C) is oval, flat and the notum is covered with large, round and tapered tubercles. The tubercles are mostly rounded on the dorsal median, becoming progressively smaller and more tapered around the median. The tubercles closest to the mantle edge are much smaller than the others. The coloration of the living animal is complex, and variegated. The ground color ranges from light to medium gray, to yellows and reddish-browns. Scattered over the mantle are mottled shades of darker hues of the major colors. On the central dorsum, is an oval of color that is more distinct than the surrounding coloration. The tubercles in this area all have the same coloration. On the tubercles towards the mantle edge, there can be a narrow, white ring at the base. Sprinkled randomly among the tubercles are tiny, dark brown or black spots. The long, tapered rhinophores are light tan at the base, with a darker tan or dark brown lamellar portion (approximately 32 lamellae) that angles posteriorly and terminates with a white tip. The six posteriorly projecting gill leaves are tripinnate and feathery and the anterior leaves are light tan with whitish flecks of color, while the posterior leaves can be a darker color similar to the central dorsal oval color. The rhinophore and gill sheaths are elevated and have tuberculate, irregular edges.

The ventral side of the specimens has retained no pigment. The oral tentacles are digitform and the foot has a rounded notch on the anterior side.

Buccal armature (Fig. 21).— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets (Fig. 21A). The radular formula of the specimen dissected is: 25 × 53.0.53 (C133935).

The innermost lateral tooth is hamate with no denticles visible on either edge (Fig. 21B). The middle radular teeth have a more elongate cusp and are also smooth (Fig. 21C). The four outermost lateral teeth, particularly the last two teeth, are much shorter than the middle or inner teeth and are denticulate with fimbriate denticles (Fig. 21D).

Reproductive system.— The reproductive system is triaulic (Fig. 22A). The ampulla is long and tubular and lies on top of the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The long, tubular prostate narrows into a long, convoluted deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct continues into the bulbous penis, which lies next to the vagina. The penis is sparsely armed on the inside with short, thorn-like structures (Figs. 23A–B). Two bulbous accessory glands lie next to the penis and vagina. These glands have long, convoluted, blind-ended, narrow ducts that terminate next to the female gland mass (Figs. 22C–D). Inside the ducts, near the junction of the muscular portion of each gland is a hollow stylet (Figs. 23C–E).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. The pyriform receptaculum seminis is much smaller than the bursa copulatrix. The bursa lies against the female gland mass and is only barely covered by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

Remarks.— Thompson's (1975) detailed description of the male reproductive organs of *Hoplodoris nodulosa* (Angas, 1864), includes an armed penis and non-hollow stylet inside a well-developed gland. We have examined three specimens from New South Wales that fit Thompson's description including the internal anatomy. In the specimen that Thompson examined, only the outer lateral teeth were denticulate, the same as we noted in the specimens from New South Wales that we examined. The specimens we examined had two hollow stylets versus a single "non-tubular" stylet described by Thompson. However, without a scanning electron microscope, the hole in the end of the stylet would have been overlooked.

Miller (1991) described several specimens from New Zealand as *Hoplodoris novaezelandiae* (Bergh, 1904). His description matches the specimens we examined from New South Wales, Australia. Based on a review of Bergh's original (1904) description of *Hoplodoris novaezelandiae*, of Miller's (1991) description of specimens from New Zealand, and our examination of specimens from and near the type locality of *Hoplodoris nodulosa* (Angas, 1864), we conclude that *Hoplodoris novaezelandiae* and *Hoplodoris nodulosa* are conspecific.

The specimens of *H. nodulosa* that we examined from the type locality in New South Wales have an armed penis and two well-developed accessory glands, each containing a hollow stylet. In addition, the four outer lateral teeth of these specimens are fimbriate.

Hoplodoris estrelyado Gosliner & Behrens, 1998

Fig. 24

(See Gosliner and Behrens, 1998:280–286 for complete synonymy and anatomy.)
= *Hoplodoris nodulosa* (Angas, 1864) misidentification in Debelius, 1998:253, bottom figures.

Material examined.— CASIZ 115343, two specimens, dissected, 40 mm, Devil's Point, Maricaban, Batangas Province, Philippine Islands. Collected by T.M. Gosliner, 15 April 1996.

Distribution.— This species is known from the Philippine Islands (Gosliner and Behrens 1998; present study), Western Australia (Debelius 1998), Vietnam (Debelius 1998), Indonesia, Marshall Islands, Solomon Islands and the Coral Sea.

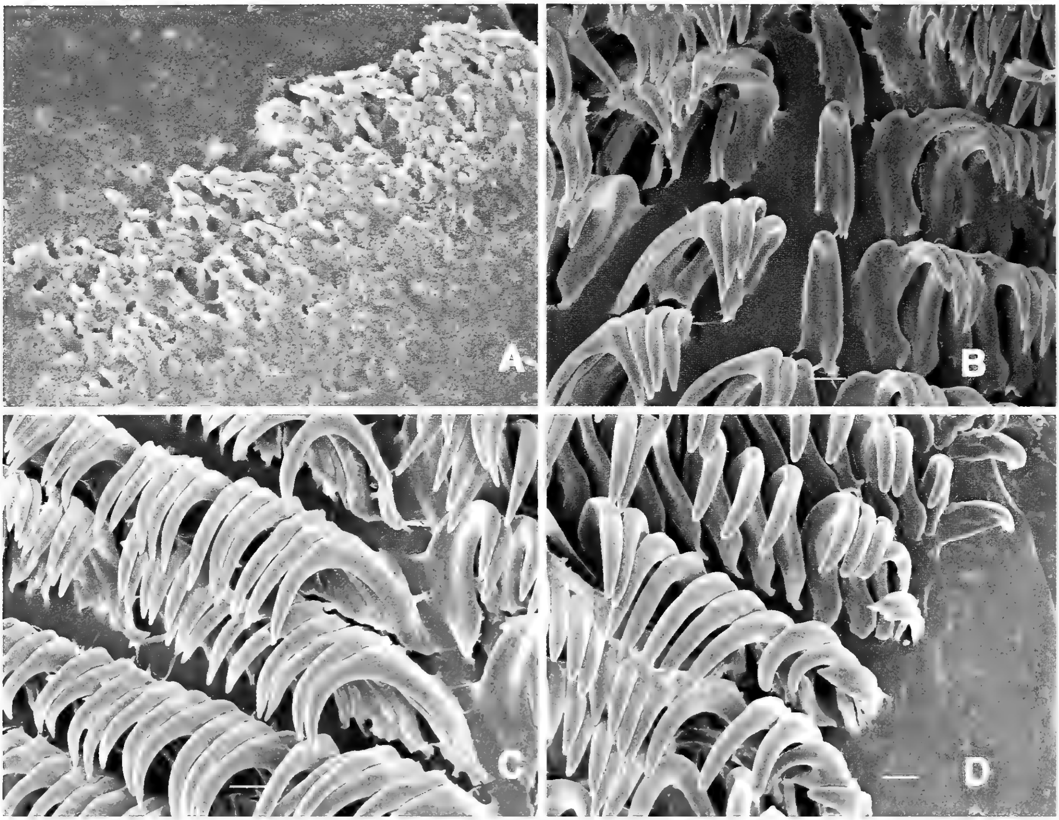


FIGURE 21. *Hoplodoris nodulosa* New South Wales (C135412).— A. Labial rods. Scale bar = 2 µm. – B. Inner lateral teeth. Scale bar = 300 µm. – C. Middle lateral teeth. Scale bar = 300 µm. – D. Outer lateral teeth. Scale bar = 20 µm.

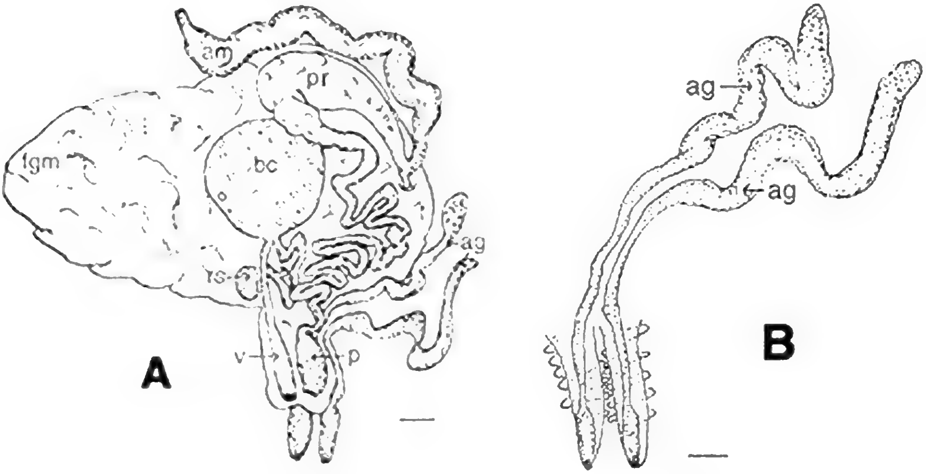


FIGURE 22. *Hoplodoris nodulosa* New South Wales (C133935). – A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. – B. Schematic expansion of accessory glands. Scale bar = 0.5 mm.

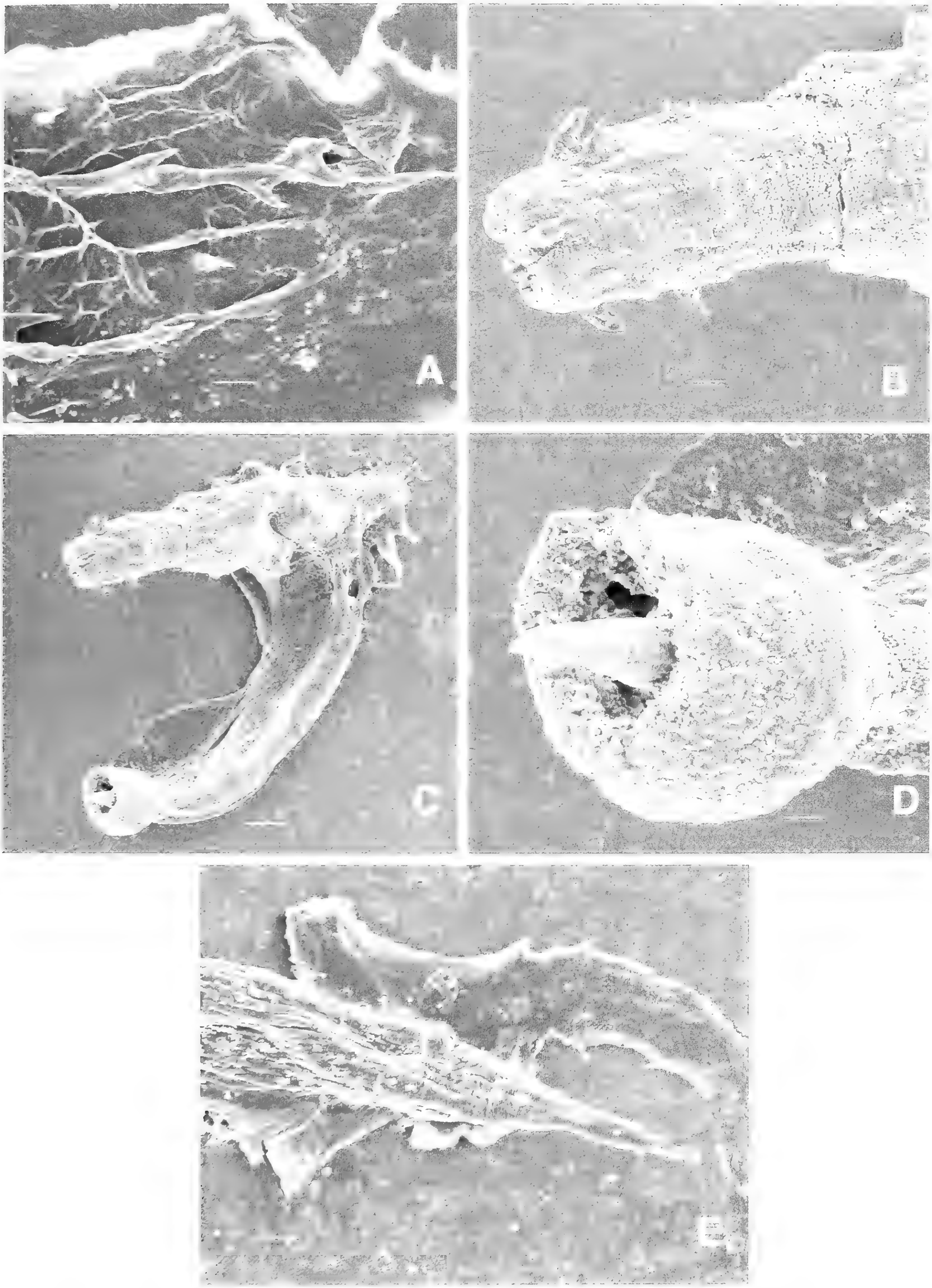


FIGURE 23. *Hoplodoris nodulosa* New South Wales (C133935). – A. Penial armament. Scale bar = 100 μm. – B. Penial spines, close-up. Scale bar = 80 μm. – C. Accessory gland stylet. Scale bar = 300 μm. – D. Accessory gland stylet, close-up. Scale bar = 100 μm. – E. Second accessory stylet, close-up. Scale bar = 100 μm.

External and Radular morphology.— The specimens examined conform to the external and radular morphology descriptions in Gosliner and Behrens.

Reproductive System.— The specimens examined conform to the reproductive morphology described by Gosliner and Behrens. The accessory gland spine (stylet) depicted by Gosliner and Behrens (1998, fig. 2) was also observed in the specimens examined for this study (Fig. 24). Observations by scanning electron microscopy also confirmed that neither the penis nor vagina is armed.

Remarks.— The specimens of *Hoplodoris estrelyado* we examined for the present study match the original description of the radular and reproductive morphology (Gosliner & Behrens1998). We can also clarify three points made in the discussion section of that publication, wherein comparison is made between *H. estrelyado* and other species of *Hoplodoris*. First, our examination of multiple *Hoplodoris* specimens revealed that *H. estrelyado* is not the only species of *Hoplodoris* in which all teeth are denticulate. All teeth of *H. bifurcata* specimens that we examined are also denticulate.

The second point is that *C. grandiflora* does have an armed penis as opposed to the Gosliner and Behrens (1998) observation that only *H.* (*C.*) *grandiflora* (Pease, 1860) and *H. estrelyado* have an unarmed penis. This detail is further considered in the remarks section of the present study where details of *H. grandiflora, C. mauritiana* and *H. desmoparypha* are described.

Lastly, neither *H. nodulosa* nor *H. estrelyado* have a solid stylet. Our electron microscopy examinations of the spines from both species revealed a hollow stylet.

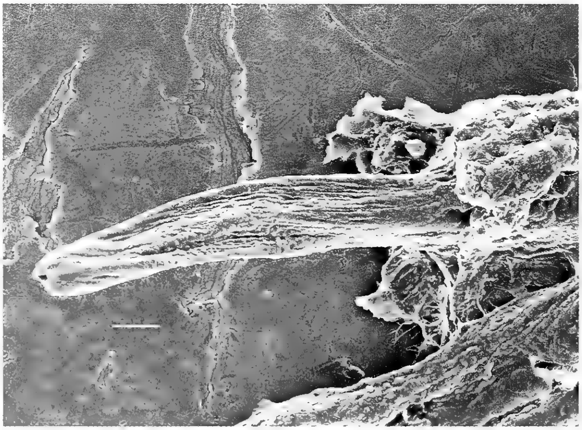


Figure 24. *Hoplodoris estrelyado* Philippines (CASIZ 115343). – A. Accessory gland stylet, showing hollow tip. Scale bar = 100 μm.

Hoplodoris flammea Fahey and Gosliner, sp. nov.

Figs. 17D, 25–27

Material Examined.— Holotype: CASIZ 139600, one specimen, 12 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. Paratypes: CASIZ 140345, one specimen, dissected, 22 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. CASIZ 140350, one specimen, 10 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. CASIZ 162234, one specimen, dissected, 24 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000.

Distribution.— This species has so far been found only in Bali, Indonesia (present study).

Etymology.— The specific name *flammea* is from the Latin meaning fiery red, the dorsal median color of this species.

External morphology (Fig. 17D).— The preserved animals range from 22–24 mm in length. The body is oval, flat and the notum is covered with large, rounded tubercles. The coloration of the living animal is complex, and variegated. The ground color is a light to medium, reddish-mottled brown or tan. In the center of the dorsum the tubercles are bright red, with white areas around them. At the base of the tubercles closer to the mantle edge, is the same white ring-like coloration around the evenly spaced clumps of smaller tubercles. Along the mantle edge are evenly spaced patches of reddish-brown tubercles. On the knobby tops of some of the brown tubercles, the coloration appears worn off and white coloration is visible. The close-set, tall rhinophores have approximately 16 lamellae and a light tan stalk with brown pigment circling the upper third of the stalk. The tip is white. The six tripinnate gill leaves are feathery and colored light gray with tan tips. The rhinophore and gill sheaths are raised with irregular edges and have small rounded tubercles on the sides and the rim.

The foot is notched anteriorly and the oral tentacles are digitform. No coloration has been retained on the ventral side of the specimens examined.

BUCCAL ARMATURE.— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets that have distinct knurls along the length (Figs. 25A–B). The radular formula of the specimen examined is: 31 × 50.0.50 (CASIZ 140345). The innermost lateral teeth of both specimens dissected are hamate with the innermost tooth having a short secondary cusp on the inner edge next to the primary cusp (Figs. 25C–D). The middle radular teeth are also hamate, with a longer cusp (Fig. 25E) with about 8 denticles along the outer margin of the cusp. The five outermost lateral teeth have minute, feathery denticles on the outer edge and are smaller than the middle and inner lateral teeth (Fig. 25F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 26). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The tubular prostate narrows into a medium length deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the narrow vagina. The penis, which is armed with sparsely scattered hooks (Figs. 27A–B) is wider than the vagina and opens into the common genital atrium.

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is about half the size of the bursa copulatrix. The bursa lies against the female gland mass and is not encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. The duct terminates into the vagina, which is not armed. A bulbous accessory gland opens into the genital atrium. The gland has a convoluted, blind-ended, narrow duct terminating near the female gland mass (Fig. 26). Inside the duct, near the junction of the muscular portion of the gland is a hollow stylet (Figs. 27C–D)

COMPARISON OF *HOPLODORIS FLAMMEA* TO OTHER *HOPLODORIS* SPECIES

Hoplodoris flammea is superficially similar to *H. bifurcata.* Both species have a central dorsum color that is distinct from the surrounding mantle coloration. *Hoplodoris flammea* has a bright red color, while the central color of *H. bifurcata* is more reddish-brown. Both species have complex, variegated coloration with mottled shades of grays and browns. Both have elongate rhinophores with deep tan lamellar regions and white tips. The gill leaves of both species are feathery and tan in color. But, *Hoplodoris flammea* lacks the small black spots on the notum that are present in *H. bifurcata.* Further, the interior anatomy, particularly the radular morphology, differs between these species. The inner lateral teeth of *Hoplodoris flammea* have a blunt cusp on the inner

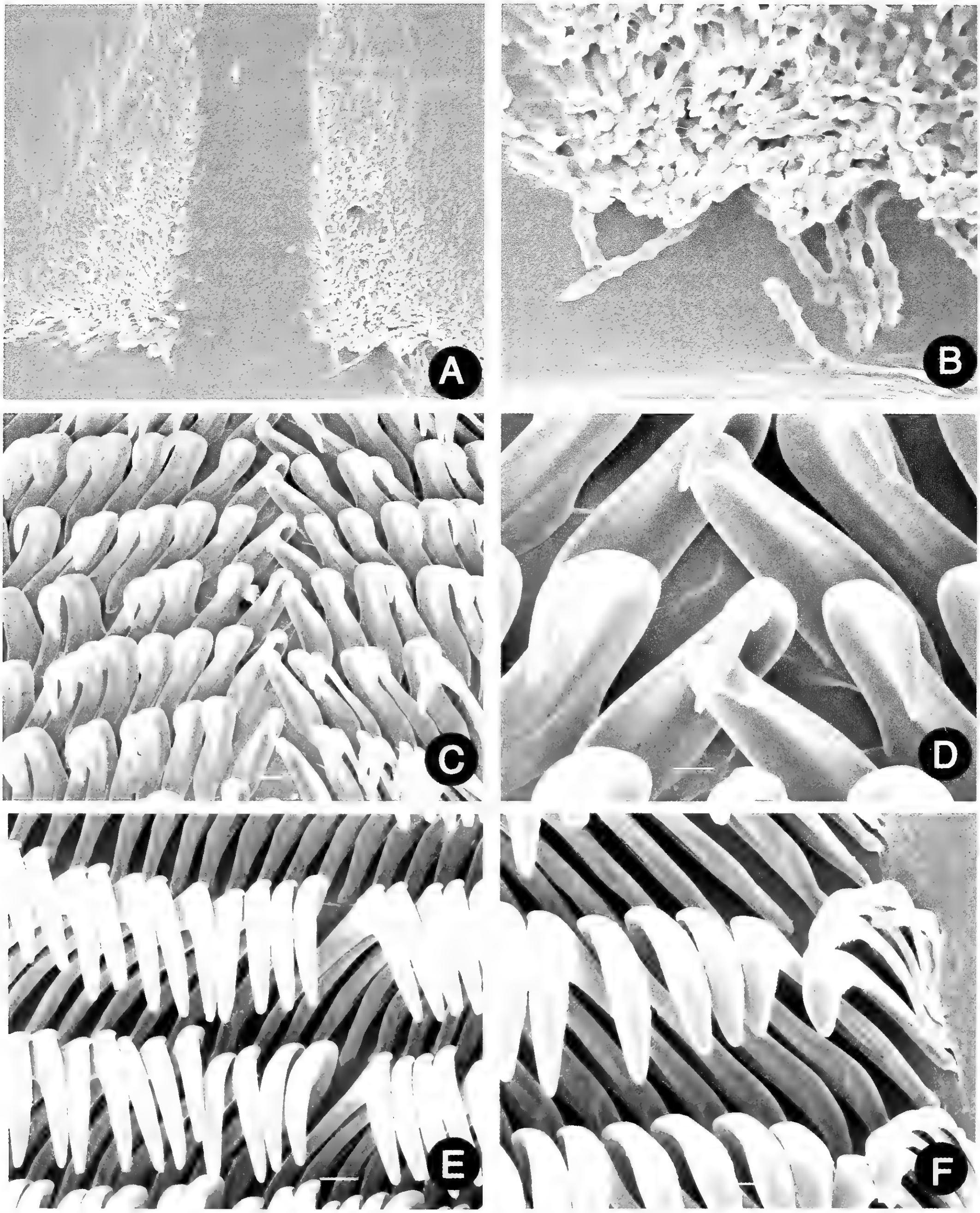


FIGURE 25. *Hoplodoris flammea* Bali (CASIZ 140345). – A. Labial rods. Scale bar = 1 µm. B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 100 µm. – D. Inner lateral teeth, close-up. Scale bar = 10 µm. – E. Middle lateral teeth. Scale bar = 15 µm. – F. Outer lateral teeth. Scale bar = 10 µm.

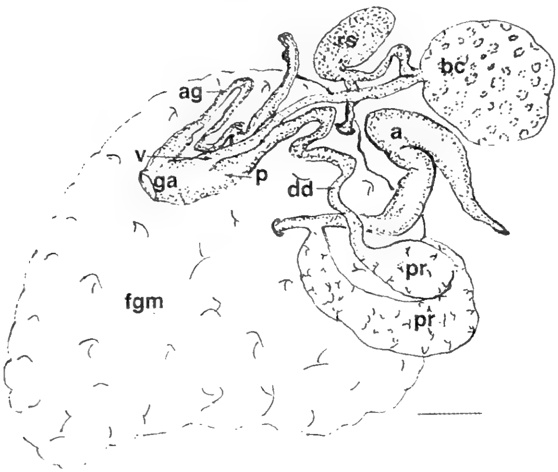


FIGURE 26. *Hoplodoris flammea* Bali (CASIZ 140345). Schematic drawing of entire reproductive system. Scale bar = 1 mm.

edge, while the inner lateral teeth of *H. bifurcata* have denticles on both the inner and outer edges of the innermost lateral tooth. The middle and outer lateral teeth of both species are denticulate, but the denticles of the middle lateral teeth of *H. bifurcata* are more pronounced. *Hoplodoris bifurcata* has three denticulate outer lateral teeth while *H. flammea* has four denticulate outer later teeth that are more brush-like. The jaw rodlets of *H. flammea* also differ in that they have distinct knobs along the length. The jaw rodlets of *H. bifurcata* are flattened plates with blunt ends.

The differences in the reproductive anatomy between the two species are as follows: the prostate of *Hoplodoris flammea* is a thick coil that does not cover the

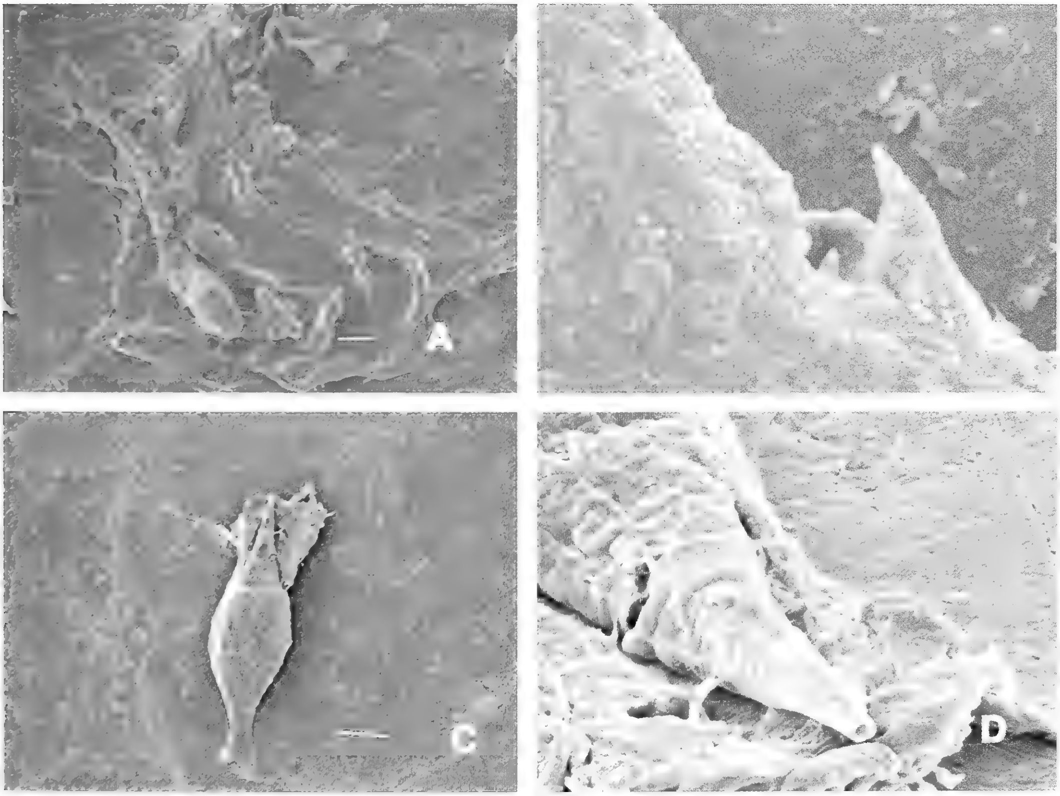


Figure 27. *Hoplodoris flammea* Bali (CASIZ 140345). – A. Penial armament. Scale bar = 100 mm. – B. Penial spines, close-up. Scale bar = 10 mm. – C. Accessory gland stylet. Scale bar = 10 mm. – D. Accessory gland stylet, close-up. Scale bar = 1 mm.

bursa copulatrix. The prostate of *H. bifurcata* covers the bursa and is a large mass rather than a coiled tube. The vagina of *H. flammea* is shorter than the deferent duct, but in *H. bifurcata* the vagina is longer than the deferent duct.

Thus, a combination of morphological characters distinguishes *H. flammea* as a separate *Hoplodoris* species.

Hoplodoris bramale Fahey and Gosliner, sp. nov.

Figs. 17E, 28–30

Material examined.— Holotype: INB 0003572316, 24 mm, Puerto Escondido, Parque Nacional Manuel Antonio, Puntarenas, Costa Rica. Iintertidal. Collected by Y. Camacho-Garcia, 18 February 2003. Paratypes: INB 0001498550, one specimen, dissected, 22 mm, Tómbolo, Punta Uvita, Osa Conservation Area, Costa Rica. Intertidal. Collected by Y. Camacho-García and D. Butvill, 6 January 2002. Two specimens (CASIZ 166813), Punta Uvita, Osa Conservation Area, Pacific coast of Costa Rica, 0–2 m depth, 15 January 2003. One specimen (CASIZ) Punta Uvita, Osa Conservation Area, Pacific coast of Costa Rica, 0–2 m depth, 15 January 2003. Six specimens (INB 0003572306) Punta Uvita, Ballena National Park, Pacific coast of Costa Rica, 0–2 m depth, 18 January 2003.

Distribution.— This species is known only from the Pacific coast of Costa Rica. It appears to be the only species of *Hoplodoris* found in the Eastern Pacific.

Etymology.— The specific name *bramale* is taken from the Latin “tuber bramale” a name given to a truffle that has the same appearance as this new species.

External morphology (Fig. 17E).— The preserved animal measures 22 mm. The body is oval, flat and the notum is covered with large, rounded tubercles. The coloration of the living animal is complex and variegated. The ground color is light to medium mottled brown or tan. At the base of the tubercles is a white area in the shape of a ring. Alongside the medial part of the dorsum are the tallest tubercles. In the middle of the dorsum, the white area decreases at the base of some tubercles, and the tubercles are shorter than those alongside the median. Along the mantle edge the tubercles are small and more densely packed than on the dorsum median. The close-set, stout rhinophores have a medium brown stalk with a lighter brown lamellar portion (approximately 10–13 lamellae) that terminates with a white tip. The six tripinnate gill leaves are feathery and light tan in color. The rhinophore and gill sheaths are low with irregular edges and have small rounded tubercles on the sides.

The foot is notched anteriorly and the oral tentacles are digitform. Some dark speckles have been retained on the ventral side of the specimens examined.

Buccal armature.— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets that have rough, irregular edges (Figs. 28A–B). The radular formula of the specimen examined is: 28 × 38.0.38. The innermost lateral teeth are hamate and narrow below the cusp (Fig. 28C). The cusp is devoid of denticles on either side. The middle radular teeth are also hamate, with a longer cusp (Fig. 28D) and lack denticles. The two outermost lateral teeth have fine denticles on the outer edge and are smaller than the middle and inner lateral teeth (Figs. 28E–F).

Reproductive system.— The reproductive system is triaulic (Fig. 29A). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The long, tubular prostate narrows into a long, looped deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct continues into the thin penis, which lies between two bulbous accessory glands.

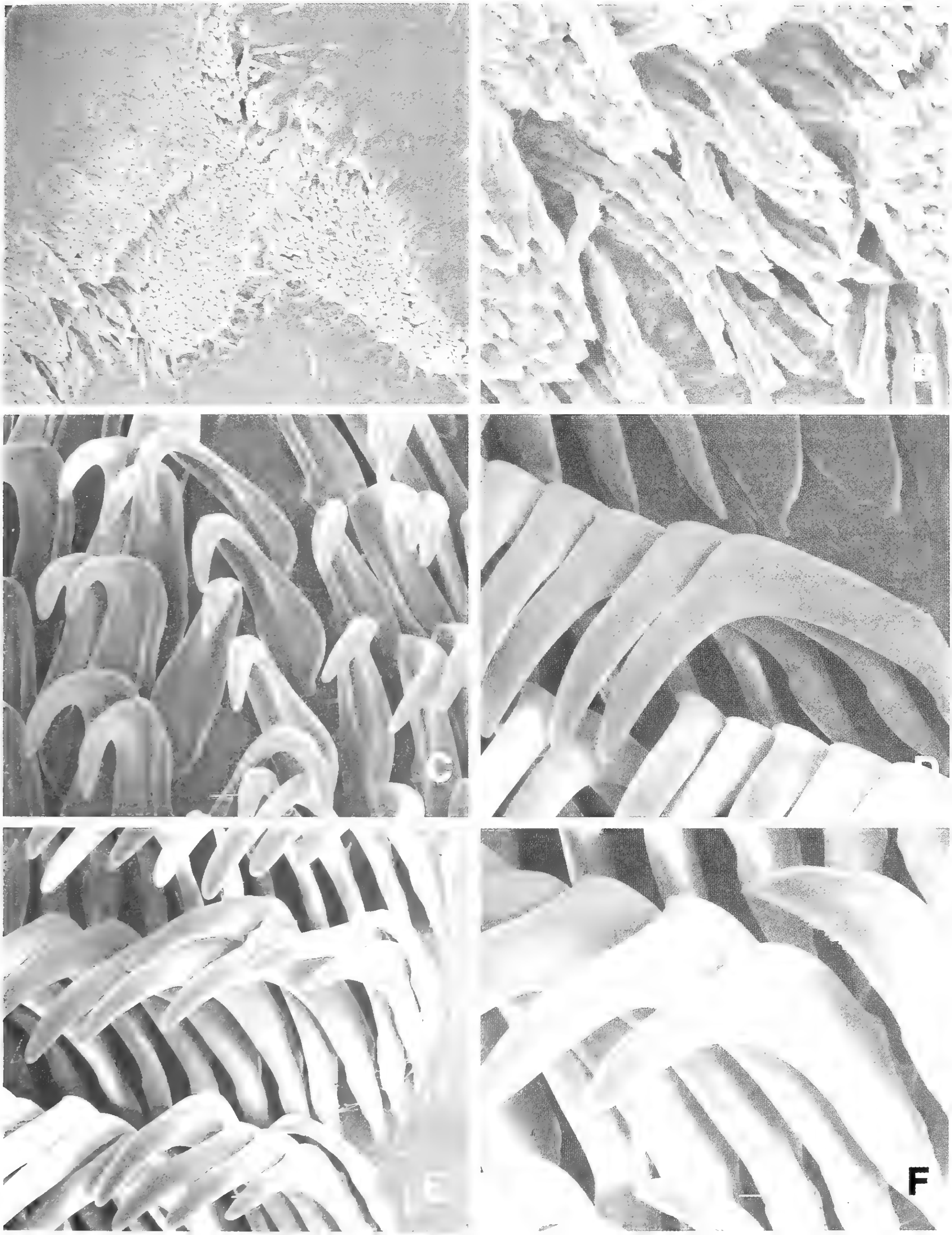


FIGURE 28. *Hoplodoris bramale* Costa Rica (INB 0001498550). – A. Labial rods. Scale bar = 10 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 300 µm. – D. Middle lateral teeth, close-up. Scale bar = 25 µm. – E. Outer lateral teeth. Scale bar = 10 µm. – F. Outer lateral teeth, close-up. Scale bar = 1 µm.

These glands have long, convoluted, blind-ended, narrow ducts that terminate near the female gland mass (Fig. 29B). Inside the ducts, near the junction of the muscular portion of each gland is a hollow stylet (Figs. 30A–B). The penis is sparsely armed on the inside with short, thorn-like structures. (Fig. 30C).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is about the same size as the bursa copulatrix. The bursa lies against the female gland mass and is partially encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

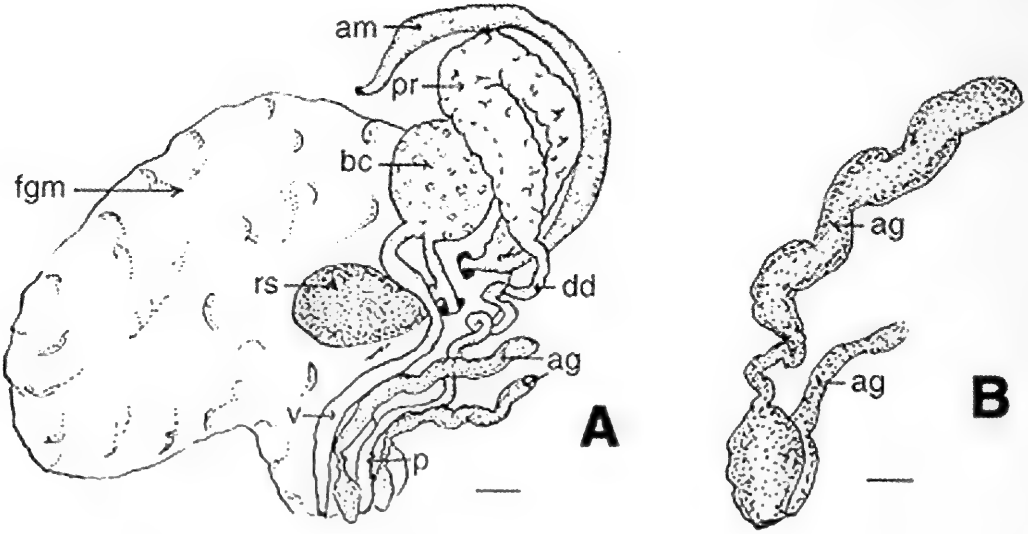


FIGURE 29. *Hoplodoris bramale* Costa Rica (INB 0001498550).– A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. – B. Schematic expansion of accessory gland. Scale bar = 0.5 mm.

COMPARISON OF *H. BRAMALE* TO OTHER *HOPLODORIS* SPECIES

Hoplodoris bramale is most similar externally to *H. grandiflora*. The notum of both species is brown, with no distinctive central oval of color. Both species have brown tubercles surrounded by a white ring at the base. The brown rhinophores have a white tip and a raised rhinophore sheath. The feathery gill leaves are light brown or tan. The gill sheath of both species is covered with small tubercles.

Differences in the internal anatomy distinguish the two species. Although the 3–4 outer lateral teeth of *Hoplodoris grandiflora* have minute denticles and are smaller than the middle lateral teeth, *H. bramale* has only one to two smaller outer lateral teeth with tiny denticles. Additionally, the middle lateral teeth of *H. bramale* have longer hooks and lack denticles while those of *H. grandiflora* are shorter and denticulate. The inner lateral teeth of both species are hamate and *H. bramale* differs by having a small, blunt cusp on the innermost tooth.

The reproductive anatomy of the two species varies considerably. *Hoplodoris bramale* has two armed accessory glands while *H. grandiflora* has one gland.

Internally, *Hoplodoris bramale* is most similar to *H. nodulosa* (Angas, 1864). *Hoplodoris* *nodulosa* also has two accessory glands but in that species, the penis does not lie between the two glands as it does in *H. bramale*. The penis of *H. bramale* is sparsely armed with short thorn-like spines as in *H. nodulosa*, while the penis of *H. grandiflora* is densely armed. The vagina of *H. bramale* is not armed; also similar to *H. nodulosa*, but the vagina of *H. grandiflora* is armed. The deferent duct of *H. bramale* is not as elongate and coiled as that of *H. grandiflora* or *H. nodulosa*. The receptaculum seminis of both *H. bramale* and *H. grandiflora* is nearly the same size as the bursa, but in *H. nodulosa* the receptaculum is much smaller than the bursa.

Externally, *Hoplodoris bramale* is quite different from *H. nodulosa*. The dark oval of coloration on the dorsum of *H. nodulosa* is not found on *H. bramale*. In addition, *H. bramale* lacks the small black spots on the notum that are generally present in *H. nodulosa*.

The particular combination of morphological characters distinguishes *Hoplodoris bramale* from other species of *Hoplodoris*.

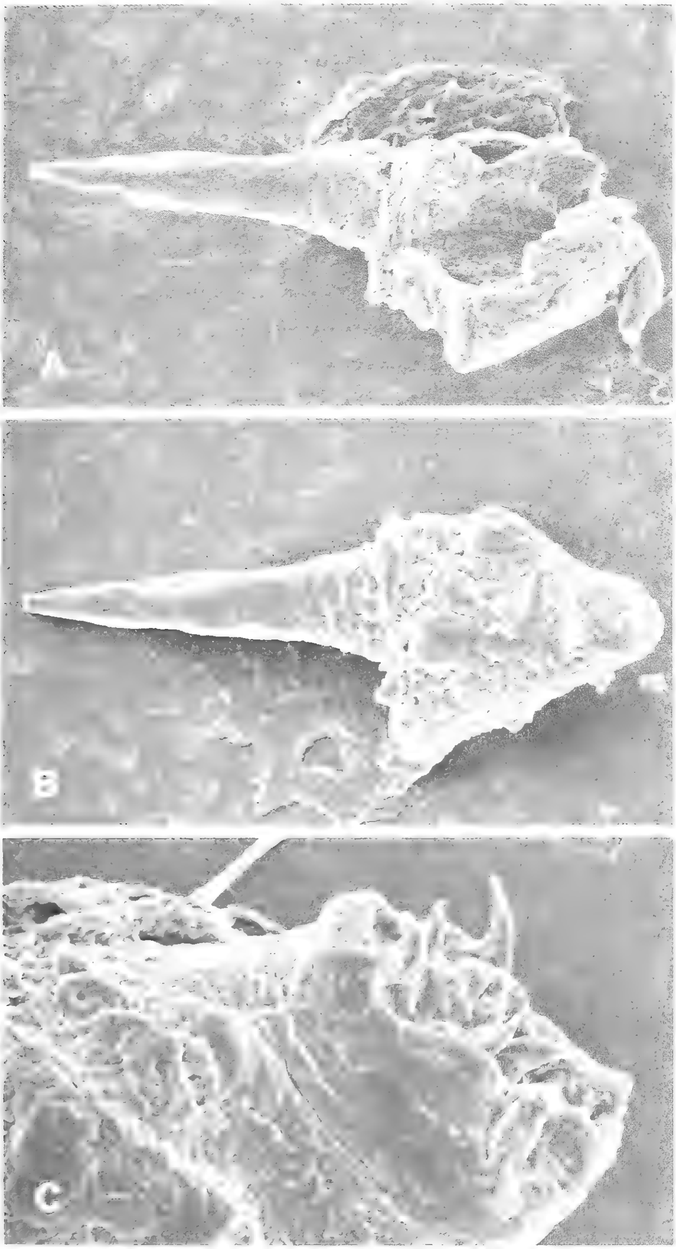


FIGURE 30. *Hoplodoris bramale* Costa Rica (INB 0001498550). – A. Accessory gland stylet, close-up. Scale bar = 100 μm. – B. Second accessory stylet, close-up. Scale bar = 100 μm. – C. Penial armament. Scale bar = 5 μm.

PHYLOGENTIC ANALYSIS

To test our hypothesis of phylogenetic relationships, we assessed the characters that could be informative. From our study, it appears that there are few characters that can be used to distinguish among these closely related taxa. For example, there are few external morphological characters that can be incorporated into phylogenetic analyses. There are also few reproductive or radular differences that can be used to distinguish between taxa.

CHARACTERS.— The following characters were considered for use in the analyses of *Hoplodoris* and *Carminodoris*. The character states are 0= plesiomorphic condition, 1, 2= apomorphic conditions. None of the character states was determined *a priori*; the result of examination of the outgroup character states. The outgroup selected, *Discodoris boholiensis* Bergh, 1877 is the type species of the genus. *Geitodoris planata* , the type species of the genus *Geitodoris* Bergh, 1894, was included in the ingroup to test the monophyly of *Hoplodoris* and *Carminodoris.* Phylogenetic analyses performed by Valdés (2002) demonstrate that both *Discodoris* and *Geitodoris* are more basally situated than *Hoplodoris*, but are nonetheless closely related. When available, we determined the character state for the taxon by examination of specimens in the California Academy of Sciences and Australian Museum collections, rather than relying on literature descriptions. Only *Carminodoris armata* Baba, 1993 was unavailable for examination.

1. *Vas deferens shape.* Both *Discodoris* and *Geitodoris* have a very long, convoluted vas deferens (0). This state is shared by the majority of *Hoplodoris* species except *H.armata, H. bifurcata, H. flammea* and *H. bramale,* which all have a shorter, although convoluted duct (1).

2. *Penial armature.* The outgroup lacks penial hooks or other armature (0), as does *Geitodoris planata* and *H. estrelyado.* All other species have penial armature (1).

3. *Vaginal armature. H. grandiflora, H. mauritiana, H. desmoparypha* each has an armed vagina (1).

4. *Vestibular gland. Discodoris* does not have a vestibular gland attached to or near the genital atrium (0). However, *Geitodoris* and all species of *Hoplodoris* and *Carminodoris* have a vestibular gland (1). Two species have two of these vestibular glands attached near the genital atrium (2), *H. nodulosa* and *H. bramale.*

5. *Vestibular gland duct.* The vestibular gland duct in *Geitodoris* is narrow, (0). All species share this state, except *H. estrelyado* and *H. armata,* which have a wide vestibular gland (1).

6. *Penis shape.* Members of the outgroup and *Geitodoris* have a wide, bulbous penis (0), as do most *Hoplodoris* species. Both *H. estrelyado* and *H. bramale* have a narrow penis (1).

7. *Stylet.* Neither *Discodoris* nor *Geitodoris* has armature (a stylet) associated with an assessory gland (0). All species of *Hoplodoris* examined in this study have a stylet (1).

8. *Stylet number.* Neither *Discodoris* nor *Geitodoris* has a stylet, so this character state is coded as inapplicable (?). All but one species of *Hoplodoris* have one stylet (0), and *Hoplodoris nodulosa* and *H. bramale* have two stylets (1).

9. *Outer lateral teeth.* The outer lateral teeth of *Discodoris* are not denticulate (0). This character state is shared by *Hoplodoris armata*. All other species have denticulate outer laterals (1).

10. *Middle lateral teeth.* Neither *Discodoris* nor *Geitodoris* have denticulate middle lateral teeth (0). Five species share this state. All other species have denticulate middle lateral teeth (1). This character was left out of the final analysis when examination of multiple specimens revealed intraspecific variation.

11. *Inner lateral teeth.* Neither outgroup has denticulate inner lateral teeth (0). Of the ingroup taxa, five have denticulate inner lateral teeth (1). This character was left out of the final analysis when examination of multiple specimens revealed intraspecific variation.

12. *Dorsal tubercle form.* Both *Discodoris* and *Geitodoris* have conical, small tubercles covering the dorsum (0). In contrast, the members of *Hoplodoris* and *Carminodoris* have prominent, rounded and tapered tubercles (1).

13. *Dorsal color.* Both *Discodoris* and *Geitodoris* have uniform dorsal coloration, which is not concentrated in the center (0). This character state is shared by most species. Three species, *H. bifurcata, H. nodulosa* and *H. flammea* have a dark median coloration (1).

14. *Penial spine density.* Of the species having a penial spine, four have densely spaced spines (0) and four have sparsely distributed spines (1).

PHYLOGENETIC ANALYSIS.— In order to perform analyses of phylogeny, character state data were entered into a data matrix using MacClade version 4.0 (Table 1). Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b10 was used to analyze the data. The optimality criterion of maximum parsimony, with the heuristic algorithm (TBR branch swapping option) was used. Multistate characters were treated as unordered with equal weight and the stepwise addition option of random trees was used with 100 repetitions for the maximum parsimony.

Bremer analyses were performed to estimate branch support. A 50% majority rule consensus tree was computed for all trees. Permutation Tests for Probability (PTP) were performed to determine if a tree as short as that found from parsimony analysis could have arisen by chance alone . Skewness tests, with evaluation of 100,000 and 1 million random trees, were performed to evaluate whether the data set contains more hierarchical structure than would be expected by chance.

RESULTS.— For the analyses using maximum parsimony as an optimality criterion, eight equally parsimonious trees were found, which were 19 steps long. Tree scores were as follows: the consistency index (CI) = 0.68, retention index (RI) = 0.70 and homoplasy index (HI) = 0.32. The strict consensus tree is shown in Fig. 31A with the character numbers and character reversals. The underlined number indicated a reversal. The 50% majority rule tree is shown in Fig. 31B. The evaluation of the randomly sampled trees for the skewness test resulted in a mean of 30.2, a standard deviation of 1.77, a *g*1 value of -0.72 and a *g*2 value of 0.51.

Bremer support analyses conducted using heuristic searches by PAUP for all trees ≤20, ≤21, ≤23 and ≤24 steps resulted in 92, 658, 3324 and 13024 trees respectively. Bremer support values are shown on Fig. 31A. *Discodoris boholiensis* remained separated from the *Hoplodoris* clade even after analysis of ≤25 steps.

TABLE 1. *Hoplodoris* data matrix

Species	*Characters* (see text)													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*
1 *H. armata*	1	1	0	2	1	0	?	?	0	0	0	1	0	0
1 *H. armata*	1	1	0	2	1	0	?	?	0	0	0	1	0	0
3 *H. grandiflora*	0	1	1	1	0	0	1	0	1	1	1	1	0	0
4 *H. mauritiana*	0	1	1	1	0	0	1	0	1	1	1	1	0	0
5 *H. nodulosa* Aust	0	1	0	2	0	0	1	1	1	0	0	1	1	1
6 *H. desmoparypha*	0	1	1	1	0	0	1	0	1	0	0	1	0	0
7 *H. estreylado*	0	0	0	1	1	1	1	0	1	1	1	1	0	?
8 *H. flammea*	1	1	0	1	0	0	1	0	1	0	1	1	1	1
9 *H. bramale*	1	1	0	2	0	1	1	1	1	0	0	1	0	1
10 *D. boholiensis*	0	0	0	0	?	0	0	?	0	0	0	0	0	?
11 *G. planata*	0	0	0	1	0	0	0	?	1	0	0	0	0	?

Discussion of Phylogenetic Analyses.— The results of these phylogenetic analyses are consistent with the recent analyses and opinions of other authors (Gosliner and Behrens 1998; Thompson 1975). First, the present analysis supports the opinion of these authors that *Carminodoris* is a junior synonym of *Hoplodoris*. However, neither taxon appears monophyletic. Instead, all species previously placed in *Carminodoris* and *Hoplodoris* appear to be members of one clade (Fig. 30). PTP tests ($P = 0.01$) indicate that a tree length of 19 steps is significantly shorter than randomly generated trees. The PTP tests generated the shortest trees of 26 steps. The retention index of 0.70 for the parsimony tree demonstrates strong statistical fit of the characters to the tree (G. Spicer, pers. commun.). The results of the randomly sampled trees, in particular the g1 value of -0.72, indicated that the data is significantly more structured than random data.

Regarding the outgroups selected for this study, Valdés' (2002) analysis indicated that *Geitodoris* is more closely related to *Hoplodoris* than it is to *Discodoris*. The present analysis supports this conclusion.

Some general comments about the phylogenetic analyses results now follow. The tree topology was affected by the selection of characters and the choice of outgroups; a situation noted by Ponder and Lindberg when examining Gastropod phylogeny. For example, adding *Discodoris lilacina* to the initial analyses doubled the number of trees but retained the same tree topology and lowered the consistency index. However, in all analyses, the general topology was maintained, that is, only one monophyletic clade resulted that united all species of *Hoplodoris* and *Carminodoris*. *Discodoris* is always positioned at the most ancestral node with *Geitodoris* more closely related to the *Hoplodoris/Carminodoris* clade.

Specific details about the taxa in this study are now discussed. In trees resulting from parsimony analyses, *Hoplodoris estrelyado* appears as the most ancestral species. In all trees, *H. grandiflora* appears in a highly derived clade and most closely related to the synonymous species, *H. desmoparypha* and *H. mauritiana*. In the parsimony analysis, the two new species each appear in a highly derived clade. *Hoplodoris bramale* from Costa Rica appears most closely related to *H. nodulosa* from the eastern coast of Australia, while *H. flammea* from Bali appears most closely related to *H. bifurcata*, also found in the tropical Indo-Pacific region.

Thompson's opinion (1975) that Kay and Young's (1969) specimen of *Carminodoris nodulosa* (identified in this study as *Hoplodoris bifurcata*) is not a conspecific of *H. nodulosa* from Australia is also supported by the present analysis. In the parsimony analysis, *H. bifurcata* (= *C. nodulosa* from Hawaii) appears in the sister clade.

Gosliner and Behrens observed that *H. estrelyado* and *H. grandiflora* (= *H. desmoparypha*) are the only two species that have a large, spherical vestibular gland situated on the end of a duct. Parsimony analysis shows *H. estrelyado* as more basally situated to *H. grandiflora*.

Our analyses, along with Valdés' (2002) publication of the phylogeny of the Cryptobranchia allowed us to compare morphological characters to determine common ancestry or independent acquisition of morphological characters. For example, several genera of dorids in clades more basal to *Hoplodoris* have penial hooks (Valdés 2000). These include *Dendrodoris, Doriopsilla, Onchidoris, Calycidoris*, and *Chromodoris*. Within the sister clade of *Hoplodoris*, six genera contain species that have penial hooks: *Alloiodoris, Platydoris, Gargamella, Baptodoris, Sclerodoris* and *Nophodoris*. In the same clade as *Hoplodoris* but more basally situated, some species of *Otinodoris* also have penial hooks. Some genera of even more basally situated clades also have penial hooks (*Onchidoris, Calycidoris, Chromodoris, Alloiodoris*). Thus, it is probable that penial hooks were inherited from a common ancestor and have been lost independently in many taxa within the Cryptobranchia.

Two characters, all radular teeth denticulate and only inner or outer radular teeth denticulate,

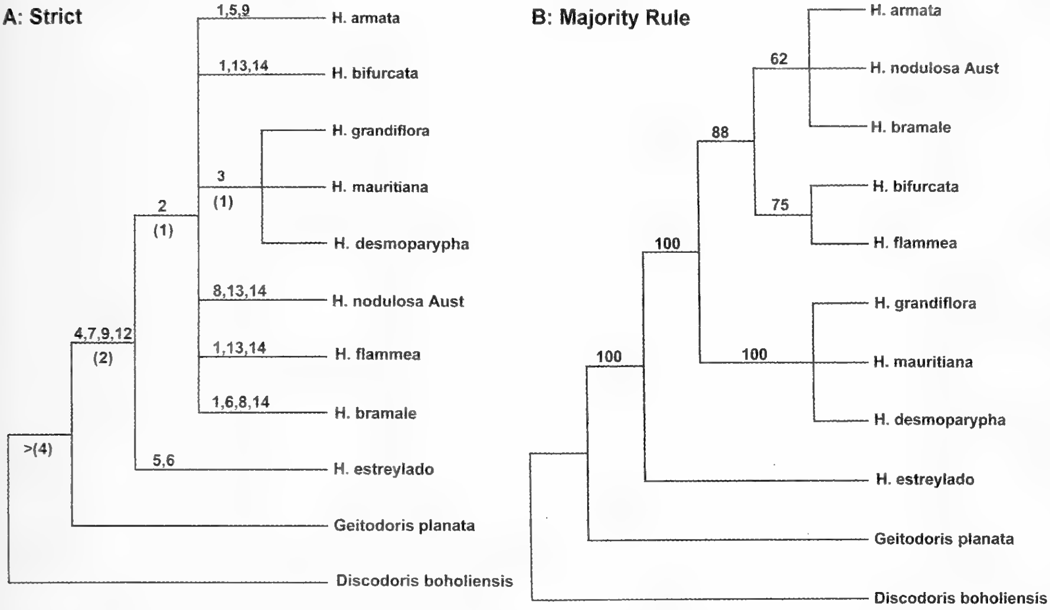


FIGURE 31. Phylogeny of *Hoplodoris/Carminodoris*. – A. Strict consensus tree of 8 most parsimonious trees. Character numbers above the branches are shown with the reversals in bold type. – B. 50% majority rule tree. Numbers shown are the percentage of trees that include that branch. Numbers in parentheses are Bremer support values. – C. Bootstrap results for most parsimonious tree. Numbers above the branches indicate support for that branch. – D. Tree obtained by distance analysis. Numbers indicate branch length.

are present in genera more basal to *Hoplodoris*. *Berthella*, the most basally situated taxon in Valdés' phylogeny of the Cryptobranchia (2002) has all radular teeth denticulate as does the clade with *Actinocyclus, Cadlina* and *Chromodoris*. The basal clade containing *Calycidoris* and *Onchidoris* has denticulate inner radular teeth. The clade containing *Goslineria* and *Pharodoris* has denticulate outer radular teeth. Thus it appears that the characters of denticulate and partially denticulate radular teeth were inherited by a common ancestor.

Two characters, an accessory gland with hard structures (spines) and vaginal hooks are not present in any Discodorididae genera basal to *Hoplodoris*. Only in the closest clade to *Hoplodoris*, are these characters present in some species. *Asteronotus, Jorunna* and *Nophodoris*, have species with an accessory gland and *Platydoris, Gargamella* and *Baptodoris* have vaginal hooks. It appears that these characters were independently acquired.

SUMMARY

The results from this study indicate that the genus *Carminodoris* Bergh, 1889 is a junior synonym of *Hoplodoris* Bergh, 1880. There are few morphological characters that can be used to justify two distinct genera. It is possible that molecular characters would shed more light on these species and would allow further testing of the species trees by comparison with the gene trees.

Carminodoris nodulosa from Hawaii and *C. bifurcata* from Okinawa appear to be the same species and should be called *Hoplodoris bifurcata* (Baba, 1993). *Hoplodoris desmoparypha* Bergh, 1880, *Carminodoris mauritiana* Bergh, 1880 and *C. grandiflora* (Pease, 1860) are conspecific and should be named *Hoplodoris grandiflora* (Pease, 1860).

Hoplodoris nodulosa (Angas, 1864) and *H. novaezelandiae* (Bergh, 1904) appear to be conspecific.

Hoplodoris nodulosa (Angas, 1864) and *Hoplodoris estrelyado* Gosliner and Behrens, 1998 should be retained as valid species.

Carminodoris armata Baba, 1993 is a synonym of *Hoplodoris armata.*

There are two new species to add to the genus *Hoplodoris: Hoplodoris flammea* and *Hoplodoris bramale*. Thus, there are seven valid species in the genus *Hoplodoris*: *H. armata, H. bifurcata, H. bramale, H. estrelyado, H. flammea, H. grandiflora,* and *H. nodulosa.*

Although the genus *Discodoris* is a closely related taxon, the genus *Geitodoris* is more closely related to *Hoplodoris.*

Important diagnostic morphological characters of *Hoplodoris* that have been inherited from a common ancestor include penial hooks and denticulate radular teeth. Newly acquired morphological characters of *Hoplodoris* species include an accessory gland with a spine and vaginal armament.

ACKNOWLEDGMENTS

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A Preliminary Report on New and Previously Known Vertebrate Paleontological Sites in Baoshan Prefecture, Yunnan Province, China

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Exploration and test excavation of new and previously known vertebrate paleontological sites in Baoshan Prefecture in southwestern Yunnan Province in October and November 2002 led to the recovery of several important Middle Pleistocene, Late Pleistocene and early Holocene mammalian faunas. The new site of Nanfeng, which appears to span the Middle to Late Pleistocene, is of particular interest because of its rich assemblage of micromammals, including numerous and diverse rodents as well as insectivores and bats. The previously known site of Wanrengang, is also of importance because its deposits appear to include the transition from the Late Pleistocene to the early Holocene; the stone tool assemblages at the site alone suggest Late Paleolithic occupation. Mammalian fossils from these sites as well as from the previously known sites of Tangzigou and Laohudong promise to shed significant light on the environmental evolution of the area, and the influence of humans on local biodiversity. Future detailed studies of the geology, geochronology, taphonomy and vertebrate paleontology of the four aforementioned sites are planned.

Yunnan Province in southwestern China is renowned for its biodiversity, and ecological and anthropological diversity. This diversity has evolved because of the great range of physical landforms and environmental conditions that exist in the province. In western Yunnan, the Hengduan Mountains, which border Myanmar, provide some of the most interesting and least well-known environments in East Asia. The Hengduan Mountains comprise three north-south trending, parallel chains of high mountain peaks separated from west to east by the Salween (locally, the Nujiang), Mekong (Lancang) and Yangtze (Jinsha) Rivers. The Hengduan orogeny preceded that of Himalayas and created some of the oldest and most isolated peaks and deeply dissected valleys in all of Asia. As the rivers cut their way through the upland, many rock types were exposed and a diversity of niches created (Ferguson 1993). Depending on the orientation and depth of the valleys, small-scale rain-shadows developed, creating a wide range of biotopes (Ferguson 1993). The Hengduan Range has been referred to by Ferguson (1993:174) as "a last resting place of a number of paleoendemics and the cradle for diverse neoendemics". The Hengduan Range and especially its westernmost chain, the Gaoligongshan or Gaoligong Mountains, are considered one of the major biodiversity "hotspots" of the world. Because of the large range of temperatures, altitudes, and latitudes represented within the Gaoligongshan, the mountains harbor many endemic species, especially at their northern extremity. The largely undocumented ecological diversity and the imminent threat of rapid human incursion due to new road-building activity in western China has prompted urgent surveys of the flora and fauna of the Gaoligongshan to be undertaken by the scientists of the California Academy of Sciences, in collaboration with their colleagues at the Kunming Institutes of Botany and Zoology.

A survey of late Tertiary and Quaternary vertebrate paleontological sites in Baoshan Prefecture of Yunnan Province was undertaken in October and November 2002 as part of the Gaoligongshan Biodiversity Survey Project of the California Academy of Sciences. A survey of the vertebrate paleofauna of the Gaoligongshan and adjacent regions was considered important to the goals of the project because it provided an opportunity to understand how the fauna of the region had evolved in relation to natural and human-induced environmental change in the latest Tertiary and Quaternary. Knowledge of the evolutionary trajectories of different vertebrate lineages under different environmental regimes provides important background for understanding how different animals may react to future environmental change. Our goal in this survey was to identify a range of paleontological sites from latest Tertiary through Neolithic age, which could shed light on faunal evolution in the region in the absence and presence of modern humans.

In this paper, we present the preliminary results of excavations at the new paleontological site of Nanfeng in addition to information on new collections made at the previously known sites of Wanrengang, Huoxinshan, Tangzigou, and Laohudong. We also briefly discuss four further sites –Yangyi, Dianjiangtai, Jiangdongshan, and Longwangtang – which were visited in November 2002, but from which no collections were made. A map of these sites is presented in Figure 1.

NEW SITE

Nanfeng (N 24° 49′ 05.4″; E 099° 06′ 09.4″; altitude 1710 m)

In 1991, the villagers of Nanfeng discovered abundant mammalian fossils during the course of road construction. Some of the fossilized long bones recovered were scraped by villagers in order to make medicinal poultices for the skin, but most had been collected and handed over intact to the Cultural Bureau of the city of Shidian, where they were safely stored until our study.

In October 2002, a test excavation at the Nanfeng site was carried out by a team led by one of us (Ji X.-P.), leading to the recovery of a small number of large mammal fossils. During the course of our November 2002 expedition, this excavation was significantly enlarged (Fig. 2). This report represents a preliminary review of what is a richly fossiliferous and taphonomically complex site. Future papers dealing with the geology, geochronology, and taphonomy of the site, along with details of the vertebrate fossil assemblage will be prepared following the completion of further investigations.

The site of Nanfeng represents a collapsed limestone cave or very deep rock shelter. Excavation carried out over the course of one week in November 2002 at Nanfeng resulted in the deepening of the test pit to a total depth of ~1.3 m, revealing four weakly defined layers of silty clay, all of which were fossiliferous. The original assemblage of mammalian fossils collected from Nanfeng in 1991 appears to have been recovered from the most superficial 0.5 m of the southern end of the site, which forms part of Layer 1 (Fig. 3). Layer 1 varies in its composition from south to north. At the southern end of the excavation – closer to the rock face – this layer includes many angular pieces of limestone from gravel through cobble size up to half-meter size (Figs. 2 and 3). These inclusions probably represent the roof of the collapsed cave. In the central and northern portions of the excavation, Layer 1 is composed mostly of brown silty clay. Layer 2 is a layer of black-

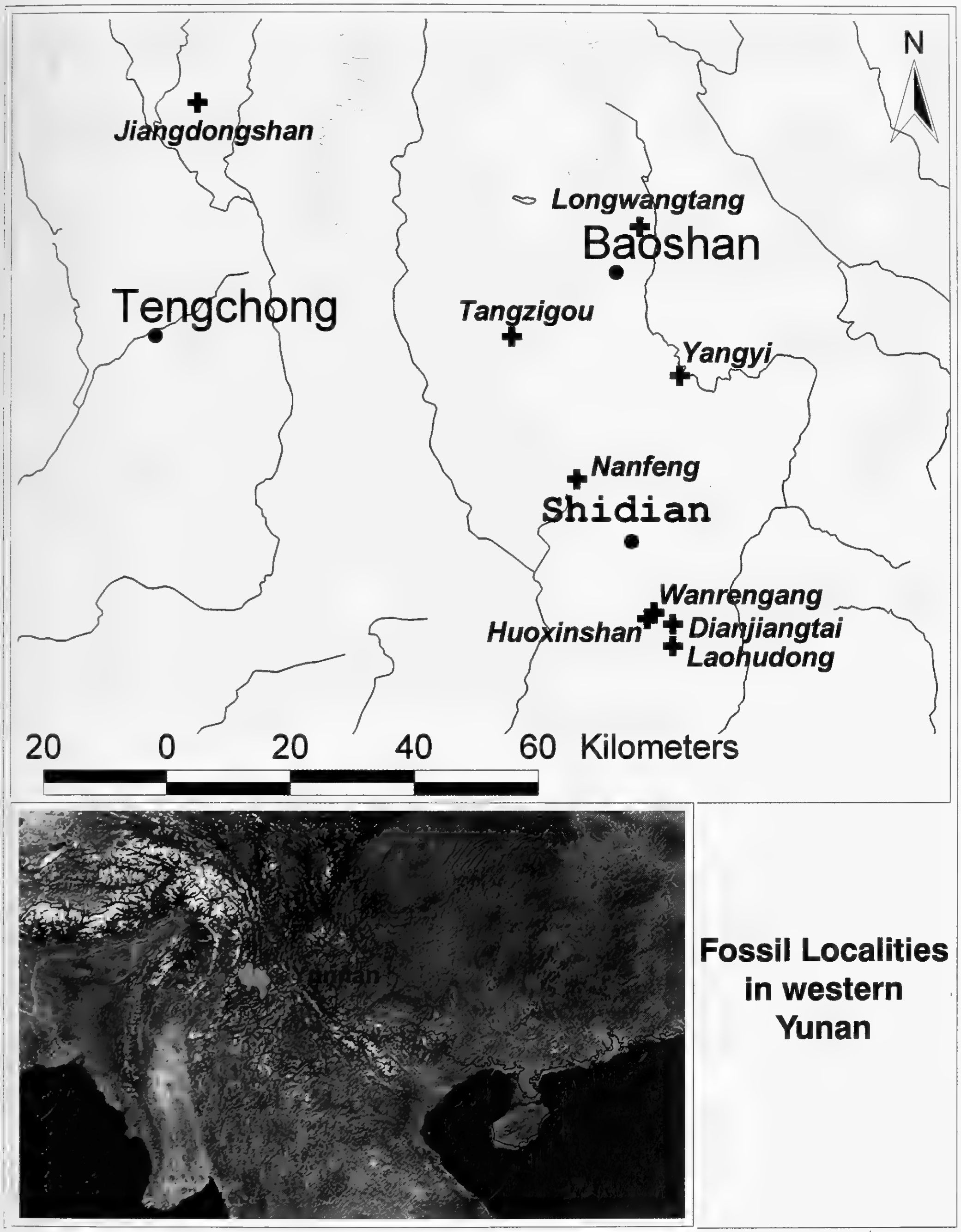


FIGURE 1. Map of Yunnan Province showing the cities of Baoshan and Shidian, with inset map showing the vertebrate paleontological sites discussed in text.

ish brown silty clay, which varies in thickness about 0.2–0.5 m; the layer is absent from the southern extremity of the excavation. Layer 3 is a 0.2–0.4 m thick layer of reddish brown silty, and Layer 4 comprises a layer of brown and black silty clay, with the black displacing the brown near the base of the excavation. The depth of Layer 4 is unclear because the excavation had not yet reached its base, but is almost certainly less than 0.5 m. Large stalagmites were found at the base of Layer 4 and throughout Layer 4 (Fig. 4). Samples of stalagmites from Layer 4 were taken for ^{230}Th/^{234}U dating. The black layer at the base of Layer 4 may represent a paleosol at or near the original floor of the cave. This attribution is suggested because the black layer is variable in thickness and slopes at an angle of about 20° toward the rock face.

Larger mammalian fossils were recovered at the site as the excavation proceeded. These bones and teeth were moderately well mineralized and required little preparation. The discovery of a muroid rodent tooth adhering to one of the specimens in the original collection led us to collect clay matrix from all four layers of the site in order to recover further remains of small mammals by wet-sieving. During our work in November 2002, matrix from Layers 1 and 4 only was washed and picked. This operation led to the retrieval of many dental and bony remains of rodents, insectivores and bats. The mammal fossils recovered from Layer 1 are fewer in number and represent fewer taxa than those of Layer 4. A detailed study of these materials is planned.

FIGURE 2. Nanfeng. The south face of the excavation; tape measure held by Yang Shengyi, Director of the Shidian Cultural Relics Bureau. Note the disturbed surface layer with large inclusions (Layer 1); these may represent the roof of the original cave or rock shelter. The rock face in the background is thought to have formed the original rear wall of the cave or rock shelter.

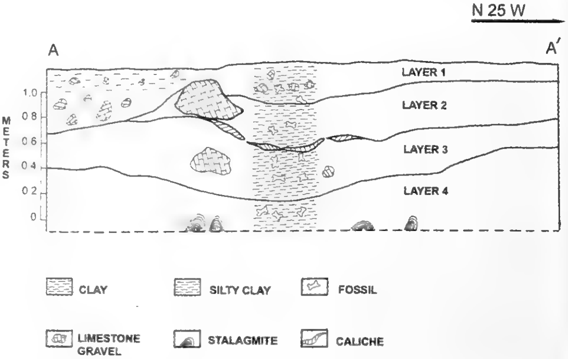


FIGURE 3. Nanfeng. Stratigraphic plan of the site. Drawing by Dr. Jean DeMouthe.

Fossils of large mammals, typical of the *Ailuropoda-Stegodon* fauna, dominate Layers 1 and 3 of the site. These fossils are most strongly concentrated at the base of Layer 1, which is interpreted as highest in the succession of the floor deposits of the former cave or rock shelter. In addition to the nominate taxa, this assemblage includes the genera *Hystrix, Rattus, Ursus, Rhinoceros, Cervus, Muntiacus,* and *Bos* (Table 1; Fig. 5). The apparent recovery of tooth plates of *Elephas* at the site by villagers in 1991 is significant, as there are no other known fossil sources in the area and the matrix adhering to the specimen and its preservation indicates that it came from the site, although this cannot be conclusively confirmed. If the co-occurrence of *Stegodon* and *Elephas* were confirmed by subsequent finds, this would support a Middle Pleistocene age for the fauna of Layer 1. Layers 2 and 3 produced relatively few large mammal fossils, mostly cervids. As of this writing, wet sieving of Layers 2 and 3 had not yet been conducted, so the nature of the small mammal assemblages in these layers is not yet known.

FIGURE 4. Nanfeng. Cross section of a stalagmite recovered from Layer 4, thought to be at or near the floor of the original cave or rock shelter.

The fossil assemblage of Layer 4 is significantly different from that of Layer 1, being dominated by small nocturnal mammals such as mice, rats, hamsters, and bats (Table 1). At least one set of associated remains (two incisors, a molar and

TABLE 1. Preliminary list of mammalian genera from Nanfeng.

Layer 1

Ailuropoda sp.
Ursus sp.
Viverridae gen. indet.
?*Hyaena* sp.
Panthera sp.
Stegodon sp.
Elephas sp.
?*Megatapirus* sp.
Rhinocerotidae gen indet.
Sus sp.
Cervus sp.
Elaphurus sp.
Muntiacus sp.
Hydropotes sp.
Cervidae gen. indet.
Antelopinae gen. indet.
Ovis sp.
Caprinae gen. indet.
Bos sp.
Rhizomys sp.
Apodemus sp.
Micromys sp.
Rattus sp.
Hystrix sp.

Layer 2

Cervidae gen. indet.

Layer 3

Viverridae gen. indet.
Cervus sp.
Muntiacus sp.
Cervidae gen. indet.

Layer 4

Erinaceidae gen indet.
?Soricidae gen. indet.
?Talpidae gen. indet.
Verspertilionidae gen indet.
Myotis sp.
Cervus sp.
Cervidae gen. indet.
Sus sp.
Bubalus sp.
Sciurotamias sp.
Sciuridae gen. indet.
Rhizomys sp.
Apodemus sp.
Micromys sp.
Rattus sp.
Myospalax sp.
Hystrix sp.
Ochotona sp.
Cricetulus sp.
Microtus sp.
?*Lepus* sp.

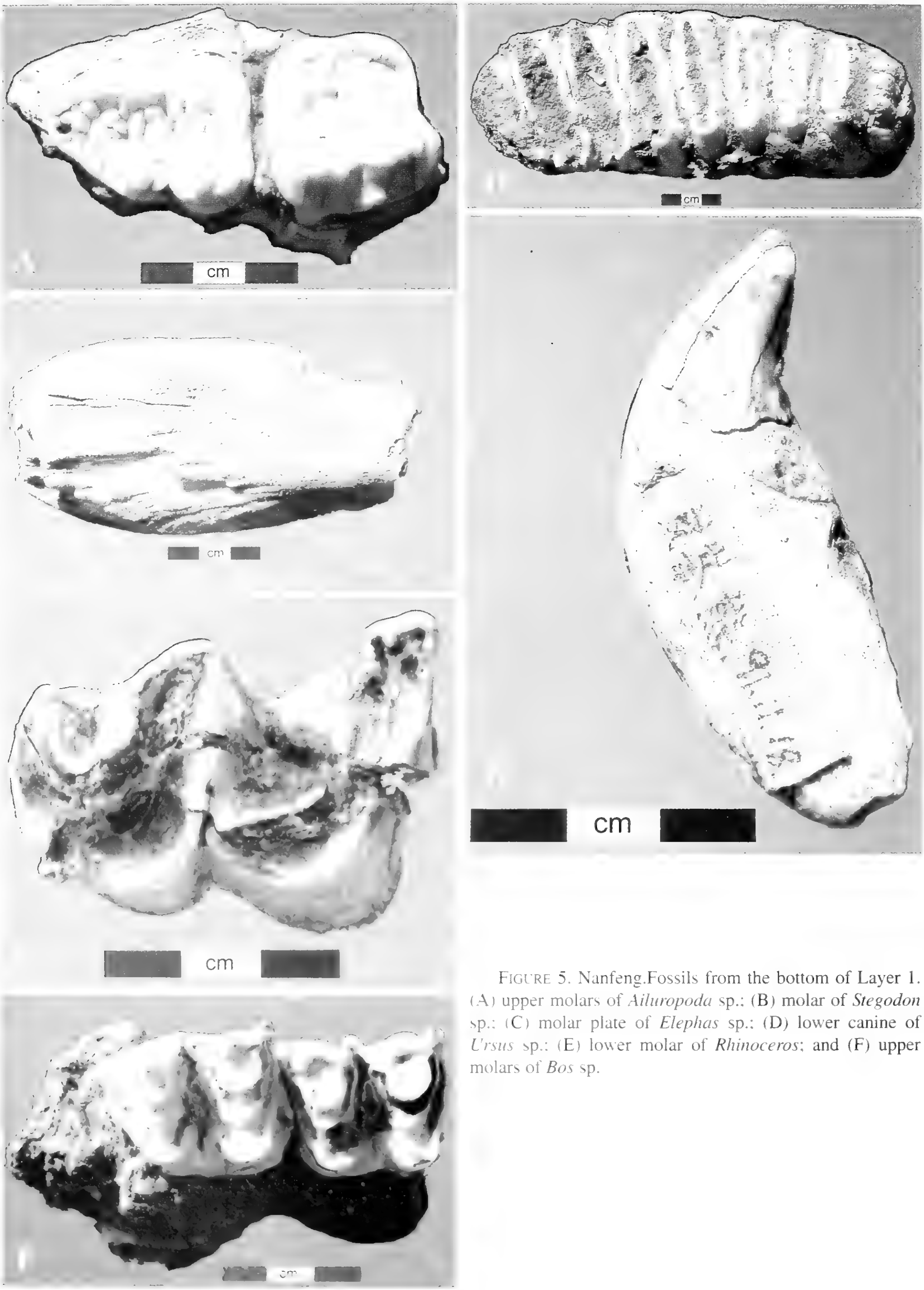


FIGURE 5. Nanfeng.Fossils from the bottom of Layer 1. (A) upper molars of *Ailuropoda* sp.; (B) molar of *Stegodon* sp.; (C) molar plate of *Elephas* sp.; (D) lower canine of *Ursus* sp.; (E) lower molar of *Rhinoceros*; and (F) upper molars of *Bos* sp.

three limb bones) of a rodent was found in one small piece of about 3 cm^3 of clay matrix. This evidence, combined with the fact that most of the mammalian taxa recovered are nocturnal or crepuscular, is consistent with the suggestion that many of the bones and teeth in Layer 4 represent the remnants of owl pellets. A complete study of the small mammal remains from Nanfeng will be undertaken in late 2003 and 2004.

A preliminary interpretation of the taphonomy of the Nanfeng site can be ventured on the basis of faunal assemblages so far recovered. Based on the preponderance of small nocturnal mammals in the oldest layer of the site, the Nanfeng cave or rock shelter is reconstructed to have had a small opening, which would have provided easy access for owls and bats, but otherwise only occasional and fatal access by larger mammals. Through time, the opening of the cave or rock shelter appears to have become larger, permitting the ingress of more and larger mammals, as witnessed by the accumulation at the base of Layer 1. Finally, the roof of the cave collapsed, possibly as a result of tectonic activity – common in the area – sealing the faunal assemblage until its accidental discovery in 1991.

The Nanfeng assemblage appears to be late Middle Pleistocene in age, based on the results of $^{230}Th/^{234}U$ dating conducted by Dr. Shen Guanjun of Nanjing University (Table 2).

TABLE 2. Results of $^{230}Th/^{234}U$ dating of stalagmites from Layer 4, Nanfeng.

Lab Number	*U Volume(ppm)*	$^{230}Th/^{232}Th$	$^{234}U/^{238}U$	$^{230}Th/^{234}U$	^{230}Th *age (ka)*
0267	0.061	21.5	1.154±0.053	0.847±0.040	188
0269	0.16	30.6	1.074±0.019	0.891±0.030	227

NEW COLLECTIONS FROM PREVIOUSLY KNOWN SITES

Wanrengang (N 24°37′24.2″; E 099°12′52.9″; altitude 1843 m)

In the Summer of 1987, poorly mineralized bones and teeth, as well as stone tools, and bone and antler tools of apparent Paleolithic age, were recovered by Mr. Yue Qi, the former director of the Shidian Cultural Relics Administration Office during his investigation at Wanrenggang rock shelter. Soon after (24–25 September 1987), experts from the Yunnan Provincial Museum and Baoshan Cultural Relics Administration Office joined them to do a test excavation. This resulted in the discovery of an almost complete hominin skull, mammalian fossils and more tools. A brief report, which described the 1987 excavation at the site and the human skull unearthed at that time, was published in 1992 (Zhang et al. 1992). This report provided a preliminary faunal list that included birds and nine species of mammals, which were referred to only by their common names in Chinese: porcupine, pig, rhesus macaque, bear, tiger, two species of deer, muntjac, and bovid.

Wanrengang is a large open rock shelter site near Xiaohanzhang village, Yaoguan country, about 23 kilometers from Shidian city (Fig. 1). Fossils and stone tools have been found over a large area, from the back wall of the current rock face (rock shelter) through an area ~30 m to the south and ~20 m below the level of the rock shelter floor (Fig. 6). The stratigraphy and geochronology of the site have not yet been studied in detail, but initial study of the archaeological remains so far recovered indicates that the site spans late Pleistocene to early Holocene, or roughly 15–7000 yr BP. A preliminary visit to the site was made by a team led by one of us (Ji X.-P.) in 2001 and a new test excavation was dug approximately 20 m south and 10 m below the level of the rock shelter floor in October 2002. Much of the site is currently under cultivation. During our visit, we did not make a formal excavation, but simply reviewed the 1987 and October 2002 excavations, combed

FIGURE 6. Wanrengang. General aspect of site. The large arrows indicate the area immediately in front (south) of the rock face (the back of the rock shelter) in which the densest accumulations of fossils and artifacts were found. The smaller arrows in the foreground indicate the cultivated field from which bones and artifacts were found at lower density.

FIGURE 7. Wanrengang. A typical accumulation of broken bone fragments from the floor of the rock shelter.

the cultivated area for fossils and dug small exploratory pits near the rock face to ascertain the extent of the site.

Wanrengang is a richly fossiliferous site, which is dominated by the remains of large deer and muntjacs, including *Cervus* sp., *Hydropotes* sp. and *Muntiacus* sp. Most of the fossils recovered are fragmentary and may have been crushed while *in situ* on a living floor (Fig. 7). This floor surface extends ~10 m from the current rock wall and appears to have been inhabited by a succession of humans from late Paleolithic times, based on the stone tools and fauna so far recovered. A preliminary faunal list for Wanrengang is provided in Table 3, and photographs of some of the specimens recovered from the site are presented in Figure 8. The limited variety of range of mammalian species recovered, the presence of only two carnivores (*Ursus* sp., *Panthera* sp.), and the large number of remains of old and immature deer and muntjacs present suggest that at least part of the site reflects a human accumulation.

While our project was not concerned with the recovery or identification of archaeological materials, one of us (G.C.) recovered an interesting tool in the course of combing the cultivated field approximately 15 m down slope in front of the Wanrengang rock shelter face. This tool represents an internal quartzite cast of a large gastropod shell, which was subsequently used by humans as a grinding tool, as judged by its highly worn convex surfaces (Fig. 9). To our knowledge, this provides one of the first examples of a fossil being fashioned and used by ancient humans as a tool.

During the course of our survey at Wanrengang, a new rock shelter site was discovered about 100 m to the west of the original site. This site, tentatively referred to as Wanrengang II (N 24°37′31.1″; E 99°12′50.1″; altitude 1807 m), is broadly part pf the same rock face and is also a rock shelter with an overhang. The deposits extend downslope about 15 meters to the south and less than 10 meters along the rock wall. This rock shelter yielded a small number of mammalian bone fragments, teeth of *Cervus* sp., and a piece of red ochre during a very short reconnaissance; further exploration will be conducted.

TABLE 3. Preliminary list of mammalian genera from Wanrengang

Macaca sp.
Homo sapiens
Panthera sp.
Ursus sp.
Rhinoceros cf. *sinensis*
Equus sp.
Sus cf. *scrofa*
Muntiacus sp.
Cervus cf. *unicolor*
Cervus sp.
Moschus sp.
Elaphurus sp.
Hydropotes sp.
Bubalus sp.
Naemorhedus sp. or *Ovis* sp.
Rhizomys sp.
Hystrix sp.

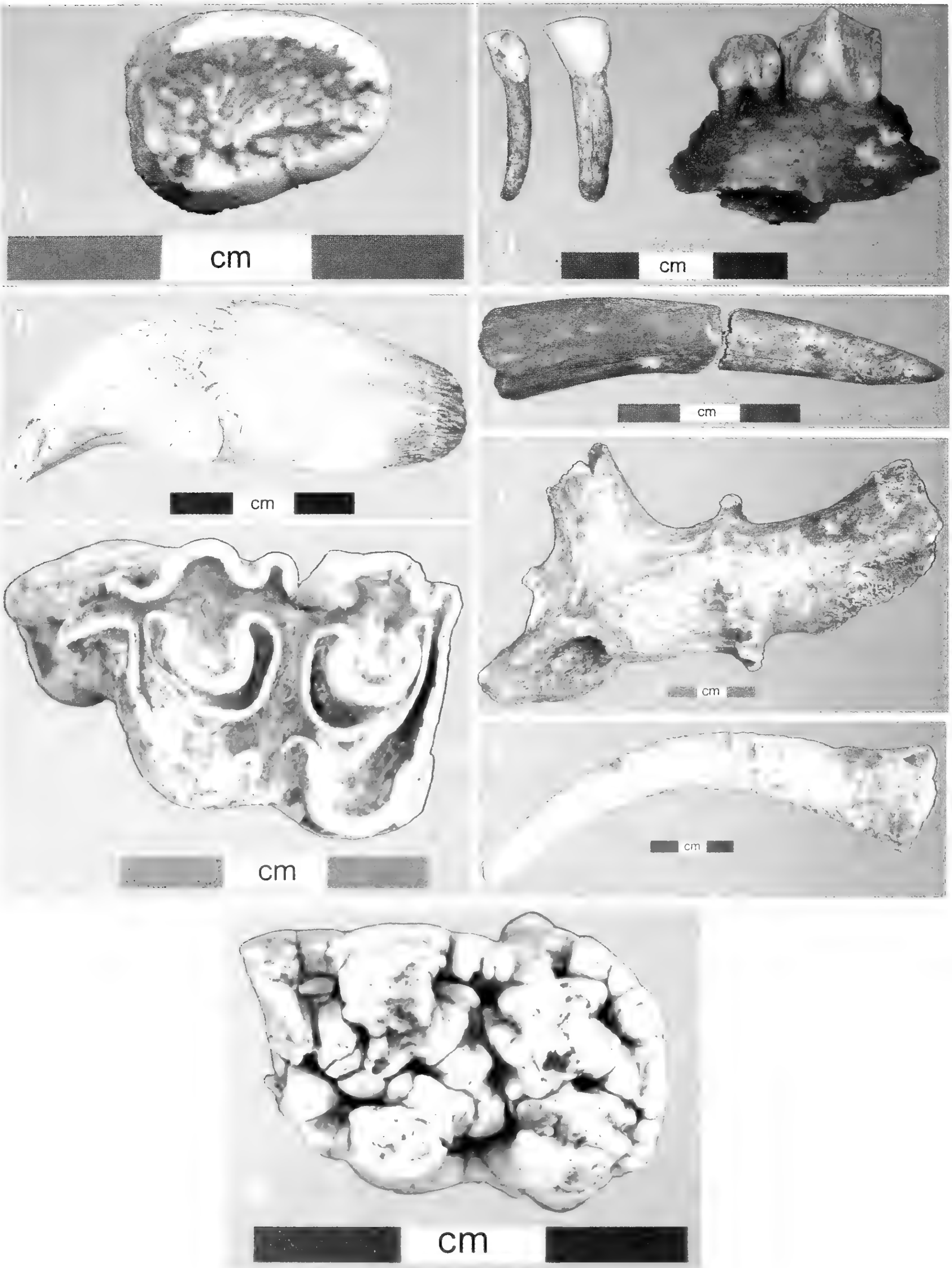
Further survey and excavation at both Wanrengang I and Wanrengang II are planned, as is study of the stratigraphy and age of both sites.

Huoxinshan (N 24°36.594′; E 099° 12.260′; altitude 1777 m)

A team from the Baoshan Cultural Bureau investigated the rock shelter site of Huoxinshan in 1987 and a brief report on the archaeological and paleontological discoveries at the site was published in 1992 (Li et al. 1992). The site yielded a large number and a wide variety of stone tools, as well as some bone tools, representing a time period spanning the late Paleolithic through the Neolithic. The fauna recovered from the site was not described in detail, but comprised *Cervus* sp., *Muntiacus* sp., *Bos* sp., *Panthera* sp., and Aves. During our short visit to the site, we slightly enlarged the previous excavation (Fig. 10), and recovered a small number of subfossil mammalian bones, bone fragments, and teeth, as well as three probable quartzite flake tools. Only one complete bone was discovered during the course of our work — a scapula of a large artiodactyl (probably *Cervus* sp.). This bone was eventually recovered in pieces and will be reconstructed. Teeth and dental fragments of *Cervus* sp., as well as isolated teeth of *Ovis* sp., *Bos* sp. and *Canis* sp. were also recovered. The estimated age of the site is 8–7000 yr BP, on the basis of a putative correlation to upper levels of the site of Tangzigou – dated by radiocarbon at 8–7000 yr BP (Li et al. 1992).

Tangzigou (N 25°01′31.0″; E 099°00′27.9″; altitude 1394 m)

The site of Tangzigou is well known for the partial skull of a Late Pleistocene hominin it has produced, sometimes referred to as "Pupiao Man" (Yunnan Provincial Museum Team, 1992; Gen and Zhang, 1992). The site has produced rich Late Pleistocene and Holocene mammalian faunas, which were described respectively by a joint team from the Yunnan Provincial Museum and Baoshan Prefecture Museum (1992) and by Zhang et al. (1992). About 29 species of mammals were reported as present at the site. In October 2002, a small test excavation at Tangzigou was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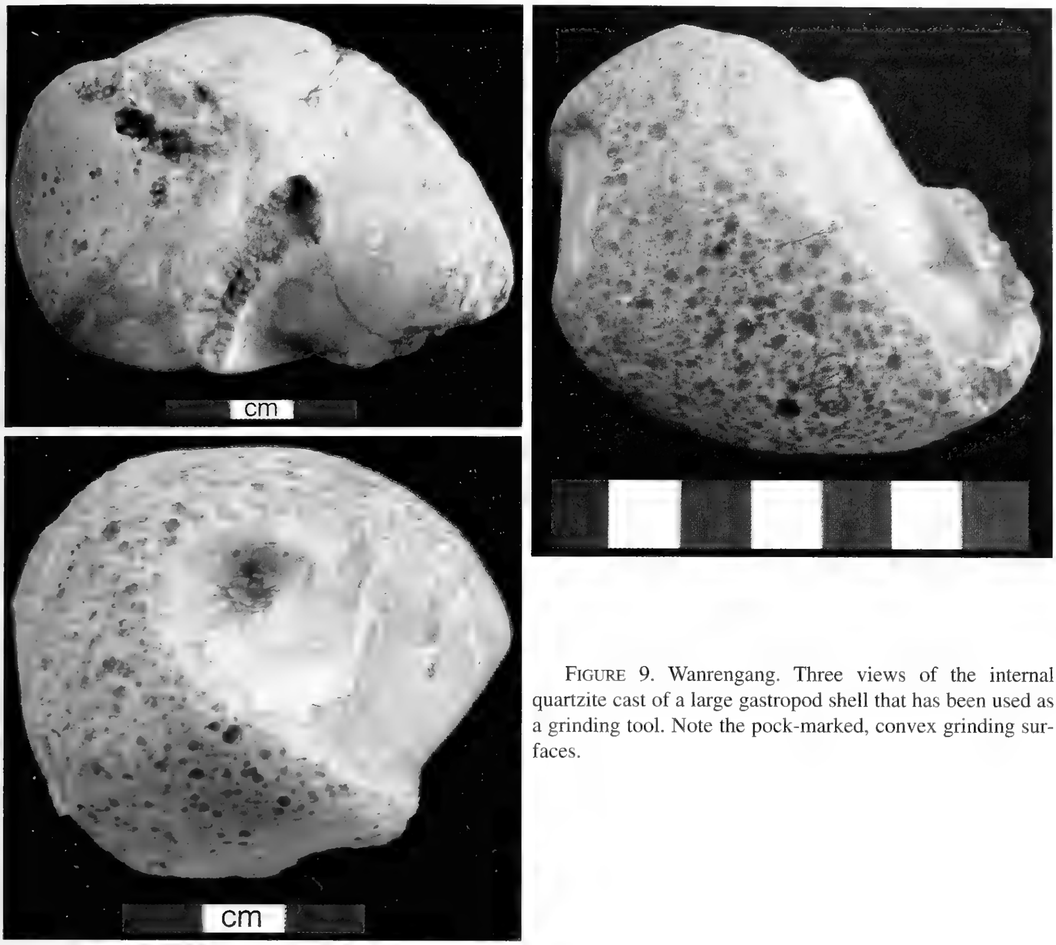

FIGURE 9. Wanrengang. Three views of the internal quartzite cast of a large gastropod shell that has been used as a grinding tool. Note the pock-marked, convex grinding surfaces.

supervised by one of us (Ji X.-P.). During our November 2002 visit to the site, a small number of vertebrate specimens, including a fragment of a molar of *Homo* sp. and remains of several cervids and a large bird were gathered from the test pit and from other areas of exposed sediment nearby. A formal excavation of the site is planned for late 2003.

Laohudong (N 24º34.551′; E 099º14.506′; altitude 1839 m)

Laohudong, "the Tiger's Cave", is a limestone cave, from which fossilized mammalian bones have been unearthed over the course of many years by local inhabitants. A brief report on the stratigraphy and archaeology of the site was published by Yue (1992). That account included a brief listing (in Chinese only) of vertebrate remains recovered from the cave: Aves (Family unknown), *Macaca mulatta*, *Rhizomys* sp., *Ursus* sp., *Mustela* sp., *Canis* sp., *Rhinoceros* sp., Cervidae (genus not specified), *Sus* sp. and Bovidae (genus not specified). The report also provided a radiocarbon

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FIGURE 8. Wanrengang. Some of the mammalian genera represented at the site. (A) *Ursus* sp. molar; (B) *Ursus* sp. canine, with rodent gnaw marks evident on surface of root; (C) *Equus* sp. molar; (D) *Muntiacus* sp. incisors and partial mandible with premolar and molar; (E) *Muntiacus* sp. horn core; (F) *Hydropotes* sp. partial antler; (G) horn core of *Ovis* sp. or *Naemorhedus* sp.; (H) *Sus* sp. partial molar. All specimens pictured except for the molar of *Ursus* sp. were recovered during the course of the October and November 2002 expeditions. The ursid molar was recovered in 1987.

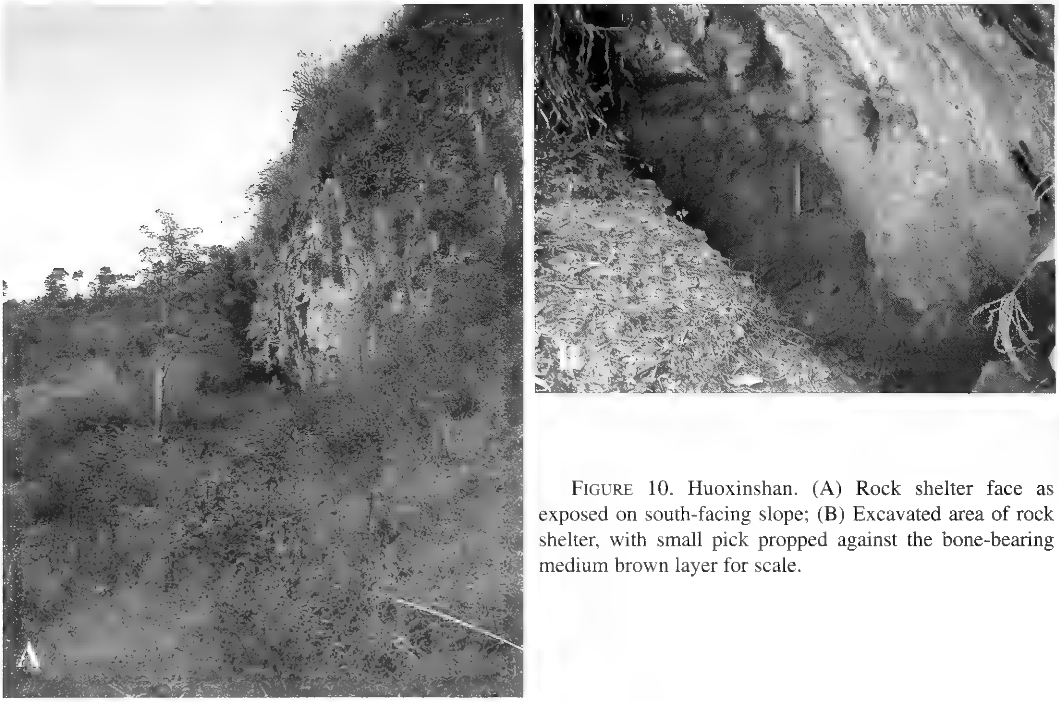

FIGURE 10. Huoxinshan. (A) Rock shelter face as exposed on south-facing slope; (B) Excavated area of rock shelter, with small pick propped against the bone-bearing medium brown layer for scale.

age on charcoal of 18,403 ± 1181 yr BP from the cave. A collection of fossils from Laohudong was deposited at the Shidian Cultural Bureau in 1989.

During our short visit to Laohudong in November 2002, we entered the cave and assessed the desirability and feasibility of conducting an excavation therein. The cave has two narrow entrances, which merge into a common aditus of about 10 m length, through which it is possible to crawl. This passageway leads to a chamber of about 3 × 4 × 2 m in which excavations had been carried out by villagers over the years. From the chamber, a tunnel of about 15 m extends until a drop off to a lower level; this was not followed because of a lack of appropriate equipment. Layers of densely fossiliferous, heavily cemented flowstone are exposed in the cave entrances and along the aditus and the walls of the chamber. The well-mineralized but generally fragmentary remains of many, mostly small to medium-sized mammals are preserved in these layers (Table 4; Fig. 11).

TABLE 4. Preliminary list of mammalian genera from Laohudong

Trachypithecus sp.
Macaca sp.
Ailuropoda sp.
Canis sp.
Ursus sp.
Cervus sp.
Muntiacus sp.
Cervidae gen. indet.
Bubalus sp.
Sus cf. *scrofa*
Rhizomys sp.
Equus sp.
Rhinoceros cf. *sinensis*
Hystrix sp.
Lepus sp.

The Laohudong accumulation almost certainly represents one that was washed into the cave by flowing water. *Hystrix* and *Muntiacus* fossils, with considerably smaller numbers of other rodent, carnivore, monkey, and large cervid remains, dominate the site. It is unclear whether the dominance of small- to medium-sized mammals at Laohudong is a taphonomic bias (due to the preferential transport and deposit of smaller elements by flowing water in the cave), or whether this represents a modern or latest Pleistocene fauna bereft of megafauna. Further explorations and excavations of the cave complex are planned, as well as new determinations of the age of the site. (The published radiocarbon date for the site based on archaeological charcoal appears much too young for what otherwise appears to be the cave's Late Pleistocene fauna.)

OTHER SITES

Yangyi (N 25°01.426′, E 099°00.514′, Altitude 1375m) and Dianjiangtai (N 24°36.487′, E 099°14.506′, Altitude 1831m)

The sites of Yangyi and Dianjiantai represent two latest Miocene or early Pliocene sites, from which fossils have been retrieved from clay strata immediately overlying lignite deposits. Both sites are active mines: Yangyi is a lignite mine, and Dianjiangtai is a lignite mine and brickworks. Yangyi has yielded a relatively diverse fauna, including two primates (Table 5), while Dianjiangtai has only produced fossils of *Stegodon* cf. *yangyiensis* and *Axis* sp. Most of these fossils were discovered by miners and workers at the site, and subsequently turned in to paleontologists. Yangyi is highly significant for having yielded a primate fossil (Gen 1995), which is thought to be the youngest Eurasian fossil hominoid so far recovered (Harrison et al. 2002). The possibility of retrieving further fossils from either of these important late Tertiary sites will depend upon the activities of the mines' employees, because active searching or deliberate excavation for fossils is precluded. At Yangyi, the mine manager informed us that the skeleton of an entire *Stegodon* had been recently unearthed and then discarded because he erroneously did not think anyone would be interested in it.

TABLE 5. Preliminary list of mammalian genera from Yangyi

Lufengpithecus sp.
Sinoadapis sp.
Zygolophodon sp.
Chilotherium yunnanensis
Stegolophodon yanyiensis
Stegodon elephantoides
Axis sp.

Natural Well on Jiangdongshan, Tengchong (N 25°22′, E 098°33′ altitude 1900–2000m)

A natural well on Jiangdongshan (Jiangdong Mountain) near the village of Gudong, west of Tengchong, was found to contain mammalian fossils by nearby villagers. A small team from the Tengchong Cultural Bureau, led by the Bureau's director, Mr. Li Zheng, undertook a preliminary exploration of this well in the mid-1990s. The natural well is estimated to be 46 m deep, with a surface opening of about 2 × 4 m. The internal shape of the well (to the extent to which it is now known) is described as pear-shaped, with diameter of about 10 m at an intermediate platform. This platform does not represent the bottom of the well, however; the bottom slopes from this base at an angle of 30–45° downward, but was not explored by Li's team because of a lack of necessary equipment. The platform is reported to be covered with a clay-like infilling of approximately 0.5 m thickness, which contained abundant mammalian fossils. During our visit to Tengchong, we interviewed Li Zheng, viewed some of the fossils unearthed, and inspected photographs of the site and of other fossils. A visit to the natural well itself was not possible because of bad weather and the remoteness of the site. The mammalian fossils retrieved from the site include a modern Asian elephant (*Elephas* sp.), three individuals of giant panda (*Ailuropoda* sp.), a large gazelle, a large deer (*Cervus* sp.), a hypsodont muntjac (probably *Muntiacus* sp.), and a very large rhizomyid rodent. We also learned that another fossil-bearing site (probably a rock shelter) exists near the well, on the same mountain. Based on the composition of the mammalian assemblage, a Late Pleistocene age for the fauna is hypothesized.

The sites at Jiangdongshan are of special importance because they are some of the few documented vertebrate paleontological sites that are west of the Nujiang River, and therefore within the

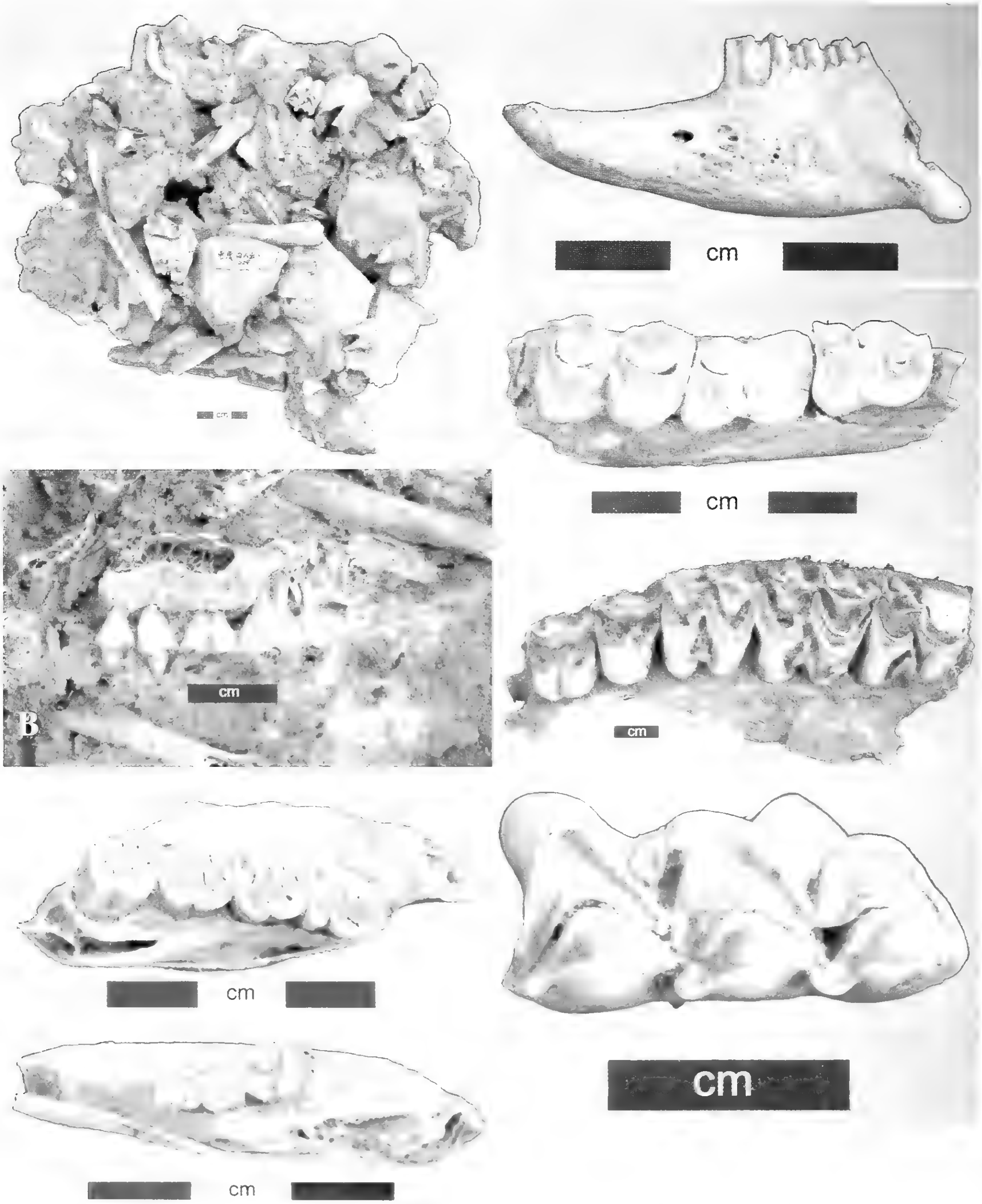

FIGURE 11a-h. Laohudong. Some of the mammalian remains recovered from the site. (A) Mammalian fossils *in situ* in calcareous flowstone recovered from the cave; (B) upper premolars and molars of *Trachypithecus* sp.; (C) molars in lower jaw of a porcupine, *Hystrix* sp.; (D) lower jaw of the bamboo rat, *Rhizomys* sp.; (E) lower jaw and molars of a rabbit, *Lepus* sp.; (F) lower molars of the water deer, *Hydropotes*; (G) upper molars of a large deer (cervid); (H) lower molar of a large deer (cervid).

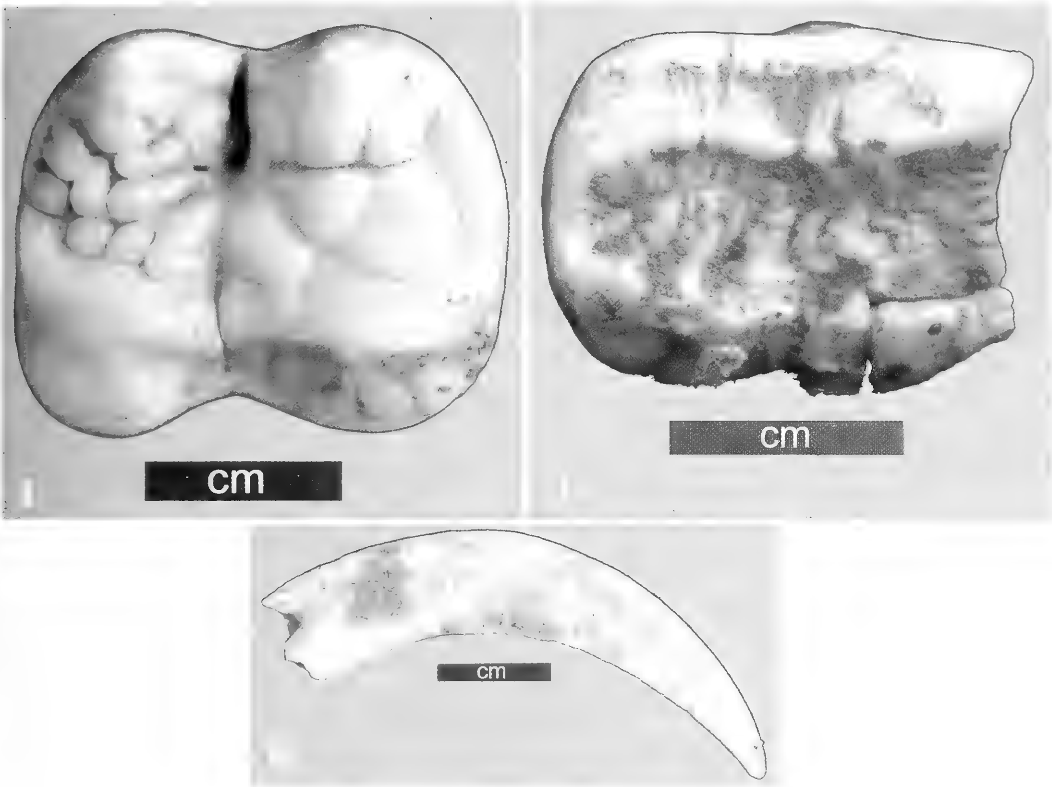

FIGURE 11 (continued). (I) lower molar of the panda, *Ailurapoda*; (J) partial lower molar of a bear, *Ursus* sp; (K) distal phalanx ('claw') of a probable bear, *Ursus* sp.

strict confines of the Gaoligongshan Range itself. To our knowledge, the retrieval of a giant panda fossil from this site marks the westernmost extent of the animal's known range in the past. Exploration of these sites and retrieval of fossils from them is planned for the coming years.

Longwangtang (N 25°11.106′; E 099°11.650′; altitude 1659m)

The site of Longwangtang was discovered by a farmer in 1984, when he unearthed some bones and teeth while getting construction materials from a cave area; these were reported to Baoshan City Museum (Gen et al. 1992). A subsequent visit to the site by representatives of the Museum confirmed the presence of fossils, including teeth of *Megatapirus* sp., and charcoal at the site. An excavation carried out at the site in 1987 led by the late Zhang Xingyong of Yunnan Provincial Museum revealed further evidence of a Late Pleistocene fauna comprising *Panthera* sp., *Canis* sp., *Ursus* sp., *Cuon* sp., *Megatapirus* sp., *Bibas* sp., *Sus* cf. *scrofa*, *Muntiacus* sp., *Cervus* sp., and *Ovis* sp. or *Naemorhedus* sp., *Rhizomys* sp., *Hystrix* sp., Sciuridae gen. indet. and *Lepus* sp., in addition to Late Paleolithic stone tools (Gen et al. 1992).

The site of Longwangtang abuts a gently sloping field system, which in turn abuts a modern limestone rock face. The site represents a collapsed cave (Gen et al. 1992), and warrants further exploration and excavation because of the abundant Late Pleistocene fauna it produced.

Discussion and Conclusions

Baoshan Prefecture is rich in vertebrate paleontological and archaeological sites (Zhang, 1992), especially Late Pleistocene and Holocene sites. Our preliminary survey of one new paleontological site (Nanfeng) and review of several previously known sites indicates that the prospects of future significant discoveries Quaternary faunas in the Prefecture are great. This is particularly so of the probable Middle to Late Pleistocene site of Nanfeng, the Late Pleistocene sites of Laohudong and Longwangtang, the Late Pleistocene to Holocene sites of Wanrengang and Tangzigou, the Late Paleolithic and Neolithic site of Huoxinshan, and a few other Neolithic sites, which straddle the Pleistocene/Holocene boundary.

Acknowledgments

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of *Semiconchula* from Central Chiapas, Mexico (Pulmonata: Xanthonychidae)

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A new species of the genus *Semiconchula* is described. It shares with *Semiconchula custepecana* the internal highly uncalcified shell and two mucus glands, one massive and the second reduced. They differ in the length of the reduced mucus gland and various structures of the reproductive tract. The new *Semiconchula* possesses an asymmetrical central radular tooth in contrast with the symmetrical central tooth of *S. custepecana*. The genus is known only from the state of Chiapas, Mexico.

Resumen

Se describe una nueva especie dentro del genero *Semiconchula*, que comparte la concha interna altamente descalcificada y dos glándulas de mucus, una masiva y la otra reducida. Las diferencias entre las dos especies está en la longitud de varias de las estructuras del aparato reproductor. Con respecto a la rádula, el diente central de la nueva especie de *Semiconchula* es asimétrico en contraste con el diente central simétrico de *S. custepecana*. El género se conoce solamente para el estado de Chiapas, México.

Examination of a semislug specimen recently donated to the California Academy of Sciences Invertebrate Collection and coming from a low mountain close to San Cristobal de las Casas, Chiapas, indicates that it belongs in the genus *Semiconchula*; however, it differs enough in various characters from the one other known species in the genus, which, until recently, was thought to be monotypic, that it must be ascribed to a new species. The type species of the genus *Semiconchula*, *Semiconchula custepecana* Naranjo-García, Polaco, and Pearce 2000, comes from southern Chiapas.

MATERIAL AND METHODS

After dissection of the preserved specimen, the reproductive organs were stained with hematoxylin and eosin, dehydrated with 95% alcohol, changed to absolute ethanol, then to 50% alcohol-toluene, and then four changes in toluene (Miller 1967). Following that procedure, the specimen was mounted in Permount, a synthetic resin. Measurements and the illustration of the reproductive structures were done from the mounted specimen. The drawing was made from the whole mount projected on paper by an overhead projector.

Semiconchula breedlovei Naranjo-García, sp. nov.

Figures 1–3

DIAGNOSIS.— Animal slug-like with a visceral hump on mid-portion of dorsum. Sole undivid-

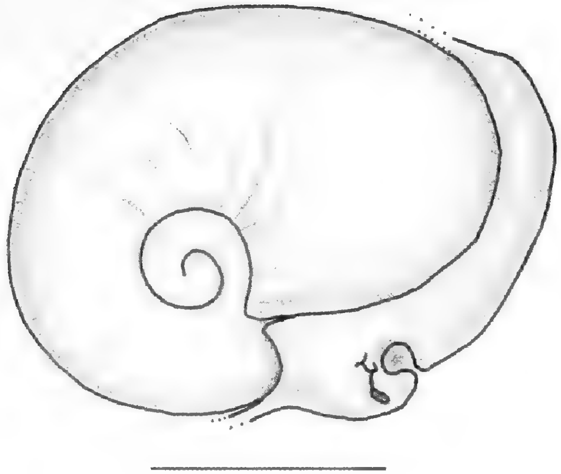

FIGURE 1. Apical view of shell of holotype. Illustration made from dissecting notes after removal of the mantle that entirely cover the shell. On the right side, the mantle collar borders the shell. Scale bar = 5 mm.

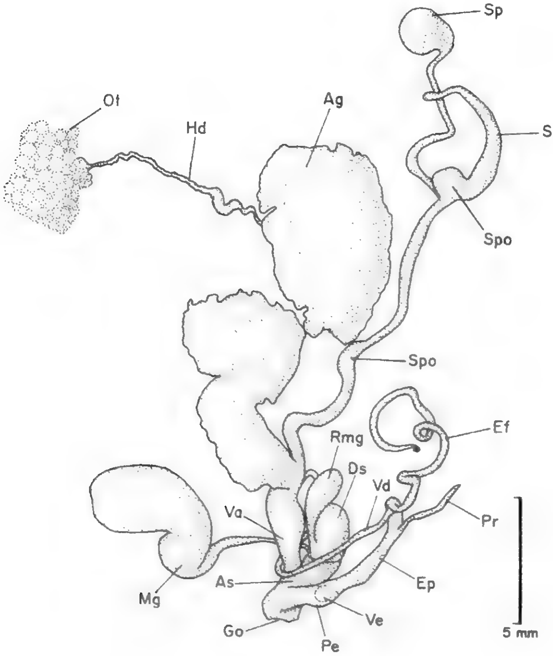

FIGURE 2. Reproductive anatomy of holotype of *Semiconchula breedlovei*, sp. nov.: Ag: Albumen gland, As: Atrial sac, Ds: Dart sac, Ef: Epiphallic flagellum, Ep: Epiphallus, Go: Gonopore, Hd: Hermaphroditic duct, Mg: Mucus gland, Ot: Ovotestis, Pe: Penis, Pr: Penial retractor muscle, Rmg: Reduced mucus gland, Sd: Spermathecal diverticulum, Spo: Spermathecal pouch, Sp: Spermatheca, Va: Vagina, Vd: Vas deferens, Ve: Verge.

ed; foot fringe holopod, without suprapedal groove. On reproductive system penis with verge, flagellum, and spermathecal diverticulum. Dart sac situated high on atrial sac.

DESCRIPTION.— Animal slug-like with visceral hump on the mid-portion of dorsum. Mantle entirely covers the reduced shell.

DESCRIPTION OF SHELL.— Shell vitriniform, internal, depressed, imperforate, delicate, extremely brittle, light brown (Fig. 1). Whorls 2-1/3 expanding rapidly. Apex smooth, body whorl of shell with uneven growth lines. Aperture large, ovate, slightly oblique, wider than high, peristome amber and translucent, soft and thin. Shell covers visceral hump entirely; the nearly uncalcified shell gradually loses more calcium towards the apex and below the hump. At the base of the hump the shell is made of a non-calcified organic sheath. Shell covered entirely by mantle. A strong connective tissue unites shell to collar on left side of body.

MEASUREMENTS OF SHELL.— Maximum diameter 11.0 mm, height 6.3 mm.

REPRODUCTIVE ANATOMY.— Penis short, elongated, cylindrical. Verge short cylindrical, tip broadly conical, slightly less than 1/3 the length of the penis. Penial retractor muscle elongated and attaches on left side of body wall at edge of mantle collar. Epiphallus long and thick, flagellum long and moderately thick originally coiled over itself. Vagina slightly conical, the widest portion apical, length about same as that of penis. Atrial sac cylindrical, wider on the apical portion, inner walls show two muscle dispositions that divide atrial sac in halves. The basal portion with parallel muscles disposed longitudinally, the upper part bearing circular parallel transverse muscles resembling a bellows. Dart sac is an ovate elongated sac situated high on the atrial sac and enters partially into atrial sac (Fig. 2).

There are two mucous glands, one large, the second reduced to about 1/3 the size of the first. The larger mucous gland sacular with inner longitudinal ridges. Second mucous gland a smooth elongated and roundish sac with a narrow inner duct with glandular walls. Each gland has a separate duct opening high in the atrial sac at side of dart sac. Spermathecal duct varies in thickness throughout its length, the inner walls of spermathecal duct with pilasters. It possesses two pouches: one pouch is located approximately half way on spermathecal duct before the fork; the second pouch is located just past the fork that ramifies to the spermathecal diverticulum and the duct that bears the spermatheca itself. Spermathecal diverticulum elongated and of irregular thickness. The spermathecal diverticulum and the first 1/3 portion of spermathecal duct (just after the fork) with glandular walls. Spermathecal diverticulum with a thick, club-shaped structure of about 5 mm, wider basally, inside is one dart, beside this structure two darts. Also, at the basal portion of spermathecal duct another dart is present. In both low and high spermathecal pouches, stiff translucent amber structures of diverse size and thickness are present, perhaps these structures could be remains of darts.

Measurement of reproductive structures (in mm) of holotype.— Penis 1.8, verge 0.5, vagina 1.9, atrial sac 1.8, dart sac 2.3, epiphallus 4.3, epiphallic flagellum 12.7, free oviduct 1.5, spermatheca 1.8, spermathecal duct (to base of diverticulum) 12.3, spermathecal diverticulum 7.5, spermathecal duct from fork to spermatheca 7.5.

External anatomy.— Anterior portion of body brown, flanks light brown-reddish, tail lighter brown than that of head, first pair of tentacles fully contracted (not visible on the surface), second pair of tentacles brown. Mantle, thick, light cream brown (not translucent), with large black raised irregular freckles without a pattern. Body skin irregularly reticulated. Mucus color bright yellow (that fades in alcohol). Tail cylindrical, tapering to the posterior end, tip roundish. A fine mid-dorsal groove runs from edge of hump to tail. No other structures (horn or caudal pore) on tail. Edge of mantle on left side of body outlined by a fine pigment accumulation. Pneumostome and anal pore are on anterior, right lower edge of visceral hump. The respiratory pore located on the upper and anal pore on the lower portion. Pneumostome with a roundish upper lappet limiting the respiratory pore and overhanging at both anterior and posterior ends. The anal pore is an oblique, semi-lunate slit with edges pointing upwards. The lappet's external wall overhangs the body and is fused with the mantle on the posterior side. Gonopore ovate, whitish and with smooth edge.

Radula and jaw of holotype.— Radular teeth tricuspid; central tooth asymmetrical with the middle cusp wide, left cusp situated low, right cusp wide with the outer edge of base thickened and rounded (Figs. 3A–B). Central cusp widest and tallest in lateral teeth. In teeth 21 to 30, the inner lateral cusp is almost of the same size as central cusp (Figs. 3C–D). In tooth 31 the central and inner lateral cusps are less pronounced. In teeth 32 to 35 the central and inner lateral cusps gradually reduce in height. In tooth 36 all three cusps are about same height, the central and inner cusps remaining slightly closer together. Tooth 37 with four cusps, two tall inner and two short outer cusps. Tooth 38 roundish (Figs. 3C, E). Jaw arched with two mid-lateral ribs extending beyond the margin of the jaw (Fig. 3F). Tooth formula 36-1-36 to 38-1-38 (Fig. 3B).

Internal anatomy.— Right ocular retractor muscle (RER) almost dorsal, slightly to the right of the mid-longitudinal line. It (RER) passes over the vagina and joins the columellar muscle passing between the reproductive organs and esophagus. The esophagus and penis are pushed to the left side of body. Reproductive organs occupy most of the anterior body cavity. The diaphragm is located below the reproductive organs (ovotestis, hermaphroditic duct and spermatheca). The columellar muscle, well developed, runs from anterior portion of foot, over the stomach, below prostate-uterus, then crosses the diaphragm and attaches to the weak shell passing between the digestive gland and ovotestis. Salivary glands flat, long and of irregular shape and appressed to the esopha-

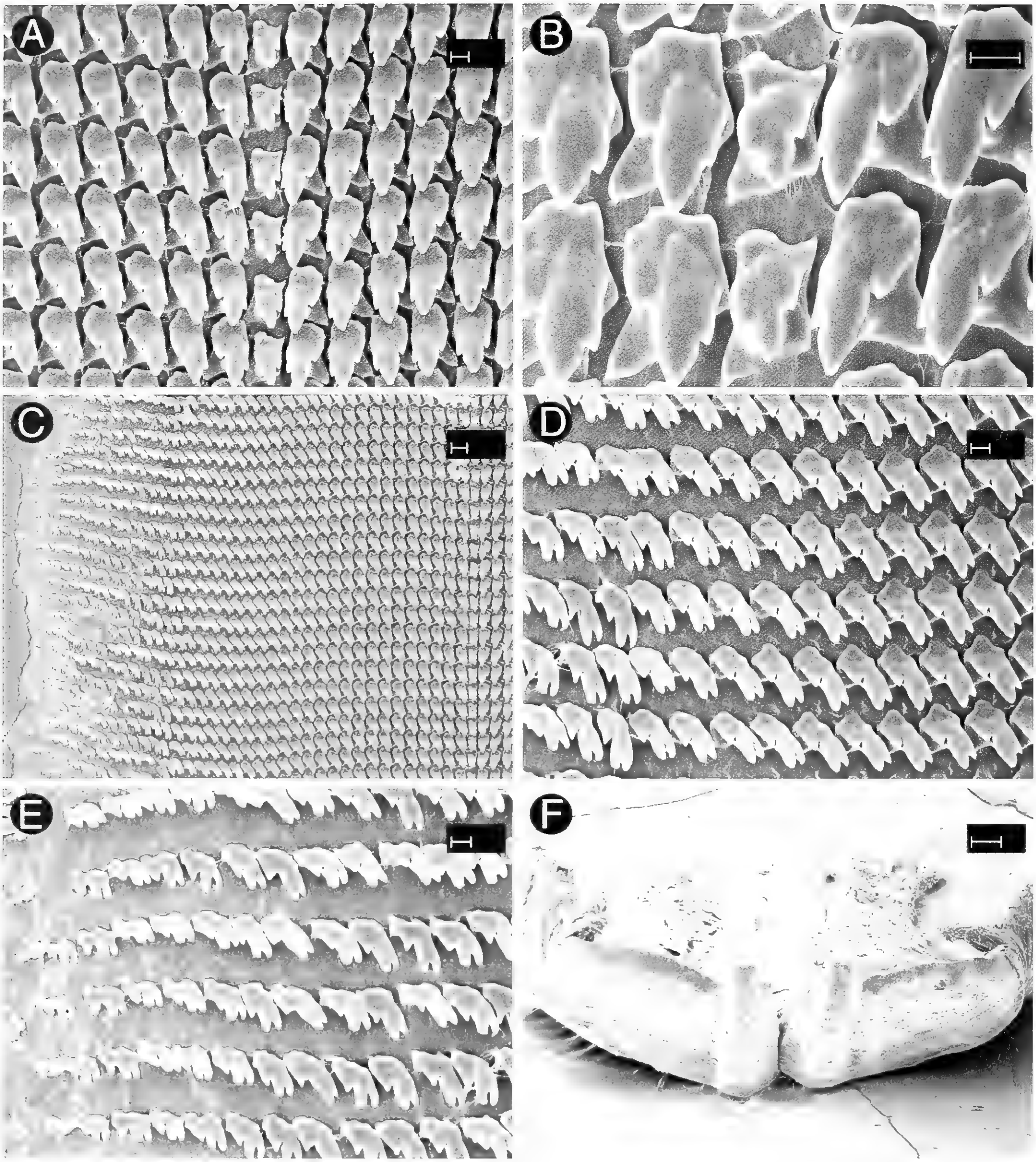

FIGURE 3. Preparation of radula and scanning electron microscope (SEM) photographs by Yolanda Camacho-García. (A) central tooth and lateral teeth 1 to 6, from central tooth to the left, scale bar =10μm. (B) central tooth close up, in middle row, scale bar =10μm. (C) general view of radula from central tooth (right hand side to the left) to marginal teeth, scale bar =30μm. (D)teeth 16 to 26 from right to left, scale bar =10μm. (E) teeth 27 to 36 from right to left, tooth formula 36-1-36 to 38-1-38, scale bar =10μm. (F) jaw of *Semiconchula breedlovei* is shown in upside down position in reference with its location on the snail body. It also should be noted that jaw broke in the mid-line during processing, scale bar =100μm.

gus and stomach. The right gland appressed to the right side, length over 7 mm. The left salivary gland is appressed to the bottom of the esophagus and stomach, length about 10 mm. The lung is on the right anterior side of visceral hump. The kidney is above it. Lung and kidney are spongy.

TYPE LOCALITY.— MEXICO, Chiapas. W of San Cristobal de Las Casas, steep, heavily wood-ed slope with *Quercus* and *Drimys* near the summit of Muk'ta vits (Cerro Huitepec). The dominant species was *Lamourouxia stenoglossa* F.W. Hunnewell and L.B. Smith from the family Scrophulariaceae. Elev. 2600 m., 25 September 1976. Collector Dennis E. Breedlove.

MATERIAL EXAMINED. — HOLOTYPE: California Academy of Science, Invertebrate Collection, CASIZ 077540. PARATYPE: Same locality as holotype, 22 October 2002, Collector Gerardo Carbot-Chanona. Colección Nacional de Moluscos, Instituto de Biología, U.N.A.M. CNMO 1203.

HABITAT.— Most of the vegetation of Cerro Huitepec is a secondary oak forest and is a reserve under the care of the group Pronatura, except for the summit that has some very reduced patches of original vegetation. According to Breedlove (1981), most of the original vegetation in the Chiapas Plateau has disappeared due to the type of agriculture employed by the Mayan farmers, who have used all the available land for cultivation.

ETYMOLOGY.— The species is name after Dr. Dennis E. Breedlove, who collected non-marine mollusks during his botanical explorations in Chiapas.

REMARKS.— The paratype presents the same general external characters as the holotype, except for the darker body and reddish color. The shell of the paratype is smaller, with maximum diameter measuring 7.8 mm and height 3.0 mm, two whorls and a sculpture of fine growth lines. The specimen is sub-adult showing the reproductive organs in early stage of development.

DISCUSSION

Semiconchula breedlovei is most closely related to *Semiconchula custepecana* (Naranjo-García, Polaco, and Pearce 2000) from the same state (Chiapas) but separated by a straight line distance of 100 km and the central depression (central depression physiographic region according to Müllerried 1957). The two species share the internal, vitriniform, depressed, imperforate, thin, fragile shell. They both possess a short penis, epiphallic flagellum and spermathecal diverticulum, single dart sac, and the two mucus glands, and both have one mucus gland massive and the other reduced. They also share the highly vascularized (spongy) lung. Nonetheless, they differ in that the delicate radial ribs of the embryonic shell of *Semiconchula custepecana* are not present in *Semiconchula breedlovei*. In *S. breedlovei* the shell is more fragile than in *S. custepecana*. They also differ in the length of the penis, the verge and the vagina, all structures being slightly larger in *S. custepecana*. The second reduced mucus gland in *S. custepecana* is a rounded vesicle while in *S. breedlovei* is an elongated roundish sac, 9 times larger. Both species share the inner circular muscles that resemble a bellows on the atrial sac; however, they differ on the basal portion of the atrial sac with parallel longitudinally disposed muscles present in *Semiconchula breedlovei* but not in *S. custepecana*.

Other differences are in the epiphallus, epiphallic flagellum, and the spermathecal duct, which are 2.7, 2.4 and 2.3 times longer, respectively, in *S. breedlovei* than in *S. custepecana*. Debris and the presence of darts inside the spermathecal duct and spermathecal pouches suggest that in *Semiconchula breedlovei* the spermatheca is also a digestive and reabsortion organ, as has been shown for *Biomphalaria glabrata* (Kitajima and Paraense 1983; Roger and Reeder 1987) and for five species of *Sonorella* (Reeder and Rogers 1979; Rogers Reeder and Shannon 1980).

The tooth formula differs between the two species; being 32-1-32 to 36-1-36 in *S. custepecana* and 36-1-36 to 38-1-38 in *S. breedlovei*. The central tooth is symmetrical in *S. custepecana* in contrast to the asymmetrical one in *S. breedlovei*. The marginal teeth are also dissimilar. Tooth 32 in *S. breedlovei* is robust with three well defined cusps, in contrast to tooth 32 in *S. custepecana*, which is small, with reduced cusps, almost obsolete.

On 19 August 1991, we (Oscar J. Polaco, three of his students, and the author) attempted to find more specimens of this new species of *Semiconchula*. However, our efforts were fruitless due to the highly modified environment at Cerro Huitepec (on one side). We were informed that the other side of the mountain possessed a more natural forest but, unfortunately, that side was (and continues to be) under the surveillance of the guerrillas, and it was not advisable to approach it. Efforts to obtain more specimens were started again by local biologists in July 2002. Fortunately, following Dr. Breedlove's directions, Gerardo Carbot-Chanona and I were able to find **a** second specimen on 22 October 2002. At this time, we again recorded the small size and patchiness of the habitat where this new species lives. *Semiconchula breedlovei* is an endangered species according to the IUCN criteria (1996) because of the highly modified habitat at Cerro Huitepec.

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I want to express my appreciation to Terry Gosliner, Elizabeth Kools, Robert Van Syoc, Peter Roopnarine, Marylin Eversole and Neil Fahy of the California Academy of Sciences for their help during my sabbatical visit. Yolanda Camacho-García prepared and took the SEM photographs of the radula. Neil Fahy and Chris Appleton revised the English and made comments on the manuscript.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of *Scelotes* from near Cape Town, Western Cape Province, South Africa

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A large new species of the scincine genus *Scelotes* is described from Bloubergstrand near Cape Town, Western Cape Province, South Africa. It lacks forelimbs, has didactyl hindlimbs, and is most similar morphologically and genetically to *S. kasneri*, a species of conservation concern occurring further north in the same province. The new species, known only from the holotype, occurs in beach dune habitat in a major metropolitan area and is probably at risk from beachfront development and human recreational activities.

The genus *Scelotes* is a monophyletic group (Whiting et al., in press) of reduced-limbed "scincine" skinks endemic to sub-Saharan Africa. Broadley (1994), in the last revision of the group, recognized 20 species, one restricted to Tanzania, and the remainder occurring in southern Africa. Twelve of the southern African taxa are restricted to eastern parts of the subcontinent (Mozambique, Swaziland, and KwaZulu-Natal, Mpumalanga, and Limpopo Provinces of the Republic of South Africa). Broadley (1994) grouped these taxa into five species groups on the basis of degree of limb reduction. Two species, *S. anguineus* and *S. cafer*, have chiefly southern distributions, the former in the region of Algoa Bay, the latter with scattered populations in both the southern and western Cape. The remaining five species are western in distribution: *S. capensis* occurs from the Richtersveld north into south central Namibia (Bauer and Branch 2003), and the Western and Northern Cape coastal regions are occupied by *S. bipes* (Mossel Bay to Saldanha Bay), *S. gronovii* (Doringbaai to Graafwater), *S. kasneri* (Vredenberg to Lambert's Bay), and *S. sexlineatus* (Stompneus Bay to Port Nolloth) (Cordes and Mouton 1996; Branch 1998).

Only *Scelotes bipes* has been recorded from the South African mainland in the immediate vicinity of Cape Town, with populations extending into the Cape Peninsula and on Robben Island (Branch 1981, 1991). *Scelotes gronovii* occurs as far south as Robben Island (Baard 1988b; Branch 1998) and Dassen Island (Branch 1981, 1991), but has mainland populations reaching only the Saldanha-Langebaan area (McLachlan 1978; Mouton et al. 1987). *Scelotes kasneri* was originally described from a single type from near Lambert's Bay by FitzSimons (1939), who later (FitzSimons 1950) signaled the presence of three additional specimens from Elands Bay. McLachlan (1978) and Mouton et al. (1987) likewise considered the range restricted to these areas, although more recently the species has been found as far south as Vredenburg (Baard 1988a;

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Cordes and Mouton 1996). We here report the discovery of a new species of *Scelotes,* allied to *S. kasneri,* from Bloubergstrand, approximately 14 km north of Cape Town.

MATERIAL AND METHODS

MORPHOLOGY.— The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.01 mm): snout-vent length (SVL; from tip of snout to vent); width at midbody (BW); depth at midbody (BD); total leg length (LL); length of digits (DL); tail length (TL); head length (HL; distance between ear and snout-tip), head width (HW; measured at angle of jaws), head depth (HD; maximum height of head, from occiput to throat); eye diameter (ED; greatest diameter of orbit); eye to snout distance (E-S; distance between anteriormost point of eye and tip of snout); and eye to ear distance (E-E; distance from ear opening to posterior corner of eye).

Scale counts and external observations of morphology were made using a Nikon SMZ-10 dissecting microscope. Scale terminology follows FitzSimons (1943). Radiographic observations were made using a Faxitron closed-cabinet x-ray system. Comparisons were made with museum material in the collection of the California Academy of Science (CAS), as well as original published descriptions and descriptions provided in broader faunal and taxonomic treatments (e.g., Broadley 1994; Branch 1998).

MOLECULAR ANALYSIS.— We examined DNA sequence variation among *Scelotes* using the mitochondrial cytochrome b (700 bp), 12S ribosomal DNA (840 bp), and 16S ribosomal DNA (555 bp) gene regions. Tissue samples from representative species of *Scelotes* were processed at field collection sites and preserved in 95% ethanol. DNA was extracted following a standard phenol/chloroform protocol, and purified using Centricon-100 purification columns (Whiting 2001). DNA templates and controls were amplified using standard PCR techniques in 50 ml reactions and products were visualized via 2% agarose gel electrophoresis. The target products were purified using the Gene Clean III kit (Bio101 Co.) and sequenced using the Perkin Elmer Big Dye cycle sequencing kit. Purified sequencing reactions were analyzed on either an ABI 377, or ABI 3100 automated sequencer. All sequences have been deposited on the GenBank database as accession numbers AY217824–26, 217830, 217833–35 (cyt b), AY218027–29, 218033, 218036–38 (12S rDNA), and AY 217978–80, 217983, 217986–88 (16S rDNA).

Sequence data were used to compute uncorrected pairwise sequence divergences in PAUP*4.0 (Swofford 2002) between multiple species of *Scelotes.* Two specimens of *Scelotes sexlineatus* were used to establish intraspecific divergence levels for this genus and the molecular markers used. Four species from the western clade (Whiting et al., in press) of *Scelotes* (*kasneri, gronovii, sexlineatus,* and *bipes*), as well as one species from the eastern clade (*arenicola*), were included in pairwise comparisons to establish interspecific levels of divergence.

Phylogenetic inference was based on maximum parsimony analysis implemented in PAUP* 4.0 (Swofford 2002). Details of the phylogenetic analysis of *Scelotes* are presented elsewhere (Whiting et al., in press).

SYSTEMATICS

Reptilia: Squamata: Scincidae

***Scelotes montispectus* Bauer, Whiting and Sadlier, sp. nov.**
Figure 1.

HOLOTYPE.— California Academy of Sciences (CAS) 223934 (field number AMB 7074).

Approximately 4.6 km north of Grootbaai, Bloubergstrand on Melkbos Rd, 33°45′02″S, 18°26′34″E. Collected by R. A. Sadlier, A. M. Bauer and A. S. Whiting, September 29 2001.

ETYMOLOGY.— The specific epithet is derived from the Latin, *montis*, meaning mountain, and *spectus*, behold, in reference to the type locality, which offers some of the finest views of Table Mountain.

DIAGNOSIS.— A very large *Scelotes* (134 mm SVL) with a robust body, wedge-shaped snout, no forelimbs, and reduced, didactyl hindlimbs. Scales in 22 rows around midbody. Dorsal color buff with faint dark markings on dorsal 7 scale rows; a dark mask from nostril through eye to nuchal scales. The combination of no external forelimbs and didactyl hindlimbs otherwise characterizes only *S. bidigittatus*, *S. kasneri*, *S. bipes*, *S. sexlineatus*, *S. guentheri*, and *S. brevipes*. The number of midbody scale rows further distinguishes the new species from all of these congeners except *S. bidigittatus* (20–22 scale rows) and *S. kasneri* (22 rows). It differs from the former in its much larger size (134 mm vs 83 mm max SVL), higher number of subdigital lamellae (5 beneath the longest digit in *S. montispectus* vs 2–3 in *S. bidigittatus*), and non-scaly lower eyelid. The new species is nearly identical in scalation to *S. kasneri* but differs from it in the absence of dark stripes on the body, chin shields in contact behind the postmental, shorter limbs (7.7% SVL vs 9.1% SVL), and in having a lower number of subdigital lamellae (5 vs 7).

DESCRIPTION (based on holotype).— Adult female, body elongate (SVL 134.00 mm), robust (BW 8.04 mm, 6% SVL; BD 6.19 mm, 4.6% SVL); regenerated tail short (TL 47.40 mm, of which 22.27 mm regenerated), strongly tapered. No forelimbs, hindlimbs small (LL 10.28 mm, 7.7% SVL), bearing two digits (3.29 and 1.52 mm), each bearing a well developed claw. Twenty-two midbody scale rows, 116 ventral scales rows from postmental to cloaca.

Head large (HL 11.31 mm; HW 6.46 mm; HD 4.90), not offset from neck and trunk; snout wedge-shaped, lower jaw countersunk; head flattened above, lateral aspect of head nearly vertical. Nostril with valvular flap, bordered by rostral and a crescentic nasal, narrowly separated by nasal from supranasal and first supralabial; no postnasal scale present; supranasals in contact behind rostral. Lower eyelid opaque, but not scaly. Frontonasal 7-sided, 1.6 times wider than long, posterior border straight; frontal trapezoidal, narrower anteriorly than posteriorly, 1.5 times wider than long, posterior border slightly convex; interparietal very large, wider than long, anterior border slightly concave; parietals narrow, separated posteriorly by interparietal, contacting third supraocular anteriorly; three supraoculars, first larger than second and third together, first and second contacting frontal, second and third contacting interparietal; four supraciliary scales, second twice as large as others; five supralabials, fourth beneath eye; four infralabials; loreal much larger than preocular; mental hemispherical, with slightly convex posterior margin; postmental roughly pentagonal; three enlarged chin shields on each side, posterior to postmental and medial to infralabials; anterormost pair of chin shields in narrow contact behind postmental. Ear opening small, but clearly visible; eye large (ED 1.73 mm) and well-formed; E-S (5.40 mm) greater than E-E (4.47 mm); parietal eye spot present.

COLORATION (in life; Fig. 1).— Dorsum buff; darker straw to yellowish-brown on dorsum of head from rostrum onto neck; two straw colored stripes on tail base; vertebral and three paravertebral rows on each side with diffuse darker spots, forming very weakly defined rows, somewhat more pronounced on forebody and from sacrum onto tail base (Fig. 1), markings on more lateral scale rows less conspicuous and more irregular. Regenerated portion of tail pinkish-brown; venter white. Blackish mask from nostril, through eye to the nuchal scales. Color in preservative similar but straw to yellow-brown pigmentation faded, regenerated tail whitish.

OSTEOLOGY.— Palatine bones in contact; atlantal arches not fused. Three cervical vertebrae, 50 trunk vertebrae with ribs, one lumbar vertebra, two sacral vertebrae, 12.5 caudal vertebrae prior

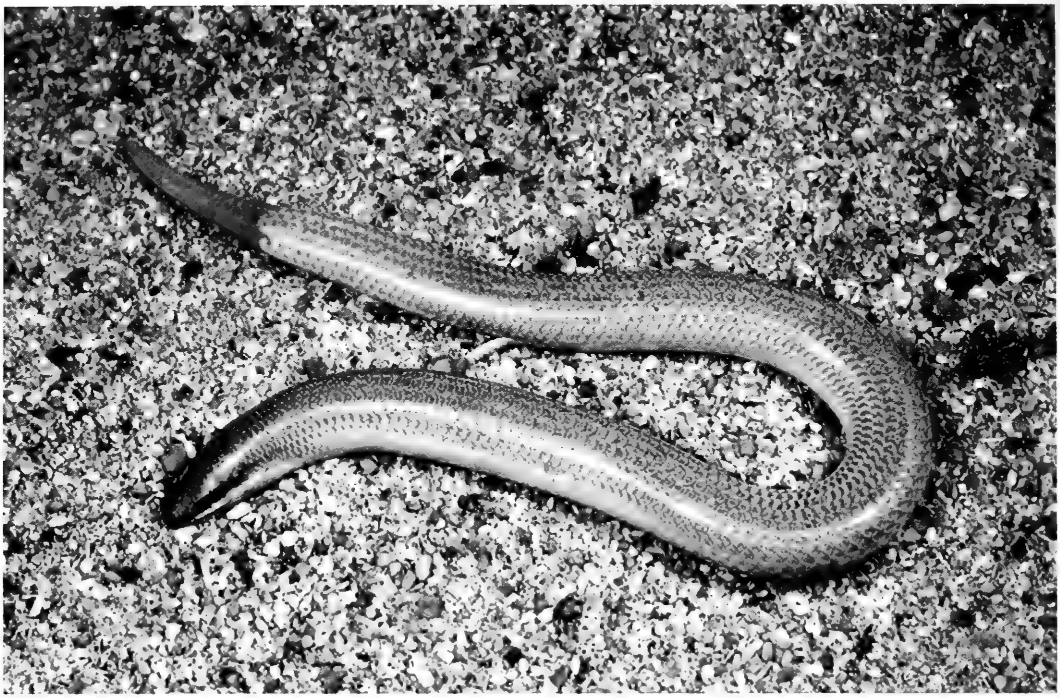

FIGURE 1. Holotype of *Scelotes montispectus* (CAS 223934) from 4.6 km north of Grootbaai, Bloubergstrand, Western Cape Province, Republic of South Africa, 33°45′02″S, 18°26′34″E. Note the lack of distinct dark bands on the body dorsum and flanks. Photo by R.A. Sadlier.

to regenerated tail. Minute pectoral remnants at level of 9th (6th trunk) vertebrae. Phalangeal formula of pes: 0.0.2.4.0.

DISTRIBUTION.— The new species is known only from the holotype collected at Bloubergstrand. Branch (1998) reported that the southernmost locality for *Scelotes kasneri,* the apparent sister taxon of *S. montispectus*, was near Vredenburg, approximately 110 km north of Bloubergstrand. The only congener with which the new species is strictly sympatric is *S. bipes.*

NATURAL HISTORY.— The specimen was collected by raking under vegetation in a narrow strip of beach dunes near Bloubergstrand, approximately 14 km north of Cape Town. *Scelotes bipes* was collected in the same habitat and *Mabuya homolacephala* and *Meroles knoxi* were collected on around the bases of strand vegetation. The habitat is similar to that noted for *S. kasneri* (Baard 1988b) and its biology is probably similar as well.

MOLECULAR COMPARISONS.— Genetic distance data cannot, in themselves, be used to establish that particular populations represent different species (Ferguson 2002). However, we considered the sequence divergence among and between species of *Scelotes* that are well accepted on morphological grounds as supplemental evidence to support the recognition of *Scelotes montispectus* as a new species. The sequence divergence between *S. montispectus* and its sister taxon *S. kasneri* (sampled localities 160 km apart) is approximately 3–8 times greater than the intraspecific divergence between the two specimens of *S. sexlineatus* (sampled localities 80 km apart) and is equivalent to the levels of divergence between other closely related species pairs (Tables 1–2).

TABLE 1: Uncorrected pairwise distance matrix for cytochrome *b* (above the diagonal) and 12S ribosomal DNA (below the diagonal). Tissues sampled from *Scelotes montispectus*, n. sp. (CAS 223934; holotype, ~4.6 km N of Grootbaai, Bloubergstrand on Melkbos Rd, Western Cape Province); *S. kasneri* (CAS 206991; 18.5 km N of jct. R365 (Leipoldtville Rd) on R27 towards Lamberts Bay, Western Cape Province); *S. gronovii* (CAS 206990; 18.5 km N of jct rd R365 on R27 towards Lambertsbaai, Western Cape Province); *S. bipes* (CAS 224005; ~4.6 km N of Grootbaai, Bloubergstrand on Melkbos Rd, Western Cape Province); *S. sexlineatus* (1, CAS 206813; Port Nolloth, Northern Cape Province; 2, CAS 206854; Brandberg, Farms Kourootje and Kap Vley, Northern Cape Province); *S. arenicola* (CAS 209635; Kosi Bay Nature Reserve, NW corner of Lake Nhlange, KwaZulu Natal Province).

	montispectus	*kasneri*	*gronovii*	*bipes*	*sexlineatus* 1	*sexlineatus* 2	*arenicola*
montispectus	–	0.08562	0.09401	0.12537	0.09292	0.10053	0.17248
kasneri	0.04686	–	0.11917	0.13798	0.12883	0.13237	0.18904
gronovii	0.07445	0.06757	–	0.14759	0.11172	0.11728	0.18660
bipes	0.10123	0.08406	0.09212	–	0.13710	0.14735	0.21459
sexlineatus 1	0.06508	0.06033	0.06756	0.09312	–	0.01189	0.17673
sexlineatus 2	0.06137	0.05660	0.06748	0.08665	0.00602	–	0.18169
arenicola	0.15731	0.14109	0.15567	0.14877	0.14993	0.14607	–

TABLE 2: Uncorrected pairwise distance matrix for 16S ribosomal DNA (specimens sampled as for Table 1).

	montispectus	*kasneri*	*gronovii*	*bipes*	*sexlineatus* 1	*sexlineatus* 2	*arenicola*
montispectus	–	–	–	–	–	–	–
kasneri	0.03846	–	–	–	–	–	–
gronovii	0.02565	0.03111		–	–	–	–
bipes	0.04419	0.05523	0.04779	–	–	–	–
sexlineatus 1	0.03479	0.04209	0.03291	0.05154	–	–	–
sexlineatus 2	0.04029	0.04210	0.04022	0.04969	0.01280	–	–
arenicola	0.07564	0.08313	0.08492	0.09185	0.08297	0.08667	–

DISCUSSION

Scelotes montispectus is clearly most similar in morphology to *S. kasneri*. It is also most similar to this form genetically, and a phylogenetic analysis of *Scelotes* (Whiting et al., in press) confirms that these two species are sister taxa. Despite obvious similarities, which are to be expected in a highly conservative group such as *Scelotes*, differences in scalation, proportion, and coloration distinguish *S. montispectus* from *S. kasneri*. Of these features, the last is the most obvious. All *S. kasneri* reported to date possess the obvious dark dorsolateral stripes initially described by FitzSimons (1939). That this pattern is ontogenetically and geographically stable is evidenced by the fact that it occurs not only in typical adult specimens (Visser 1984), but also in very large adults

(FitzSimons 1939, 1943) and in juveniles (FitzSimons 1950; CAS 206991) from near the type locality at Lamberts Bay as well as in specimens from elsewhere in the range of the species (Branch 1998).

In recent years there have been numerous descriptions of new taxa from South Africa, including some within a few km of major population centers. The discovery of *Pseudocordylus nebulosus* from Landdroskop, only 15 km from Somerset West (Mouton 1995), and *Afroedura hawequensis* from the Hawekwa Mountains, 10 km from Paarl (Mouton and Mostert 1985), are two such examples. This species, discovered only 14 km from Cape Town in a public beach area in Bloubergstrand is another such example. It highlights the inadequacy with which the herpetofauna of even suburban parts of South Africa has been surveyed and underscores the need for further research on the cryptic fauna of the Western Cape.

Both *Scelotes gronovii* and *S. kasneri* were listed in the first *South African Red Data Book* (McLachlan 1978); the former as rare due to restricted distribution and the latter simply as rare. In the more recent *Red Data Book* (Branch 1988), both species were listed as restricted. Subsequent research has expanded the known range of these two species (e.g., Cordes and Mouton 1996), but because of their fossorial habits, the true status of these and other *Scelotes* is difficult to assess. Partly because of this, Mouton et al. (1987) suggested that *Scelotes gronovii* and *S. kasneri* should be research priorities among the southwestern Cape red data lizards. Baard (1988a) regarded degradation of sand dune habitat, including conversion to parking lots and off-road vehicle use, as the major threat to *S. kasneri.* This is certainly also the case for *S. montispectus*. Indeed, the only known locality for this species lies within the Cape Town metropolitan area in a narrow sand dune strip between a busy road and a heavily used public beach.

ACKNOWLEDGMENTS

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A New Species of *Aristochroa* Tschistschérine (Coleoptera: Carabidae: Pterostichini) from the Gaoligongshan of Western Yunnan Province, China

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A new species of the genus *Aristochroa* Tschitschérine, *A. abrupta* Kavanaugh and Liang, sp. nov., is described from the Gaoligongshan of western Yunnan Province, China (type locality: Danzhu He drainage, 2830 m, Gongshan County). Members of this species are distinguished by the abrupt sinuation of the lateral margin of the pronotum in all adults and the long, triangular, right-deflected lamella of the aedeagus in males. Illustrations are provided for these and other structures. This species is unusual also in its occurrence at lower elevations (2770 to 3400 m) than most other members of the genus.

The pterostichine carabid genus *Aristochroa* was described by Tschitschérine (1898) to include a total of five Chinese species. Since then, 12 new species have been added to the genus (Tschitschérine 1903; Straneo 1938; Xie and Yu 1993; Sciaky and Wrase 1997; Zamotajlov and Fedorenko 2000; Liang and Yu 2002).

In July 2000, while conducting fieldwork for an inventory of the carabid beetle fauna of the Gaoligongshan of western Yunnan Province, China, we collected several specimens of *Aristochroa* at localities in each of two separate river valleys on the eastern slope of the mountain range, in Gongshan County, Nujiang Prefecture. In May and September 2002, several more specimens of the genus were collected in or near these valleys. Subsequent morphological comparison of these specimens with representatives and/or descriptions of all other known species has convinced us that they represent a species previously unknown to science. A description of this new species follows.

Aristochroa abrupta Kavanaugh and Liang, sp. nov.

(Figures 1–2, 4, 6, 8, 10–11)

TYPES.— Holotype, a male, deposited in Institiute of Zoology, Chinese Academy of Sciences, Beijing (IOZ), labelled: "CASENT1006544" / "China, Yunnan Province, Nujiang Prefecture, Gongshan County, Danzhu He drainage, 13.5 airkm SW of Gongshan, 2830m" / "N 27.62947°/E 98.62010°, 30 June – 5 July 2000, Stop # 00–17K, D.H. Kavanaugh, C.E. Griswold, Liang H.-B., D. Ubick, and Dong D.-Z. collectors". A total of 21 paratypes (11 males and 10 females) are deposited in the California Academy of Sciences (CAS), Kunming Institute of Zoology (KIZ), and IOZ (see specimen data below, under Geographical distribution).

TYPE LOCALITY.— Danzhu He drainage, 2830 m, N 27.62947°/E 98.62010°, Gongshan County, Yunnan Province, China.

FIGURE 1. Digital photograph of habitus of holotype of *Aristochroa abrupta* sp. nov., dorsal aspect.

DIAGNOSIS.— Adults of *A. abrupta* sp. nov. can be distinguished from all other known species of *Aristochroa* by the following combination of character states: pronotum with lateral margins deeply and abruptly sinuate in posterior one-fifth, parallel anterior to base, with four (three or five in a few specimens) lateral setae anterior to middle, hind angles rectangular, basal foveae smooth, impunctate; pro-, meso-, and metepisterna smooth, impunctate; elytral interval 3 with two (one in a few specimens) discal setiferous pores; elytral intervals 1, 3, 5 and 7 strongly convex, microsculpture distinct on all intervals.

If one were to use the key to species of *Aristochroa* provided by Liang and Yu (2002), specimens of *A. abrupta* would key out at couplet 13, with specimens of *A. gratiosa* Tschitschérine and *A. militaris* Sciaky and Wrase. However, that key does not include the three species described by Zamotajlov and Fedorenko (2000) (namely, *A. sciakyi, A. dimorpha*, and *A. kangdingensis*) and is therefore incomplete. We choose not to provide a new key to all known species at this time because it seems likely that additional new species will continue to be found in the near future. Instead, we simply mention characters useful for distinguishing *A. abrupta* adults from those of *A. gratiosa, A. militaris, A. sciakyi, A. dimorpha*, and *A. kangdingensis.*

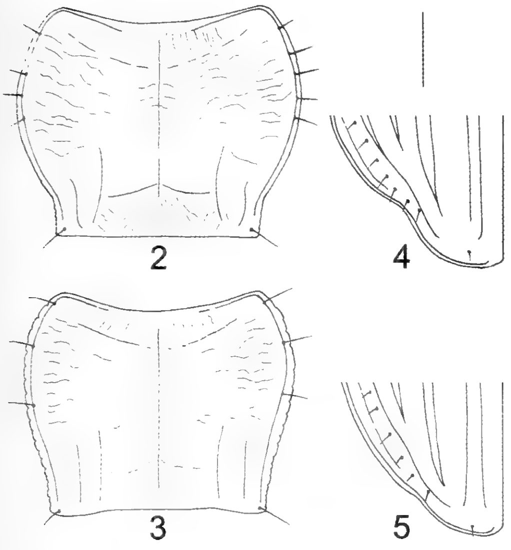
Adults of *A. abrupta* are most similar to those of *A. gratiosa*, but differ with them in having the lateral margin of the pronotum more deeply and abruptly sinuate and less crenulate (compare Figs. 2 and 3), the lateral longitudinal grooves of the basal foveae shorter and slightly S-shaped (long and straight in *A. gratiosa*), the subapical sinuation of the elytral margin much deeper (compare Figs. 4 and 5), and the shape of the aedeagus in males and the gonostylus of the ovipositor in females distinctly different (compare Figs. 6 and 7 and Figs. 8 and 9, respectively). They differ with adults of *A. militaris* in both pronotal shape and shape of the male aedeagus (compare Figs. 2 and 6 here with Figs. 45 and 20, respectively, in Sciaky and Wrase 1997). They differ with *A. dimorpha* adults in having intervals 1, 3, 5, and 7 markedly convex (only faintly convex in the latter), with *A. sciakyi* adults in having deeply sinuate lateral pronotal margin (only slightly sinuate in the latter), and with *A. kangdingensis* adults in having the deep pronotal lateral sinuation (faintly sinuate in the latter), smooth basal foveae (coarsely rugose in latter), and distinct microsculpture in intervals 1, 3, 5 (absent from these intervals in the latter).

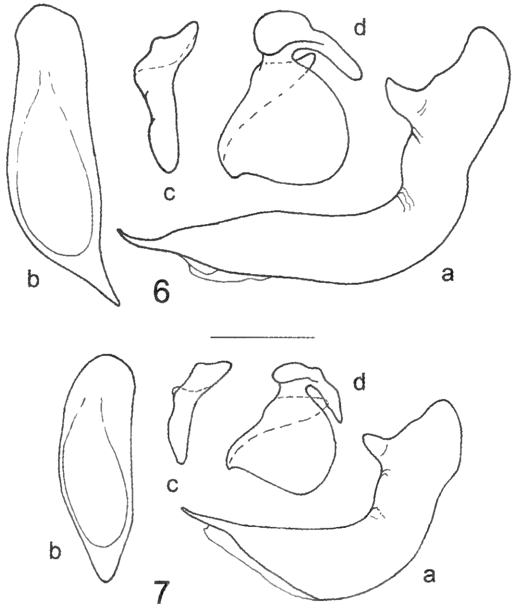
Description.— Total length (measured along midline from apex of longer mandible to apex of longer elytron) 12.9–14.5 mm in males and 12.4–14.6 mm in females; width (measured across greatest width of elytra) 4.8–5.4 mm in males and 5.0–5.7 mm in females. Antennae, mandibles, labrum, femora, tibiae and ventral surface black or reddish black; palpi and tarsi reddish brown; head, pronotum, and elytra with distinct coppery luster (with faint to moderately distinct green highlights in most individuals, most distinct on head and pronotum).

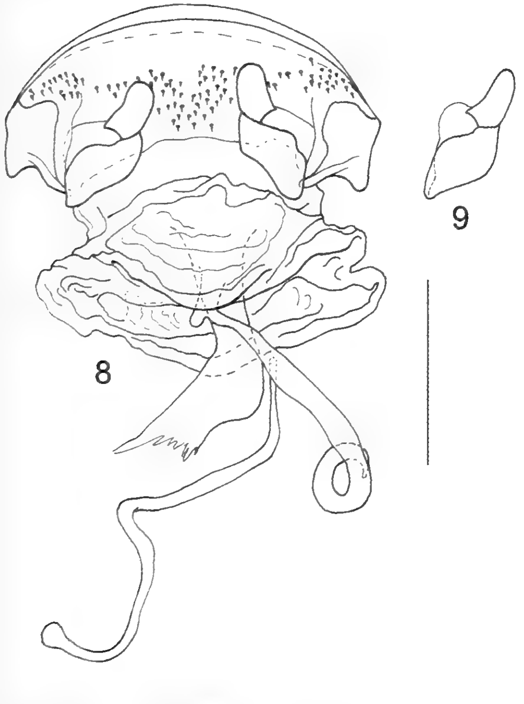
Mandible short, faintly rugose on dorsal surface, hooked and pointed at apex. Labrum transverse, slightly emarginate at apex, with six setae. Clypeus convex. Frontal furrows deep, impunctate, divergent and slightly bifurcate posteriorly. Vertex convex, smooth, impunctate, microsculpture mesh pattern transverse, indistict. Eyes large, convex. Tempora short, oblique. Antennae extended posteriorly to basal one-eighth of elytra, pubescent from apical half of antennomere 4, antenomere 3 slightly longer than the scape. Terminal labial palpomere slightly dilated toward apex, apex truncate. Mentum tooth wide, moderately emarginate. Ligula widely dilated at apex, with four apical setae.

Pronotum (Fig. 2) large, transverse, widest at or slightly anterior to middle, ratio of pronotal width to length (PW:PL) = 1.33 (range 1.25–1.36 in males, 1.26–1.40 in females), base not or only slightly narrower than apex. Microsculpture mesh pattern transverse, most distinct in lateral furrows and basal foveae. Apical margin slightly emarginate, apical margination widely interrupted in the middle. Apical angles rounded, slightly projected anteriorly. Lateral margins with only a few shallow crenulations, smoothly arcuate from apical angles to one-third from base, then abruptly sinuate to basal angles. Lateral furrow narrow, with four (three or five in a few specimens) setae anterior to the middle, one seta near the basal angle. Basal angles rectangular. Disk convex, sparsely and transversely rugose laterally, longitudinally rugose at middle both apically and basally, basal area deeply depressed. Medial longitudinal impression deep, except shallow at or terminated before both apical and basal margins. Anterior transverse impression shallow, posterior transverse impression deep. Basal foveae smooth, impunctate, outer longitudinal groove slightly S-shaped, one-half as long as inner groove. Prosternum impunctate, with a longitudinal depression in the middle, microsculpture mesh pattern transverse. Pro-, mes-, and met-episterna impunctate, microsculpture mesh pattern distinct, transverse.

Elytra ovate, convex, widest and highest slightly posterior to the middle, ratio of elytral length to width (EL:EW) = 1.51 in males (range 1.45–1.59), 1.38 in females (range 1.33–1.43). Microsculpture mesh pattern distinct, isodiametric. Intervals 1, 3, 5, 7 strongly convex; interval 3 about 2.2 times as wide as interval 4 in the middle, with two dorsal setiferous pores, basal one adjoining stria 3 and apical one (absent in some individuals) adjoining stria 2. Stria shallow, punctures indis-







FIGURES 2–5. Figs. 2–3: Pronotum, dorsal aspect. Fig. 2: *Aristochroa abrupta* sp. nov. Fig. 3: *Aristochroa gratiosa* Tschitschérine. Figs. 4–5: Elytral apex, male, dorsal aspect. Fig. 4: *Aristochroa abrupta*. Fig. 5: *Aristochroa gratiosa*. Scale line = 1.0 mm.

FIGURES 6–7. Male genitalia; a. median lobe, left lateral aspect; b. apex of medial lobe, dorsal aspect; c. right paramere, lateral aspect; d. left paramere, lateral aspect. Fig. 6: *Aristochroa abrupta* sp. nov. Fig. 7: *Aristochroa gratiosa* Tschitschérine. Scale line = 1.0 mm.

FIGURES 8–9. Female genitalia, ventral aspect. Fig. 8: *Aristochroa abrupta* sp. nov. Fig. 9: *Aristochroa gratiosa* Tschitschérine, left ovipositor only. Scale line = 1.0 mm.

tinct, stria 7 with one setiferous pore near the apex. Scutellum smooth, scutellar striole shallow, parascutellar setiferous pore absent. Humerus well-marked, round, slightly tuberculate. Basal margin straight or slightly concave anteriorly, forming an obtuse angle with lateral margin at the humerus. Lateral margin markedly sinuate anterior to apex (Fig. 4). Abdominal sterna impunctate, sparsely rugose laterally. Sternum VII with two pairs of posterior paramedial setae in males (one pair or two pairs with a third seta unilaterally in a few individuals), two pairs of setae in females.

Male with aedeagus distinctly bent at the middle, thickened ventrally anterior to apex, apex thin and slightly bent ventrad in lateral view (Fig. 6a); apical lamella long, triangular, markedly deflected right and apically narrowed in dorsal view (Fig. 6b). Parameres as in Figures 6c and 6d.

Female genitalia as in Figure 8. Gonostylus broad, arcuate. Spermatheca pointed and slightly coiled apically, spermathecal gland elongate, tubular.

Sexual dimorphism.— Males with antennae slightly (about 5%) longer than females; females with elytra relatively wider and with greatest elytral width more distinctly posterior to middle than in males.

Geographical distribution.— At present known only from the eastern slope of the Gaoligongshan in Gongshan County, Nujiang Prefecture, western Yunnan Province, China. We have examined a total of 22 specimens (including the holotype and 21 paratypes) from the following localities: Danzhu He drainage [13.5 air km SW of Gongshan, 2830m, N 27.62947°/ E 98.62010°, 30 June – 5 July 2000, Stop # 00-17K, D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong collectors (3 males and 1 female); 13.5–13.8 airkm SSW of Gongshan, 2720–2840m, N 27.63267°/ E 98.60861° to N 27.63331°/E 98.60356°, 30 June – 5 July 2000, Stop # 00–17E, D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong collectors (1 female); 13.5 to 15.7 airkm SSW of Gongshan, 2700–3100m, N 27.63063°/E 98.62074° to N 27.62705°/ E 98.59204°, 30 June –5 July 2000, Stop # 00–17A, D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong collectors (2 males, 1 female)]; Qiqi He drainage [Dongshaofang-Yakou, 27°41′40″ N, 98°28′47″ E, 3400m, 1 May 2002, G. D. Yang collector (1 male); No. 12 Bridge camp area, 16.3 airkm W of Gongshan, N 27.71503°/E 98.50244°, 2775m, 15–19 July 2000, Stops # 00-23D and E, D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong collectors (2 males and 5 females); same locality, 2 May 2002, H.B. Liang and W.D. Ba collectors (4 males)]; Pula He drainage [Dabadi, 41 km W of Gongshan on Dulong Valley Road, 3000m, N 27.79655°, E 098.50562°, 27 September to 6 October 2002, Stop # DHK-2002-031F, D.H. Kavanaugh, P.E. Marek, H.B. Liang, X.C. Liang, & D.Z. Dong collectors, (2 females)].

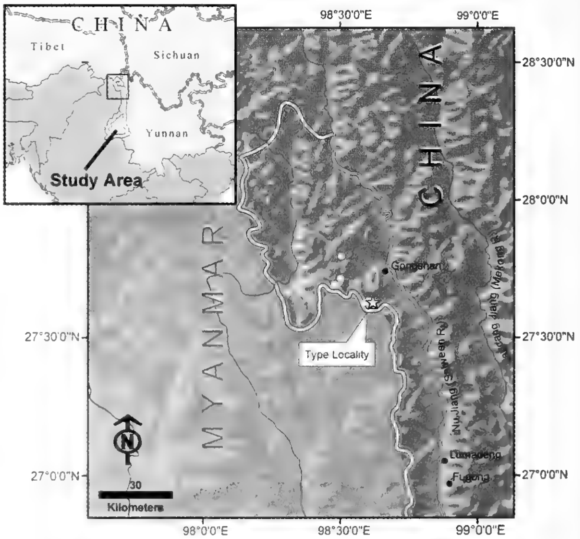


FIGURE 10. Map of the Gongshan study area (insert; study area outlined in white; black box locates area of enlargement). Sites at which specimens of *Aristochroa abrupta* sp. nov. were collected are identified by solid white circles and the type locality by a star.

Geographical variation.— No locality-specific morphological differences have been observed among individuals from the different localities sampled for this species.

Habitat distribution.— Adults of this species have been collected from several localities on the eastern slope of the Gaoligongshan, in two different major drainage systems: the Danzhu He and Pula He systems. Compared with most other known species of *Aristochroa*, the new species occurs at lower elevations, ranging from 2770m to 3400m. Most *Aristochroa* species are restricted to montane regions above 4000 m (range for the genus from 2500–5000 m), with all known records below 4000 m confined to areas well north of the known range of *A. abrupta* (in Sichuan and

FIGURES 11–12. Photographs of habitat for *Aristochroa abrupta* sp. nov., eastern slope of the Gaoligong Shan, Gongshan County, western Yunnan Province, China. Fig. 10. Forest in valley of Qiqi He at No. 12 Bridge Camp, 16.3 km W of Gongshan, 2775 m; adult beetles collected mainly in pitfall traps placed on the forest floor in this habitat (at locations marked by pink flagging tape in photograph). Fig. 11. Type locality, valley of Danzhu He, 13.5 km SW of Gongshan, 2380 m; adult beetles collected at night along road cut near or on large granitic boulders.

Shaanxi provinces), except for *Aristochroa dequinensis* Xie and Yu (1993), also from northern Yunnan, with a known altitudinal range from 3450–4650 m. The only species know to occur at elevations as low as *A. abrupta* is *Aristochroa militaris* Sciaky and Wrase (1997) (with a known altitudinal range of 2500–3300 m), which occurs at the northern distributional limit for the genus in Shaanxi Province (at 33.51°N).

At each of the known localities, *A. abrupta* adults have been found in mixed conifer and broadleaf deciduous forest, either on the forest floor, which includes a moist, mossy and shrubby understory (Fig. 11), or along road cuts through granitic sandy soils and boulders. In the latter habitat, beetles were collected by hand, mainly at night, on or near large boulders (Fig. 12).

ETYMOLOGY.— The specific epithet is derived from the Latin, *abruptus*, meaning broken off or cut off, in reference to the deep and abrupt basolateral sinuation cut into the lateral margin of the pronotum.

ACKNOWLEDGMENTS

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Designation of Types for the New Diatom (Bacillariophyta) Taxa Described by Robert Hagelstein from Puerto Rico

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A total of 10 holotypes are identified, and 30 lectotypes and 2 isotypes are designated for the names of the taxa described by Robert Hagelstein in his work on diatoms from Puerto Rico. Marine, estuarine and freshwater taxa are included in this treatment. The groups are mostly raphid forms, with only one centric species being described as new. Illustrations and an emended description are provided for *Pinnularia laterittata* var. *minor*, which was not illustrated in the original publication. Transfer of Hagelstein's collection from the New York Botanical Garden (NYBG) to the Diatom Collection of the California Academy of Sciences (CAS) has required designation of CAS numbers, and they are listed along with Hagelstein's numbers for the type slides.

Robert Hagelstein had diverse interests, being not only a successful businessman, but also someone who published scientific works on diatoms (1939) as well as slime molds (1944). He amassed a diverse collection of diatom slides and samples, including the large collection of D.B. Ward, as well as a variety of associated manuscripts, illustrations and photographs from a variety of well- and lesser-known diatomists. He was a regular correspondent with contemporaries such as Charles Boyer and Albert Mann, with whom he exchanged slides, material and ideas. His collection was originally deposited at the New York Botanical Garden (Burke 1940), but just last year it was given to the Diatom Collection of the California Academy of Sciences (CAS).

Hagelstein's only published contribution was on the diatoms from Puerto Rico. In that work, he described 42 new taxa (25 new species and 17 new varieties), while making 1 new combination (*Caloneis disticha* (A. Schmidt) Hagelstein, comb. nov., basionym: *Navicula disticha*) and proposing 1 new name (*Navicula borinquensis* Hagelstein, based on the basionym *Navicula notanda* Østrup). While all of his new taxa are validly published (according to the International Code of Botanical Nomenclature-Greuter et al. 2000), he did not indicate in his manuscript the slides he used to base his descriptions, nor did he designate type slides for his new taxa. This is the same situation encountered by Simonsen relative to the Friedrich Hustedt collection, and the result in that case was the 3 volume set composed of a catalogue and illustrations of Hustedt's types (Simonsen 1987). The present contribution attempts to make explicit the slides Hagelstein used to base his descriptions and to designate type slides for the new taxa, but not to illustrate again the new taxa.

To best understand Hagelstein's approach and method, a large card file kept by him for his floristic project on the diatoms of Puerto Rico was reviewed. The file is organized by taxon, and has his notes on valve morphology, descriptions and notes as to which slides (and at which locations on the slides) he identified diatom taxa. This card file was extremely helpful to sort out where Hagelstein saw taxa, what his concept of the taxon was, and where specimens might be found.

Unfortunately, the file does not indicate exact locality information for the slides or samples, thus it is difficult to near impossible to match up the locality information listed in Hagelstein's manuscript with the existing samples. Matching up specimens to those presented as photographs in his 1939 work was difficult since the images were cut out along the margins, so as to leave out any other context for the specimens. However, in most cases, matching up specimens to those present in the 1939 work was done without too much trouble, since Hagelstein indicated which of the specimens he used for illustrations in his flora, by the abbreviation "Fig." associated with the location of the specimen.

I have followed Simonsen's (1987) approach to typification. In his work on Hustedt's types, Simonsen designated holotypes only in the instances where there were marked specimens on a single slide. When there are no such marked specimens, or when more than a single slide with marked specimens was encountered, Simonsen, designated lectotypes. In the case of the Hagelstein Collection, instead of searching for marked slides, his notes were used as guides to relate the specimens and slides.

The present report lists the new taxa described by Hagelstein, including the page number and plate and figure number for each new taxon. Habitats listed by Hagelstein where the taxon was found in his study are then followed by comments related to the slide(s) where specimens were found, designation of type slides, and in a few cases taxonomic status. All types are deposited at the Diatom Collection of the California Academy of Sciences (San Francisco), and provided herein are the new CAS slide numbers.

RESULTS AND DISCUSSION

Amphora bigibba var. ***capitata,*** Hagelstein, page 325/Pl. 3, fig. 7

HABITAT: Naval dock, San Juan Bay; Harbor of Christiansted, St. Croix

COMMENTS: Hagelstein's notes indicate he viewed specimens on slide 94D3 only. Observations in the context of the present report support Hagelstein's, and the specimen indicated as the type in his notes is present on 94D3. This slide is here designated as the lectotype.

Caloneis liber var. ***incerta,*** Hagelstein, page 336/Pl. 4, fig. 2

HABITAT: San Juan Bay

COMMENTS: Hagelstein's notes indicate he saw a single specimen of this new variety on slide 94D3. This individual specimen is present on the slide, the same one photographed and presented by Hagelstein. Slide 94D3 is the holotype for this taxon.

Campylodiscus cordatus, Hagelstein, page 337/Pl. 4, fig. 3

HABITAT: San Juan Bay

COMMENTS: Hagelstein encountered this new species of *Campylodiscus* in a large number of slides, including 91B1, 95A1, 117A2, 117B1, 118B1, 128B1, and 128B4. Presence of this species in each of these slides is confirmed. A single specimen on slide 118B1 was photographed and presented by Hagelstein, and this slide is here designated as the lectotype for the name of this species.

Cocconeis singularis, Hagelstein, page 343/Pl. 4, figs 7, 8

HABITAT: Ponce

COMMENTS: A single valve of this taxon was observed by Hagelstein on slide 73B1. Its presence is confirmed on that slide, which is the holotype.

Cyclotella insolita, Hagelstein, page 345/Pl. 4, fig. 9

HABITAT: Canal de Martin Peña

COMMENTS: Hagelstein's notes indicate this colonial *Cyclotella* is present on slides 165-2 and 165-3. It is easily found on both slides, which are of plankton. Slide 165-3 is here designated as the lectotype and slide 165-2 as an isotype for this species.

Cymbella coamoensis, Hagelstein, 347/Pl. 4, fig. 11
HABITAT: Coamo Springs
COMMENTS: A specimen conforming to the descripton of Hagelstein was found on slide 57A1. His illustration is of a initial valve, while his notes indicate this specimen is "perfect". The specimen photographed could not be located, therefore slide 57A1 is here designated as the lectotype for the name of this species.

Diploneis gravelleana, Hagelstein, 352/Pl. 5, fig. 2
HABITAT: San Juan Bay and adjoining marshes
COMMENTS: This species is present on Hagelstein slide 29B1, as indicated in his notes. It is here designated as the lectotype.

Diploneis smithii var. ***adversa*,** Hagelstein, 354/Pl. 5, fig. 3
HABITAT: Harbor of Christiansted, St. Croix
COMMENTS: Numerous specimens are present on Hagelstein slide 149-2A. This slide is here designated as the lectotype.

Eunotia indica var. ***undulata*,** Hagelstein, 357/Pl. 5, fig. 4
HABITAT: Near Carolina
COMMENTS: A single specimen was found on Hagelstein slide 228D1, as indicated in his notes. The slide is here designated as the lectotype.

Eunotia lunaris var. ***duolineata*,** Hagelstein, 357/Pl. 5, fig. 5
HABITAT: spring near Hato Rey
COMMENTS: Numerous specimens are found on Hagelstein slide 23A4, which is here designated as the lectotype. The acute "knick" on the ventral margin is the diagnostic feature of this taxon, according to Hagelstein's notes.

***Gomphonema carolinense*,** Hagelstein, page 360/Pl. 5, fig. 6
HABITAT: Rio Grande de Loiza at Trujillo Alto; Carolina; pools on the sandy plain adjacent to Carolina
COMMENTS: A specimen conforming to the description and illustration in Hagelstein for this taxon was found on slide 143A1, which is here designated as the lectotype. It is surprising that in her consideration of this species, Patrick (in Patrick and Reimer 1975) did not consult Hagelstein's type. The image offered by Krammer and Lange-Bertalot (1991, plate 87, figure 12) of this taxon from an unknown locality appears quite different from Hagelstein's taxon, particularly in the shape of the valve and the organization of the central striae. Further research may suggest the two are not conspecific.

Gyrosigma acuminatum var. ***angulatum*,** Hagelstein, 365/Pl. 5, fig. 7
HABITAT: Quintana Spring
COMMENTS: Several specimens of this new variety were found on Hagelstein slide 248-2B1, including the specimen included in Hagelstein's publication. Slide 248-2B1 is here designated as the lectotype.

***Gyrosigma variipunctatum*,** Hagelstein, 367/Pl. 5, fig. 8

HABITAT: Quarantine Station, San Juan Bay

COMMENTS: The specimen photographed by Hagelstein is present on slide 203A-1; his notes indicate it is known from a single specimen. Slide 203A-1 is the holotype.

***Gyrosigma variistriatum*,** Hagelstein, 367/Pl. 5, fig. 9

HABITAT: Quarantine Station, San Juan Bay

COMMENTS: The single specimen presented by Hagelstein is present on slide 115B2. His notes indicate this new *Gyrosigma* is known from a single specimen only. Hagelstein slide 115B2 is the holotype.

Homeocladia vidovichii var. ***nodulosa*,** Hagelstein, 369/Pl. 5, fig. 11

HABITAT: San Juan Bay; Fajardo; Mayaguez

COMMENTS: This diatom is listed in Hagelstein's notes as occurring on slides 18C1 and 106B1, and as common on the latter slide. The two specimens observed on 18C1 did not match the illustration on plate 5. We have not been able to match any one of the literally hundreds of specimens on 106B1, but it seems safe to suggest it should serve as the lectotype for this new variety. Thus, slide 106B1 is here designated as the lectotype.

***Mastogloia obliqua*,** Hagelstein, 375/Pl. 5, figs 12, 13

HABITAT: Fajardo

COMMENTS: Hagelstein indicates this taxon is present on a single slide, 230C1, in the Hagelstein collection. This slide is the holotype of this species.

***Mastogloia sancti-johannis*,** Hagelstein, 376/Pl. 6, fig. 1

HABITAT: Naval Dock, San Juan Bay

COMMENTS: The specimen illustrated by Hagelstein was found on slide 91B2, and this slide is here designated as the lectotype.

***Navicula congerana*,** Hagelstein, 382/Pl. 6, figs 8, 9

HABITAT: Mangrove marsh at Miramar

COMMENTS: Hagestein's notes indicate he saw this new species on two slides, 116A3 and 116B1, and that the figures were of specimens from slide 116B1. Observations from this study confirm the presence of this new *Navicula* on both slides, and that the specimens illustrated by Hagelstein are on slide 116B1, which is here designated as the lectotype for this taxon.

***Navicula expansa*,** Hagelstein, 384/Pl. 6, fig. 10

HABITAT: Canal de Martin Peña

COMMENTS:A population of this new *Navicula* species occurs only on Hagelstein slide 31A, and it is the holotype.

***Navicula guaynaboensis*,** Hagelstein, 385/Pl. 6, fig. 11

HABITAT: near Guaynabo

COMMENTS: The specimen illustrated by Hagelstein may be found on slide 138B1, and this slide is here designated as the lectotype for this taxon.

***Navicula howeana*,** Hagelstein, 385/Pl. 7, fig. 1

HABITAT: Harbor of Christiansted, St. Croix

COMMENTS: No card for this taxon was found in Hagelstein's file, and no other written materials related to the taxon have been uncovered. Slides from the locality indicated by Hagelstein have yielded no specimens. With the apparent loss of the original specimens, the illustration provided by Hagelstein is here designated as the lectotype, in accordance with the provision of Article 9.2 of the International Code of Botanical Nomenclature (Greuter et al. 2000), which states "A lectotype is a specimen or illustration designated from the original material as the nomenclatural type . . ."

Navicula incomposita, Hagelstein, 386/Pl. 7, fig. 2

HABITAT: Park Loiza; Laguna San José

COMMENTS: Hagelstein's notes indicate he observed this diatom from a variety of samples and slides, including 10B2, 83B2, 112A, 112B, 113A, 113B, 204, 217B1 and 217B2. The specimen illustrated is present on slide 112A1 and this slide is here designated as the lectotype. Slide 112A6 appears to be an isotype.

Navicula incomposita var. ***minor***, Hagelstein, 386/Pl. 7, fig. 3

HABITAT: Park Loiza; Santa Isabel; San Juan marshes

COMMENTS: According to Hagelstein's notes, this new variety was observed on the following slides: 82B1, 255A1, and 255C1. While many more specimens are indicated in the notes to have been seen on sample 255 slides, his notes indicate the specimen figured came from slide 82B1, which is here designated as the lectotype for this species.

Navicula lyra var. ***irregularis***, Hagelstein, 388/Pl. 7, figs 5, 6

* HABITAT: San Juan Bay and marshes; Fajardo; Ponce

COMMENTS: The specimens illustrated in figures 5 and 6 on plate 7 were found on slide 115A1, which is here designated as the lectotype for this new variety.

Navicula mannii, Hagelstein, 388/Pl. 7, figs 7, 8

HABITAT: Quarantine Station; Fajardo; San Juan Bay

COMMENTS: Hagelstein lists two slides, 203B and 256B2, on which he identified this new variety. Though he indicates a single specimen on slide 256B2 "…seems to be [the] best specimen" the individual could not be found on the slide. The taxon is common on slide 203B and, coupled with its absence on slide 256B2, this recommends here designating slide 203B as the lectotype.

Navicula tubulosa var. ***rhomboidea***, Hagelstein, 391/Pl. 7, fig. 13

HABITAT: San Juan Bay and marshes

COMMENTS: This new variety was identified by Hagelstein from two slides, 18C1 and 118B1, but only a single specimen was identified from the slides (from slide 18C1), and this single specimen did not match the illustration. While there is original material extant from which Hagelstein based his description, slide 18C1 is here designated as the lectotype of this new variety.

Nitzschia brittonii, Hagelstein, 393/Pl. 7, fig. 14

HABITAT: San Juan Bay and marshes

COMMENTS: No card for this Hagelstein was found. With the apparent loss of the original specimens, the illustration provided by Hagelstein is here designated as the lectotype, in accordance with the provision of Artcle 9.2 of the International Code of Botanical Nomenclature (Greuter et al. 2000).

Nitzschia hemistriata, new species, 396/Pl. 8, fig. 1

HABITAT: Canal de Martin Peña

COMMENTS: Hagelstein's notes suggest this new species can be found on two slides, 29B1 and 31B1, but he only showed a reference point for one of the slides. The specimen illustrated by

---

*common in freshwater

Hagelstein was found on slide 31B1, recommending this slide to be here designated as the lectotype.

Nitzschia miramarensis, Hagelstein, 398/Pl. 8, figs 4, 5

Habitat: Marsh at Miramar

Comments: On the single slide listed by Hagelstein to possess this taxon, the specimens illustrated by him were found. The slide, 116B1, is the holotype.

Nitzschia obtusa var. ***lata***, Hagelstein, 399/Pl. 8, figs 6, 7

Habitat: Mangrove marshes at San Juan

Comments: Specimens were found on the following slides: 26A1, 29A1, 29B1, 164A1, 164B1, 164C25 and 164C26. Specimens illustrated by Hagelstein are to be found on slide 164A1, and it is here designated as the lectotype.

Nitzschia obtusa var. ***undulata***, Hagelstein, 399/Pl. 8, figs 8, 9

Habitat: Marshes at martine Peña; Santurce

Comments: This taxon was found only on slide 220B1, which is here designated as the lectotype.

Nitzschia ponciensis, Hagelstein, 401/Pl. 8, fig. 13

Habitat: Naval Dock at San Juan Bay; Ponce

Comments: This species was found on a single slide, and one specimen on this slide corresponds to the one illustrated by Hagelstein. Slide 73B1 is the holotype slide.

Nitzschia quickiana, Hagelstein, 401/Pl. 8, fig. 14

Habitat: Mangrove marsh at Miramar

Comments: This species was found on slides 31B1 and 164B1. The figured specimen was found on 164B1, and this slide is here designated as the lectotype.

Pinnularia laterittata var. ***minor***, Hagelstein, 407/not figured

Comments: Hagelstein did not provide illustrations of this new variety in his original work. While lack of illustrations does not render this taxon invalid, since algae described prior to 1958 do not require illustrations for valid publication (Article 39.1, Greuter et al. 2000), figures and an emended described are provided herein.

Emended description: Valves straight with slightly tumid middle and ends rounded, 98.0–126.0 μm long, 15.5–17.5 μm broad. Striae radiate, becoming parallel then convergent at the ends, longitudinal lines cross the striae about 1/3 the distance from the axial area to the margin, 7–8 striae in 10 μm. Raphe lateral, undulate, external distal raphe ends bayonnet-shaped, helictoglossae distinct. Figures 1–8.

Hagelstein (p. 406) discusses the possible implications of *Pinnularia latevittata* Cleve and its varieities producing (in the current terminology) *cis* frustules, that is the orientation of features one each valve of a frustule in the same direction. A wide range of naviculoid diatoms had been known to only produce *trans* frustules, where the orientation of features of valves of a frustule is in opposite directions. In *P. laterittata* var. *minor*, both *cis* (figs 6–8) and *trans* (figs 1, 2) frustules were observed. This phenomenon of a single species producing both *cis* and *tran*s valves, which occurs in other *Pinnularia* species, was described and analyzed by Mann (1983).

Slide 131A1 is here designated as the lectotype. Hagelstein reports this taxon from a several slides, including 57A1, 130B1, 143D1, 143D2, 145A1, 145A2 and 145B1.

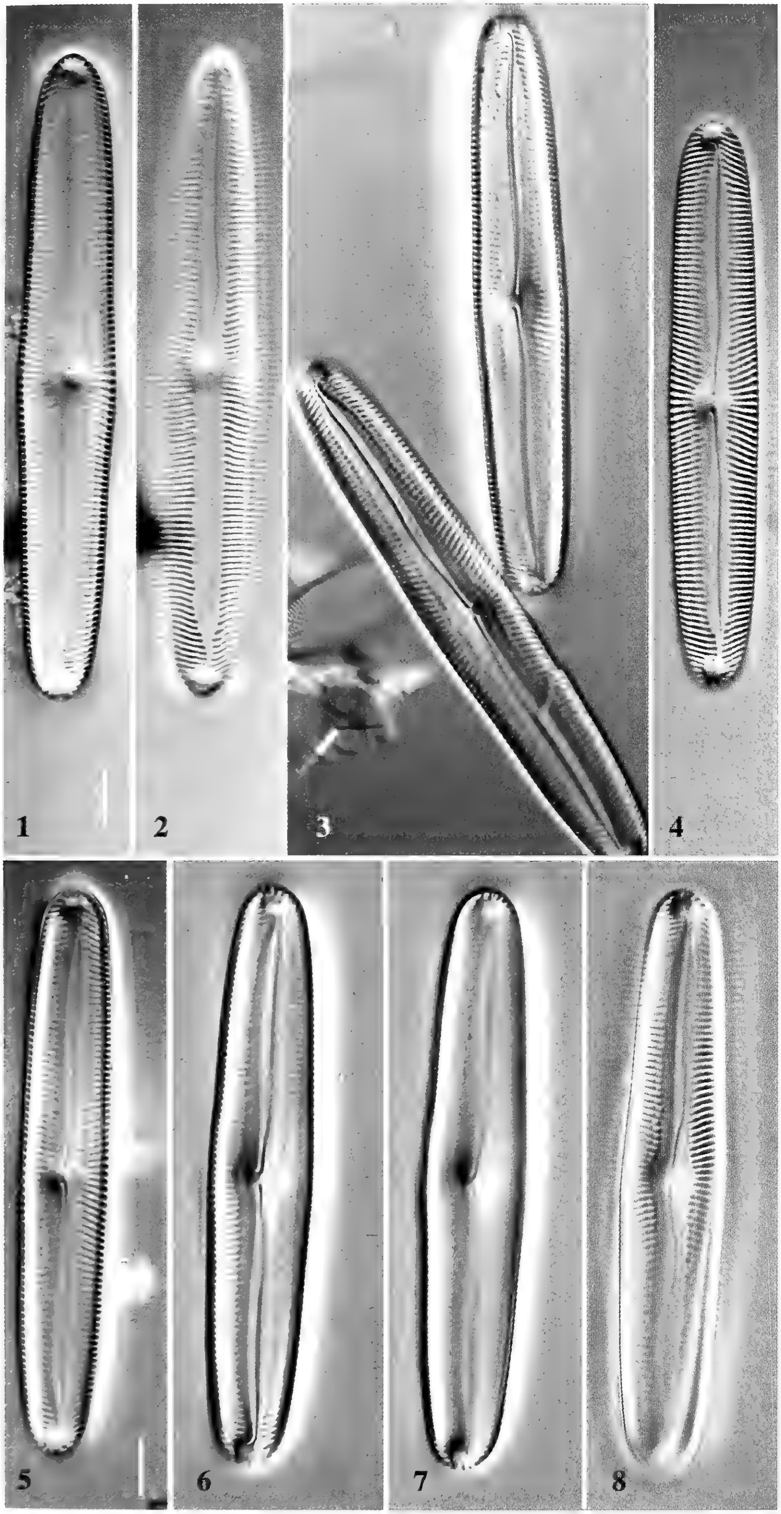

Plate 1. Light microscopy. Figures 1-8. *Pinnularia laterittata* var. *minor* Hagelstein. Size range of this taxon is documented. Figures 1 and 2 are from the same frustule showing *trans* valves. Figs. 6-8 are of the same frustule, showing *cis* valves. Scale bar in figure 1=10 μm, same for all figures.

Pinnularia titusiana, Hagelstein, 408/Pl. 9, figs 2, 3

HABITAT: common at Coamo Springs

COMMENTS: This species was identified from slides 52A1 and 170A, as indicated by Hagestein in his notes. The specimens figured by Hagelstein were found on slide 52A1, and it is here designated as the lectotype.

Pinnularia viridis var. ***subconstricta***, Hagelstein, 409/Pl. 9, fig. 4

HABITAT: Coamo Springs; ditches south of Santurce

COMMENTS: Hagelstein indicated this new variety can be found on slides 52A1, 168, 170A and 174. The illustrated specimen was found on slide 52A1, and this slide is here designated as the lectotype.

Pleurosigma angusti-convexum, Hagelstein, 409/Pl. 9, fig. 5

HABITAT: Canal de Martin Peña

COMMENTS: This new *Pleurosigma* species was found only on slide 165-2 which is the holotype.

Pleurosigma portoricense, Hagelstein, 412/Pl. 9, figs 6, 7

HABITAT: Rio Grande de Loiza; pools on the sandy plain near Carolina

COMMENTS: This species was found on slides 143B3 and 226B1. The illustrated specimens were both found on slide 143B3, and it is here designated as the lectotype.

Pleurosigma strigosum var. ***incisum***, Hagelstein, 414/Pl. 9, figs 8, 9

HABITAT: near Park Loiza

COMMENTS: This new variety was found on the only slide indicated in Hagelstein's notes, slide 110A1. This slide is the holotype.

Stauroneis similaris, Hagelstein, 421/Pl. 9, fig. 12

HABITAT: ditch near Park Loiza

COMMENTS: This specimen was found on slide 111A1, and it is here designated as the lectotype.

Trachyneis aspera var. ***atomus***, Hagelstein, 428/Pl. 9, fig. 14

HABITAT: Harbor of Christianstedt, St. Croix

COMMENTS: Hagelstein's notes indicate that this new *Trachyneis* variety is to be found on slides 149-2A3 and 149-1B2. The specimens encountered on these slides do not appear to be the same as those illustrated in the publication, although Hagestein indicates in his notes the illustrated specimen should be on slide 149-2A3. Unlike the situation described by Kociolek and de Reviers (1996), where Manguin material from Lake Karluk had been lost, and therefore illustrations were designated as holotypes, we have located specimens used by Hagelstein to describe this variety. Slide 149-2A3 is here designated as the lectotype for this taxon.

Tropidoneis van-heurckii var. ***maxima***, Hagelstein, 430/Pl. 9, fig. 15

HABITAT: marsh at Miramar

COMMENTS: This new variety occurs on slides 255A1 and 255C1. The specimen illustrated is found on slide 255A1, and it is here designated as the lectotype. Subsequent research on this taxon may find it to represent the larger end of the size diminution series of the nominate variety.

A summary of the typification of Hagelstein's taxa is provided in Table 1.

TABLE 1. Lisiting of original slide numbers, type status taxon, and new CAS number for each of the taxa described by Hagelstein.

Original Number	*Type status*	*Taxon*	*CAS*
94D3	Lectotype	*Amphora bigibba* var. *capitata*	221057
	Holotype	*Caloneis liber* var. *incerta*	
118B1	Lectotype	*Campylodiscus cordatus*	221058
73B1	Holotype	*Cocconeis singularis*	221059
165-3	Lectotype	*Cyclotella insolita*	221060
165-2	Isotype	*Cyclotella insolita*	221061
	Holootype	*Pleurosigma angusti-convexum*	
57A1	Lectotype	*Cymbella coamoensis*	221062
29B1	Lectotype	*Diploneis gravelleana*	221063
149-2A	Lectotype	*Diploneis smithii* var. *adversa*	221064
228D1	Lectotype	*Eunotia indica* var. *undulata*	221065
23A4	Lectotype	*Eunotia lunaris* var. *duolineata*	221066
143A1	Lectotype	*Gomphonema carolinense*	221067
248-2B1	Lectotype	*Gyrosigma acuminatum* var. *angulatum*	221068
203A-1	Holotype	*Gyrosigma variipunctatum*	221069
115B2	Holotype	*Gyrosigma variistriatum*	221070
106B1	Lectotype	*Homeocladia vidovichii* var. *nodulosa*	221071
230C1	Holotype	*Mastogloia oblique*	221072
91B2	Lectotype	*Mastogloia sancti-johannis*	221073
116B1	Lectotype	*Navicula congerana*	221074
	Holotype	*Nitzschia miramarensis*	
31A	Holotype	*Navicula expansa*	221075
138B1	Lectotype	*Navicula guaynaboensis*	221076
112A1	Lectotype	*Navicula incomposita*	221077
112A6	Isotype	*Navicula incomposita*	221078
82B1	Lectotype	*Navicula incomposita* var. *minor*	221079
115A1	Lectotype	*Navicula lyra* var. *irregularis*	221080
203B	Lectotype	*Navicula mannii*	221081
18C1	Lectotype	*Navicula tubulosa* var. *rhomboidea*	221082
31B1	Lectotype	*Nitzschia hemistriata*	221083
164A1	Lectotype	*Nitzschia obtusa* var. *lata*	221084
220B1	Lectotype	*Nitzschia obtusa* var. *undulata*	221085
73B1	Holotype	*Nitzschia ponciensis*	221086
164B1	Lectotype	*Nitzschia quickiana*	221087
131A	Lectotype	*Pinnularia laterittata* var. *minor*	221088
52A1	Lectotype	*Pinnularia titusiana*	221089
	Lectotype	*Pinnularia viridis* var. *subconstricta*	
143B3	Lectotype	*Pleurosigma portoticense*	221090

TABLE 1 (*continued*). Lisiting of original slide numbers, type status taxon, and new CAS number for each of the taxa described by Hagelstein.

Original Number	*Type status*	*Taxon*	*CAS*
110A1	Holotype	*Pleurosigma strigosum* var. *incisum*	221091
111A1	Lectotype	*Stauroneis similaris*	221092
149-2A3	Lectotype	*Trachyneis aspera* var. *atomus*	221093
255A1	Lectotype	*Tropidoneis van-heurckii* var. *maxima*	221094

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A New Species of *Tritonia* from Okinawa (Mollusca: Nudibranchia), and its Association with a Gorgonian Octocoral

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A new species of tritoniid nudibranch is described. *Tritonia bollandi* sp. nov. is known from its type locality of Seragaki Tombs, Okinawa, and from Indonesia, and has been found at depths of 58 to 75 m. The animal reaches 88 mm in length, and mature specimens are olive green in color, with lighter colored branchial plumes, nearly white rhinophores, and a thin white margin along the notal margin. The body appears granular due to the presence of small low tubercles on all parts of the body, except for the foot. The oral veil is slightly bilobed and bears 12 to 14 elongate digitiform processes, many of which are apically bifid. The notal margin extends along and slightly overhangs the sides of the body. From the notal margin are produced 9 to 14 pairs of arborescent branchial plumes, and the sheaths of the rhinophores, whose margins are undulate and flange-like. The rhinophore shafts are retractable, and are palmate in appearance, with a central clavus surrounded by a stepped series of pinnate processes. External genitalia are on the right side of the animal, behind the third anterior branchial plume. The anus and nephroproct are also on the right side, behind and just below the 4th branchial plume, close to the notal margin. The anterior foot margin is rounded. Buccal armature includes a pair of jaws with 2 to 4 rows of microscopic denticles along the masticatory border. The radula has a tricuspid rachidian, a differentiated first lateral tooth, and a series of hamate to falcate lateral teeth. There are no cuticular plates within the stomach. *Tritonia bollandi* sp. nov. has been observed to feed upon gorgonian octocorals of the family Ellisellidae (Gray, 1859), in particular *Verrucella aurantia* (Gray, 1869). Sclerites produced by the octocoral were isolated from nudibranch digestive system contents and compared with sclerites isolated from octocoral samples, providing further evidence of the association between *Tritonia bollandi* sp. nov. and the octocoral family Ellisellidae. This is the first record of predation by a nudibranch on this family of octocoral.

During 1995 and 1997, eight specimens were collected by Robert F. Bolland while scuba diving at a site off the island of Okinawa. With one exception, all of these specimens were found in association with a red gorgonian octocoral. Two of the specimens were observed by the collector to be feeding on the gorgonian, and five other specimens were found on this gorgonian. Specimens of the gorgonian were collected along with the nudibranchs in almost all cases, and in one case a nudibranch egg mass was collected on the gorgonian sample taken near the nudibranch. Detailed examination of the morphology and anatomy of the nudibranch specimens indicate they belong to the genus *Tritonia.* Comparison was made between the specimens with descriptions of similar species, as well as direct comparison of the morphology with a type specimen of a similar, described species from Indonesia (*Tritonia olivacea* Bergh, 1905). *Tritonia bollandi* sp. nov. does not match this or any other previously published descriptions of tritoniids, and is described herein.

Nudibranchs of the family Tritoniidae are well documented as feeding on octocorals, including sea pens, soft corals and gorgonians (McDonald and Nybakken 1999). In many cases, the feeding may be limited to a single species or family. Animals are often cryptic upon their prey species. Substances sequestered from their prey (Avila et al. 1999) may chemically protect other species. Unless an animal has been seen directly feeding on a prey species, it can be difficult to connect it to a specific prey. In this study, direct observation of feeding is combined with collections and photographs of associated prey. In addition, digestive tract contents provide sclerites of the prey coral, allowing direct comparison among samples, and identification of the prey octocoral as belonging to the family Ellisellidae Gray, 1859. This is the first record of a nudibranch feeding on this family of gorgonians.

Methods.— Nudibranchs were relaxed in ethylene phenoxytol, fixed in 10% buffered formalin for 24 hours, then transferred to 75% EtOH. Coral specimens were placed directly into 75% EtOH. Anatomical drawings have been produced with the aid of a drawing tube attached to a binocular dissecting microscope. Dissections of the animals have been performed by a ventral incision through the length of the sole of the foot and around the genital and anal openings, allowing the removal of the entire visceral mass in one piece. Jaws and radulae were freed from the buccal masses by partially dissolving them in 10% KOH solution. Digital photos of corals, egg mass, and jaws were produced using a MDS100 Kodak digital camera. Jaws and radulae were air dried, then mounted on aluminum stubs and sputter-coated with a mixture of gold and palladium in preparation for electron microscopy. Scanning electron micrographs (SEMs) were taken using a Hitachi S-520 Scanning electron microscope, then scanned into a Macintosh computer system and edited using Adobe Photoshop™ 5.5. Digestive contents and coral samples were treated with undiluted household bleach to dissolve the tissue, releasing the sclerites. Sclerites were then collected with micropipettes, washed 3 times in de-ionized water, then rinsed in 75% EtOH. Samples were then dispersed on aluminum stubs, and sputter coated with gold/palladium for scanning electron microscopy, and also made into permanent glass slides for optical microscopy.

Species Description

Suborder Dendronotacea Odhner, 1934
Family Tritoniidae Lamarck 1809
Tritonia Lamarck, 1801

Tritonia bollandi Smith and Gosliner, sp. nov.

Tritoniid sp. 8, Rudman, 2003.

Type Material.— All type material has been deposited at California Academy of Sciences Department of Invertebrate Zoology (CASIZ). All material was collected by Robert F. Bolland at Seregaki Tombs 26.00°30.40′N 127.00°52.60′E, Okinawa, on a substratum of mixed sand and coral rubble. Holotype: CASIZ 105327, 85 mm in length, collected 12 May 1995 at 64 meters along with sample of octocoral upon which it was found. Paratypes: CASIZ 105302, 88 mm in length, dissected, collected 7 July 1995 at 75 m along with sample of octocoral upon which it was feeding. CASIZ 115750, 69 mm in length, dissected, collected 4 May 1997 at 58 meters from a partially eaten octocoral; CASIZ 105329, 17 mm in length, collected 7 July 1995 at 75 meters along with sample of octocoral upon which it was feeding; CASIZ 105300, 88 mm in length, collected 3 August 1995 at 74 meters along with sample of octocoral upon which it was found; CASIZ 115738, 65 mm in length, collected 1 March 1997 at 72 meters along with egg mass and octocoral sample upon which it was found; CASIZ 115821, 82 mm in length, collected at 59 meters.

Additional material examined.— Zoölogisch Museum, Universiteit van Amsterdam (ZMA), paratype of *Tritonia olivacea* Bergh, 1905, 17 mm in length collected on the Siboga Expedition by Bergh, with an additional pair of jaws, possibly from the holotype, which is missing.

External Morphology.— The largest specimen (CASIZ 105302) was 88 mm in length in life (Figs.1a–b) This preserved specimen is 73 mm in length, 12 mm across widest portion of notum, and 12 mm from top of notum to bottom of foot. The body is elongate and limaciform, with greatest diameter just anterior to mid-body. Another preserved specimen (CASIZ 115750) measured 47 mm in length, and 10 mm in width and height (Figs. 2a–b). Posterior to mid-body the animals taper gradually to the posterior end of the foot. The body shape is trapezoidal in cross-section, with the widest portion being the notum. Color in life ranges from nearly white to dark olive green with some preserved specimens retaining some of this olive green coloration. The paratype illustrated in Figures 1a and 1b shows a thin white margin along the edge of the notum, with nearly white rhinophoral shafts and lighter colored branchial plumes. All of the preserved animals show some degree of translucency, with some details of the internal organs visible through the body wall. The preserved animals all have a finely granular texture due to the small rounded low tubercles present on the body surfaces except the foot. Anterior to the foot and rhinophores is the characteristic oral veil (also referred to as the frontal veil or velum) extending forward from around the mouth opening. The velum is a flattened contractile projection, somewhat bilobed in form with elongate digitiform processes produced along the margins of each lobe. There are 6 or 7 processes on each lobe, the outermost on each side consisting of an oral tentacle with a distinct groove and a spatulate or rolled distal portion. Of the remainder, the most medial processes are always the shortest, increasing in length to the 3rd or 4th process, then generally decreasing in length to the 5th or 6th on each side. Some or all of the velar processes are apically bifid. In general the longer ones show this tendency more (Fig. 2b). The edges of the notum extend out slightly over the body, forming a distinct notal margin or ridge. From this margin are produced the sheaths of the rhinophores (Fig. 2c) and the branchial plumes (Fig. 2d). The notal margin extends up the sides of the widely spaced, tubular rhinophoral sheaths. The margins of the rhinophoral sheaths are simple and undulate. In most of the specimens examined, the flange is anteriorly lower, giving a notched appearance, and is more expanded at the posterior margin, where it tended to fold over or extend somewhat. The rhinophore shaft is contractile within the sheath. The shape of the rhinophore is characteristic of the family, and has been described by various workers as palmate. A central digitiform clavus arises from the apex of the shaft, surrounded by a series of bi-pinnately divided projections, lowest in the anterior portion and rising in a stepped fashion posterolaterally (Fig. 2c). There are 9 to 14 distinctive arborescent branchial plumes per side on the animals examined. A thickened trunk extends from the notal margin forming the base of each plume, dividing to produce 5 radial branches, each of which then divides 2 or more times to terminate in simple pinnate processes (Fig 2d). The largest and most developed plumes are just anterior to the mid-body, and the plumes are smaller and more simply developed towards the anterior and posterior of the animal. The external mouth opening is a ventral longitudinal slit anterior to the foot, surrounded by labia (Fig 2b). The foot is linear and narrow, with a bluntly rounded anterior margin. The basal, medial portion of the foot is smooth, and the anterior portion in the area below the buccal mass is wider than the remainder of the foot, which tapers acutely at the tail. A labiate margin surrounds the basal portion of the foot, and is distinctly wider in this anterior, buccal portion. The interior portion of the foot margin is rugose, showing fine longitudinal folds. The external genitalia are on the right side of the animal, located posterior to the third anterior branchial plume at approximately the midline of the side of the body (Figs. 1a, 2f). The largest projection is the most ventral, and consists of a folded skin flap surrounding the oviduct. The gonopore occurs dorsal to this flap, and near it is the small penial papilla. The anus is located posterior to the fourth branchial plume, close to the notal margin, and is at the apex of a short, tubular anal papilla. The nephroproct is located just anterior to the anus, on the same plane as the anal opening (Fig. 1a).

INTERNAL ANATOMY.— Dissection of two specimens (CASIZ 115750 and 105302) provides the basis for anatomical descriptions.

Digestive system: The muscular buccal mass is white, with some reddish tinge from the jaws showing through. The jaw arches are exposed, and are visible on the dorsal aspect of the buccal mass. Situated along either side of the posterior margin of the buccal mass is a pair of floccose salivary glands. From the ventral aspect, a thin-walled transparent aorta extends from the posterior margin of the buccal mass posteriad to the pericardial region (Fig. 3). The buccal armature consists of a pair of jaws and a radula. The jaws are translucent, reddish brown in color, and stout, with the masticatory edge folded over and not serrate. The pair measured (CASIZ 115750) was 6.25 mm long by 6.875 mm wide, before drying. The jaws of another paratype (CASIZ 105302) were not measured before drying but were somewhat larger (Figs. 7a–b). The masticatory borders appear smooth to the naked eye, but SEM images (Figs. 4a–d) reveal the presence of two to four rows of denticles on the masticatory borders. The more newly formed denticles (Figs. 4d–e) possess multifid distal ends, with the older ones (Figs. 4a–b) appearing peg-like. The radular formulae are 66 × (78.1.1.1.78) and 55 × (59.1.1.1.59) for CASIZ #s 105302 (Figs. 5a–d) and 115750 (Figs. 6a–d), respectively. The base of the rachidian is roughly rectangular. The rachidian tooth is tricuspid, with the central cusp being largest. The emarginate central cusp is sharply acuminate, with a thickened central ridge adding structural support. In many cases there is some folding at the shoulders of the central cusp. The two shorter outer cusps are stouter and blunter than the central cusp, and curve inward towards it. Some of these outer cusps show considerable distal folding, while others are more simple in form. The first lateral tooth on each side is differentiated from the remainder, being stout and blunt in comparison to the remainder of the sharper, hamate outer laterals. These innermost laterals have folds and thickenings that give them a buttressed appearance, with the holotype showing a distinct peg-like ridge. The remaining laterals on each side are hamate, with sharp points. Those closest to the rachidian are stouter, gradually becoming finer and more blade-like towards the outer margins of each half-row.

The gross anatomy of the visceral mass is illustrated in Figure 3. The esophagus exits from the dorso-medial buccal mass, arching posteriad. Beyond the ganglia and the encircling nerve ring, the esophagus narrows before turning to the left and enlarging into a crop-like sac. There are fine spots of greenish pigment dispersed on portions of the esophagus and crop, as well as the stomach and intestine of one of the animals dissected. The inside of the crop has a girdle of longitudinal folds and ridges, but is devoid of any chitinous plates. The crop narrows, and opens ventrally into the narrow proximal portion of the esophagus. Continuing posteriad in a straight line, it passes through a groove dividing the ventral side of the genital mass, before widening and curving dorsally to enter the stomach. The major portion of the muscular stomach is visible on the dorsal side of the animal. It sits atop the genital mass and the smaller anterior digestive gland, nestled in a hollow in the anterior portion of the posterior digestive gland mass. It is completely uncovered by the digestive gland. The interior of the stomach has a series of longitudinal folds and ridges, but is devoid of chitinous plates. The stomach narrows and curves to the right, forming the intestine, which curves dorsally to terminate at the anus. The contents of the crop, esophagus, stomach and intestine contain bits of coral and digested material. The digestive gland consists of a smaller, anterior portion attached to a larger posterior lobe, each of which has separate ducts entering to the stomach. Though not shown in the illustration, approximately six openings in the posterior digestive glands give rise to thin-walled, transparent branchial aorta, which ramify, connecting with the bases of each branchial plume (Fig. 2e). These branchial aorta do not ramify into the branchial plumes.

Reproductive system (Fig. 8a).— The reproductive system is triaulic, with three separate genital openings, but with no duct connecting the vagina or bursa copulatrix to the female gland mass or oviduct. The ovotestis is difficult to discern by gross examination, but appears to lie on the surface of the digestive gland masses. The narrow, thin-walled hermaphroditic duct enters the muscular, "C" shaped ampulla. Distally, the ampulla connects with the female gland mass, and it is not possible to discern exactly where the duct divides into male and female branches.

The vas deferens exits from the female gland mass, terminating distally in an unarmed penial papilla. There is no discrete prostate gland, but the proximal portion of the vas deferens is thickened and glandular in appearance. The oviduct exits the female gland mass proximal to the vaginal opening. The female gland mass makes up the bulk of the reproductive system, consisting of the smaller albumen and the larger mucous and membrane glands. The muscular bursa copulatrix is rounded-elongate connecting to the vagina by a narrow duct that is approximately equal in length to the bursa.

Nervous system.— The cerebral and pleural ganglia are well fused and are joined by short connectives to the pedal ganglia, which are joined by a paired circum-esophageal commisure (Fig. 8b). A pair of buccal ganglia (Fig. 8c) are present on the ventral esophagus, anterior to the circum-esophageal ring. The buccal ganglia are touching each other. Giant nerve cells are present on the surface of all the ganglia. A pair of sub-dermal eyes is present posterior to the bases of the rhinophore sheaths, each connected by a nerve to the cerebropleurals.

Egg mass.— On the octocoral sample collected along with CASIZ 115738 is an egg mass, which likely belongs to this nudibranch. It is a white string about 0.5 mm across, wrapped around the branches of the coral sample (Fig.7c). There is a single egg per capsule. The white eggs are spherical and approximately 0.1 mm in diameter.

Distribution.— *Tritonia bollandi* sp. nov. is only known from its type locality in Okinawa and from Indonesia (Rudman 2003).

Etymology.— The species is named after Robert F. Bolland in recognition of his many contributions to the knowledge of invertebrate biodiversity, particularly the opisthobranchs.

Discussion.— While searching the literature, a plate of *Tritonia olivacea* Bergh, 1905 (pl. XX, fig. 18) appeared to closely resemble *T. bollandi* (Fig. 7d). A translation of the original description (Bergh 1905) failed to provide enough information to determine if these animals were the same as those described in the present study. Although the holotype of *Tritonia olivacea* could not be located, a paratype specimen was obtained. Comparison of the specimens show significant differences in several important features. In *T. olivacea*, the oral veil has a total of 8 papillae, all simple, with dark pigmentation retained on the distal ends, while *T. bollandi* has 12 to 14 papillae, many of which are apically bifid and without pigmentation. The location of the genital and anal openings also differs between species, with *T. olivacea* having the external genitalia between the 4th and 5th branchial plume and the anus between the 5th and 6th, while in *T. bollandi* they are located between the 3rd and 4th, and 4th and 5th respectively. Other differences exist between the specimens, but it is difficult to determine which may be artifacts of fixation or preservation. A pair of jaws was sent along with the paratype, assumed to belong to the holotype or another paratype specimen. Examination under an optical microscope did not reveal any denticulation of the masticatory border, which is in agreement with Bergh's description, and differs from the denticulate jaw of *Tritonia bollandi* sp. nov.

Although the cosmopolitan family Tritoniidae is readily discerned by its general body shape, oral veil and characteristic rhinophore shape, it has presented many problems to workers trying to unravel its taxonomy and systematics. Early descriptions are poor, often lacking details of internal anatomy, and are usually without illustrations of the animal in life. Many of the Indo-Pacific species are relatively rare, adding to the difficulty of sorting out the tangle of named species that presently exist in the literature. To date, the bulk of the work of classification has been undertaken by Odhner (1936). He expanded this work by focusing on the Tritoniidae (Odhner 1963) in a publication that may have created more confusion than it resolved. At issue with some modern workers is the systematic importance of characters pertaining to the division of the digestive gland (Avila et al. 1999; Willan 1988; Wägele and Willan 2000). We agree with those who think that the progression from a holohepatic state to a distinctly lobed and/or branched cladohepatic state of the digestive gland represents a homoplasy within the nudibranchs. The relative homogeneity of reproductive and nervous system morphology within the Tritoniidae requires the finding of more meaningful characters from other sources. As fresh collection efforts are undertaken, perhaps molecular data can help unravel some of the problems with this group.

Until further work can be undertaken to review the taxonomy of the Tritoniidae, we will follow the basic taxonomic structure proposed by Odhner, and place our new species in the genus *Tritonia* based on the absence of stomach plates, the undivided digestive gland, radular form with tricuspid rachidian, blunt differentiated first lateral teeth, and simple hamate outer laterals, as well as the simple penial papilla.

INTRODUCTION TO OCTOCORAL STUDY

Gorgonians are octocorals characterized by a tough, flexible axis composed of the scleroprotein gorgonin, with varying amounts of calcareous material included in the axis, as well as in the living tissue where it takes the form of sclerites. The family Ellisellidae Gray, 1858 is part of the group *Calcaxonia* Grasshoff, 1999, and is composed of gorgonians with a solid axis containing heavy calcareous deposits of calcite or aragonite. Sclerites in the shape of spindles, clubs and double heads are present in the fleshy covering of the axis (coenenchyme) as well as in the non retractable polyps (Brill et al. 1983; Bayer and Grasshoff 1994; Grasshoff 1999). Morphology of the sclerites, along with growth form is used in identification to species level. Gradations between these forms can make species identification of small samples difficult.

OCTOCORAL EXAMINED.— Octocoral samples are either stored in the same bottle as the nudibranchs examined for the description, or were split out from the nudibranchs and assigned new numbers, and the catalog numbers are listed without repeating collection information already listed. CASIZ 115736 and CASIZ 115738 each had a sample of red octocoral upon which the animal was collected included in the same lot. CASIZ 105328 is a sample of red octocoral identified as Ellisellidae that had the animal in CASIZ 105327 associated with it. CASIZ 105330 is an ellisellid octocoral identified as *Verrucella aurantia* upon which was found the animal in CASIZ 105329. CASIZ 105303 and CASIZ 105300–105301, are also identified as *Verrucella aurantia* and are associated with CASIZ 105302 and CASIZ 105300 respectively. CASIZ 104850, 1 specimen identified as *Verrucella* sp., collected on mixed sand and coral rubble, 1.3 km ENE of Maeki-zaki, Seragaki Tombs, Okinawa, 14 April 1995, collected by Robert Bolland.

OBSERVATIONS AND RESULTS.— CASIZ 105302, a paratype of *Tritonia bollandi* sp. nov. was photographed with its prey CASIZ 105303 (Fig. 1b) and was observed by the collector to be feeding upon it. Portions of the coral can be seen to be stripped of living material down to the axis. Sclerites from the digestive tract of the nudibranch (Fig. 10) are compared with sclerites taken directly from the octocoral sample (Fig. 11). A paratype of *Tritonia bollandi* sp. nov. (CASIZ

105329) was also observed by the collector to be feeding on the octocoral collected with it (CASIZ 105330). While this nudibranch specimen was not dissected to obtain digestive tract contents, the sclerites from the prey coral sample are shown in Figure 12. In the case of CASIZ 115738, a unique opportunity was presented to observe digestive tract contents without dissection. The nudibranch was collected along with the octocoral upon which it was found. Although the nudibranch was not observed feeding on the coral, parts of the sample appear to have been eaten. A large fragment of hard red material consisting of partially digested coral was found protruding from the anus of the nudibranch. SEM's of this material (Figs. 13a–b, e–f) show gorgonian sclerites, along with some ossicles belonging to an unidentified sea cucumber (Figs. 13c–d). Comparison with sclerites from the coral sample (Figs. 13g, i–k) shows similar sclerites in both samples. Figure 13h shows a sea cucumber ossicle similar to that collected from the nudibranch. The paratype CASIZ 115750 was collected from a partially eaten, unidentified octocoral. A specimen of the coral was not taken, but stomach contents are illustrated in Figure 16. The holotype (CASIZ 105327) was found on and collected with a small octocoral (CASIZ 105328). Figure 14 illustrates the sclerites from a sample of this coral. Paratype CASIZ 105300 was found on and collected with a coral sample represented by CASIZ 105301. Sclerites from this sample are illustrated in Figure 15.

The association between *Tritonia bollandi* sp. nov. and its prey is supported by several lines of evidence: direct observation of the nudibranch feeding upon the octocoral, observation of the nudibranch and/or its suspected spawn on the suspected prey, visual evidence of the coral having been stripped of living material, and comparison of sclerites from the digestive tract of nudibranchs with sclerites freed from octocoral samples. The strongest evidence for specific predation occurs with the holotype specimen, which was directly observed feeding. The prey species was subsequently identified as *Verrucella aurantia* (Gray, 1869) by Gary C. Williams of the California Academy of Sciences by means of sclerite morphology and growth form. Comparison of sclerites (both SEM and optical microscopy) from the digestive tract of the nudibranch with sclerites taken from the prey coral show a similarity of forms consisting of variations on the dumbbell and double head shape, with more or less distinct waist areas, free from tubercles. These forms intergrade with longer spindle shapes, some of which have no waist areas. The paratype CASIZ 105329 was also directly observed feeding on the octocoral (CASIZ 105330), also identified as *Verrucella aurantia* by growth form and sclerite morphology. CASIZ 105328 is the lot containing both the paratype nudibranch and the coral sample with spawn. Feeding was not observed, but comparison of sclerites show similar morphology. The appearance of the sclerites, as well as the growth form suggest that this coral is also *Verrucella aurantia.* The spawn mass found on the coral is consistent with nudibranch spawn, and suggests a close relationship between the nudibranch and coral. The presence of ossicles belonging to an unidentified sea cucumber (Gosliner et al. 1996:8; Lambert 1997) from both the coral and the nudibranch also strengthen the assumption that the nudibranch was feeding on this particular coral. It was suggested that these ossicles were incidental, probably stuck to the mucus found on the coral and ingested with it (G.C. Williams, pers. commun.). The remaining 3 specimens that were found associated with red octocorals all had sclerites from the corals that were similar to the others found, and while a species level identification is not possible it can be said with confidence that they belong to the family Ellisellidae, which consists of 10 genera. The absence of club shaped sclerites narrows the possible identification to the ellisella group, which contains the genera *Ctenocella, Viminella, Ellisella, Verrucella,* and *Phenilia* (Grasshoff 1999).

Discussion.— The nudibranch *Tritonia bollandi* sp.nov. appears to be a specialist predator on gorgonian octocorals of the family Ellisellidae (Gray 1858) in general, and is known to feed in particular on *Verrucella aurantia* (Gray 1869). This is the first record of this family of octocoral being used as a nudibranch food source. Many members of the family Tritoniidae are known or suspected specialist predators on octocorals, often limited to a single species or group of species within a single family. In some cases, the nudibranch may be cryptic in form or coloration, becoming difficult to see on its host. This does not appear to be the case with *Tritonia bollandi* sp. nov., which contrasts sharply with the color of its prey. However, at the depth that these animals are found (56–75 meters) visibility probably becomes a moot point. Tritoniid nudibranchs may also utilize toxic or distasteful compounds sequestered from their prey as a means of discouraging their own predators (Avila et al. 1999; Gosliner and Ghiselin 1987; Gosliner et al. 1996; Willan 1998). At present, no chemical work has been done to see if this might be the case with these species.

ACKNOWLEDGMENTS

The authors would like to thank Dr. Robert Bolland of the Asian Division of the University of Maryland for collecting and providing the material for this study, as well as the photographs in Fig. 2. Henrik Woehlk provided the translation of Bergh's original description of *Tritonia olivacea*. This work would not have been possible without the help and support of the staff of the Department of Invertebrate Zoology and Geology at the California Academy of Sciences, San Francisco. Special thanks go to Gary Williams for his help in octocoral identification, and for his comments and suggestions.

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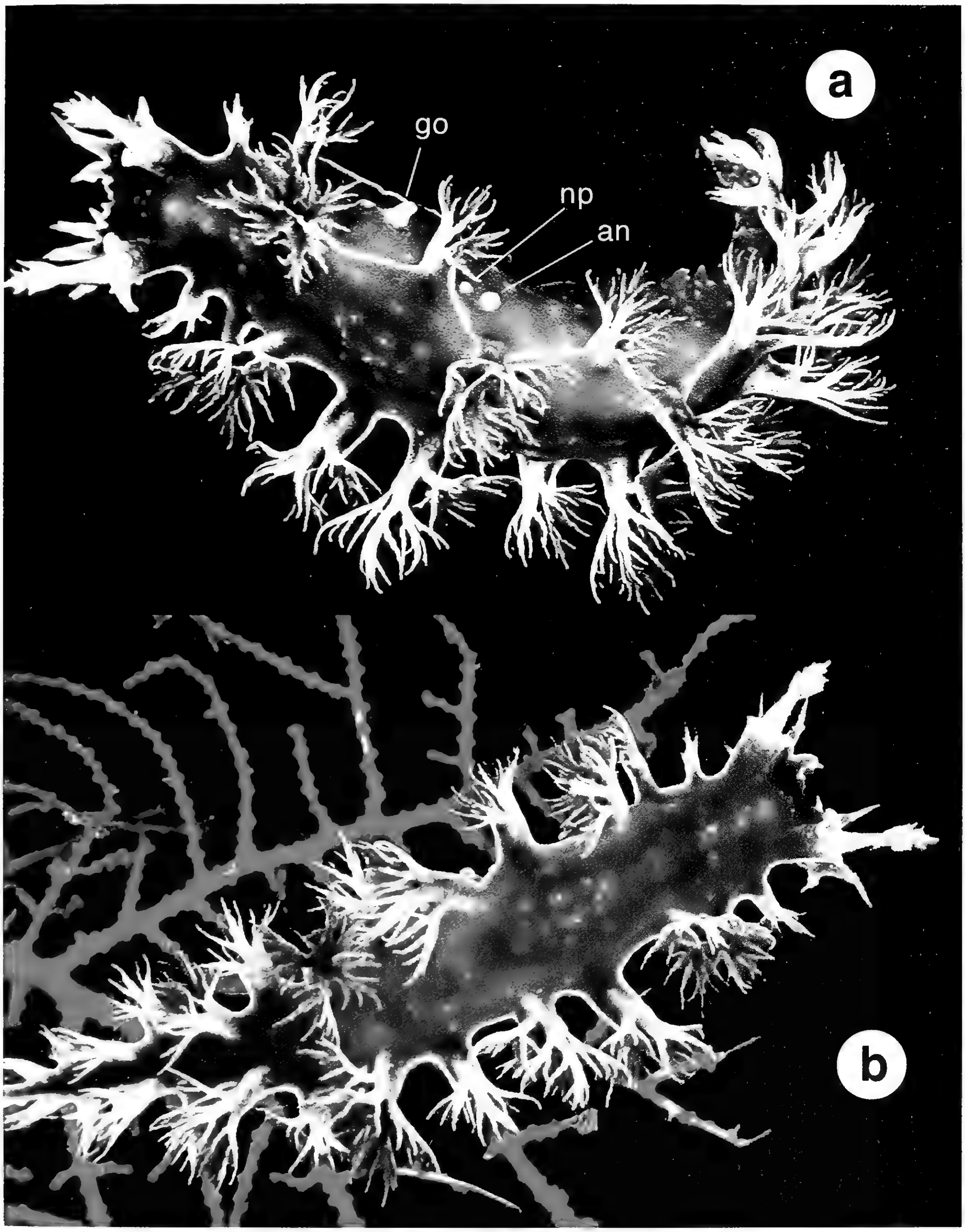

FIGURE 1.(a) Photograph of living animal (CASIZ 105302), 88 mm long, showing general structure and external features on right side. (b) Photograph of same specimen upon the octocoral it was found feeding on. an = anus; go = genital opening; np = nephroproct.

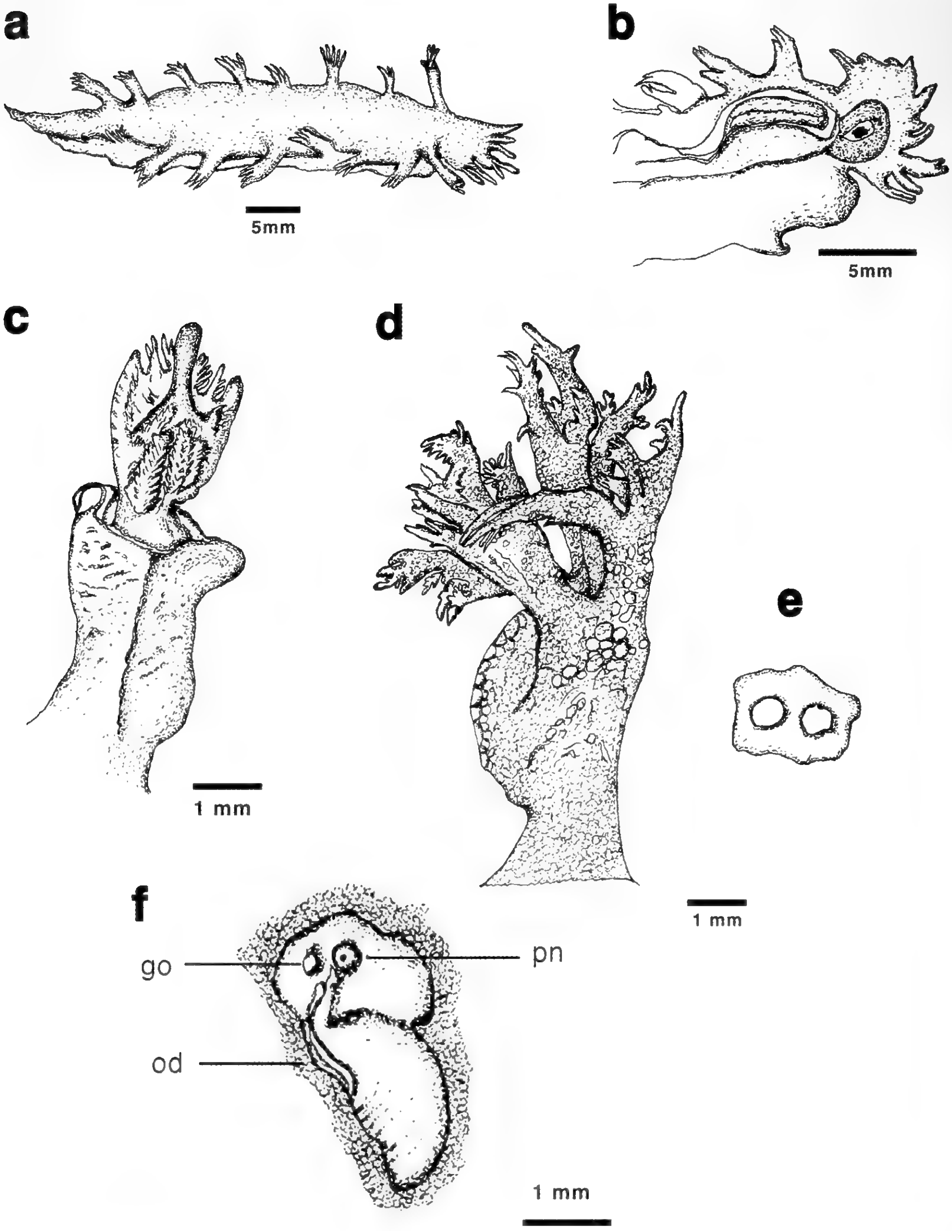

FIGURE 2. Paratype (CASIZ 115750) external features. (a) drawing of preserved specimen, dorsal view. (b) ventral view of anterior portion of animal, showing mouth, anterior foot, and oral veil. tg = tentacular groove. (c) detail of rhinophore. (d) detail of branchial plume. (e) detail of base of branchial plume, same scale as (d). (f) detail of external genitalia. go = gonopore; od = oviduct; pn = penial papilla.

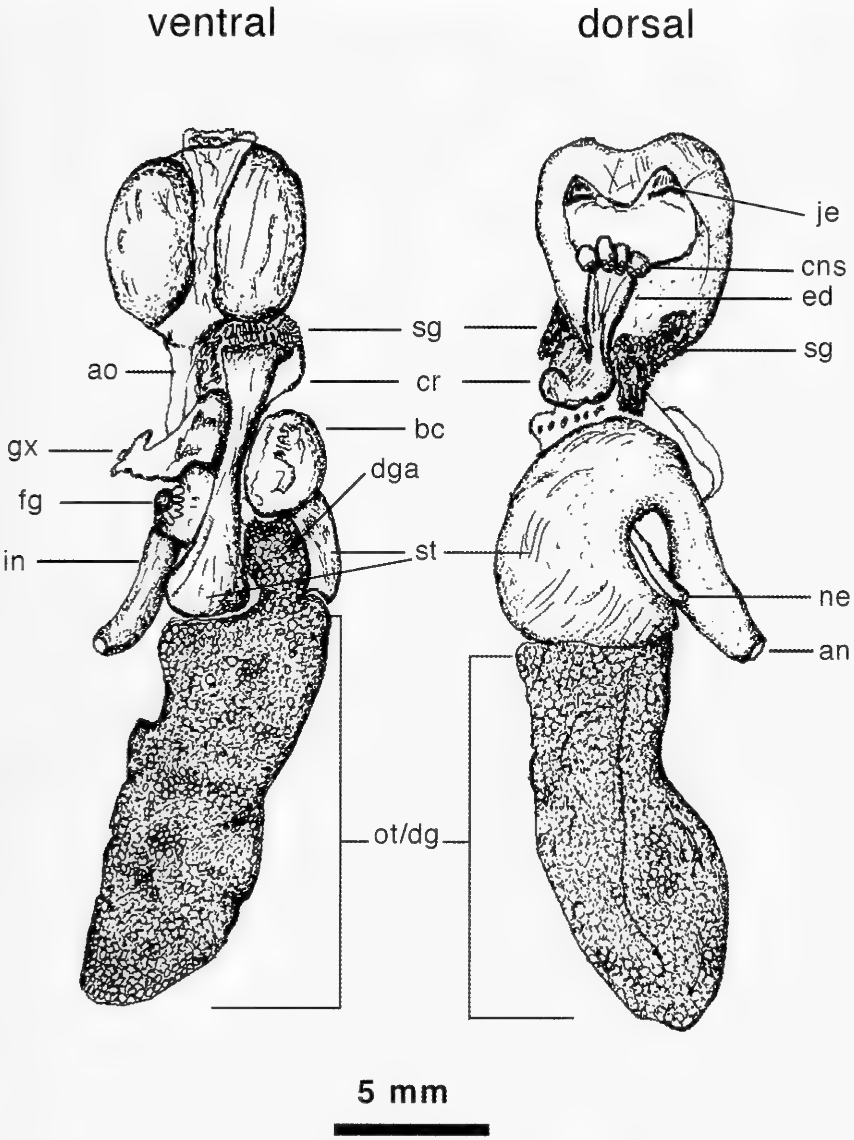

FIGURE 3. Visceral mass of paratype (CASIZ 115750) in ventral and dorsal views. an = anus; ao = aorta; bc = bursa copulatrix; cns = central nervous system; cr = crop; dga = anterior digestive gland; ed = distal esophagus; fg = female gland mass; gx = external genitalia; in = intestine; je = jaw edge; ne = nephroproct; ot/dg = ovotestes/digestive gland; sg = salivary glands; st = stomach.

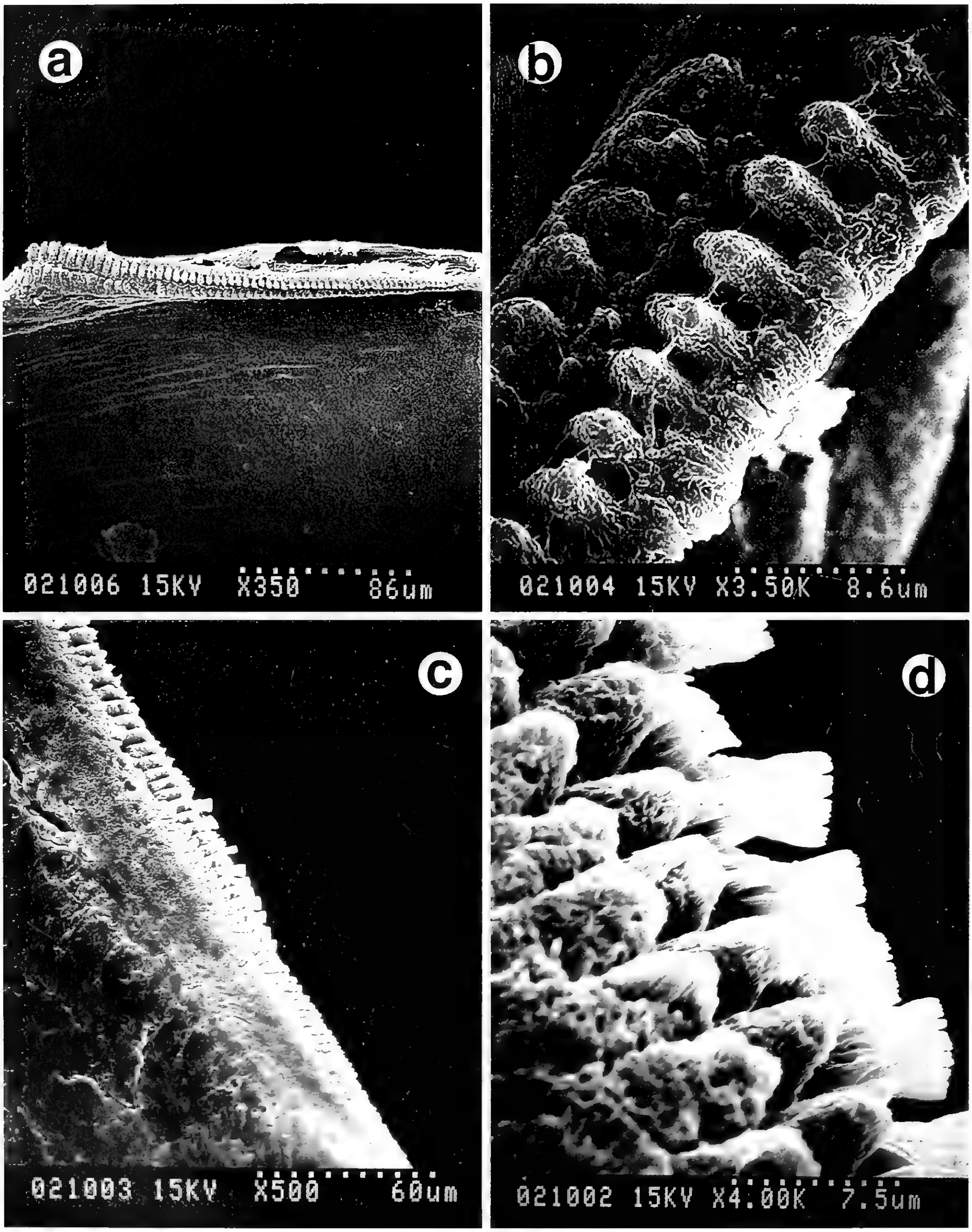

FIGURE 4. (a–b) SEM's of masticatory border of CASIZ 115750. (c–d) SEM's of masticatory border of CASIZ 105302, showing older, worn peg-like structures and newer multifid denticles.

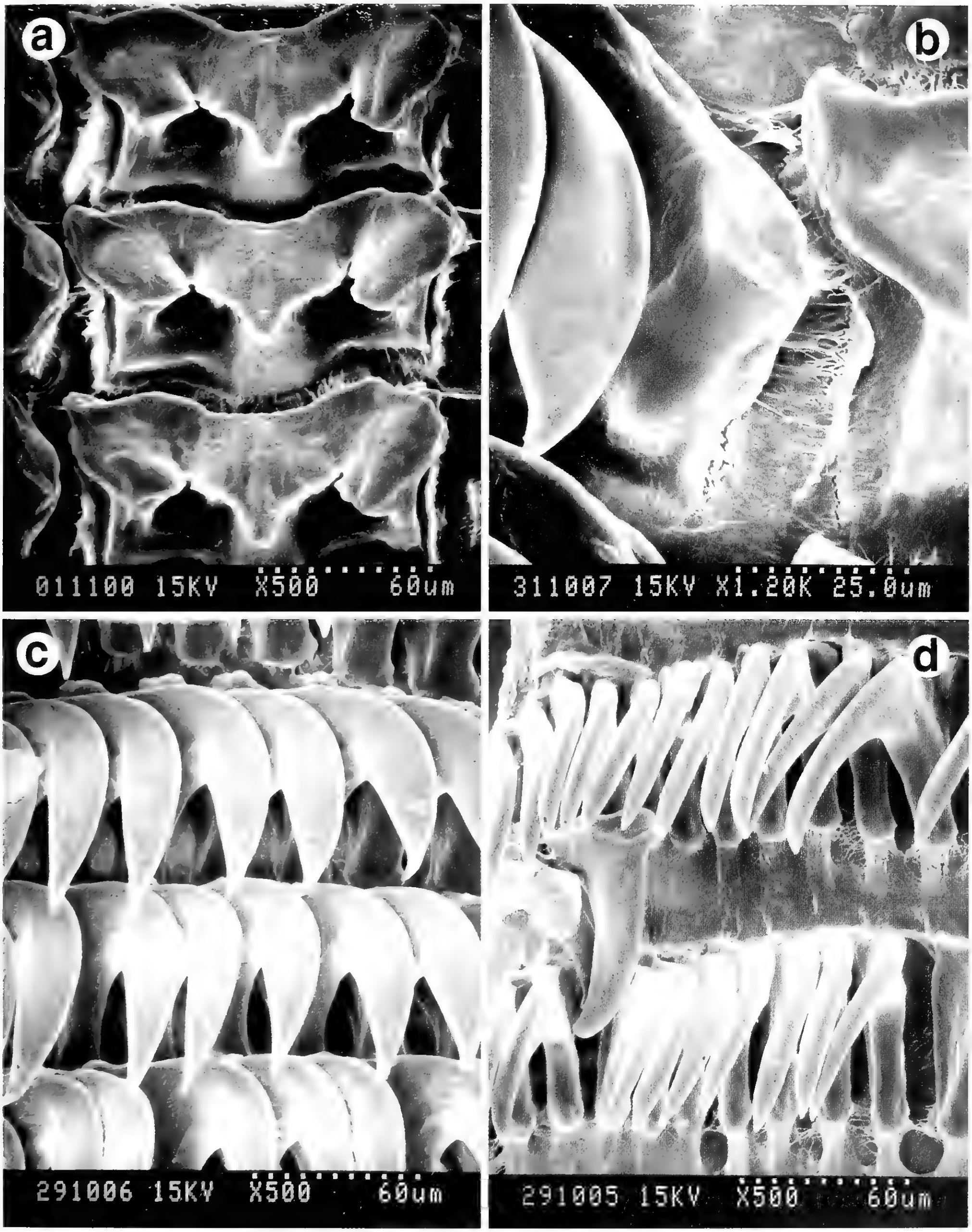

FIGURE 5. SEM's of radula of CASIZ 105302. (a) Rachidian teeth and first laterals near new end of radula. (b) Detail of first lateral and first inner lateral. (c) Inner lateral teeth of portion of half-row. (d) Outer lateral teeth of portion of half-row.

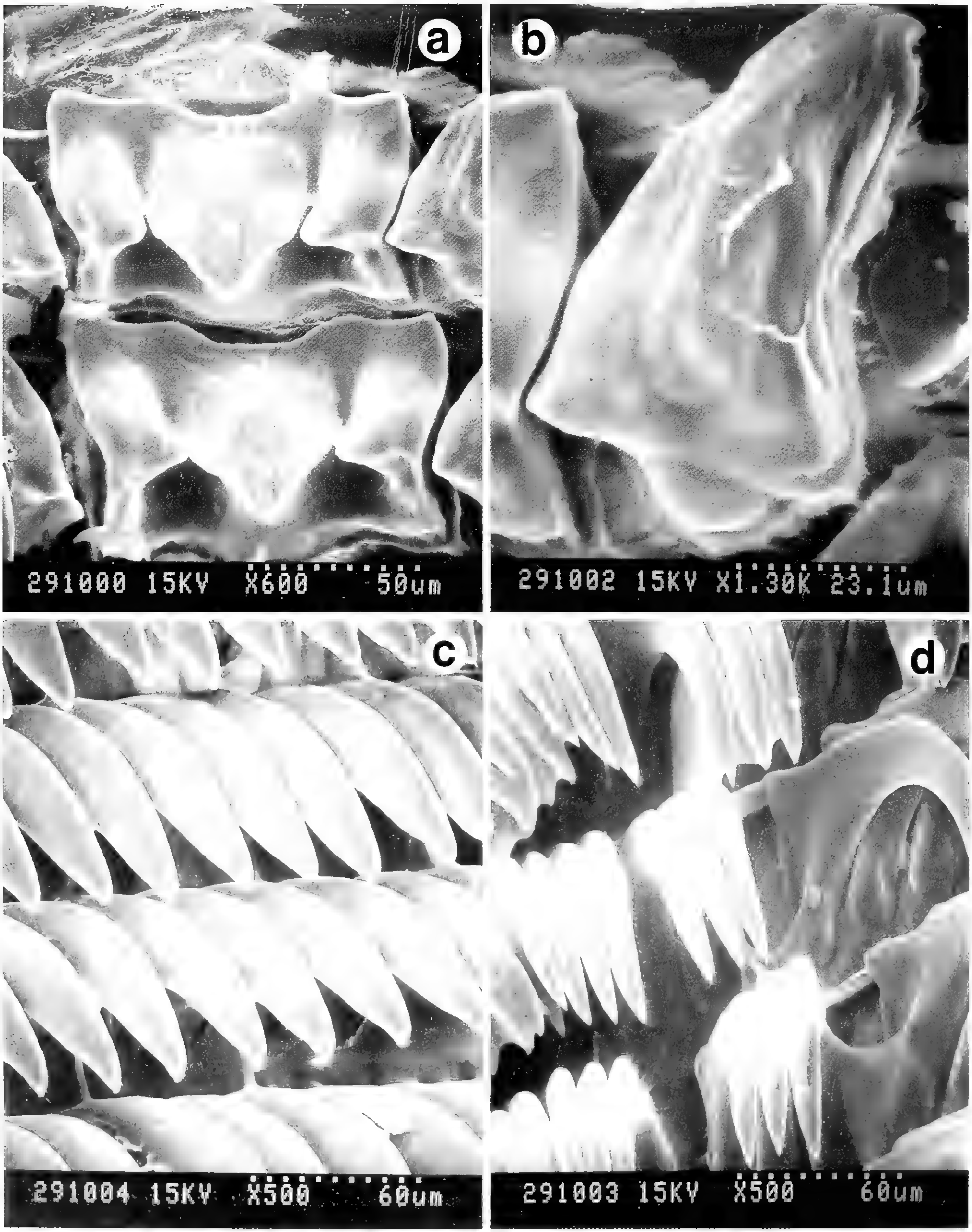

FIGURE 6. SEM's of radula of CASIZ 115750. (a) Rachidian teeth and first laterals near new end of radula. (b) Detail of first lateral and first inner lateral. (c) Inner lateral teeth of portion of half-row. (d) Outer lateral teeth of portion of half-row.

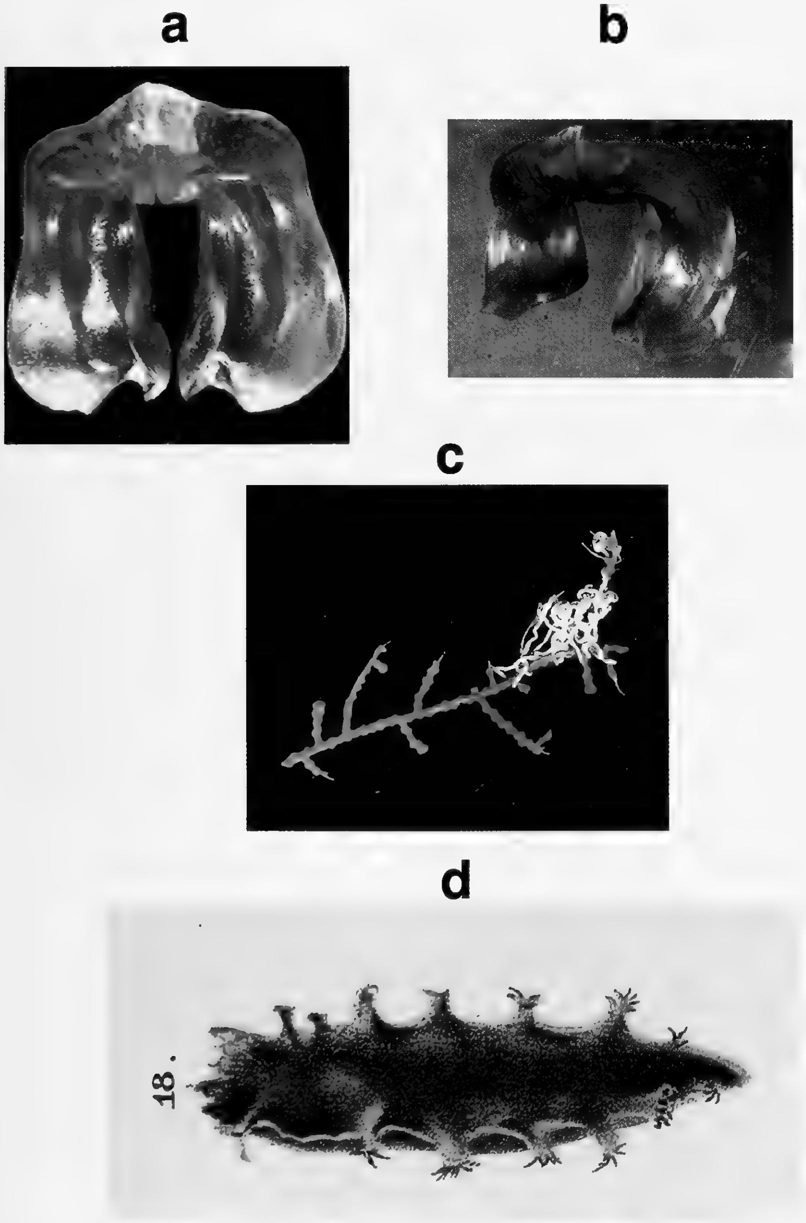

FIGURE 7. (a) Digital photo of jaws of paratype CASIZ 105302. (b) Digital photo of jaws of paratype CASIZ 115750. (c) Digital photo of coral sample and egg mass, CASIZ 115738. (d) Scanned image of plate of *Tritonia olivacea* Bergh, 1905.

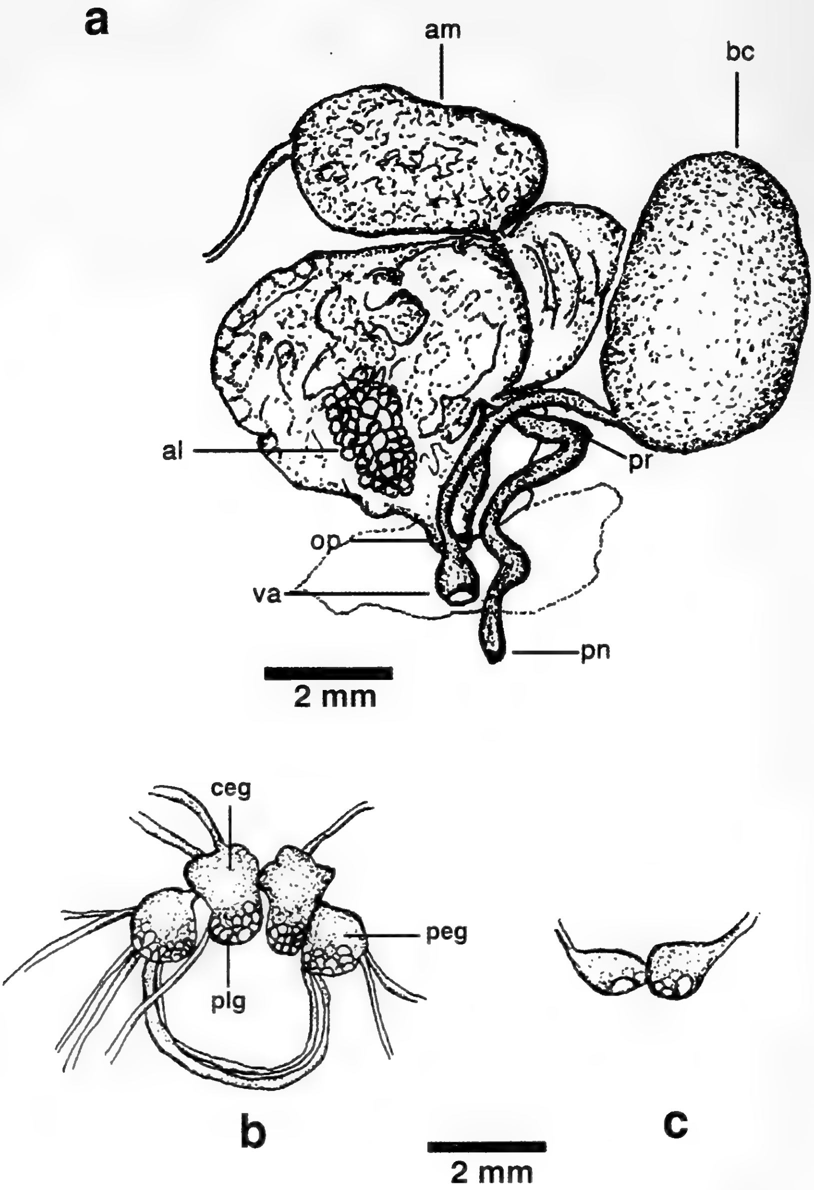

FIGURE 8. Details of internal anatomy of holotype CASIZ 105302. (a) Reproductive system. al = albumen gland; am = ampulla; bc = bursa copulatrix; od = oviduct; pn = penis; pr = prostatic portion of vas deferens; va = vagina. (b) Central nervous system. ceg = cerebral ganglia; peg = pedal ganglia; plg = pleural ganglia. (c) Buccal ganglia.

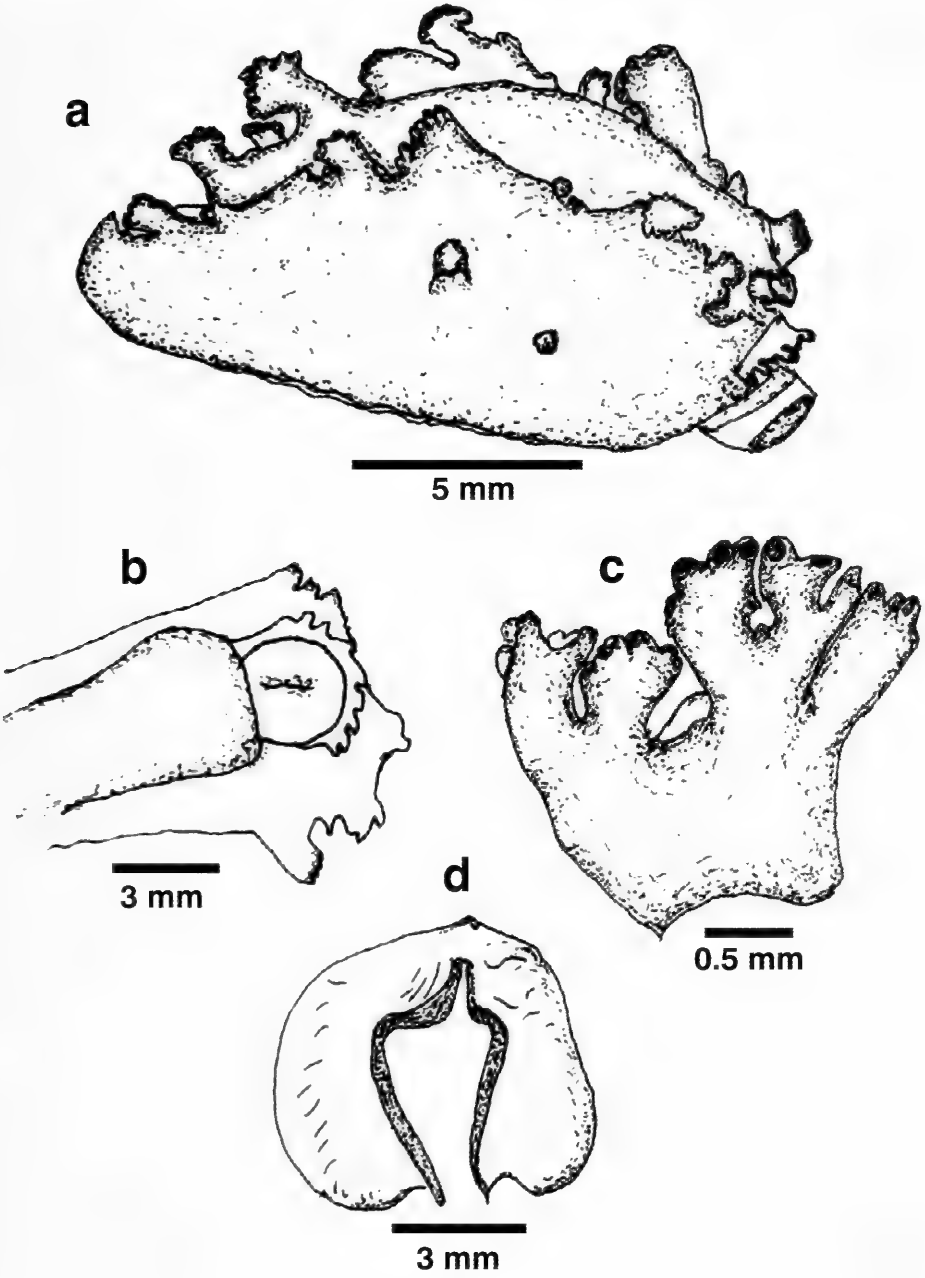

FIGURE 9. Drawings made from paratype of *Tritonia olivacea* Bergh, 1905. (a) Body of preserved specimen, right side. (b) Anterior ventral view. (c) Isolated branchial plume. (d) Jaw, possibly from holotype.

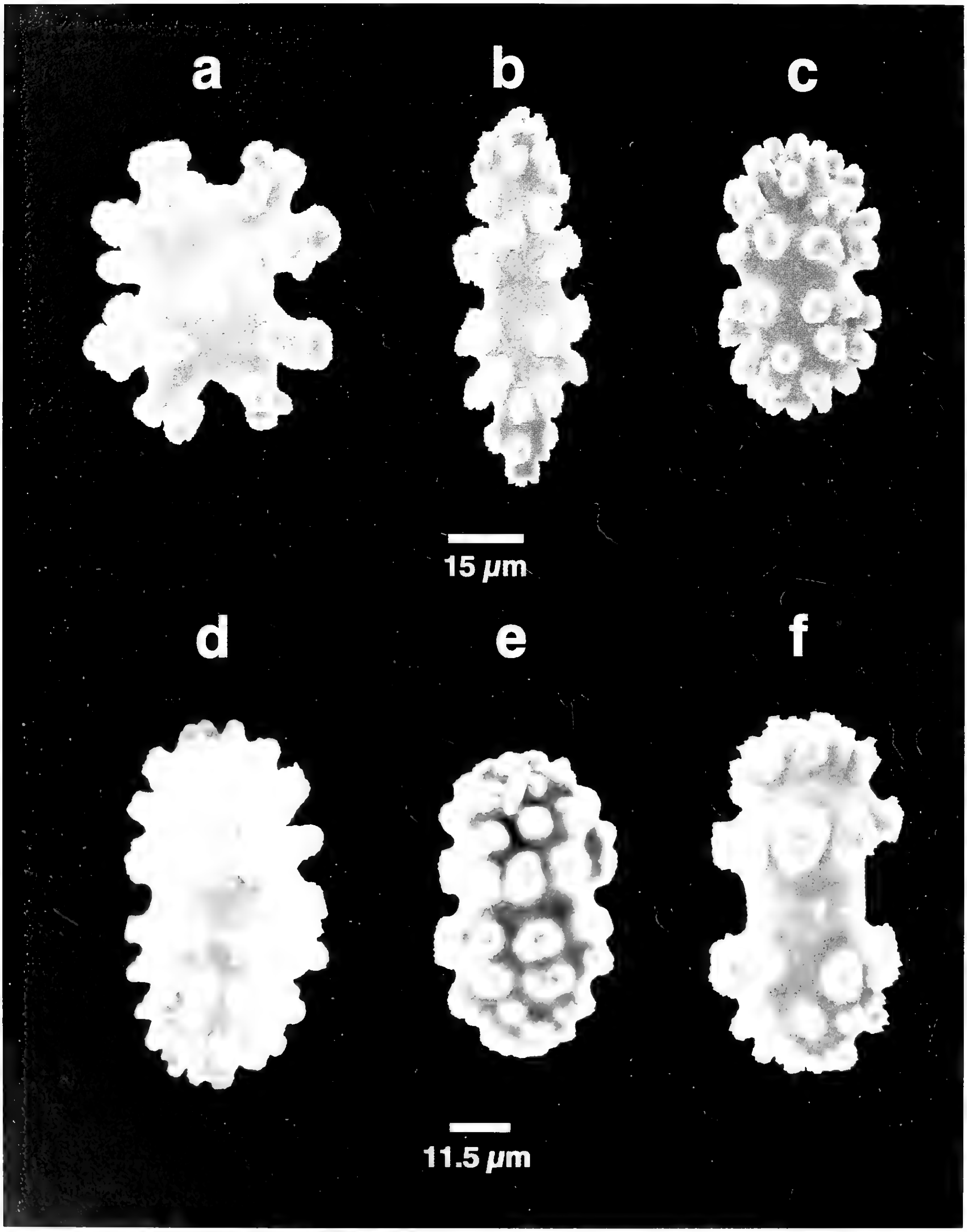

FIGURE 10. (a–f) SEM's of sclerites taken from the digestive tract of nudibranch CASIZ 105302.

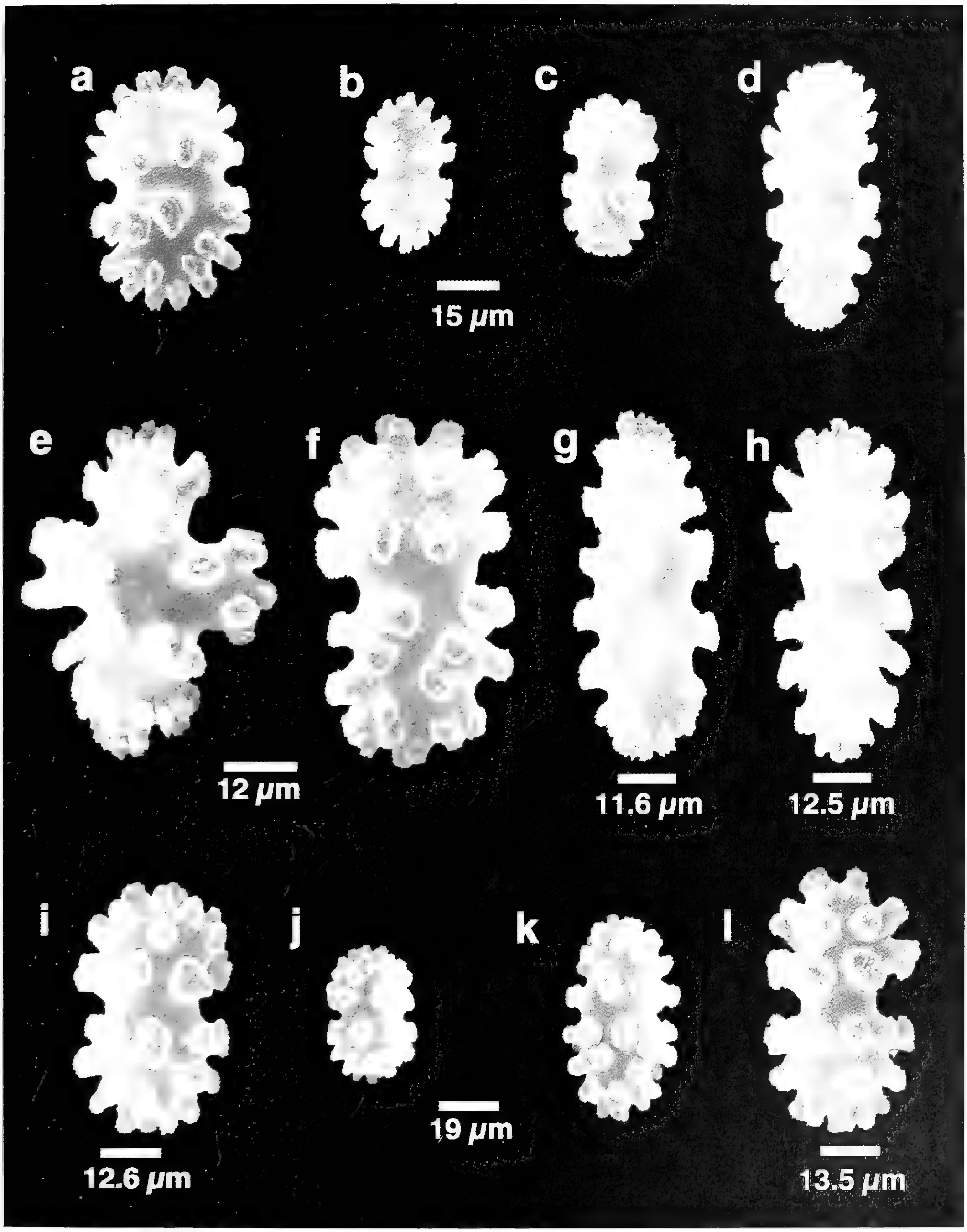

FIGURE 11. (a–l) SEM's of sclerites from coral sample CASIZ 105303 collected along with nudibranch CASIZ 105302.

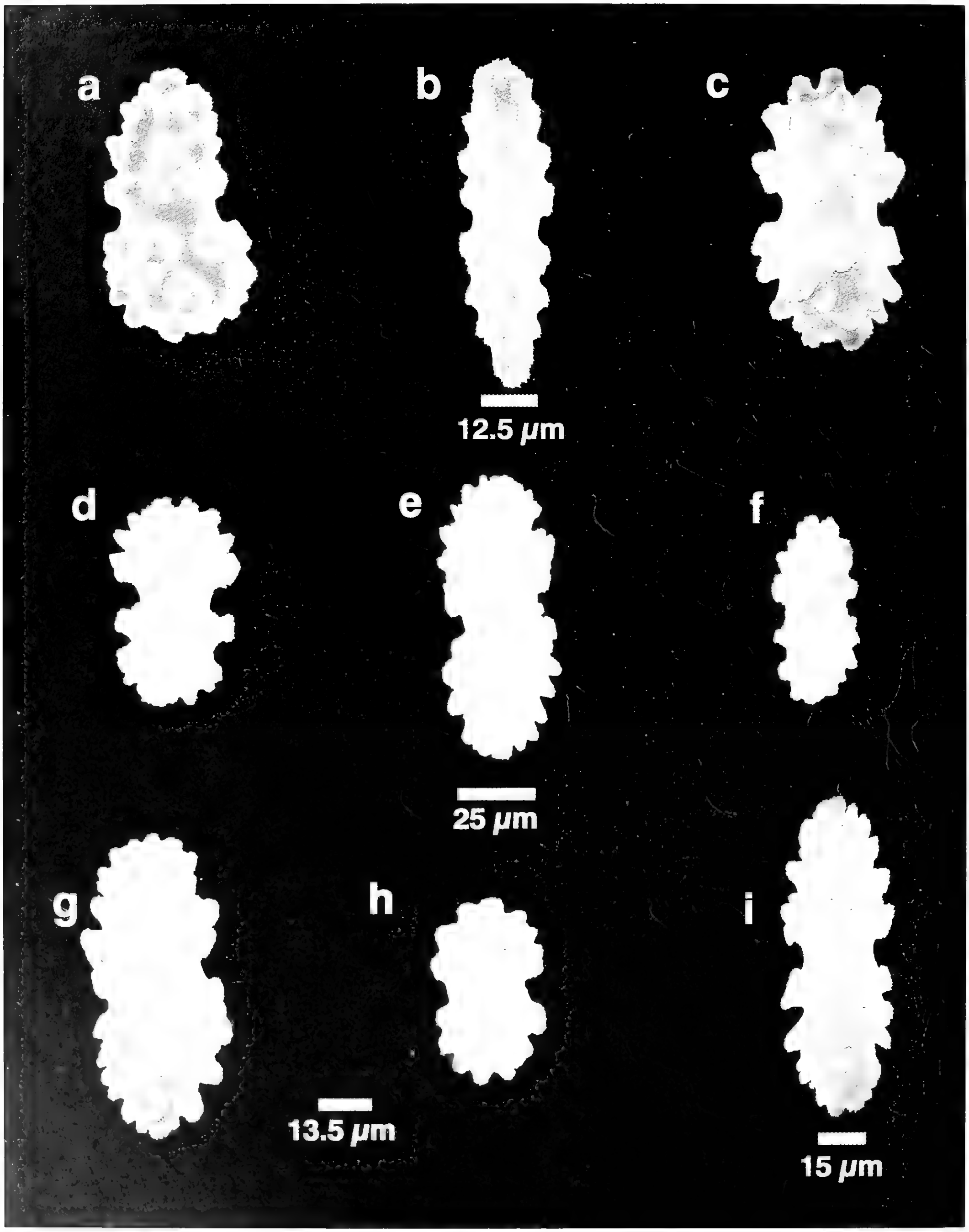

FIGURE 12. (a–i) SEM's of sclerites from coral sample CASIZ 105330, prey of nudibranch CASIZ 105329.

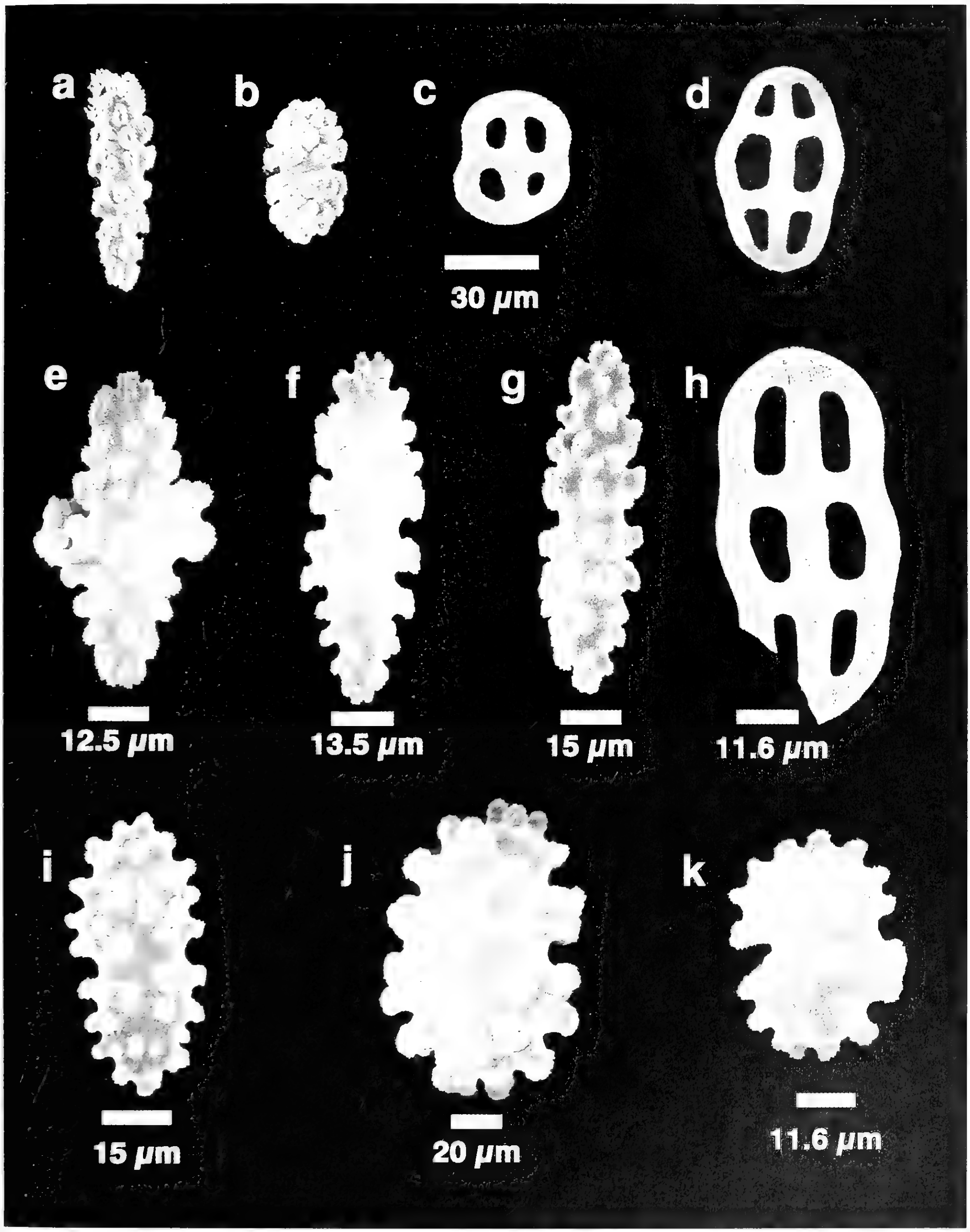

FIGURE 13. (a–f) SEM's of sclerites from coral sample collected with nudibranch CASIZ 115738. (g-k) Sclerites taken from material collected at anus of nudibranch

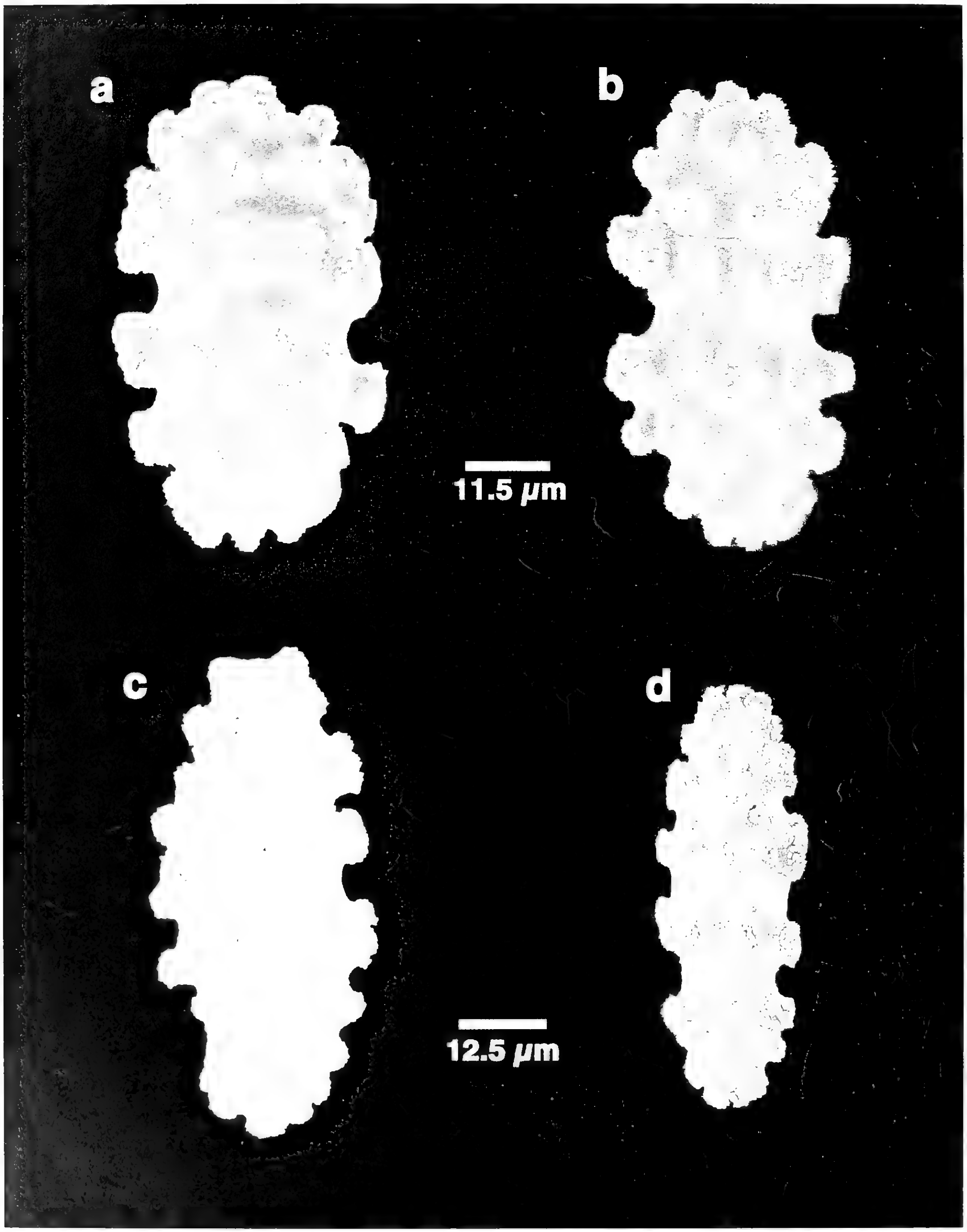

FIGURE 14. (a–d) SEM's of sclerites from coral sample CASIZ 105328.

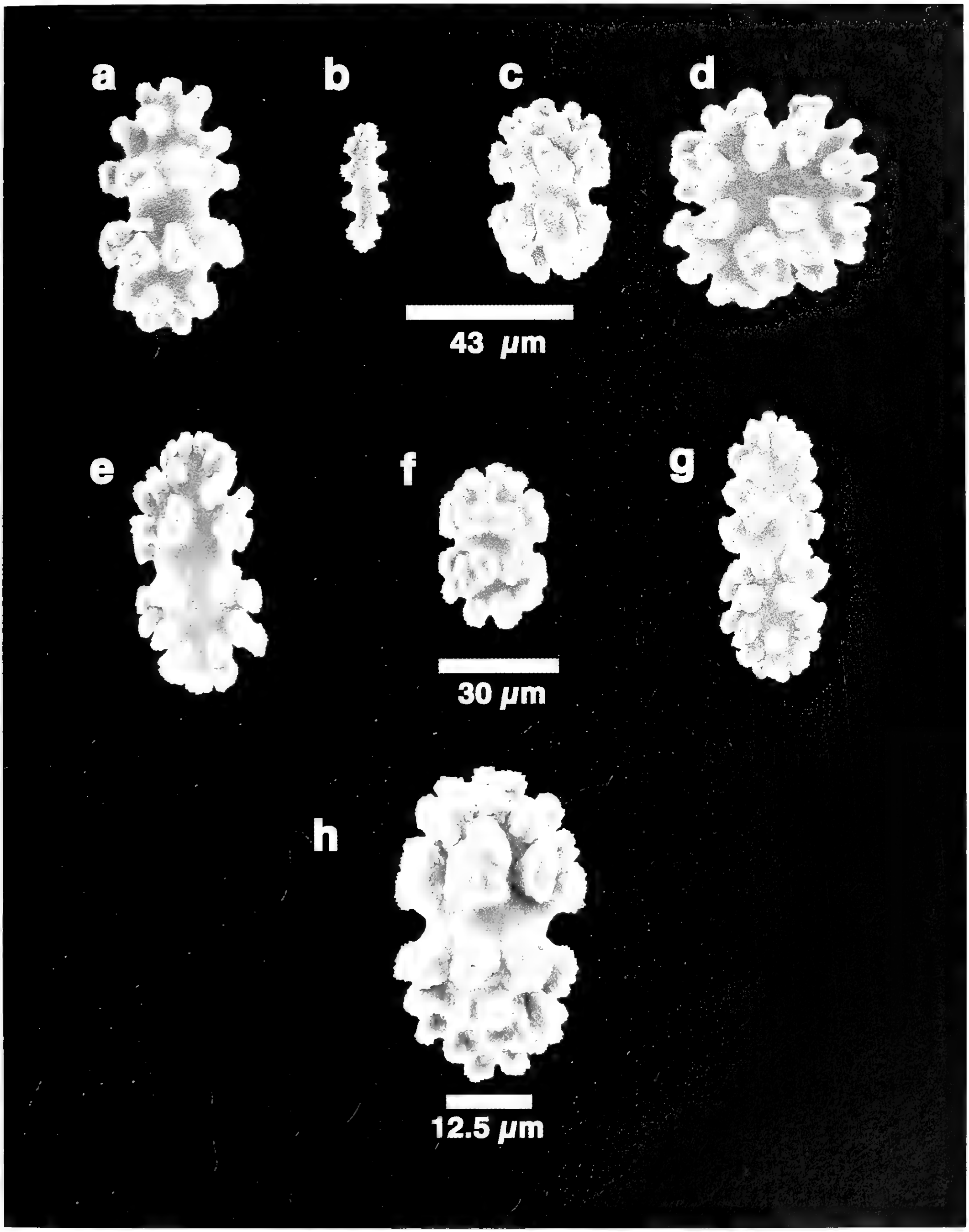

FIGURE 15. (a–h) SEM's of sclerites from coral sample CASIZ 105301, collected along with nudibranch CASIZ 105300.

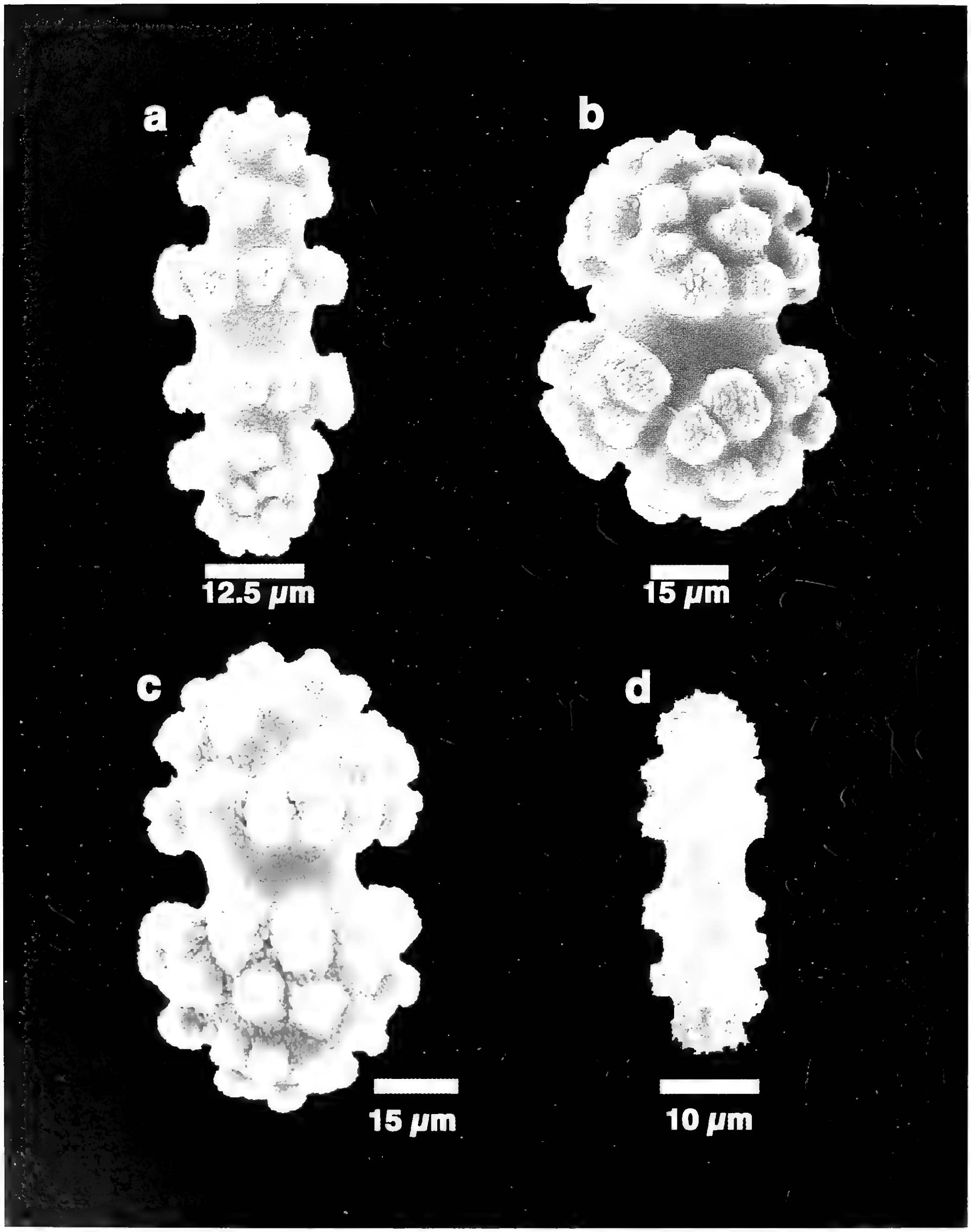

FIGURE 16. (a–d) SEM's of sclerites from stomach contents of CASIZ 115750.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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The Grenadier Genus *Mataeocephalus* Berg, 1898 (Teleostei, Gadiformes, Macrouridae), with Descriptions of Two New Species

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We recognize six species of *Mataeocephalus: M. acipenserinus, M. adustus, M. cristatus* n.sp., *M. tenuicauda, M. kotlyari* sp. nov., and *M. hyostomus*. The last species was formerly considered to belong to *Hyomacrurus*, a genus that was thought, based on its six branchiostegal rays, to be most closely related to *Coryphaenoides*, but differing in the advanced placement of the anus. We consider *Hyomacrurus* to be a synonym of *Mataeocephalus*, but retain it as a subgenus containing two species, *M. kotlyari* and *M. hyostomus*. *Mataeocephalus microstomus* Regan and *M. nigrescens* Smith and Radcliffe are relegated to the synonymy of *M. acipenserinus*. A revised diagnosis of *Mataeocephalus* is provided, and its status within the group of macrourids with seven branchiostegal rays is discussed.

From the mid-1960s through the 1980s research vessels of the former Soviet Union conducted extensive exploratory trawling cruises in the Atlantic, Indian and Pacific oceans. Many of the areas explored had previously been infrequently or never before sampled. The thalassobathyal fish fauna of oceanic elevations (e.g., sea mounts, guyots, ridges, plateaus, etc.) within the tropical and subtropical waters of the Indian Ocean and western Pacific is particularly rich in grenadiers of the families Bathygadidae and Macrouridae (Shcherbachev et al. 1979; Shcherbachev 1984, 1987). Our studies of these grenadiers have resulted in the description of numerous new species and new records for the area, as well as resolution of a number of difficult taxonomic problems (Sazonov and Shcherbachev 1982, 1985; Shcherbachev and Piotrevsky 1982; Merrett et al. 1983; Iwamoto and Sazonov 1988; Iwamoto and Shcherbachev 1991; Shcherbachev et al. 1986, 1992; Iwamoto and Sazonov 1994; Shcherbachev and Iwamoto 1995; Iwamoto and Williams 1999).

The genus *Mataeocephalus* was represented in several of these collections, certain members of which were from localities that have helped resolve some perplexing questions of identification. Included among these specimens was an undescribed species taken at widely separated localities in the western Pacific and Indian Ocean. No representative of subgenus *Hyomacrurus* was collected by Soviet vessels, but in 1995, the Taiwanese research vessel *Fishery Researcher I* made a series of trawl hauls off the east coast of southern Luzon, Philippines. One of those trawls in the Lagonoy

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[4] Deceased.

[5] Send reprint requests to Iwamoto.

Gulf near the type locality of *Macrourus hyostomus* Smith and Radcliffe, 1912 resulted in the collection of six specimens of that species, all in good condition. Those specimens allowed us to compare the species with one previously recorded as an undescribed species of *Mataeocephalus* (Iwamoto and Merrett 1997; Merrett and Iwamoto 2000; Iwamoto and Graham 2001) and collected by the French in the Loyalty Islands, Vanuatu, and the Chesterfield and Bellona Plateau, and by the Australians off the northwestern and southeastern corners of Australia. The two species are closely similar, but sufficient differences were found to justify designating the latter as a new species. A third species, *H. heyningeni* (Weber, 1913), had been assigned to the genus by Gilbert and Hubbs (1916:423) without their having examined specimens. Two of us (YIS, YNS) have examined the types and determined that they represent a species of *Coryphaenoides*.

The purpose of this paper is to record the new material of *Mataeocephalus*, redefine the diagnosis of the genus, describe two new species, and discuss the relationships of the two subgenera.

MATERIALS AND METHODS

This study was initiated by Sazonov, who with Shcherbachev, had examined a substantial number of specimens collected by vessels of the former Soviet Union. Those collections were augmented by types and other *Mataeocephalus* material Sazonov had examined in the USNM and CAS in 1993 during a visit to the U.S. Sazonov and Shcherbachev also examined material in the Zoological Museum of Copenhagen University in 1989 and the Zoological Museum of Hamburg University in 1995 and 2001. Sazonov had prepared a rough draft of a manuscript in which he had descriptions of four species (including the two new ones) of *Mataeocephalus*, a key to the species, and two large tables of measurements and counts. He sent this draft to Iwamoto for comment and additions. Partly on account of other commitments, but also because of some misgivings about Sazonov's treatment of certain species, Iwamoto declined to participate in the project, but encouraged Sazonov to publish his results with Shcherbachev. However, about that same time, Sazonov's research emphasis took a turn towards the alepocephaloids, especially those from Australia and New Caledonia. Consequently, nothing further was done on the *Mataeocephalus* manuscript. His sudden and most-unexpected death in March 2002 left the project hanging, and Shcherbachev took over the job of completing those papers that Sazonov had in the works. It was with Shcherbachev's encouragement that Iwamoto agreed to help complete the paper. The manuscript was completely reworked and a substantial amount of information was added, notably the introductory remarks, the remarks under the genus and subgenera, and the section on *Hyomacrurus,* including the description of *H. hyostomus*. Sazonov's descriptions of *M. cristatus and M. adustus* remain relatively intact, but all others were extensively modified.

Our study specimens are deposited in AMS, BMNH, CAS, CSIRO, MNHN, USNM, ZMB, ZMH, ZMMSU, and ZSI. Institutional abbreviations are taken from Leviton et al. (1988) and later amended in Leviton and Gibbs (1985). The reader is referred to Eschmeyer's (1998) *Catalog of Fishes* for detailed references and authorities to taxonomic names used. Methods for taking counts and making measurements follow procedures of Gilbert and Hubbs (1916) and slightly modified by Iwamoto (1970) and Iwamoto and Sazonov (1988).

DESCRIPTIONS

Genus *Mataeocephalus* Berg, 1898

Coelocephalus Gilbert and Cramer, 1897 (type species *Coelocephalus acipenserinus* Gilbert and Cramer 1897, by monotypy).

Mataeocephalus Berg, 1898 (replacement name for *Coelocephalus* Gilbert and Cramer, 1897, preoccupied by *Coelocephalus* Clark 1860, in Coleoptera).

Hyomacrurus Gilbert and Hubbs, 1920 (type species *Macrourus hyostomus* Smith and Radcliffe, 1912, by original designation)

DIAGNOSIS.— Branchiostegal rays 6 or 7; precaudal vertebrae 12–14; anal pterygiophores before first caudal vertebra 10–18. Retia and gas glands two, drumming muscles in males. Anus situated within a small to medium-sized periproct which is variously removed from anal fin origin. A rudimentary to small light organ usually developed before anus. Spinous second ray of first dorsal fin with rudimentary to well-developed serrations along leading edge; ray greatly elongated in some. Mouth small, length upper jaw usually about one-third length of head. Barbel short, thick at base, rapidly tapering to fine tip. Gill membranes broadly attached across isthmus, without broad free fold, greatly restricting opercular opening. Gill arches restricted at upper and lower ends by broad membrane folds connecting adjacent arches; first arch broadly connected laterally to gill cover by membrane or folds of skin, greatly restricting outermost gill slit. Outer series of rakers on first gill arch absent or few and rudimentary, consisting of one or more tiny spinules in each. Dentition in bands in both jaws; those in upper jaw in short, broad, truncated band in most species, in tapered band in others. Teeth in lower jaw in tapered band, short in some not reaching to end of rictus, longer in others reaching to end of rictus. Underside of head either covered with small scales or mostly naked. Tip of snout armed with a pair of stout conical tubercular scales covered with small, short spinules and joined mesially near their bases; leading edge of snout with characteristic series of (usually) seven stout spiny scales between scutes at terminal and lateral angle. Numerous conspicuous free neuromasts along leading edge of snout and on ventral surfaces. Behind leading edge of snout a deep scaleless groove connecting to a longitudinal groove running along each side of broad median ridge of scales. Suborbital ridge sharp and angular in cross section in most species, dividing head into dorsal and ventral parts; a broad shelf dorsally armed with coarsely spinulated scales above edge and separated from an upper smaller series of scales by a groove lined with a file of free neuromasts.

REMARKS.— The genus *Coelocephalus* was established by Gilbert and Cramer (1897) for their new Hawaiian species *C. acipenserinus.* Because the genus name had been previously used in Coleoptera, Berg (1898) provided the replacement name *Mataeocephalus.* The genus was based solely on its difference from *Caelorinchus* in having the second dorsal spine serrated, a point not lost by Gilbert and Cramer (1897:423), who stated that the character “is of doubtful value, especially in view of the rudimentary serrae present on the second dorsal spine of *Coelorhynchus gladius.*”

Despite this inauspicious beginning, the genus concept persisted, and in 1899, Garman described *Macrurus tenuicauda* from the Gulf of Panama and recognized the close similarity of his new species to *M. acipenserinus.* He made the interesting observation: ”branchiostegal rays commonly seven, frequently six; in each case there are seven either on one side or the other or on both sides” (Garman 1899:216). Regan (1908:221) described *Macrurus microstomus* from a single 18-cm specimen taken off Saya de Malha Bank in the western Indian Ocean. In his brief description, he gave six as the number of branchiostegal rays.

In 1912, Radcliffe described two other species (*M. adustus* and *M. nigrescens*) from the rich *Albatross* collection from the Philippines. He, too, saw similarities in the genus to *Caelorinchus*, especially in head shape, but he noted that "the spinous occipital ridges characteristic of the species of that genus are lacking," (Radcliffe 1912:125). He described two other characters of importance, "the spinigerous tubercle that is normally bifid" at the tip of the snout, and "the submarginal groove anterior to" the side of the snout. Radcliffe noted the presence of this latter character in *Macrourus hyostomus* and concluded, "the intergradations are such as to suggest the desirability of considering *Mataeocephalus* and *Coelorhynchus* as subgenera under *Macrourus" (loc. cit.).*

In their monumental work "The macrouroid fishes of the Philippine Islands and East Indies," Gilbert and Hubbs (1920:563) stated: "This genus [*Mataeocephalus*] is not intermediate between *Macrourus* and *Coelorhynchus* as Radcliffe has suggested. It is really related to *Lionurus* in a manner analagous [*sic.*] to that by which *Coelorhynchus* is related to *Coryphaenoides (Macrourus).* The similarity . .in snout. . .and infraorbital ridge, is due to convergence rather than to common origin." (It should be noted that their concept of *Lionurus* corresponds to certain genera currently accepted as members of the seven-branchiostegal-rayed group, including *Kumba, Kuronezumia, Lucigadus, Nezumia, Sphagemacrurus, Ventrifossa*, and a few others. Currently, *Lionurus* is recognized as a member of the six-branchiostegal-rayed group, and often treated as a subgenus of *Coryphaenoides*.)

More than half a century after Gilbert and Hubbs's (1920) revision, Marshall (1973) published his extensive work on the Macrouridae of the western North Atlantic. Marshall provided a key to all genera of grenadiers and a diagnosis of *Mataeocephalus* that included several new characters that he had discovered, among which were "no outer gill rakers on 1st arch, abdominal vertebrae 13–14,.swim bladder with 2 retia mirabilia," and "anus variable in position, either just before the origin of the anal fin or between the origins of the pelvic and anal fins" (*ibid,* p. 618). In his key and diagnosis, Marshall recorded the number of branchiostegal rays as seven, despite Garman (1899) and Regan's (1908) findings of variability in that count.

Iwamoto (1979:144–145) modified Marshall's diagnosis of the genus and placed emphasis on the broad naked area surrounding the anus and its location relative to the anal and pelvic fins, but recognized the variable nature of this character, especially as it concerned *M. adustus*, which he considered the most primitive member. He considered the genus to be closest to *Nezumia* Jordan, 1904, based on the presence of seven branchiostegal rays and the nature of the periproct region, among other characters.

The diagnosis we provide above is highly tentative and in need of more definitive characters, as most of those listed are plesiomorphic for the seven-branchiostegal-rayed macrourids or are found among a large number of species. The character differences between *Mataeocephalus* and *Hyomacrurus* are weak, with only the lanceolate scale spinules and invariable six branchiostegal rays in the latter seemingly of importance. Lanceolate scale spinules, however, are known in many grenadier genera, and the presence of six or seven branchiostegal rays in *M. tenuicauda* suggests that the character can be variable within a taxon. On this basis, we consider *Hyomacrurus* to be a synonym of *Mataeocephalus*, although warranting subgeneric standing. The entire classification of macrourids with seven branchiostegal rays must be considered uncertain, as no comprehensive phylogenetic analysis has been made of this large group. The genera are for the most part poorly defined, and it is our feeling that several, perhaps many, may prove to be paraphyletic or polyphyletic.

The following key and descriptions should allow the reader to identify with confidence adults of the *Mataeocephalus* species so far as we know them. Owing to the breadth of geographic coverage represented by our examined material, we feel it unlikely that additional species will be found except by division of currently accepted ones, in which case the widespread *M. acipenserinus* is a likely candidate (see below). The genus is confined to subtropical and tropical waters of the Indo-Pacific (Iwamoto 1979:144). It is the only grenadier genus with more than one species that is absent from the Atlantic.

Key to Species of *Mataeocephalus*

1a. Underside of snout fully or almost fully covered with scales. 2
1b. Underside of snout naked except for characteristic overlapping series along anterior leading edge. 4

2a. Branchiostegal rays 7; spinules on body scales slender, conical 3
2b. Branchiostegal rays 6; spinules on body scales narrowly lanceolate. (subgenus *Hyomacrurus*) 5

3a. Spinules on median row of body scales not enlarged; scales along narrowest part of suborbital shelf in 4–6 rows, those immediately below orbit small, not thickened; height 1D much greater than head length . . . . *Mataeocephalus* (*M.*) *adustus*
3b. Spinules on median row of body scales slightly enlarged, giving a faintly striated appearance to body surface; scales on suborbital shelf in 2 or 3 distinct rows, the lower row separated from those above by a line of sensory neuromasts, the lower row thickened, stoutly spinulated; height 1D less than 135% HL (usually 50–90%) . . *Mataeocephalus* (*M.*) *cristatus* n.sp.

4a. A dermal window of light organ extending anteriorly from periproct; 5.5–9.5 (usually 7–9) scale rows below origin of second dorsal fin . . . . *Mataeocephalus* (*M.*) *acipenserinus*
4b. No dermal window of light organ before periproct; 9–11 (rarely 8) scale rows below origin of second dorsal fin . . . . *Mataeocephalus* (*M.*) *tenuicauda*

5a. Pyloric caeca 16–19; scales below mid-base 1D 4.0–5.5, below 2D 4.5–5.5; V 7, rarely 6; height 1D 88–119% HL . . . . *M.* (*Hyomacrurus*) *kotlyari* n.sp.
5b. Pyloric caeca 8–13; scales below mid-base 1D 3.5–4.5, below 2D 5.0–7.5; V 7–8, rarely 9; height 1D 124–295% HL . . . . *M.* (*Hyomacrurus*) *hyostomus*

Subgenus *Mataeocephalus* Berg, 1897

Diagnosis. Branchiostegal rays 7, rarely 6. Body scales densely covered with slender, reclined, needleshaped spinules. Anus situated close before anal fin or far anterior, between anal and pelvic fins. Underside of head scaled or naked.

Mataeocephalus acipenserinus (Gilbert and Cramer, 1897)

Fig. 1; Table 1

Coelocephalus acipenserinus Gilbert and Cramer, 1897:422–423, pl. 42, fig. 1 (lectotype USNM 47721; Hawaiian Is.; 545–686 m).
Macrurus (*Coelorhynchus*) *acipenserinus*: Lloyd, 1909:159 (Bay of Bengal; 1134 m).
Macrurus macrolophus (*nec* Alcock): Brauer 1906:266 (Somalia; 628–1134 m).
Mataeocephalus acipenserinus: Berg, 1898: 41. Gilbert, 1905:676–677 (Hawaii; 406–911 m). Iwamoto, 1990: 246, fig. 555 (compiled). Sazonov and Iwamoto, 1992:70 (Sala-y-Gomez; 730–800 m). Iwamoto and Merrett, 1997:533–534, fig. 26 (Chesterfield and Bellona Plateau, Loyalty Islands, Wallis and Futuna Islands; 760–900 m). Iwamoto and Williams, 1999:188–189, fig. 38 (WA, Australia; 650–945 m). Merrett

and Iwamoto, 2000: 769 (Vanuatu, Wallis and Futuna Islands; 748–1220 m). Iwamoto and Graham, 2001: 484, fig. 98 (NSW, Australia; 823–933 m).

Macrourus microstomus Regan, 1908: 221, pl. 23, fig. 2 (Saya de Malha Bank; 549–914 m).

Mataeocephalus microstomus: Norman, 1939:52 (Zanzibar and Maldive areas; 640–797 m); Shcherbachev, 1987: 7 (listed; Saya de Malha and off Sumatra; 600–875 m).

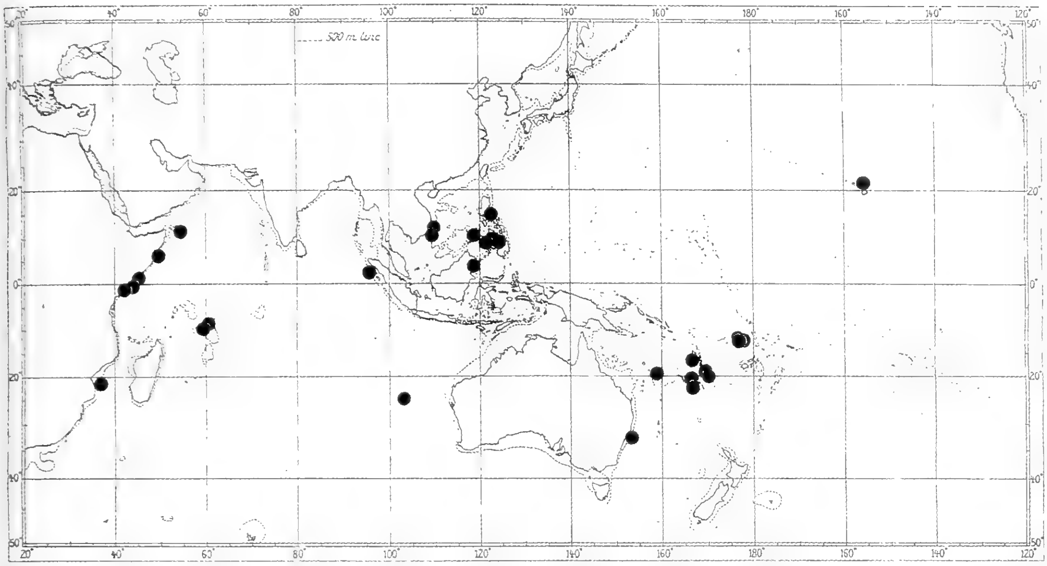
Mataeocephalus nigrescens Smith and Radcliffe in Radcliffe, 1912: 125, pl. 28, fig. 2 (holotype USNM 72492; Philippines; 1344 m). Gilbert and Hubbs, 1920: 563 (Philippines; listed). Iwamoto, 1990:245, fig. 553 (in key).

Diagnostic description.— Branchiostegal rays 7; V 7–8, P i17–i25; precaudal vertebrae 13–14 (n = 4); anal pterygiophores before first caudal vertebra 17–18 (n = 4). Snout length 34–43% of HL; orbit diameter 27–35%; interorbital width 18–24%; orbit to angle of preopercle 27–36%; upper jaw 19–28%. Teeth in lower jaw in short lunate patch. Underside of head anterior to lower jaw naked; scales on vertical portion of infraorbital shelf enlarged, scutelike, in two rows, those in lower series largest. Second ray of 1D with 4–11 sparsely set denticles and a filamentous tip, sometimes notably elongated. Body scales with reclined conical spinules in 5–12 parallel to slightly diverging rows; rarely, spinules in middle row slightly enlarged. Light organ variably developed, appearing as only a slightly thickened anterior portion of periproct to a subtriangular or pear-shaped anterior extension of periproct. Anus within periproct and removed from anal-fin origin, usually closer to anal fin than to insertion of pelvic fin.

Counts and measurements (see Table 1).

Distribution.— Widely distributed in tropical waters of the Indo-Pacific region (Fig. 1). In the Indian Ocean the species has been recorded from the Saya de Malha Bank (type locality of *M. microstomus*), off Zanzibar and the Maldives (Norman 1939), near the coast of Mozambique and Somalia, off Socotra, near Indostan, off Sumatra, and off Western Australia. In the Pacific Ocean it has been recorded from Hawaii (type locality of *M. acipenserinus*), Philippine seas (type locality of *M. nigrescens*), South China Sea, Tasman Sea off the southeastern coast of Australia, off New Caledonia, and the Sala y Gomez Ridge (Sazonov and Iwamoto 1992). Capture depths range from about 600 to 1300 m.

Remarks.— We have not examined the holotype of *M. microstomus*, which was inadequately described in the original description. We did, however, examine a good series of *Mataeocephalus* from Saya de Malha Bank on the Mascarene Plateau (Table 1), the type locality of the species, which support our synonymizing of the species with *M. acipenserinus.* Our comparison of the type specimens of *M. nigrescens* with specimens of *M. acipenserinus* from the Indian Ocean found them indistinguishable in almost all characters except for a slightly higher range of upper jaw lengths (ca. 22–28% HL compared with 19–24% in *acipenserinus*) and a relatively shorter anterior projection of the anterior dermal window of the light organ. Such differences hardly suffice to separate the two at the species level. Similarly, *M. acipenserinus* from the type locality (Hawaii) are essentially indistinct from those taken off the Sala-y-Gomez Ridge in the southeastern Pacific. Iwamoto (1990) used the distance orbit to angle of preopercle to distinguish *M. nigrescens* and *M. acipenserinus*, but from our data (see Table 1) this character shows such overlap as to be of no value. Other characters, including suborbital width, interdorsal space, and upper-jaw length, varied slightly from population to population, but in general, the differences were insufficient to recognize more than a single species. For example, the type specimens of *M. nigrescens* differ from the type specimens of *M. acipenserinus* in their shorter external projection of the light organ, fewer scales between the lateral line and middle of the first dorsal fin, and longer distance anus to anal-fin origin. However, fishes from the South China Sea and Indian Ocean are intermediate in those characters. The supposed difference between the two nominal species in number of



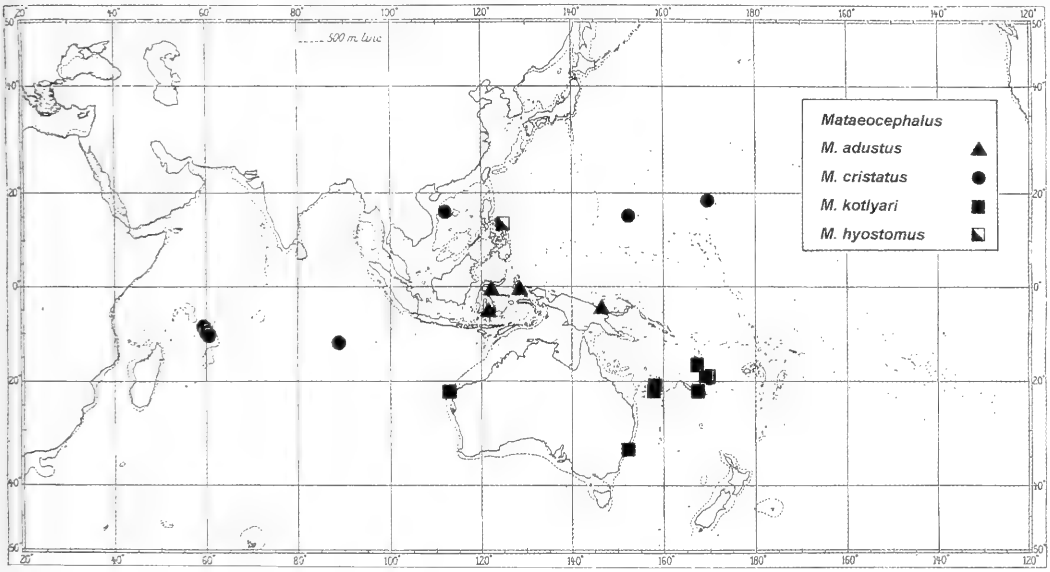


FIGURE 1 (above). Collection localities of *Mataeocephalus acipenserinus* in the Indo-West Pacific. Captures in the southeastern Pacific (Sala y Gomez Ridge) are not shown.

FIGURE 2 (below). Collection localities of *Mataocephalus adustus, M. cristatus, M.* (*Hyomacrurus*) *hyostomus* and *M.* (*Hyomacrurus*) *kotlyari* in the Indo-West Pacific.

spinule rows on body scales (5–6 in *M. acipenserinus*, 8–10 in *M. nigrescens*) is likely attributable to size, with smaller specimens having 5–9 rows and larger ones having 8–12. The extreme variability in the shape and length of the dermal window of the light organ also does not allow us to use this character for diagnostic purposes. The geographic variation in morphometric characters we have seen in this species resembles that recorded by Sazonov and Shcherbachev (1997) for *Sokodara misakia* and *S. johnboborum*, viz., fishes from the western Indian Ocean are closer to

TABLE 1. Counts and measurements of *Mataeocephalus acipenserinus* from different localities. Counts within parentheses are rare for specimens in each area. The western Indian Ocean specimens come from Socotra, Somalia, Mozambique & the Mascarene Plateau

Locality	*w. Indian Ocean*	*India*	*Sumatra*	*Western Australia*	*South China Sea*	*Philippines*	*e. Australia*	*Hawaii*	*Sala y Gomez*
No. of spec.	n=32	n=1	n=5	n=10	n=26	n=12	n=2	n=14	n=21
TL, mm	141+--254+	160+	211+--235+	145+--188+	151+--217+	139+--247+	246+--275+	92+--177+	118--250
HL, mm	27.7–64.2	34.7	45.6–59.5	36–46	31.5–48	35.3–55	51.2–53.5	25.3–51.5	26.5–54
	In percent of head length								
Snout len.	35–43	38	38–39	36–42	34–41	37–40	40–41	37–42	39–44
Orbit	27–34	27	29–32	28–33	28–35	29–33	29–29	27–34	29–34
Interorb.	17–21	20	19–22	21–23	18–23	19–24	22–24	20–24	20–23
Postorb.	28–34	32	31–33	28–32	30–33	31–36	32–33	30–33	26–33
Orb-preop	27–34	31	31–34	29–32	30–34	32–36	31–31	27–31	28–35
Suborb.	13–16	16	13–16	15–17	14–17	16–17	14–15	13–15	14–17
Up. jaw	19–24	31	19–24	20–24	22–25	22–28	21–23	21–24	20–28
Barbel	4—7	4	4–8	5–7	5–7	4—8	6–6	3–6	4–9
Anus-A.	4—13		11–18	8–14	11–25		11–15	5–13	6–12
Depth	47–68		54–61	50–58	49–59	55–65	57–63	49–61	47–60
1D. ht.	54—132*		79–92	51–62	57–59		59	59–63	50–63
P. len.	44–52		42–46	38–50	37–49	39–44	46	42–59	41–57
V. len.	39–57		42–54	44–58	36–56	38–49	48	42–51	45–70
1D.-2D.	27–41		31–49	20–36	27–41	30–39	29–34	17–33	14—32
	Counts								
1D.	II,8–10	II,10	II,8–9	II,8–9	II,7–10	II,8–10	II,9	II,8–10	II,8–10
P.	i,18–23	I,20	i,19–24	i,18–22	i,19–23	I,17–21	i,18–23	i,19–25	i,20–25
V.	(7)8	7	8	(7)8	(7)8	8	8	8	(7)8
GR-I(int.)	6–7	6	6	6–7	6–8	6–8	6–8	6–7	6–8
Scales 1D.	7–8(9)	7–8	6–7	7–8	6–7	(6)7–8	8–9	8–9	8–9
--mid-1D	5–6.5(7.5)		5–6.5	5–6	5–6.5	5–6.5	5.5–6.5	6–7.5	6–7.5
--2D.	(5.5)6.5–8		6.5–8.5	7–8.5	7.5–8	5.5–7.5	8–9	8–8.5	7–9
Pyl.caeca	10–19	10	13–17	14—16	13–15				14–15

those from the South China Sea than to fishes from the Sala-y-Gomez Ridge or Hawaiian Islands (the type locality).

For the reasons given above, we cannot support continued recognition of *M. nigrescens* and *M. microstomus* as species distinct from *M. acipenserinus.* Minor differences between populations of *M. acipenserinus* appear to exist, but our materials are insufficient to analyze intrapopulational relationships. We recognize *M. tenuicauda* as a separate species based on a number of differences from *M. acipenserinus.* It has a greatly reduced internal lens of the light organ, lacks an anterior projection of the periproct, has 8.5–11 scale rows between the lateral line and origin of the second dorsal fin, and attains a somewhat larger size than *M. acipenserinus* (to about 71 mm HL, vs. about 64 mm). The two species have 17–18 anal pterygiophores before first caudal vertebra, many more than the 9–11 of the other species.

Material examined.— Lectotype (here designated): USNM 47721 (39.6 mm HL, 134+ mm TL) and Paralectotypes USNM 47721 (3, 24–47.5 HL, 118+-161+ TL); Kaiwi Channel, 21°12′N, 157°38′30″W; 375 fm [686 m]; ALBATROSS sta. 3474.

Pacific Ocean. **Hawaiian Islands**: USNM 47728 (7, 25.3–47.5 HL, 92+-176+ TL); 21°08′N, 157°43′W; 642 m; ALBATROSS sta. 3475. CAS-SU 3142 (4, 44–51.5 HL, 161+-177+ TL); 21° 08'30"N, 157°49′W; 627 m; ALBATROSS sta. 3470. **Philippines**: USNM 72942 (holotype of *M. nigrescens*, 51 HL, 247+ TL); 9°12′45″N, 125°20′E; 735 fm [1344 m]; ALBATROSS sta. 5492. USNM 149306 (paratypes of *M. nigrescens*, 44 HL, 203+ TL); 9°37′05"N, 121°12′37″E; 340 fm [622 m]; ALBATROSS sta. 5424. USNM 149307 (paratypes of *M. nigrescens*, 41.5 HL, 182+ TL); 9°37′45″N, 121°11′E; 495 fm [905 m]; ALBATROSS sta. 5425. USNM 149309 (4 paratypes of *M. nigrescens*, 43–55 HL, 162+-225+ TL); 9°38′30″N, 121°11′E; 508 fm [929 m]; ALBATROSS sta. 5423. USNM 149310 (paratype of *M. nigrescens*, 49.2 HL, 239+ TL); 8°34′48″N, 124°01′E; 700 fm [1280 m]; ALBATROSS sta. 5515. USNM 149311 (2 paratypes of *M. nigrescens*, 40–41.8 HL, 150+-154+ TL); 4°06′50″N, 118°47′20″E; 347 fm [635 m]; ALBATROSS sta. 5586. USNM 149312 (paratype of *M. nigrescens*, 35.3 HL, 139+ TL); 10°57′45″N, 118°38′15″E; 375 fm [686 m]; ALBATROSS sta. 5348. USNM 149313 (2 of 3 paratypes of *M. nigrescens*, 47–52.8 HL, 178+-215+ TL); 13°21′00″N, 122°18′45″E; 530 fm [969 m]; ALBATROSS sta. 5219. **Sala-y-Gomez Ridge**: see Sazonov and Iwamoto (1992: 71) for list of specimens. **South China Sea**: ZMMSU P-19496 (5, 36–48 HL, 160+-217+ TL); 11°33.2′N, 109°48.2′E; 900–1300 m; ODISSEY tr. 50. ZMMSU P-19497 (18, 31.5–47 HL, 151+-209+ TL); 10°10′N, 110°02′E; 680–750 m; ODISSEY tr. 52. ZMMSU P-19498 (3, 42–46 HL, 175+-188+ TL); 10°40.8′N, 110°03′E; 760–800 m; ODISSEY tr. 57. **Australia off New South Wales**: AMS I.29742-002 (51.2 HL, 275 TL); 32°09′S, 153°09′E; 1079–1143 m; KAPALA sta. K89-17-07. AMS I.29753–009 (4, 37.4–51.0 HL, 170+-215+ TL); 31°53′S, 153°16′E; 878–933 m; KAPALA sta. K89-17-06. AMS I.30304-007 (1 spec.); 32°12′S, 153°06′E; 823–860 m; KAPALA sta. K89–17–09. **Southwestern Pacific off New Caledonia and vicinity:** see specimen list in Iwamoto and Merrett (1997:533) and Merrett and Iwamoto (2000: 769)

Indian Ocean. **Bay of Bengal**: ZSI 1097/1 (34.7 HL, ca. 160+ TL); INVESTIGATOR sta. 321. **Maldives**. BMNH 1939.5-24-723-724 (2, 48.4–53.2 HL, 159+-232+ TL); 797 m; DISCOVERY sta. 143. Socotra. ZMMSU P-19499 (58.3 HL, 254+ TL); 12°20'N, 53°03.7′ E; 1000–1120 m; VITYAZ-II cr. 17, sta. 2565; 28 Oct. 1988. **Somalia**: ZMB 12999 (57.7 HL, 240+ TL); 1°49'N, 45°29.5′E; 1134 m; VALDIVIA sta. 256. ZMB 22342, 22343 (2, 59.5, 49.7 HL, 234–211 TL); 1°40.6′S, 41°47.1′E; 693 m; VALDIVIA sta. 251. ZMB 17643 (64.2 HL, 254+ TL); 0°24.3′S, 42°49.4′E; 1019 m; VALDIVIA sta. 252. ZMB 24128 (43.5 HL, 179 TL); VALDIVIA sta. unknown, Somalia region. ZMB 22587 (35.8 HL, 191 TL); 6°24.1′N, 49°31.6′E; 628 m; VALDIVIA sta. 265. **Mozambique**: ZMMSU P-19517 (3, 46.0–49.5 HL, 170+- 253 TL); 20°58.5′S, 35°56.2′E; 950–900 m; VITYAZ-II cr. 17, sta. 2621; 20 Nov. 1988. **Mascarene Ridge**: ZMMSU P-19492 (5, 30.5– 45.0 HL, 133+-202+ TL); 8°39′S, 59°45′E; 820–790 m; FIOLENT cr. 9, tr. 54; 3 Sep. 1977. ZMMSU P-19494 (5, 35.5–45.5 HL, 147+-179+ TL); 9°32.7'S, 60.02′E; 800 m; FIOLENT cr. 9, tr. 156. ZMMSU P-19518 (6) and CAS 82135 (2, 27.7–51.0 HL, 141–231 TL); 9°34′S, 59°55′E; 830–430 m; VITYAZ II cr. 17, sta. 2816; 9 Jan. 1989. ZMMSU P-19519 (53.3 HL, 247 TL); 8°32′S, 59°40′E; 960–1300 m; VITYAZ-II cr. 17, sta. 2820; 10 Jan. 1989. **Mentavay Ridge off Sumatra**: ZMMSU P-19495 (5, 45.6–59.5 HL, 211+-235 TL); 3°46′N, 95°00′E; 800–850 m;

PROF. MESIATZEV cr. 7, tr. 7; 28 Feb. 1979. **West Australia off Carnarvon**: ZMMSU P-15356 (10, 36–46 HL, 145+-188+ TL); 23°57.9′S, 112°14.2′E; 834–831 m; VITYAZ sta. 4564; 1 Dec. 1959. ZMMSU P-15356 (10, 36–46 HL, 145+-188+ TL); 23°57.9’S, 112°14.2′E; 834–831 m; VITYAZ sta. 4564.

Mataeocephalus adustus Smith and Radcliffe, 1912

Figs. 2; Table 2

Mataeocephalus adustus Smith and Radcliffe in Radcliffe, 1912:126–127, pl. 28, fig. 3 (holotype USNM 72943; off Celebes, 1472 m). Merrett and Iwamoto, 2000:769–771, fig. 26 (Vanuatu, 1058–1191 m).

Diagnostic description.— Branchiostegal rays 7; V 7; P i15-i17; precaudal vertebrae 13 (n = 3); anal pterygiophores before first caudal vertebra 9 (n = 3). Snout relatively short, 34–37% HL (one juvenile with 41%), 1.2–1.5 times longer than orbit; orbit diameter 24–28% HL, 1.1–1.3 times longer than interorbital width; orbit to angle of preopercle 38–41% HL; interspace between dorsal fins usually more than 34% HL (10% HL in one juvenile). Jaw teeth in tapered bands, those on premaxillary extending to rear of rictus. Underside of head entirely scaled; suborbital scales small, not modified into enlarged, spiny scutes, those on upper half in four to six rows. Second ray of first dorsal fin with few or no denticles, tip filamentous, often notably elongated. Body scales with reclined conical spinules in 12–18 parallel rows, none enlarged. Dermal window of light organ absent; periproct relatively small. Anus variable in position, about midway between anal and pelvic fins in small juveniles, closer to anal fin origin in adults.

Counts and measurements.— (See Table 2.)

Distribution.— Philippines, n. of New Guinea, Vanuatu (Fig. 2). Depth range 919–1472 m.

Remarks.— *Mataeocephalus adustus* appears in some ways to be the most generalized member of the genus, and its placement here is debatable and tentative. Several characters of the species differ to various degrees from those of other members of the genus, including: (1) relatively high non-depressed snout and deep head; (2) fine spinulation on, and the non-thickened nature of, scales along the leading edge of the snout; (3) long tapered band of premaxillary teeth spanning most of rictus; (4) relatively large mouth that is not markedly U-shaped; (5) small periproct and poorly developed light organ; (6) posterior position of the anus, close before or slightly removed from the anal fin; (7) greatly reduced serrations on spinous dorsal ray; and (8) only nine anal pterygiophores anterior to the first caudal vertebra. This last count is the lowest we have found among representatives of the genus. All of these differences, however, are relative and do not represent a sharp, clearly defined divergence. Other characters of the species support unification as they appear to represent synapomorphies of the genus. They include (1) distinctive, bifid, terminal snout scute composed of two, relatively slender, forwardly pointed, cone-shaped halves joined along the basal midline; (2) deep, scaleless, crescentic grooves behind the dorsal leading edge of the snout on each side, each connected to a deep longitudinal groove running between the median nasal crest and the lateral nasal ridges; (3) either no gill rakers on the lateral side of the first gill arch or few extremely small and rudimentary rakers. This last character is shared with *Caelorinchus* and *Macrourus,* both of which have characteristically six branchiostegal rays.

Material examined.— Holotype: USNM 72943 (47.5 mm HL, 225+ mm TL); Indonesia, Gulf of Boni, Celebes; 3°42′S, 120°45′50″E; 805 fm [1472 m]; ALBATROSS sta. 5654; 18 Dec. 1909. Paratypes: **Indonesia**: USNM 149273 (2, 25.5–48 HL, 112+-197 TL); south of Patiente Strait; 00°56′30″S, 128°05′00″E; 569 fm [1041 m]; ALBATROSS sta. 530; 2 Dec. 1909. USNM 149247 (26 HL, 151 TL); Gulf of Tomini, Celebes; 00°21′33″N, 121°04′01″E; 747 fm [1366 m];

TABLE 2. Counts and measurements of *Mataeocephalus adustus* from different localities.

	Indonesia			*off Papua New Guinea*			*off Vanuatu*		
Cat. No.	USNM 149274	USNM 72943*	USNM 149273	ZMMSU P-15355			MNHN 1995-846	MNHN 1995-978	MNHN 1995-978
TL, mm	151+	225+	197+	94+	269+	286+	307+	146+	183+
HL, mm	40	47.5	48	24.9	71.5	75	61.8	31.2	43
	In percent of head length								
Snout len.	35	35	34	41	37	35	37	38	39
Preoral		30	28		30	30	30	33	35
Orbit	29	27	26	28	25	24	23	25	24
Interorb.	23	23	24	23	23	22	22	22	20
Postorb.	40	40	39	37	39	41	41	40	40
Orb-preop	41	41	39	38	40	40	40	39	38
Suborb.		15	14		16	14	16	15	15
Up. jaw	26	24	28	27	28	29	27	25	24
Barbel	10	4	10	9	8	6	5	8	7
Depth	54	64	63	54	67	70	63	61	63
1D. ht.		112					157		
P. len.	51	47					52	51	
V. len.	51	30					53	46	
1D.-2D.	55	44	43	10	57	48	43	29	33
	Counts								
1D.	II,10	II,9	II,7	II,10	II,7	II,8	II,9	II,8	II,9
P.	i,17	i,15	I,16	i,16–17	I,16	I,16–17	I,19	I,18–17	I,17
V.	7	7	7	7	7	7	7	7	7
GR-I(int.)	8	8	8	7	8	8	7	9	9
Scales 1D.		6	7		6	7	7		4
--mid-1D		4.5	4.5		4.5	4.5	5		
--2D.			5.5		7	6	6.5	6	
Pyl.caeca			15			16		18	

* Holotype

ALBATROSS sta. 5605; 16 Nov. 1909. OTHER MATERIAL. **Papua New Guinea**: ZMMSU P-15355 (3, 24.9–75 HL, 94+-286+ TL); 5°22′S, 146°14′E; 1380–1400 m; DMITRY MENDELEYEV cr. 18, sta. 1542; 14 Feb. 1977. **Vanuatu**: MNHN 1995-846 (61.8 HL, 307+ TL); 15°53.81′S, 167°30.42′E; 1100–1191 m; MUSORSTOM 8, sta. CP 1076; 4 Oct. 1994. MNHN 1995-854 (43 HL, 183+ TL); 18°03.70′S, 168°54.40′E; 1058–1086 m; MUSORSTOM 8, sta. CP 1037; 29 Sep. 1994. MNHN 1995-978 (31 HL, 146+ TL); 18°53.29′S, 169°52.65′E; 919–1000 m; MUSORSTOM 8, sta. CP 1008; 25 Sep. 1994.

Mataeocephalus cristatus Sazonov, Shcherbachev and Iwamoto, sp. nov.

Figs. 2–4; Table 3

Diagnostic description.— Branchiostegal rays 7; V 7; P i17-i21, usually i18 or more; precaudal vertebrae 12 (n=2); anal pterygiophores before first caudal vertebra 11 (n=2). Snout length 35–41% of HL, 1.4–2.0 times longer than orbit; orbit diameter 21–25% HL, about equal to (0.8–1.1 times) interorbital width; orbit to angle of preopercle 33–38% HL; interspace between dorsal fins usually less than 30% HL. Head shallow, usually wider than deep, dorsal surface of snout slightly convex, its dorsal profile straight or slightly concave, top of head at mid-orbit flat or slightly concave. Snout (Fig. 4) depressed and narrowly pointed in lateral view; broadly triangular in dorsal view; tipped with two stout spiny conical scutes pointed forward and joined mesially at base. Leading edges of snout covered with small, non-imbricate scales, each covered with short, conical spinules, the scales broadly overlapping dorsal and ventral surfaces and interspersed with short, thick sensory papillae. Above and behind leading edge of snout a deep groove. Naked membrane of nasal fossa restricted by surrounding scaled ridges. Mouth small, U-shaped and inferior; a small short barbel below tip of lower jaw. Oral valves covered with thick short papillae. Jaw teeth in short, broad, non-tapered bands, the upper tooth bands each somewhat truncated posteriorly, the two halves of lower jaw forming a broad crescent; none of teeth enlarged. Underside of head usually entirely scaled, although some specimens with median swath on underside of snout naked; upper (shelf) portion of suborbital with two rows of somewhat enlarged, coarsely modified scales in narrowest portion; a line of free neuromasts between each row. Gill membranes broadly united across isthmus restricting opening of operculum; no free posterior fold. Gill arches restricted by membranes across upper and lower arms; outer gill slit narrow; outer rakers on first arch absent. Spinous second ray of first dorsal fin with weak serrations on leading edge. Body scales with needle-like spinules in 12–18 parallel rows, the middle row enlarged in most scales, forming parallel striations on the body surfaces. Dermal window of light organ absent; periproct relatively small. Anus removed from anal fin in juveniles and adults, situated about midway between origin of anal fin and base of pelvic fin. Pyloric caeca finger-like, simple, with no branching above base.

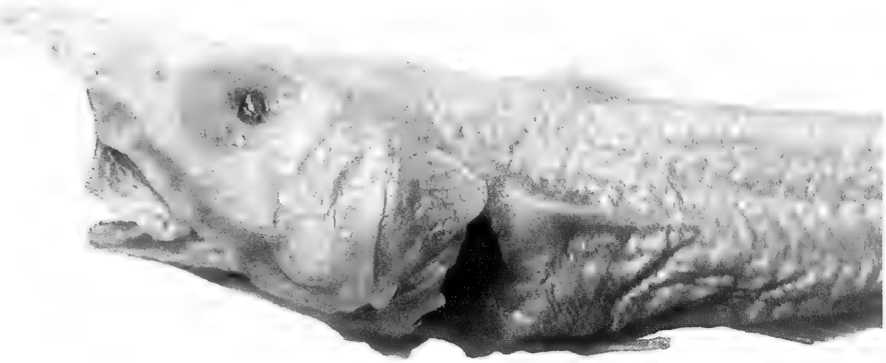
Counts and measurements (see Table 3).

Distribution.— Indian Ocean (Saya de Malha Bank, Mascarene Ridge, Markus-Necker Ridge, Ninety East Ridge), and western Pacific Ocean (South China Sea) (Fig 2). Depth range 1000–1720 m.

Etymology.— From the Latin *crista*, a crest, in reference to the slightly enlarged middle row of spinules on most body scales.

Remarks.— The count of 12 precaudal vertebrae in this species contrasts with the 13–14 found in other *Mataeocephalus*. We examined 21 specimens of *M. cristatus,* 15 of which came from the Mascarene Plateau in the western Indian Ocean. Three specimens were represented from the Ninety-East Ridge in the eastern Indian Ocean, one was from the South China Sea, and two were from the Markus-Necker Ridge in the western Pacific. Inadequate representation from the last three areas prevented us from estimating populational differences, although based on Table 1, one might suspect that fishes from the Markus-Necker Ridge had the shortest snout, those from the Ninety East Ridge had the smallest orbit, and all specimens from eastern localities had the widest interorbital and longest upper jaw.

Type Specimens.— Holotype: ZMMSU P-15345 (48.0 mm HL, 215 mm TL); Ninety East Ridge, 11°31′S, 88°55′E; 1600–1700 m; PROF. MESIATZEV cr. 7, tr. 5; 18 May 1979. Paratypes: **Indian Ocean**: **Ninety East Ridge**: ZMMSU P-15346 (33 HL, 152 TL); same data as for holotype. ZMMSU P-15347 (57.5 HL, 271 TL); 11°45′S, 88°47′E; 1600 m; FIOLENT cr. 9, tr. 24; 14 June



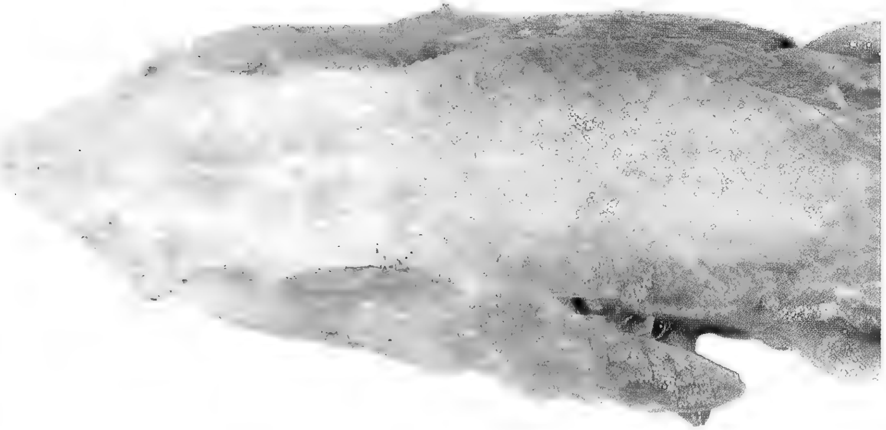


FIGURE 3 (above). Lateral view of paratype of *Mataeocephalus cristatus* (CAS 82136, 51.6 mm HL) from the Mascarene Ridge in 1300-1240 m.

FIGURE 4 (below). Dorsal view of head of paratype of *Mataeocephalus cristatus* (CAS 82136).

1977. **Saya de Malha Bank**: ZMMSU P-15350 (52.0 HL, 255 TL); 1280 m; CHATYR-DAG cr. 4, tr. 16; 28 Aug. 1974. **Mascarene Ridge**: ZMMSU P-15351 (44.0 HL, 152+ TL); 8°26′S, 59°29′E; 1300–1260 m; FIOLENT cr. 9, tr. 52; 2 Sep. 1977. ZMMSU P-15352 (5: 42–55 HL, 200–267 TL) and CAS 82136 (2: 51.6–53.0 HL, 212+-230+ TL); 8°57'S, 59°19′E; 1300–1240 m; FIOLENT cr. 9, trawl 53; 2 Sep. 1977. ZMMSU P-15353 (52.5 HL, 241 TL); 8°08'S, 59°37.6′E; 1247–1269 m; ZVEZDA KRYMA cr. 6, tr. 210; 9 Nov. 1976. ZMMSU P-19490 (53.5 HL, 230 TL); 9°38′S, 60°56′E; 1700–1650 m; VITYAZ-II cr. 17, sta. 2814; 9 Jan 1989. ZMMSU P-19491 (3: 54.0–58.0 HL, 267–271 TL); 9°40′S, 60°31′E; 1520–1720 m; VITYAZ-II, cr. 17, sta. 2815; 9 Jan. 1989. **Pacific Ocean**: **South China Sea**: CAS 38331 (44.7 HL, 217 TL); off Vietnam, Paracel Is., 15°38′N, 111°54′E; 1234–1264 m; STRANGER sta. NAGA60-67; 29 Feb. 1960. **Markus-Necker Ridge**: ZMMSU P-15354 (52.0 HL, 249 TL); 19°08′N, 171°09′E; 1000–1250 m; MYS UNONY tr. 62; 24 Aug. 1979. ZMMSU P-19489 (53.0 HL, 245+ TL); 15°42′N, 152°05′E, 1355–1381 m; CHRONOMETER tr. 59.

Mataeocephalus tenuicauda (Garman, 1899)

Fig. 5

Macrurus tenuicauda Garman, 1899:216–217, pl. 49, fig. 1 (Gulf of Panama, 838 m; Albatross sta. 3384).
Mataeocephalus tenuicauda: Gilbert and Hubbs, 1916:146 (list). Iwamoto, 1979:145–147, figs. 8, 9a (Panama, Ecuador, Galapagos; 700–1159 m); 1990:247, fig. 557 (compiled).

Diagnostic description.— Branchiostegal rays 6–7, usually 7; V 8–9; P i21-i25; precaudal vertebrae 13–14 (n=2); anal pterygiophores before first caudal vertebra 17–18 (n=2). Snout length 36–42% of HL; orbit diameter 26–30%; interorbital width 19–22%; orbit to angle of preopercle 28–33%; upper jaw 19–28%. Head shallow, about as wide as deep, dorsal surface of snout gently convex, essentially flat or slightly convex over orbits. Snout depressed and narrowly pointed in lateral view, broadly triangular in dorsal view, tipped with two spiny conical scutes pointing forward and adjoined at base. Leading edge of snout covered with coarse, tubercular, nonimbricate scales, with short, thick, sensory papillae filling interspaces between these scales. Above and behind scaled leading edge of snout, a deep groove followed by a broad naked area with a slender mesial arm extending posteriorly alongside median nasal ridge. Underside of head entirely naked except for small patch of scales on ventral surface of preopercle and a narrowly overlapping series of scales along leading edge of snout. Nasal fossa broadly naked. Suborbital shelf with two rows of coarsely modified scales; a line of free neuromasts separating each row. Mouth small, U-shaped, and inferior; a small short barbel below tip of lower jaw. Gill membranes broadly united across isthmus restricting opening of operculum; no free posterior fold. Gill arches restricted by membranes across upper and lower arms; outer gill slit narrow; outer rakers on first arch absent or reduced to three or four small plates. Jaw teeth in short, broad, cardiform bands, the upper tooth bands each truncated posteriorly, the two halves of the lower jaw forming a broad crescent. None of teeth enlarged. Spinous second ray of first dorsal fin with strong but widely spaced serrations along leading edge. Body scales with slender needle-like spinules in sharp ridgelike rows; in juveniles (CAS 86531) spinule rows parallel, giving striated appearance to body surfaces. Pyloric caeca short, thick, simple, with no branching, 16–21 total. Periproct relatively large; dermal window of light organ absent; anus situated within middle third of distance between origin of anal fin and base of pelvic fin. Two juveniles collected by the deep-submersible vehicle *Johnson Sea-Link* off the Galapagos had a polka-dotted color pattern (Fig. 5), much as has been recorded in *Malacocephalus* and *Mesobius.*

Distribution.— Confined to tropical waters of the eastern Pacific, from Panama south to Ecuador and west to the Galapagos. Depth range about 700–1159 m.

Remarks.— *Mataeocephalus tenuicauda* closely resembles *M. acipenserinus* but can be distinguished by features provided in the key to species. See also the discussion in the description of

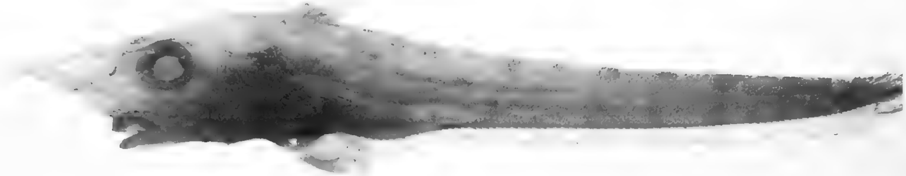


Figure 5. Juvenile of *Mataeocephalus tenuicauda* (CAS 86531, 25.4 mm HL) collected off James Bay, Isla San Salvador, Galapagos, in 3000 ft [914 m] by the JOHNSON SEALINK deep-submersible vehicle.

M. acipenserinus. *M. cristatus* is also very similar to *M. tenuicauda*, but that species has scales on the underside of the snout and most scales dorsally on the trunk and anteriorly on the tail have the median spinule row slightly enlarged.

Material examined.— See Iwamoto (1979) for list of material examined of this species, to which add: CAS 86531 (2, 25.4–26.5 mm HL, 153–155 mm TL); Galapagos, Isla San Salvador, James Bay; 3000 ft [914 m]; collectors J.E. McCosker et al., *Johnson Sealink* sta. JSL 3977; 26 Nov. 1995. CAS-SU 57034 (61 HL, 290 TL); "Pacific. Deep-sea. Arcturus" [no other locality; mislabeled as from Chesapeake Bay].

Subgenus *Hyomacrurus* Gilbert and Hubbs, 1920

Diagnosis.— Branchiostegal rays 6; precaudal vertebrae 13–14; anal pterygiophores before first caudal vertebra 10–11. Anus remote from anal fin, usually within middle third of distance from insertion of pelvic fins to origin of anal fin. Body scales densely covered with lanceolate spinules. Underside of head almost entirely covered with scales.

Remarks.— In their 1920 revision of the macrouroid fishes, Gilbert and Hubbs (1920:423) commented on the remarkable nature of the fish they called *Coryphaenoides hyostomus* in its having six branchiostegal rays and an anus that was remote from the origin of the anal fin. All other species they included in *Coryphaenoides* had the anus immediately before the anal fin. Based on the anterior position of the anus, they erected the subgenus *Hyomacrurus*. *Macrurus heyningeni* Weber, 1913, from the Timor Sea, was described as having this same unique combination, and although Gilbert and Hubbs did not assign that species to *Hyomacrurus*, their implications were clear, and Marshall (1973:564) apparently agreed when he considered that species as a member of *Hyomacrurus*. (Two of the current authors (YIS,YNS), however, examined the holotype of *M. heyningeni* in April 1985 and determined that it belongs in the genus *Coryphaenoides*.) Marshall's concept of *Hyomacrurus* followed that of Gilbert and Hubbs in that he considered the genus "...most closely related to *Coryphaenoides* but differs in the position of the anus... and number of retia mirabilia in the swim bladder (2 *cf.* 4)." These two characters, however, are shared by members of the tribe Malacocephalini (*Malacocephalus, Ventrifossa, Nezumia, Lucigadus*) and most other macrourid genera with seven branchiostegal rays. We suspect that those authors were overly swayed by the branchiostegal ray count in allocating the species to the *Coryphaenoides*-related lineage.

The close relationship of *Mataeocephalus* and *Hyomacrurus* was suggested by Radcliffe (1912) when he described *M. nigrescens* and *M. adustus*. He noted two characters of importance, "the spinigerous tubercle that is normally bifid" at the tip of the snout, and "the submarginal groove anterior to" the side of the snout, and the presence of the latter in *Macrourus hyostomus*. These characters, however, are also developed to various degrees in many species of the related genera *Nezumia* and *Sphagemacrurus*, rendering them unusable as synapomorphies.

The presence or absence of a luminescent organ appears to vary within the genus, with species such as *M. acipenserinus* having a relatively large organ intruding into the abdominal wall anterior to the anus, with a well-developed external dermal window extending as a shallow fossa from the naked anal surround (the periproct). In other species the dermal window is lacking, and the luminescent organ is of moderate size (*M. tenuicauda, M. cristatus, M. hyostomus, M. kotlyari*) to almost indiscernible (e.g., *M. adustus*).

The branchiostegal ray count has been accorded considerable value in defining the genera and higher- category taxa within the grenadiers. *Coryphaenoides* and *Hyomacrurus* are characterized as having six branchiostegal rays as opposed to seven in *Mataeocephalus*. Bearing this in mind, it is important to recall Garman's (1899:216) remark in his description of *Macrurus tenuicauda*: "Branchiostegal rays commonly seven, frequently six; in each case there are seven either on one side or the other or on both sides." We are uncertain as to how many specimens formed the basis of Garman's observation, but the MCZ lot (cat. no. 28555) containing the type specimens currently includes only three specimens. We have not had the opportunity of checking this character in all specimens of *Mataeocephalus* used in our previous studies, as they are now scattered to all corners of the earth. However, one specimen of *M. tenuicauda* (CAS-SU 57034) not previously recorded by us had six branchiostegal rays on each side. Should the branchiostegal ray count prove to be as variable as Garman's and our limited data suggest, its value as a phylogenetic character is seriously compromised for this group. It is for this reason that we treat *Hyomacrurus* as a subgenus within *Mataeocephalus,* and the only characters that appear to separate the two are the somewhat lanceolate scale spinules and the presumably invariable six branchiostegal rays in the former.

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

Fig. 2, 6; Table 3

Macrourus hyostomus Smith and Radcliffe, in Radcliffe, 1912:121–122, pl. 27, fig. 1 (type locality: se. Luzon, Philippines, 1024 m; also Sibuku Bay, Borneo, 750 m, and Buton Strait, Celebes, 1022 m).
Coryphaenoides (*Hyomacrurus*) *hyostomus*: Gilbert and Hubbs, 1920:422–424 (descr. compiled).
Coryphaenoides hyostomus: Gilbert and Hubbs, 1916:144 (listed). Weber and de Beaufort, 1929:33–34 (descr. compiled).
Hyomacrurus hyostomus: Marshall 1973:564 (listed).

Diagnostic description.— V 7–8, rarely 9; P i16-i20; pyloric caeca 8–13. (Most of the features described for *M. kotlyari* apply to this species and are generally not repeated here.) Head about as broad as high at level of posterior orbital margin; snout rather broad, moderately pointed and protruding more than half orbit diameter beyond mouth. Jaws extend posteriorly to below posterior one-third to one-quarter of orbit. Lips thick, papillaceous. Barbel short, rapidly tapered to filamentous tip. Terminal scute of snout small, bifid. Underside of snout and head scaled. Body scales densely covered with long, slender, somewhat flattened (lanceolate, with concave anterior surface), recurved, greatly reclined spinules arranged in somewhat convergent or divergent rows. Anus about

Figure 6. *Mataeocephalus* (*Hyomacrurus*) *hyostomus* (CAS 212549, 64 mm HL) taken from the type locality, Lagonoy Gulf, Luzon, Philippines, in 1037-1100 m.

TABLE 3. Counts and measurements of *Mataeocephalus cristatus* from different localities.

Locality	*South China Sea*	*Markus-Necker Ridge*		*Ninety East Ridge*			*Mascarene Plateau*
Cat. No.	CAS 38331	P-15344	P-19489	P-15316	P-15345	P-15347	(see text)
No. of spec.	n=1	n=1	n=1	n=1	n=1	n=1	n=26
TL, mm	214+	249+	243+	152+	215+	271+	152+–271+
HL, mm	44	52	58	33	48	57.5	42–58
	In percent of head length						
Snout len.	38	36	35	39	37	39	38–41
Preoral	31	33	30		35	33	30–40
Orbit	23	23	25	21	23	21	22–25
Interorb.	25	28	25	28	26	25	22–26
Postorb.	35						35–38
Orb-preop	35	35	36	38	37	38	33–38
Suborb.	12	15	13	15	13	11	12–16
Up. jaw	25	25	25	27	26	25	20–26
Barbel	10	8		6		5	7–10
Depth	55	63	67	56	58	63	54–62
1D. ht.	71	60	64	62	64		63–84
P. len.	47	51			48	44	38–50
V. len.	44	55	45	42	47	49	32–58
1D.-2D.	13	17	16	27	29	28	11–34
	Counts						
1D.	II,9	II,9	II,10	II,8	II,9	II,7	II,8–10
P.	i,18	I,20–21	i,19–20	i19	i18–17		i17–22
V.	7	7	7	7	7	7	7–8
GR-I(int.)	8	8	8	6	7	7	6–8
Scales 1D.	5	6	6		6	6	5–7
--mid-1D	4	3.5	5		4	4	4–5
--2D.	6	5	7		7	7	5–7
Pyl.caeca						16	10–14

midway between insertion of pelvic fin and origin of anal fin. Spinous second ray of first dorsal fin very long, 1.5 to more than twice length of head, with a few weak denticulations confined to basal portion. Teeth in both jaws in broad bands; dentary band tapered and ending at angle of mouth; premaxillary band falls slightly to well short of end of rictus and truncated or broadly rounded, outer premaxillary teeth not much larger than those more inward. Pyloric caeca count in four specimens 8, 11, 13, 13.

Overall color medium to light brownish, abdomen darker, somewhat purplish, with margin of scale pockets almost black; operculum dark, overlain with silvery. Underside of head and snout generally lighter brown. Branchiostegal membrane black except along isthmus. Thin black eye ring, usually incomplete along ventral orbital margin. Upper jaw to end of rictus very dark, abruptly changing to pale posteriorly; lower lips faintly pigmented. Gums pale, mouth cavity dark gray but paler around mouth opening. Gill cavity dark. First dorsal fin black; pelvic and pectoral fins blackish; anal fin dusky.

Other counts and measurements.— 1D II,8–9; GR-I (inner) 5–8, GR-II (outer/inner) 5–7/6–9; scales below 1D 5–6 (one spec. with 8), below mid 1D 3.5–4.5, below 2D 5–7.5. Total length 185–383+ mm; head length 40.6–65.5 mm. The following in percent of head length: snout length 30–36; ventral length of snout 22–30; internasal width 23–26; interorbital width 22–26; orbit diameter 22–25; suborbital width 14–15; postorbital length 46–50; distance orbit to angle of preopercle 40–44; length upper jaw 28–31; length barbel 7–10; length outer gill slit 9–10; preanal length 152–171; body depth 57–68; interspace between first and second dorsal fins 17–27; height 1D 145–295; length P 31–52; length V 41–61.

Distribution.— Known only from off Luzon, Philippines, Borneo, and Celebes (Fig. 2). Depth range 760–1100 m.

Material examined.— USNM 72938 (holotype: 58.8 mm Hl, 280 mm TL); Lagonoy Gulf, Luzon, Philippines; 13°37′30″N, 123°41′09″E; ALBATROSS sta. 5470; 1024 m. CAS 212549 (3 spec., 40.6–65.5 HL, 202–283 TL); Lagonoy Gulf, Luzon, Philippines: 13°21′19″N, 124°12′16″E; 1037–1100 m; FISHERY RESEARCHER I sta. TERI-Phi-5-95; 24 Sep. 1995. CAS 214046 (3 spec., 36.5–46.0 HL, 160+-205+ TL); Camarines Sur, Luzon, Philippines; 14°50′28″N, 123°17′18″E; 760–770 m; FISHERY RESEARCHER I sta. TERI-Phi-12-95; 27 Sep. 1995.

Mataeocephalus kotlyari Sazonov, Shcherbachev and Iwamoto, sp. nov.

Figs. 2, 7

Hyomacrurus sp. A: Williams et al., 1996:149 (listed; Western Australia, 685 m).

Mataeocephalus sp.: Iwamoto and Merrett, 1997:62–63, fig. 7 (Loyalty Is., Chesterfield and Bellona Plateau, Wallis and Futuna Islands; 412–970 m). Iwamoto and Williams, 1999: 189, fig. 39 (1 spec., NW Cape, Western Australia; 650–685 m). Merrett and Iwamoto, 2000: 771 (20 spec., Vanuatu; 690–1000 m). Iwamoto and Graham, 2001:484–485, fig. 99 (1 spec., New South Wales, Australia; 896–960 m).

Diagnostic description.— V 7 (one specimen with 6 on right fin, 7 on left fin); P i17-i20; pyloric caeca 15–19. Snout sharply pointed in lateral view, broadly triangular in dorsal view; leading edges rounded and fleshy but fully covered with small, tightly adherent modified scales. Tip of snout armed with a pair of small, stoutly spined, somewhat cone-shaped scutes. A deep crease dorsally behind leading snout margins, each connected to a shallow longitudinal trough medial to each supranarial ridge. Interorbital broad, flat, about equal to orbit diameter. An angular ridge from tip of snout to anterior end of preopercle dividing dorsal and ventral head surfaces, with a row of small, slightly modified scales below orbit along dorsal edge of ridge and separated by a narrow gap from a second and third row of similar scales. Free neuromasts of sensory lateralis system scattered over head surfaces, but concentrated on snout; sensory pores small and poorly developed. Scales of body densely covered with relatively narrow to broadly lanceolate spinules (much as in *Nezumia aequalis*). No reticulate pattern on the anterior, unexposed field. Scales almost completely cover entire head; naked only along margin of jaws, anteriorly on lower jaws, medially on underside of snout, and over gill membranes. Premaxillary teeth in short broad band, extending less than half length of entire premaxillary and occupying somewhat more than half length of rictus; outer series scarcely larger than other teeth in jaw. Mandibular teeth in narrow band, about three teeth

FIGURE 7. Paratype of *Mataeocephalus* (*Hyomacrurus*) *kotlyari* (CAS 86481, 48.1 mm HL) collected off the Chesterfield and Bellona Plateau, 412-430 m.

wide near symphysis, tapering to one or two laterally, ending just short of end of rictus. Dorsal fin high, second spinous ray somewhat longer than head length in some individuals, succeeding rays shorter, tapering rapidly; leading edge of spinous ray with a few rudimentary denticulations proximally (difficult to detect) in some, with as many as 14 serrae in others. Pectoral fin relatively broad and short, its distal tip falling at or short of anal fin origin. First dorsal and pelvic fin origins about on same vertical, that of pectoral slightly in advance. Pelvic fins small, most rays falling well short of anal fin origin; outer ray produced into slender filament extending to near fourth anal ray. Periproct region moderate in size, almost equal in diameter to that of pupil, far removed from anal fin and closer to pelvic fin insertions. Light organ scarcely discernible from exterior, but present in body wall as a small pocket with large lens-like structure immediately anterior to anus. Pyloric caeca long, slender, 15–19 total in eight specimens.

Color of first dorsal fin entirely black in some specimens, but in others black distally, pale along base; pectoral and pelvic fins also black, but free distal end of outer pelvic ray completely pale; base and lowermost portion of pectoral usually paler; anal fin with anterior four rays black or blackish, following rays with dusky distal margin, darker near end of tail. Body overall brownish to swarthy, much darker over abdomen, underside of head including barbel rather pale or dirty whitish; branchiostegal membrane blackish with purplish tinge, but mostly pale ventrally towards base of rays.

OTHER COUNTS AND MEASUREMENTS.— 1D II,8–9; total GR-I (outer/inner) 0–3/7–8, GR-II (outer/inner) 6–7/6–7; scales below 1D 4.5–7.0, below mid 1D 4.0–6.0, below 2D 4.5–6.5. Total length 120+-232 mm; head length 30–55 mm. The following in percent of head length: snout length 31–36; ventral length of snout 24–30; internasal width 22–25; interorbital width 20–25; orbit diameter 18–26; suborbital width 12–15; postorbital length 41–46; distance orbit to angle of preopercle 36–42; length upper jaw 26–31; length barbel 5–10; preanal length 155–167; body depth 59–74; interspace between first and second dorsal fins 13–24; height 1D 88–119; length P 42–50; length V 41–56.

DISTRIBUTION.— Known from northwestern and southeastern Australia, New Caledonia, Vanuatu (Fig. 2). Depth range 412–1000 m, most frequently captured between 700 and 900 m.

ETYMOLOGY.— Named after our colleague, Alexander Kotlyar, of the P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, for his contributions to the study of deep-sea fishes and for his untiring efforts in collecting fishes, including some of the specimens used in this study.

Remarks.— This species was the source of much confusion for us. We initially recognized its similarity in several fundamental features to species of *Mataeocephalus* but were impressed by how different it was compared to others of that genus, especially in its relatively deep head, short snout, poorly developed light organ, lanceolate scale spinules, and six branchiostegal rays. A subsequent search of the literature and examination of specimens led us to conclude that it was most closely related to *Hyomacrurus hyostomus*. We were fortunate to acquire a series of specimens of that species from near the type locality during a cruise of the Taiwanese vessel FISHERY RESEARCHER I in 1995. Our conclusions were immediate on comparison of the two taxa–they were very similar but distinct, and they represented a clade distinct from other *Mataeocephalus.*

Type specimens [note: complete collection data for these specimens are available in Iwamoto and Merrett (1997), Iwamoto and Williams (1999), Merrett and Iwamoto (2000) and Iwamoto and Graham (2001)].— Holotype: MNHN 1994–960 (55 HL, 225+ TL); Chesterfield and Bellona Plateau; 21°15.01′S, 157°51.33′E; 970 m. Paratypes: **Australia**: AMS I.29804-002 (1 spec.), Newcastle, NSW; 896–960 m. CSIRO H22549-13 (1 spec.) NW Cape, WA; 650–685 m. **Chesterfield and Bellona Plateau**: CAS 86481 (2, 39.2–48.1 HL, 180+-214+ TL); 412–430 m. **Loyalty Islands**: MNHN 1994-961 (40.5 HL), BMNH 1996.7.19:27 (51.5 HL); 760–790 m. **Vanuatu**: MNHN 1997-679 (33–44 HL, 160-192+ TL); 775–748 m. MNHN 1995-969 (33 HL, 148+ TL); 780–783 m. MNHN 1997-678 (12, 30–46 HL, 120+-221+ TL); 764–786 m. MNHN 1995-874 (41 HL); 690–750 m. MNHN 1995-856 (51 HL); 775–798 m. MNHN 1997-677 (39 HL); 764–786 m.

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IN MEMORIAM

Yuri Shcherbachev and Tomio Iwamoto dedicate this paper to the memory of the first author, Yuri Igorevich Sazonov, who passed away at the age of 51 years on 21 March 2002. He was struck down with a severe cold during a very chilly January and February, when his laboratory in the Zoological Museum of Moscow State University dropped to very low temperatures because of ongoing repairs to the roof of the building. Despite the extremely cold conditions in the unheated room, he continued his work unstinted. That behavior was typical of Yuri, who was always a strong, robust man inured to normal hardships and completely dedicated to his ichthyological studies. It was not until his condition deteriorated dangerously that he allowed himself to be taken to the hospital. He was there for less than a week before he succumbed.

Yuri was born on 14 Oct. 1950 in the city of Gorodok in Belorussia. He graduated from Moscow State University in 1972, after which he worked under Nikolai V. Parin in the Oceanic Ichthyofauna Laboratory of the Institute of Oceanology, Academy of Sciences of the SSSR (now Russian Academy of Sciences). Between 1974 and 1987 he participated in four expeditions to the Indian and Pacific oceans. In 1989 he defended his Ph.D. thesis "Morphology and classification of the fishes of the family Platytroctidae (Salmoniformes, Alepocephaloidei)." From 1990 until his death, Yuri was curator of the marine fish collection of the Zoological Museum of Moscow State University. He published extensively (more than 70 papers) and was known worldwide as an expert on the alepocephaloids, macrouroids, and morids, groups in which he described more than 60 new taxa. His expertise garnered him numerous invitations to visit museums in Europe, the United States, Australia, and India. Yuri was reaching the apex of his professional career and was widely recognized as one of the premier systematic ichthyologists in Russia. The ichthyological community has lost a productive, dedicated scientist with a keen eye and insightful mind, and his friends and colleagues around the world bemoan the loss. [Parts of this were extracted from a manuscript prepared by Nik Parin and Sergei Evseenko for publication in *Voprosy Ikhtiologii*, for which we thank the authors.]

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Systematic Review and Phylogenetic Analysis of the Nudibranch Genus *Melibe* (Opisthobranchia: Dendronotacea) with Descriptions of Three New Species

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Three new species of the genus *Melibe* are described: *Melibe digitata* sp. nov. and *M. tuberculata* sp. nov. are recorded from the Philippines. Specimens of *M. minuta* sp. nov. have been found only from Okinawa, Japan. Specimens of *Melibe engeli* Risbec, 1937 are recorded and described from the Hawaiian Islands and the Philippines and an additional photo is noted from southern Japan. These represent the first published records of this species since its original description. The anatomy of an additional nine species of *Melibe* is re-examined. These include: *M. australis* (Angas, 1864), *M. bucephala* Bergh, 1902, *M. leonina* (Gould, 1852), *M. liltvedi* Gosliner, 1987, *M. megaceras* Gosliner, 1987, *M. papillosa* (de Filippi, 1867), *M. pilosa* Pease, 1860, *M. rosea* Rang, 1829 and *M. viridis* (Kelaart, 1858). Consistent anatomical differences suggest that *M. pilosa* and *M. papillosa* represent distinct species. This review of the morphological variability within the genus provides the basis for a phylogenetic analysis of the group. *Melibe* is shown to represent a monophyletic clade. Members of the genus *Tethys* represent the sister group of *Melibe*.

The dendronotacean genus *Melibe* Rang, 1829 is one of two genera comprising the family Tethydidae. Several of these species are known only from their original descriptions, and most species have been only superficially described with an emphasis on external anatomy. Gosliner (1987) reviewed aspects of the systematics and anatomy of *Melibe* and described two new species. He considered the genus as containing 15 valid species from throughout the world. Collections of three apparently undescribed species from the Philippines and Okinawa have prompted a review of the genus to provide data for adequate morphological comparison as well as evidence for constructing a phylogenetic hypothesis of relationships within the family and genus. Specimens of nine additional species were examined to amplify previous descriptions and examine characters for phylogenetic analysis. In cases where portions of the anatomy have been described elsewhere, only new information or data that do not agree with previous descriptions are included here.

Species Descriptions

Family Tethydidae Rafinesque, 1815

Genus *Melibe* Rang, 1829

Type species: *Melibe rosea* Rang, 1829, by monotypy.

Synonyms.— *Chiroraera* Gould, 1852 (type species: *C. leonina* Gould, 1852). *Jacunia*

Filippi, 1867 (type species: *J. papillosa* Filippi, 1867). *Melibaea* Angas, 1864 (type species: *M. australis* Angas, 1864). *Meliboea* Kelaart, 1858 (type species: *M. viridis* Kelaart, 1858). *Propomelibe* Allan, 1932 (type species: *P. mirifica mirifica* Allan, 1932).

Melibe australis (Angas, 1864)

Melibaea australis Angas, 1864:62, pl. 6., fig. 2.
Melibe australis (Angas, 1864) Burn, 1957. Wells and Bryce, 1993:174, fig. 225. Debelius, 1996:228, middle fig.

Material examined.— Natural History Museum, London, BMNH 1965400, 8 specimens, Torkay and Point Londsdale, Victoria, Australia, 1 January, 1965, R. Burn.

Distribution.— Known from New South Wales, Victoria, Tasmania and Western Australia, Australia (Angas 1864; Burn 1957; Wells and Bryce 1993; Debelius 1996).

External morphology.— The preserved specimens examined here are small, up to 7 mm in length. The body surface is covered with low tubercles. The oral hood is relatively small and smooth with only a single row of tentacles along the margin. Papillae are absent from the outer surface of the hood, but are present on the inner surface around the mouth. The rhinophores are well separated and lack papillae or posterior ornamentation on the rhinophore sheath. The foot is narrow and linear without papillae on the anterior margin. The cerata are globular with irregular low tubercles. The genital opening lacks papillae around the aperture.

Digestive System.— The buccal mass is wide, but is devoid of jaws or salivary glands. The esophagus is short and widens into the stomach, which lacks any chitinous plates. The anterior digestive gland is a compact mass that surrounds the stomach, but none of its ducts enter the cerata. The posterior gland is also compact and none of its ducts enter the cerata.

Central nervous system.— The ganglia are all smooth and rounded, devoid of tubercles. The cerebral and pleural ganglia are fused. The pedal commissure is elongate. The buccal ganglia are well separated.

Reproductive system.— The reproductive system was not well preserved and probably was not fully mature in the small animals examined here. The compound ovotestis follicles form a solid mass.

Discussion.— From the subsequent phylogenetic analysis, it appears that *Melibe australis* is the sister species to all of the Indo-Pacific species. *Melibe australis*, like other members of the larger clade to which it belongs, has a small oral hood that has been secondarily enlarged in some members of the clade, a papillate mouth surface and a relatively narrow foot, that has been secondarily widened in some members of the clade. *Melibe australis* has two autapomorphic features: loss of stomach plates and salivary glands.

Melibe bucephala Bergh, 1902

(Fig. 2a–d)

Melibe bucephala Bergh, 1902:205, pl. 3, figs. 6–10. O'Donoghue, 1929:803, fig.220. Debelius, 1996:286, bottom fig., 287.

Material examined.— Natural History Museum, London, BMNH 1933.6.30.35, 1 specimen, Suez Canal, H. M. Fox. This is the same specimen described by O'Donoghue (1929).

Distribution.— Known from Thailand (Gulf of Siam) (Bergh 1902) and the Red Sea (O'Donoghue 1929; Debelius 1996).

External morphology.— Living animals may reach 100 mm (Debelius 1996). The preserved specimen examined is large, 40 mm in length. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a slightly elevated dorsal hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Rounded to slightly conical papillae are present on the notum and cerata. The papillae on the body are smaller than those on the cerata. The wide, linear foot has a rounded, entire, anterior margin, which becomes somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The oral hood is large with anteriorly and posteriorly incised margins. The margin of the hood has three to five rows of cylindrical papillae, which taper to conical points, with the innermost row the longest. There are scattered papillae on the surface of the oral hood. The well-separated perfoliate rhinophores have 6 to 7 lamellae and arise from the surface of the oral hood within cylindrical sheaths. Extending from the posterior portion of the sheath is a laterally compressed, posteriorly directed sail, which bears low tubercles and terminates in an apical papilla. There are six cerata per side of the body. They are somewhat flattened, saccate, oval to triangular with a papillate surface. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is dorsal and slightly posterior to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras. A circle of 14 small, conical papillae surrounds the gonopore.

Digestive System.— (Figs. 2b,d) The coarsely papillate interior of the oral hood connects with the elevated, papillate mouth. The buccal mass had previously been removed, but was recorded by O'Donghue (1929) as being devoid of a radula, but containing a pair of chitinous jaws with an undulate border. The surface of the remains of the buccal mass is papillate. A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior portion of the stomach contained 24 triangular, chitinous plates, with thin, eccentric apices arranged in an alternating manner. The plates also alternate between large and small in size. The intestine leaves the posterodorsal portion of the stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the basal portion of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral portion of the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately after its emergence from the stomach, this branch ramifies into more than half of the length of the anteriormost ceras on the left. The anterior portions of the digestive gland also ramify around the stomach. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into most of the length of the next two pairs of posterior cerata. Posteriorly from this point the branch continues to ramify posteriorly, but does not enter into any of the remaining cerata.

Central nervous system.— The ganglia are not entirely intact, but it is evident that the cerebral, pleural and pedal ganglia are almost entirely separate but are situated in close proximity to each other. All of these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells (Fig. 2c). An elongate commisure joins the pedal ganglia. The paired buccal ganglia lie adjacent to each other on the ventral surface of the esophagus, and are connected to the pedal ganglia by paired nerves. Each buccal ganglion is smooth.

Reproductive system.— The dissected specimen has more than 20 compound, spherical, congested ovotestis bodies (Fig. 2d). The narrow preampullary duct widens and enters the s-shaped ampulla posteriorly (Fig. 2a). The ampulla constricts slightly before forming the distal portion, which branches into the oviduct and vas deferens. The slender vas deferens enters almost immediately into the spherical prostate before exiting, enlarging, and making a bend before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate, probably serving as a serial receptaculum seminis, based on its position and thicken muscularized structure. The oviduct bifurcates, one branch expanding into a pyriform bursa copulatrix, the other leading to the vagina. A distinct banded vaginal gland is present internally around the vagina (Fig. 2a).

Discussion.— *Melibe bucephala* appears to be the sister species of *M. viridis*. These species share two synapomorphies. Both have a coarsely papillate inner surface of the oral hood and a wide foot. *Melibe bucephala* has two autapomoprhies: an absence of ceratal papillae and a papillate buccal mass

Melibe digitata Gosliner and Smith, sp. nov.

(Figs. 1a, 3–5)

Type material.— Holotype: CASIZ 106449, one specimen, collected at 10 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April, 1996, T.M. Gosliner. Paratypes: CASIZ 103754, six specimens, with egg mass, collected at 10 m depth, Pinnacle Rock, Hamilo Bay, Batangas Province, Luzon Island, Philippines, 4 March 1995, T.M. Gosliner. CASIZ 096242, two specimens, with egg mass, collected at 12 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon Island, Philippines, 14 March 1994, T.M. Gosliner. CASIZ 103756, twelve specimens, with egg mass, collected at 1 meter depth, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 27 February, 1995, T.M. Gosliner. CASIZ 110380, two specimens, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 19 April, 1997, T.M. Gosliner. CASIZ 110425, four specimens collected at 12 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 20 February, 1997, T.M. Gosliner.

Distribution.— Thus far, specimens of *Melibe digitata* have been found on several occasions in the Batangas Province of the Philippines in the vicinity of Maricaban Island and Hamilo Bay. This species has not been found from other localities.

Etymology.— The name *digitata* refers to the highly digitate branching of the cerata.

External Morphology.— The color of the living animals is creamy white to greenish brown, with darker green coloration towards the distal ends of the cerata. The animal is translucent or semi-transparent and the viscera are readily visible through the surface of the living and preserved animals (Fig. 1a). The preserved specimens reach a maximum length of 25 mm. The body is limaciform, somewhat compressed anterolaterally, and is elevated dorsally in a hump at the midbody region. Posterior to the hump, the body tapers abruptly into a narrow posterior portion of the foot (Fig. 3a). The notum is smooth, with a scattering of very fine white glandular dots or tubercles. The foot is more opaque, narrow and linear with the anterior margin rounded and entire. The remainder of the margin is somewhat undulate. There are one to five small conical papillae on or immediately proximal to each side of the anterior foot margin. The oral hood is small relative to the body, (6 mm in diameter for the largest specimen) and is produced from a distinctly narrowed base. The hood is semi-transparent, and has many very fine whitish glandular dots or tubercles over its surface. The partially opaque hood margin has an inner and outer row of narrowly tapering tentacular papillae with acute or acuminate apices. The tips of the inner row tend to be curled, and the two rows are of equal length. The dorsal hood surface has from 10–20 larger and less acutely tapering papillae that are denser near the margin. In many of the specimens one or two of these papillae were bifid or trifid. The perfoliate rhinophores (Fig. 3b) have 5–7 lamellae and are born within long cylindrical sheaths arising close together from the narrow portion of the body posterior to the hood. The length of the sheaths is nearly equal to the hood diameter. The distal margin of the sheath thickens and expands to produce a coronate row of 5 to 11 short papillae on the anterior margin, and a single fingerlike papilla on the posterior margin, which may exceed the length of the exposed rhinophore. The arborescent, inflated cerata arise from cylindrical bases, and reach aproximately 2/3rds of the body length (Fig. 3c). The basal 2/3rds of the cerata are unbranched or have few simple branches. The distal portions are highly ramified and terminate in multifid acutely tapering apices. The basal portions are semi-transparent and colored like the notum, but the ramified portions are more opaque, and in the living animal (Fig. 1a) exhibit a pronounced greenish-brown coloration probably denoting the presence of zooxanthellae. There are 4–7 cerata per side arranged close to the midline of the dorsum. The anteriormost cerata are opposite, with the remainder alternating. The posteriormost few cerata are smaller with less developed branching. The anus is located just anterior to the second right ceras. The nephroproct is just dorsal to the anus. The gonopore is well ventral to the most anterior right ceras, near the lateral midline of the body. Many of the observed specimens have one or two conical papillae ventral to the anteriormost right ceras, proximal to the gonopore.

DIGESTIVE SYSTEM.— The finely papillate inner surface of the oral hood connects to the raised, papillate mouth, which opens into a muscular buccal mass (Fig, 4b). The buccal mass is of intermediate width compared with the other new species described. The mass is devoid of a radula, but a pair of chitinous jaws with a smooth masticatory margin is present (Fig. 5a). A pair of elongate salivary glands is present near the middle of either side of the buccal mass. An elongate esophagus emerges from the posterior end of the buccal mass and expands into the muscular saccate stomach. In one dissected specimen, the posterior portion of the stomach contained 17 thin triangular plates of subequal size with their eccentric apices arranged in an alternating fashion (Figs. 5b, c). The intestine is produced from and is contiguous with the posterodorsal portion of the stomach, curving posteriorly before recurving slightly to the anal opening. The diffuse digestive gland originates from the lateral portion of the stomach, is relatively compact and undeveloped posteriorly, and covers the surface of the ovotestis in an undulating fashion. A separate branch comes from the right side of the stomach and ramifies into the anteriormost right ceras. A branch on the left side of the stomach ramifies into the remaining cerata.

CENTRAL NERVOUS SYSTEM.— The smoothly textured cerebral and pleural ganglia are fused, and are connected by a short commissure to the smaller pedal ganglia (Fig. 4b). The eyes are situated at the end of short nerves that join them to the dorsal surface of the cerebral ganglia. The small, spherical buccal ganglia are situated on the ventral surface of the buccal mass in such a way that they touch each other, and are joined to the cerebral ganglia by thin, short nerves.

REPRODUCTIVE SYSTEM.— The arrangement of the reproductive system is triaulic (Fig. 4a). Seven compactly congested ovotestis follicles were found in one specimen dissected, and were held together by the digestive gland branches on the surface of each. The narrow preampullary duct enters the dorsal portion of the proximal lobe of the relatively large, bilobed, saccate, inflated ampulla. The ampulla narrows briefly before expanding to form the second lobe that narrows distally, bifurcating into the oviduct and the vas deferens. The oviduct widens into a serial, fan-shaped receptaculum seminis, narrows again forming two convolutions and widens slightly before entering the pyriform bursa copulatrix. Proximal to its exit is a duct that joins the vagina at the proximal end, where a compact mass of nodular globules forms a distinct vaginal gland. The female gland mass is composed of a large, smooth mucous gland, and the smaller membrane and albumen glands. After exiting the ampulla, the narrow vas deferens enters almost immediately into the relatively large, spherical prostate, which is composed of many small globose bodies. Exiting the prostate, the vas deferens makes several bends before entering the base of the relatively short, conical penis. The penis is within the penial sac, which then joins with the vagina at the genital opening.

Development.— A flatly coiled whitish egg ribbon arranged as a three-tiered spiral whorl was also found. It contained numerous clear gelatinous capsules approximately 0.12 mm in diameter, each with a single opaque white egg.

Natural history.— The species has been found in 1–12 meters of water. Specimens are generally found on or under the surface of rounded basaltic stones, and have been found on two occasions with specimens of *Melibe tuberculata.*

Discussion.— *Melibe digitata* can readily be distinguished from other members of the genus by its highly ramified cerata. Its golden greenish to brownish body color makes individuals of this species highly cryptic in its natural environment, and probably denotes the presence of zooxanthellae. *Melibe digitata* appears to be the sister species of *M. tuberculata* according to the subsequent phylogenetic analysis. The two species share numerous apomorphies. In both species the rhinophores are inserted close to each other basally and the serial receptaculum seminis is expanded. Both species have a secondarily smooth body and smooth jaws. In both taxa, the rhinophoral sail and ceratal tubercles appear to have been secondarily lost and the number of stomach plates is less than 20. Both species have a poorly developed posterior digestive gland.

Melibe digitata differs from *M. tuberculata* in several significant regards. The most obvious difference between the two is the presence of acutely pointed papillae in *M. digitata* versus rounded papillae in *M. tuberculata*. The bursa copulatrix of *M. digitata* is pyriform whereas in *M. tuberculata* it is more spherical. The ovotestis follicles of *M. digitata* are close to each other whereas in *M. tuberculata* they are well separated. In *M. digitata* the digestive gland enters more than half of the ceratal length, whereas in *M. tuberculata* the gland is only found in the basal half. In *M. digitata* the buccal mass is moderately narrow, while in *M. tuberculata* it is much wider. The salivary glands are elongate in *M. digitata* and much shorter in *M. tuberculata*. The pleural ganglia of *M. digitata* are largely fused while in *M. tuberculata* they are well separated.

Melibe engeli Risbec, 1937

(Figs. 1d, 6–9)

Melibe engeli Risbec, 1937:160. Risbec, 1953:114, fig. 68 a–g. Catala, 1986:83, fig. 30.

Material examined.— CASIZ 105680, one specimen, collected at 12 m depth, The Head, Hamilo Bay, Batangas Province, Luzon Island, Philippines, 4 March, 1995, M. Miller. CASIZ 085887, one specimen, collected at 23 m depth, Layaglayag Point, N.W. side of Maricaban Island, Batangas Province, Luzon, Philippines, 22 March 1993, T.M. Gosliner. CASIZ 096241, one specimen, collected at 4 m depth, Seafari Beach, Anilao, Batangas Province, Luzon Island, Philippines, 17 March 1994, T.M. Gosliner. CASIZ 106396, one specimen, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April 1996, T.M. Gosliner. CASIZ 110389, four specimens, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 20 April 1996, T.M. Gosliner. CASIZ 093685, one specimen, collected at 20 m depth, in an algal mat, Makena, Maui, Hawaii, 16 January 1993, M. Severns. CASIZ 089652, three specimens, collected at 1 meter depth, on *Acanthophora spicifera* at night, Hekili Point, Maui, Hawaii, 26 September, 1993, C. Pittman. CASIZ 093678, two specimens, collected in low intertidal on *Acanthophora spicifera*, Hekili Point, Maui, Hawaii, 16 October 1993, C. Pittman. CASIZ 093676, three specimens, collected in shallow subtidal, Hekili Point, Maui, Hawaii, 11 October, 1993, C. Pittman.

Distribution.— This species has been recorded from New Caledonia (Risbec, 1937, 1953; Catala, 1986 and has most recently been collected from Japan (A. Ono, pers. commun., http://online.divers.ne.jp/ono/seaslug3/room3-12.html), Hawaii (present study) and the Philippines (present study).

External morphology.— The living animals are virtually transparent, with a slight greenish yellow coloration and white and cream colored internal organs (Fig. 1d). The preserved specimens reach a maximum of 30 mm in length and are white to pale yellow, extremely transparent, with the internal organs and muscle fibers clearly visible (Fig. 6a). The body is limaciform and elongate, somewhat compressed anterolaterally, tapering posteriorly into a narrow rounded posterior portion of the foot. The body surface has few to many conical papillae, tapering to acute or acuminate apices. There are scattered fine white dots or tubercles on or near the body surface, which are more numerous on the papillae. The foot is narrow and linear, opaque white, with the anterior margin rounded and entire. There are 2–4 small conical papillae tapering to acute or acuminate apices on or proximal to the anterior margin of the foot. The circular oral hood is small compared to the rest of the body. The margin of the hood is entire in the majority of the specimens observed, although in some it is indented slightly, usually basally. In all specimens there is an inner and an outer row of long, tapering, conical, tentacular papillae with recurving tips. These are most often found in an opposite arrangement, but may also be found alternating. Some specimens exhibit up to 5 rows, most often near the basal margin. These rows are more or less equal in length, and have a visible axial fiber extending from the hood margin out to the tip, and a concentration of fine white spots. There are additional papillae on the dorsal surface of the hood, generally resembling those on the body surface, and more concentrated towards the anterior margin. The rhinophores are sheathed and born within separated processes that arise from the dorsal surface of the oral hood (Fig. 6b). The sheaths are somewhat inflated and cylindrical with spreading circular margins that produce a flattened, leaf-like posterior process. There is a great deal of variation among specimens, but a "cockscomb" of 3–5 obtuse to acutely pointed papillations is typical present, creating an effect that resembles the outline of a typical ceras. The cerata are inflated, and variable in outline, ranging from oval, saccate, or pyriform, to elongate and cylindrical (Fig. 6c). The surface may be smooth, or covered with low tubercles that give it a broadly warty look, or that may give the margins a lobed or undulating appearance. In the living animals these may appear more papillate (Fig. 1d). The distal margins range from plain and oval to papillately ornamented. The ornamentation may range from low obtuse papillae to one to three flattened processes bearing 3–6 elongate triangular pappilae in a "cockscomb" pattern. This wide range of variability may be due in part to the dehiscence or autotomy of the cerata at the basal end. Specimens have been observed with few to many missing cerata, and with cerata in different stages of apparent regeneration and growth. The cerata are transparent, and the branches of the digestive gland within them are visible. There are fine white spots or tubercles, possibly glandular in nature, visible on the surface of the cerata, and concentrated on the margins and the papillae. There are 3–6 cerata on each side of the dorsal midline. The anteriormost left and right cerata are opposite, with the remaining cerata most often alternating. The anus is located on the right side in the gap between the first and second anterior cerata, midway or slightly more proximal to the anteriormost ceras. The nephroproct is immediately dorsal to the anus. The gonopore is well ventral to and on a line with or just anterior to the anteriormost right ceras. There are no papillae associated with the gonopore.

Digestive system.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass is wide and muscular, devoid of a radula, but containing a pair of denticulate, chitinous jaws (Figs. 9a–b). A pair of compact, nodular salivary glands lies on either side of the middle portion of the buccal mass (Figs. 7a–b). The narrow, elongate esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Figs. 9c–d). The plates also alternate between large and small in size. In the present study, one specimen dissected contained 15–16 plates, and the other contained 22. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies well into the first anterior ceras on the right side. Another large branch of the digestive gland originates from the posterolateral side of the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into the remaining cerata.

Central nervous system.— The cerebral and pleural ganglia are smooth and fused (Figs. 7a–b). They are joined to the pedal ganglia by a short commisure. A short pedal commissure joins the pedal ganglia. A pair of nerves joins with each of the small, spherical buccal ganglia lying on the ventral esophagus, touching each other. The small, dark eyes are situated on anterodorsal portions of the cerebral ganglia.

Reproductive system.— The dissected specimen has 9 simple, spherical, well separated ovotestis bodies (Fig. 7a). The narrow preampullary duct enters the saccate ampulla ventrally (Figs. 8a–b). The ampulla constricts slightly before forming the distal portion that then branches into the oviduct and vas deferens. The slender vas deferens enters almost immediately into the spherical prostate. It then exits from the prostate, enlarges, and makes a bend before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct widens slightly before forming an "S" curve, which probably serves as a serial receptaculum seminis. The oviduct bifurcates, one branch expanding into a pyriform bursa copulatrix, the other leading to the vagina. A distinct, nodular vaginal gland lies alongside the vagina. In one of the dissected specimens, a distinct muscular band was observed around the neck of the vagina, just distal to the vaginal gland and proximal to the terminus of the penial sac.

Natural history.— This species has been found under rocks and on clumps of the brown alga *Padina* sp., as well as on *Acanthophora* sp.

Discussion.— *Melibe engeli* has only been recorded from the type locality, New Caledonia. These new records from Hawai'i and the Philippines represent significant range extensions. This species is remarkable by its transparent body and may easily be overlooked in the field. Specimens studied do not differ markedly from those described by Risbec (1937, 1953). This species appears to be the sister species to *M. digitata* and *M. tuberculata*. These three species share six synapomorphies. All three species have a series of papillae situated immediately dorsal to the anterior end of the foot. The papillae of the oral hood are equal in length in *M. digitata, M. engeli* and *M. tuberculata.* In these taxa the esophagus is elongate, the digestive gland is ramified only within the cerata and the pedal commisure is short. The ovotestis folicles are well separated in *M. engeli* and *M. tuberculata*, but are congested in *M. digitata*.

Melibe engeli can readily be distinguished from other members of the genus by its transparent body and form of the rhinophoral sheaths and cerata. Internally, *M. engeli* is distinct from its sister taxa *M. digitata* and *M. tuberculata* in having stomach plates that alternate in size. Based on the subsequent phylogenetic analysis, other taxa in other lineages appear to have developed this apomorphic state independently.

Melibe leonina (Gould, 1852)

Chioraera leonina Gould, 1852:310. Gould, 1856: pl. 26, figs. 404a,b.

Material examined.— CASIZ 07161, one specimen, 0.9 km w. of Moss Landing, Monterey County, California, on *Macrocystis*, 7 October 1970, G. McDonald.

Distribution.— Known from the Pacific Coast of North America from Kodiak Island, Alaska to Bahía de los Ángeles, México (Behrens 1991).

External morphology.— Most of the external anatomy of this species has been previously described (MacFarland 1966; Gosliner 1987). The body is smooth without any trace of tubercles or papillae on the notum, cerata or anterior margin of the wide foot. Rounded tubercles are present on the notum and cerata. The cerata and body appear to lack zooxanthellae. The gonopore lacks associated papillae.

Digestive System.— The smooth interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, devoid of jaws or radula. The esophagus is short and the salivary glands are compact. The posterior of the stomach lacks chitinous plates. A glandular pouch is present on either side of the dorsal surface of the stomach that expands into the digestive gland ducts. The digestive gland is diffuse and ramifies only within the cerata. A branch of the digestive gland originates from the right side of the stomach and ramifies into the more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches to each of the posterior cerata and ramifies well within the remaining cerata.

Central nervous system.— Gosliner (1987) described the arrangement of the tuberculate ganglia. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are well separated from each other and are smooth in texture.

Reproductive system.— The arrangement of the reproductive organs has been previously described and figured (MacFarland 1966, pl. 54, fig. 1; Gosliner 1987, fig. 2b). The 40–60 ovotestis bodies are arranged in congested somewhat compound clumps of 2–4 bodies.

Natural history.— Specimens of *Melibe leonina* are found frequently on the blades of the kelp *Macrocystis* spp. and less commonly on eel grass, *Zostera marina* where they feed upon crustaceans (Ajeska and Nybakken 1976; Gosliner 1987).

Discussion.— Based on the subsequent phylogenetic analysis, *Melibe leonina* is the most basal member of the genus. Despite its basal position within the genus, *M. leonina* has numerous derived features: flattened cerata, elongate outer row of oral hood papillae, tuberculate ganglia, an elongate penis, somewhat compound ovotestis follicles that are congested, a difuse digestive gland and digestive gland branches that are ramified into the cerata.

Melibe liltvedi Gosliner, 1987

Melibe liltvedi Gosliner, 1987:402, figs. 1b, 3, 8e, 9d, 10d.

Material examined.— CASIZ 073951, three specimens, Llandudno, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 30 m depth, 1 February 1983, W.R. Liltved.

DISTRIBUTION.— Known from the Atlantic coast of the Cape Peninsula, South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY.— Gosliner (1987) described the external anatomy of this species and details were confirmed from examination of material in this study. Papillae are absent from the anterior border of the foot. The cerata and body appear to lack zooxanthellae. The gonopore lacks associated papillae.

DIGESTIVE SYSTEM.— The smooth interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, devoid of jaws or radula. The esophagus is short and the salivary glands are compact. The posterior portion of the stomach possesses 5–6 chitinous plates that are triangular in shape and equal in size. They are arranged in a uniform distributional pattern. The digestive gland is a compact mass that is ramified around the stomach. A branch of the digestive gland originates from the right side of the stomach and ramifies into the more than half of the first anterior ceras on the right side. Another large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches into each of the posterior cerata and ramifies well within the remaining cerata.

CENTRAL NERVOUS SYSTEM.— Gosliner (1987) described the arrangement of the smooth major ganglia. The pleural ganglia are well seperated from the cerebral ganglia. An elongate commissure joins the pedal ganglia. The paired buccal ganglia are adjacent to each other and are smooth in texture.

REPRODUCTIVE SYSTEM.— The arrangement of the reproductive organs has been previously described (Gosliner 1987, fig. 3d). The ovotestis forms a solid mass of compound bodies.

DISCUSSION.— *Melibe liltvedi*, together with its sister species, *M. rosea*, forms a relatively basal clade within the genus. Both species in this clade share three synapomoprhies, the presence of a semi-serial receptaculum seminis, pleural ganglia that are well seperated from the cerebral ganglia and the buccal ganglia that are adjacent to each other. This latter feature has also developed independently in other lineages of *Melibe*. *Melibe liltvedi* differs in several regards from its sister species. The most obvious difference in distinguishing *M. liltvedi* from *M. rosea* is the coloration of the living animals. *Melibe liltvedi* is opaque white, whereas *M. rosea* is pink to orange in color. In *M. liltvedi*, the rhinophore sheath is ornamented with papillae, whereas in *M. rosea* they are absent. The inner surface of the oral hood is smooth in *M. liltvedi* and finely papillate in *M. rosea*. Internally, *M. liltvedi* lacks any remnant of jaws, whereas they are present in *M. rosea*. The bursa copulatrix of *M. liltvedi* is pyriform and spherical in *M. rosea*.

Melibe megaceras Gosliner, 1987

Melibe megaceras Gosliner, 1987:404, figs. 1c, 4, 5, 8g, 9f, 10e.

MATERIAL EXAMINED.— CASIZ 076164, one specimen, Coconut Island, Kaneohe Bay, Oahu, Hawaii, 3 July 1981, T.M. Gosliner. CASIZ 076165, one specimen, collected from sand bar, Kaneohe Bay, Oahu, Hawaii, 25 October 1986, T.M. Gosliner.

DISTRIBUTION.— This species was previously known only from the Hawaiian Islands (Gosliner 1987). A photograph from Carole Harris and second from Burt Jones and Maurine Shimlock indicate that this species is also present from Dubai and Indonesia, respectively. Additional photographs from Malaysia are posted on the Sea Slug Forum (Rudman 2003). These additional records suggest that this species is widely distributed in the Indo-Pacific.

External morphology.— The external anatomy for this species was described by Gosliner (1987) and details were confirmed from material examined in this study. The body is covered with uniformly scattered, elongate papillae. The smooth, elongate cerata are inflated and have 2–4 elongate apical branches. The rhinophore sheaths have a single elongate papilla on the posterior surface. Papillae are absent from the anterior border of the wide foot. The oral hood is small and bears two rows of tentacles along the anterior margin. The outer row consists of uniformly small tentacles, while the inner row has tentacles of alternating large and small sizes. The cerata and body appear to contain zooxanthellae. The gonopore lacks associated papillae.

Digestive System.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass is wide and muscular, devoid of jaws or radula.

There is a small, compact, globular salivary gland on either side of the buccal mass. The buccal mass connects to the short esophagus, which expands abruptly into the muscular, saccate stomach, which contains 20–24 thin triangular plates with eccentric apices in the posterior portion of the specimens dissected. The majority of the plates is nearly equal size, and is aligned in a regular fashion. Three to four smaller plates are found in some specimens, but these smaller plates do not alternate with the larger ones in a regular manner. The digestive gland is diffuse and surrounds the stomach. The two anterior branches of the digestive gland enter more than half of the two anteriormost cerata. The posterior digestive branch is not well developed and simply surrounds the stomach. No branches of the posterior digestive gland enter any of the posterior cerata.

Central nervous system.— The smooth cerebral and pleural ganglia are completely fused together. An elongate commissure joins the pedal ganglia. The paired, smooth, spherical buccal ganglia are adjacent to each other on the ventral portion of the esophagus. Darkly pigmented eyes are present on the dorsal surface of the cerebral ganglia.

Reproductive system.— The arrangement of the reproductive system is triaulic and was previously described by Gosliner (1987). Additional details are added here. The thirteen simple ovotestis follicles are congested. The preampullary duct enters the saccate ampulla, bifurcating distally into an oviduct and vas deferens. The vas deferens directly enters the spherical prostate, emerging as a thin tube within the penial sac, entering the base of the short, flat, spatulate penis. The oviduct widens slightly into a serial receptaculum seminis, then narrows slightly, proceeding distally towards the junction of the spherical bursa copulatrix and the duct of the female gland mass near the gonopore. The vagina contains a nodular gland near its distal opening.

Discussion.— The subsequent phylogenetic analysis indicates that *Melibe megaceras* is the sister species to a large clade containing seven Indo-Pacific taxa (Fig. 25). All members of this large clade share several synapomorphies. These eight taxa have papillae on the surface of the oral hood, papillae on the rhinophore sheaths (which have secondarily been lost in *M. viridis*), a papillate body surface (which has been secondarily modified in *M. digitata and M. tuberculata)* and the presence of a nodular vaginal gland that is either external or internal. *Melibe megaceras* can be most easily distinguished from the other members of this clade, as well as from other members of the genus, by its elongate cerata with 2–4 elongate branches, a posterior digestive gland branch that does not enter any of the cerata and a flattened paddle-shaped penis. *Melibe megaceras* is similar to *M. digitata* and *M. tuberculata* in that ceratal tubercles are absent.

Melibe minuta Gosliner and Smith, sp. nov.

(Figs. 1b, 10–12)

Type material.— Holotype: CASIZ 078529, one specimen, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 16 July 1991, R.F. Bolland. Paratypes: CASIZ 078517, 10 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 30 May 1991, R.F. Bolland. CASZ 078518, 22 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 18 May 1991, R.F. Bolland. CASIZ 078519, 20 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 18 May 1991, R F. Bolland. CASIZ 078521, five specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 19 May 1991, R.F. Bolland. CASIZ 078522, three specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 2 June 1991, R.F. Bolland. CASIZ 078533, four specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 9 June 1991, R.F. Bolland. CASIZ 086601, seven specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 9 March 1992, R.F. Bolland. CASIZ 087918, one specimen, collected at 1.5 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 13 July 1992, R.F. Bolland.

Distribution.— Locally common, but so far limited only to the Horseshoe Cliffs area of the Ryukyu Islands in Okinawa.

Etymology.— This species is named *minuta* owing to the small size of the adult specimens.

External morphology.— The living animals are translucent and are brownish green in color (Fig. 1b). The preserved specimens range in size from 3–10 mm in length and are firm and fleshy (Fig. 10a). The general body shape is limaciform, somewhat elongated, and not compressed anterolaterally. Posterior to the oral hood, the body is humped and rounded in the cardiac and visceral region, tapering abruptly into the posterior portion of the foot, which is often tapered and curled. Ventral to the visceral and cardiac area the rounded body flattens somewhat to form the sides of the foot. The body surface is mostly smooth, with some rugose areas around the neck, ceratal bases, and the side of the foot. There may be some low tubercles on the dorsal portion of the neck, and some small opaque, apparently glandular spots or tiny tubercles in the area dorsal to the foot margin. The foot has a narrow, entire, anterior margin, which is rounded in ventral view (Fig. 10b). There are no associated foot papillae. The foot becomes wider near the middle of the body, with a clearly defined sole and foot margin visible when viewed from above. The foot tapers posteriorly and projects behind the body proper. Posterior to the projecting, entire, anterior portion, the foot margin becomes undulate. The oral hood is produced from a narrowed base, which lies posterior to the projecting anterior foot margin. The hood is small relative to the body, and its entire, circular margin typically bears an inner and an outer row of cylindrical papillae with rounded or bulbous apices (Fig. 10b). The outer row is significantly longer and larger, and the inner row may be so short in places that it could be described as a series of tubercles. In some specimens additional rows or partial rows of papillae are present, usually in the anterior portion, to a maximum of 4 rows. The hood surface tends to be more translucent than the margin, and in some specimens is covered with fine white glandular dots, which appeared as low rounded tubercles in others. There are no accessory papillae on the hood surface. The widely seperated rhinophoral sheaths arise from the hood surface just anterior to the neck (Figs. 10a,e). In general, they are cylindrical and simple, with no sail or large projections, widening and thickening at the distal portion to produce a flanged margin that may be entire and simple, or ornamented with bead-like projections, or short crenulations with rounded apices. In detail, the form varies between an elongate cylinder that widens gradually at the apex to a distinct, shorter, somewhat annulate basal portion with a seperately defined distal cup or calyx. The rhinophores are perfoliate with three or four lamellae (Fig 10e). There are 4–6 cerata on each side of the dorsum, the anteriormost being opposite in arrangement, becoming more alternate posteriorly (Fig 10a). The fleshy cerata arise from a cylindrical base and spread and flatten into fan shaped, oval, or spatulate distal portions which tend to become concave on the inner surfaces, the margins thickened and inrolled. The margins bear a complex combination of multifid projections and papillations, single papillae, crenulations, and tubercles. The convex inner surfaces bear similar protuberences, while the outer surfaces range from bearing low glandular opaque spots to circular raised tubercles creating a nodular appearance (Figs.10c–d). While the cerata of the living animals may be somewhat translucent, it is not possible to externally ascertain the presence of branches of the digestive gland within them. In the preserved specimens the cerata are firmly held nearly vertical or in a "V". It appears that autotomy or dehiscence is less apt to occur in this species as there are few detached cerata present. The anus is located on a distinctly raised papilla located anterodorsal to the second anterior ceras on the right side. The nephroproct is immediately dorsal to the anus. The gonopore is anteroventral to the most anterior right ceras. There are no papillae associated with the gonopore. In many of the specimens a subdermal black eyespot is observable on the left side below the anteriormost ceras. The right eyespot is most often hidden by the genital organs.

DIGESTIVE SYSTEM.— The finely papillate oral hood interior leads to the papillate mouth. The oral tube does not significantly expand into the buccal mass, which is narrow, lacks musculature, and is devoid of any vestiges of jaws or radula. There is a small, compact, globular salivary gland on either side of the buccal mass. The buccal mass is continuous with the elongate esophagus, which expands abruptly into the muscular, saccate stomach, which contained 8 or 9 thin triangular plates in the posterior portion of the specimen dissected (Figs. 12a–c). The plates are of near equal size, and are aligned in a regular fashion. The arrangement of the digestive gland is much the same as described for *Melibe tuberculata.*

CENTRAL NERVOUS SYSTEM.— The smooth cerebral and pleural ganglia are fused (Fig. 11b). An elongate commissure joins the pedal ganglia together. Each of a pair of spherical buccal ganglia is touching side by side on the ventral portion of the esophagus. Darkly pigmented eyes are present on the dorsal surface of the cerebral ganglia.

REPRODUCTIVE SYSTEM.— The arrangement of the reproductive system is triaulic (Fig. 11a). The five simple ovotestis follicles are congested. The preampullary duct enters the saccate ampulla, bifurcating distally into an oviduct and vas deferens. The vas deferens directly enters the spherical prostate, emerging as a thin tube within the penial sac, entering the base of the short, conical penis. The oviduct widens slightly into a serial receptaculum seminis, then narrows slightly, proceeding distally towards the junction of the pyriform bursa copulatrix and duct of the female gland mass near the gonopore. A vaginal gland is not present.

NATURAL HISTORY.— This species has been found at depths between 1.5 and 4 meters, on or within chunks of living and dead hermatypic coral with growths of *Acanthophora* sp. (R.F. Bolland, pers. commun.)

DISCUSSION.— *Melibe minuta* is the most basal member of the tropical Indo-Pacific clade of *Melibe* species. All of these species are unique in possessing brownish coloration that is most likely indicative of the presence of zooxanthellae. Most members of this clade have a papillate body surface (except for *M. digitata* and *M. tuberculata* where they have been secondarily lost) and papillae on the cerata (with the exception of *M. megaceras* where they have been secondarily lost). *Melibe minuta* is easily recognizable externally by its small body size and the flattened cerata with an inrolled margin. The outer row of papillae on the oral hood is the longest.

Melibe papillosa (de Filippi, 1867)

(Figs. 13, 14)

Jacunia papillosa de Filippi, 1867:233–234.
Melibe papillosa (de Filippi, 1867).
Melibe fimbriata Debelius, 1996, misidentification: 288, upper photo.

MATERIAL EXAMINED.— CASIZ 076181, one specimen, intertidal zone, Choshaga Saki, Sagami Bay, Honshu, Japan, 21 June 1970, F. Steiner. CASIZ 089005, one specimen, 41 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 29 November, 1992, R.F. Bolland. CASIZ 075960, one specimen, 2 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 20 July, 1991, R.F. Bolland.

DISTRIBUTION.— Known from the Japan (De Filippi 1867; Baba 1949), Okinawa (present study) and Indonesia (Debelius 1996).

EXTERNAL MORPHOLOGY.— The living animals as seen in photos not published in the present study have a golden brown ground color, with brown and opaque white blotches present on notum and cerata, along with dispersed patterns of tiny white flecks or glandular dots. The animal is translucent to transparent, and portions of internal organs and the substratum can be seen through the body. The preserved specimens reach a maximum length of 50 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Thin, elongate papillae are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin with two rows of cylindrical papillae, which taper to conical points, with the innermost row being the longer. There are scattered papillae on the surface of the oral hood. The well-separated, perfoliate rhinophores (Fig.13a) have 12 lamellae and arise from the surface of the oral hood within cylindrical sheaths that have a narrow posterior sail with a simple elongate dorsal projection. The three to six pairs of cerata (Fig.13b) are apically flattened with a regular wedge shaped margin, bearing a few thin papillae along the margin. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras and bears a circle of papillae around the genital aperture.

DIGESTIVE SYSTEM.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth (Fig. 13c). The buccal mass is wide and muscular, devoid of a radula, but containing a pair of thin, chitinous jaws with a denticulate masticatory border (Fig. 14a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 23 triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Fig. 14b). The plates also alternate between large and small in size. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into more than half of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into more than half of the next pair of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

CENTRAL NERVOUS SYSTEM.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other (Fig. 13c). All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia lie adjacent to each other on the ventral surface of the esophagus, and are connected to the cerebral ganglia by paired nerves. Each buccal ganglion is smooth with an additional outlying esophageal ganglion lateral to each buccal ganglion.

REPRODUCTIVE SYSTEM.— The dissected specimen has more than 50 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of two bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posteriorly (Fig. 13d). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

DISCUSSION.— This species has been the subject of considerable confusion. Several workers have considered *M. papillosa* (de Filippi, 1867) and *M. vexillifera* Bergh, 1880 as synonyms of *M. pilosa* (Pease, 1860) (Eliot 1907; Odhner 1936; Edmunds and Thompson 1972; Gosliner 1987). However, after re-examination of specimens of these taxa in this study, it is evident that the three taxa are closely related, but distinct from each other. *Melibe papillosa* is the sister species to the clade containing *M. viridis* (*M. vexillifera* appears to be a synonym of this species) and *M. bucephala*. Members of this clade have buccal ganglia that are adjacent to each other and stomach plates that alternate in size. *Melibe papillosa* differs from these other two species in having two rows of papillae on the oral hood while *M. bucephala* and *M. viridis* have 3–5 and 2–5 rows, respectively. In *M. papillosa*, the posterior digestive gland enters only the first post cardiac cerata while in *M. bucephala* and *M. viridis* the digestive gland enters the first two ceratal rows.

In its general body form *Melibe papillosa* most closely resembles *M. pilosa*. This resemblance has created confusion in their taxonomic distinction. Following examination of specimens of these two taxa in the present study, several consistent anatomical differences were confirmed. The jaws of *M. pilosa* have a smooth masticatory, border while those of *M. papillosa* are denticulate. *Melibe pilosa* has stomach plates that are all relatively large while in *M. papillosa* they are alternating in size and alignment. In *M. papillosa*, the branches of the posterior digestive gland entering only the first posterior cerata while in *M. pilosa* they enter the first two of the posterior cerata. In *M. papillosa* the buccal ganglia are adjacent to each other, while in *M. pilosa* they are in contact with each other.

Melibe pilosa Pease, 1860

(Figs.15–17)

Melibe pilosa Pease, 1860:34. O'Donoghue, 1929:803, fig. 220.

MATERIAL EXAMINED.— CASIZ 061506, intertidal to 1 m depth, Diamond Head Beach Park, Oahu, Hawaiian Islands, 8 February 1986, M.T. Ghiselin. CASIZ 061501, 2 m depth, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 10 February 1986, T.M. Gosliner. CASIZ 016677, shallow water, Waikiki Beach, Oahu, Hawaiian Islands, 11 March 1939, D.P. Abbott. CASIZ 087402, Easter Island, L. De Salvo.

DISTRIBUTION.— Known from the Hawaiian Islands (Pease 1860; Gosliner 1987) and Easter Island (present study).

EXTERNAL MORPHOLOGY.— The translucent living animals as seen in photographs not shown in the present study have a grayish brown ground color, with brown and opaque white blotches present on notum and cerata, along with dispersed patterns of tiny brown spots. The preserved specimens reach a maximum length of 80 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Thin, elongate papillae are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin with three rows of cylindrical papillae, which taper to conical points, with the innermost row much longer and thicker than the outer ones. There are scattered papillae on the surface of the oral hood. The well-separated, perfoliate rhinophores (Fig. 15b) have 10 lamellae and arise from the surface of the oral hood within cylindrical sheaths that have a narrow posterior sail with a simple elongate dorsal projection. There are four to nine pairs of cerata (Fig. 15a) which are apically flattened with a regular wedge shaped margin, bearing a few thin papillae along the margin. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras and bears a circle of papillae around the genital aperture.

DIGESTIVE SYSTEM.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass (Fig. 16b) is wide and muscular, devoid of a radula, but containing a pair of thin, chitinous jaws with a smooth masticatory border (Fig. 17a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 17 triangular, chitinous plates, with thickened, eccentric apices arranged uniformly (Figs. 17b–c). The plates are subequal in size, but do not alternate between large and small plates. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. This branch ramifies around the stomach. Bifurcating immediately, another branch ramifies into more than half of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into more than half of the next two pairs of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

CENTRAL NERVOUS SYSTEM.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other (Fig. 16b). All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are in contact with each other on the ventral surface of the esophagus, and are connected to the cerebral ganglia by paired nerves. Each buccal ganglion is smooth with an additional outlying esophageal ganglion lateral to each buccal ganglion.

REPRODUCTIVE SYSTEM.— The dissected specimen has more than 20 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of 2–3 bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posteriorly (Fig. 16a). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally at the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

Natural history.— *Melibe pilosa* is found relatively commonly in shallow waters of 0.5–10 meters depth. Generally it is found in association with a variety of marine algae including *Padina* sp. and *Acanthophora* sp.

Discussion.— As discussed previously under the discussion of *M. papillosa*, *M. pilosa* has been the subject of considerable taxonomic confusion. It is clearly distinct from *M. papillosa* and *M. viridis*. *Melibe pilosa* is the sister taxon to the clade containing *M. papillosa* (de Filippi 1867), *M. bucephala* Bergh, 1902 and *M. viridis* Kelaart, 1858. Members of this clade share several apomorphies. They share several external features including a large oral hood, flattened cerata, a circle of papillae surrounding the genital aperture, and an oral hood with two or more rows of papillae. Their central nervous system has tuberculate ganglia with well-separated cerebral and pleural ganglia. The digestive system contains elongate salivary glands and the digestive gland ducts enter only the first one or two cerata of the posterior digestive branch. All four species have an internal vaginal gland.

Melibe pilosa and *M. viridis* differ from *M. papillosa* and *M. bucephala* in having a smooth rather than denticulate masticatory margin of the jaws. *Melibe pilosa* has fewer stomach plates (16–17) than the other members of this clade, which have more than 20 plates. In *M. pilosa* the plates are arranged uniformly, while in the three species that comprise the sister taxon have plates whose apices alternate in their arrangment.

Melibe rosea Rang, 1829

(Figs. 18a, b)

See Gosliner (1987) for synonymy and references.

Material examined.— CASIZ 061503, two specimens, dissected, Algoa Bay, Cape Province, South Africa, 10 m depth, 14 May 1984, W.R. Liltved. SAM A33980, four specimens, dissected, Dale Brook, False Bay, Cape Province, South Africa, on the underside of intertidal rocks, 18 November 1979, T.M. Gosliner.

Distribution.— This species is known only from the temperate waters of southern Africa from Port Nolloth on the Atlantic coast to Port Alfred in the Indian Ocean (Gosliner 1987).

External morphology.— Gosliner (1987) described the external anatomy for this species and details were confirmed from material examined in this study. The oral hood is large and devoid of small papillae over its surface. It has two or three rows of papillae along the anterior margin that are more or less equal in length. The cerata are inflated and bear numerous rounded tubercles. Papillae are absent from the anterior border of the foot. The cerata and body lack zooxanthellae. The well- separated rhinophore sheaths are simple, without papillae or appendages. The gonopore lacks associated papillae.

Digestive System.— The finely papillate interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, and contains a pair of chitinous jaws (Fig.18a). The jaws have 14–22 rounded denticles along either masticatory margin. The esophagus is short and the salivary glands are compact. The posterior of the stomach possesses 7–8 chitinous plates that are symmetrically triangular in shape and equal in size (Fig. 18b). They are arranged in a uniform distributional pattern. The digestive gland is a compact mass that is ramified around the stomach. A branch of the digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches to each of the posterior cerata and ramifies well within the remaining cerata.

Central nervous system.— The arrangement of the smooth major ganglia was described by Gosliner (1987). The pleural ganglia are well separated from the cerebral ganglia. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are adjacent to each other and are smooth in texture.

Reproductive system.— The arrangement of the reproductive organs has been previously described (Gosliner 1987, fig. 3d). The ovotestis forms a solid mass of compound bodies.

Discussion.— As mentioned under the discussion of *M. liltvedi*, *M. rosea* is the likely sister species of *M. liltvedi*. Both species have a semi-serial receptaculum seminis and buccal ganglia that are adjacent to each other. In addition to the external differences noted above, *Melibe rosea* has denticulate jaws while *M. liltvedi* lacks any vestige of jaws. *Melibe rosea* has a spherical bursa copulatrix while the bursa is pyriform in *M. liltvedi*.

Melibe tuberculata Gosliner and Smith, sp. nov.

(Figs. 1c, 19–21)

Type Material.— Holotype: California Academy of Sciences, CASIZ 105639, one specimen, collected at 1.5 m depth, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 27 February, 1995, T.M. Gosliner. Paratype: CASIZ 106394, one specimen dissected, collected at 8 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April, 1996, T.M. Gosliner.

Distribution.— This species has thus far been reported only from the Batangas Province of the Luzon Island in the Philippines.

Etymology.— The name *tuberculata* refers to the rounded tubercles covering the surface of the cerata.

External morphology.— The living animal (Fig. 1c) has a translucent, brownish green body, with the cerata possessing a more vivid, opaque green appearance. The preserved specimens are 11 mm and 15 mm in length. The body is limaciform, somewhat compressed anterolaterally, humped over the visceral region, tapering posteriorly to a rounded posterior portion of the foot (Fig. 19a). The preserved body is pale yellow-white in color and is semi-transparent, with the organs and a criss-crossing network of muscle fibers visible through the body wall. The texture of the dorsum is essentially smooth, with very fine opaque glandular spots or tubercles scattered throughout, but more concentrated near the margin of the foot. The foot is narrow and linear, with an opaque margin that is somewhat undulate along its length, and an anterior margin that is entire and rounded. There are 2 small papillae on or proximal to each side of the anterior margin of the foot. The oral hood is quite small compared to the body, and has an entire, circular margin

(Fig.19a). An inner and an outer row of papillae are present, which are more or less equal in length, with the anteriormost appearing slightly longer. The papillae are cylindrical, with the inner row tapering to acute apices, while the outer row tends to be less tapered and more rounded apically.

The dorsal surface of the hood bears larger club shaped or bulbous papillae, arranged in two rows with the most basal row being the largest. Small white glandular dots or tubercles are present on the translucent surface of the hood, while the hood margin appears more opaque. The well-separated rhinophoral sheaths arise just posterior to the slightly constricted neck separating body from hood. The sheaths are elongate and cylindrical, widening at the distal margin into a corona of 6–12 anterior tubercles and a single posterior elongate papilla (Fig. 19c). The smooth arborescent cerata arise from cylindrical bases into trunks extending approximately 1/4th of the total length before producing multiple branches which terminate in elongate, bulbous, rounded papillae (Fig. 19b). The cerata are dehiscent along their base, and appear to be shed or autotomized easily, as most are no longer attached. There appear to be 4–5 cerata per side, arranged close to the midline. The anus is located on a low elevation located just anterior to the second anterior ceras on the right side, slightly dorsal to the ceratal midline. The nephroproct is immediately dorsal to the anus, on the anal papillae. The gonophore is directly ventral to the anteriormost right ceras, proximal to the lateral midline. There are no papillae associated with the gonopore. One specimen was observed to have a single slightly lobed papilla on an elevated base located medially, proximal to the midline of the dorsum. The second specimen had a much smaller papilla without the elevated base located just anterior to the posteriormost left ceras (Fig. 19a).

Digestive system.— The finely papillate inner surface of the oral hood leads to a mouth with a papillate surface. A wide muscular buccal mass leads to an elongate esophagus, which widens into a saccate muscular stomach. A pair of compact salivary glands lies one on each side of the muscular portion of the buccal mass. A radula is entirely lacking, but a pair of chitinous jaws with smooth masticatory surfaces was present in the muscular fold of the buccal mass (Fig. 21a). The posterior portion of the stomach contained 16 chitinous plates of subequal size, with alternately arranged eccentric apices (Figs. 21b–c). The wide intestine emerges from the dorsal stomach, narrowing as it curves anteriorly, recurving posteriorly before reaching the anus. The diffuse digestive gland originates ventrolaterally on the left side of the stomach. A thin branch proceeds anterodorsally, crossing over the esophagus and entering the first ceras on the right side, where it ramifies into less than half the length of the ceras. A second slightly wider branch proceeds dorsally to enter and ramify into the first ceras on the left side. A larger branch of the digestive gland proceeds posteriorly, entering and ramifying into the remaining cerata.

Nervous system.— All of the ganglia are smooth in texture, with the pleural ganglia well separated (Fig. 20b). The pedal ganglia are joined by a short pedal commisure. The smooth spherical buccal ganglia are situated on the ventral esophagus in such a way that they are touching each other. Each of a pair of dark eye-spots are located on either lobe of the cerebral ganglia.

Reproductive system.— The arrangement of the reproductive system (Fig. 20a) is triaulic. There are four simple, well-separated ovotestis follicles. The preampullary duct enters the proximal lobe of the expanded ampulla, with the distal lobe bifurcating into a tubular vas deferens, and an oviduct. The vas deferens proceeds in a linear manner for a distance equal to the length of the ampulla before recurving and entering the spherical prostate. Emerging from the prostate, the thinner distal portion undergoes several convolutions before entering the proximal portion of the conical penis, the distal end of which lies near the gonopore. After emerging from the ampulla, the oviduct immediately enters a serial, expanded receptaculum seminis, which then narrows, making two convolutions before joining with the female atrium distal to the nodular vaginal gland, where it is joined by the elongate duct from the spherical bursa copulatrix. The female gland mass is also connected to the atrium, and consists of a larger, smooth, mucous gland, a smaller, folded membrane gland, and a nodular albumen gland.

Natural history.— This species has been found in shallow water underneath rocks, and in both occurrences it was found under the same rock as specimens of *Melibe digitata.*

Discussion.— *Melibe tuberculata* appears to be the sister species of *M. digitata* and the synapomorphies shared by these taxa are described in the discussion of *M. digitata.* Differences between the two taxa are also noted in this discussion.

Melibe viridis (Kelaart, 1858)

(Figs. 22, 23)

Meliboea viridis Kelaart, 1858:113.
Melibe fimbriata Alder and Hancock, 1864:138, pl. 33, figs. 6–7.
Melibe vexillifera Bergh, 1880:162, pl. 2, figs. 1–11, pl. 3. figs. 1–3.
Propomelibe mirifica Allan, 1932:314, pl. 24, figs. 1–8.

Material examined.— CASIZ 103727, two specimens, 8 m depth, Seafari Beach, Balayan Bay, Batangas Province, Luzon Island, Philippines, 24 February, 1995, L. Losito. CASIZ 083671, three specimens, 5 m depth, Seafari Beach, Balayan Bay, Batangas Province, Luzon Island, Philippines, 17 February, 1992, T.M. Gosliner. CASIZ 061505, Inhaca Island, Mozambique, 1 July 1955, W. Macnae. CASIZ 078516, one specimen, 64 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 20 July, 1991, R.F. Bolland.

Distribution.— Known from the Indian and western Pacific Oceans from Mozambique (Macnae and Kalk 1958), Zanzibar (Eliot 1902, 1907), Sri Lanka (Kelaart 1858), India (Alder and Hancock 1864), Vietnam (Dawydoff 1952; Risbec 1956), Japan (Bergh 1880; Baba 1949), Okinawa (present study); Philippines (present study) and Australia (Allan 1932; Coleman 1989; Wells and Bryce 1993). This species has also been found in the Mediterranean Sea from Greece and has probably migrated there through the Suez Canal (Thompson and Crampton 1984).

External morphology.— The living animal as seen on a photo slide not shown in the present study has a tan ground color, with brown blotches present on notum and cerata, along with dispersed patterns of tiny white flecks or glandular dots. The animal is translucent to transparent, and portions of internal organs and the substrate can be seen through the body. The preserved specimens reach a maximum length of 130 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Rounded tubercles are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin that produces two to five rows of cylindrical papillae, which taper to conical points, with the innermost row being the longest. There are scattered papillae or tubercles on the surface of the oral hood. The well-separated perfoliate rhinophores have 5 to 7 lamellae and arise from the surface of the oral hood within cylindrical sheaths bearing low tubercles. A posterior sail is absent from the rhinophore sheath, but a simple papilla is commonly present on the posterior side of the sheath of most of the animals examined. The five to nine cerata are somewhat flattened, saccate, oval to cylindrical with tubercular and papillate surfaces whose dark blotches persist in preservation (Fig.22c). They are arranged in two rows on either side of the dorsum, the anteriormost opposite, with the remainder alternate and increasingly offset toward the posterior. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras. A ring of papillae is associated with the gonopore.

Digestive System.— The coarsely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass is wide and muscular, devoid of a radula, but containing a pair of thick, chitinous jaws with a smooth masticatory border (Fig. 22a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 23 triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Fig. 22b). The plates also alternate between large and small in size. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into the basal portion of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into the basal portion of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into the basal portions of the next two pairs of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

Central nervous system.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other. All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia (Fig. 23b) lie adjacent to each other on the ventral surface of the esophagus, and are connected to the pedal ganglia by paired nerves. Each buccal ganglion consists of four or five well-fused cells, with an additional distinct esophageal ganglion lateral to each buccal ganglion.

Reproductive system.— The dissected specimen has more than 50 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of 2–4 bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posteriorly (Fig. 23a). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

Natural history.— These animals appear to be feeding on crustaceans, which they are able to ingest intact. The stomach of the 13 cm specimen from Mozambique contained the carapace of a crab, 13 mm across, nearly completely intact. The stomach contents of the 11 cm specimen from the Philippines included several intact ostracods, each approximately one mm in length, and a hermit crab in a snail shell two mm in height. In the field in the Philippines, specimens have been observed to feed on mysid shrimp at night. However, the mysids were attracted to a diver's underwater light and this may simply be an opportunistic feeding event rather than one that occurs under natural light conditions.

Discussion.— As noted above, in the discussion of *M. papillosa*, there has been much confusion surrounding the Indo-Pacific species of *Melibe* that have flattened cerata. In addition to *M.*

papillosa and *M. pilosa*, several names have been used to describe Indo-Pacific species with these kinds of cerata. The earliest name available is *Meliboea viridis* Kelaart, 1858, described from Sri Lanka (as Ceylon). Subsequent authors have largely ignored this species. The next most recent name is *Melibe fimbriata* Alder and Hancock, 1864, from India. Bergh (1880) described *Melibe vexillifera* from Japan. Most recently, Allan (1932) described *Propemelibe mirifica* from northern Queensland, Australia. Several workers considered *M. vexillifera* to be a synonym of M. *pilosa*, but have regarded *M. fimbriata* as a distinct species (Eliot 1907; Odhner 1936; Edmunds and Thompson 1972; Gosliner 1987).

Edmunds and Thompson (1972) suggested *that M. fimbriata* differs from *M. pilosa* and in several regards. They stated that in *M. pilosa* a distinct papilla is present on the posterior end of the rhinophore sheath but this is absent in *M. fimbriata*. However, Thompson and Crampton (1984) indicated that a papilla is present in Mediterranean specimens of *M. fimbriata*. The present study indicates that a small papilla is usually present in *M. fimbriata*. In *M. pilosa* and *M. papillosa* a posterior expansion of the rhinophore sheath forming a sail is present, while in *M. fimbriata* it is absent. Edmunds and Thompson stated that the pharynx and esophagus of *M. pilosa* are slightly longer than in *M. fimbriata*. However, examination of specimens of *M. papillosa*, *M. pilosa* and *M. viridis* in the present study, indicates that there is no significant difference in the length of these portions of the digestive tract in these three species. Edmunds and Thompson (1972) suggested that in *M. pilosa* a jaw is usually present while in *M. fimbriata*, it is generally absent. The specimen that they identified as *M. pilosa* from Tanzania had a pair of jaws, but it is unclear whether the masticatory margin was smooth or denticulate. Alder and Hancock (1864) did not describe specifically whether jaws were present or absent in their specimen of *M. fimbriata*, but indicated that jaws were typically absent in species of *Melibe*. Eliot (1902) recorded *M. fimbriata* from Tanzania and indicated that jaws were absent in the specimen he examined. Later, he (Eliot, 1907) re-examined the specimen from Tanzania and found that jaws were indeed present. He noted that he re-examined Alder and Hancock's specimen, but as the material was so poorly preserved, he could not determine whether jaws were present. In the same paper he indicated that jaws were absent in a specimen of *M. pilosa* he examined from Japan. Examination of material of all three species in the present study indicates that jaws were present in all specimens studied. In *M. pilosa* and *M. viridis*, the masticatory margin is smooth, while in *M. papillosa* it is denticulate. The specimens that Edmunds and Thompson identified as *M. pilosa* and Thompson and Crampton identified as *M. fimbriata* are clearly conspecific with *M. viridis* described here. The specimens described by Edmunds and Thompson and Thompson and Crampton clearly have multibranched papillae and dark rounded tubercles at the base of the cerata. These are characteristics found only in *M. viridis*. Their specimens have as many as 5 rows of papillae along the margin of the oral hood that is found only in *M. viridis* and *M. bucephala*. *Melibe pilosa* has a maximum of three rows of papillae while *M. papillosa* has only two rows.

Allan (1932) described *Propemelibe mirifica* as distinct species and genus. She stated that "[W]hile no anatomical studies have been undertaken from specimens collected in Australia…", published color photos from Queensland (Coleman 1989:61, middle photo) and Western Australia (Wells and Bryce 1993:175, lower photo) show large animals with distinct dark rounded tubercles and branched papillae that are diagnostic features of *M. viridis*. We therefore consider *P. mirifica* to be a junior synonym of *M. viridis*.

Kelaart's name, *Meliboea viridis,* has been largely ignored by subsequent authors. Rudman (1999) noted that Alder and Hancock stated that *M. viridis* was probably a juvenile of the animal that they named *M. fimbriata*, but objected to the name *viridis*, since their specimen was not greenish in color. Rudman stated that he could find no consitent basis for separating the two species. We agree with Rudman and consider *M. fimbriata*, *M. vexillifera* and *M. mirifica* all to represent junior synonyms of *M. viridis*.

Species Taxonomy and Nomenclature

In the last review of the genus (Gosliner 1987) fifteen valid species were recognized. In the present study, three new species are described and *M. papillosa*, *M. pilosa* and *M. viridis* are recognized as distinct species. Several species have been incompletely described and have not been subsequently studied. *Melibe capucina* described from the Philippines (Bergh 1875) is not identifiable with any of the four species subsequently collected from the Philippines. Its taxonomic status remains uncertain. *Melibe japonica* Eliot, 1913 was not fully described and none of the anatomical features were illustrated. From the external description, it appears that this species may be synonymous with *M. viridis*. In the same paper, Eliot (1913) appears to have confused *M. vexillifera* (=*M. viridis*) with *M. papillosa*. *Melibe maugeana* Burn, 1960, on the basis of the illustrations of the rhinophores and cerata, appears to differ from the other temperate Australian species, *M. australis* (Angas, 1864). Details of its anatomy have not been described, nor has it been documented in collections since the original description. *Melibe mirifica* (Allan, 1932), considered as a valid species by Gosliner (1987), is here regarded as a junior synonym of *M. viridis*. *Melibe ocellata* Bergh, 1888 and *M. rangi* Bergh, 1875 were not completely described and have not been observed since their original descriptiona. Their taxonomic status remains uncertain.

On the basis of the present study, the following species appear to be distinct and recognizable:

Melibe australis (Angas, 1864)
Melibe bucephala Bergh, 1902
Melibe digitata Gosliner and Smith, n. sp.
Melibe engeli Risbec, 1937
Melibe leonina (Gould, 1852)
Melibe liltvedi Gosliner, 1987
Melibe maugeana Burn, 1960
Melibe megaceras Gosliner, 1987
Melibe minuta Gosliner and Smith, n. sp.
Melibe papillosa (de Filippi, 1867)
Melibe pilosa Pease, 1860
Melibe rosea Rang, 1829
Melibe tuberculata Gosliner and Smith, n. sp.
Melibe viridis (Kelaart, 1858) = *Melibe fimbriata* Alder and Hancock, 1864 = *Melibe vexillifera* Bergh, 1880 = *Propomelibe mirifica* Allan, 1932
= ? *Melibe japonica* Eliot, 1913

Doubtful species include the following:

Melibe capucina Bergh, 1875
Melibe ocellata Bergh, 1888
Melibe rangi Bergh, 1875

Phylogenetics

Character Analysis

In order to study the phylogenetic relationships of members of the Tethydidae and to test the monophyly of *Melibe*, a phylogenetic analysis has been undertaken. To examine these relationships of these taxa, 47 anatomical characters were surveyed in 15 taxa. In addition to the thirteen taxa of *Melibe* included in this study, data for the other member of the Tethydidae, *Tethys fimbria* (Linnaeus, 1767) was examined. *Marionia* was used as the outgroup of the Tethydidae, since it represents one of the most basal members of the Dendronotacea (Odhner 1936).

The following characters were examined and coded (see also table [Fig. 24]):

1. *Body surface*: The body surface of the outgroup *Marionia* is ornamented with rounded tubercles. Members of the ingroup may have a smooth body surface (0), a surface with tubercles (1) or one with papillae (2).

2. *Foot width*: In the outgroup and some members of the ingroup the foot is moderately wide (1), while in some ingroup taxa the foot is narrow (0).

3. *Foot papillae*: In some species of *Melibe* a series of elongate papillae are present (1) on the anterodorsal surface of the foot. These structures are absent (0) in the outgroup, *Tethys* and several members of *Melibe*.

4. *Oral hood*: An oral hood is a distinctly expanded portion of the head that is used by members of the Tethydidae to capture crustacean prey. It absent (0) in the outgroup and present (1) in all members of the ingroup.

5. *Oral hood size*: This character is absent (2) within the outgroup and may be either a large (0) or small (1) structure within the Tethydidae.

6. *Oral hood margin*: This character is not applicable (?) to the outgroup. The oral hood margin within the ingroup may contain one row of papillae (0), two rows of papillae (1) or more than two rows of papillae (2).

7. *Oral hood papillae*: This character is not applicable (?) to the outgroup. In the ingroup the papillae on the oral hood are equal in length (0), the inner row is longest or the outer row is longest.

8. *Papillae on oral hood*: This character is not applicable (?) within the outgroup. Papillae may be either absent (0) or present (1) on the surface of the hood in members of the ingroup.

9. *Rhinophores*: The rhinophores are chemosensory organs situated on either side of the dorsal surface of the head. They are present in all taxa studied here. In the outgroup and most members of the ingroup the bases of the rhinophores are well-separated from each other (0). In *M. digitata* and *M. tuberculata* they are adjacent (1) to each other.

10. *Rhinophore sheath sail*: In the outgroup and most members of the ingroup the posterior end of the rhinophore sheath lacks any posterior extension (0). In some members of the ingroup the posterior end of the sheath has a membranous, sail-like extension (1).

11. *Rhinophore sheath papilla*: In some members of the ingroup a distinct papilla is present at the apex of the posterior end of the rhinophore sheath (1). It is absent in *Marionia* and many members of the ingroup (0).

12. *Gills*: A series of dendritic respiratory structures are found on the lateral margins of the notum in the outgroup and in *Tethys* (0), but are absent (1) in species of *Melibe*. These structures have often been called gills, but are not homologous to the ctenidium of other mollusks.

13. *Cerata*: Elongate appendages are found on the lateral margins of the members of the ingroup (1). These structures, generally called cerata, often contain branches of the digestive gland. They are absent (0) from members of the outgroup.

14. *Ceratal shape*: Ceratal shape is not applicable (?) to the outgroup. Within the ingroup, the cerata may be either inflated (0) or laterally flattened (1).

15. *Ceratal tubercles*: In many ingroup taxa the surface of the cerata bears rounded tubercles (1). Other members of the ingroup lack tubercles on the cerata (0). This character is not applicable to the outgroup (?).

16. *Ceratal papillae*: This character is not applicable (?) to the outgroup, since species of *Marionia* lack cerata. Some ingroup members lack elongate papillae on the surface of the cerata (0), while they are present in others (1). This character is independent of the previous one, since some taxa may have both tubercles and papillae.

17. *Genital opening*: In the outgroup the genital aperture has no distinct papillae with which they are associated (0). In some members of the ingroup, there are no distinct papillae, or 3 or less papillae, which is also coded as absent (0). In other ingroup taxa there are distinct papillae around the margin of the genital atrium, arranged in a circular manner (1).

18. *Inner oral hood surface*: In *Marionia*, this character is not applicable since and oral hood is not present (?). In members of the ingroup an oral hood is present and its inner surface is either smooth (0), finely papillate (1), or coarsely papillate (2).

19. *Mouth surface*: In the outgroup and some members of the ingroup the surface of the tissue surrounding the oral opening is smooth (0). In some ingroup taxa it bears a series of papillae around the opening (1). Presumably, these papillae serve a sensory function.

20. *Buccal mass*: In the outgroup and most members of the ingroup, the buccal mass is wide (0). In *M. digitata* it is of intermediate width (2), while in *M. minuta* it is narrow (1). This multistate character is treated as unordered.

21. *Jaws*: In the outgroup a pair of jaws with a denticulate masticatory margin is present (0). In members of the ingroup, the jaws may be denticulate, have a smooth masticatory margin (1), or be entirely absent (2).

22. *Salivary glands*: In the outgroup and several members of the ingroup a pair of elongate salivary glands is present on either side of the junction of the esophagus with posterior end of the buccal mass (1). In several ingroup taxa, the salivary glands are compact (0). In *M. australis* salivary glands appear to be entirely absent (2).

23. *Esophagus*: In the outgroup and some members of the ingroup the esophagus, between the posterior end of the buccal mass and the stomach, is a relatively short duct (0). In a few ingroup taxa the esophagus is more elongate (1).

24. *Stomach plates*: In the outgroup taxon the stomach contains more than 20 chitinous plates that are presumably used to crush the calcareous sclerites of cnidarian prey (2). The ingroup taxa feed on crustaceans. Many of them have 20 or more stomach plates, some have 10–19 plates (1), some have fewer than 10 plates (0) and in others plates are entirely absent (3).

25. *Stomach plate alignment*: In the outgroup and several members of the ingroup the apices of the chitinous plates that line the stomach are all aligned with the highest point near the middle (0). In some members of the ingroup the apices of the plates alternate in position from the right and left side of the median line (1).

26. *Stomach plate size*: In the outgroup and in some members of the ingroup, the stomach plates are more or less uniform in size (0). In other ingroup taxa the plates alternate between large and small plates (1).

27. *Stomach plate shape*: In the outgroup and some members of the ingroup, the stomach plates are bilaterally symmetrical with a apex in the middle of the plate (0). Other members of the ingroup have plates with an eccentric apex (1).

28. *Digestive gland:* In the outgroup and several members of the ingroup, the digestive gland forms a compact mass (0) while in other ingroup members it is more diffuse (1).

29. *Digestive gland enters first cerata*: In the outgroup the digestive gland does not extend to the dorsal surface (2). In some of the ingroup taxa the digestive gland penetrates less than the basal half of the cerata (1), while in others it penetrates well beyond the middle of each ceras (0).

30. *Digestive gland branches*: In the outgroup the digestive gland forms a solid mass that is not ramified (2). In the ingroup taxa the digestive gland is always ramified. In some cases it is ramified only within the cerata (1), in others it is ramified around the stomach and in the cerata (0).

31. *Posterior digestive gland branch*: In *Marionia* and most ingroup taxa the posterior branch of the digestive gland is well developed (0). In a few members of the ingroup this posterior branch is poorly developed (1).

32. *Posterior digestive gland entry*: In the outgroup, the posterior digestive gland does not extend dorsally towards the notal surface (2). In the ingroup, the posterior branch of the digestive gland extends dorsally and enters some of the posterior cerata. In some cases it enters all of the cerata (3), in others only the anteriormost pair of post-cardiac cerata (0) and in other cases only the anterior 2 post-ceratal pairs (3).

33. *Ganglia*: *Marionia*, the outgroup taxon, has ganglia with a smooth external margin (0). In members of the ingroup the ganglia may be smooth or have an irregular outline due to presence of large peripheral nerve cells (1).

34. *Pleural ganglia*: In the outgroup and most members of the ingroup the pleural ganglia are well-separated from the cerebral ganglia (0), while in some members of the ingroup these ganglia are largely fused (1).

35. *Pedal commissure*: In the outgroup and the majority of members of the ingroup, the commissure joining the pedal ganglia is elongate (1). In a few taxa this commissure is short (0).

36. *Buccal ganglia*: In the outgroup and many ingroup members, the buccal ganglia are well-separated from each other (1). In some ingroup members the ganglia are adjacent to each other (2) or, in other cases, they actually touch each other (0).

37. *Buccal ganglia texture*: In the outgroup and virtually all members of the ingroup the buccal ganglia have a smooth texture (0), while in *M. viridis*, the ganglia appear tuberculate (1) owing to the presence of large peripheral nerve cells.

38. *Ovotestis follicles:* In the outgroup and several ingroup taxa the ovotestis follicles are united in compound masses (2). In some ingroup taxa the follicles are only somewhat (two or three follicles together some or all of the time) compound (0) or form simple masses (1).

39. *Ovotestis development*: In the outgroup and several members of the ingroup, the follicles form a solid mass (2). In other ingroup members the follicles are either congested (0) or well separated (1).

40. *Receptaculum seminis*: In the outgroup and *Tethys*, a receptaculum seminis is indistinct (2). In members of the ingroup a distinct receptaculum seminis is present. It may be either serial (1), or enter via a distinct duct, where it is termed semi-serial (0).

41. *Serial receptaculum seminis*: In some ingroup taxa with a serial receptaculum seminis, the receptaculum may be either narrow (0) or expanded (1). This character is not applicable in the outgroup and in several of the ingroup taxa (?).

42. *Bursa copulatrix*: The bursa copulatrix of the outgroup and several members of the ingroup is pyriform (1). In a few ingroup taxa the bursa is spherical (0).

43. *Vaginal gland*: In the outgroup, a distinct vaginal gland is absent (0). In some members of the ingroup a gland is present. It may be either external and nodular (2) or internal and smooth (1). This multistate character is treated as unordered.

44. *Prostate gland*: In *Marionia* the vas deferens lacks a distinctly thickened prostate gland (0). In all of the ingroup members a distinct prostate is present (1).

45. *Penis*: In the outgroup and the vast majority of ingroup taxa, the penis is conical (0). In *Melibe leonina* the penis is elongate (1), while in *M. megaceras* the penis is flattened and paddle-shaped (2).

46. *Accessory penial sac*: In the outgroup and most members of the ingroup, the accessory penial sac is absent (0). In *Tethys fimbria* an accessory sac is present (1).

47. *Zooxanthellae*: Members of the outgroup and some members of the ingroup lack brownish pigment and apparently lack zooxanthellae as symbionts (0). All of the tropical species of *Melibe* have brownish pigment and it has been demonstated that in the two species examined histologically (Kempf 1984) that this is due to the presence of zooxanthellae (1).

PHYLOGENETIC ANALYSIS

It was decided that species for which there was insufficient data would be excluded from the analysis. These were species for which no type material was available for comparison with the existing literature. This resulted in the exclusion of *M. capucina* Bergh, 1875; *M. ocellata* Bergh, 1888; *M. maugeana* Burn, 1957 and *M. rangi* Bergh, 1875. *Tethys fimbria* (Linnaeus, 1767) was included in the matrix, as it is the best described member of the second genus in the family Tethydidae. The genus *Marionia* was used as the outgroup. This analysis was performed using PAUP 3.1.1, with MacClade 3.01 for the data matrix. This resulted in an analysis of 15 taxa, using 47 characters. All characters were treated as un-ordered and unweighted. Heuristic search and branch and bound searches were undertaken using the DELTRAN option, resulting in a single tree with a length of 123 steps, a consistency index of 0.569 and retention index of 0.671 (Fig. 25).

DISCUSSION

The resultant phylogeny supports the hypothesis that *Melibe* represents a monophyletic taxon. The four most basal species in the tree are all found in temperate regions, (California, South Africa and Australia, respectively) while the large more derived, monophyletic clade consists of all of the tropical Indo-Pacific species. This pattern of distribution, with basal temperate species and derived tropical ones, is consistent with what is seen with other groups of nudibranch molluscs, eg. *Flabellina* (Gosliner and Kuzirian 1990), *Hallaxa* (Gosliner and Johnson 1994) and *Platydoris* (Dorgan, Valdés, and Gosliner 2002). The most basal taxon within *Melibe* is *M. leonina.* This species retains more plesiomorphic attributes but has also several autapomorphies, related to most organ systems. *Melibe rosea* and *M.liltvedi*, both from South Africa, are sister taxa at the next highest node. They share apomorphies of their reproductive and nervous systems. The other temperate species, *M. australis* is the sister species to all of the Indo-Pacific taxa. This species has two autapomorphies, the absence of jaws and salivary glands. Kempf (1984) described the presence of zooxanthellae in some tropical species of *Melibe.* It appears that all members of the Indo-Pacific clade share the apomorphy of having zooxanthellae in their tissues. This may be an adaptation to living in less productive tropical waters. Within this clade there are certain morphological adaptations which may support the utilization of zooxanthelae. These include a transparent or highly translucent body allowing good light transmission to the symbionts, and cerata that are arranged in an alternating pattern that minimizes shading and optimizes control of light intensity. In addition, the members of this clade all have branches of the digestive gland within the cerata. While this relationship has not been studied, the digestive gland branches might aid in the transport of ingested symbionts to the ceratal tissues, and in the uptake of photosynthetic products by the host. The transparency of these animals, along with the color imparted by the symbiont may also provide many of these species with a high degree of crypsis, allowing them to almost disappear against their normal background. The Indo-Pacific clade has undergone considerable speciation, with nine recognized nominal species.

The biogeographical relationships of the Indo-Pacific taxa are complex and sister taxa do not exhibit markedly vicariant distributions. In both cases where sister taxa are well defined, the sister species are sympatric, for at least a portion of their ranges. *Melibe viridis* is one of the most widespread species, known from the western Indian Ocean to the western Pacific. In the Red Sea and the Gulf of Thailand it is found sympatrically with its sister species, *M. bucephala*. The other pair of sister species, *M. digitata* and *M. tuberculosa*, is sympatric in the Philippines. Knowledge of distributional ranges of many species is likely incomplete. Since *M. megaceras* was first described from the Hawaiian Islands (Gosliner 1987), two additional specimens have been recorded here from Dubai and Indonesia, greatly extending the known distribution of this species. *Melibe engeli* has only been observed a few times since its original description, although it can be sporadically abundant in some habitats (present study). Several species have never been recorded since their original descriptions and their systematic and biogeographical status remain in doubt. Incomplete records of other species may greatly impact our understanding of natural ranges for species of *Melibe*. The cryptic color patterns and small body size of many species likely compound our poor knowledge of these distributional patterns.

The Tethydididae are highly modified dendronotoideans. All species of both *Tethys* and *Melibe* have lost the radula and in many taxa the jaws are also reduced or entirely lost. Most dendronotoideans are specialized predators upon coelenterates (McDonald and Nybakken 1999). In contrast, species of *Melibe* and *Tethys* are predators upon crustanceans and have altered their external body form and digestive system to accommodate this dietary modification.

ACKNOWLEDGMENTS

This work was supported largely by the National Science Foundation REU grant (REU 9820251) for the Summer Systematics Institute at the California Academy of Sciences. Many individuals kindly facilitated completion of this work. Bob Bolland, Lou De Salvo, Michael Ghiselin, Carole Harris, Burt Jones, Laura Losito, Michael Miller, Cory Pittman, Maurine Shimlock and Mike Severns all provided specimens and photographic records of fresh material examined in this study. Joan Pickering and Kathy Way of the Natural History Museum, London kindly made preserved material available for examination.

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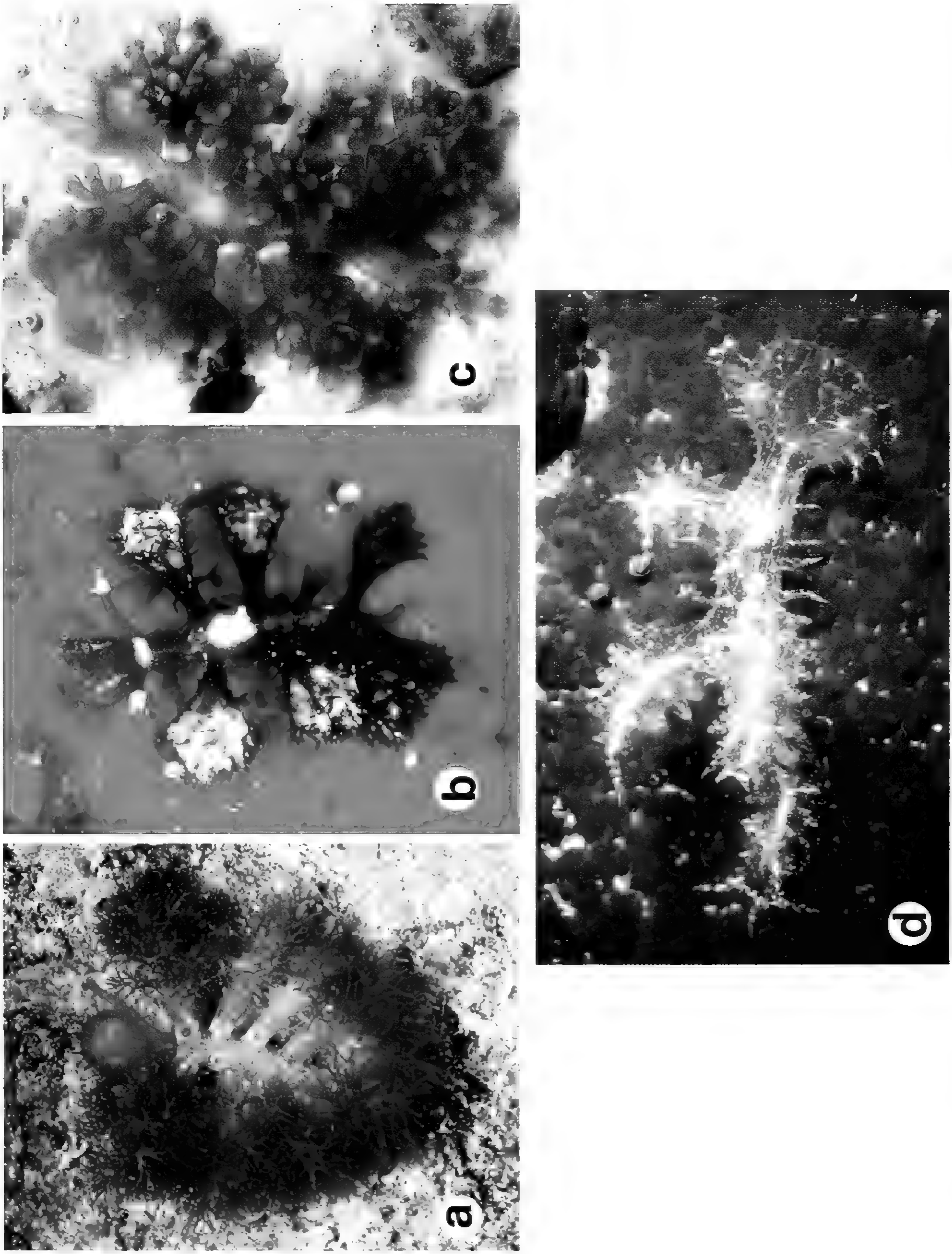

Figure 1. Photographs of living animals. A: *Melibe digitata* sp. nov. B:*Melibe minuta* sp. nov. C:*Melibe tuberculata* n. sp.. D: *Melibe engeli* Risbec, 1951.

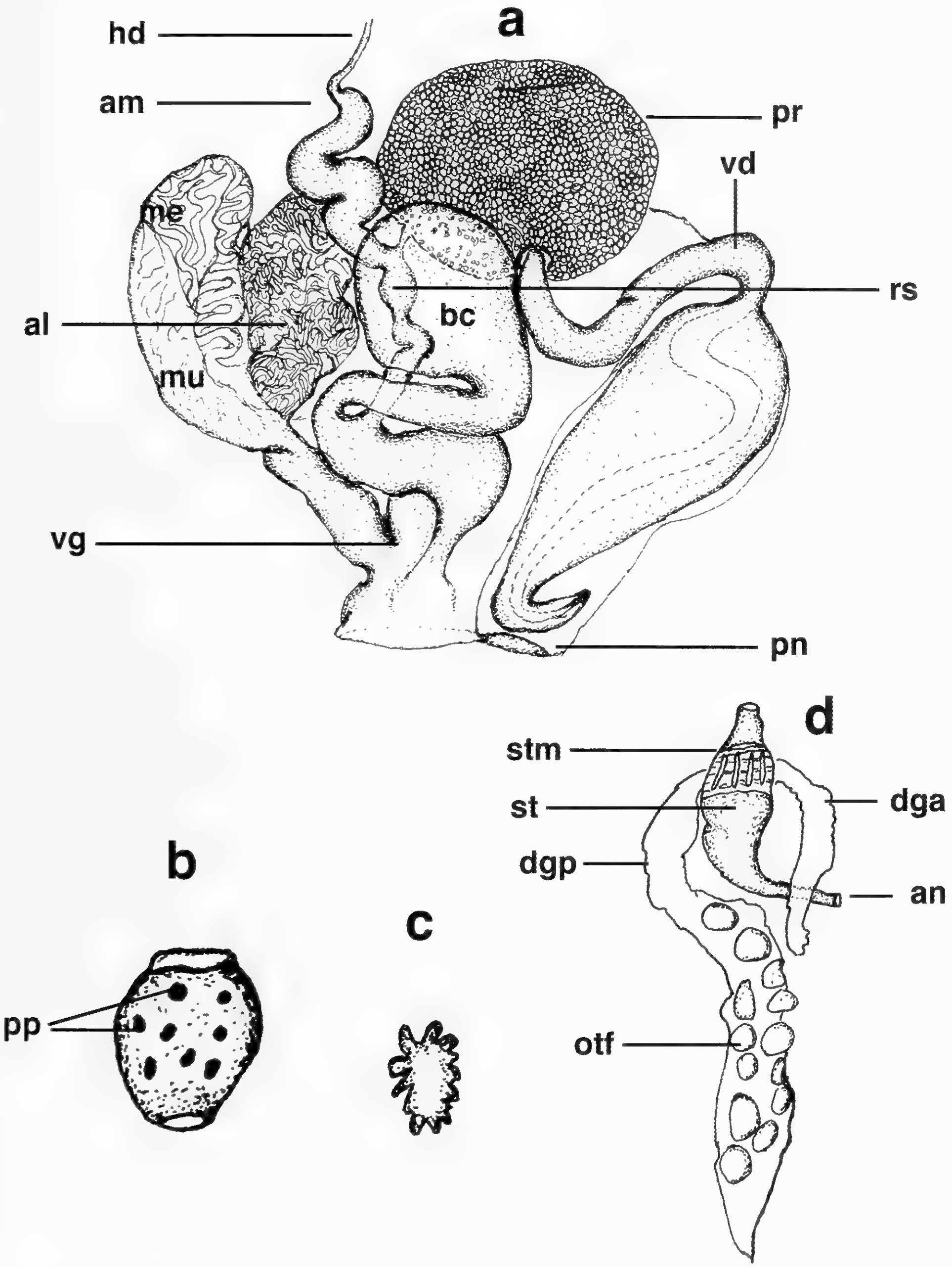

FIGURE 2. *Melibe bucephala* Bergh, 1902, anatomy (BMNH1933.6.30.35). A: Reproductive system. al = albumen gland; am = ampulla: bc = bursa copulatrix; hd = hermaphroditic duct; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate gland; rs = receptaculum semenis; vd = vas deferens; vg = vaginal gland. B: Buccal mass. pp = papillae. C: Portion of viscera. An = anus; dga = anterior digestive gland; dgp = posterior digestive gland; otf = ovotestis follicles; st = posterior portion of stomach; stm = muscular portion of stomach. D: portion of central nervous system.

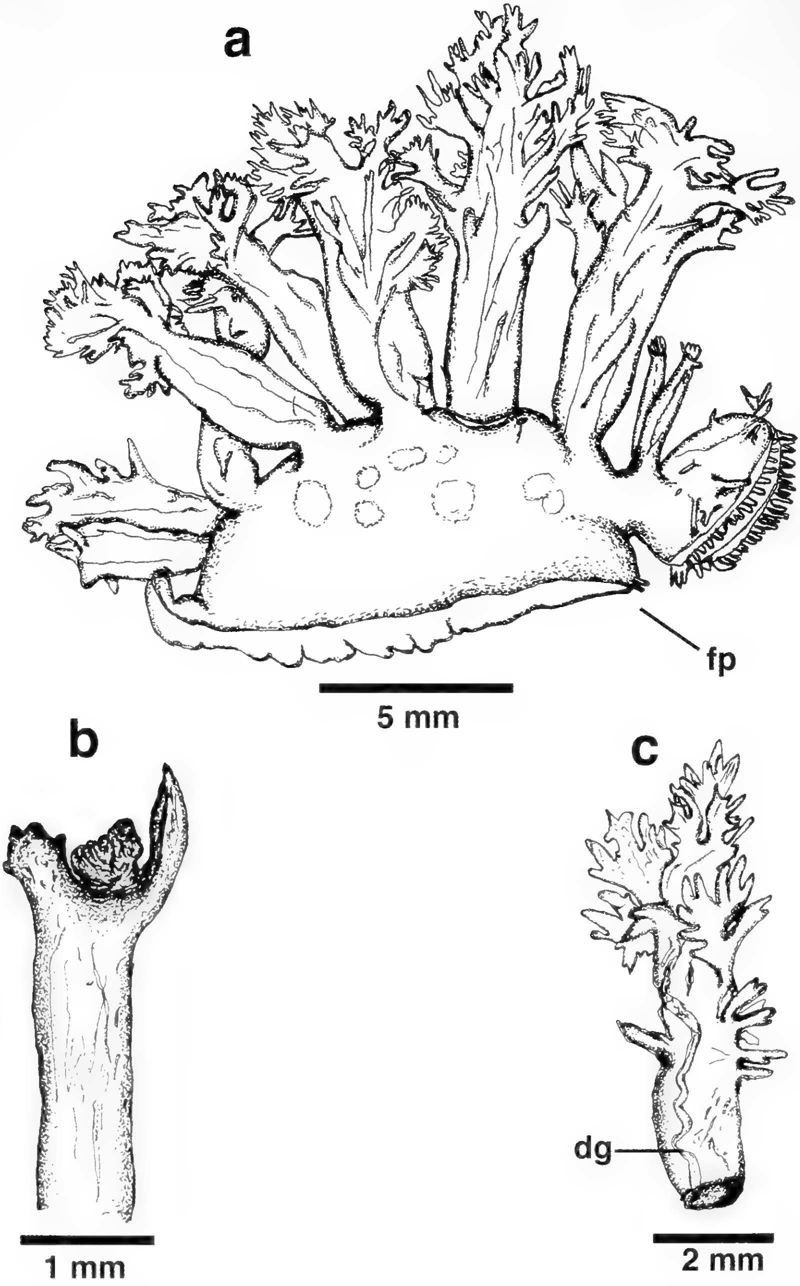

FIGURE 3. *Melibe digitata* sp. nov., morphology. A: Body of preserved specimen (CASIZ 110425). fp = foot papillae. B: Rhinophore (CASIZ 103754). C: Detached ceras (CASIZ 103754).

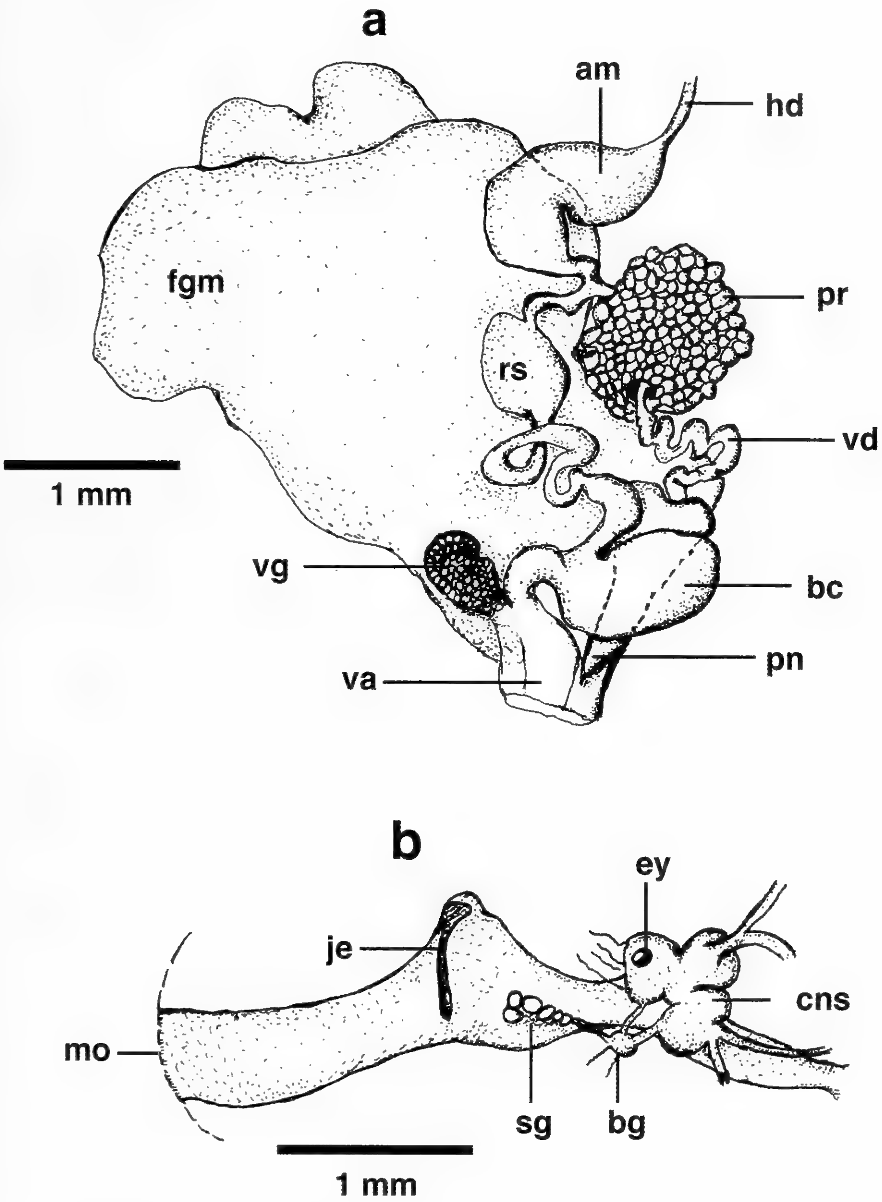

FIGURE 4. *Melibe digitata* sp. nov., anatomy (CASIZ 110425). A: Reproductive system. am = ampulla; bc = bursa copulatrix; fgm = female gland mass; hd = hermaphroditic duct; pn = penis; pr = prostate; rs = receptaculum semenis; va = vaginal atrium; vd = vas deferens; vg = vaginal gland. B: Buccal mass. bg = buccal ganglia; cns = central nervous system; ey = eye; je = jaw edge; mo = mouth; sg = salivary glands

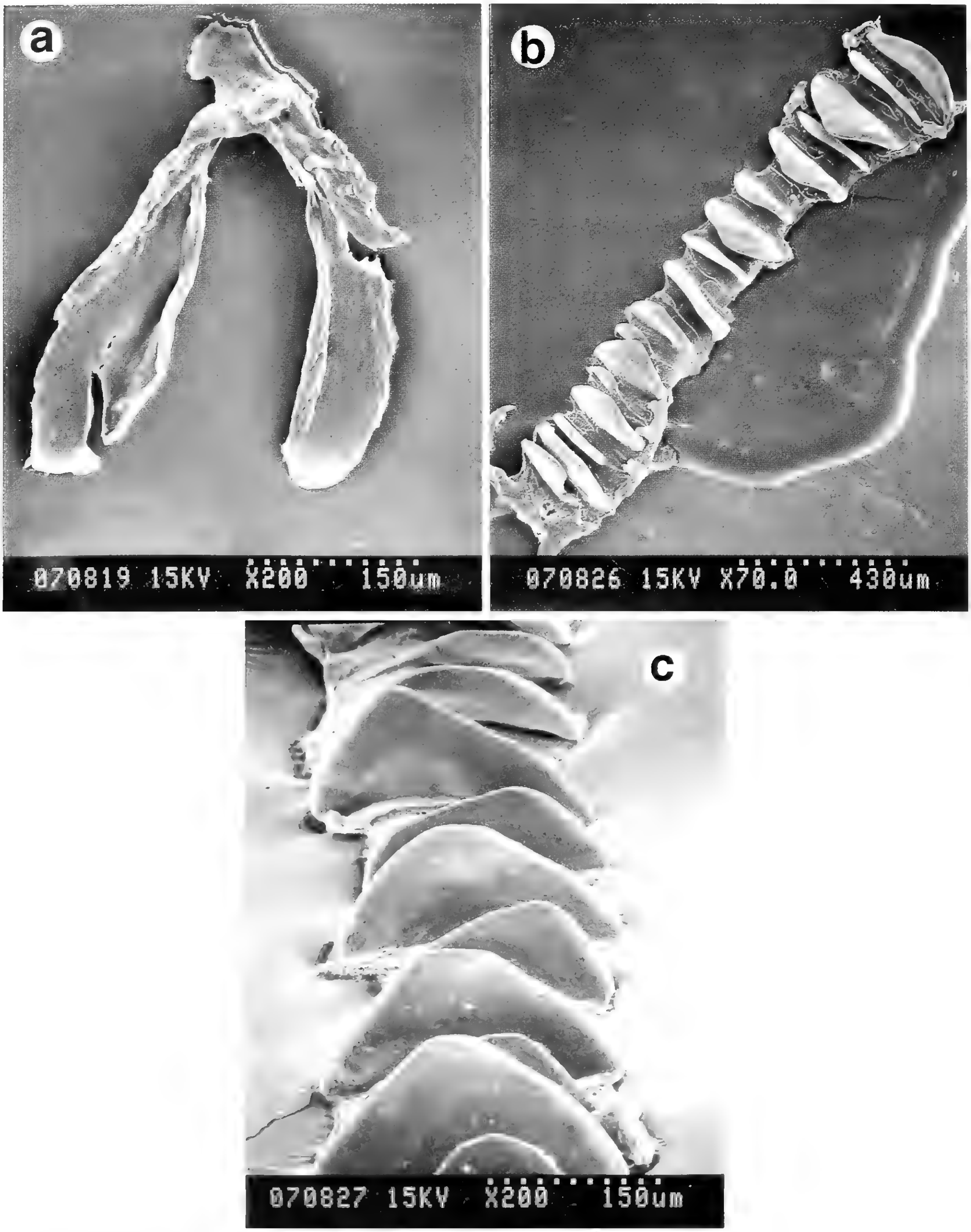

FIGURE 5. *Melibe digitata* sp. nov. (CASIZ 110425). A: Jaws. B-C: Stomach plates.

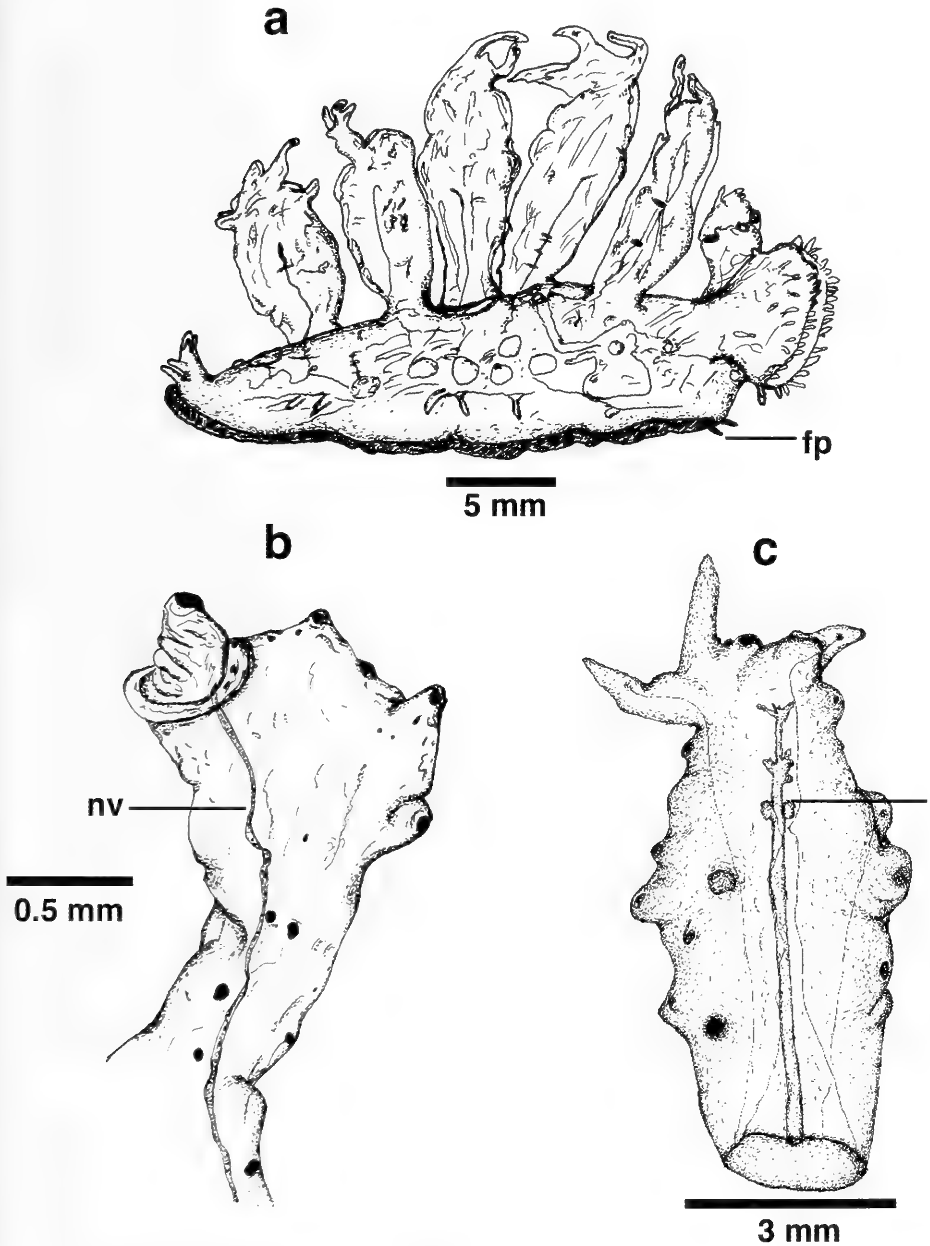

FIGURE 6. *Melibe engeli* Risbec, 1937, morphology. A: Body of preserved specimen (CASIZ 110389). fp = foot papillae. B: Rhinophore CASIZ 106396). nv = nerve. C: Detached ceras (CASIZ 93676). dgb = branch of digestive gland.

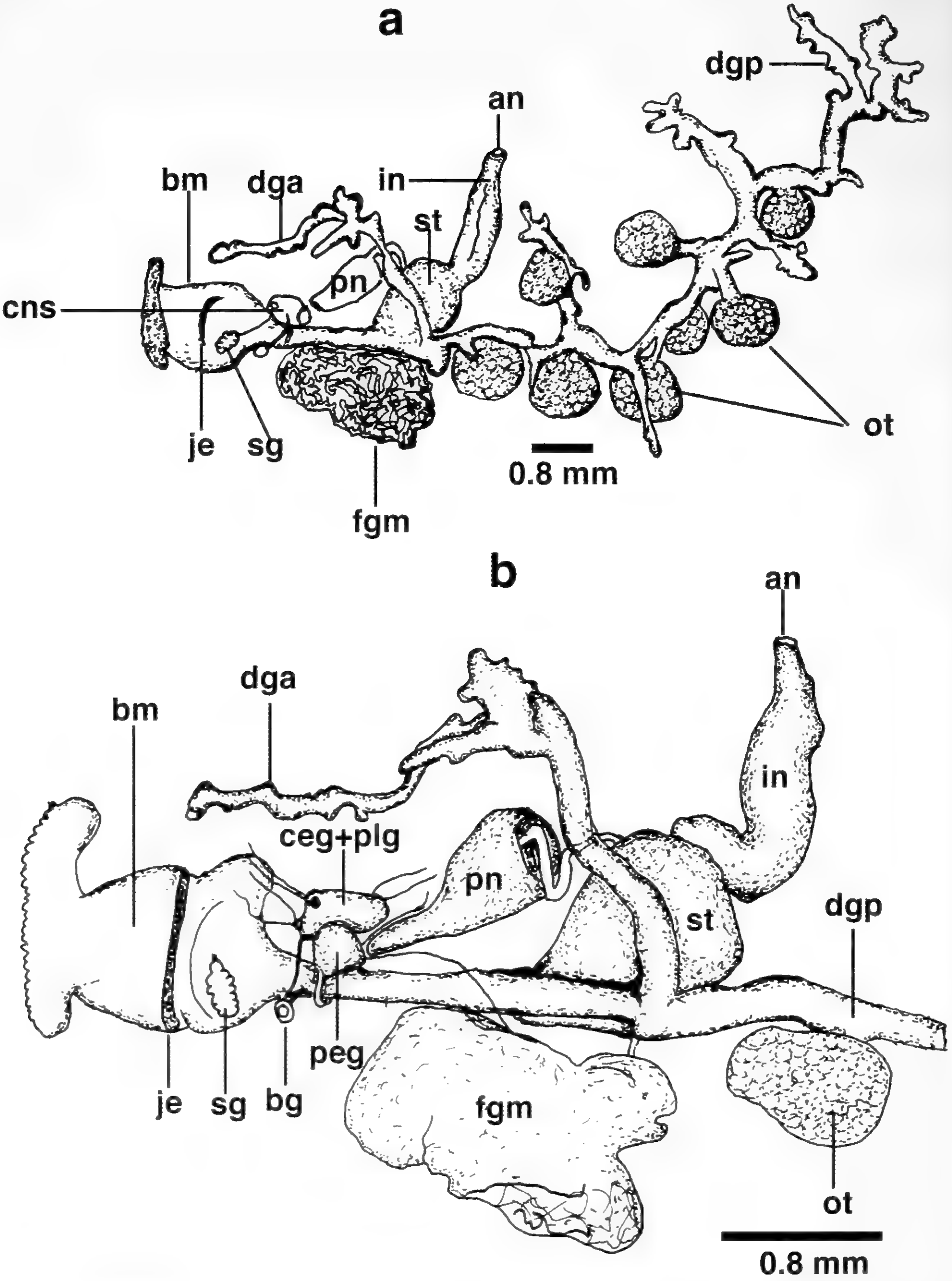

FIGURE 7. *Melibe engeli*, two views of visceral mass (CASIZ 105680). A: Visceral mass removed nearly intact. B: Close up view of anterior portion. an = anus; bg = buccal ganglia; bm = buccal mass; ceg = cerebral ganglia; cns = central nervous system; dga = anterior digestive gland; dgp = posterior digestive gland; fgm = female gland mass; in = intestine; je = jaw edge; ot = ovotestis; peg = pedal ganglia; plg = pleural ganglia; pn = penis; sg = salivary gland, st = stomach.

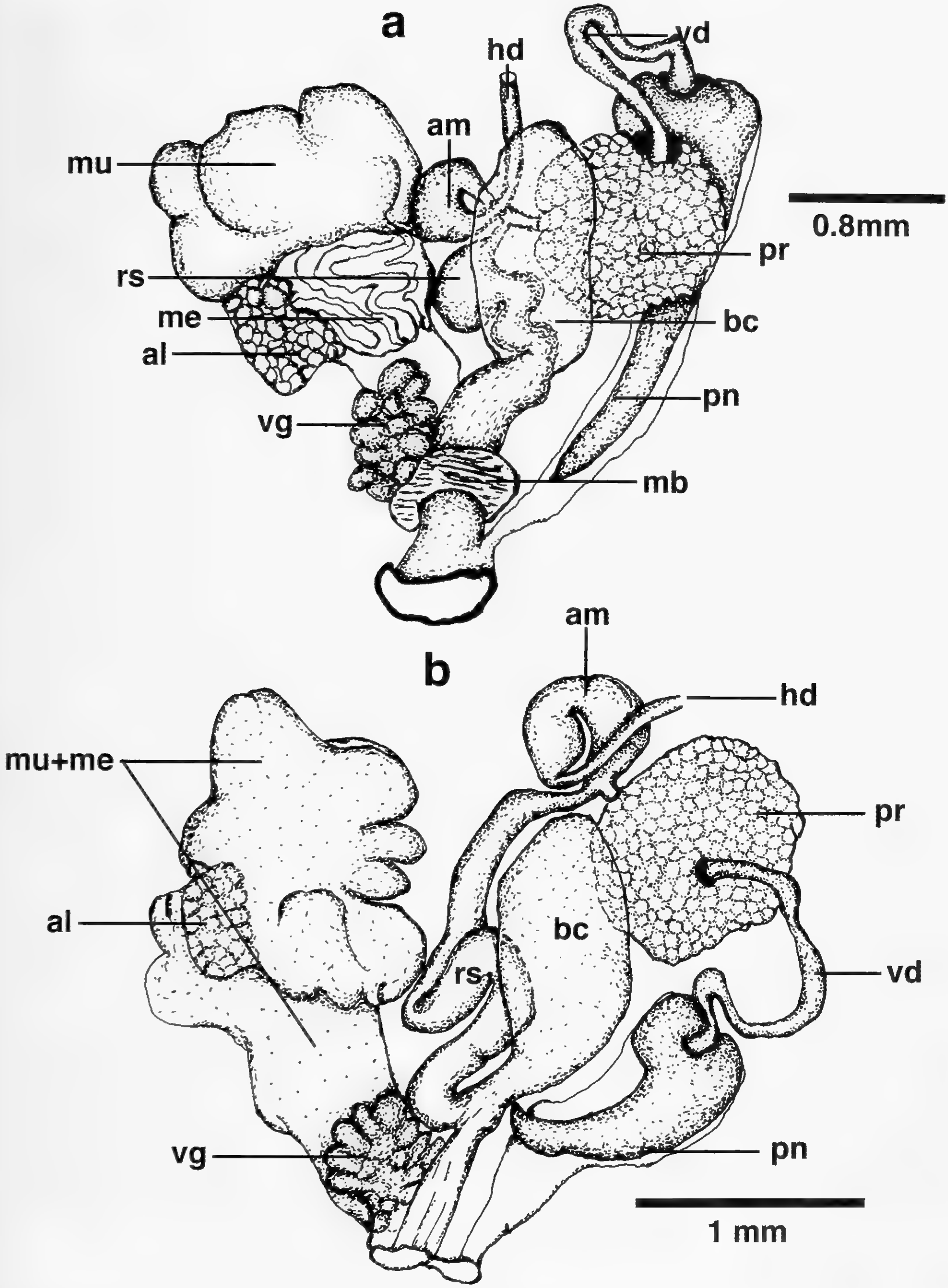

FIGURE 8. *Melibe engeli,* comparison of reproductive systems. A: Philippine specimen (CASIZ 105680). B: Hawai‘ian specimen (CASIZ 89652). al= albumen gland; am = ampulla; bc = bursa copulatrix; mb = muscular band; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate; rs = receptaculum semenis; vd = vas deferens; vg = vaginal gland.

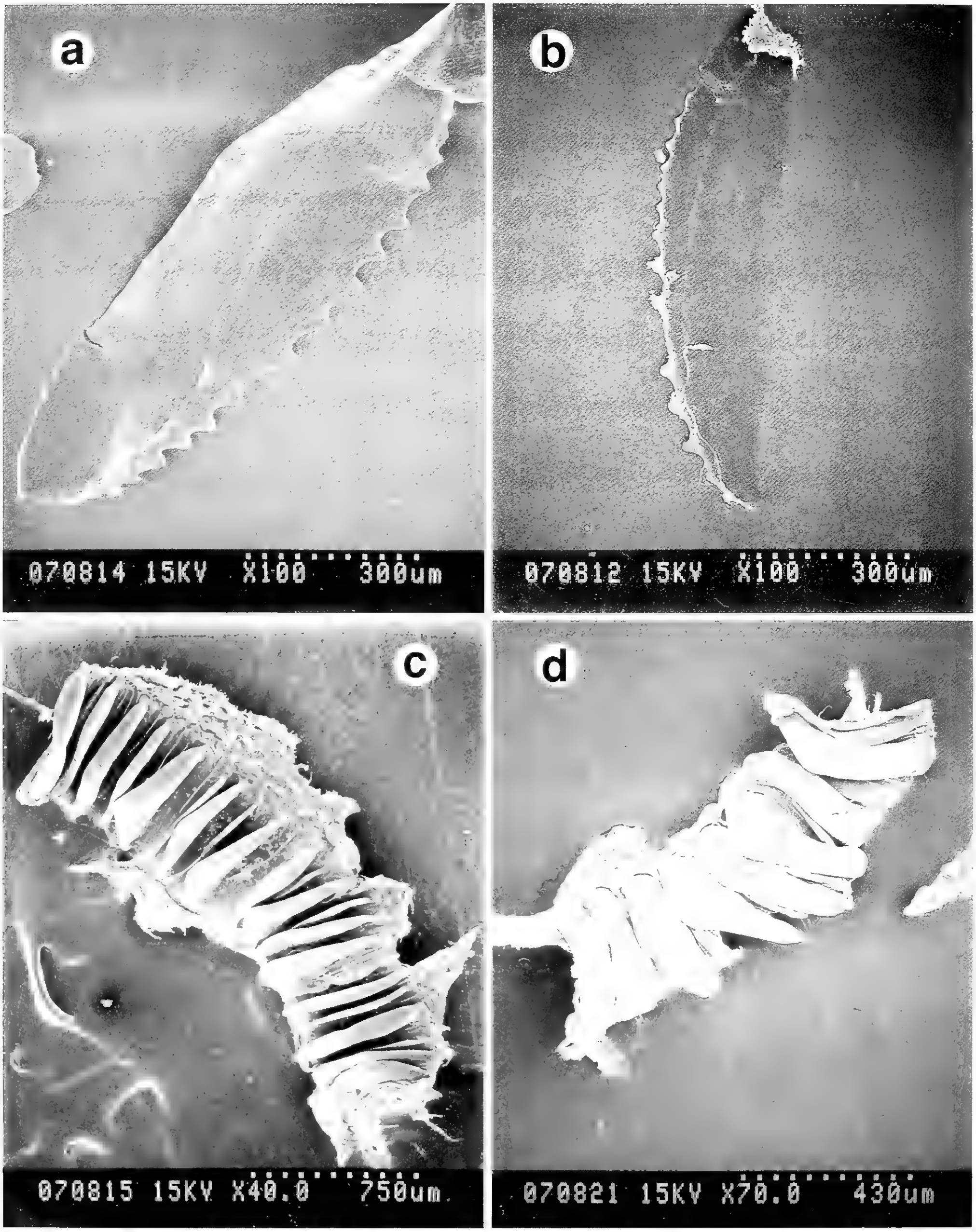

FIGURE 9. *Melibe engeli*, comparison of digestive armature. A: Jaw of CASIZ 89652 (Hawai'i). B: Jaw of CASIZ 105680 (Philippines). C: Stomach plates of CASIZ 89652. D:Stomach plates of CASIZ 105680.

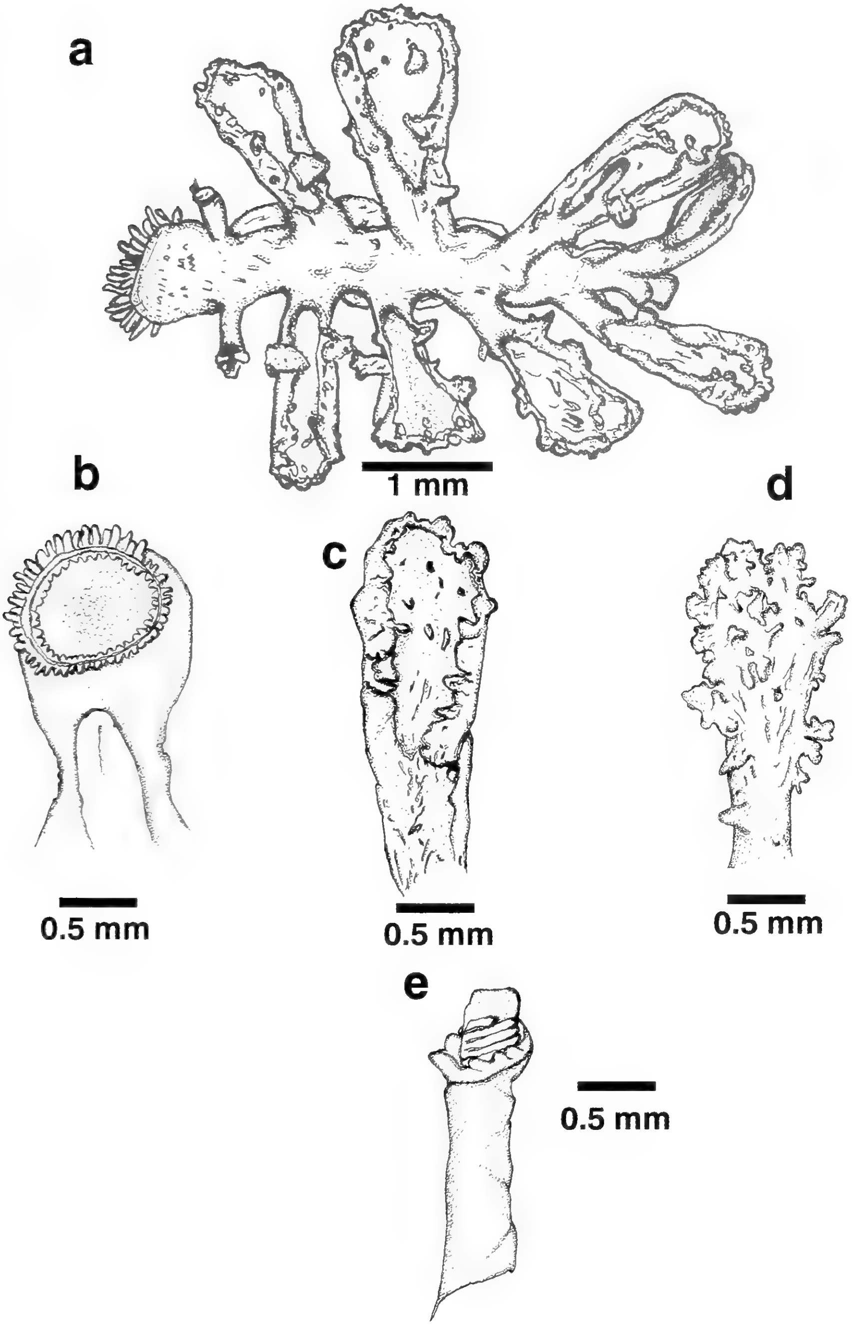

FIGURE 10. *Melibe minuta* sp. nov., External morphology. A: Dorsal view of animal (CASIZ 78517). B: Ventral view of oral hood, mouth, and anterior foot (CASIZ 78533). C: Detail of inward facing surface of ceras CASIZ 78529). D: Detail of outward facing side of ceras (CASIZ 78529). E: Detail of rhinophore (CASIZ 78517).

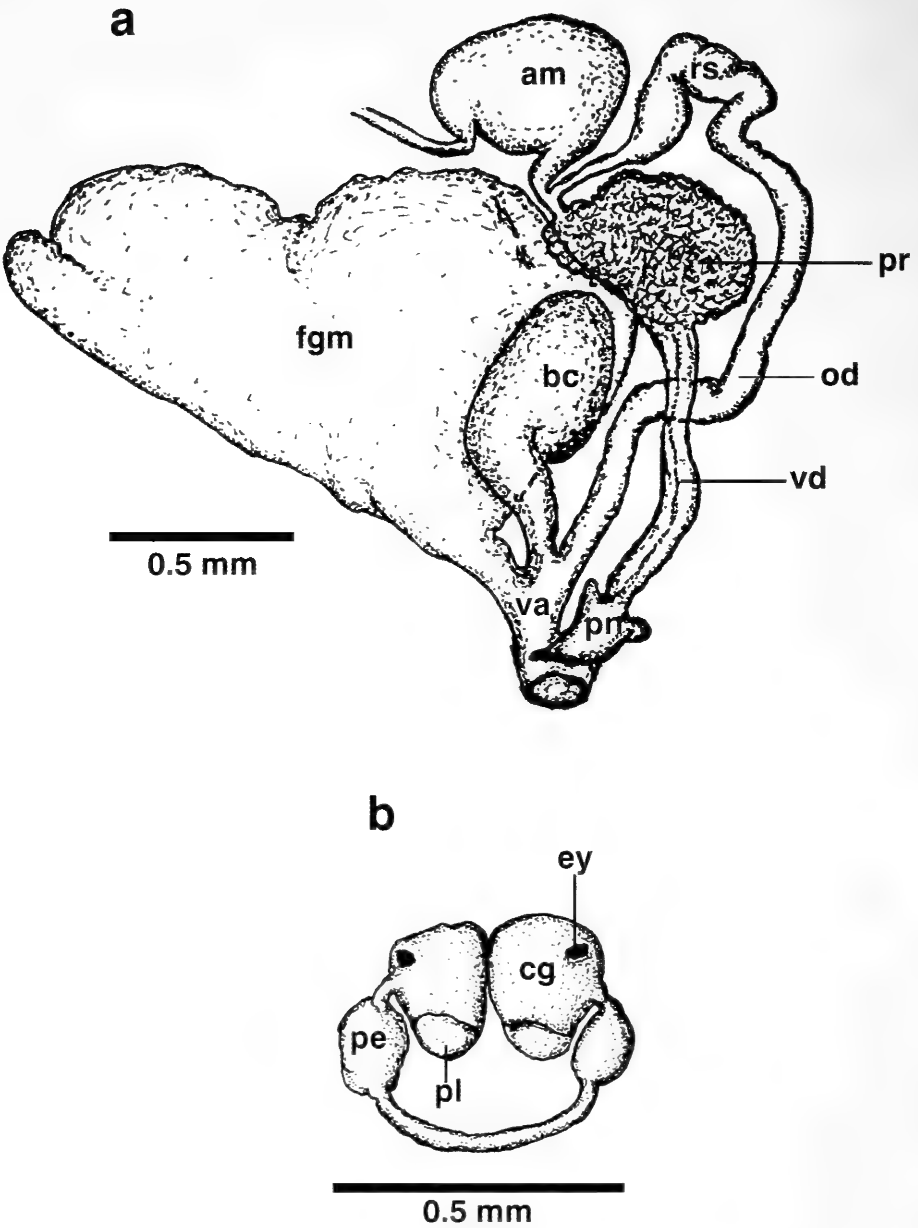

FIGURE 11. *Melibe minuta* sp. nov.., anatomical details. A: Reproductive system (CASIZ 78533). B: Central nervous system. am = ampulla; bc = bursa copulatrix; cg = cerebral ganglion; ey = eye; fgm = female gland mass; od = oviduct; pe = pedal ganglion; pl = pleural ganglion; pn = penis; pr = prostate; rs = receptaculum semenis; va = vagina; vd= vas deferens.

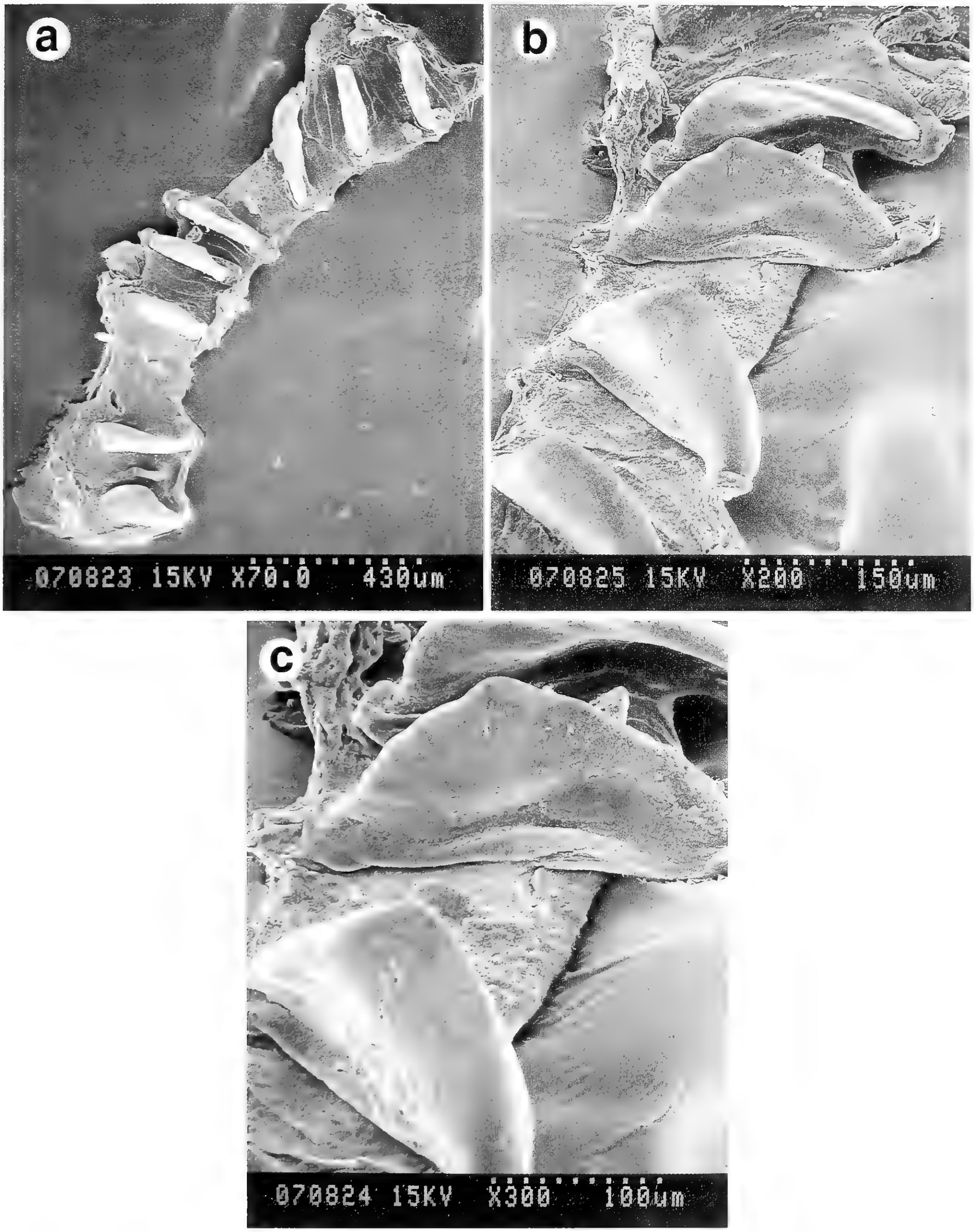

FIGURE 12. *Melibe minuta* sp. nov., SEM's of stomach plates (CASIZ 87918). A: Entire band of stomach plates. B-C: Details of stomach plates.

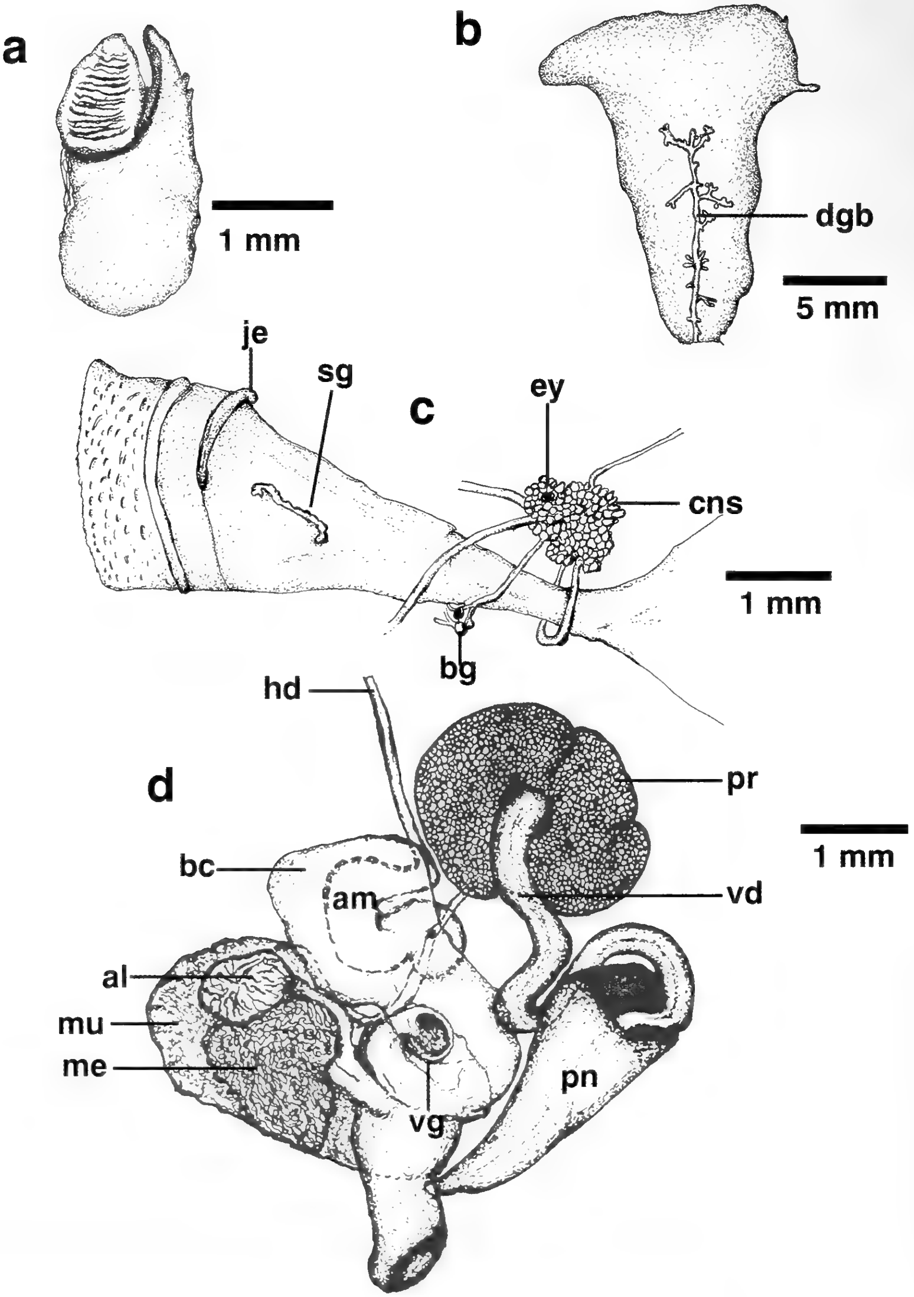

FIGURE 13. *Melibe papillosa* (de Filippi, 1867), morphology and anatomy (CASIZ 89005). A: Rhinophore. B: Ceras. C: Buccal mass and central nervous system. D: Reproductive organs. am = ampulla; al = albumen gland; bc = bursa copulatrix; bg = buccal ganglia; cns = central nervous system; dgb = digestive gland branch; ey = eye; je = jaw edge; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate; sg = salivary gland; vd = vas deferens; vg = vaginal gland.

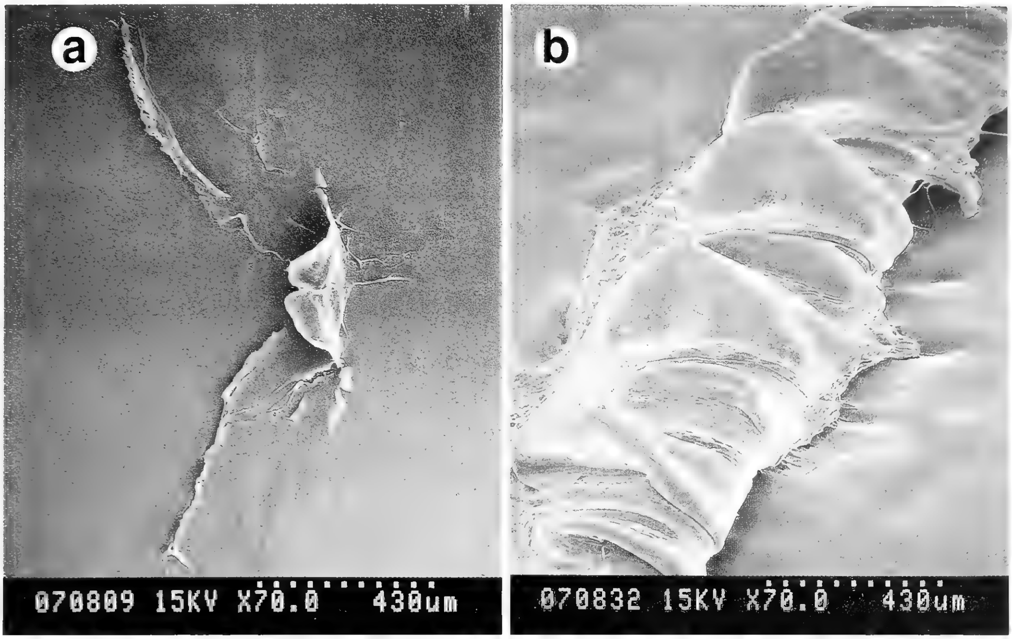

FIGURE 14. *Melibe papillosa*, digestive armature (CASIZ 89005). A: Jaws. B: Stomach plates.

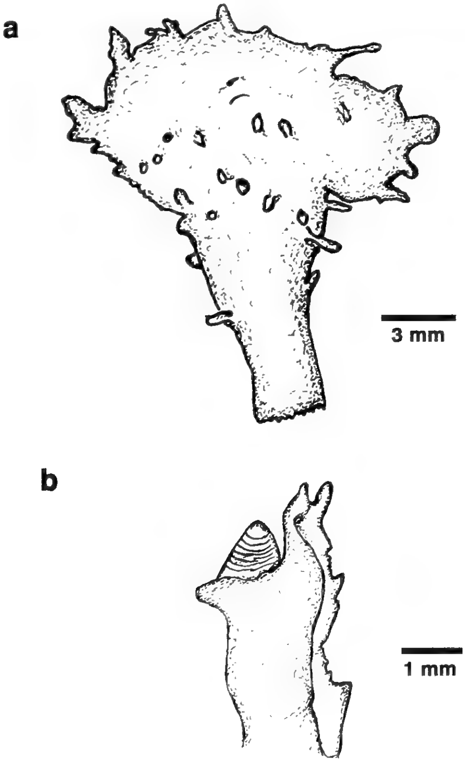

FIGURE 15. *Melibe pilosa* Pease, 1860, external morphology. A: Detail of ceras (CASIZ 61501). B: Detail of rhinophore (CASIZ 16677).

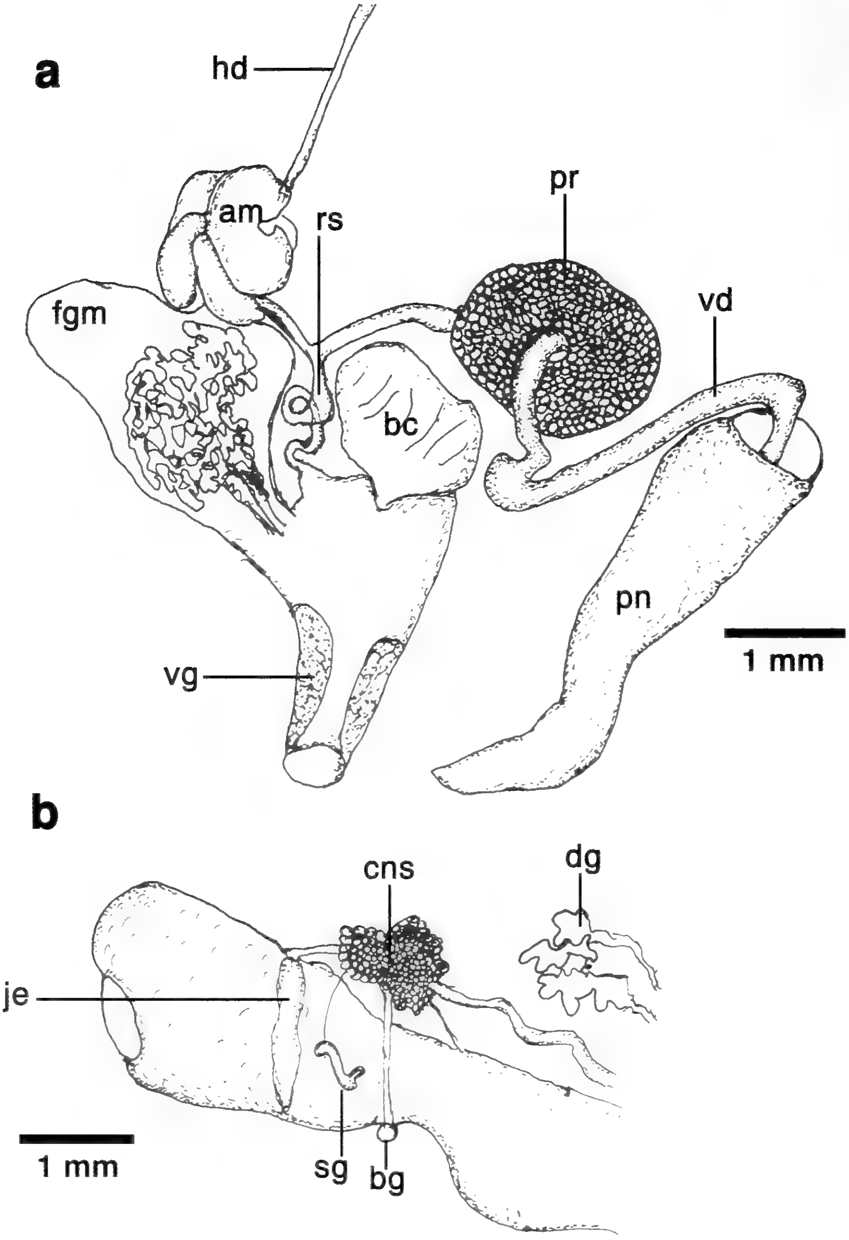

FIGURE 16. *Melibe pilosa*, anatomy. A: Reproductive organs (CASIZ 61516). B: Buccal mass and anterior visceral organs CASIZ 16677). am = ampulla; bc = bursa copulatrix.; bg = buccal ganglia; cns = central nervous system; dg = digestive gland; fgm = female gland mass; hd = hermaphroditic duct; je = jaw edge; pn = penis; pr = prostate; rs = receptaculum semenis; sg = salivary gland; vd = vas deferens; vg = vaginal gland.

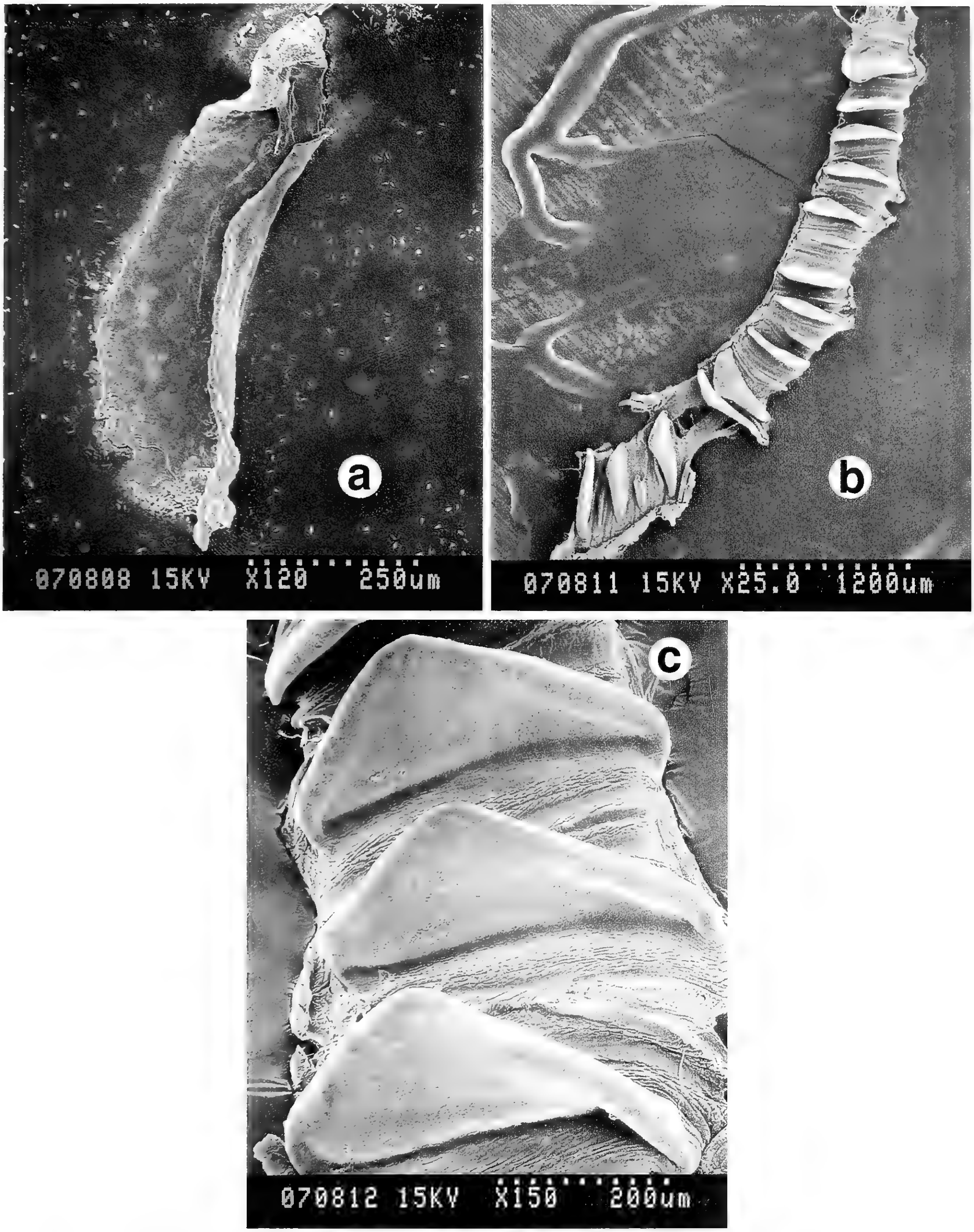

FIGURE 17. *Melibe pilosa*, digestive armature (CASIZ 61506). A: Jaws. B: Girdle of stomach plates. C: Detail of stomach plates.

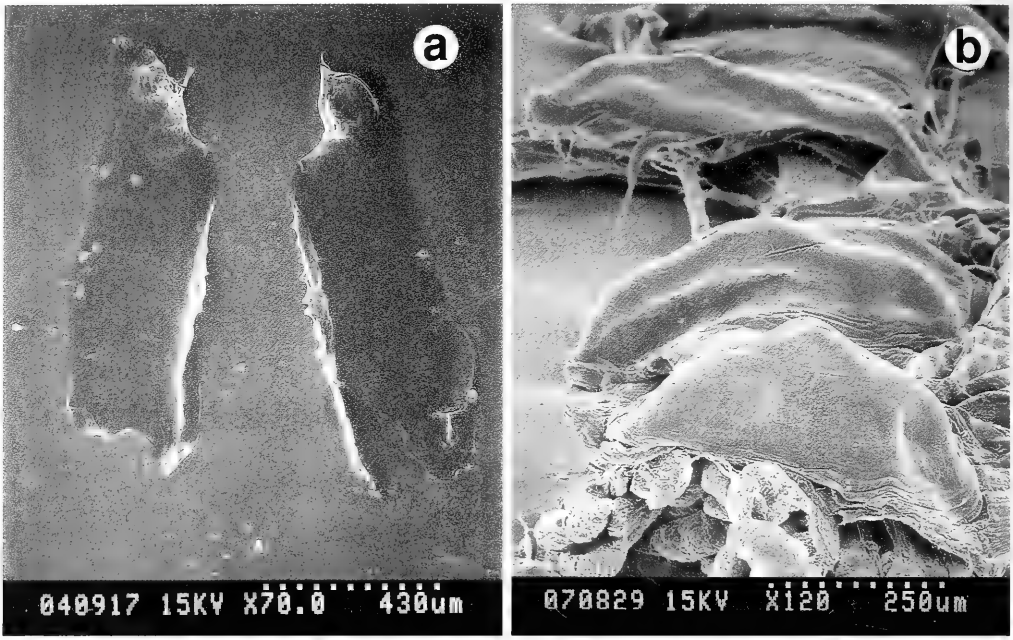

FIGURE 18. *Melibe rosea* Rang, 1829, digestive armature. A: Jaws. B: detail of stomach plates.

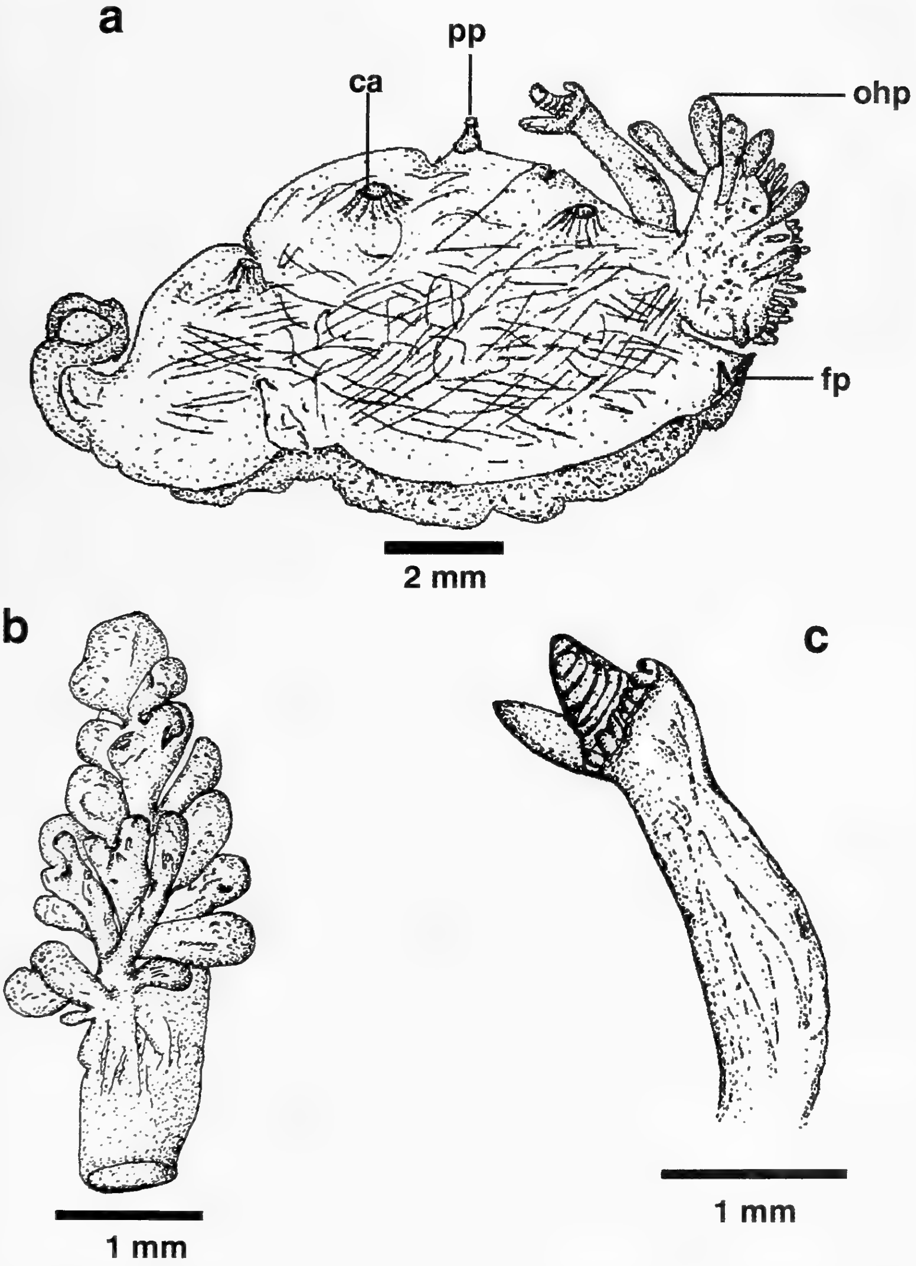

FIGURE 19. *Melibe tuberculata* sp. nov., external morphology. A: Body of preserved specimen without cerata (CASIZ 105639). B: detached ceras (CASIZ 106394). C: Detail of rhinophore (CASIZ 105639). Ca = point of ceratal attachment; fp = foot papillae, ohp = oral hood papillae; pp = unique papillae.

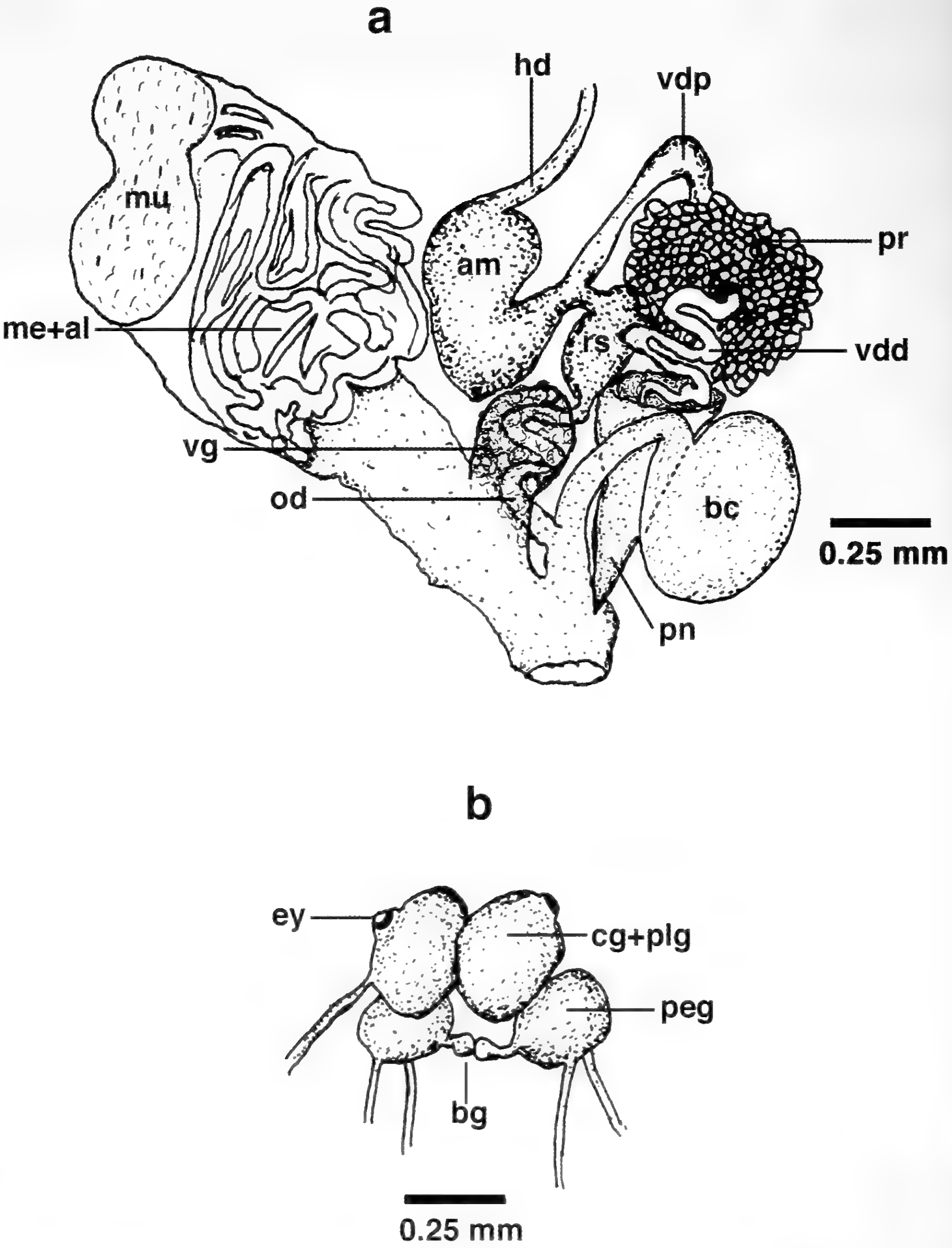

FIGURE 20. *Melibe tuberculata* sp. nov., anatomical details CASIZ 106394). A: Reproductive organs. B: Central nervous system. al = albumen gland; am = ampulla; bc = bursa copulatrix; bg = buccal ganglia; cg = cerebral ganglion; ey = eye; me = membrane gland; mu = mucous gland; od = oviduct; peg = pedal ganglion; plg = pleural ganglion; pn = penis, pr = prostate gland; rs = receptaculum semenis; vg = vaginal gland; vdd = distal vas deferens; vdp = proximal vas deferens.

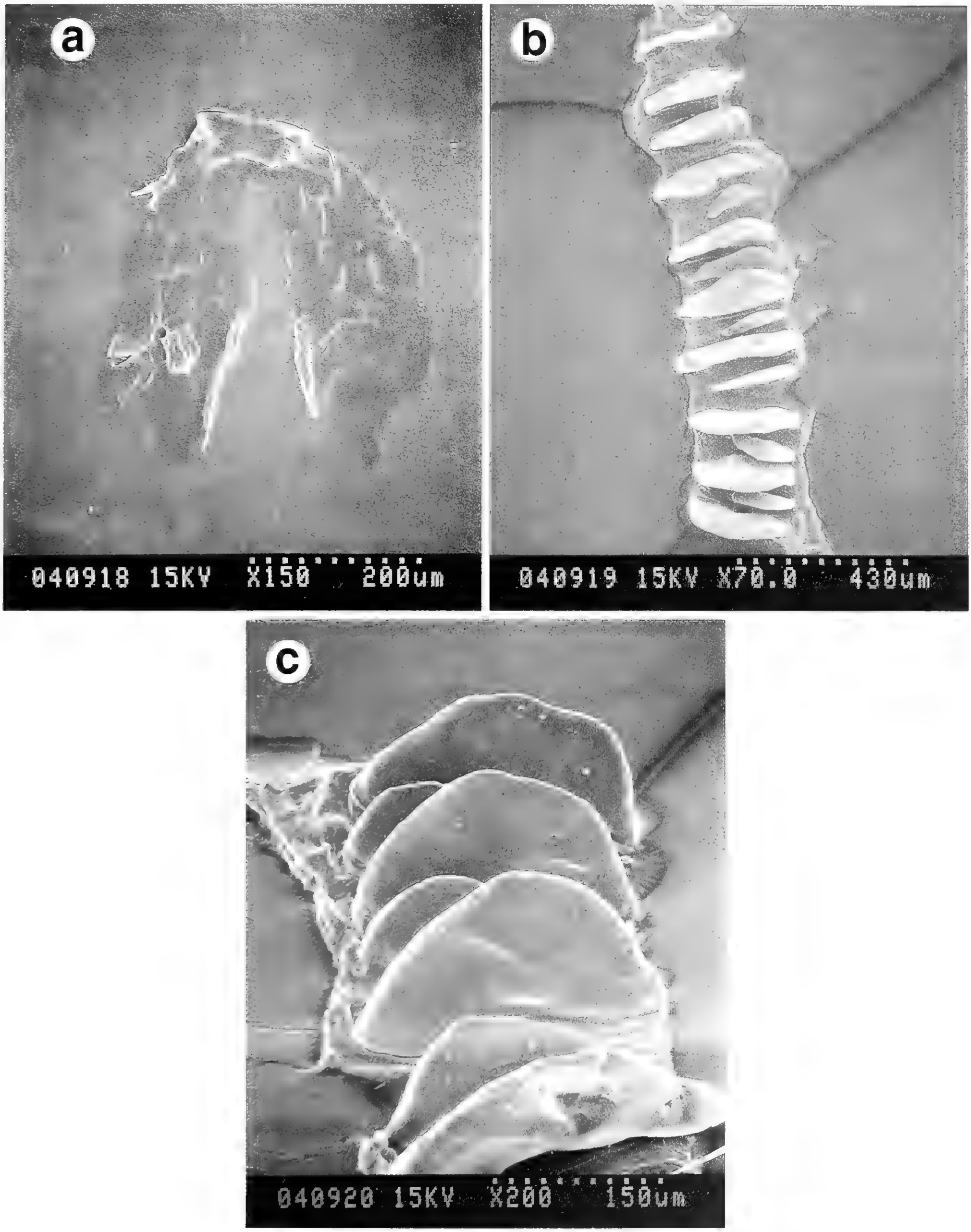

FIGURE 21. *Melibe tuberculata* sp. nov., digestive armature (CASIZ 106394). A: Jaws. B: Girdle of stomach plates. C: Detail of stomach plates.

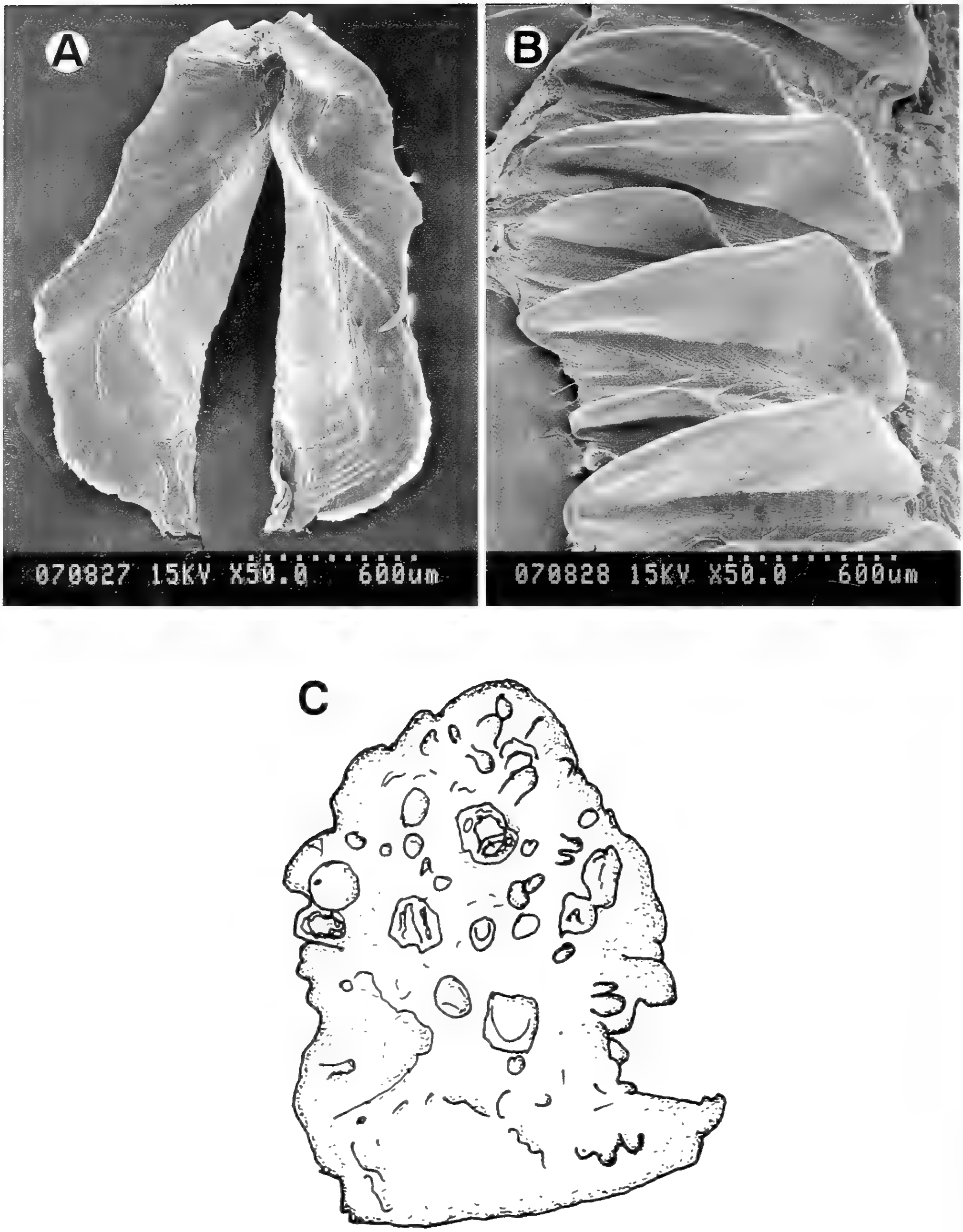

FIGURE 22. *Melibe viridis* (Kelaart, 1858). A: Jaws. B: Detail of stomach plates. C: Detail of ceras (CASIZ 83671).

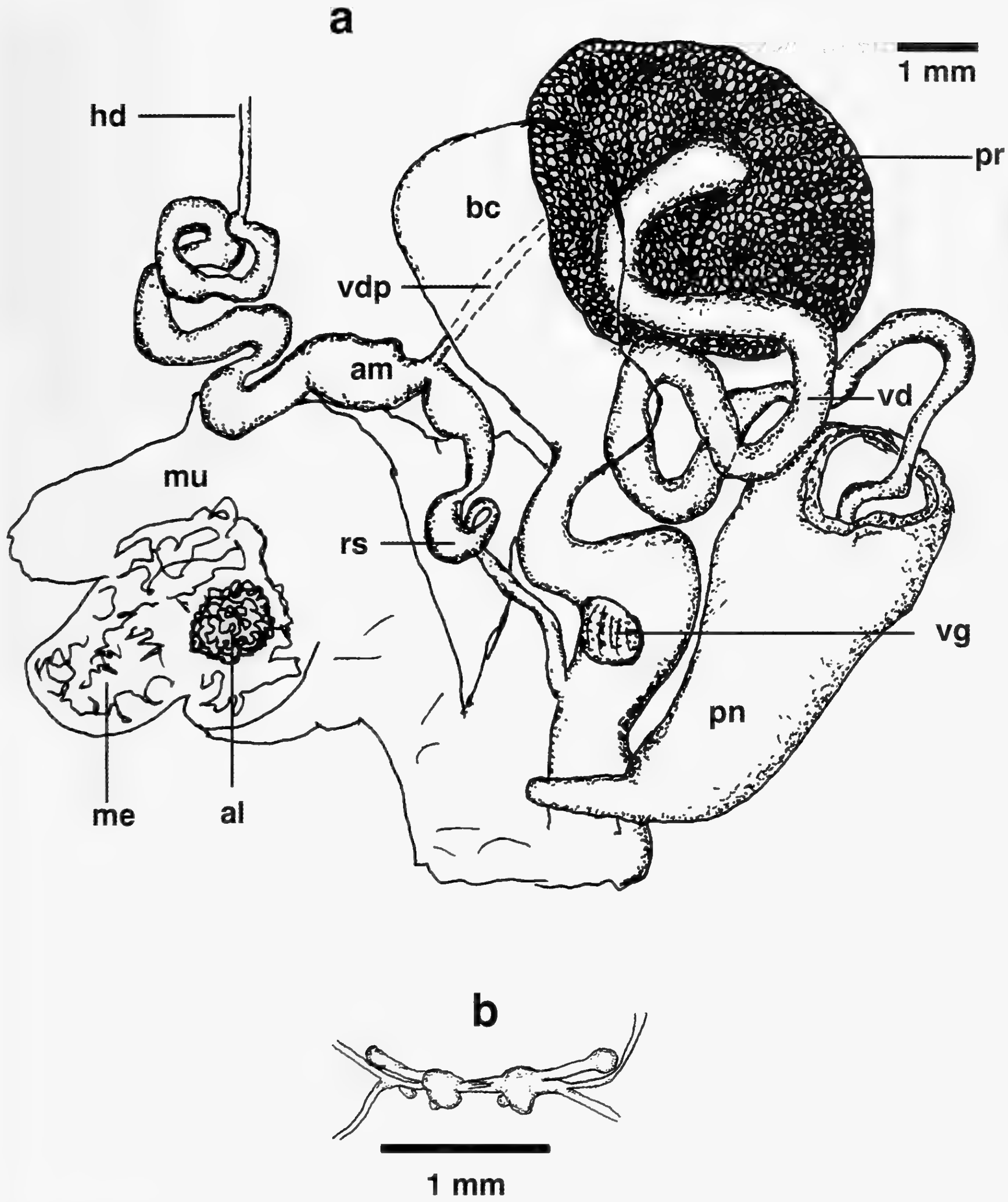

FIGURE 23. *Melibe viridis*, anatomy. A: Reproductive organs (composit drawing of CASIZ 61505 and 103727). B: Detail of buccal ganglia (CASIZ 83671). Al = albumen gland; am = ampulla; bc = bursa copulatrix; hd = hermaphroditic duct; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate gland; rs = receptaculum semenis; vd = distal vas deferens; vdp = proximal vas deferens; vg = vaginal gland.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Marionia	2	1	0	0	2	?	?	?	0	0	0	0	0	?	?	?	0	?	0	0	0	1	0	2	0	0	0	0	2	2	0	2	0	0	1	1	0	2	2	2	?	1	0	0	0	0	0
Fimbria	0	1	0	1	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1	0	5	?	?	?	0	0	0	0	3	0	0	1	1	0	2	2	2	?	1	0	1	0	1	0
australis	?	0	0	1	1	0	?	0	0	0	0	1	1	0	1	0	0	1	1	0	2	2	0	5	?	?	?	0	?	0	0	?	0	1	1	1	0	2	2	?	?	1	0	1	0	0	0
bucephala	1	1	0	1	0	2	1	1	0	1	1	1	1	1	1	0	1	2	1	0	0	1	0	2	1	1	1	1	0	0	0	0	1	0	1	2	0	2	0	1	0	1	1	1	0	0	1
digitata	0	0	1	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	?	1	1	1	1	1	0	1	1	0	1	1	3	0	1	0	0	0	1	0	1	1	1	2	1	0	0	1
engeli	1	0	1	1	1	2	0	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	2	1	1	1	1	0	1	0	3	0	1	0	0	0	1	1	1	0	1	2	1	0	0	1
leonina	0	1	0	1	0	1	2	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0	3	?	?	?	1	0	1	0	3	1	0	1	1	0	0	0	1	0	1	0	1	2	0	0
liltvedi	2	1	0	1	0	2	1	0	0	0	1	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0	1	2	0	2	2	0	?	1	0	1	0	0	0
megaceras	1	1	0	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	0	2	0	0	2	0	0	1	1	0	0	1	2	0	1	1	2	0	1	0	1	0	0	2	1	1	0	1
minuta	0	1	0	1	1	1	2	0	0	0	0	1	1	1	1	1	0	1	1	1	2	0	1	0	0	0	0	1	1	1	1	3	0	1	1	0	0	1	0	1	0	1	0	1	0	0	1
papillosa	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	2	1	1	1	1	0	0	0	1	1	0	1	2	0	0	0	1	0	1	1	1	0	0	1
pilosa	1	0	0	1	0	2	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0	1
rosea	2	1	0	1	0	2	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	2	0	2	2	0	?	0	0	1	0	0	0
tuberculata	0	0	1	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	3	0	0	0	0	0	1	1	1	1	0	2	1	0	0	1
viridis	1	1	0	1	0	2	1	1	0	0	1	1	1	1	1	1	1	2	1	0	1	0	0	2	1	1	1	1	1	1	0	0	1	0	1	2	1	2	0	1	0	1	1	1	0	0	1

FIGURE 24. Matrix of species and characters used in phylogenetic analysis

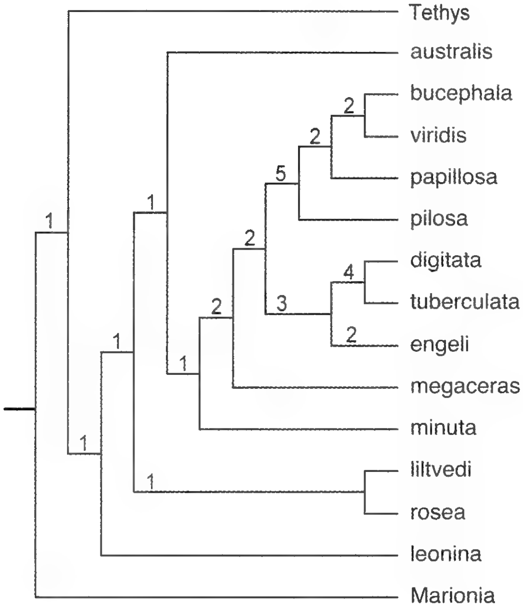

FIGURE 25. Tree resulting from phylogenetic analysis of data. Bremer support values shown at nodes.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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On the Egg-guarding Behavior of a Chinese Symphytognathid Spider of the Genus *Patu* Marples, 1951 (Araneae, Araneoidea, Symphytognathidae)

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The eggsacs and egg-guarding behavior of a species of *Patu* from montane forests in the Gaoligongshan of western Yunnan Province, China, mirror that reported by Marples (1951) for *P. samoensis* from Samoa. The eggsacs are deposited as a loose group on the frame near the periphery of the spiral portion of the web.

Symphytognathid spiders are known for their small size and beautiful, finely-woven, horizontal orb webs. Most adults are less than 1mm in total length and, with an adult female at 0.55mm or less, *Anapistula caecula* Baert and Jocqué from West Africa may be the world's smallest spider (Baert and Jocqué 1993). Symphytognathids appear to be common in moist environments in the tropics and south temperate regions but their small size has made them rare in collections. They are most often collected by sieving leaf litter, a technique that reveals little of their life style. *Curimagua bayano* from Panama is unique in being a kleptoparasite in the webs of diplurid spiders, but most other symphytognathids appear to be free-living web-builders (Forster and Platnick 1977). Symphytognathid webs have been described from several continents. The majority of these observations are of horizontal, 2-dimensional orb webs with many accessory radial lines that anastomose before reaching the hub (Forster and Platnick 1977, fig. 1; Coddington 1986, fig. 12.24; Hiramatsu and Shinkai 1993, fig. 1). Most observations are on the webs of various *Patu* species from Samoa (Marples 1951), Fiji (Marples 1951; Forster 1959), Central America (Coddington 1986; Eberhard 1987) and Japan (Hiramatsu and Shinkai 1993). Undescribed *Patu* species from Tanzania, Madagascar and Australia make similar webs (Griswold, unpublished data). A Puerto Rican *Anapistula* makes a similar web (Coddington 1986, fig. 12.23; Griswold et al. 1998, fig. 3c). Hickman (in Forster and Platnick 1977:3) reported that the Tasmanian *Symphytognatha globosa* Hickman, 1931 makes a web of a few irregular horizontal threads. This is unique among symphytognathids, and at least the South African *Symphytognatha imbulunga* Griswold, 1987 makes a horizontal orb typical for the family (Griswold, unpublished).

Eggsacs of Symphytognathidae have previously been reported by Hickman in the original description of the family (Hickman 1931) for captive spiders reared in the lab and by Marples for spiders in the field (Marples 1951). We here report on the eggsacs of a *Patu* species from southwestern China, which resemble those described by Marples for the Samoan *P. samoensis* Marples, 1951 and Fijian *P. vitiensis* Marples, 1951 fifty years previously.

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STUDY SITE

Symphytognathids were observed at 2000m elevation near Qiqi He in the Nujiang State Nature Reserve, Yunnan Province, China. This nature reserve is in the Gaoligongshan (Gaoligong Mountains), which extend north-south along the border between China and Myanmar, dividing the watersheds of the Irrawaddy (Dulong Jiang) and Salween (Nu Jiang) Rivers. Because of its physical isolation and long-standing political instability the area is less disturbed than most other regions in Yunnan. Large tracts of old growth forest with a rich flora of hardwood and coniferous trees persist in the mountains. *Taiwania*, a relictual genus of Taxodiaceae, occurs in this area. Affinities of known spiders are with the Himalayas (Griswold et al. 1999). This area, part of the 'East Himalayan Region,' has been recognized as an area of biotic richness and endemism (Myers 1988).

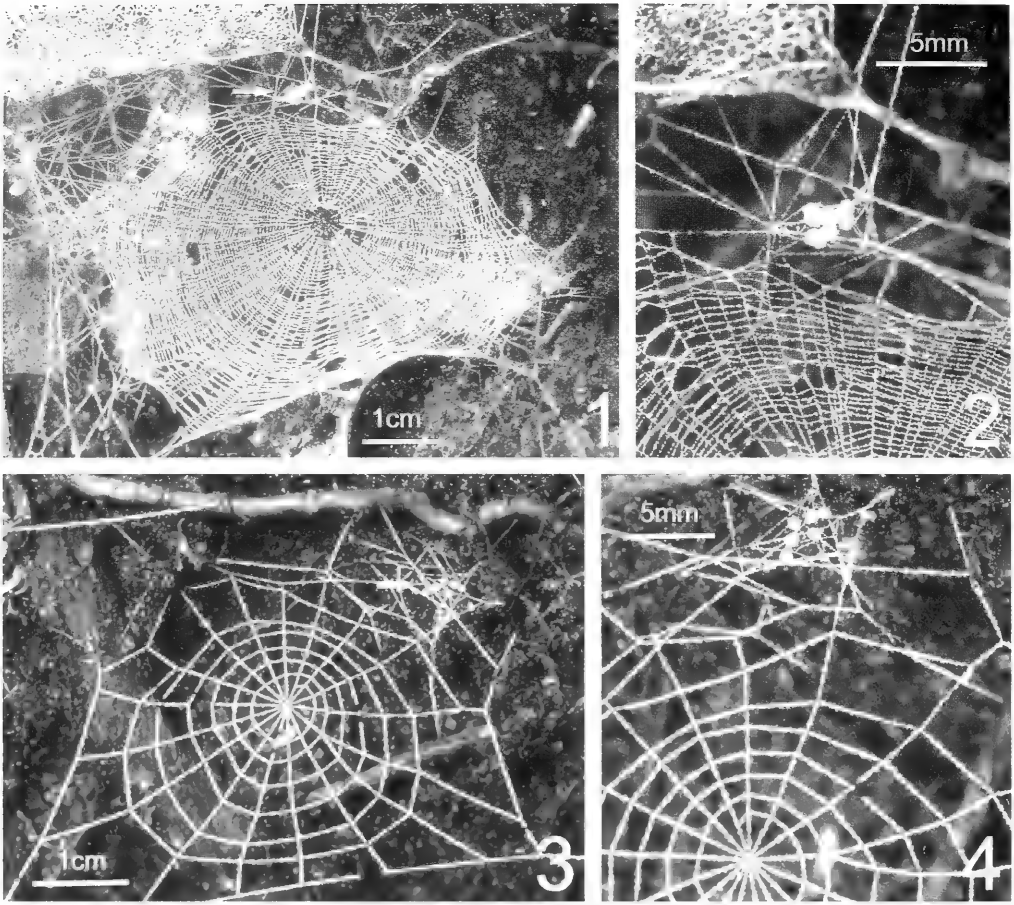
MATERIALS AND METHODS

Dark, shaded embankments along stream courses and hillsides, the sides of fallen logs, and tree trunks were searched for symphytognathid webs. Because of their fine structure and the dark environment in which they occur, webs were invisible, although those containing eggsacs could be located by noticing these tiny, white objects. Corn starch was broadcast into suitable habitats and clung to small webs, including those of symphytognathids, making them visible. Spiders were collected by visualizing the web with corn starch, locating the spider (in most cases hanging at the hub), placing a spoon beneath the web, and gently tapping the center of the web, causing the spider to drop into the spoon. A description of the method and photos of the site and spiders are available at: *http://www.calacademy.org/research/cnhp/* and *http://www.calacademy.org/science_now/archive/academy_research/griswald_10172000.html*. The locality record is China: Yunnan Province: Nujiang Prefecture: Nujiang State Nature Reserve, Qiqi He, 9.9 air km W of Gongshan, 27°43′N, 98°34′E, 2000m, 9–14 July 2000, C.E. Griswold, H.–M. Yan, and D. Ubick. Close up photos of the eggsacs and female (Figs. 5–6) were taken with a Leica MZ12.5 stereomicroscope and the numerous photos with different focal planes were digitally montaged into one in-focus image using the software package Automontage® made by Syncroscopy. Voucher specimens are deposited in the College of Life Science, Hunan Normal University (CASENT Nos. 9000339, 341, 342, 369, 371 and 9000372) and Department of Entomology, California Academy of Sciences (CASENT Nos. 9000338, 340, 343, 370, 373, and 9000374).

OBSERVATIONS

Sixty adult females, two juveniles and eight adult males were collected during five days of collecting. All individuals were taken from horizontal 2-D orb webs (Figs. 1, 3) that were typical of those previously described for symphytognathids. Although at the time of collecting it was not possible to determine the sex or maturity of the spiders, occasionally two would drop from the center of the same web suggesting that males and females could be found there together. The spiders were identified as an undescribed species of *Patu*, having the characters diagnostic for that genus (Forster and Platnick 1977:15): chelicerae fused only near the base, an elevated pars cephalica and six eyes in three diads. The male and female genitalia are unlike those of any described species.

Eggsacs were found attached to frame lines on the periphery of the webs of six adult females (Figs. 1, 3), always on that side of the web nearest the surface of an embankment, log or tree trunk. If eggsacs were present the female hung close to them. Females without eggsacs hung from the hub at the center of the web. The eggsacs were attached to the web by one or a few silken lines and were separate (Fig. 4) or contiguous (Fig. 2). In some cases bits of moss, wood (Fig. 5) or other

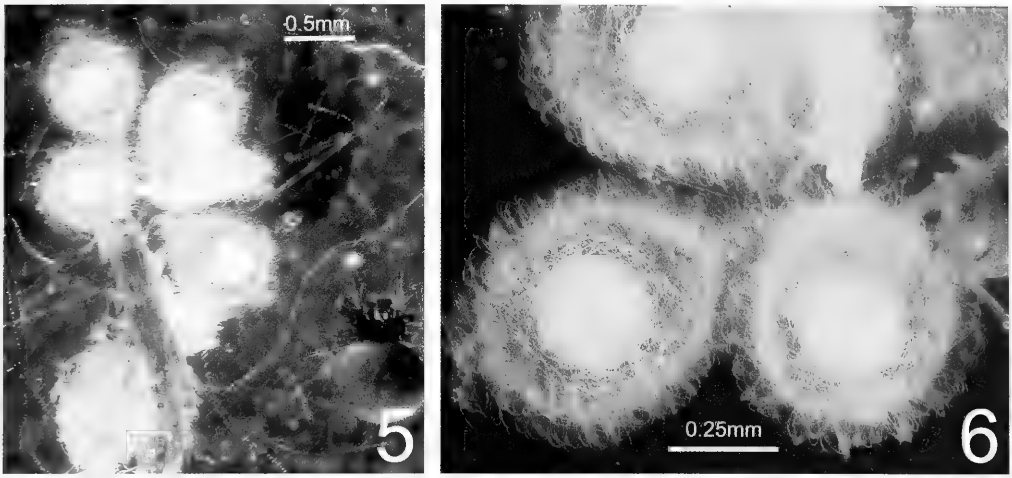


FIGURES 1–4. Webs and eggsacs of *Patu* sp. from QiQi, Gaoligongshan, China. Webs and eggsacs have been dusted with corn starch to enhance their visibility. 1. Completed web; arrow to eggsacs at top of photo (Voucher CASENT 9000342). 2. Close up of eggsac group on frame at periphery of web (Voucher CASENT 9000342). 3. Incomplete web with temporary spiral; arrow to eggsac at upper right of photo (Voucher CASENT 9000340). 4. Close up of eggsac group on frame at periphery of web (Voucher CASENT 9000340). Photos 1 and 2 by L. Dong, 3 and 4 by C. Griswold.

debris were attached to one or more of the eggsacs, but in all cases the eggsacs were clearly exposed. There was no attempt to camouflage the eggsacs. The number of eggsacs per group ranged from four to eleven ($\bar{X} = 7$, $N = 6$). The eggsacs were about the same size as the female that made them (Fig. 5): females ranged from 0.74 to 0.96 mm in total length, whereas the eggsacs ranged from 0.64 to 1.00mm in diameter (N eggsacs measured = 35, X diameter = 0.82mm). Eggsacs contained either a single egg or developing embryo and all were translucent but rendered conspicuous even in their low light habitats by the single bright white egg or embryo within each one. Each eggsac consisted of a sphere of fine silk woven loosely and covered with loops of silk projecting from the surface (Fig. 6). This is exactly the form described by Marples (1951:51) for the "cocoons" of *P. samoensis*.

DISCUSSION

The eggsac placement discovered in this new Chinese species of *Patu* is identical to that found by Marples fifty years earlier for *Patu* species from Samoa and Fiji. The only other symphytog-



FIGURES 5–6. Eggsacs of *Patu* sp. from QiQi, Gaoligongshan, China, preserved specimens. 5. Five eggsacs with female at lower right (Voucher CASENT 9000340). 6. Close up of eggsacs (Voucher CASENT 9000340).

nathid for which the eggsac is known, *Symphytognatha globosa* Hickman from Tasmania, makes a strikingly different, densely woven, triangular eggsac studded with sharp silken points (Hickman 1931, Plate I, fig. 3). The uniformity of eggsacs within *Patu* and their difference from *Symphytognatha* suggest that eggsac form may be an informative character within the Symphytognathidae.

Griswold, Coddington, Hormiga and Scharff (1998) placed the Symphytognathidae in the "Symphytognathoids", which comprised the Anapidae, Mysmenidae, Symphytognathidae and Theridiosomatidae and were characterized by the unambiguous synapomorphies of posteriorly truncate sternum, loss of the claw on the female palp, greatly elongate fourth tarsal median claw, and double attachment of the eggsac near the hub. Schütt (2003) considered the same taxa, with the addition of the Microphocommatidae, as Symphytognathidae *sensu lato*. In neither of those papers, nor in an earlier quantitative treatment of araneoid phylogeny (Coddington 1990), was symphytognathid eggsac attachment behavior scored for this family because Marples' field observation was overlooked and Hickman's lab observations were considered possibly artifactual. Character 91 in Griswold et al. (1998) was "Eggsac doubly attached: (0) absent; (1) present". The authors noted that "basal theridiosomatid genera such as *Ogulnius, Plato, Naatlo, Epeirotypus*, the anapids *Anapis, Anapisona*, and the mysmenids *Mysmena* and *Maymena* retain their eggsacs at or near the hub of their webs . . . attached by two silk lines within the web or with one line attaching to the substrate" (Griswold et al. 1998:45). This behavior should be more precisely defined as eggsac doubly attached during construction, because whereas some taxa leave the eggsac doubly attached others, e.g., distal theridiosomatids (some *Plato*), cut the bottom attachment so that the eggsac appears singly attached (J. Coddington, pers. commun.). The previous second attachment may be visible as a nubbin on the eggsac. The results of the analysis of Griswold et al. (1998) implied such behavior for the Symphytognathidae. It is uncertain if this is the case for this species of *Patu*, but at least the upper eggsac in Figure 5 has a small nubbin on the rounder end that may be the vestige of a former double attachment.

Other questions remain. Although numerous *Patu* have been observed on several continents, eggsacs have been observed only for the Samoan and Fijian species (Marples 1951) and this Chinese species. Why should this behavior be so rarely observed? The haphazard arrangement of the eggsacs on the frame of the web suggests that they may have been transported there after construction. Perhaps other *Patu* species transport the eggsacs farther, where they are overlooked.

Behavioral characters will undoubtedly help to clarify the evolution of these minute spiders. We hope that Arachnologists, armed with corn starch, spoons, patience and good eyesight, will add to our growing store of observations of these cryptic but fascinating animals.

ACKNOWLEDGMENTS

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Two New Labrid Fishes of the Genus *Oxycheilinus* from the South Pacific

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The fish family Labridae, popularly called wrasses, is the second largest family of marine fishes in the world (after the Gobiidae), with 453 species (Parenti and Randall 2000). Most species (82%) are found in the tropical and subtropical Indo-Pacific region, and ones previously unknown to biologists continue to be discovered. In a phylogenetic study of labrid fishes of the tribe Cheilinini, Westneat (1993) recognized two lineages, a "cheiline" lineage of five genera, all but one with species confined to the Indo-Pacific, and a "pseudocheiline" lineage. The genera of the "cheiline" lineage are *Cheilinus*, *Doratonotus*, *Epibulus*, *Oxycheilinus*, and *Wetmorella*. *Oxycheilinus* was proposed by Gill (1862) for *Cheilinus arenatus* Valenciennes. His genus was not recognized by Bleeker and Pollen (1874), Jordan and Snyder (1902), and later authors. However, Westneat provided characters to distinguish it from *Cheilinus*, and he has been followed by most recent authors. In addition to *O. arenatus*, Westneat classified the following species in *Oxycheilinus*: *O. bimaculatus* (Valenciennes), *O. celebicus* (Bleeker), *O. digrammus* (Lacepède), *O. mentalis* (Rüppell), *O. orientalis* (Günther), and *O. unifasciatus* (Streets).

In 1971, while diving in 49 m off Henderson Island in the Pitcairn Islands, the first author speared an unknown labrid fish with narrow dark stripes that seemed to be a species of *Cheilinus* (*Oxycheilinus* then not separated from *Cheilinus*), but it tore free. Later the same year off Tahiti in 76 m he speared the same species, but again it escaped. Richard L. Pyle collected what is probably the same species while diving in 85 m off Rarotonga, Cook Islands in 1991 and made it available for our description. It clearly represents an undescribed species of *Oxycheilinus*.

We also have nine specimens of a second new species of *Oxycheilinus* collected from 1988 to 2001 in the Chesterfield Bank of the Coral Sea, off New Caledonia, and New South Wales. The purpose of the present paper is to describe these two species to make the names available for a book on reef and shore fishes of the South Pacific that has been prepared by the first author. A revision of *Cheilinus* and *Oxycheilinus* is in progress by us which will provide a key, diagnoses, and illustrations of all the species.

MATERIALS AND METHODS

Specimens of the new species of *Oxycheilinus* were deposited at the following institutions: Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); Museum Victoria, Melbourne (NMV); and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

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Lengths given for specimens are standard length (SL), the straight-line distance from the front of the upper lip to the base of the caudal fin (posterior end of the hypural plate). Head length is measured from the same median anterior point to the end of the opercular membrane, and snout length from the same point to the fleshy edge of the orbit. Body depth is the maximum depth, and body width the greatest width just posterior to the gill opening. Orbit diameter is the greatest fleshy diameter, and interorbital width the least fleshy width. Caudal-peduncle depth is the least depth; caudal-peduncle length is measured horizontally from the rear base of the anal fin to the caudal-fin base. Dorsal and anal-fin spines are measured from the tip to the point where they emerge from the body. Caudal-fin length is measured horizontally from the fin base to a vertical at the tip of the longest ray.

Pectoral-ray counts include the uppermost rudimentary ray. Gill-raker counts were made on the first gill arch and include rudiments; the upper-limb count is given first, and the raker at the angle is contained in the lower-limb count.

Proportional measurements are presented in Table 1 as percentages of the standard length; those in the text are rounded to the nearest 0.05. Data in parentheses in the descriptions that follow refer to paratypes, if any, and if different from those of the holotype.

SPECIES DESCRIPTIONS

Oxycheilinus lineatus Randall, Westneat and Gomon, sp. nov.

Plate 1, Fig. A; Table 1.

MATERIAL EXAMINED.— HOLOTYPE: BPBM 39091, male, 159.5 mm, Cook Islands, Rarotonga, east side, off residence of Charles J. Boyle, ledge on slope above drop-off, 85 m, hand net, R. L. Pyle, 5 January 1991.

DIAGNOSIS.— Dorsal rays IX,10; anal rays III,8; pectoral rays 13; lateral-line interrupted, the pored scales to caudal-fin base 16 + 7; gill rakers 4 + 8; body moderately elongate, the depth about 3.4 in SL; head length about 2.5 in SL; snout long and pointed, about 2.5 in head; dorsal profile of snout nearly straight, of nape slightly convex; lower jaw slightly projecting; maxilla ending a half-eye diameter before anterior margin of orbit; caudal fin (of adult male) slightly rounded, the upper three principal rays a little prolonged; membranes of spinous portion of dorsal fin incised one-third to one-half length of spines; pectoral fins short, about 3.2 in head; body below lateral line with 12 narrow, slightly irregular, dark brown stripes separated by white lines; body above lateral line with similar but more irregular bands; head with narrow dark brown bands radiating from eye except anteriorly; snout bluish gray with brown dots; a blackish blotch on basal half of first membrane of dorsal fin.

DESCRIPTION.— Dorsal rays IX,10; anal rays III,8; all dorsal and anal rays branched, the last to base; pectoral rays 13, the first rudimentary, the second unbranched; pelvic rays I,5; principal caudal rays 13, the middle 11 branched; upper procurrent caudal rays 5; lower procurrent caudal rays 4; lateral-line interrupted, the pored scales 16 + 7; 2 pored scales on caudal-fin base, the last very large and pointed; scales above lateral line to base of dorsal spines 1.5; scales below lateral line to origin of anal fin 5.5; median predorsal scales 5 (+ 1 or more embedded anteriorly); gill rakers 4 + 8; pseudobranchial filaments 19; branchiostegal rays 5; vertebrae 23.

Body moderately elongate, the depth 3.4 in SL; body width 1.95 in depth; head length 2.45 in SL; snout long and pointed, 2.5 in head; dorsal profile of snout nearly straight, of nape slightly convex; orbit diameter 5.55 in head; interorbital space strongly convex, the least fleshy width 3.9 in head; caudal-peduncle depth 2.7 in head; caudal-peduncle length 3.4 in head.

Lower jaw slightly projecting and mouth a little oblique, forming an angle of about 20° to horizontal axis of body; maxilla ending a half orbit diameter before anterior edge of orbit, the upper-jaw length 2.8 in head; a pair of broadly spaced incurved canine teeth anteriorly in each jaw, the lowers about half as long as uppers and fitting inside uppers when mouth closed; a row of 15 closely set conical teeth of moderate size along side of upper jaw, the largest anterior to mid-side; lower jaw with a row of 17 comparable conical teeth on side of lower jaw, but a little smaller on average than those of upper jaw; no inner rows of small teeth in jaws, and no teeth on palate. Tongue slender, the tip rounded, reaching anteriorly only a little more than half distance to front of jaws. Lips thick but not fleshy; no flap on side of lower lip. Gill rakers small and simple, those on lower limb nearly sessile; longest gill raker on lower limb about equal to longest gill filaments, about one-third orbit diameter. Nostrils as small as sensory pores, the anterior in a low membranous tube with a short posterior flap about three-fourths orbit diameter before upper part of eye; posterior nostril behind and slightly dorsal to anterior nostril, the internarial space about equal to pupil diameter.

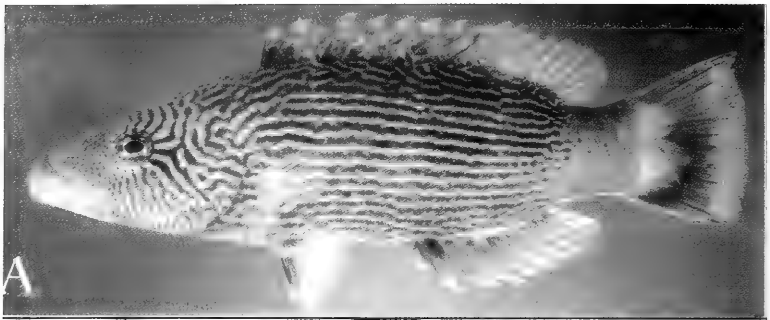
Upper part of posterior edge of preopercle covered by a scale to level of a pupil diameter below orbit; ventral edge of preopercle free nearly to a vertical at posterior end of maxilla; outer and ventral part of preopercle thin and membranous, with a slight indentation in margin above rounded corner.

Scales cycloid, thin, and membranous, but adherent; head scaled except for membranous flange of preopercle, snout, chin, and anterior interorbital space; predorsal scales ending in an embedded lateral pair of scales in posterior interorbital space; scales of lateral line with a single horizontal tubule, ending in a pore; first lateral-line scale at upper end of gill opening; anterior lateral line following dorsal contour of body, the posterior part midlateral on caudal peduncle; scales on thorax only slightly smaller than largest on side of body; no scales on base of dorsal or anal fins except a few in middle of soft portions with about half scales extending onto base of fins; caudal fin with scales on basal half, the most posterior a vertical row of three very large scales, the middle one the last scale of lateral line; paired fins without scales except for a slender midlateral scaly process extending posteriorly from base of pelvic fins a little more than half length of pelvic spines; a slender axillary scale above base of pelvic fin, partly covered by an unusually large scale between bases of pelvic and pectoral fins.

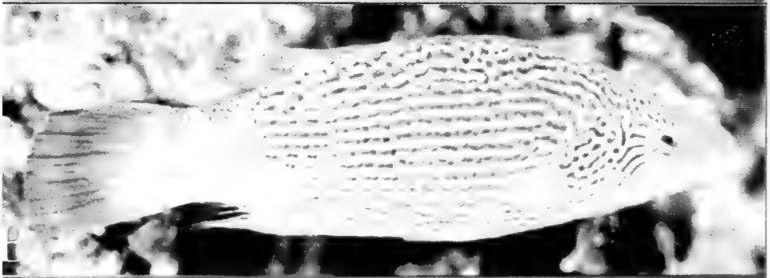
Origin of dorsal fin on a vertical at posterior end of opercular membrane, the predorsal length 2.4 in SL; dorsal spines progressively longer, the first 6.45 in head, and the ninth 3.7 in head; membranes of spinous portion of dorsal fin incised one-third to one-half length of spines; each interspinous membrane of dorsal and anal fins extending above spine tips with support of a stout cirrus from near tip of each spine; first dorsal soft ray longest, 3.25 in head (but remaining rays except last two nearly as long); origin of anal fin below base of eighth dorsal spine, the preanal length 1.55 in SL; first anal spine 7.2 in head; second anal spine 4.35 in head; third anal spine 3.8 in head; first anal soft ray longest, 3.3 in head; caudal fin slightly rounded, the three uppermost principal rays a little prolonged, the fin length 4.0 in SL; fourth pectoral ray longest, 3.25 in head; origin of pelvic fins slightly posterior to lower base of pectoral fins, the prepelvic length 2.35 in SL; pelvic spine 3.7 in head; first pelvic soft ray longest, not approaching anus, 2.45 in head.

Color of holotype in alcohol: light brown with 12 slightly irregular, narrow, dark brown stripes on body below lateral line, the paler interspaces a little broader than dark stripes; dark stripes ending posteriorly below rear base of dorsal fin; a few scattered dark dots on upper half of caudal peduncle; body above lateral line and on nape with similar narrow bands but progressively more irregular dorsally and anteriorly, those extending from nape onto opercle forming a convoluted pattern; head otherwise light brown with narrow dark brown bands radiating from eye except posteriorly, the anterior ones dotted, the upper ones breaking into dots in interorbital; snout light grayish

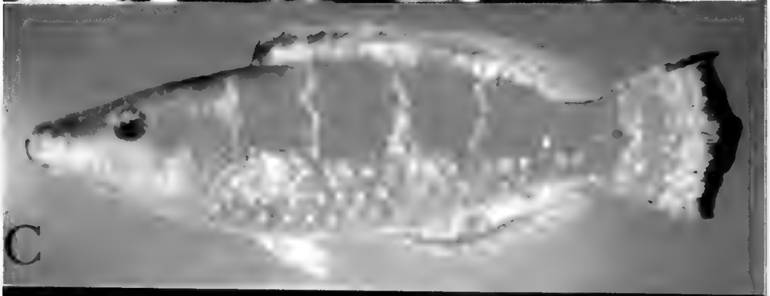
Plate 1



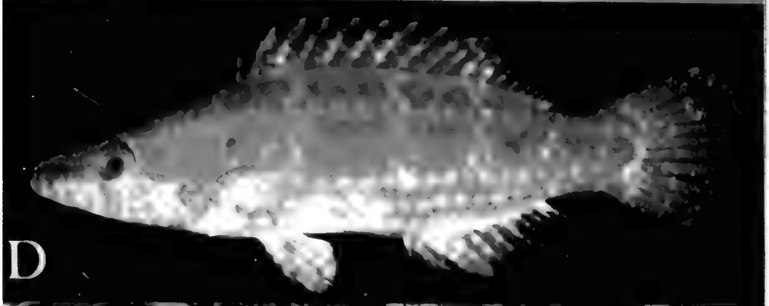
A. Holotype of *Oxycheilinus lineatus* (BPBM 39091), male, 159.5 mm SL, Rarotonga, Cook Islands, 85 m (J. Randall).



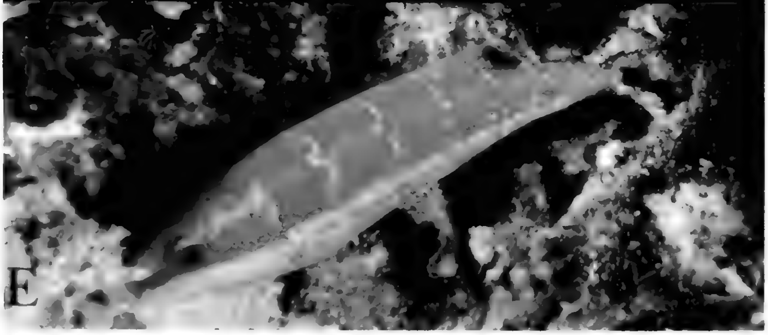
B. Underwater photograph of *Oxycheilinus lineatus*, Rurutu, Austral Islands, 70 m (Y. Lefevre).



C. Holotype of *Oxycheilinus nigromarginatus*, BPBM 33686, male, 111.6 mm SL, Chesterfield Bank, Coral Sea, 10 m (J. Randall).



D. Paratype of *Oxycheilinus nigromarginatus*, BPBM 37942, male, 79.0 mm SL, Tongatapu, 12 m (J. Randall).



E. Underwater photograph of *Oxycheilinus nigromarginatus*, Chesterfield Bank, Coral Sea (J. Randall).

brown with dark brown dots; lips and chin without markings; dorsal fin with very faint pale yellowish brown markings in spinous portion, a blackish blotch in lower half of first membrane, and a lesser blotch on second membrane; anal and caudal fins slightly dusky, paler posteriorly; pectoral fins pale; pelvic fins dusky at base.

Color of holotype when fresh (Pl. 1A): body with narrow dark purplish brown stripes as described above, but the stripes now about twice as wide as pale interspaces which are pinkish white dorsally and bluish white ventrally (the edges of the dark stripes in the fresh specimen are not as darkly pigmented, and only the dark middle part remains in preservative); caudal peduncle brown except for a few scattered dark brown dots on upper half; head light lavender-gray, with narrow dark purplish brown bands radiating from eye except anteriorly, those extending ventrally from eye breaking into dashes or dots on lower part of head, and those dorsally into dots into interorbital space; snout with yellowish brown dots, a few extending onto basal part of upper lip; outer triangular part of each interspinous membrane of dorsal fin whitish, the supporting cirrus of each pale pink; first interspinous membrane with a large subtriangular purplish black spot on basal half; second membrane with a similar but smaller spot and less strongly pigmented, and the next membranes with similar but progressively smaller and lighter basal blotches; rest of spinous portion of fin light yellowish brown with small brown blotches; soft portion of dorsal fin pale brown anteriorly, gradually shading to translucent with pale yellowish rays posteriorly; anal fin brown anteriorly, the pigment nearly covering all of membranes, the lower part of first two membranes dark brown; brown portion of fin progressively shorter posteriorly, the rest of fin with translucent membranes and pale yellowish rays; caudal fin brown on proximal third except the three large basal scales which are pale yellowish, whitish on distal third; pectoral fins translucent with pale yellowish rays; pelvic fins purplish brown proximally and whitish distally, except for spine, first membrane, and first ray, purplish to tip.

Etymology.— This species is named *Oxycheilinus lineatus* from the Latin *linea* for line, in reference to the strong linear pattern.

Remarks.— Although described from a single adult male specimen from Rarotonga in the Cook Islands, the species is known from Tahiti and Henderson Island in the Pitcairn Islands where it was nearly collected by the first author. We also have an underwater photograph of it taken by Yves Lefevre in the Austral Islands (Pl. 1B). That fewer specimens have not been collected or photographed is undoubtedly due to its occurrence on deep reefs; the known depth range is 49–85 m.

Oxycheilinus lineatus is easily distinguished by its strong linear pattern. There appear to be no important differences in meristic data or body proportions to separate it from the other species of the genus. However, it can be separated, at least as an adult, by the strong incision of each interspinous membranes of the dorsal fin and the short pectoral fins, their length about 3.2 in the length of the head.

Oxycheilinus nigromarginatus Randall, Westneat and Gomon, sp. nov.

Plate 1, Figs. C–E; Table 1

Material examined.— Holotype: BPBM 33686, male, 111.6 mm, Coral Sea, Chesterfield Bank, southeast end of lagoon, 19°53.5′S, 158°28.2′E, sand with small thickets of *Acropora*, 10 m, spear, J.E. Randall, 28 August 1988. Paratypes: BPBM 37942, male, 79.0 mm, Tongatapu, Monuafe Islet, southwest side, 12 m, spear, J.E. Randall, 28 February 1983; BPBM 33693, female, 73.2 mm, Coral Sea, Chesterfield Bank, southeast end of lagoon, at anchorage, 27–28 m, small coral heads and patches of foraminifera sand, spear, J.-L. Menou and J.E. Randall, 27 August 1988; CAS 216844, 69.7 mm, Coral Sea, Chesterfield Bank, M. Kulbicki, 21 August 1988; NSMT-

TABLE 1. Proportional measurements of type specimens of two species of *Oxycheilinus* expressed as percentages of the standard length.

	O. lineatus	*O. nigromarginatus*						
	Holotype	Holotype	Paratypes					
	BPBM 39091	BPBM 33686	NSMT 65066	BPBM 33693	NMV A8578	NMV A8578	NMV A11834	USNM 371349
Sex	male	male	female	female	female	intersex	male	male
Standard length (mm)	159.5	111.6	64.3	73.2	82.3	99.8	101.0	113.4
Body depth	29.7	29.8	28.3	28.3	28.5	31.0	32.2	30.0
Body width	15.1	15.8	15.9	14.8	15.3	15.2	15.7	14.9
Head length	40.5	40.7	41.1	41.2	40.0	40.1	39.7	39.6
Snout length	16.2	15.1	14.3	15.2	14.3	14.6	14.7	15.3
Orbit diameter	7.3	6.5	8.8	8.2	7.7	6.8	7.0	6.6
Interorbital width	10.3	9.4	9.4	9.5	9.6	9.8	9.9	9.9
Upper-jaw length	14.3	15.6	14.4	14.6	13.8	14.6	14.6	15.2
Caudal-peduncle depth	15.1	13.4	12.8	12.3	13.4	14.1	14.4	13.6
Caudal-peduncle length	11.8	11.6	11.2	11.9	10.9	12.0	11.8	11.2
Predorsal length	41.6	39.5	41.7	40.4	41.5	40.2	38.8	39.6
Preanal length	64.8	64.7	65.8	65.2	64.6	65.1	64.6	64.4
Prepelvic length	42.8	41.4	43.2	42.6	41.6	42.8	42.1	41.2
Dorsal-fin base	50.7	52.8	52.8	51.0	54.5	53.0	55.4	54.5
First dorsal spine	6.3	6.0	6.1	7.1	7.2	7.0	6.4	6.2
Ninth dorsal spine	11.0	11.5	11.7	11.5	11.0	11.2	11.0	deformed
Longest dorsal ray	12.5	12.6	14.0	14.9	13.2	13.9	13.0	14.0
Anal-fin base	25.1	25.6	20.9	23.8	24.2	25.2	24.3	26.4
First anal spine	5.6	4.0	4.2	5.5	5.6	4.2	4.0	4.8
Second anal spine	9.3	7.8	8.3	9.5	8.2	7.6	7.9	8.1
Third anal spine	11.7	12.1	12.0	12.9	12.1	12.0	12.4	11.9
Longest anal ray	12.3	12.4	12.3	14.1	13.3	14.0	12.8	13.5
Caudal-fin length	25.0	24.4	21.4	24.6	25.1	27.2	25.8	25.7
Pectoral-fin length	12.5	15.2	14.0	15.3	14.8	14.1	14.9	15.2
Pelvic-spine length	10.9	11.0	11.7	11.0	12.3	11.3	11.9	10.0
Pelvic-fin length	16.5	16.9	16.2	17.5	16.4	17.3	17.5	17.9

P65066; female, 64.3 mm, same data as preceding; USNM 371349, male, 113.4 mm, same data as holotype; NMV A8578, females and intersex, 3: 81.3–99.8 mm, New Caledonia, St.Vincent South, 15 m, M. Kulbicki, 18 October 1989; NMV A11834, male, 101 mm, Australia, New South Wales, Sydney Harbor, Camp Cove, 33°50′S, 151°16′E, R.H. Kuiter, May 1991.

DIAGNOSIS.— Dorsal rays IX,10; anal rays III,8; pectoral rays 13; lateral-line interrupted, the pored scales to caudal-fin base 15 + 6; gill rakers 5-6 + 8-9; body moderately elongate, the depth 3.1–3.55 in SL; head length 2.45–2.55 in SL; snout long and pointed, 2.6–2.8 in head; dorsal profile of snout straight or with a slight concavity of snout to above eye; lower jaw slightly projecting; maxilla reaching or nearly reaching a vertical at anterior margin of orbit; caudal fin of females slightly rounded, the upper three principal rays slightly prolonged; fin of males rhomboid with the upper three rays more strongly projecting; pectoral fins 2.6–2.95 in head; body and fins pale yellowish in preservative with a blackish posterior margin on caudal fin, broader and black in male; first interspinous membrane of dorsal fin dusky; red in life on about upper half of body with five irregular pale bars, pale red on lower half with three pale stripes containing small white spots; posterior edge of caudal fin blackish to black.

DESCRIPTION.— Dorsal rays IX,10; anal rays III,8; all dorsal and anal rays branched, the last to base; pectoral rays 13, the first rudimentary, the second unbranched; pelvic rays I,5; principal caudal rays 14, the middle 12 branched; upper procurrent caudal rays 5 ; lower procurrent caudal rays 5; lateral-line interrupted, the pored scales to caudal-fin base 16 + 7; 2 pored scales on caudal-fin base, the last very large and pointed; scales above lateral line to base of dorsal spines 1.5; scales below lateral line to origin of anal fin 5.5; median predorsal scales 5, preceded by a lateral pair of scales in posterior interorbital space, usually with a small scale anterior to these (often embedded); gill rakers 5 + 8 (5-6 + 8–9); pseudobranchial filaments 19 (19–23); branchiostegal rays 5; vertebrae 23.

Body moderately elongate, the depth 3.4 (3.1–3.55) in SL; body width 1.95 in depth; head length 2.45 (2.4–2.55) in SL; snout long and pointed, 2.7 (2.6–2.8) in head; dorsal profile of snout straight or with a slight concavity on snout to over eye; orbit diameter 6.25 (4.7–6.0) in head; interorbital space strongly convex, the least fleshy width 4.35 (4.0–4.4) in head; caudal-peduncle depth 3.05 (2.75–3.35) in head; caudal-peduncle length 3.4 (3.45–3.65) in head.

Lower jaw slightly projecting; mouth oblique, forming an angle of about 20° to horizontal axis of body; maxilla ending about a half orbit diameter before anterior edge of orbit, the upper-jaw length 2.6 (2.6–2.9) in head; a pair of broadly spaced, incurved, canine teeth anteriorly in each jaw, the lowers a little smaller than uppers and fitting inside uppers when mouth closed; a row of close-set conical teeth of moderate size along side of upper jaw (19 in holotype); lower jaw with a row of smaller conical teeth on side (23 in holotype); no inner rows of small teeth in jaws, and no teeth on palate. Tongue slender, the tip rounded, reaching anteriorly about two-thirds distance to front of jaws. Lips thick but not fleshy; a ventrally directed flange on side of lower lip. Gill rakers small and simple, those on lower limb nearly sessile; longest gill raker on lower limb about three-fourths length of longest gill filaments, about equal to pupil diameter. Nostrils as small as sensory pores, the anterior in a low membranous tube with a short posterior flap equal in perpendicular distances to edge of orbit and edge of snout above upper lip; posterior nostril behind and slightly dorsal to anterior nostril, the internarial space about 4 in orbit diameter.

Upper part of posterior edge of preopercle covered by a scale to level of lower edge of orbit; the ventral edge of preopercle free nearly to a vertical at anterior edge of orbit; outer and ventral part of preopercle thin and membranous, with a slight indentation in margin above rounded corner.

Scales cycloid, thin, and membranous, but adherent; head scaled except for membranous flange of preopercle, snout, chin, and anterior interorbital space; predorsal scales ending in a lateral pair of scales in posterior interorbital space, usually with a small median scale before (often embedded); scales of lateral line with a single horizontal tubule, ending in a pore; first lateral-line scale at upper end of gill opening; anterior lateral line following dorsal contour of body, the posterior part midlateral on caudal peduncle; scales on thorax only slightly smaller than largest on side of body; no scales on base of dorsal or anal fins; caudal fin with scales on basal half, the most posterior a vertical row of three very large scales, the middle one the last scale of lateral line; paired fins without scales except for a slender midlateral scaly process extending posteriorly from base of pelvic fins a little more than half length of pelvic spines; a pointed axillary scale above base of pelvic fin, its lower edge straight.

Origin of dorsal fin slightly anterior to a vertical at posterior end of opercular membrane, the predorsal length 2.55 (2.4–2.6) in SL; dorsal spines progressively longer, the first 6.8 (5.6-6.75) in head, and the ninth 3.55 (3.5–3.65) in head; membranes of spinous portion of dorsal fin of holotype not incised (membranes of smallest female incised at most nearly one-half spine length); each interspinous membrane of dorsal fin supported distally by a stout cirrus, but extending at most slightly above spine tips; first dorsal soft ray longest, 3.2 (2.75–3.05) in head (but remaining rays except last two nearly as long); origin of anal fin below base of eighth dorsal spine, the preanal length 1.55 (1.5–1.55) in SL; first anal spine 10.1 (7.2–9.8) in head; second anal spine 5.15 (4.35–5.25) in head; third anal spine 3.35 (3.2-3.4) in head; first anal soft ray longest, 3.3 (2.85–3.35) in head; caudal fin of holotype rhomboid, the three uppermost principal rays slightly prolonged, the fin length 4.1 (3.7–4.7) in SL; fourth pectoral ray longest, 2.7 (2.6–2.95) in head; origin of pelvic fins below lower base of pectoral fins, the prepelvic length 2.4 (2.3–2.4) in SL; pelvic spine 3.7 (3.25–3.95) in head; first pelvic soft ray longest, not approaching anus, 2.4 (2.2–2.5) in head.

Color of holotype in alcohol: pale yellowish with a faint dusky stripe on side of snout; three faint purplish brown lines across anterior half of upper lip, the posterior two continuing more faintly across lower lip, but the first leading to a broader purplish band across lower lip, the two bands converging and joining on chin; spinous portion of dorsal fin with slightly dusky membranes, the darkest on first membrane; soft portion of dorsal fin and all of anal fin with near-transparent membranes and pale yellowish rays; caudal fin with transparent membranes and pale yellowish rays except for a broad dark purplish brown posterior margin that is more than a half orbit diameter at broadest place; paired fins pale.

Color of holotype when fresh (Pl. 1C): upper half of body red with four irregular narrow whitish bars (from white edges on scales) and a similar short bar on nape; lower half of body light red with small white spots, mainly in three lengthwise series (the lower on abdomen); a small red spot midlaterally on body below base of fifth dorsal soft ray; head red, paler ventrally, with narrow light orange lines radiating from eye, those passing ventrally most numerous, sometimes broken and branching on lower part of head; numerous white dots on postorbital head, larger posteriorly; a broad diffuse dusky stripe on side of snout extending narrowly onto front of upper lip; a few near-vertical light orange lines on side of snout, some crossing those extending anteriorly from eye; three faint dusky-edged light orange lines crossing side of lips; a broad dark purplish brown bar on each side of upper lip, converging onto chin; dorsal fin pale red with scattered whitish flecks and red blotches along base; first membrane of fin black; a dusky-edged orange stripe in outer part of spinous portion of fin, continuing faintly without dusky edges onto soft portion of fin; posterior half of soft portion of fin with transparent membranes and whitish rays blotched with red; anal fin pale red with scattered white flecks and red blotches on basal half, and a light orange-red stripe near middle of fin; caudal fin pale red, dotted with white, the rays with narrow red transverse bands; posterior edge of caudal fin with a broad black border, the black continuing more proximally on second principal ray; a small dusky spot on first basal pored scale of caudal fin; pectoral fins with pale orange rays and transparent membranes; pelvic fins pale red with small whitish flecks.

Color of 79-mm paratype when fresh (Pl. 1D): pale red, finely blotched with red; narrow whitish bars on body and nape as in holotype; a faint whitish stripe following lateral line, and three ventral pale stripes, each containing a series of small white spots; a small but prominent midlateral red spot below base of fifth dorsal soft ray, and a slightly smaller one on penultimate lateral-line scale on caudal-fin base; head with whitish lines radiating from eye except anteriorly, separated by indistinct broader red lines; postorbital head with white dots; a dusky stripe on side of snout in line with lower half of eye and extending onto upper lip; white dots and vertical white lines on snout, the dots mainly dorsal and onto dusky, stripe and the lines ventral, including lips, chin, and a few on isthmus; spinous portion of dorsal fin, first two membranes of soft portion, anterior two-thirds of anal fin, and pelvic fins translucent whitish with oblique red bands and indistinct white spots, the posterior part of dorsal and anal fins with transparent rays and pale rays with red and white spots basally; caudal fin pale red with irregular red cross bands, white spots, and a posterior reddish black border (does not show well on Pl. 1D due to black background); pectoral fins with transparent membranes and pale rays narrowly edged in red.

Etymology.— This species is named *Oxycheilinus nigromarginatus* from the Latin, meaning black-margined, in reference to the conspicuous black posterior margin on the caudal fin, the only obvious color marking persisting in preservative.

Remarks.— *Oxycheilinus nigromarginatus* appears to be restricted to the southwest Pacific. We have specimens from New South Wales, Chesterfield Bank in the Coral Sea, New Caledonia, and Tonga. They were collected in protected waters of lagoons or harbors on mixed sand and coral-reef habitats in the depth range of 10–27 m.

This species is most closely related to *Oxycheilinus orientalis* (Günther 1862), a new name for *Cheilinus coccineus*, non Rüppell, Bleeker, type locality Batjan, Indonesia.

Randall and Khalaf (2003) showed that *C. rhodochrous* Günther in Playfair and Günther, 1867, type locality Zanzibar, is a synonym of *O. orientalis*, redescribed the species, and recorded it from the Red Sea, Lombok in Indonesia, Okinawa, and the Marshall Islands.

Oxycheilinus nigromarginatus shares such characters with *O. orientalis* as a slender body, pointed snout with projecting lower jaw, caudal-fin shape, interspinous membranes of dorsal fin incised in females but extending to spine tips in males, fin-ray and gill-raker counts, and some features of color, such as the following: red with five narrow whitish bars on upper half of body (less distinct in *orientalis*, especially in males*)*, two small midlateral deep red spots posteriorly, becoming dusky in males, a black area posteriorly on eye (more readily seen by rotating the eyeball forward), and white lines ventrally on head (or in the case of the male *O. nigromarginatus*, of pale orange lines). *O. orientalis* differs in having 12–14 anterior lateral line scales, compared to 15 for *O. nigromaginatus*, in dentition (upper jaw of *O. orientalis* with a row of 4 or 5 canine teeth on each side, with 1–4 stout conical teeth between canines; *O. nigromarginatus* with only an anterior pair of canines); a large black blotch usually present in humeral region of adults, and in lacking a black posterior margin on the caudal fin, three longitudinal series of white spots ventrally on the body, and white dots on postorbital head except for a few on nape sometimes extending onto upper part of opercle.

Acknowledgments

We thank foremost Richard L. Pyle for collecting our only specimen of *Oxycheilinus lineatus* and Rudie H. Kuiter and Michel Kulbicki for collecting paratypes of *O. nigromarginatus*. Thanks are also due Yves Lefevre for his photograph of *O. lineatus* from the Austral Islands, Loreen R. O'Hara for X-rays, and Arnold Y. Suzumoto for curatorial help at the Bishop Museum.

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A Reconsideration of *Megalostoma* (Acanthaceae), a New Species, and Recognition of a New Section of *Justicia*

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Based on macromorphological and palynological evidence, *Megalostoma* (Acanthaceae) is reduced to sectional status within *Justicia*. Two previously described species, *J. tabascina* and *J. valvata*, and a newly described species, *J. dendropila*, show affinities to the only known species of *Megalostoma* and are also included in the section. A new combination in *Justicia* is proposed for *M. viridescens*.

Leonard (1940) described *Megalostoma* based on plants from Guatemala and noted that relatives of this unispecific genus were not known. Nevertheless, he placed the genus in "section" (undoubtedly a mistake for "tribe") Louteridieae because the "irregular coriaceous calyx and tubercular pollen grains suggest a possible relationship to *Louteridium* Wats." Other than noting its superficial similarities to *Louteridium*, remarking upon its "widely divergent corolla lobes," and providing a brief description, Leonard (1940) did not indicate other diagnostic features of *Megalostoma*.

Louteridium possesses a 3-parted calyx, four androecial elements (i.e., either four stamens or two stamens and two staminodes), and spheric-pantoporate pollen (Daniel 1995a, 1998; Richardson 1972; Scotland 1993; Scotland and Vollesen 2000), characteristics not found in the species described by Leonard. Scotland and Vollesen (2000) included *Louteridium* in tribe Ruellieae subtribe Ruelliinae whereas they treated *Megalostoma* in Ruellieae subtribe Justiciinae. Indeed, *Megalostoma* has a basically five-parted calyx (see below), a corolla with a rugula, two stamens, and a complex type of 3-aperturate pollen that indicate a relationship with *Justicia* of that subtribe.

Since the description of *M. viridescens*, a similar species from Mexico has been described as *Justicia valvata* (Daniel 1993). In addition, the Mexican genus *Tabascina* Baill. was shown to be indistinct from *Justicia* (Daniel 1990) and its sole species shares numerous characters with *J. valvata* (Daniel 1993). Based on the morphological similarities of *M. viridescens* to these two species of *Justicia*, *Megalostoma* is herewith reduced to synonymy within *Justicia*. Recent collections of a distinctive and undescribed species from the Yucatan Peninsula of Mexico reveal another relative of the previously described taxa in this alliance. The combination of several shared macromorphological and palynological features in these four species appears to be unique among American Acanthaceae and suggests taxonomic status at a suprageneric level. *Justicia* section *Megalostoma* is herewith recognized to accommodate these species.

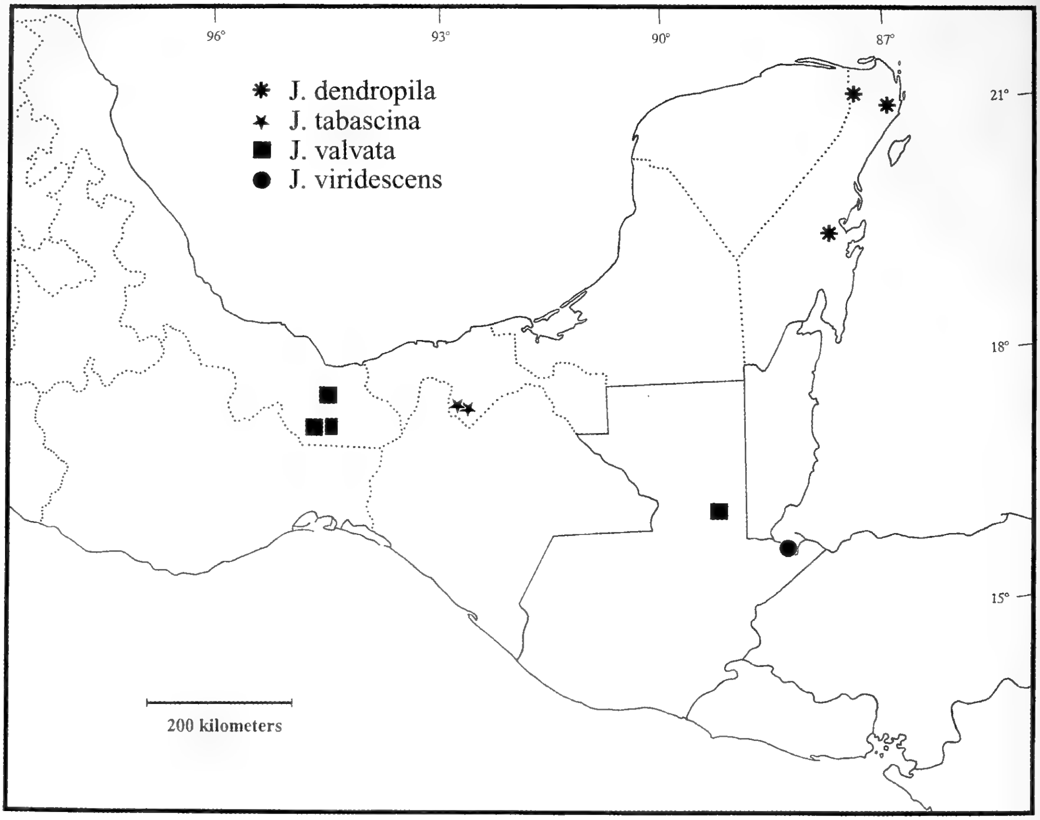

FIGURE 1. Map of southern Mexico and western Central America showing distributions of the species of *Justicia* sect. *Megalostoma*.

Justicia section ***Megalostoma*** (Leonard) T.F. Daniel, stat. nov. *Megalostoma* Leonard, J. Wash. Acad. Sci. 30:503. 1940.

TYPE. *Megalostoma viridescens* Leonard.

Shrubs or small trees. Inflorescence of dichasiate spikes (dichasia sessile) or thyrses (dichasia pedunculate). Bracts and bracteoles often caducous. Flowers subsessile to short pedicellate. Calyx with 5 valvate lobes, lobes separating distally in various ways (e.g., sometimes separating into 2 lobes and appearing somewhat spathelike, sometimes 4-lobed with anterior lobes not separating, sometimes separating into 5 lobes), posterior lobe usually larger than others, lobes ± coriaceous and relatively broad (2–7 mm wide). Corolla greenish or yellowish, externally pubescent with glandular trichomes, upper lip erect, internally rugulate, lower lip spreading ± perpendicular to (or forming an obtuse angle with) upper lip, 3-lobed. Stamens with thecae subparallel to subsagittate, subequally to unequally inserted, pubescent or glabrous, lacking basal appendages; pollen euprolate to perprolate (polar diameter 1.8–2.7 times longer than equatorial diameter), 3–4-aperturate, apertures flanked on each side by 1 (–2) row(s) of insulae. Capsules (known from only two species) 4-seeded.

The section consists of four species from southern Mexico and Guatemala (Fig. 1). Three of the species occur in moist to wet forests whereas *J. dendropila* occurs in a dry forest formation.

Using Graham's (1988) infrageneric classification of *Justicia* (which was based on a subset of species), section *Megalostoma* cannot be readily identified with any of the suprageneric taxa recognized. These species share some affinities with her sects. *Plagiacanthus* (e.g., spicate inflorescence units, corollas less than 50 mm long, thecae with small or no appendages, and smooth seeds) and *Drejerella* (e.g., 3-aperturate pollen and smooth seeds). It differs from section *Plagiacanthus* by its greenish or yellowish corollas (vs. red or purplish) and 3–4-aperturate (vs. 2-aperturate) pollen, and from section *Drejerella* by its unappendaged thecae (vs. thecae with a basal appendage). Section *Megalostoma* differs from all other infrageneric taxa recognized by Graham (1988) by the combination of characters noted in the sectional description above. The relatively large, variously fused, and coriaceous calyx lobes and pollen varying from 3 to 4-aperturate (with the apertures usually flanked on each side by 1 row of insulae) appear to be especially distinctive features of the section. Following the key to species, abridged descriptions that incorporate new data are provided for those species that have been treated recently and a more detailed description is given for the newly described species, *J. dendropila*.

Key to Species of *Justicia* Section *Megalostoma*

1a. Young stems, leaves, bracts, bracteoles, calyx lobes, and corolla pubescent with branched (dendritic) trichomes; pollen with interapertural surfaces tuberculate-echinate; plants of seasonally dry forests in the Yucatan Peninsula. . . . . 1. *J. dendropila*
1b. Young stems, leaves, bracts, bracteoles, calyx lobes, and corolla glabrous or pubescent with unbranched trichomes; pollen with interapertural surfaces coarsely reticulate; plants of moist to wet forests in southern Mexico (Veracruz and Tabasco) and Guatemala 2

2a. Corolla 35–41 mm long; thecae 7–7.5 mm long; pollen 3-aperturate; style 37–39 mm long . . . . 2. *J. viridescens*
2b. Corolla 18–25 mm long; thecae 4–5.3 mm long; pollen 4-aperturate; style 15–24 mm long . 3

3a. Young stems and rachises bifariously pubescent; dichasia solitary at inflorescence nodes, sessile; calyx externally glabrous . . . . 3. *J. valvata*
3b. Young stems and rachises evenly pubescent; dichasia paired at inflorescence nodes, pedunculate; calyx externally pubescent . . . . 4. *J. tabascina*

1. ***Justicia dendropila*** T.F. Daniel, sp. nov. (Figure 2.)

TYPE: MEXICO: **Quintana Roo**: Mpio. Benito Juárez, 9 km W of Hwy. 307 in Puerto Morelos along road to Central Vallarta, 20°51.5′N, 86°59.1′W, 7 m, evergreen seasonal forest, 19 February 2003 (flr. & frt.), *T. Daniel 10287* (holotype: MEXU!; isotypes: BR!, CAS!, CICY!, CIQR!, ENCB!, F!, K!, MICH!, MO!, NY!, UCAM!, US!).

Frutices inclinati usque ad 4 m alti, pubescentes trichomatibus dendriticis. Folia petiolata, laminae anguste ellipticae vel ellipticae, 37–165 mm longae, 11–64 mm latae. Inflorescentia floribus in spicas terminales; dichasia alterna, sessilia, uniflora. Bracteae ellipticae vel subcirculares vel obovatae, 12–28 mm longae. Bracteolae lineares vel lanci-lineares, 12–18.5 mm longae. Calyx 5-lobus, 10–11 mm longus, lobis ovato-ellipticis vel ellipticis. Corolla viridi-flava, 37–48 mm longa. Stamina thecis 4.8–6 mm longis, subsagittatis vel subparallelis, basi ecalcaratis; pollinis granae 3-aperturatae. Capsula 11.5–15 mm longa, glabra.

Leaning shrubs to 4 m tall. Young stems subquadrate, densely and evenly pubescent with den-

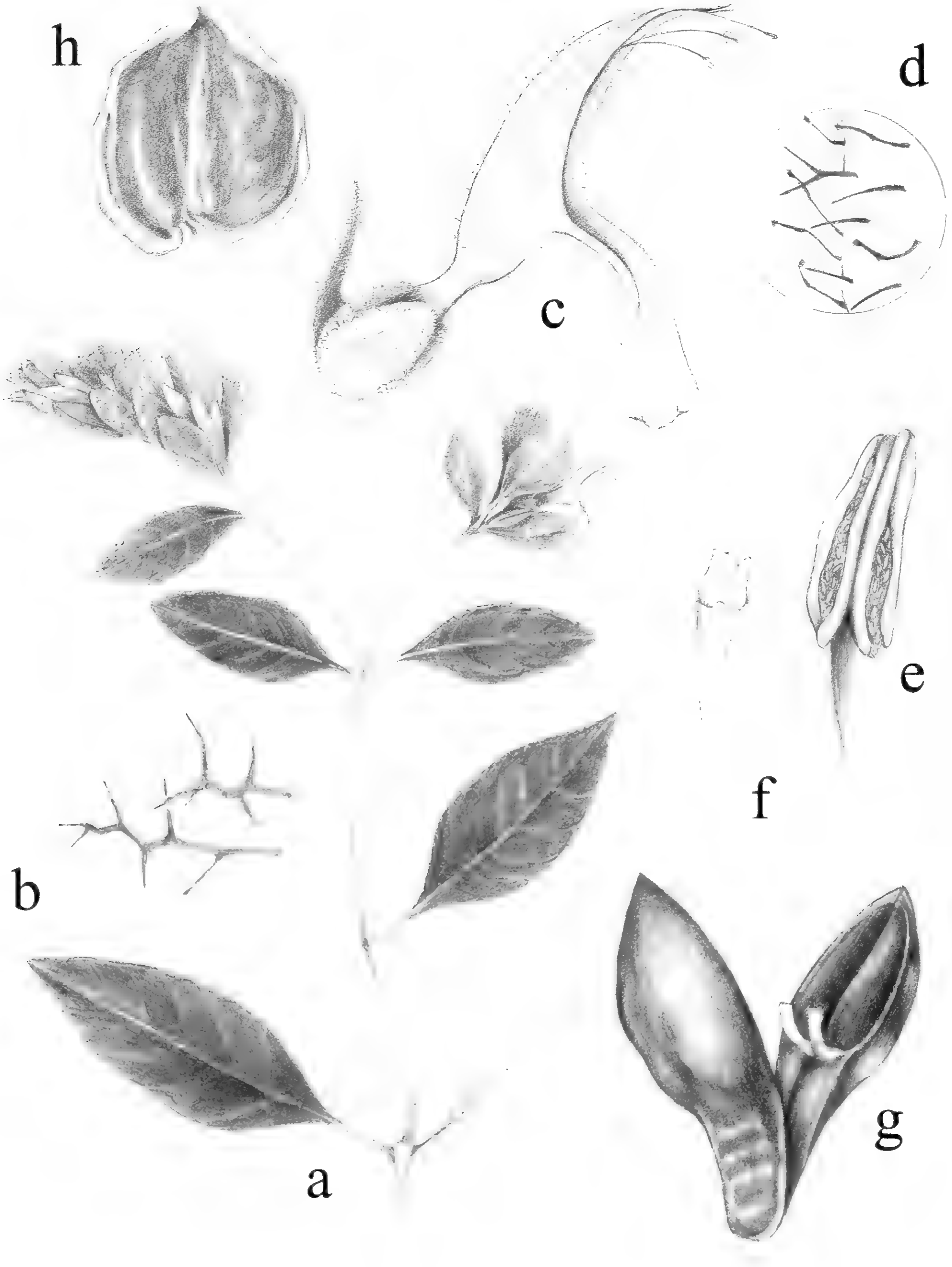

FIGURE 2. *Justicia dendropila* (*Daniel 10287*). a. Habit, × 0.5. b. Dendritic trichomes, × 33. c. One bracteole and flower, × 1.8. d. Pubescence of corolla, × 20. e. Anther, × 6. f. Stigma, × 17. g. Capsule, × 3.8. h. Seed, × 7. Drawn by Victoria Saxe.

dritic trichomes 0.2–0.5 mm long. Leaves petiolate, petioles to 20 mm long, blades narrowly elliptic to elliptic, 37–165 mm long, 11–64 mm wide, 1.9–4.8 times longer than wide, acute to subacuminate at apex, acute to attenuate at base, surfaces pubescent with dendritic trichomes, margin entire. Inflorescence of terminal dichasiate spikes, rachis pubescent like young stems; dichasia alternate, sessile, 1 (–2)-flowered. Bracts green with maroon near apex, elliptic to subcircular to obovate, 12–28 mm long, 6–18 mm wide (sometimes larger and subfoliose at base of spike), abaxial surface pubescent with cauline type trichomes. Bracteoles linear to lance-linear (to oblanceolate), 12–18.5 mm long, 1–3.4 mm wide, abaxial surface pubescent like bracts. Flowers sessile to subsessile (i.e., pedicels to 0.5 mm long). Calyx 10–11 mm long, 5-lobed, lobes ovate-elliptic to elliptic, 8–9 mm long, 3–4.4 mm wide, abaxially pubescent with cauline type trichomes, margin densely pubescent with intertwined flexuose dendritic trichomes to 1.7 mm long. Corolla greenish yellow, 37–48 mm long, externally pubescent with flexuose glandular trichomes 0.1–0.4 mm long and unbranched or stellate to dendritic eglandular trichomes to 0.7 mm long, tube 18–20 mm long, narrow proximal portion 8–10 mm long, 4 mm in diameter, abruptly expanded at apex into throat, throat 7–11 mm long, 6–11 mm in diameter near midpoint, upper lip 20–31 mm long, 2-lobed at apex, lobes 0.3 mm long, lower lip 17–25 mm long, lobes 3.4–5 mm long, 3–3.4 mm wide. Stamens inserted near midpoint of throat, 33–36 mm long, filaments greenish yellow, glabrous distally, thecae brownish (immature) turning greenish yellow when mature, 4.8–6 mm long, subsagittate to subparallel, subequally inserted, subequal (distal theca slightly longer), lacking basal appendages, pubescent with eglandular trichomes (these sometimes obscured or appearing absent following dehiscence); pollen (Fig. 3) 3-aperturate, apertures flanked on each side by 1 (–2) rows of insulae, exine tuberculate-echinate. Style 34–50 mm long, glabrous, stigma subcapitate, 0.5 mm long. Capsule 11.5–15 mm long, glabrous, stipe 4–5 mm long, head 7.5–10 mm long, obovoid to ellipsoid. Seeds 4, lenticular, 4.2–4.8 mm long, 3.2–3.6 mm wide, surfaces ± smooth to rugose, lacking trichomes, margin entire and ± swollen.

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

DISTRIBUTION AND HABITATS.— Known only from the Yucatán Peninsula (Quintana Roo) of southeastern Mexico; evergreen seasonal forests; 7–15 m.

PARATYPES.— MEXICO: **Quintana Roo**: Mpio. Carrillo Puerto, 6–10 km NE de Felipe Carrillo Puerto sobre el camino a Vigía Chico, *E. Cabrera et al. 16380* (CAS); Mpio. Benito Juárez, 15 km N de Puerto Morelos hacia Cancún, 1 km hacia la autopista Cancún–Mérida, 21°01′N, 86°52′W, *R. Durán et al. 3079* (CICY); Mpio. Benito Juárez, 8 km W del entronque a Vallarta, partiedo de la carr. Cancún–Tulúm, 20°52′N, 86°57.5′W, *I. Olmsted et al. 342* (CICY, MEXU); Mpio. Lázaro Cárdenas, camino blanco de Kantunilkin, rumbo a San Isidro, 21°08′N, 87°32′W, *E. Ucan 1994* (CICY).

This species is unusual among Mexican *Justicia* in its dendritic pubescence. *Justicia stellata* (Greenm.) T.F. Daniel, a species from Jalisco, is the only other Mexican species in the genus with branched (varying from stellate to dendritic) trichomes. Unlike *J. dendropila*, *J. stellata* has reddish purple corollas and 2-aperturate pollen (Daniel 2002). Indeed, *J. dendropila* shares all of the characteristics of section *Megalostoma*, and appears most similar to *J. viridescens*. Both species have relatively large corollas and 3-aperturate pollen (Fig. 3). They can be distinguished by the following couplet:

1a. Plants with dendritic trichomes ± throughout; young stems evenly pubescent; leaves acute to subacuminate at apex; inflorescence a terminal spike; bracts and bracteoles persistent; calyx 10–11 mm long; thecae 4.8–6 mm long; pollen with exine echinate-tuberculate; plants of dry forests in Quintana Roo, Mexico . . . . *J. dendropila*

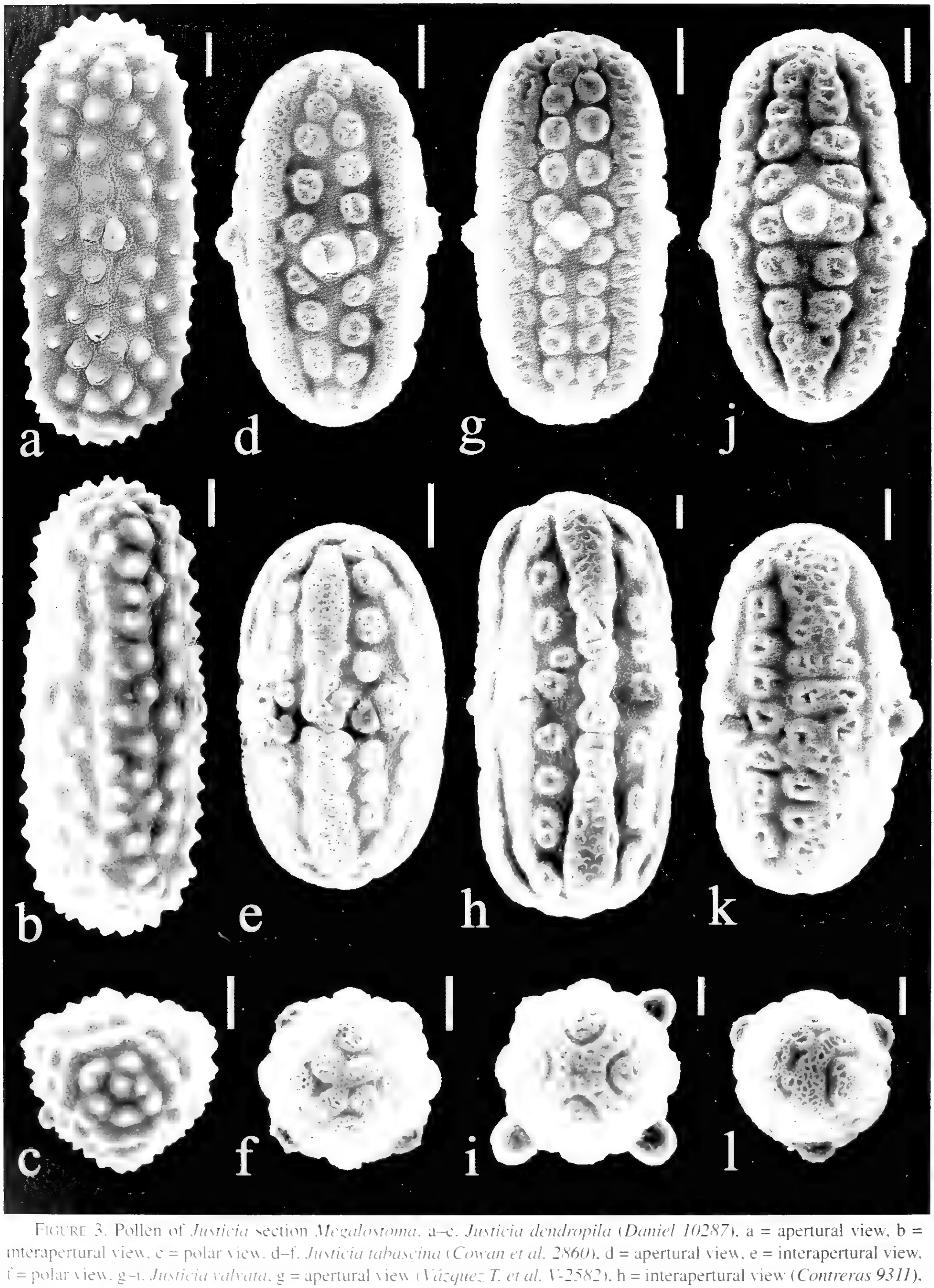

FIGURE 3. Pollen of *Justicia* section *Megalostoma*. a–c. *Justicia dendropila* (*Daniel 10287*). a = apertural view, b = interapertural view, c = polar view. d–f. *Justicia tabascina* (*Cowan et al. 2860*). d = apertural view, e = interapertural view, f = polar view. g–i. *Justicia valvata*. g = apertural view (*Vázquez T. et al. V-2582*). h = interapertural view (*Contreras 9311*). i = polar view (*Vázquez T. et al. V-2582*). j–l. *Justicia viridescens* (*Martínez S. et al. 23668*). j = apertural view, k = interapertural view, l = polar view. All scales = 10 µm.

1b. Plants lacking dendritic trichomes; young stems bifariously pubescent; leaves long-acuminate to caudate at apex; inflorescence a terminal panicle; bracts and bracteoles caducous; calyx 12–19 mm long; thecae 7–7.5 mm long; pollen with exine coarsely reticulate; plants of wet forests in Izabal, Guatemala . . . . *J. viridescens*

2. ***Justicia viridescens*** (Leonard) T.F. Daniel, comb. nov. *Megalostoma viridescens* Leonard, J. Wash. Acad. Sci. 30:503. 1940.

TYPE: GUATEMALA: **Izabal**: Escoba, across bay (W) from Puerto Barrios, near sea level, wet forest, 3 May 1939, *P. Standley 72948* (holotype: F!; isotype: US!).

Shrubs or small trees to 6 m tall. Young stems quadrate, bifariously pubescent with antrorse eglandular trichomes 0.05–0.1 mm long. Leaves subsessile to petiolate, petioles to 5 mm long, blades ovate-elliptic to elliptic, 55–125 mm long, 18–44 mm wide, 2.2–3.5 times longer than wide, long-acuminate to caudate at apex, rounded to acute at base, surfaces glabrous or nearly so, margin entire to subsinuate. Inflorescence of axillary and terminal pedunculate spikes, collectively forming a terminal panicle, rachises ± evenly pubescent with antrorse eglandular trichomes 0.05–0.2 mm long; dichasia 1-flowered, solitary at nodes (i.e., alternate), not appearing secund, sessile. Bracts subtending dichasia caducous, not seen. Bracteoles caducous, not seen. Flowers subsessile to short pedicellate, pedicels to 2 mm long. Calyx 12–19 mm long, abaxially glabrous or nearly so, lobes ± lunate (i.e., curved), 3–7 mm wide, margins sometimes inconspicuously ciliate. Corolla green to greenish white, 35–41 mm long, externally pubescent with erect to flexuose glandular trichomes 0.1–0.2 mm long, tube 14.5–17 mm long, upper lip 22–27 mm long, apex not seen, lower lip 19–22 mm long, lobes not seen. Stamens 24 mm long, thecae 7–7.5 mm long, glabrous; pollen (Fig. 3) 3-aperturate, exine coarsely reticulate. Style 37–39 mm long, stigma subhemispheric, equally 2-lobed, lobes 0.2 mm long. Capsule and seeds not seen.

PHENOLOGY.— Flowering: May, September; fruiting: unknown.

DISTRIBUTION AND HABITATS.— Known only from eastern Guatemala (Izabal); lowland rain forests; near sea level–120 m.

ILLUSTRATION.— J. Wash. Acad. Sci. 30: 502. 1940.

ADDITIONAL SPECIMENS EXAMINED.— GUATEMALA: **Izabal**: Mpio. Pto. Barrios, en el Río las Escobas, camino entre Pto. Barrios y Punta de Palma, *E. Martínez S. et al. 23668* (MEXU, MO); Escoba, across bay (W) from Puerto Barrios, *P. Standley 73025* (F).

Megalostoma viridescens was described from the type and two paratypes, all from the same locality in eastern Guatemala. *Martínez S. et al. 23668*, a recent (1988) collection from the vicinity of the type locality, allows this species to be more fully characterized and reveals that the species still persists in eastern Guatemala.

Justicia viridescens and *J. valvata* appear more similar to one another than either does to *J. tabascina*. They differ from the latter species by their bifarious cauline pubescence, sessile dichasia that are solitary at the inflorescence nodes, and abaxially glabrous calyces. Pollen of *J. viridescens* (based on *Martínez S. et al. 23668* and *Standley 73025*) differs from that of both *J. valvata* and *J. tabascina* by having only three apertures (Fig. 3).

3. ***Justicia valvata*** T.F. Daniel, Contr. Univ. Michigan Herb. 19:282. 1993.

TYPE: MEXICO: **Veracruz**: Mpio. Hidalgotitlán, KM 7 camino a la Escuadra, 140 m, selva alta perenifolia, 10 September 1974, *J. Dorantes et al. D-3538* (holotype: CAS!; isotypes: MEXU!, MO!).

Shrubs to small trees to 5 m tall. Young stems quadrate, bifariously pubescent with antrorse eglandular trichomes 0.2–0.4 mm long, soon glabrate. Leaves subsessile to petiolate, petioles to 16 mm long, blades elliptic, 35–240 mm long, 14–73 mm wide, 2.4–3.3 times longer than wide, intergrading with bracts, acuminate to subfalcate at apex, acute to attenuate at base, adaxial surface glabrous, abaxial surface glabrous or with scattered eglandular trichomes at junctions of major veins. Inflorescence of axillary and terminal pedunculate spikes, collectively forming a terminal panicle, rachis pubescent like young stems; dichasia 1-flowered, solitary at nodes (i.e., alternate), secund, sessile. Bracts subfoliose, caducous, lance-elliptic to lance-linear, 3.5–12 mm long, 0.7–3 mm wide, glabrous or sparsely pubescent with antrorse-appressed eglandular trichomes. Bracteoles caducous, lance-linear, 2.5–3 mm long, 0.5–0.6 mm wide, pubescent like bracts. Flowers subsessile (i.e., borne on pedicels to 1 mm long). Calyx 8–11.5 mm long, abaxially glabrous, lobes ovate-triangular, 2–3.5 mm wide. Corolla greenish-yellow with purplish markings, 18–25 mm long, externally pubescent with glandular trichomes 0.2–0.3 mm long, tube 9–14 mm long, upper lip 8–12 mm long, emarginate at apex, lower lip 7–9 mm long, lobes 1–2 mm long, 1.5–2 mm wide. Stamens 11–13 mm long, thecae 4–5 mm long, glabrous; pollen (Fig. 3) 4-aperturate, exine coarsely reticulate. Style 18–24 mm long, stigma 0.2 mm long, subcapitate to minutely 2-lobed. Capsule and seeds not seen.

PHENOLOGY.— Flowering: September-December; fruiting: unknown.

DISTRIBUTION.— Southern Mexico (Veracruz) and northern Guatemala (Petén); lowland rain forests; 100–150 meters.

ILLUSTRATION.— Contr. Univ. Michigan Herb. 19: 284. 1993.

ADDITIONAL SPECIMENS EXAMINED.— GUATEMALA: **Petén**: Los Arcos, Cadenas Road, on km 143, west, *E. Contreras 9311* (F, K, LL, MO, PH, S). MEXICO: **Veracruz**: Mpio. Hidalgotitlán, Benito Juárez segundo, 17°47′N, 94°39′W, *G. Castillo C. 364* (F, IEB, MEXU); Mpio. Hidalgotitlán, 7 km NW del Campamento Hermanos Cedillo por la brecha a La Escuadra, 17°16′N, 94°36′W, *M. Vázquez et al. V-1752* (F); Mpio. Jesús Carranza, 2 km N de Poblado 2, Ejido F. J. Mina, 17°16′N, 94°40′W, *M. Vázquez T. et al. V-2582* (CAS, MEXU).

Pollen of this species (based on *Contreras 9311*, *Dorantes et al. D-3538*, and *Vázquez T. et al. V-2582*) is 4-aperturate and thus appears more similar to that of *J. tabascina* than to that of either *J. viridescens* or *J. dendropila* (Fig. 3). Variation in pollen of this species was discussed by Daniel (1993). Four-aperturate pollen in *Justicia* was unknown to Graham (1988), but has been noted to occur in at least nine Mexican species (including *J. tabascina* and *J. valvata*) of the genus (Daniel 1995b, 1995c, 1998; Wasshausen and Daniel 1995). Pollen of the other seven species (i.e., *J. angustiflora* D.N. Gibson, *J. jitotolana* T.F. Daniel, *J. masiaca* T.F. Daniel, *J. multicaulis* Donn. Sm., *J. nelsonii* (Greenm.) T.F. Daniel, *J. nevlingii* Wassh. & T.F. Daniel, and *J. warnockii* B.L. Turner) with 4-aperturate pollen differs from that of section *Megalostoma* in various characteristics and these species do not appear to be closely related to *J. tabascina* and *J. valvata* based on macromorphological characteristics.

4. ***Justicia tabascina*** T.F. Daniel, Proc. Calif. Acad. Sci. 46:284. 1990. *Tabascina lindenii* Baill., Hist. Pl. 10: 445. 1891, as "*lindeni*," *non Justicia lindenii* Houllet (1870).

TYPE: MEXICO: **Tabasco**: forêts de Teapa, October, *J. Linden s.n.* (holotype: P!).

Shrubs to 2.5 m tall. Young stems subquadrate to quadrate, evenly pubescent with antrorse eglandular trichomes 0.3–0.6 mm long, internodes often constricted just above nodes. Leaves petiolate, petioles to 33 mm long, blades ovate-elliptic to elliptic, 36–180 mm long, 12–83 mm wide, 2–3 times longer than wide, acuminate at apex, acute to subattenuate at base, surfaces pubescent with cauline type trichomes mostly or entirely restricted to major veins. Inflorescence of 1–4 terminal thyrse(s) to 7.5 cm long, rachis evenly pubescent with flexuose to antrorse eglandular trichomes to 0.6 mm long; dichasia 1-flowered, paired at nodes (i.e., opposite), pedunculate, peduncles to 12 mm long, pubescent like rachis. Bracts often caducous, linear, 4–7 mm long, 0.6–1.5 mm wide, pubescent like rachis. Bracteoles linear, 2.5–6 mm long, 0.8–1 mm wide, pubescent like rachis. Flowers sessile to short (to 1 mm) pedicellate. Calyx 10–16 mm long, abaxially pubescent with erect to flexuose eglandular trichomes to 0.5 mm long, lobes asymmetrically elliptic to lance-elliptic to ovate-elliptic to elliptic, 2–5 mm wide. Corolla yellow or greenish white, 20–24 mm long, externally pubescent with glandular trichomes 0.05–0.2 mm long, tube 12–13 mm long, upper lip 9–11 mm long, entire at apex, lower lip 7–10 mm long, lobes 1.5–3 mm long, 1.5–2.5 mm wide. Stamens 9 mm long, thecae 3.8–5.3 mm long, dorsally pubescent with eglandular trichomes; pollen (Fig. 3) 4-aperturate, exine coarsely reticulate. Style 15–18 mm long, stigma more or less capitate, 0.2 mm long. Capsule 17–22 mm long, glabrous, stipe 7–9 mm long, head 10–13 mm long. Seeds 4, lenticular, subcircular in outline, 4.2–5 mm long, 3.5–4.8 mm wide, surfaces smooth.

PHENOLOGY.— Flowering: March, June, October; fruiting: February–March, June.

DISTRIBUTION.— Southern Mexico (Tabasco); lowland rain forests, lower montane rain forests; 20–140 m.

ILLUSTRATION.— None found.

ADDITIONAL SPECIMENS EXAMINED.— MEXICO: **Tabasco**: Mpio. Tacotalpa, Cerro de Madrigal, 7 km de las Est. Tacotalpa hacia Tapijulapa, *C. Cowan et al. 2860* (CAS, MEXU); Mpio. Teapa, Grutas de Joconá, 3 km NE de Teapa, *E. Martínez S. et al. 3098* (CAS, MEXU); Mpio. Teapa, Alrededores de las Grutas de Coconá, 17°33′N, 92°55′W, *P. Tenorio L. & M. Sousa S. 19545* (EAP, MEXU); Mpio. Teapa, Cerro del Coconá, *S. Zamudio R. 349* (MEXU).

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