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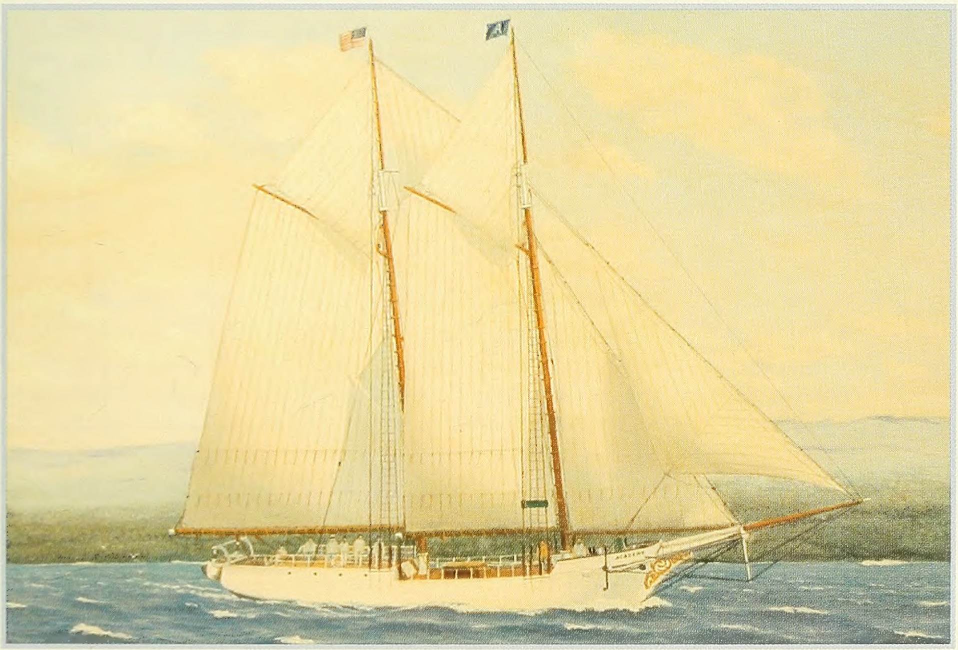

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COVER IMAGE

Painting by E. Helgason (1964) of Academy's schooner *Academy* (U.S. register #202055), the former U.S. Navy schooner *Earnest*, decked out for its 17-month voyage to the Galápagos Archipelago with new paint and new rigging. The schooner had been purchased from the Navy in May 1905 for $1000 plus an additional $50 for a new set of sails and binnacle. It was further refurbished and equipped for the Galápagos expedition at a cost of $4,550. The vessel measured 85 feet in length, 23.5 feet in width, and had a gross weight of 114 tons. The expedition departed from San Francisco 28 June 1905 and returned 29 November 1906. Its 10-man crew included Rollo Beck, expedition leader and ornithologist; Edward W. Gifford, ornithologist; Joseph S. Hunter, ornithologist; Ernest S. King, assistant herpetologist; Frederick T. Nelson, mate; Washington H. Ochsner, geologist and conchologist; J.J. Parker, navigator; Joseph R. Slevin, herpetologist; Alban Stewart, botanist; and Francis X. Williams, entomologist.

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Two New Species of Dorid Nudibranchs (Gastropoda, Opisthobranchia) from the Indian Ocean

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Two new species of cryptobranch dorid nudibranchs are described from the Indian Ocean. *Chromodoris cazae* sp. nov. is known from the United Arab Emirates, Gulf of Oman. This species is characterized by having a smooth white body with several irregular patches of deep red-maroon found scattered on the mid-dorsal region. Each of these patches has a number of smaller irregular orange spots within it. *Aldisa andersoni* sp. nov. is found from Sri Lanka. This species has a series of rows of low tubercles on the blue dorsum. Black pigmentation demarcates the rows of tubercles. The species also has an opaque yellow saddle posterior to the rhinophores, and other yellow marks on the dorsum. Other species having similar coloration and that also appear to mimic phyllidid nudibranchs are discussed. Both species are distinguished from other described taxa based on differences in body coloration and external and internal morphology and anatomy.

During the past several years, the described opisthobranch taxa of the western Pacific has increased dramatically (Brunckhorst 1993; Gosliner 1993, 1994; Gosliner and Draheim 1996; Gosliner and Behrens 1997; 1998a and b, 2000; Johnson and Gosliner 1998; Gosliner and Fahey 1998; Gosliner and Johnson 1999; Carlson and Hoff 2000; Fahey and Gosliner 1999a and b; Fahey and Gosliner 2001, 2003; Hamatani 2001; Yonow 2001; Dorgan et al. 2002; Ortiz and Gosliner 2003; Smith and Gosliner 2003; Gosliner and Smith 2003). The Indian Ocean, however, has a richly diverse but reasonably unknown opisthobranch gastropod fauna (Gosliner 1994; Gosliner and Behrens 2000; Valdés, Mollo, and Ortea 1999; Yonow 1984, 1994, Yonow et al. 2002). Increasing awareness of differences in opisthobranch morphology by sharp-eyed, dedicated recreational divers has produced a number of interesting finds. Two such new discoveries are described here.

The family Chromodorididae comprises one of the most colorful and morphologically diverse groups of dorid nudibranchs. More than 600 species have been described to date belonging to the 16 genera within the Chromodorididae. The morphological characteristics and the systematic relationships of members of the family have been comprehensively discussed in recent years (Rudman 1984, 1986, 1987, 1995; Baba 1994, 1995; Hamatani 1995; Gosliner and Behrens 1998a, 2000; Johnson and Gosliner 1998; Gosliner and Johnson 1999; Schrödl 1999; Valdés et al. 1999). The *Chromodoris* species described here broadens the basis for the genus and adds new records to the fauna of a little studied area of the Gulf of Oman.

Millen and Gosliner (1985) defined the diagnostic characters of the genus *Aldisa*, listing eleven species. The genus is characterized by having elongate denticulate teeth, penial spines, conical tubercles and reduced oral tentacles. Several additional species have been added since then (Ortea and Ballesetros 1989; Elwood et al. 2000; Perrone 2001). Perrone (2001) listed twenty species of *Aldisa* worldwide. He overlooked two species described the year before (Elwood et al. 2000). All but three of these species are white, yellowish or red in color. Perrone (2001) included in his list several undescribed species and the specimen shown in Debelius (1996:213 as *Chromodoris* sp.) as a junior synonym to *Aldisa erwinkoehleri*. We were fortunate to acquire the specimen (pictured in Debelius) from its collector, Dr. Charles Anderson, and describe it here as a new species. To paraphrase Dr. Bill Rudman (Sea Slug Forum, March 13, 2002), we too "used to think of *Aldisa* as a genus of red dorids which mimicked sponges, but now it seems they include a group of nodulose species which mimic phyllidiids."

This paper describes the anatomy and systematic relationships of two new species, one *Chromodoris*, from the United Arab Emirates and the one *Aldisa* mentioned above, from Sri Lanka. Specimens examined in this study are housed in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ).

Species Descriptions

Chromodorididae Bergh, 1891
Chromodoris Alder and Hancock, 1855

Chromodoris cazae Gosliner and Behrens, sp. nov.
(Figs. 1A, 2–3)

Chromodoris sp. Coleman, 2001:76.

Material examined.— Holotype (CASIZ 168299). Rashid Wreck, Khawr Fakkan, United Arab Emirates, 12 m, December 1, 1999. Paratype (CASIZ 168300). Jumeirah Reef, Khawr Fakken, United Arab Emirates, 12m, December 23, 2000.

Distribution.— Known only from the Gulf of Oman, United Arab Emirates.

Etymology.— *Chromodoris cazae* is named in recognition of Carole Harris, Dubai, United Arab Emirates, who was the first to bring this species to our attention and was instrumental in collecting the type specimens. The name *cazae* refers to Carole's childhood nickname (Caz).

External morphology.— The living animals are 40–70 mm in length. The body is oval and high, the notal surface is smooth (Fig. 1A), but with low pigmented elevations. The anus is situated within the ring formed by the gill branches. The perfoliate rhinophores have 18–26 lamellae. The branchial plume is made up of nine unipinnate branches. The background color of the body is translucent white. There are several irregular patches of deep red-maroon found scattered on the mid-dorsal region. Each of these patches has a number of smaller irregular orange spots within it. The number of orange spots varies greatly from zero to sixteen or more. Some specimens, as indicated in photographs of specimens not collected, have orange spots outside of the maroon patches, within the white regions. Each colored patch and spot is slightly elevated or raised from the otherwise smooth notal surface. The margin of the mantle has an irregular series of similar patches. Some specimens have a thin blue line along the edge of the mantle. In some specimens the rhinophoral sheaths have a small maroon patch on the posterior side. The gills and rhinophores are uniformly white, with opaque white specks and lines. Ventrally (Fig. 2B), the foot is about a quarter of the width of the notum. The genital aperture is located on the right side in the anterior third of the body. The triangular, conical oral tentacles are well separated from each other.

Mantle glands.— The mantle glands (Fig. 2A) are continuous around the lateral margins of the mantle and are absent from anterior and posterior portions of the notum. The glands consist of simple spherical bodies that are well separated from each other.

Buccal armature.— The buccal mass is composed of an oval to rounded buccal bulb and

FIGURE 1. Living animals. A, *Chromodoris cazae* sp. nov., specimen from Khawr Fakken, United Arab Emirates, photograph by Carole Harris. B. *Aldisa andersoni* sp. nov., specimen from Sri Lanka, holotype (CASIZ 167461), photograph by Charles Anderson.

the short, glandular oral tube (Fig. 2C). The muscular portion is about two-thirds the length of the oral tube. A pair of elongate salivary glands extends posteriorly from the junction of the posterior portion of the buccal bulb and the esophagus. At the anterior end of the muscular portion of the buccal mass there is a chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 3A) have a short base and a curved apex that may be undivided or, more commonly, a short bifid apex. The radular formula of the paratype is 33 × 42.1.42. The rachidian row of teeth is well-developed (Fig. 3B). The rachidian teeth are short, triangular and devoid of denticles. The innermost lateral teeth (Fig. 3B) have a broad triangular cusp. On the inner side of the primary cusp is a single rounded inner denticle. There are 4–5 small, acutely pointed denticles on the outer side of the primary cusp. The subsequent inner lateral teeth lack the inner denticle and possess 5–6 outer denticles. The middle lateral teeth (Fig. 3C) are elongate and sharply curved with 5–6 acutely pointed denticles on the outer side of the primary cusp. The three to four outermost teeth (Fig. 3D) are more elongate with a broad base. They have 3–4 rounded denticles on the outer side of the small primary cusp.

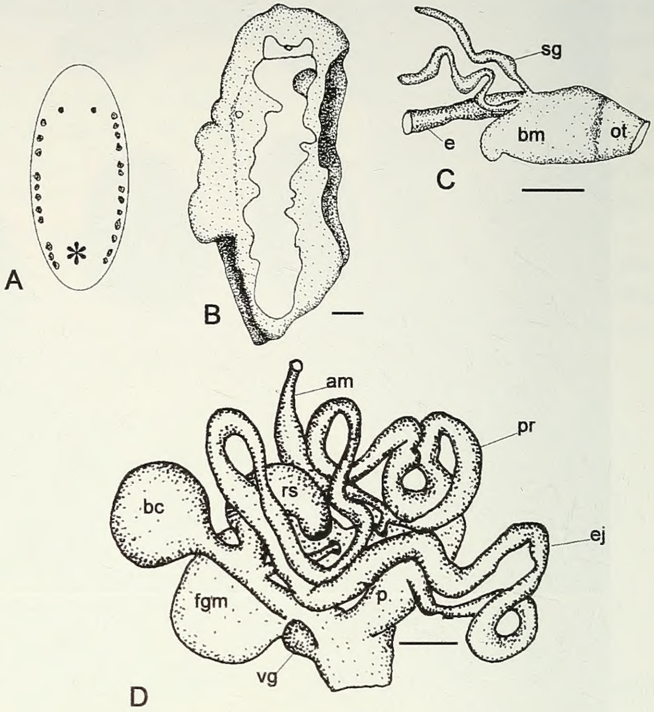

FIGURE 2. *Chromodoris cazae* (CASIZ 168300). A. Schematic distribution of mantle glands. B. Ventral view of anterior border of the foot, scale bar = 1.0 mm. C. Buccal mass, scale bar = 1.5 mm. D. Reproductive system; scale bar = 0.3mm. Abbreviations: am, ampulla; bc, bursa copulatrix; bm, buccal mass; e, esophagus; ej, ejaculatory duct; fgm, female gland mass; o, oral tube; ot, oral tentacle; p, penis; pr, prostate; sg, salivary gland; rs, receptaculum seminis; vg, vestibular gland.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 2D). The ampulla is relatively short and curved. From its proximal end it bifurcates into the short, thick, slightly convoluted prostate and the short oviduct that enters the female gland mass. From the prostatic portion of the vas deferens, the duct narrows somewhat and changes texture as it becomes the long and convoluted ejaculatory segment. More proximally to the genital atrium, the ejaculatory duct narrows and again abruptly expands into the short muscular penial sac. The thick vaginal duct opens into the genital atrium adjacent to the penis and a short, globular vestibular gland. Proximally, the vaginal duct connects directly with the spherical bursa copulatrix. The curved, pyriform receptaculum seminis enters the vagina immediately below the bursa copulatrix. Just below the entrance of the receptaculum seminis, the vagina is joined by the short, narrow uterine duct, which enters the female gland mass. The female gland mass is large and completely developed.

DISCUSSION.— *Chromodoris cazae* is unique in its white color with patches of maroon with smaller orange spots inside the patches. A few other species have similar colors. *Chromodoris kitae* Gosliner, 1994, has purple spots extending from the edge of the notum and covering the entire dorsal surface. There is a ring of orange patches along the submarginal area of the mantle. The gills and rhinophores are grayish white with opaque white spots. This species is known only from Madagascar. *Chromodoris naiki* Valdés, Mollo, and Ortea, 1999, from India, also has a white body but with purple and orange markings. In this case, the orange markings are not restricted to a sub-

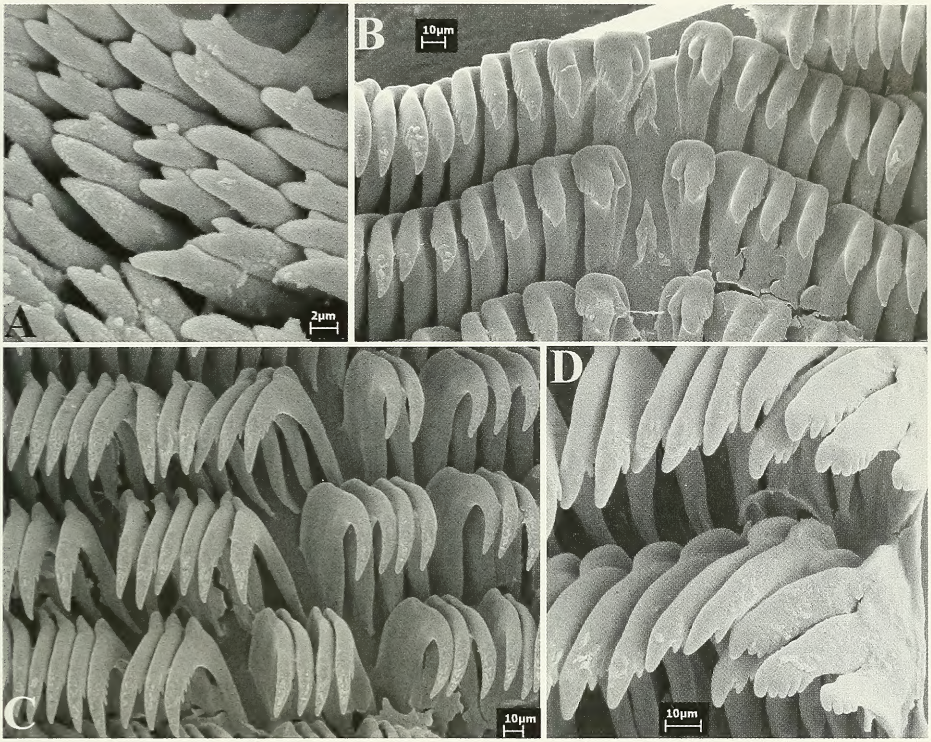

FIGURE 3. *Chromodoris cazae* sp. nov., holotype (CASIZ 168299). A, Scanning electron micrographs. A. Jaw rodlets, scale bar = 2 µm. B. Inner lateral teeth, scale bar = 10 µm. C. lateral teeth from the central portion of half-row, scale bar = 10 µm. D. Outer lateral teeth, scale bar = 10 µm.

marginal band and are found on the notum as well. This differs from the color pattern of *C. cazae*, where the orange spots are much smaller than the purplish ones. Additionally, *C. naiki* bears small opaque white spots on the notum that are absent in both *C. kitae* and *C. cazae*.

Internally, the three species differ as well. In *C. naiki*, a rachidian row of radular teeth is absent, whereas in *C. cazae* and *C. kitae* a row of triangular rachidian teeth is present. In *C. cazae*, the rachidian teeth are far more prominent than in *C. kitae*. In the reproductive system of *C. naiki* and *C. kitae*, the elongate and coiled receptaculum seminis enters directly into the base of the bursa copulatrix at the distal end of the vagina. In *C. cazae*, the receptaculum is pyriform with a shorter duct and enters the vagina in a position that is more proximal to the genital atrium.

Aldisidae Bergh, 1891

Aldisa Bergh, 1878

Aldisa andersoni Gosliner and Behrens, sp. nov.

(Figs. 1B, 4–5)

Chromodoris sp. Debelius, 1996:213 (bottom of page).
Aldisa erwinkoehleri Perrone, 2001: misidentification of specimen in Debelius, 1996.

MATERIAL EXAMINED.— HOLOTYPE (CASIZ 167461). Pigeon Island, Trincomal, Sri Lanka, March 7, 1995, 8 m deep, Charles Anderson. Photographs of two additional specimens taken on the same dive the holotype was collected, taken by Dr. Charles Anderson.

DISTRIBUTION.— Known only from Pigeon Island, Trincomal, Sri Lanka.

ETYMOLOGY.— *Aldisa andersoni* is named in recognition of Charles Anderson, Malé, Maldives, who was the first to bring this species to our attention and was instrumental in collecting the holotype.

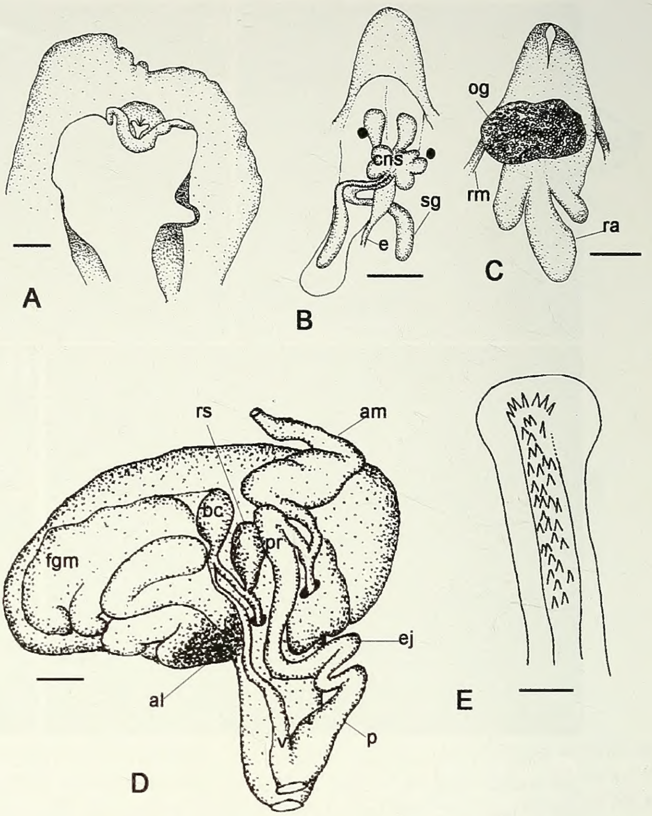

FIGURE 4. *Aldisa andersoni* sp. nov., holotype (CASIZ 167461) A. Ventral view of the anterior border of the foot, scale bar = 1.0 mm. B. Buccal mass, dorsal view, scale bar = 0.6mm. C. Buccal mass, ventral view, scale bar = 0.5 mm. D. Reproductive system; scale bar = 2.3 mm. E. Penial hooks, scale bar = 35 µm. Abbreviations: al, albumen gland; am, ampulla; bc, bursa copulatrix; cns, central nervous system; e, esophagus; ej, ejaculatory duct; fgm, female gland mass; og, oral gland; p, penis; pr, prostate; ra, radular sac; rm, retractor muscle; rs, receptaculum seminis; sg, salivary glands; v, vagina.

EXTERNAL MORPHOLOGY.— The living animals are 20–30 mm in length. The body is oval and the notal surface covered with a series of low conical tubercles (Fig. 1B). The tubercles form distinct ridges running longitudinally along the center of the notum, and perpendicular laterally along the margin of the notum. Rows of these tubercles are situated in regions of opaque blue pigment. These regions are separated by areas of black. There is an opaque, bright yellow saddle across the notum behind the rhinophores. This saddle extends right to the edge of the mantle. A few bright yellow patches may partially encircle the gill pocket. Some specimens have yellow patches posterior to the rhinophores. The anus is positioned dorso-ventrally. The perfoliate rhinophores have 17 lamellae. The gill is made up of seven tripinnate branches. The rhinophores and gill are the same blue as the notum. Each rhinophoral pocket has two equally-sized tubercles on either side. The gill sheath has a single row of twelve tubercles along its margin. The anterior portion of the foot (Fig. 4A) is smooth lacking a notch and the oral tentacles are rudimentary, typical of *Aldisa*.

BUCCAL ARMATURE.— The buccal mass is composed of an oval to rounded buccal bulb and the glandular oral tube (Fig. 4B–C). The esophagus opens on the dorsal side of the buccal mass, where two large, darkly pigmented salivary glands attach. Below the posterior end of the oral tube portion of the buccal mass lies a large granular oral gland mass (Fig 4C). The radular formula is impossible to determine given the elongate intertwining radular teeth (Fig. 5A). There is no trace of a rachidian row of teeth. The teeth are all extremely narrow and elongate with a broad, triangular base. The inner lateral teeth (Fig. 5C) are much longer than the outer ones. The inner teeth bear 7–8 sharp denticles with a wide groove extending from the apex to about the middle of each den-

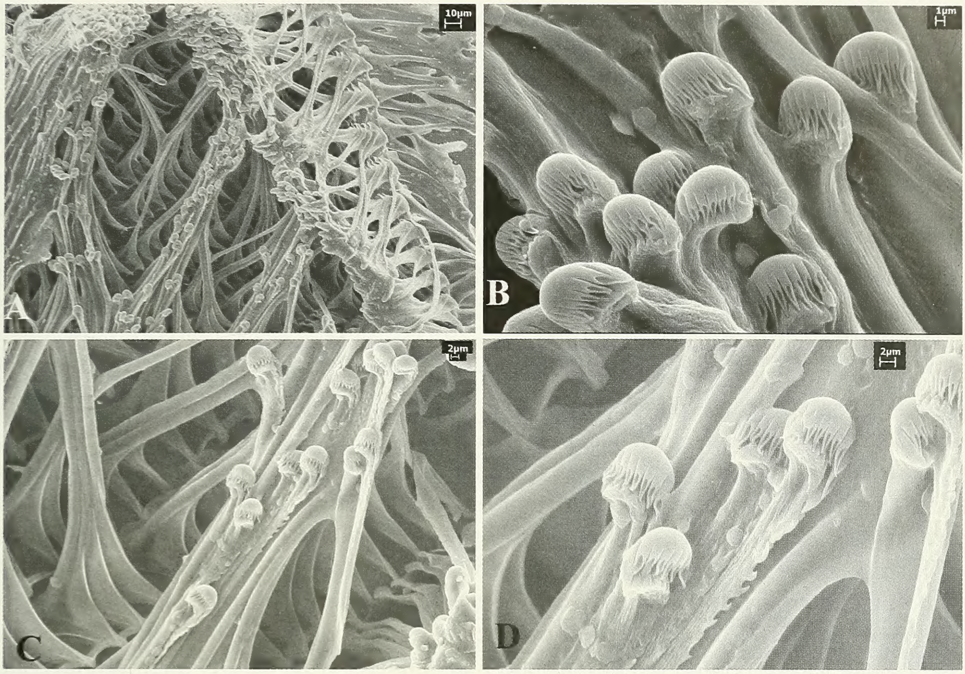

FIGURE 5. *Aldisa andersoni* sp. nov., holotype (CASIZ 167461). Scanning electron micrographs. A. Lateral teeth, scale bar = 10 µm. B. Close up of inner lateral teeth from the central portion of half-row, scale bar = 1 µm. C. Inner lateral teeth, scale bar = 2 µm. D. Close up of inner lateral teeth, scale bar = 2 µm.

ticle (Fig. 5B, D). A series of approximately ten smaller, simply upturned denticles are present along the distal portion of the tooth below the grooved denticles.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 4D). The ampulla is tubular and thick, winding back on itself before narrowing where the distal portion emerges at the prostate and oviduct. The oviduct connects with the female gland mass beneath the prostate. The prostate is granular and tubular, convoluted, distally narrowing and expanding again into the short muscular ejaculatory portion. The distal portion of the deferent duct exits at a separate genital atrium. The penial bulb is armed with approximately 6 rows of minute hooks (Fig 4E). The hooks have a wide base tapering to a long curved cusp. The vaginal duct is about the same length as the deferent duct, and opens into the bursa copulatrix. The bursa copulatrix is rounded and connects with the seminal receptacle by a short duct. Near the seminal receptacle this duct is joined by the uterine duct, which enters the female gland mass. The pyriform receptaculum seminis is equal in size to the bursa copulatrix.

DISCUSSION.— The revision of the genus *Aldisa* by Millen and Gosliner (1985) diagnosed the genus with the following characteristics: elongate radular teeth with multiple denticulations, a dorsum with low conical tubercles (except *Aldisa pikokai* Bertsch and Johnson, 1982, which lacks tubercles), a ring of tubercles around the rhinophoral and branchial pockets, bi- and tri-pinnate gills, penial spines in most species, absence of oral tentacles and the anterior portion of the foot smooth with no notch.

Aldisa andersoni exhibits all the characteristics of the genus *Aldisa* noted above. Elwood, et al. (2000) added a previously unnoticed character when describing *Aldisa albatrossae* and *A. williamsi*: the presence of a pair of unique hamate radular teeth, which are much wider and more robust than the thin denticulate ones.

Aldisa andersoni is the fourth described tropical Indo-Pacific species exhibiting bright blue coloration with black and/or yellow markings. It is similar, in this regard, to *Aldisa albatrossae*, *A. williamsi* and *A. erwinkoehleri* Perrone, 2001, but it differs in a number of characteristics. All other species, except *Aldisa barlettai* Ortea and Ballesteros, 1989, are species exhibiting subdued white, green, tan, or red coloration making them cryptic on their sponge prey.

In *Aldisa andersoni*, the low conical tubercles are clearly arranged in rows or ridges. Tubercles on the notum of *Aldisa albatrossae*, *A. williamsi* and *A. erwinkoehleri* are randomly distributed. The black coloration on *A. williamsi* and *A. erwinkoehleri* forms concentric rings, and in *A. albatrossae* **it** forms a rectangle on the dorsum with a T-shape mark anterior to the rhinophores. In *A. andersoni*, the black pigmentation is found uniformly over the mantle separating the rows of tubercles. The opaque yellow pigmentation on *Aldisa andersoni* is quite similar to that found on *A. albatrossae* and *A. erwinkoehleri*. There are, however, consistent differences that clearly separate them. *A. williamsi* has no yellow pigmentation. The yellow pigmentation covers the tubercles in *A. erwinkoehleri* and in *A. andersoni*, but not in *A. albatrossae*, where it occurs between the tubercles. The yellow color markings on *A. andersoni* are far more extensive than in the other species, with a yellow saddle extending to the very edge of the mantle that is not isolated into smaller broken patches, as in *A. erwinkoehleri*.

The rhinophores differ in color among all four species. In *Aldisa albatrossae*, they are white-grey; in *A. williamsi*, pale brown; in *A. erwinkoehleri*, black; whereas in *A. andersoni* they are the same blue as the body. The arrangement of tubercles around the rhinophoral pockets also differs among the four species. *Aldisa albatrossae* has four similarly sized equally separated tubercles; *A. erwinkoehleri* has two large and two small tubercles, whereas *A. andersoni* and *A. williamsi* have two equally sized tubercles, which are separated on either side of the pocket. Differences exist also in the tubercles around the gill sheath. *A. albatrossae* has a double row of tubercles; *A. williamsi* has a single row of eight tubercles; *A. erwinkoehleri* a single series tubercles; and *A. andersoni* has a single series of twelve tubercles around the sheath.

Internally, the radular teeth vary in one significant regard. In *Aldisa albatrossae* and *A. williamsi*, there is a pair of smooth, hamate teeth in addition to the elongate teeth typical of species of *Aldisa*. These hamate teeth are absent in *A. andersoni* and were not described either in *A. erwinkoehleri*. A massive granular gland on the ventral surface of the buccal mass is present in *A. andersoni*. Re-examination of type specimens of *A. williamsi* and *A. albatrossae* revealed the presence of a similar gland, but it is proportionately much smaller in these two species than that found in *A. andersoni*.

A few differences were found in the reproductive systems of the four species. The penial spines of *Aldisa andersoni* are similar in shape to those found in *A. williamsi*, but they differ from those of *A. albatrossae*. Perrone (2001) reports no armature at all in the penial bulb of *A. erwinkoehleri*. In the description of *A. erwinkoehleri*, the prostatic portion of the vas deferens was not differentiated, as it is in the other three species. It is not certain whether these discrepancies are due to morphological differences, but they are more likely the result of incomplete description in the case of *A. erwinkoehleri*. The bursa copulatrix is relatively small in all four species, being approximately equal to the receptaculum seminis in size.

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Pacific Coast Nudibranchs, Supplement II New Species to the Pacific Coast and New Information on the Oldies

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***Pacific Coast Nudibranchs — A Guide to the Opisthobranchs Alaska to Baja California* (Behrens 1991) presented taxonomic and biological information on 217 species of opisthobranch molluscs found within the geographic range of the title. Only a few species were excluded at that time, because of depth or rarity. Since its printing many new species have been discovered and the ranges of others found to occur within the coverage of the original work. Researchers have learned a great deal about morphological variation and the ecology of many species. The goal of this supplement is to bring current the biological, biogeographical, morphological and taxonomic information concerning those species found along this coastline by incorporating both published material and confirmed observations of field workers and opishtobranch enthusiasts. The opisthobrach fauna of the Pacific Coast, from the Bering Strait of Alaska to Cabo San Lucas, Baja California Sur, Mexico, now totals some 252 documented species.**

This supplement is intended to update the contents of *Pacific Coast Nudibranchs*, second edition, (Behrens 1991) by providing information on newly discovered species, unknown at the time of publication of that edition, and new occurrences, range extensions and ecological information, as well as, changes to and additions of species names published since 1991.

This new information is compiled not only from the publication of recent scientific journal articles, but also from observations and collections shared with the author by opisthobranch researchers and enthusiasts up and down the Pacific Coast. Without this collaborative effort, accumulation of scientific knowledge in this area would certainly not be as extensive as it is today. Included here are 26 species new to the region covered by the 1991 edition. This supplement also includes species, previously undescribed, which now have names, several newly discovered foreign introductions, and 23 additional undescribed species, bringing the total number of opisthobranch species from the Bering Strait, Alaska to the tip of Baja California, Mexico, to 252 species.

Interest in opisthobranch mollusks has a broadening audience as indicated not only by the number of new publications featuring this taxonomic group, but by the media attention being given it. Nudibranch or sea slug is becoming a household word.

The recent report of the introduction of a *Philine* from New Zealand waters to San Francisco Bay and its rapid population spread to other coastal bays and estuaries in California received television and newspaper coverage across the country.

With the growth of the Internet has come its concomitant use by opisthobranch enthusiasts to share information. It all began with Bernard Picton and C. Morrow's entire book entitled *A Field*

Guide to the Nudibranchs of the British Isles presented on a Web Site. Since then, Nudibranch web sites have sprung up all over the World. On the West Coast of the United States, we have two web sites. "The Slug Site" features a collection of color photos from various regions around the world, whereas "The Opisthobranch" web site contains online editions of the current month's *Opisthobranch Newsletter*, a bibliography of Opisthobranchia, a nudibranch bibliography compiled by Gary McDonald with gopher search capabilities, a list of color illustrations of opisthobranchs on the net, a taxonomic and systematic list of Opisthobranchia, and the addresses of persons following this group of marine animals. Internationally, the Australian Museum's — "Sea Slug Forum" has become the largest and most active site providing realtime communication among sea slug enthusiasts and scientists alike. Lastly, Erwin Koehler's *Opisthobranchs of the World* is a list of every photograph of an opisthobranch on the world wide web.

New information was accepted for this supplement up until September 30, 2003.

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SPECIES NEW TO THE PACIFIC COAST

The following species were not known by the author to occur between Alaska and the tip of the Baja California peninsula during the preparation of the second edition of *Pacific Coast Nudibranchs* in 1991. Some are new discoveries, some were published in obscure publications, and some where purposely excluded from the 1991 edition due to their depth of occurrence below that of the average SCUBA diver. The new records are presented here in phylogenetic order.

Order Cephalaspidea

Family Acteonidae

Acteon sp.

Gosliner (1996) reports an undescribed species of *Acteon* from the Santa Maria Basin, California.

Identification.— The shell is white and 3 mm long with 22 finely, punctate spiral lines on the body whorl (Gosliner 1996) (Fig. 1). It has three whorls. This species has a large operculum. The species is reported to be similar to *Acteon panamensis* Dall, 1908, but different from *A. traskii*, which has rose colored bands on the shell (Gosliner 1996).

Radula.— Each half row has more than 50 minute teeth, each with 16–18 denticles along the inner edge.

Size.— 1–3 mm in length.

Range.— Santa Maria Basin, off Purisima Point, California (Gosliner 1996).

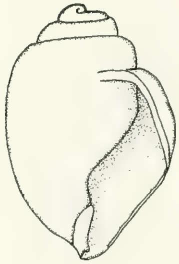


Figure 1. *Acteon* sp. Drawing of shell. (After Gosliner 1996.)

Family Hydatinidae

Parvamplustrum sp.

Gosliner (1996) reports an undescribed species of *Parvamplustrum* from the Santa Maria Basin, California.

Identification.— A tiny species, the animal has a short, triangular foot (Gosliner 1996). It has bifid head tentacles. The shell is bulloid.

Radula.— Gizzard plates are absent and the jaws are unarmed polygonal rodlets (Gosliner 1996). The radular formula is 20 × 1.0.1. The lateral teeth are curved with broad denticles.

Size.— Less than 1 mm in length.

Range.— Santa Maria Basin, off Purisima Point, California (Gosliner 1996).

Family Cylichnidae

***Cylichna diegensis* (Dall, 1919)**

Gosliner (1996) reports *Cylichna diegensis* from the Santa Maria Basin, California.

Identification.— The shell is bulloid (Fig. 2A) with fine spiral striae and brown periostrical lines at each end (Gosliner 1996). The body of the animal is brown in the preserved state.

Radula.— The jaws have multifid rodlets (Fig. 2B). The radular formula is 13 × 3–4.1.1.1.3–4 (Gosliner 1996). The rachidian teeth are bifid with 5–7 denticles (Fig. 2C). The inner lateral teeth have 9–11 denticles (Fig. 2D). The three gizzard plates are equal in size and shape (Gosliner 1996).

SIZE.— The shell is 3–7mm in length.

RANGE.— Pt. Loma, San Diego, California (9–191 fathoms) to the Santa Maria Basin, off Point Sal, California (Gosliner 1996).

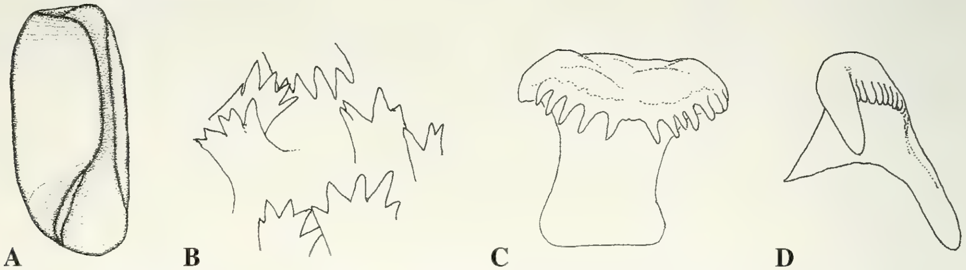


FIGURE 2. *Cylichna diegensis* (Dall, 1919). A. Drawing of shell. B. Jaw rodlets, C. Rachidian tooth, D. Lateral Tooth. (After Gosliner 1996.)

Acteocina eximia (Baird, 1863)

Gosliner (1996) discusses nomenclatural issues surrounding the subspecies originally assigned to *Acteocina culcitella.* He concludes that the subspecies, *Acteocina culcitella eximia*, is in fact a distinct species in the California fauna.

IDENTIFICATION.— Externally similar to *Acteocina culcitella* (Species #4 in Behrens 1991), but with a shorter spire and no columellar pleat (Gosliner 1996) (Fig. 3A).

RADULA.— The radular formula is 19–28 × 1.0.1 (Gosliner 1996). The lateral teeth have a strong central denticle, with 30–50 short denticles along the margin (Fig. 3B). There are three gizzard plates, two large and concave and one small one that is laterally compressed and concave (Gosliner 1996).

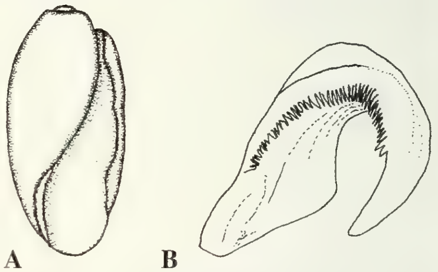


FIGURE 3. *Acteocina eximia* (Baird, 1863). A. Drawing of shell. B. Lateral Tooth. (After Gosliner, 1996.)

SIZE.— 4–10mm in length.

NATURAL HISTORY.— Found in deep water, 22 m in its northern range to 60 m in the southern areas.

RANGE.— Vancouver, British Columbia, to San Diego, California (Gosliner 1996).

Family Retusidae

Retusa zystrum Dall, 1919

Gosliner (1996) reports *Retusa zystrum* from the Santa Maria Basin, California.

IDENTIFICATION.— The shell is bulloid with numerous characteristic longitudinal striae (Gosliner 1996).

Buccal Morphology.— Jaws are absent. The gizzard plates are not equal in size, one being larger than the other two (Gosliner 1996). The plates are covered with tubercles, the largest being on the inner side.

SIZE.— 1.5 mm in length.

RANGE.— Described from San Diego and San Pedro, California. Now known from the Santa Maria Basin off Point San Luis and Purisima Point, California (Gosliner 1996).

Volvulella californica Dall, 1919

Volvulella californica Dall, 1919, is reported by Gosliner (1996) from the Santa Maria Basin, Califonia, just north of its type locality.

Identification.— Shell smooth, without sculpture (Figure 4A). Widest in middle, tapered at both ends. Posterior project acute, elongate (Gosliner 1996).

Radula.— None

Natural History.— Little is known. Specimens were collected at between 90–345 m depth.

Size.— 1–3 mm in length.

Range.— Santa Cruz, California, to Todos Santos Bay, Baja California (Abbott 1974).

Etymology.— Named for the State of California, its type locality.

Volvulella panamica Dall, 1919

Volvulella panamica, on the other hand, was known only from Panama, and it too is noted because of its recent collection in the Santa Maria Basin (Gosliner, 1996).

Identification.— Shell smooth, without sculpture, and with a prolonged posterior projection (Fig. 4B). Posterior end of outer lip originating at base of posterior projection (Gosliner 1996).

Radula.— None

Natural History.— Little is known about the biology of this species. Specimens were collected from 90–197 m depth.

Size.— 2.5–5 mm in length.

Range.— Santa Maria Basin, California (Gosliner 1996), to Panama (Abbott 1974).

Etymology.— Named for the type locality, Panama Bay, Panama.

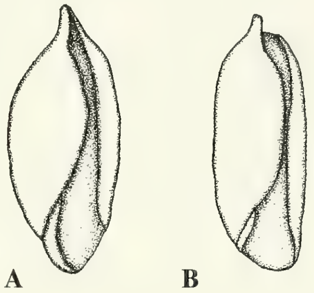


Figure 4. Drawings of shells of (left) *Volvulella californica* and (right) *Volvulella panamica*. (After Gosliner 1996.)

Family Philinidae

A white species of *Philine* was first noted in San Francisco Bay when it was observed in trawl samples collected in conjunction with the on-board educational program offered by the Marine Science Institute of Redwood City, in the summer of 1992. It was identified by Gosliner (1995) as *Philine auriformis* Suter, 1909. Rudman (*www.seaslugforum /philcali.htm*) refutes this identification, stating the California species is quite different in internal anatomy from the New Zealand *Philine auriformis*. Since that time, similar white *Philine* have become abundant along the entire California coastline. As a result of careful study, a total of four species of white *Philine* have now been identified throughout the region (see discussions on the Sea Slug Forum — *www.seaslugforum/philcali.htm*). Three more deepwater species are reported from the Santa Maria Basin, California, by Gosliner (1996).

Philine aperta (Linnaeus, 1767)

Identification.— The animal is white like *P. auriformis, P. orientalis* and *P. japonicus*.

Buccal Morphology.— Gizzard plates same as *P. orientalis* and *P. japonicus*, two larger mirror imaged and a third smaller plate. All have small holes in the center.

Size.— To 70 in length.

Range.— Atlantic coast of South Africa. California (T. Gosliner, pers. commun.).

Philine auriformis Suter, 1909

Identification.— The animal (Plate 1A) is transparent white to yellow in color. The Hancock's organs are reddish brown, and the darker visceral mass and gizzard plates are clearly visible through both the dorsal and ventral surfaces of the body (Gosliner 1995). This species also has a broad, shallow internal shell, with a spiral beaded sculpture.

Buccal Morphology.— There are equally sized spindle shaped gizzard plates with grooves on the outer surface (Gosliner 1995) (Fig. 5B). The radular formula is 21 × 1.1.0.1.1. There are 30–50 fine denticles along the inner masticatory edge on the inner lateral tooth (Fig. 5A). The outer tooth is smaller but similar in morphology.

Natural History.— This species is found on muddy bottoms, intertidally to 15–20 ft. deep. Egg masses are large, ovoid, mucous masses attached to the substrate by a thread. They contain numerous spirals of egg capsules, each capsul containing two eggs (see Gosliner (1995) for details). This voracious carnivore feeds on the clam *Gemma gemma* and several species of *Transennella*.

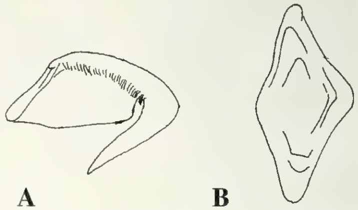


Figure 5. *Philine auriformis* Suter, 1909. A. Lateral radular tooth; B. Gizzard plate.

Size.— 15–30mm in length.

Range.— South San Francisco Bay and Bodega Harbor, California (Gosliner 1995). Also reported from Dillon Beach (H.E. Smith, pers. commun.), Morro Bay (M. Behrens, pers. commun.) Elkhorn Slough (G. McDonald, pers. commun.), Mission Bay (D. Cadien, pers. commun.), and Coos Bay, Oregon (Jeff Goddard, pers. commun.), Barkley Sound, Vancouver Island, British Columbia (S. Millen, pers. commun.).

Philine japonica Lischke, 1872

Identification.— The animal is white like *P. aperta, P. auriformis, and P. orientalis.*

Buccal Morphology.— Gizzard plates same as *P. aperta and P. orientalis*, two larger mirror imaged and a third smaller plate. All have small holes in the center.

Size.— To 50 mm in length.

Range.— Japan and Tomales Bay, California (Gosliner, pers. commun.).

Philine orientalis A. Adams, 1854

Identification.— The animal is white similar to *P. aperta, P. auriformis, and P. japonicus.*

Radula.— Gizzard plates are relatively large. Two are mirror images of one another. The third is smaller and symetrical in shape. Each plate has a pair of pin holes in the center (Fig. 6A). The radular formula is 1.0.1. The teeth are hook-like with a denticulated edge, like that of *P. auriformis* (Fig. 6B).

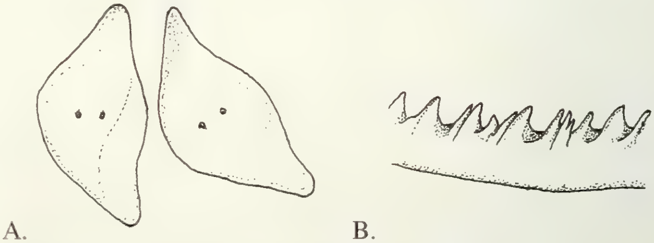


Figure 6. *Philine orientalis* A. Adams, 1854. A. Gizzard plate. B. Radular dentition.

Natural History.— Found on intertidal mudflats. Periodically in dense populations, dozens per square meter (M. Chow, pers. commun.).

SIZE.— To 50 mm in length.

RANGE.— Originally described from "eastern seas," it has been reported from the Philippines by Watson (1886) and from Hong Kong by Morton and Chiu (1990). Bodega Bay and San Francisco Bay, California (M. Chow and T. Gosliner, pers. commun.).

Philine polystrigma (Dall, 1908)

Orignally named *Clistaxis polystrigma* Dall, 1908, Gosliner (1996) reports this species from the Santa Maria Basin, California and reassigns the species to the genus *Philine*.

IDENTIFICATION.— Typical *Philine* body shape, the preserved specimens were light tan (Gosliner 1996). The anterior head shield is rounded at both ends. The posterior shield has a blunt lobe on either side (Figure 7A).

RADULA.— The radular formula is 16 × 1.0.1. The lateral teeth have 25–30 fine, triangular denticles (Gosliner 1996) (Fig. 7B). The three gizzard plates are long, oval and equal in size and shape (Fig. 7C).

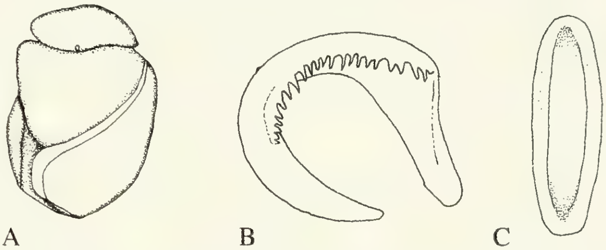


FIGURE 7. *Philine polystrigma* (Dall, 1908). A. Drawing of animal. B. Lateal tooth. C. Gizzard Plate. (After Gosliner 1996.)

SIZE.— 0.5 to 3.0 mm in length.

RANGE.— Described from South Coronado Island. Gosliner extends the range to the Santa Maria Basin, off Point San Luis and Point Sal, California.

Philine sp. 1

Gosliner (1996) reports two undescribed species from the Santa Maria Basin, California.

IDENTIFICATION.— *Philine* sp. 1 is morphologically similar to *P. polystrigma* as discussed above (Gosliner 1996) (Fig. 8A). The shell has a characteristic pointed lobe (Fig. 8B).

RADULA.— The radular formula is 15 × 1.1.0.1.1. The inner lateral teeth have 22–34 elongate denticles (Gosliner 1996) (Fig. 8C). The outer lateral teeth are simple and smooth. The three gizzard plates are equal in size. They have a prominent ridge down the centerline (Gosliner 1996).

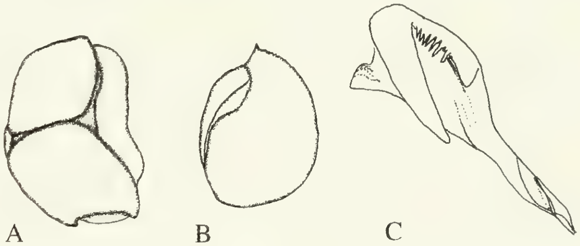


FIGURE 8. *Philine* sp. 1. A. Drawing of animal. B. Lobe of shell. C. Inner Lateral tooth. (After Gosliner 1996.)

NATURAL HISTORY.— Collected only on fine soft sediments in 90–155 m of water. Probably feeds on Foraminifera (Gosliner 1996).

SIZE.— 1–5 mm in length.

RANGE.— Known from the Santa Maria Basin, off Point San Luis and Point Sal, California (Gosliner 1996).

Philine sp. 2

Gosliner (1996) reports a second undescribed *Philine* from the Santa Maria Basin, California.

Identification.— A tiny species, the anterior shield is short and rounded posteriorly, whereas the posterior shield is elongate, terminating in skirt-like lobes (Gosliner 1996).

Radula.— This species has a unique radular formula of 13 × 6.1.0.1.6 (Gosliner 1996). The inner lateral teeth are broad and hook-shaped and bear no denticles (Gosliner 1996). The outer lateral teeth are narrow hook-shaped and are also free of secondary denticles (Gosliner 1996).

Size.— Approximately 1 mm in length.

Range.— Known only from the Santa Maria Basin, off Point San Luis, California (Gosliner 1996).

Family Aglajidae

Aglaja sp.

A new, undescribed species of *Aglaja* is reported from Santa Maria Basin, California (Gosliner 1996).

Identification.— The body is a uniform whitish brown. Both ends of the head shield are rounded. The posterior shield terminates in an elongate tail on the left side of the body and a shorter lobe on the right side (Gosliner 1996).

Buccal Morphology.— There are no radula or gizzard plates (Gosliner 1996).

Size.— 0.5–1 mm in length.

Range.— Known only from the Santa Maria Basin, off Purisima Point and Point Sal, California (Gosliner 1996).

Family Philinoglossidae

Philinoglossa sp.

Nine specimens of this undescribed species have been collected on a fine sand bottom in 65 ft. of water off San Diego (Cadien 1998). The specimens ranged in size from 1–2 mm in length, suggesting that this species may be quite common but overlooked due to its small size (Plate 1B). According to Cadien (1998), the species is ovate-elongate and lacks a head shield, parapodia, external gills, rhinophores, oral tentacles, attenuated foot corners, posterior mantle lobes surface eyes and an external shell.

The color is tan, with darker reddish brown visceral mass showing through. Internally there is no shell, jaws or gizzard plates. The radula formula is 15 × 2.1.0.1.2. The lateral teeth are flat and appressed, the cusp simple, curved and acute (Plate 1C). The lateral tooth is larger, stronger and strong shouldered. The central cusp is curved with some small marginal denticles.

Family Akeridae

Akera sp.

The benthic monitoring program carried out in southern California, referred to a Bight '98 EMAP project, has collected an unidentifiable species determined to belong to the genus *Akera* (Ron Veralde and Kelvin Barwick, pers. commun.). The specimen was collected in 40 m of water near the south western shore of Santa Catalina Island. As seen in Plate 1D, the body of the animal is cream colored. The internal organs can be seen through the external coiled shell, which has a depressed spire.

Order Anaspidea

Family Aplysiidae

***Aplysia parvula* Güilding in Mörch, 1863**

This species occurs worldwide in warm temperate waters and has recently been observed in southern California (Bruce Wright, pers. commun.).

Identification.— Typical sea hare body form. Mottled brown in color, the parapodia has a dark blue-black line along the edge of the parapodia (Plate 1E). The parapodia encloses the mantle cavity.

Size.— To 50 mm in length.

Range.— Worldwide tropical to sub-tropical. Along the Pacific Coast of North America from the Gulf of California to Galápagos Islands (Gosliner 1991), and San Clemente Island.

Order Notaspidea

Family Pleurobranchidae

***Pleurobranchus* cf. *areolatus* (Mörch, 1863)**

Although originally thought to be a new species of *Pleurobranchus*, because it was so far outside of the range of *P. areolatus* and because it lacked the characteristic white speckles on the rhinophores and white snow flakes over the notal tubercles, internal anatomical similarities suggest we should refer to it as a color variation of *P. areolatus* until further studies are conducted, suggesting otherwise.

Identification.— A large pleurobranch, the notal surface is covered with large smooth tubercles (see Plate 1F). The largest tubercles are brown whereas smaller ones are golden brown. In juveniles, the border between the tubercles is white whereas in larger specimens is ~~a~~ light tan to peach color. The rolled rhinophores are tan to orange.

Radula.— 90 × 230.0.230.

Size.— To 190 mm in length (Angulo-Campillo et al. 2001).

Range.— The new occurrences outside the Gulf of California, include: Isla Revillagigedos, Mexico (K. Kaiser), San Benitos Island (E. Houcke), La Jolla (P. Hughes) and San Clemente Island (M. Tegner, K. Miller and C. Gramlick), San Diego County, Anacapa and Catalina Islands, California (J. Engle, E. Erikson, R. Herrmann and D. Richards). Previously, Atlantic coast, Florida and Caribbean to Canal Zone, Barbados and Curacao, and Gulf of California to Panama.

Order Sacoglossa

Family Stiligeridae

***Placida* sp.**

Discovered by Jim Lance and Wes Farmer, the species is undescribed.

Identification.— Aeolid-like in appearance, this sacoglossan has a cream colored head and green cerata covered with white specks and have white tips (Plate 1G). The long cephalic tentacles are also white at the tips.

Radula.— Unknown

Natural History.— This species lives on intertidal mudflats and feeds on the green alga, *Codium magnum.*

Size.— To about 15 in length.

Range.— To date known only from Bahía San Quintin, Baja California, Mexico.

Order Nudibranchia
Suborder Doridacea (= Doridina)
Family Gnathodoridoidea

Bathydoris aioca **Marcus and Marcus, 1962**

Originally described from Guadalupe Island, Baja California, Mexico, I was unaware of any photographs of this species and, due to its depth of occurrence, I excluded it from the 1991 edition of *Pacific Coast Nudibranchs*. The species has now been dredged off the Oregon coast.

Identification.— Valdés and Bertsch (2000) report that although the color of the living animal is unknown, the dorsum is smooth and preserved specimens give no evidence of spots or other color markings (Plate 1H). The rhinophores are quite long and bear 45 lamellae. The gill consists of 18 bipinnate branchial leaves.

Radula.— The radular formula is 53–64 × 64–81.1.64–81.

Natural History.— Dredged from depths of 2700–2850 m.

Size.— To 71 mm in length.

Range.— Known only from the type locality off Guadalupe Island, Mexico, and Oregon (Valdés and Bertsch 2000).

Family Goniodorididae

Okenia **sp. 1**

A new species of *Okenia* has been showing up regularily in southern California (Plate 1I). It has been encountered at diver depths off Huntington Beach, Newport Beach, San Onofre and Redondo Beach on worm tubes on soft bottoms (Don Cadien, pers. commun.). Further south in San Diego, the species is found in association with the solitary tunicate, *Mogula* sp. (Ron Velarde and Megan Lilly, pers. commun.). Preliminary evaluations indicate that the species is undescribed but shares some anatomical features with *Okenia aspersa* (Alder and Hancock, 1845) from British waters (D. Cadien, pers. commun.).

Okenia **sp. 2**

A second undescribed species of *Okenia* is reported from the Santa Maria Basin, California (Gosliner 1996).

Identification.— The notum has 3–4 papillae present along either lateral margin of the notum (Gosliner 1996). There are four gills arranged in a semi-circle (Gosliner 1996).

Radula.— The radula formula is 18 × 1.1.0.1.1. The inner lateral teeth are large, curved with 7–8 denticles on the inner side (Gosliner 1996). The outer lateral teeth are narrow and bicuspid.

Size.— 1 mm in length.

Range.— Known only from the Santa Maria Basin off Point Sal, California (Gosliner 1996).

Family Onchidorididae

Calycidoris guentheri **Abraham, 1876**

The distribution of this species has previously been given as Arctic Seas to Bering Strait in 14–44 meters of water. Nora R. Foster and Rae Baxter were responsible for the first collections of this species in the northern Pacific, the southern most being from the central Bering Sea. It is a synonym of *Doris* (*Adalaria*) *sibirica* Aurivillius, 1887 (= *Calycidoris guentheri*, *fide* T. Gosliner, pers. commun.). See complete description below.

Identification.— Typically doridoid in shape, the body is large, slightly wider in front and depressed. It is densely covered with small conical spiculose tubercles which vary in size. The ground color is tan to dark brown, often with reddish pink to purple. The head is a narrow, thick, veil. It has 18–23 pinnate gills in a circle around a central anus, which contract into a sheath.

Radula.— The radular formula is 25–28 × 3.1.0.1.3.

Natural History.— Dredged from depths of 9–270 m, usually 9–60 m (Roginskaya 1972).

Size.— To 32 mm in length.

Range.— Widespread in the Arctic Ocean from the Barents Sea to the Chukchi Sea and Bering Strait (Roginskaya 1972); also found across the Beaufort Sea to Liverpool Bay, North WestTerritory (S. Millen, pers. commun.). Specimens are also reported from the Bering Sea (Goddard and Foster 2002).

Etymology.— Named for Dr. Albert Günther of the British Museum of Natural History.

Family Discodorididae

Diaulula greeleyi (MacFarland, 1909)

Peltodoris nayarita Ortea and Llera, 1981, was described from the Nayarit coast of Mexico by Ortea and Llera (1981). Since then it has been collected within the coverage of *Pacific Coast Nudibranchs*, 2nd ed., at Punta Eugenia (Bertsch et al. 2000). Camacho-García and Valdés (2003) report that this species is synonymous with *Diaulula greeleyi* (MacFarland, 1909).

Identification.— An orange red dorid with brown blotches (Plate 2A). The dorsum is tuberculate, bearing caryophyllidia. The rhinophores and gills pockets are elevated.

Radula.— The radular formula is 37 × 55.0.55. The lateral teeth are hamate, having a single cusp and lacking denticles.

Size.— To 100 mm in length.

Range.— Florida, Brazil, South Carolina, Isla Isabela, Nayarit, Mexico and Punta Eugenia, Baja California, Mexico, and the Pacific Coast of Costa Rica (Camacho-García and Valdés 2003).

Family Polyceratidae

A recent, deepwater study in the Santa Maria Basin of Central California has produced a number of previously undescribed species (Gosliner 1996). The following genus, new to the Pacific Coast of North America, was represented among specimens collected during that study. The new species has yet to be described.

Holoplocamus sp.

Among the new species collected in the Santa Maria Basin study (Gosliner 1996) was this primitive polyceratid. Coincidentally, Shrake (1977) reported the collection of five specimens taken in 600 ft of water at locations, also in the Santa Maria Basin (Platform Harvest and Platform Hildago), of a species identified at the time, as *Triopella* sp., another primitive polyceratid. Subsequent discussions with Don Cadien, who originally identified the specimens as *Triopella*, have led to the conclusion that those specimens were likely the same as Gosliner's species reported here as *Holoplocamus* sp.

Identification.— The body is elongate with 11–15 spiculate velar tentacles and 4–6 lateral appendages per side of the body (Fig. 9). The three gills are unipinate to bipinnate. The mouth is flanked by a pair of elongate tentacles (Gosliner 1996).

Radula.— The radular formula is 30 × 7–8.2.1.2.7–8. See Gosliner (1996) for SEMs of the radular morphology.

Natural History.— Collected by trawl net on both hard and soft bottoms.

Size.— To 0.5–1.5 mm.

Range.— Know only from the Santa Maria Basin, Platform Harvest and Platform Hildago (Shrake 1977) and off Morro Bay and Purisima Point, San Luis Obispo County, California (Gosliner 1996).

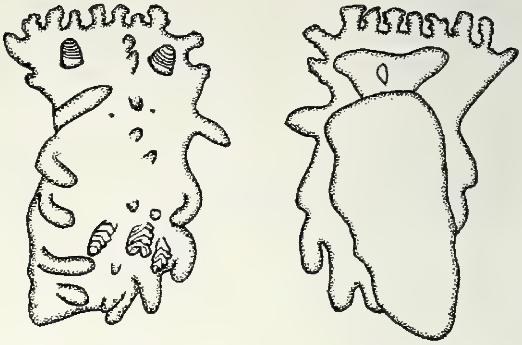


Figure 9. *Holoplocamus* sp. Drawings of preserved specimen. Dorsal and ventral views. (After Gosliner 1996.)

Colga pacifica Bergh, 1894

Identification.— This phanerobranch dorid looks very much like a *Triopha*. The notum has a pre-branchial notal processes. A main row of elongate processes runs down the middle of notum and usually a pair of rows of similar processes accompanied it along both sides. In some specimens these lateral rows are almost the same length as the middle row. Specimens vary from pure white with yellow gills and rhinophores shown above, and as described originally by Bergh, to specimens that are completely orange (Plate 2B).

Radula.— The radular formula is 15 × 5–6.1.1.1.1.1.5–6. Drawings of the jaw and radula are presented in Fig. 10.

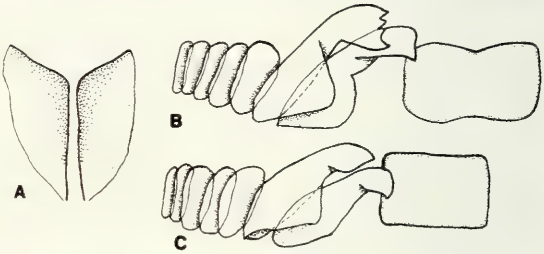


Figure 10. *Colga pacifica*. Drawing of jaw and radula. (After Martynov and Baranets 2002)

Natural History.— This species feeds on various bryozoans. The specimens shown here were collected between 90–275 m deep.

Size.— To about 20 mm.

Range.— Alaska to Shikotan Island (southern Kuril Islands); southwest Greenland.

Family Dendrodorididae

Doriopsilla spaldingi Valdés and Behrens, 1998

This recently discovered species has probably been passed over for years as a common yellow porostome (*Doriopsilla albopunctata* or *Dendrodoris fulva*) with a light margin. The collection of several specimens from the La Jolla area bearing a distinctive blue margin has drawn attention to the identity of this species (J. Lance, pers. commun.).

Identification.— As mentioned above, this species looks strikingly similar to *Doriopsilla albopunctata* (= *Dendrodoris fulva*). Gills and rhinophores are yellow-orange and the notum has evenly distributed low tubercles. The margin is the key identifying feature; it is highly undulated and white to iridescent blue in color (Plate 2C). Close analysis by Jim Lance indicates that in iridescent blue specimens, the tissue morphology is similar to that of the blue in the aeolid *Hermissenda*, being a concentration of coalesced sacs acting as vesicles that hold the color platelets together.

Radula.— None

Natural History.— Collected in depths of 200 feet in Scripp's Canyon, to 80 feet, and in the Channel Islands. This species lays a flat coiled egg mass, which produces direct development or lecithotrophic larvae (J. Lance, pers. commun.).

Size.— To 83 mm.

Range.— South Coronado Island, Baja California, La Jolla Submarine Canyon and Pt. Loma, San Diego County, and San Miguel Island, California. It has also been observed at 210 ft. at The Pinnacles, Carmel, California (Clinton Bauder, pers. commun.).

Etymology.— Named for George E. Spalding III of Solana Beach, California, who discovered this species.

Suborder Dendronotacea (= Dendronotina)

Family Tritoniidae

***Tritonia pickensi* Marcus and Marcus, 1967**

Identification.— Similar in appearance to *Tritonia myrakeenae*, the body is translucent and bears an opaque white region mid-dorsally, which branches to extend to the base of each gill (Plate 2D). There are approximately 12 gill tufts.

Natural History.— Found on the red gorgoniam, *Lophogorgia chilensis*, to depths of 65 ft or more.

Size.— To about 25 mm.

Range.— La Jolla Canyon, San Diego and California Channel Islands, California; Bahía de los Ángeles to Cabo San Lucas, Baja California (Skoglund 2002), Puerto Vallarta, Mexico (Hermosillo-González 2003) and Costa Rica (INBIO 2003).

Etymology.— Named to honor Dr. Peter E. Pickens, University of Arizona, who collected extensively in the Gulf of California for the Marcus'.

Family Scyllaeidae

***Crosslandia daedali* Poorman and Mulliner, 1981**

This species had been known only from the mainland of Mexico and the Gulf of California.

Identification.— The species has lobed parapodia, the first of which is largest (Plate 2E). The edges of the lobes are irregularly notched and digitate and have numerous branchial tufts along the edges. The color varies from orange to green and red. There are fine brown lines along the body as well as some brown spots. The species also has a series of 5–6 bight blue spots along the sides and dorsally.

Natural History.— On the mainland, the species was found on the alga *Padina* sp., where it grazes on small hydroids that live on the alga.

Size.— To 25 mm in length.

Range.— First reported on this coast from Punta Eugenia, Baja California (Bertsch et. al. 2000), the species is now known to range to Guaymas in the Gulf of California and south to Puerto Vallarta, Mexican mainland (Hermosillo-González 2003).

Family Dendronotidae

***Dendronotus* sp.**

It is not known if this is the same as *Dendronotus* sp. 1, (Species #148), which is known from

Alaska and as far south as the California Channel Islands, as I have no specimens to make this determination. What is known is that this very large species, reaching over 7 inches, matches no other species recorded from along this coast. I have received several photographs of this species but as yet no specimens by which to set the record straight. Note the white specks on a red body as described for *Dendronotus* sp. 1, but the handsome specimen shown in Plate 2F has a wide patch of opaque white along its mid-dorsal line.

Identification.— A large, red-bodied *Dendronotus* with white specks covering the entire body. Some specimens may have a wide patch of opaque white along its mid-dorsal line.

Radula.— Unknown.

Natural History.— Nothing is known of this species' habits.

Size.— Large, to 180 mm in length.

Range.— Seymour Inlet, Tredwell Bay, Vancouver area, British Columbia.

Suborder Arminacea (= Arminina)

Family Arminidae

Armina cordellensis Gosliner and Behrens 1996

Identification.— Grey in color, the notum is granular with irregularly spaced, low, rounded tuberacles (Fig. 11).

Radula.— 46 × 42.1.69. The rachidian teeth are broad with a large triangular central cusp, flanked by 8–13 elongate denticles per side (Fig. 12). The lateral teeth are triangular with 7–9 short triangular denticles (Fig. 12).

Natural History.— The type specimen was collected at a depth of 46–52 m.

Size.— 60 mm.

Range.— Known only from Cordell Banks, 20 km off Point Reyes, California.

Etymology.— Named for the type locality, the Cordell Bank.

Figure 11. *Armina cordellensis* Gosliner and Behrens. 1996. Drawing of preserved specimen.

Figure 12. *Armina cordellensis* Gosliner and Behrens, 1996. Radular teeth.

Janolus sp.

Identification.— Similar in coloration to *Dirona pellucida* Volodchenko, 1941(= *Dirona aurantica* [Hurst. 1966]), the body being transparent to orange with white specks and a white line up each ceras and each rhinophore. The digestive gland is clearly seen within each ceras (Plate 3A), unlike *D. pellucida*, where the gland is absent.

Radula.— Unknown.

Natural History.— Nothing is known of this species' habits.

Size.— 30–40 mm.

Range.— Photographed in Quarry Bay, Nelson Island, British Columbia in 60 feet of water by Bernard P. Hanby (Andy Lamb, pers. commun.).

Suborder Aeolidacea (= Aeolidina)

Family Flabellinidae

Flabellina bertschi Gosliner and Kuzirian 1990

Until recently, this species was known only from the Pacific coast of Panama and within the Gulf of California. Goddard and Schickel (2000) have reported the species from the outer coast of Baja California.

Identification.— This species is typically flabellinid in shape. The body is translucent with an opaque white band on the notum (Plate 3B). The cerata are orange-red with white tips. The rhinophores are smooth. The oral tentacles and rhinophores are tipped with white.

Radula.— The radular formula is 24–31 × 1.1.1. The rachidian tooth has 6–8 denticles, the laterals 9–11 denticles.

Natural History.— Little is known about this species.

Size.— To 30 mm length.

Range.— Known from Pacific coast of Panama (Gosliner 1994), Puerta Vallarta, Mexico (Hermosillo-González 2003), Costa Rica (INBIO 2003), Gulf of California (Gosliner and Kuzirian 1990), Punta Rosarita on the west coast of Baja California (Goddard and Schickle 2000), and Little Farnsworth, Catalina Island, California (E. Erikson, pers. commun.). Also from the Galápagos (Gosliner 1994).

Etymology.— Named to honor marine biologist and friend, Hans Bertsch.

Flabellina cf. *islandica* (Odhner, 1937)

This species is possibly the same as *Flabellina islandica,* which is known from Iceland (Sandra Millen, pers. commun.).

Identification.— This species is typically flabellinid in shape, but slightly stouter and wider, an adaptation believed to be related to its soft bottom existence. The ground color is translucent pinkish cream with stubby red cerata (Plate 3C). Opaque white specks occur on the dorsal surface and cerata, the ends of the smooth rhinophores and the extremely long oral tentacles.

Radula.— The radular formula for specimens from Iceland is 15 × 2.1.1. The rachidian has 5–7 denticles, the laterals are smooth and there is a small outer lateral on the left side of some specimens.

Natural History.— Shallow subtidal on mud bottoms in the spring and summer.

Size.— To 22 mm length.

Range.— Known from southern British Columbia, Victoria Harbor (Vancouver Island) and Vancouver Harbor (mainland) (Neil McDaniel and Sandra Millen, pers. commun.). Similar animals have been found in the Sea of Japan (Sandra Millen, pers. commun.).

Family Tergipedidae

Cuthona sp.

Identification.— Another transparent tergipedid with brown ceratal cores. Internal anatomy indicates it is a new species (J. Lance, pers. commun.). There are 8–9 rows of cerata, tipped with a white cnidosac. The tips of the rhinophores and cephalic tentacles are white encrusted.

Radula.— Unknown.

Natural History.— Found on the hydroid, *Tubularia* sp., on boat docks (J. Lance, pers. commun.).

Size.— 5–9 mm in length.

Range.— San Diego, California (J. Lance, pers. commun.).

Family Aeolidiidae

Aeolidia herculea Bergh, 1894

Aeolidia farallonensis Gosliner and Behrens, 1996 (synonym).
Aeolidia grandis Volodchenko, 1941 (synonym).

Gosliner and Behrens (1996) described two new deepwater species from northern California. One was *Aeolidia farallonensis*, described from several specimens collected from 510 and 1400 m deep off the Farallon Islands, Gulf of the Farallons, California. At the time the authors described *A. farallonensis*, *A herculea* was regarded as a synonym of *Aeolidia papillosa* (Linnaeus, 1781) (Marcus 1961). At the suggestion of colleague A.V. Martynov, the authors reviewed Bergh's original description and found these species to be identical.

Identification.— Similar in external morphology to *Aeolidia papillosa* (Linnaeus, 1761) (Species no. 212) except the rhinophores are rugose (Fig. 13A) rather than smooth, and it has fewer rows of cerata, but with nearly twice the number of cerata per row (Gosliner and Behrens 1996). Internal anatomies clearly differentiate these two species. The color of the living animal is unknown.

Radula.— 30 × 0.1.0. Each tooth bears 38–53 shallow triangular denticles (Fig. 13B). The jaws (Fig. 13C) are twice as long and more than twice as wide as those of a similar size *A. papillosa*. The jaws of *A. herculea* are similar in size and shape to those described for *A. farallonensis*.

Natural History.— Specimens have been collected from 510 and 1400 m deep.

Size.— 25 mm.

Range.— Originally described from Alaska. Gosliner and Behrens (1996) add the Farallon Islands, Gulf of Farallons, California. Additional collections have been recorded from Monterey Bay, 570–700 m deep (Jim Nybakken, pers. commun.).

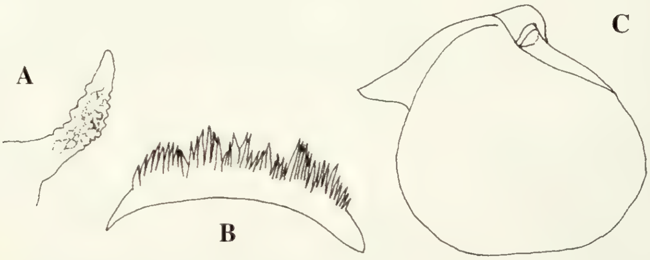
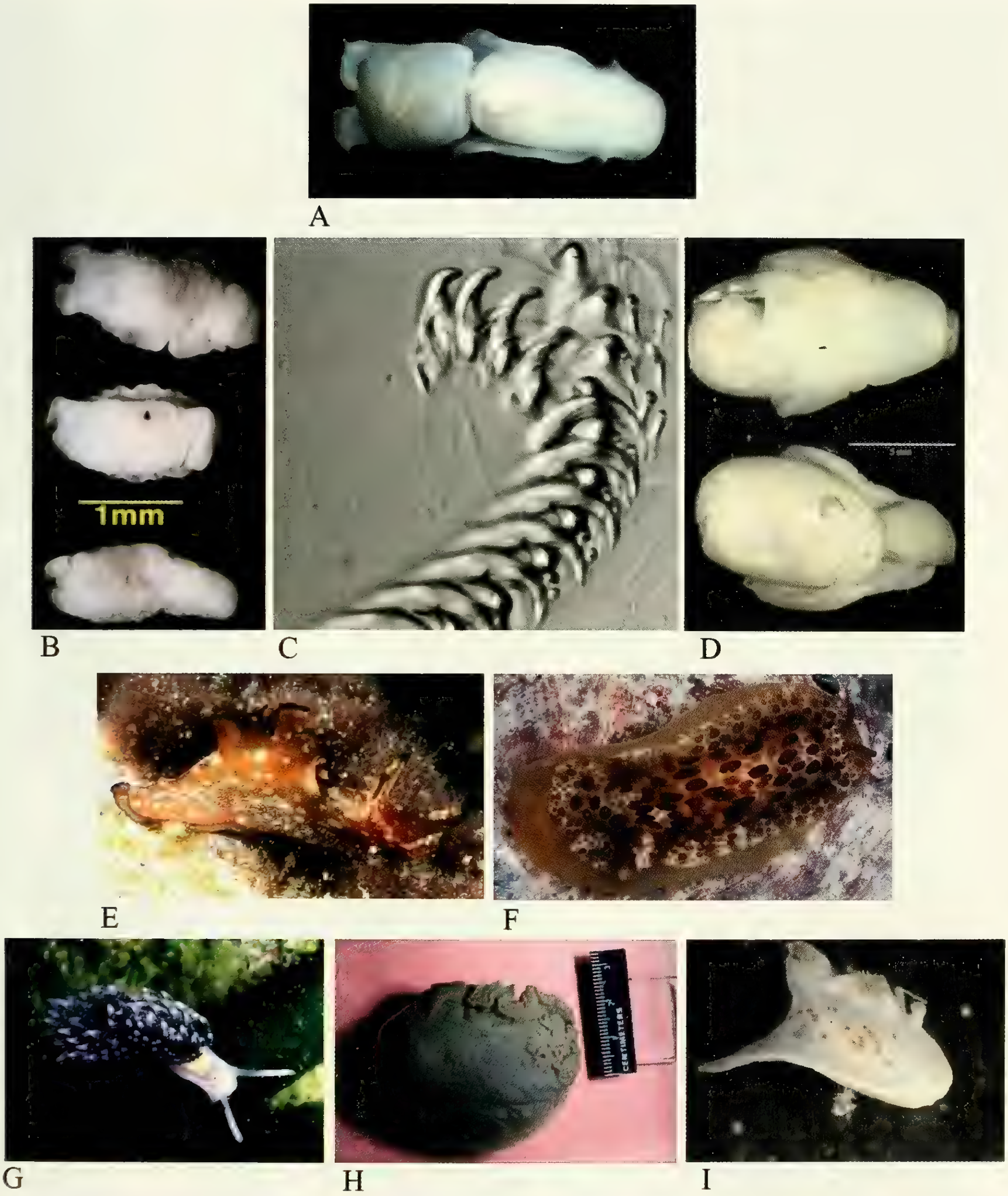


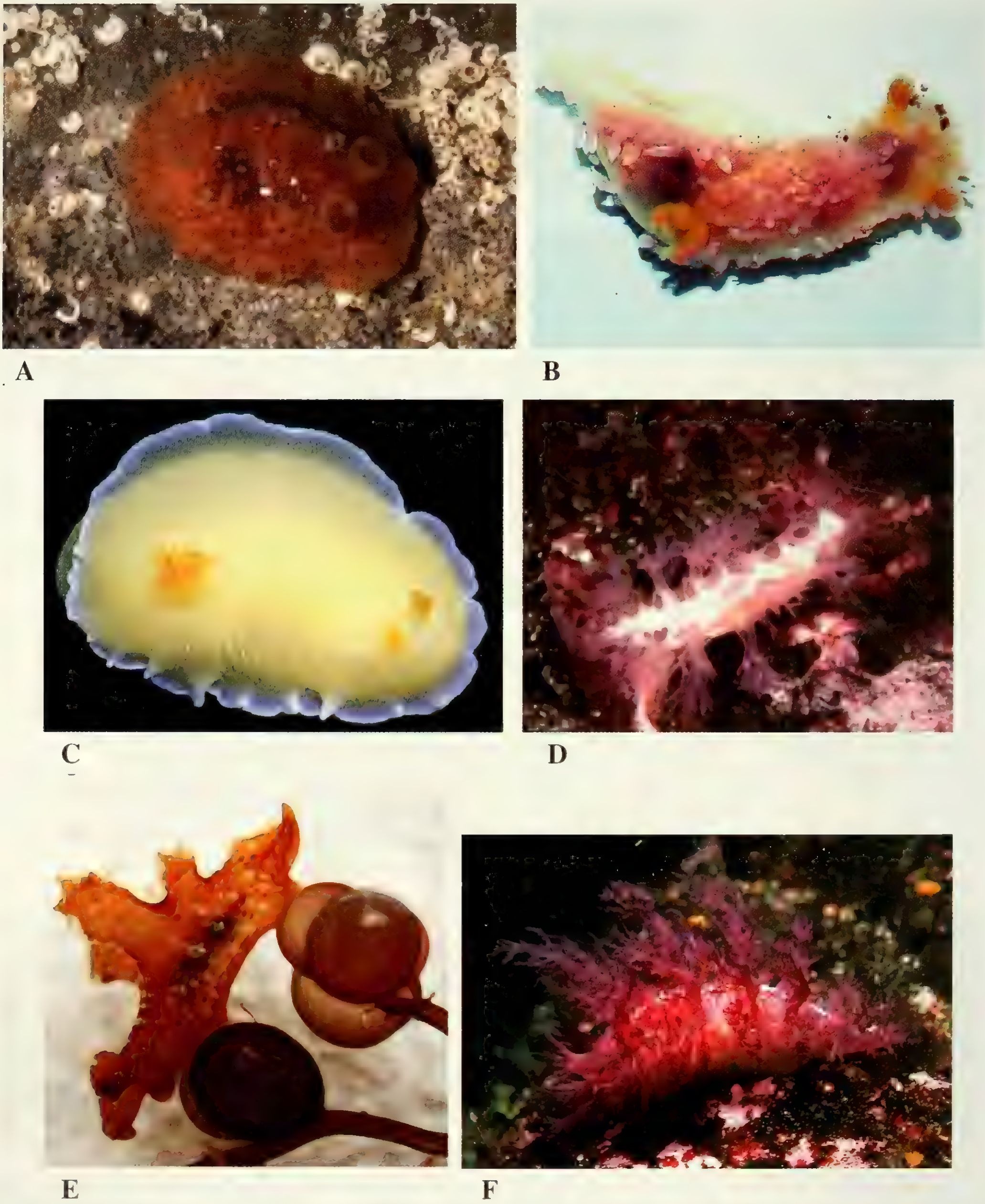
Figure 13. *Aeolidia herculea*, Bergh, 1894. A. Rhinophore; B. Radular tooth; C. Jaw. (Drawings after Gosliner and Behrens 1996.)

Plate 1



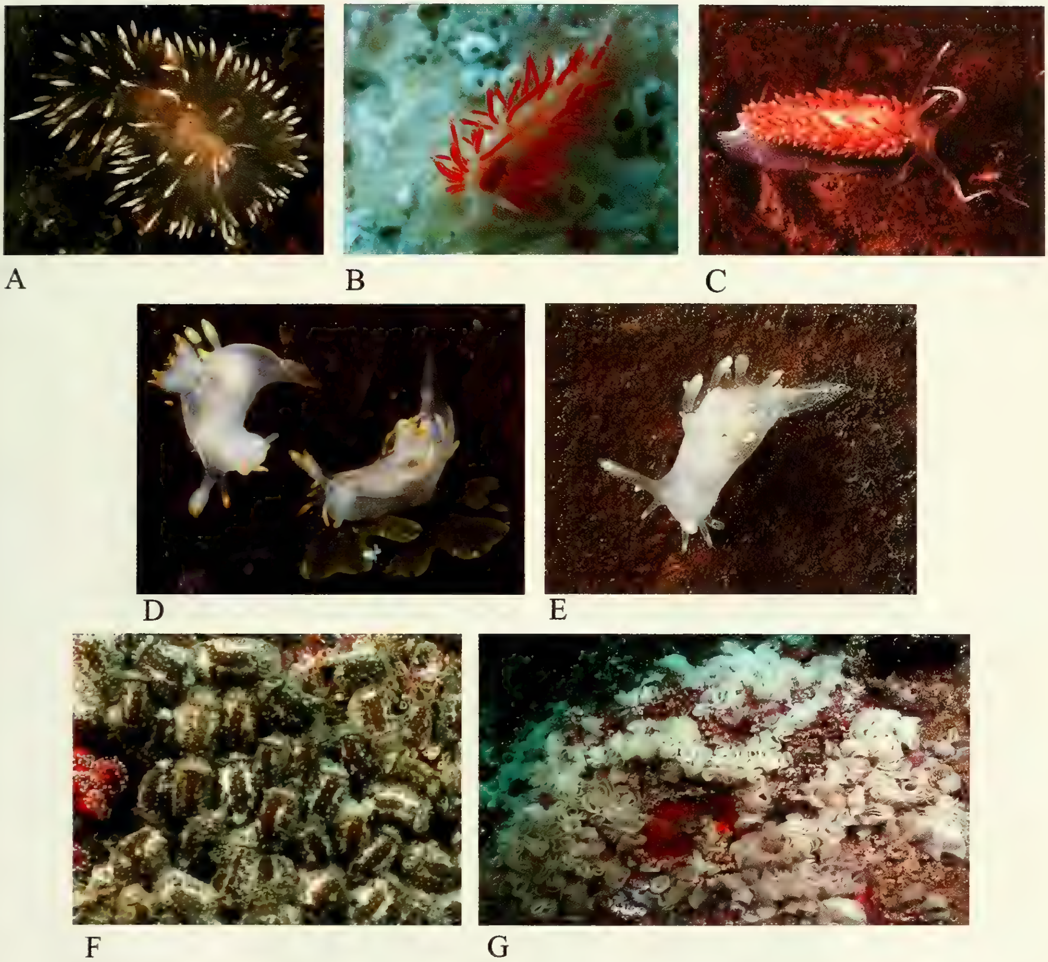
A. *Philine auriformis* Suter, 1909, living animal, San Francisco Bay, California (T. Gosliner); B. *Philinoglossa* sp. Dorsal and ventral views of preserved specimens, San Diego, California (Kelvin Barwick); C. *Philinoglossa* sp. Radula; D. *Akera* sp., preserved specimen, dorsal and ventral view, Santa Catalina Island, California (Kelvin Barwick); E. *Aplysia parvula*. living animal San Clemente Island, California (Bruce Wright). F. *Pleurobranchus* cf. *areolatus*, living animal, La Jolla, California (David Behrens); G. *Placida* sp., living animal, Bahía San Quintin, Baja California, Mexico (Wes Farmer and Jim Lance); H. *Bathydoris aioca*, preserved specimen, Oregon (Hans Bertsch); I. *Okenia* sp., freshly preserved specimen, Huntington Beach, California (Sarah Douglass).

Plate 2



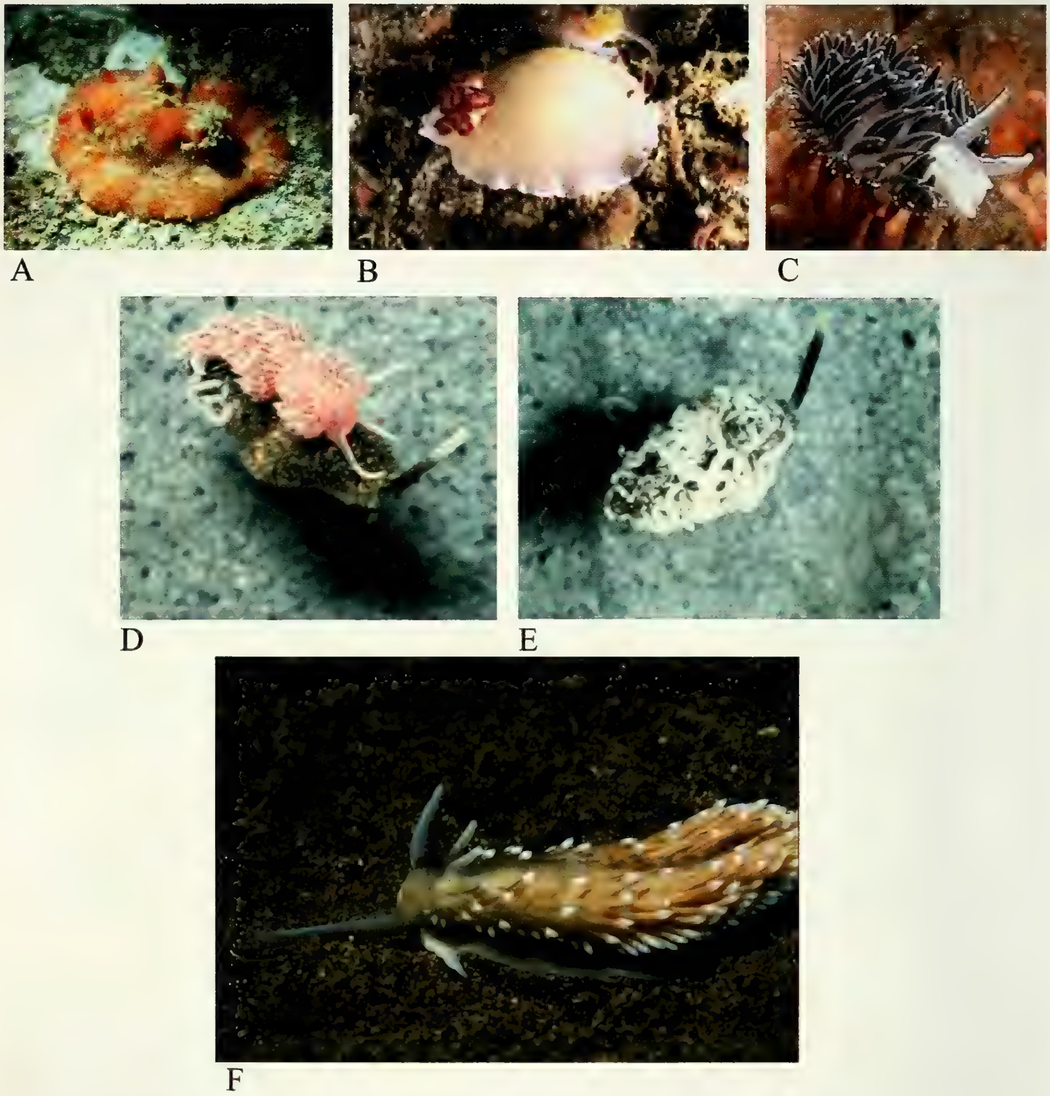
A. *Diaulula greeyeli* (MacFarland, 1909), living animal, Punta Eugenia, Baja California, Mexico (Hans Bertsch); B. *Colga pacifica*, living animal, Kuril Islands, Alaska (Roger Clark); C. *Doriopsilla spaldingi* Valdés and Behrens 1998, living animal, San Diego, California (Mike Miller); D. *Tritonia* cf. *pickensi*, living animals, Channel Islands, California (Kathy deWet); E. *Crosslandia daedali*, living animal, Puerto Vallarta, Mexico (Ali Hermosillo-González); F. *Dendronotus* sp., living animal, Seymour Inlet, Tredwell Bay, Vancouver, British Columbia (Bernard P. Hanby).

Plate 3



A. *Janolus* sp., living animal, Quarry Bay, Nelson Island, British Columbia (Bernard P. Hanby); B. *Flabellina bertschi*, living animal, Puerto Vallarta, Mexico (Ali Hermosillo-González). C. *Flabellina* cf. *islandica*, living animal, Victoria Harbor, Vancouver Island, BC, Canada (Neil McDaniel). D. *Ancula gibbosa*, living animals, Southern California (Bruce Wright); E. *Ancula gibbosa*, living animals, Vancouver, British Columbia area (Charlie Gibbs); F. *Onchidoris bilamellata*, mass feeding on barnacles in Monterey, California (Clinton Bauder); G. *Onchidoris bilamellata*, mass spawning in Monterey, California (Clinton Bauder).

Plate 4



A. *Taringa aivica*, living specimen, Puerto Vallarta, Mexico (Ali Hermosillo-González); B. *Dendrodoris* sp. 2., living animal (Clinton Bauder); C. *Flabellina trophina*, living dark color morph, Coronation Island, Alaska (Clinton Bauder); D. *Anetarca armata*, feeding on hydoids living on shell of living *Decipifus californicus*, Bahía de Los Angeles, Baja California, Mexico (James R. Lance); E. *Decipifus californicus* covered with *Anetarca* egg ribbon, Bahía de Los Angeles, Baja California, Mexico (James R. Lance); F. *Cerberilla* cf. *pungoarena*, living animal, Channel Islands, California (Kathy deWet).

NEW INFORMATION AND NOMENCLATURAL CHANGES

The following is an update to the information presented in the second edition of *Pacific Coast Nudibranchs* (Behrens 1991). The numbers listing the species below correspond to the species identification numbers used in that text. Included in brackets are new names given species that were reported as undescribed in 1991, synonymies and nomenclatural changes. New information on color variation and possible taxonomic confusion, and extensions of the known ranges are also presented.

A comprehensive study of the food preferences of nudibranchs worldwide was published by McDonald and Nybakken (1997) Referencing the prey species of the nudibranchs of this coast here would be too voluminous and the mere number of references would surely triple the length of this document. I refer you to the original document at — http://www.veliger.org/nudibranch_food.html.

Order Cephalaspidea

1. *Rictaxis punctocaelatus* (Carpenter, 1864)

Mikkelson (1996) reviewed the Cephalaspidea and proposed moving the Opisthobranch family Acteonidae from the Opisthobranchia, to the Gastropod subclass Heterobranchia. I do not support this move here. The range of this species should be extended into the Gulf of California to Bahía San Carlos, Sonora, Mexico (Poorman and Poorman 1988).

5. *Acteocina harpa* (Dall, 1871)

The range of this species is extended south to Rocas Alijos, Mexico (McLean and Coan 1996).

8. *Cylichna alba* (Brown, 1827)

This little known species has been observed recently in Boundary Bay, Vancouver, British Columbia on the estuary's mud flat, hidden in drying mats of drift eel grass (Bill Merilees, pers. commun.). This species has been found in the guts of western sandpipers.

11. *Diaphana californica* Dall, 1919

The range of this species is extended north to Kayostla Beach, Olympic Peninsula, Washington (Jeff Goddard et al. 1997).

21. *Navanax inermis* (Cooper, 1863)

The range of this species is extended north to Bolinas Lagoon, Marin County, California, where adult specimens were collected in December 1992 during that year's El Niño event.

22. *Navanax polyalphos* (Gosliner and Willaims, 1972)

The species is now reported as far south as Costa Rica (Camancho-Garcia, pers. commun.).

23. *Philine bakeri* Dall, 1919 [now: *Philine alba* Mattox, 1958]

The correct designation for the photo of the *Philine* shown in Behrens, 1991, photo 23, has been bantered back and forth. Due to the size of the specimen (15 mm), it should be listed as *Philine alba.*

Order Anaspidea

Family Aplysiidae

24. *Aplysia californica* Cooper, 1863

The range of this species has been extended to Hachijo Island, Japan where several 70-cm specimens have been collected (Jun Imamoto and Nishina Masayoshi, pers. commun.) and to El Salvador (Hernandez C. 1992).

Order Notospidea

Family Pleurobranchidae

30. *Berthella californica* (Dall, 1900)

A specimen closely matching *Berthella californica* was recently trawled from 400 feet in the Galápagos Islands (T. Gosliner, pers. commun.). This extension should be considered tentative, however. Martynov (1997) reports this species from Beringa Island, Peter the Great Bay, Sea of Russia.

32. *Berthella strongi* (MacFarland, 1966)

The range of this species is extended north from Moss Beach, California, to Nanaimo, British Columbia (Mike Miller, pers. commun.), and south from Santa Cruz Island to Punta Rosarito, Baja California (Goddard and Schickel 2000).

33. *Berthella engeli* (Gardner, 1936) [now: *Berthellina ilisima* Marcus and Marcus, 1967]

For sometime there has been uncertainty concerning the proper placement of the bright orange pleurobranchs on this coast and elsewhere. *Berthella engeli* and *B. citrina* have been used interchangably throughout the literature. A recent study of all the smooth orange *Berthella's* worldwide undertaken by Terrence Gosliner and Lucas Cervera concludes that the eastern Pacific species is *Berthellina ilisima* (Juan Lucas Cervera, pers. commun.).

Order Sacoglossa

A review of the natural history of the sacoglossans of the northeastern Pacific can be found in Trowbridge (2002).

36. *Elysia hedgpethi* Marcus, 1961

Hermosillo-González (2003) reports this species from Puerto Vallarta, Mexico.

38. *Ercolania boodleae* (Baba, 1938)

The range is extended into the Gulf of California at Puerto Peñasco (Trowbridge 2002).

39. *Placida dendritica* (Alder and Hancock, 1843)

The range of this species is extended north to Bertha Bay, Chichagof Island, Alaska, where it has been collected on *Codium fragile* (Rita O'Clair, pers. commun.), and south into Gulf of California at both Bahía de los Ángeles, Baja California, and Bahía San Carlos, Sonora, Mexico (Trowbridge 2002), on *Codium setchelli* (Cynthia Trowbridge, pers. commun.).

41. *Stiliger fuscovittatus* Lance, 1962

Please note that the photo in the 1991 edition of *Pacific Coast Nudibranchs* shows a specimen on the algae, *Microcladia*. This algal species is not fed upon by *Stiliger* and, additionally, is rarely associated with it (Cynthia Trowbridge, pers. commun.).

42. *Alderia modesta* (Loven, 1844)

This species was previously reported as far south as Newport Bay, California. It has now been reported from San Quintin, Baja California, Mexico (J. Lance, pers. commun.). The range is also extended north to Prince William Sound, Alaska (Goddard and Foster 2002).

Krug (1998) reports that *Alderia modesta* practices poecilogony, or the production of eggs of different sizes that yield either planktotrophic veligers or lecithotrophic veligers, depending on their available yolk supply. Back crosses of these two forms yield the same ratio of reproductive types seen initially and give evidence of their conspecificity. Starved individuals, which had previously spawned exclusively or primarily lecithotrophic larvae, switiched to production of planktotrophic larvae after a short period of no food. Whether larvae are planktonic or not significantly affects the dispersal potential of a spawning event.

43. *Aplysiopsis oliviae* (MacFarland, 1966) [now: *Hermaea oliviae* (MacFarland, 1966)]

The taxonomic placement of this species has changed several times. As I suspected (Behrens 1991), the morphology of the radular teeth places this species in *Hermaea* (Kathe Jensen, Sea Slug Forum, 7 November 2001).

The range of this species is extended south to El Morro, Isla Cedros (Bertsch et al. 2000) and north to Seymour Inlet, British Columbia (Marli Wakeling, pers. commun.).

44. *Aplysiopsis enteromorphae* (Cockerell and Eliot, 1905)

The color of the body in adults (15–25mm) is yellowish-white with patches of greenish black. Small specimens (<5–10mm in length) are much darker than their larger peers (Cynthia Trowbridge, pers. commun.). Trowbridge also points out that specimens feeding on *Chaetomorpha* are browner than those feeding on *Cladophora*, infact they shimmer with a golden-reddish reflectance. The range is extended south to Bahía San Quintin, Baja California (C. Trowbridge, per. comm.), and Puerto Vallarta, Mexico (Hermosillo-González 2003).

45. *Hermaea vancouverensis* (O'Donoghue, 1924)

This species feeds on *Isthmia nervosa* in Oregon (C. Trowbridge, per. comm.) as was previously documented by Williams and Gosliner (1973).

46. *Olea hansineensis* Agersborg, 1923

The range of this species is extended to Prince William Sound, Alaska (Goddard and Foster 2002), where it was found feeding upon the egg mass of the cephalaspidean, *Melanochlamys diomedea*. Specimens of this species may reach 13 mm (Chia and Skeel 1973).

Order Nudibranchia
Suborder Doridacea (= Doridina)

47. *Corambe pacifica* MacFarland and O'Donoghue, 1929

The genus *Corambe* has been subjected to several nomenclautural reviews and changes in recent years. Martynov (1994) divided *Corambe* into several newly defined genera and assigned *C. pacifica* to the genus *Gulbinia*. More recently, Valdés and Bouchet (1998) have reexamined the value of the characters Martynov used to differentiate the new genera and have simplified the taxonomy to three genera, reestablishing, this species as *Corambe pacifica*.

The range of this species is extended to the south to Mismaloya, Puerto Vallarta, Mexico (Hermosillo-González 2003).

48. *Corambe* sp. 1 [now: *Loy thompsoni* (Millen and Nybakken, 1991)]

This species has now been described in the scientific literature and given the name *Corambe thompsoni* by Sandra Millen and Jim Nybakken (1991). The trivial name *thompsoni* is given in recognition of the British opisthobranch researcher Dr. Thomas Thompson. Martynov (1994) reassigned the species to the genus *Psammodoris*. Valdés and Bouchet (1998), in their reorganization, placed it in the genus *Loy* Martynov (1994).

The radular teeth, which were not included in PCN Supplement I — Rabula (Behrens 1992), are shown here (Fig. 14). The radular formula for this species is 45–48 × 5–6.1.0.1.5–6. The lateral tooth has a rectangular base with a long, denticulate hook. Also shown is the arrangement of the spicules in the mantle tissue.

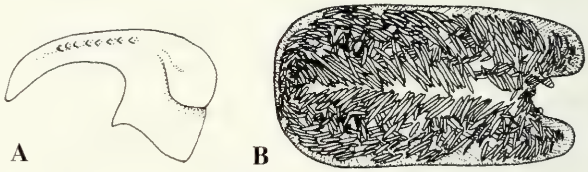


FIGURE 14. *Loy thompsoni* (Millen and Nybakken, 1991). A. Radular tooth. B. Drawing of arrangement of mantle spicules. (After Millen and Nybakken 1991.)

The range of the species is extended to Port Valdez, Alaska (Nora Foster, pers. commun.).

49. *Doridella steinbergae* (Lance, 1962) [now: *Corambe steinbergae* (Lance, 1962)]

Like other corambid species, *Doridella steinbergae* has also undergone some recent nomenclatural revision. Martynov (1994) created the genus *Suhinia* for *D. steinbergae*. Swennen and Dekken (1995, p. 104), placed this species in a newly established genus, *Paracorambe*. Here again, Valdés and Bouchet (1998), in their reexamination of the value of the characters used to differentiate the eleven proposed genera of Martynov (1994) and Swennen and Dekker (1995), simplified the taxonomy, referred this species to the genus *Corambe*.

The range of this species is extended north to Little Takli Island, Alaska (Goddard and Foster 2002).

50. *Okenia angelensis* Lance, 1966

The range of this species is extended south to Chile, South America (Fischer and Ortea 1996).

51. *Okenia plana* Baba, 1960

Rudman (1995), in his review of the Chromodorididae of New Caledonia and the *Noumea* *romeri* color group, when describing *Cadlinella hirsuta*, he clarified some taxonomic confusion in this genus that resulted in the combination of a number of species, including *Okenia plana* Baba, 1960, under *Doris eolida* and its placement in the genus *Hopkinsia*. Gosliner (2004:144), however, places this species in the genus *Okenia*.

52. *Okenia vancouverensis* O'Donoghue, 1921

The range of this species is extended south to Sechelt Inlet, Vancouver, British Columbia (Donna Gibbs and Andy Lamb, pers. commun.).

54. *Ancula lentiginosa* Farmer *in* Farmer and Sloan, 1964

The range of this species is extended south to Islote Mosquera, Isla Galápagos, Ecuador (Fischer and Ortea, 1996). It has been collected on several occasions (1995 and 2002) in 2300 ft of water off San Diego, California (Ron Velarde, pers. commun.). This disjunct occurrence is likely related to water temperature similarities between shallow Canadian and deep California waters.

55. *Ancula pacifica* MacFarland, 1905 [now: *Ancula gibbosa* (Risso, 1818)]

This species has been synonymized with *Ancula gibbosa* (Risso, 1881) by Thompson and Brown (1984).

The range of this species is extended north to Prince William Sound (Goddard and Foster 2002) and Beringa Island, Sea of Russia (Martynov 1997).

On an ecological note, during the summer of 1996, hundreds of specimens were observed feeding on the entoproct, *Barentsia*, in Diablo Cove, San Luis Obispo, California (Mike Behrens, pers. commun.).

In the Vancouver area, specimens of two color variations occur together. The color form shown in Plate 3D is typical of the color originally described for *Ancula gibbosa* and has not been recorded from the southern part of the range on this coast. Plate 3E depicts the more typical southern color and the one shown in the 1991 edition of *Pacific Coast Nudibranchs*.

56. *Trapania velox* (Cockerell, 1901)

The range of this reasonably uncommon species is extended north to Morro Bay, San Luis Obispo County, California, where it has be observed and collected commonly in deep holes in this coastal estuary (Michael Behrens and Duke McPherson, pers. commun.).

57. *Trapania* sp. 1 [now: *Trapania goslineri* Millen and Bertsch, 2000]

This beautiful little goniodorid was named to honor my friend and opisthobranch researcher, Terrence Gosliner, invertebrate zoologist and Provost of the California Academy of Sciences. With the description now published, we can now cite the radular formula of 37–41 × 1.0.1. The spawn is a narrow, white, upright ribbon, of 1 ½ coils, 5–6 mm in diameter (Millen and Bertsch 2000).

Hermosillo-González (2003) extends the range to Puerto Vallarta, Mexico.

58. *Hopkinsia rosacea* MacFarland, 1905 [now: *Okenia rosacea* (MacFarland, 1905)]

In Gosliner's (2004) review of the genus *Okenia*, he concluded that the genus *Hopkinsia* and its included species had to be referred to *Okenia*, which is the senior synonym. Gosliner expressed his regrets in having to take this action, but he believes it is justified based on recent phylogenetic analyses of the relevant morphological data (Gosliner, pers. commun.).

61. *Acanthodoris lutea* MacFarland, 1925

Publication of the northernmost collections of this species was overlooked during the preparation of the second edition of *Pacific Coast Nudibranchs*. Goddard (1987) reports this species occurrence as far north as Punta Gorda, Humboldt County, California. Goddard has now collected this species at North Cove, Cape Argo, Oregon, feeding on *Alcyonidium* sp. Subsequently, I have learned of this species occurrence in 60 feet of water at Indian Arm, near Vancouver, British Columbia (Andy Lamb, pers. commun.).

62. *Acanthodoris nanaimoensis* O'Donoghue, 1921

The range of this species is extended north to Kachemak Bay, Alaska, near Homer, where it has been collected intertidally (Jane Middleton, pers. commun.).

64. *Acanthodoris rhodoceras* Cockerell and Eliot, 1905

The range of this species is extended south into the Gulf of California, to Bahía de los Ángeles (Hans Bertsch, pers. commun.) where it occurs in January, and north to the mouth of the Umpqua River, Oregon (Jeff Goddard, pers. commun.).

65. *Adalaria jannae* Millen, 1987

The range of this species is extended north to Prince William Sound (Goddard and Foster 2002) where it was found feeding on the bryozoan *Membranpora*, which was living on the kelp *Laminaria*.

66. *Adalaria* sp. 1

The range of this species is extended north to Prince William Sound (Goddard and Foster 2002).

70. *Onchidoris bilamellata* (Linnaeus, 1767)

This barnacle-grazing dorid is not particularly common along the Pacific Coast, but when it is found, it is usually in large swarms. Clinton Bauder documented huge aggregations of this species in Carmel Bay, California, in December 2001 (Plate 3F). The presence of the nudibranch followed a massive settlement of the barnacle, *Balanus crenatus*. As the barnacle population declined, mass spawning by the nudibranchs occurred (Plate 3G). Similar observations of these large population explosions have been made by Bernard Picton (pers. commun.) in Galway, Ireland and by Jim Anderson (pers. commun.) off Scotland.

72. *Aegires albopunctatus* MacFarland, 1905

The range of this species is extended north to Mountain Point, Ketchikan, Alaska (Kurtis Morin and A. Murray, pers. commun.).

73. *Crimora coneja* Marcus, 1961

This is a rare species, previously reported to occur from Point Loma, San Diego, California, to Cape Arago, Oregon. Within this range it has only been found at two locations: rocky intertidal at Punta Gorda, California (Jeff Goddard pers. commun.) and subtidally within Morro Bay, California (Michael Behrens, pers. commun.). Goddard reports that it has been found in abundance only once, when 66 specimens were collected on a single low tide. In that area, *Crimora* feeds on the encrusting bryozoan, *Hincksina minuscule*.

74. *Laila cockerelli* MacFarland, 1905 [now: *Limacia cockerelli* (MacFarland, 1905)]

The genus *Laila,* described by MacFarland in 1905, has been synonymized with the older *Limacia* Müller, 1781 (Vallés et al. 2000).

Limacia cockerelli has several color morphs and it has been speculated that these might represent distinct species. The distinctive color form of *Limacia* with the large red blotches was thought to occur just in California as reported previously. Darcy Kehler (pers. commun.) photographed specimens exhibiting this color pattern at the very northernmost extreme of its range, in Bedwell Bay, Vancouver, British Columbia. Additionally, its range must now be extended north to Mountain Point, Ketchikan, Alaska (K. Morin and A. Murray, pers. commun.).

75. *Polycera alabe* Collier and Farmer, 1964

The range of this species has been extended south to Puerto Vallarta, Mexico, Costa Rica (INBIO, 2003), and Chile (Schrödl 2003) and north, within Baja California to the Coronado Islands (Jerry Allen, pers. commun.), La Jolla Canyon (G. Spalding and M. Miller, pers. commun.), and Catalina, Anacapa, and Santa Barbara Islands (Erik Erikson, Dan Richards, and Kathy deWet, pers. commun.; also Lonhart and Tupen 2001).

77. *Polycera hedgpethi* Marcus, 1964

The range of this species is extended to Balboa, Panama (D. Cadien, pers. commun.) and to the Izu Pennisula and Suruga Bay, Japan (Okutani 2000).

78. *Polycera tricolor* Robillard, 1971

The range of this species is extended north to Hayden Passage, British Columbia (Jeff Rosenfeld, pers. commun.) and to Settler Cove, Ketchikan, Alaska (K. Morin and A. Murray, pers. commun.).

79. *Polycera zosterae* O'Donoghue, 1924 [now: *Palio dubia* (M. Sars, 1829)]

Polycera zosterae has been reassigned to the genus *Palio* by Rivest (1984). Goddard and Foster (2002) report *P. zosterae* as a junior synonym of the northern Sea of Japan species, *Palio dubia* (M. Sars 1829). Angulo-Campillo (2002) reports *P. zosterae* from La Paz, Baja California Sur, Mexico. Because this species is clearly temperate, further study is necessary to confirm the identity of the Mexican species.

80. *Polycerella glandulosa* Behrens and Gosliner, 1988

This species is now reported along the Pacific Coast of Central America to Costa Rica (INBIO 2003).

81. *Tambja eliora* (Marcus and Marcus, 1967)

Recently, members of the University of California at San Diego dive club, The Sea Deucers, have documented large numbers of this species as far north as Ensenada Bay. Individuals varied in size from 45–68 mm (Mike Miller, pers. commun.). The species is also reported from Puerto Vallarta (Hermosillo-González 2003) and Costa Rica (INBIO 2003).

82. *Tambja fusca* Farmer, 1978 [now: *Tambja abdere* Farmer, 1978]

Tambja fusca and *T. abdere* were both described by Farmer in 1978. These two species have been determined to be color variations of a single species; the name *T. abdere* takes precedence as it appears first in the publication. With the synonymy, it should be noted that the range of the species now extends south to Huatulco, Oaxaca, Mexico. Hermosillo-González (2003) reports it from Puerto Vallarta, and INBIO (2003) reports the species from Costa Rica.

83. *Triopha catalinae* (Cooper, 1863)

The range of this species is extended northwest to Slemya Island in the Aleutians (Goddard and Foster 2002).

In a laboratory study, Geiger and Holyoak (1996) demonstrated that *T. catalinae* prefers shaded area over lighted conditions even though its primary prey, erect bryozoans, occurs in both light and shaded environments.

84. *Triopha maculata* MacFarland, 1905

The range of this species is extended from Punta Cono to Punta Rosarito, Baja California (Goddard and Schickel 2000), and Beringia and Mednyi Islands, Sea of Russia (Martynov 1997).

85. *Triopha* sp. 1 [now: *Triopha catalinae* (Cooper, 1863)]

The correct location of the collection that includes the specimen shown in the photograph (Behrens 1991) for this species is Boardman State Park, Oregon (Jeff Goddard, pers. commun.). Since his original collection, other specimens have been photographed by Steve Horvath and Marli Wakeling at Seymour Narrows, British Columbia, Canada.

Based on an examination of the internal anatomy of specimens that were colleceted from Washington, British Columbia, and Alaska, Sandra Millen determined it to be a color morph of *Triopha catalinae*.

86. *Cadlina flavomaculata* MacFarland, 1905

The range of this species is extended to La Paz, Baja California Sur (Angulo-Campillo, 2002) and to Costa Rica (INBIO 2003). The specimens from Costa Rica may prove to be a new species (R. Johnson, pers. commun.).

90. *Cadlina sparsa* (Ohdner, 1921)

Although this species was reported from the Juan Fernandez Island, far offshore of Chile, it has now been collected from the Chilean shoreline at Bahía de Coliumo, Chile (Schrödl 1997), and Argentina (Schrödl 2003).

91. *Chromodoris galexorum* Bertsch, 1978

Previously known only as far north as Guadalupe Island, Baja California, this species quite surprising showed up at Catalina Island, California (Jack Engle and Erik Erikson, pers. commun.).

92. *Chromodoris macfarlandi* Cockerell, 1901

Goddard (2000b) reports that this dorid feeds on both the pink sponge, *Aplysilla glacialis* and the deep red sponge, *Aplysilla polyraphis* in the La Jolla, California, portion of its range.

94. *Glossodoris dalli* (Bergh, 1879)

Gosliner (1991), reports two specimens collected intertidally on Isla Fernandina and Isla Santa Cruz, Galápagos Archipelago.

99. *Tyrinna evelinae* (Marcus, 1958)

The range of this species has been extended south to Costa Rica (Camacho-Garcia, pers. commun.) and to El Rubio, Peru (Schrödl and Millen 2001).

101. *Jorunna pardus* Behrens and Henderson, 1981

Since its original description, collection of numerous additional specimens has shown some degree of color variation. Individual specimens have been collected ranging from white with sparse black speckling to deep yellow with large round spots, the largest of which being dorso-medially positioned. A few specimens have been collected with no spots on the foot or tail. The degree of black pigment on the gills also varies from dense black to white tipped only slightly with black.

103. *Aldisa albomarginata* Millen, 1985 *in* Millen and Gosliner 1985

The range of this species is extended to Agamemnon Channel, Vancouver, British Columbia (D. Gibbs and A. Lamb, pers. commun.).

105. *Aldisa sanguinea* (Cooper, 1863)

The northernmost range of this species has been extended by Jeff Goddard, who has collected three specimens at Otter Crest, Lincoln County, Oregon.

107. *Rostanga pulchra* MacFarland, 1905

Some clarification of the sponges *Rostanga* feeds upon should note that *R. pulchra* is chemically attracted to and feeds on *Ophlitaspongia pennata* Labbe. Anderson (1971) adds *Esperiopsis originalis* and *Plocamia karykina* to the list of authenticated prey sponges.

108. *Atagema alba* (O'Donoghue, 1927)

This species was recently collected from a depth of 120 feet in Scripps Canyon, San Diego County, California. (Jim Lance, pers. commun.).

109. *Sclerodoris tanya* (Marcus, 1971)

This species has been collected in Puerto Vallarta, Mexico (Hermosillo-González, 2003).

110. *Archidoris montereyensis* (Cooper, 1862) [now: *Doris montereyensis* Cooper, 1863]

Bergh (1878) introduced the genus *Archidoris* based on *Doris tuberculata*, *Doris montereyensis* and others. *Doris montereyensis* has simple round tubercles, with spicules that do not protrude from the dorsal surface. For this reason, Valdés (2002) referred *Archidoris* to the synonymy of *Doris* Linnaeus, 1758.

Aside from the obvious presence of this species' preferred food, the encrusting sponges *Haliclona* sp. and *Halichondria* sp. in shaded habitats, a study reported by Geiger and Holyoak (1996) indicates that intertidally this dorid unquestionably prefers shaded over lighted conditions. Geiger and Holyoak's study was conducted in the high intertidal and did not take into account the effects of current strength. Ryan Murphy (pers. commun.) suggests in his study, in an area of strong currents, that no preference was found between shaded and unshaded conditions.

111. *Archidoris odhneri* MacFarland, 1966 [now: *Doris odhneri* (MacFarland, 1966)]

As reported above for *Doris montereyensis*, because *Doris odhneri* also has simple round tubercles, with spicules that do not protrude from the dorsal surface, it has been transferred to *Doris* Linnaeus, 1758 (Valdés 2002).

The range of this species is extended north to the Bering Sea side of the Alaska Peninsula (Goddard and Foster 2002).

112. *Anisodoris lentiginosa* Millen 1982 [now: provisionally listed as cf. *Peltodoris lentiginosa* (Millen 1982)]

The placement of *Anisodoris lentiginosa* is problematic (see the discussion below for *Peltodoris nobilis*). Because *Anisodoris lentiginosa* is also not a caryophyllidia-bearing species, it is provisionally listed here as *Peltodoris* until a more complete analysis of this species is published.

113. *Anisodoris nobilis* (MacFarland, 1905) [now: *Peltodoris nobilis* (MacFarland, 1905)]

Anisodoris nobilis was originally placed in the genus *Montereina* (MacFarland 1905) and later transferred to the genus *Anisodoris*. Valdés and Gosliner (2001), having conducted a careful review of caryophyllidia-bearing dorid nudibranchs, noted that the type species of *Anisodoris* was caryophyllidia-bearing and they, therefore, transferred it to *Diaulula*. *Anisodoris nobilis*, however, unlike the type species of the genus, has small rounded tubercles with no protruding spicules on the dorsal surface. Because it does not have caryophyllidia, this species recently has been transferred to the genus *Peltodoris* Bergh, 1880 (Valdés 2002).

115. *Diaulula sandiegensis* (Cooper, 1863)

The range of this species is extended northward to Kachemak Bay, Alaska (Jane Middleton, pers. commun.) and the central Aleutian Islands (Goddard and Foster 2002), and to Peter the Great Bay (Martynov 1997). In a study by Geiger and Holyoak (1996), this species prefers shaded over lighted conditions. Ryan Murphy's findings mentioned above dispute this preference.

Behrens and Valdés (2001) in their examination of the *Doris* (*s.l.*) species described the variability in radular morphology of *D. sandiegensis* and presented evidence that the hamate teeth of *Diaulala* may have denticles in some specimens.

116. *Diaulula* sp. 1 [now: *Diaulula sandiegensis* (Cooper, 1863)]

In the 1980 edition of *Pacific Coast Nudibranchs*, I referred to this species as *Doris* (*s.l.*)

species MacFarland (1966). In the 1991 edition, it was suggested that this species more properly belongs in the genus *Diaulula*. Behrens and Valdés (2001) examined the single specimen of *Doris* (*s.l.*) species referred to in MacFarland (1966) and other material collected from southern California that matched the external coloration of *Doris* (*s.l.*) species. The internal anatomy was found to be identical to that of *Diaulula sandiegensis*. In that study, *Doris odonoghuei* Steinberg 1963 (= *Doris echinata* O'Donoghue, 1922) was also found to be a junior sysnomym of *D. sandiegensis*.

117. *Discodoris* sp. 1 [now: *Diaulula aurila* (Marcus and Marcus, 1967)]

In their review of caryophyllidia-bearing dorids, Camacho-García and Valdés (2003) placed *Discodoris aurila* in the genus *Diaulula* based on the presence of caryophyllidia. During their study, they were unaware of the specimen collected by T. Gosliner and shown in Behrens (1991). This specimen is identical of *D. aurila* (T. Gosliner, pers. commun.).

The range of this species is now extended north from Ft. Kobbe Beach, Canal Zone, Panama (Camacho-García), to Punta Rosarito, Baja California, Mexico (Goddard and Schickel 2000).

119. *Geitodoris heathi* (MacFarland, 1905)

The range of this species is extended north to Prince William Sound (Goddard and Foster 2002).

120. *Taringa aivica timia* Marcus and Marcus, 1967 [now: *Taringa aivica* Marcus and Marcus, 1967)

The subspecies *T. a. timia* appears to be a color morph of the nominal species *T. aivica*, so this subspecific designation is dropped (Camacho-García and Valdés 2003). The range is extended to Puerta Vallarta, Mexico (Hermosillo-González 2003). Hermosillo-González (2003) reports that the color varies widely from that reported in Behrens (1991) (see Plate 4A).

123. *Thordisa rubescens* Behrens and Henderson, 1981

Valdés (2002) provides a much more detailed description of the internal anatomy of this species than given by Behrens and Henderson (1981), adding information on the central nervous and reproductive systems, as well as SEMs of the radula, dorsal papillae and penial armature.

The range of this species has been greatly extended to the south with the collection of a 6 mm specimen at Punta Eugenia, Baja California by Hans Bertsch (pers. commun.).

124. *Peltodoris* sp. 1 [now: *Peltodoris mullineri* Millen and Bertsch, 2000]

The descriptive material in the 1991 edition of *Pacific Coast Nudibranchs* is unchanged, but we now have the radular formula which is 23–24 × 42–63.0.42–63. Sandra Millen and Hans Bertsch named this species to honor their friend Dave Mulliner of San Diego, California.

The range of this species is extended north to Santa Barbara and Anacapa Islands (Marc Shargel, pers. commun.), and south to Isla de Malpelo, Columbia (Kaiser and Bryce 2001). It has also been found in the Gulf of California at Bahía de los Ángeles (Hans Bertsch and Allen Grant, pers. commun.).

126. *Platydoris macfarlandi* Hanna, 1951

This rare species had only been collected once since its description in 1951 (Behrens and Henderson 1983). With the collection of two additional specimens, the range is extended south to Bahía San Cristobal, Baja California (Bertsch et al. 2000).

127. *Dendrodoris fulva* (MacFarland, 1905) [now: *Doriopsilla albopunctata* (Cooper, 1863)]

After years of fielding questions concerning the identification of this species and difficulty distinguishing *Dendrodoris fulva* from *Doriopsilla albopuntata*, a careful study of the internal anatomy, has shown the two to be synonymous (Gosliner, Schaefer, and Millen 1999). *D. albopunctata*, being the older of the two names, takes precedence.

128. *Dendrodoris krebsii* (Mörch, 1863) [now: *Dendrodoris fumata* Rüppell and Leuckart, 1830]

The Caribbean and Eastern Pacific species referred to as *Dendrodoris krebsii* are actually distinct species (Valdés, Ortea, and Ballestros 1996). Brodie, Willan and Collins (1997) refer to color photographs in Valdés et al. (1996) labeled as *D. nigra* (Stimpson, 1855), that the Pacific coast species should be referred to as *D. fumata* Rüppell and Leuckart, 1830. Gosliner (1991) and Valdés et al. (1996) report this species from the Galápagos Islands, and Kaiser and Bryce (2001) at Isla de Malpelo, Columbia.

129. *Dendrodoris nigromaculata* (Cockerell *in* Cockerell and Eliot, 1905)

This species is reported south to Costa Rica (INBIO 2003).

130. *Dendrodoris* sp. 1 [now: *Doriopsilla gemela* Gosliner, Schaefer, and Millen, 1999]

The photograph of species #130 *Dendrodoris* sp. 1 was taken of an intertidal specimen collected in San Luis Obispo, California. Since the publication of Behrens (1991), several "yellow gilled" porostomes have been discovered along this coast. *Doriopsilla gemela*, is the species shown in photograph #130, but is thought to be distinct from an identical looking deep water species found in La Jolla Canyon (Jim Lance, pers. commun.).

IDENTIFICATION.— Identical in color to *Doriopsilla albopunctata* except that the branchial plume is orange. The body and gills are bright yellow to orange or orange-brown. The minute tubercles on the surface of the notum have small white specks.

RADULA.— None

NATURAL HISTORY.— Found intertidally (Bertsch 2002). The egg mass is distinctive and differs from that of *D. ablopunctata*. The coil consists of about three whorls of yellow eggs which lie flat on the substrate, rather than on edge, as in *D. ablopunctata*. Bertsch (2002), in some detail, also describes its ecology and natural history in Bahía de los Ángeles.

SIZE.— To 40 mm in length.

RANGE.— Gulf of California and along the Pacific coast of North America from Bahía Tortugas, Baja California Sur, Mexico, to Elkhorn Slough, Monterey County, California.

ETYMOLOGY.— The name *gemela* comes from the Spanish for twin, as the species is so close in appearance to *D. albopunctata*.

131. *Dendrodoris* sp. 2

Two additional sightings of this still undescribed species have been made in 150 and 170 feet of water in La Jolla Canyon (George Spalding, pers. commun.). Additionally, a specimen was photographed by Clinton Bauder in Carmel Bay, at 180 ft. on July 12, 2000 (Plate 4B). The specimen measured 30 mm in length. Bauder's photograph is a much better representation of the living animal than the moribund specimen figured in Behrens (1991). This species remains undescribed.

132. *Dendrodoris* sp. 3

This yet undescribed porostome species (currently under study by Sandra Millen and Hans Bertsch) is becoming increasingly more common along the mainland coast where it has been collected south to Bird Rock, La Jolla, California (Jim Lance, pers. commun.). Subtidal observations have also been made at Quast Rock at 60 feet (George Spalding, pers. commun.).

Suborder Dendronotacea (= Dendronotina)

136. *Tritonia diomedea* Bergh, 1894

An unpublished doctoral thesis by James Murray (1966) presents fascinating new information on *Tritonia diomedea*. The following notes are extracted from from Murray (1966):

Tritonia diomedea feeds on pennatulacean cnidarians — the sea pen *Ptilosarcus gurneyi* (unpublished), and the sea whips *Virgularia* (McDonald and Nybakken 1978), *Stylatula elongata* (Willows, pers. commun.) in Washington and British Columbian waters, and *Acanthoptilum* in Californian waters as deep as 200 m (Rim Fay, pers. commun.). *T. diomedea* will also feed on the sea pansy, *Renilla köllikeri* (G. Brown, R. Longley, pers. commun.), in the laboratory, although it is unknown if they do so in nature. It appears that geographically isolated groups of *Tritonia* will eat only one prey species, and this prey species varies among groups. *Virgularia* beds tend to be found in silty mud at greater depths (>25 m) than the sandy beds of *Ptilosarcus* (<20 m).

Tritonia diomedea found among *Virgularia* tend to be smaller (0.5–20 cm) than those found among *Ptilosarcus* (8–30 cm). Also, those found among *Ptilosarcus* tend to be orange (like *Ptilosarcus*), with distinct tubercles on the dorsum, whereas those found among *Virgularia* tend to be redder in hue, from brick red to pale pink, and have a smoother dorsum (MacFarland 1966 for color illustration). There also appears to be variation in the number of embryos per egg mass capsule among geographically separated groups that is not related to prey items (C.E. Lee, unpublished).

Tritonia diomedea lives among beds of these soft corals on flat or gently sloping soft bottoms of sand or silt. The silty surface of *Virgularia* beds (~30 m deep) is softer than the sandy surface of *Ptilosarcus* beds (4–18 m deep), presumably due to lower water flow rates in the deeper *Virgularia* beds that allow the finer silt to settle out of suspension. This correlates with the observation that *T. diomedea* found among *Virgularia* can orient to lower flow rates than those found among *Ptilosarcus* (unpublished). *T. diomedea* can grow to 30 cm in length and to a mass of 1700 g.

137. *Tritonia festiva* (Stearns, 1873)

James Murray also reports that during the studies described above on *Tritonia diomedea*, he collected *T. festiva* up to 10 cm in length near Tofino, British Columbia.

138. *Tritonia myrakeenae* Bertsch and Mozqueira, 1986

This species has been collected as far south as Costa Rica (INBIO, 2003).

139. *Hancockia californica* Macfarland, 1923

The range of this species is extended to Fort Bragg, California (C. Schooley and M. Ellen Hill, pers. commun.), inside the Gulf of California at Bahía de los Angeles (Hans Bertsch and Jim Lance, pers. commun.), and south to Puerto Vallarta (Hermosillo-González 2003) and Costa Rica (INBIO 2003).

145. *Dendronotus iris* (Cooper, 1863)

The range of this species is extended to Cabo San Lucas, Baja California (Jim Lance, pers. commun.).

The color of this species varies widely. Behrens (1980) described three distinct morphs, but later (Behrens 1991) he mentions only the red and white morphs. The color of this species varies tremendously from white through grey, orange and red. The color of the gill tufts is also variable — white, orange or purple, depending on the overall body color. The most distinctive character is the white line along the edge of the foot. This characteristic is found in every specimen.

148. *Dendronotus* sp. 1

La Jolla Shores, San Diego County can be added to locations at which this undescribed species has been photographed (Steve Gardner, pers. commun.). Also, see the description of a new *Dendronotus* in "Newly Discovered Species" section.

149. *Doto amyra* Marcus, 1961

Goddard (1996) provides an excellent study of the larval development of this species. In this paper, he points out that *D. amyra*, as currently accepted, may include at least two and possibly four distinct species. The following is a brief review of the distinctions Goddard reports for the four forms:

Doto amyra Marcus, 1961 — Feeds on the hydroids *Abietinaria* sp., *Garveia* sp., *Coryne* sp., and *Sertularia furcata* and reaches a length of 14 mm. The larvae are lecithotrophic. The body and head are translucent white and occasionally have an irregular scattering of fine-grain subcutaneous brown to black pigment. The five to eight pairs of cerata have pale yellow to light pinkish-orange or orange-brown colored cores. The cerata possess four to seven rings of tuberacles and lack dark pigment. The rhinophores are translucent and contain opaque white grains.

Doto form A — Feeds on small athecate hydroids and measures up to 7 mm. This form is similar in color to the previous, but with no dark pigment. It has five to six pairs of cerata, usually with orange to pinkish cores. Because of the presence of semi-translucent white glands in the tuberacles, they appear whiter that in the previous form. The larvae are planktotrophic.

Doto form B — This form occurs on *Aglaophenia*. It differs from the above two in having dark pigment on the cerata, which are smooth or bear only low tuberacles. Specimens lack the opaque white grains in the rhinophores. It is similar to *D. columbiana* O'Donoghue, 1921.

Doto form C (from La Jolla, California) — Similar to *Doto* form A, above, it has planktotrophic larvae and feeds on short, unidentified hydroids.

Hermosillo-González (2003) extends the range of this species to Puerto Vallarta, Mexico.

152. *Doto lancei* Marcus and Marcus, 1967

The range of this species is extended northward from Mission Bay, California to Monterey Bay (Lovell and Libby Langstroth, pers. commun.). Lovell and Libby Langstroth's specimen was dark in color, similar to the species referred to as *Doto columbiana* in Behrens (1980, Species #92). The range of this species is extended south to Puerto Vallarta, Mexico Hermosillo-González (2003) and Costa Rica (INBIO, 2003).

Suborder Arminacea (= Arminina)

156. *Armina californica* (Cooper, 1863)

The range of this species is extended to the Aleutian Akutan Islands (Goddard and Foster 2002).

158. *Dirona aurantia* Hurst, 1966 [now: *Dirona pellucia* Volodchenko, 1941]

Dirona aurantia was reported to be a junior synonym of *D. pellucida* (Martynov 1997). The species complete range now would include Charleston, Oregon (Jeff Goddard, pers. commun.) to Norton Sound, Alaska, across the Bering Sea and the Sea of Japan to Russia (Martynov 1997). It is found to 60 m. In Oregon, the individuals were found on the bryozoan *Bugula pacifica,* living on floating boat docks (Jeff Goddard, pers. commun.).

159. *Dirona picta* MacFarland *in* Cockerell and Eliot, 1905

Previously known only to Charleston, Oregon, this species has now been collected on the south side of Cape Mearnes, Tillamook County, OR (Jeff Goddard, pers. commun.).

160. *Janolus barbarensis* (Cooper, 1863)

The range of this species is extended south to Puerta Vallarta, Mexico (Hermosillo-González 2003).

161. *Janolus fuscus* (O'Donoghue, 1924)

The range of this species is extended north to Homer, Alaska (Goddard and Foster 2002). It has also been documented from Sado island, Sea of Japan and Onagawa and Hokkaido, Pacific Ocean side in Japan (Nishina Masayoshi, pers. commun.).

Suborder Aeolidacea (= Aeolidina)

163. *Chlamylla* sp. 1 [now: *Flabellina* sp. and/or *Flabellina intermedia* (Bergh 1899)]

Currently, there is some confusion concerning whether we have one or two new species of *Chlamylla* in the 1991 edition of *Pacific Coast Nudibranchs.* On review, the species in the photograph probably belongs to the genus *Flabellina* (S. Millen, pers. commun.).

The specimen shown in the photograph as species #163 of the 1991 edition was collected in the Strait of George, British Columbia, was 9 mm in length, and was found on a solitary *Tubularia* sp. This specimen is considered to be an undescribed *Flabellina* (S. Millen, pers. commun.). The rhinophores can be extended the length of the body, although they are contracted in the 1991 photo. The ground color is transparent grey with pale peach suffused on the dorsum. Lanceolate cerata are continuous and irregularly arranged on notal flange. Ceratal cores are peach-pink with white cnidosacs, inside a clear sheath. The rhinophores, and long, cylindrical oral tentacles are dusted with opaque white at the ends.

The other specimens referred to in the 1991 edition are nearly identical to this photo but have been collected in deep water trawl nets off the coast Oregon by Goddard (1990), and in Alaska. These specimens are yellow in color and are considered to be *Flabellina intermedia* (Bergh 1899) (Alan Kuzirian, pers. commun.).

165. *Flabellina fusca* (O'Donoghue, 1921) [now: *Flabellina trophina* (Bergh, 1894)]

Flabellina fusca (O'Donoghue, 1921) is a junior synomyn to *Flabellina trophina* (Bergh, 1894) (Roginskaya 1990).

Flabellina trophina is often confused with *Flabellina verrucosa*, both species having reddish ceratal cores. The primary distinguishing characters are that *F. triopina* has a pointed snout, which is often upturned, and the cerata are continuous on a flange rather than in clusters inserted directly on the notum. Plate 4C shows a dark color morph of the species from Alaska.

In a message to the Sea Slug Forum from Irina Roginskaya, it appears that this species has a wide diet feeding on other aeolid nudibranchs as well as polychaete worms.

166. *Flabellina iodinea* (Cooper, 1862)

The range of this species is extended to San Benitos Islands, Baja California, Mexico (Hermosillo-González 2003).

167. *Flabellina marcusorum* Gosliner and Kuzirian, 1990

This species is known from the Pacific and Atlantic Oceans. Its range along this coast has been extended south to the Gulf of Chiriqui, Panamá and to Islas Galápagos, Ecuador (Gosliner 1994), and along the Atlantic Coast, it ranges north to Venezuela and Curacao in the Caribbean and to Santa Marta Bay, Columbia, and to Brazil (P. Montoya, pers. commun.; Humann and DeLoach 2002; Sea Slug Forum).

169. *Flabellina salmonacea* (Couthouy, 1838) [now: *Flabellina japonica* (Volodchenko, 1941)]

According to Sandra Millen (pers. commun.), Pacific Coast specimens differ from the Atlantic Coast sibling species, *F. salmonacea*, by their yellow cerata and penial morphology; they are actually *Flabellina japonica*. Thus, the range should be changed to Sea of Japan and British Columbia, Canada. The species was named for the Japan Sea.

172. *Flabellina* sp. 1

It has been suggested that this species might be a *Cumanotus* due to its wide body and basally joined rhinophores (S. Millen, pers. commun.). The photo in the 1991 edition of *Pacific Coast Nudibranchs* is of a specimen collected at Mission Bay, California. The reference to the British Columbia specimens was likely to a similar looking *Cumanotus*.

This species has a unique swimming style, where the cerata move in unison, forward and backwards in a rowing manner (Neil McDaniel, pers. commun.).

173. *Flabellina* sp. 2 [now: *Flabellina vansyoci* Gosliner, 1994]

This colorful aeolid from the southern portion of this coast has been recently described by Terry Gosliner (Gosliner 1994), and given the name *Flabellina vansyoci*; the name honors California Academy of Sciences' biologist Robert Van Syoc.

The radular formula for the species is 36 × 1.1.1. The rachidian tooth bears 5–6 triangular denticles as shown here (Fig. 15). The margin teeth bear 15–20 denticles.

The size of the species ranges from 15–30mm. Originally, the species was documented to occur at Magdelena Bay, Baja California and Islas Ladrones, Panama. Bertsch *et al.* (2000) extended the range northward to Punta Eugenia, Baja California. The species has also been observed further south, at La Paz, Baja California Sur (Angulo-Campillo 2002) and Puerto Vallarta (Hermosillo-González 2003), Mexico, and along the west coast of Costa Rica (INBIO 2003).

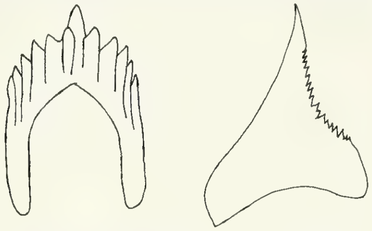


FIGURE 15. *Flabellina vansyoci* Gosliner, 1994. Radular teeth.

174. *Flabellina* sp. 3 [now: *Flabellina amabilis* Hirano and Kuzirian, 1991]

This species is *Flabellina amabilis* from northern Sea of Japan (Sandra Millen, pers. commun.). Its radula is triseriate, with a formula of 13–17 × 1.1.1. The rachidian teeth have 4–8 denticles and the lateral teeth 5–8 denticles.

175. *Babakina festiva* (Roller, 1972)

Redfern (2001) documents the presense of *Babakina festiva* in the tropical Atlantic, in the Bahamas.

178. *Eubranchus olivaceus* (O'Donoghue, 1921) [now: *Eubranchus rupium* (Möller, 1842)]

Just and Edwards (1985) and Martynov (1998) indicated that the northeast Pacific *Eubranchus olivaceus* is a synonym of the north Atlantic *Eubranchus rupium*. The range of this species on this coast is thus extended to Amalga Harbor, north of Juneau, Alaska. It has been observed feeding on the hydroid species *Obelia* (Rita O'Clair, pers. commun.). More recently, the range has been extended to Homer, Alaska (Goddard and Foster 2002).

181. *Eubranchus steinbecki* Behrens, 1984

The range of this species is extended to La Paz, Baja California Sur, Mexico (Angulo-Campillo 2002).

184. *Catriona rickettsi* Behrens, 1984

Previously known only from San Francisco Bay and La Jolla, California, Jeff Goddard reports large numbers of this species were found on large patches of *Tubularia* sp. on the ocean side of the south jetty, Umpqua River, Douglas County, Oregon, during February 1994, 1996 and 1997. Also, Bertsch *et al.* (2000) extended the range south to Punta Eugenia, Baja California, Mexico.

[**Note concerning *Cuthona***: Martynov (2002) recommends a number of taxonomic changes for Pacific coast *Cuthona* returning several species to the genus *Trinchesia*. I cannot support these recommendations and do not follow them here.]

186. *Cuthona albocrusta* (MacFarland, 1996)

The range of this species is extended north to Cordova Marina, Prince Williams Sound, Alaska, and south to Bird Rock, La Jolla, California (Goddard 2000a), Bahía Tortugas (Bertsch et al. 2000) and La Paz, Baja California Sur, Mexico (Angulo-Campillo 2002)

187. *Cuthona cocoachroma* Williams and Gosliner, 1979

The northern limit of this species is extended from Oregon to Kayostla Beach, Olympic Peninsula, Washington (Goddard et al. 1997).

190. *Cuthona flavovulta* (MacFarland, 1996)

The northern limit of this species is extended from Oregon to Kayostla Beach, Olympic Peninsula, Washington (Goddard et al. 1997).

191. *Cuthona fulgens* (MacFarland, 1996)

The northern limit of this species is extended from Oregon to Kayostla Beach, Olympic Peninsula, Washington (Goddard et al. 1997).

193. *Cuthona lagunae* (O'Donoghue, 1926)

The range of this species is extended north to Humbug Mountain, Curry County, Oregon (Jeff Goddard, pers. commun.), and south to Bahía Tortugas, Baja California (Bertsch et al. 2000).

194. *Cuthona perca* (Marcus, 1958)

Perrone (1995) reports the occurrence of this species in the Mediterranean, and he discusses taxonomic variation between several of the populations of this global species.

195. *Cuthona phoenix* Gosliner, 1981

This species has now been reported from Costa Rica (INBIO 2003).

197. *Cuthona pustulata* (Alder and Hancock, 1854)

The range of this species is extended northward to Homer, Alaska (Goddard and Foster 2002) where it was found feeding on the hydroid, *Sarsia* sp.

198 *Cuthona rolleri* Behrens and Gosliner, 1988

A recent deepwater study conducted in the Santa Maria Basin in Central California collected a specimen of *C. rolleri* at a depth of 575 m. This is the first subtidal collection of this species, which previously was known only from intertidal collections, and it extends the range south to Point Sal, San Luis Obispo County, California (Gosliner 1996).

200. *Cuthona viridis* (Forbes, 1830)

The range of this species is extended south to Bremerton, Washington (Andy Lamb, pers. commun.). Roginskaya (2000) reports that in summer *C. viridis* is the most common nudibranch in the intertidal zone of the Murman coast of the Barents Sea. Roginskaya also gives a detailed account of this species' reproductive biology and development.

203. *Fiona pinnata* (Eschscholtz 1831)

Schrödl (2003) reports this species from the southern hemisphere along the coast of Chile.

204. *Anetarca armata* Gosliner, 1991

Since the description of the species in 1991, it has been determined that it occurs on both coasts of Baja California. Farmer (1990) describes studies conducted by Jim Lance in Bahía de los Angeles, Gulf of California, Mexico that report a fascinating association of this nudibranch i.e., where it lives, feeds, and lays its eggs, on a symbiotic hydroid species (Plate 4D), which occurs solely on the shelled gastropod, *Decipifus californicus* (Plate 4E). Reported also from Puerto Vallarta, Mexico (Hermosillo-González 2003) and Costa Rica (INBIO 2003).

206. *Facelina stearnsi* Cockerell, 1901

Specimens have been recently collected at a depth of 110 ft. in La Jolla Canyon, San Diego, California (Peter Brueggeman and George Spalding, pers. commun.). The range of the species is extended southward to La Paz, Baja California where numerous specimens have been observed on an offshore shipwreck (Bob Sinclair, pers. commun., and Angulo-Campillo 2002).

208. *Hermosita sangria* Gosliner and Behrens, 1986

This species has been reported from Costa Rica (INBIO, 2003).

209. *Noumeaella rubrofasciata* Gosliner, 1991

The range is extended to Puerto Vallarta (Hermosillo-Gonzales 2003) and Guanacaste, Costa Rica (Peter Ajtai, pers. commun.).

210. *Phidiana hiltoni* (O'Donoghue, 1927)

The range of this species is extended northward to Duxbury Reef, Marin County, California (T. Gosliner, pers. commun.).

212. *Aeolidia papillosa* (Linnaeus, 1761)

Goddard and Schickel (2000) extend the geographic range of this cosmopolitan species along the Pacific Coast south to Punta Rosarito, Baja California. Schrödl (1997) reports a variation of *Aeolidia papillosa*, *Aeolidia papillosa* var. *serotina* from Bahía de Coliuma, Chile and in the Falkland Islands and Argentina (Schrödl 2003).

213. *Aeolidiella chromosoma* (Cockerell and Eliot, 1905)

Along the West Coast, the range of this species is extended to Costa Rica (INBIO 2003); in the eastern Pacific it has recently been reported from the Izu Peninsula and Sagami Bay, Japan (Jun Imanoto and Nishina Masayoshi, pers. commun.).

214. *Aeolidiella indica* Bergh, 1888 [now: *Anteaeolidiella indica* (Bergh, 1888)]

Aeolidiella indica is placed in a new genus, *Anteaeolidiella*. Miller (2001) reviewed the aeoid nudibranchs of New Zealand. His review included the report of *A. indica* from that region. Because of internal anatomical features found in *A. indica*, which separated it from other species in *Aeolidiella*, he created a new genus *Anteaeolidiella* for it.

The range for this species should include the Galápagos Islands, Ecuador (Hickman and Finet 1999).

216. *Cerberilla mosslandica* McDonald and Nybakken, 1975

Jeff Goddard (pers. commun.) reports a single specimen matching the description of *C. mosslandica* from 65 m of water, 6.4 km west of Bandon State Beach, Oregon.

217. *Cerberilla* sp. 1 [now: *Cerberilla* cf. *pungoarena* Collier and Farmer, 1964]

This species has become common in the Channel Islands. (Plate 4F) (Kathy deWet, pers. commun.). This speciesis considered to be *Cerberilla pungoarena* Collier and Farmer, 1964, from Puerto Refugio, Isla Ángel de la Guardia, Gulf of California, Mexico.

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The Panamic Gorgonian Genus *Pacifigorgia* (Octocorallia: Gorgoniidae) in the Galápagos Archipelago, with Descriptions of Three New Species

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The eastern Pacific gorgonian genus *Pacifigorgia* Bayer, 1951, is here described from the northwestern fringe of the Galápagos Archipelago. The two small islands of Darwin and Wolf are relatively isolated from the rest of the archipelago. Two of the new taxa are apparently endemic to these outer islands, as previous subtidal surveys of the other Galápagos Islands, as well as other regions of the Panamic Biogeographic Province, have not encountered conspecific material. The third new species is apparently restricted to central islands of the archipelago. The previously described *P. darwini* (Hickson, 1928) is the most common and widespread species and is found throughout the archipelago, except for the outlying islands of Darwin and Wolf. A taxonomic assessment of Hickson's *Gorgonia darwinii* var. *douglasii* is also included. The genus is restricted to the eastern Pacific (Gulf of California to Peru), with the exception of *Pacifigorgia elegans*, endemic to the tropical western Atlantic (Trinidad to Brazil). The addition of the new taxa described here makes twenty-one species belonging to the genus that are considered valid.

The marine fauna of oceanic islands have been subjects of great scientific interest chiefly because of their biogeographic relevance. Endemism, dispersal patterns, and other aspects of evolutionary biology might be better understood through comparisons to mainland faunas (Quammen 1996).

The main oceanic islands and archipelagos situated in the tropical eastern Pacific are Isla del Coco (Costa Rica); Isla Malpelo (Columbia); Islas Revillagigedo (Mexico), Île Clipperton (France); and Islas Galápagos (Ecuador). Even though numerous expeditions to explore the flora and fauna of these islands have been made, the octocorallian fauna remains as one of the least known faunal elements.

The literature pertaining to the Galápagos octocoral fauna is depauperate. The main sources here include Hickson (1928), Bayer (1978), and Breedy and Guzman (2003). Sources relevant to the genus *Pacifigorgia* are Bayer (1951, 1953, 1956), Breedy (2001), and Breedy and Guzman (2002, 2003). Hickson (1921, 1928) and Deichmann (1941) provided the first records of shallow water octocorals of the Galápagos Archipelago. Hickson (1921) described *Cavernularia darwinii* (Pennatulacea) from Isla Cristobal (Chatham Island), and then seven years later, he described two new species of *Pacifigorgia* (under the generic name *Gorgonia*) (Hickson, 1928). Deichmann (1941) described the species *Muricea galapagensis* (Plexauridae) from Isla Isabela (Albemarle

Island), which was pulled up on an anchor chain from 53 fathoms (97 m depth). The validity of this species has to be corroborated.

Aside from Hickson's two species and the recently described *Pacifigorgia curta* Breedy and Guzman, 2003, from Isla del Coco, there are not published records from other oceanic islands of the tropical eastern Pacific. Two presently undetermined species of *Pacifigorgia* are known from Islas Revillagigedo. These are represented by two dried preserved specimens, CAS 097905 and CAS 097906.

The only published records of the genus *Pacifigorgia* from the Galápagos, appeared in Hickson's publication "The Gorgonacea of Panama Bay." He described two taxa: *Pacifigorgia darwinii* (Hickson, 1928), *and Pacifigorgia darwinii* var. *douglasii* (Hickson 1928). *Pacifigorgia darwinii* was revised and redescribed by Breedy and Guzman (2002), whereas *P. darwinii* var. *douglasii*, was originally figured only from sclerites, which is all that is known to exist from the type specimen (Breedy and Guzman 2002).

In this paper, we monograph all the known taxa from the Galápagos Archipelago, which includes the descriptions of three new species, based on the study of recently discovered taxa, and material found in several collections. The two previously described taxa are also included in the present paper, making a total of five species of the genus *Pacifigorgia* presently known to inhabit the shallow coastal waters of the Galápagos Archipelago. Four of these are considered valid, whereas one is here considered to be of dubious status.

The three new species of sea fans (gorgonian corals) were discovered during SCUBA operations conducted during the 1994 California Academy of Sciences marine expedition to the Galápagos Islands, Ecuador. McCosker (1994) briefly describes this expedition.

The genus *Pacifigorgia* was described by Bayer (1951:94) for net-like reticulated species with sclerites as spindles and capstans (scaphoids absent), geographically confined to the Pacific coast of tropical America (with one exception from the tropical western Atlantic). The following genera are known to comprise the shallow-water gorgonian fauna (<50 m) of the Galápagos Archipelago. These five genera represent approximately eleven species in the two families Plexauridae and Gorgoniidae: *Adelogorgia* (1 species), *Eugorgia* (1 species), *Leptogorgia* (1 species), *Muricea* (ca. 4 species), and *Pacifigorgia* (4 valid species, plus 1 dubious species) (pers. observ. and Cleve Hickman — pers. commun.).

METHODS

Specimens were collected by the senior author (GCW) from several islands in the Galápagos Archipelago, between 2°N to 1.5°S Latitude, and 89°W to 92°W Longitude, during the California Academy of Sciences marine expedition to the Galápagos Islands in May of 1994. All material was collected by SCUBA in shallow water (<50 m depth), and preserved in 70% ethanol. The specimens for study came from this recent collection as well as from expeditions by C. Hickman and P. Humann (1993–2001). Other material came from the collections of the California Academy of Sciences, San Francisco; the Charles Darwin Research Station, Galápagos; the voucher collection of the Museum of Comparative Zoology of Harvard University, Boston, made available to us by Ardis Johnston; and type specimens and microscope slides from The Natural History Museum, London, through the kindness of Sheila Halsey. Most of this material was collected by hand using SCUBA or skin diving. Most of the specimens are preserved in 70–75% ethanol and were originally fixed in ethanol. A few of the specimens were preserved dried. All collection sites are indicated on the maps (Figs. 5, 9, 16, 23), along with a range comparison map (Fig. 24).

Sclerites were isolated using sodium hypochlorite (household bleach); see the website:

http://www.calacademy.org/research/izg/OctoResearchTech.htm (Octocoral Research Center or Octocoral Home Page — Research Techniques), and Breedy and Guzmán (2002:784) for details. Also of relevance here are Bayer (1961:23–24), and Fabricius and Alderslade (2001:38).

The subject for Figure 1A was photographed in a small glass aquarium from freshly collected material, using a Pentax 35 mm camera, with a 50 mm macro lens and flash unit. Figure 1C is a scanprint made directly from the holotype, using a Umax Astdra 1200S flatbed scanner. Micrographs for figures 1B and 2 were made using a Nikon Coolpix 990 digital camera, a Nikon SMZ-10 dissecting microscope, and an Olympus CH-2 compound microscope. Scanning electron micrographs were made using a Leo 1400 Series or a N-2360 Hitachi scanning electron microscope. Sclerite drawings were made using an Olympus CH-2 compound microscope with an attached drawing tube. Digital images and plates of photographs, micrographs, and scanning electron micrographs were made using Adobe Photoshop software. Abbreviations used in the text are BM or NHM (The Natural History Museum, London; formerly British Museum — Natural History); CAS (California Academy of Sciences, San Francisco); CDRS (Charles Darwin Research Station, Puerto Ayora, Isla Santa Cruz, Galápagos Islands); MCZ (Museum of Comparative Zoology, Harvard University, Boston).

Specimens examined in this study are deposited in the CAS octocoral collection (Department of Invertebrate Zoology and Geology), the CDRS, and the MCZ. Type specimens were obtained by loan from the BM. Previous records of some species have been acquired from literature sources (Hickson, 1928; Stiasny, 1941, 1943; Breedy and Guzmán, 2002), as well as from personal observations and museum specimens.

Terminology used in this paper conforms to that of Bayer, Grasshoff and Verseveldt (1983), and Breedy and Guzmán (2002).

SYSTEMATIC ACCOUNT

Family Gorgoniidae Lamouroux, 1812

Pacifigorgia Bayer, 1951

Rhipidigorgia (partial) Valenciennes, 1855:13. Milne Edwards and Haime, 1857:173. Horn, 1860:233.

Rhipidogorgia (partial) Verrill, 1864:32. Duchassaing and Michelotti, 1864:20. Verrill, 1869:424.

Litigorgia (partial) + *Eugorgia* (partial) Verrill, 1868:414.

Leptogorgia (partial) Verrill, 1869:420. Verrill, 1870:548.

Gorgonia Bielschowsky, 1918:32. Kükenthal, 1924:338. Bielschowsky, 1929:141. Stiasny, 1941:268. Stiasny, 1943:74.

Pacifigorgia Bayer, 1951:94. 1953:103. 1956:212. Breedy, 2001:182. Breedy and Guzmán, 2002:791. 2003:3.

DIAGNOSIS.— Sea fans composed of reticulated networks by anastomosis (as in the western Atlantic genus *Gorgonia*), but with sclerites similar to those of the genus *Leptogorgia* from the eastern Pacific and Atlantic Ocean. The coenenchymal sclerites are girdled spindles and radiates, whereas scaphoids are absent. Color permanent, incorporated in the sclerites.

TYPE SPECIES.— *Gorgonia stenobrochis* Valenciennes, 1846; subsequent designation by Bayer, 1951:94.

DIVERSITY AND DISTRIBUTION (see Fig. 5, inset).— Twenty species from the Eastern Pacific (Baja California to Chile, Cocos Islands, Revillagigedo Islands and Galápagos Islands); one species in the western Atlantic (Trinidad and Venezuela to Brazil).

Pacifigorgia dampieri Williams and Breedy, sp. nov.

(Figs. 1–5, 24)

Material examined.— Holotype: CAS 097040, Ecuador, Galápagos Islands, Isla Darwin, 15–21 m depth, (Station G8), 13 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. Paratype: CAS 097021, Ecuador, Galápagos Islands, Isla Wolf, 9–15 m depth, (Station G5), 12 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol.

Other material: CAS 097022, Ecuador, Galápagos Islands, Isla Wolf, 12–18 m depth, (Station G4), 12 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. CAS 097023, Ecuador, Galápagos Islands, Isla Wolf, 12–18 m depth, (Station G4), 12 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. CAS 097025, Ecuador, Galápagos Islands, Isla Wolf, 9–15 m depth, (Station G5), 12 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. CAS 097025, Ecuador, Galápagos Islands, Isla Wolf, 9–15 m depth (Station G5), 12 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. CAS 147483, Ecuador, Galápagos Islands, Isla Darwin, 15–21 m depth, (Station G8), 13 May 1994, collected by G.C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen, preserved in 75% ethanol. CDRS 02–39, Ecuador, Galápagos Islands, Isla Wolf, depth not recorded, 19 May 2001, collected by C. Hickman.

General description.— Fans are relatively stiff, planar or comprised of a main fan with several secondary fans in different planes, which radiate outward from the central region of the main fan. Secondary fans may radiate perpendicularly from the main fan. Colonies are wider than high, often irregularly-shaped, up to 200 mm in height and 270 mm in width. Multiple fans are interconnected by relatively thick branches (up to 8 mm in width) that diverge upwards from the holdfast. In some cases, fans with separate holdfasts anastomose to produce a maze-like appearance. The fusion between fans may take place in the coenenchyme of the main stem or main branches. Colonies often have strong, encrusting, orange-colored holdfasts. In smaller colonies, the holdfast may spread out conspicuously over the substratum.

Networks are intricate, regular, and of open meshes. The meshes are often more-or-less square, but are also variable: circular, rounded-rectangular, elliptical or triangular meshes 2–5 mm long by 1–3 mm wide; elongated and trapezoidal meshes 4–12 mm long by 0.7–6.0 mm wide. Colonies average approximately six meshes/cm^2. Mesh branches are thin, up to 1.0 mm in diameter. Prominent, rounded midribs , up to 7 mm in width, extend up into the fans, or reach a short distance upwards from the base of the fans. They are of a distinct orange color, with distinct longitudinal grooves of yellow and orange sclerites, very apparent in dried specimens. The terminal branchlets are short, 2–5 mm in length. Free twigs emanating from the interior of the fans are short (up to 2 or 3 mm long) and scarce. The mound-like protuberances resulting from the retracted polyps are small (mostly ≤ 1 mm long), oval in shape with slit-like apertures, slightly raised, and red-orange at the bases with yellowish apices. These mounds are disposed in more-or-less distinct, usually four longitudinal rows along the branches. On a particular face of the fan, the mounds are arranged biserially, alternately so on narrow branches, alternate to opposite on thicker branches. Polyps are milky white with very thin points-like arrangements of sclerites.

The coenenchymal sclerites are mostly girdled spindles with blunt, rounded ends, but a dominance of spindles with acute ends is also observed in some specimens (e.g., CAS 097025). The spindles vary in length from 0.08 mm -0.16 mm and are up to 0.04 mm in width. They have 4–6 whorls of tubercles, with both ends acute or blunt, or with one end acute and the other blunt. Compact, relatively wide radiates or capstans (0.40–0.60 mm long), and relatively elongated eight radiates (0.60 mm–0.80 mm long and up to 0.04 mm wide), are also common in all the specimens. These characteristically have two whorls of tubercles and warty ends. The coenenchymal sclerites are entirely red or yellow, whereas some are bicolored (red and yellow). Anthocodial sclerites are elongated yellowish rods (up to 0.11 mm in length and 0.02 mm in width), with lobed or scalloped margins, and with short tubercles at the ends.

Color in life is brick-red to rust-orange, often with orange main branches. The mounds formed by retracted polyps are mostly brick-red to dull orange. The color is conserved in alcohol-preserved specimens or is slightly paler in dried specimens.

DESCRIPTION OF HOLOTYPE.— Growth form and size (Fig. 1A–B): The holotype measures 77 mm high by 163 mm wide, and is comprised of a single planar fan. Secondary fans are absent. The main stem is very short above the holdfast (<5 mm long). A strong main trunk-like branch is absent. Instead, two thickened branches (each approximately 4 mm in width) emanate from the basal stem, which form a more-or-less V-shape, and subtend the fan. The free terminal branches are 2–10 mm long. Networks are composed of relatively large, open meshes of variable shape. The meshes are mostly quadrilateral , trapezoidal, or deltoid in shape, whereas some are elongated. Meshes vary from 2–8 mm long and 2–3 mm wide; mostly 6–8 meshes/cm^2. Mesh branches are narrow, mostly 1.0–1.5 mm wide.

Polyps (Fig. 1B): The polyps are all retracted and form mound-like, rounded protuberances in longitudinal rows along the branches. The mounds are approximately 1.0 mm long, usually oval in shape with slit-like apertures.

Sclerites (Figs. 1C–D, 2–4): The coenenchymal sclerites are girdled spindles, some with blunt to rounded ends and others with acute tips, mostly 0.08–0.14 mm in length. Eight radiates are also present, mostly 0.05–0.07 mm long (Figs. 1C–D, 2–4). The terminal branches have a predominance of spindles (Fig. 2A–E, G–J, M), whereas the holdfast region has mainly radiates (Fig. 3). Some of these are ornately sculptured (Fig. 3J–K, O), but others are more sparsely ornamented (Fig. 3A, E–F, M). The anthocodial sclerites are bisquit-shaped rods, 0.03–0.04 mm long (Fig. 2K, N–P), or elongated rods with more or less scalloped margins, up to 0.06 mm long (Fig. 2F, L). Sclerites are red, yellow, or bicolored (Figs. 1C–D). The various kinds of sclerites are shown at the same scale in Fig. 4.

Color (Fig. 1A–B): The coenenchyme is brick-red to rust-orange throughout, with brick-red to dull orange mounds formed by the retracted polyps. The sclerites are mostly deep-red or bright yellow, whereas some are bicolored red and yellow. Wet preserved specimens appear deep red, dried specimens pale orange.

ETYMOLOGY.— This species is named for William Dampier, English explorer, naturalist, and buccaneer, who visited the Galápagos Archipelago between 31 May and 12 June of 1684, and described various aspects of the flora and fauna, over a century and a half before Charles Darwin's visit of 1835 (Dampier, 1927:75–83).

DISTRIBUTION.— Apparently restricted to outlying Darwin and Wolf Islands, in the extreme northwestern fringe of the Galápagos Archipelago; 9–21 m in depth (Figs. 5, 22).

REMARKS.— All colonies examined, including the holotype, have numerous pinkish white ophiuroids attached to the them (Fig. 1A). These brittle stars measure approximately 10–15 mm in length and presumably represent a single species, which is unidentified at present.

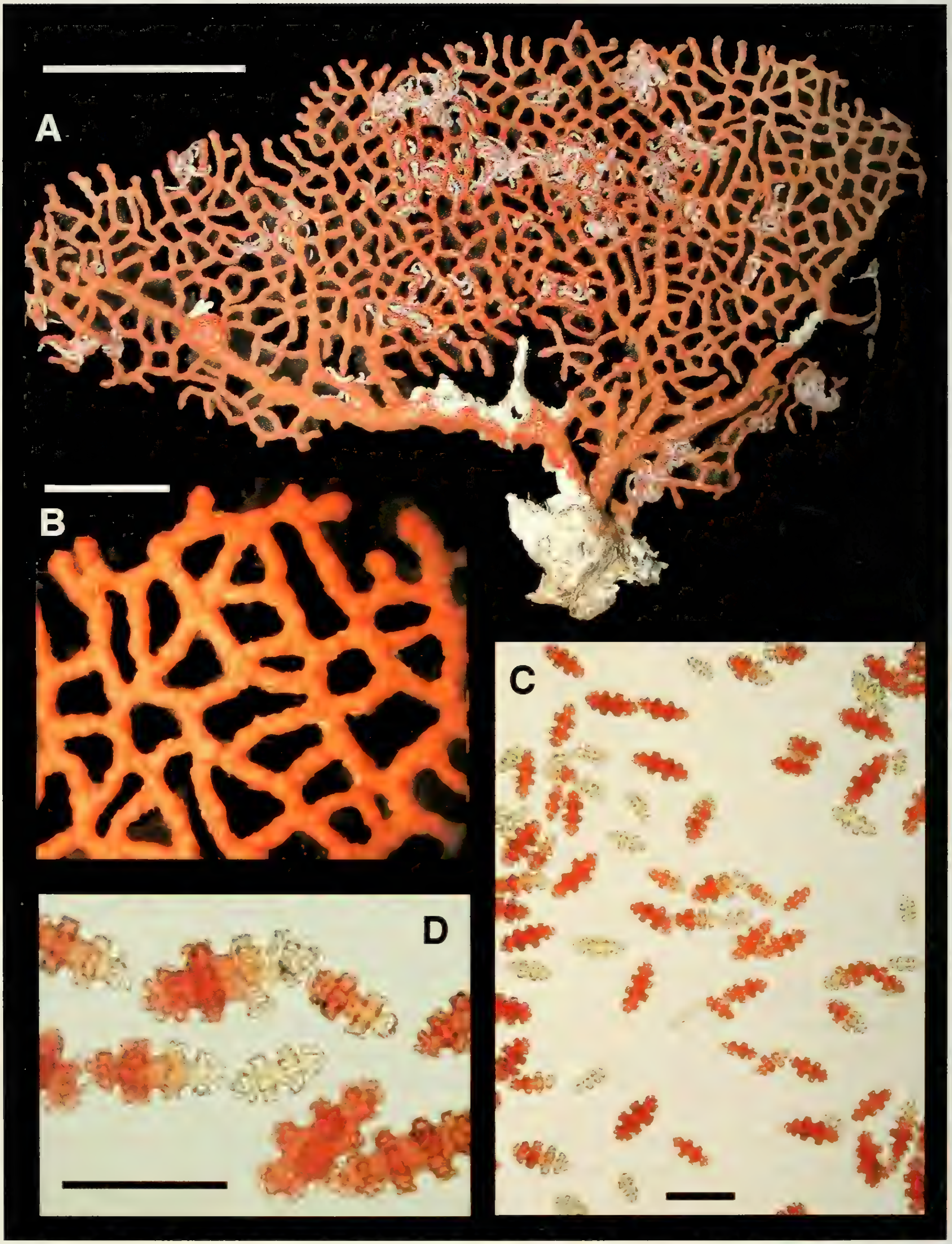

FIGURE 1. Holotype of *Pacifigorgia dampieri* sp. nov. A. Whole colony, wet-preserved; scale bar = 30mm. B. Detail of branching pattern; scale bar = 6 mm. C. Micrograph of coenenchymal sclerites; scale bar = 0.10 mm. D. Micrograph of coenenchymal sclerites including bicolored ones; scale bar = 0.08 mm.

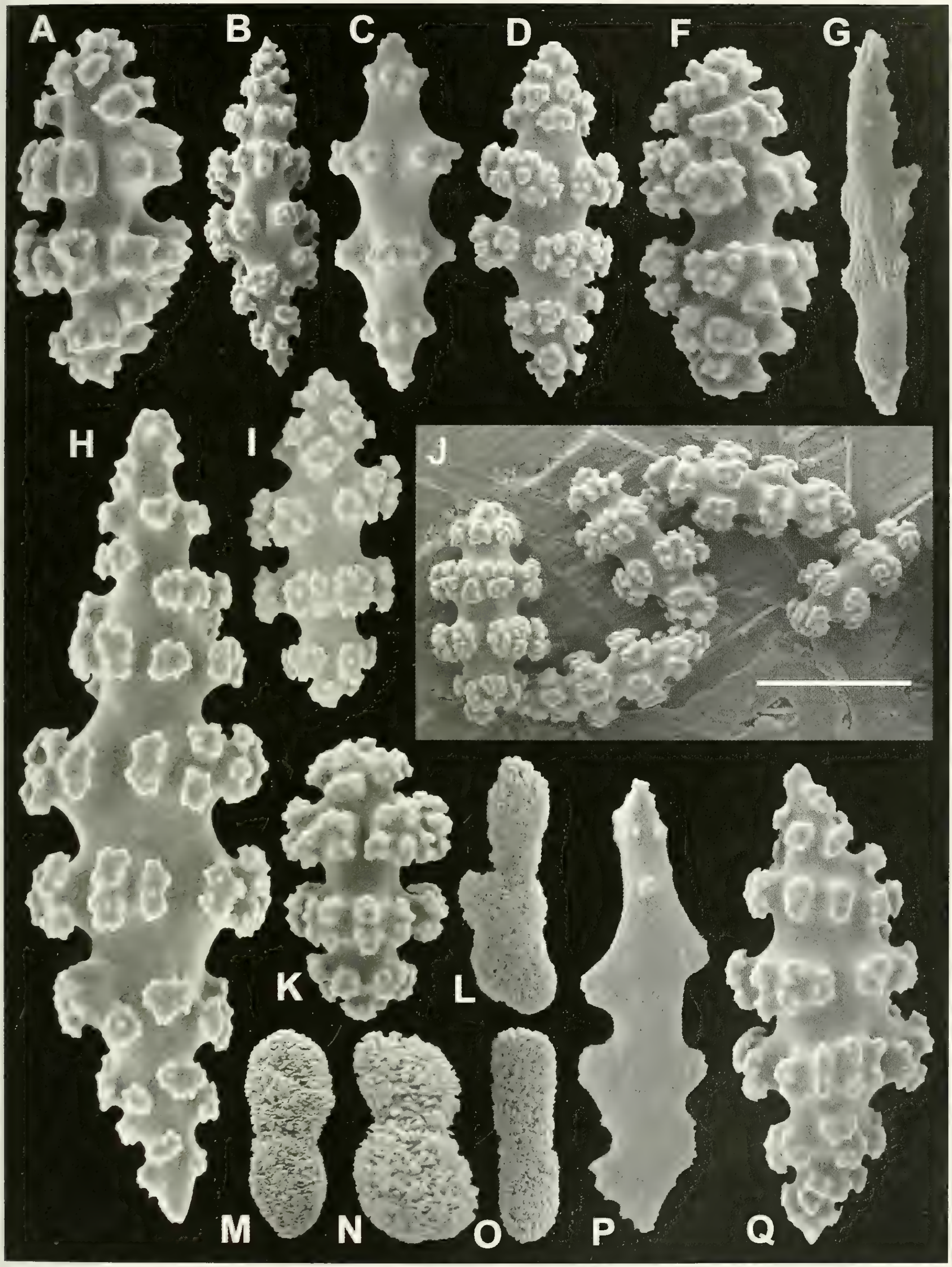

FIGURE 2. Holotype of *Pacifigorgia dampieri* sp. nov. Scanning electron micrographs of coenenchymal and anthocodial sclerites from the outermost branch tips. A. 0.06 mm. B. 0.11 mm. C. 0.08 mm. D. 0.09 mm. E. 0.05 mm. F. 0.06 mm. G. 0.14 mm. H. 0.06 mm. I. Scale bar = 0.06 mm. J. 0.05 mm. K. 0.03 mm. L. 0.06 mm. M. 0.10 mm. N. 0.04 mm. O. 0.03 mm. P. 0.04 mm. Anthocodial sclerites: K, N, O, P; all others are coenenchymal sclerites.

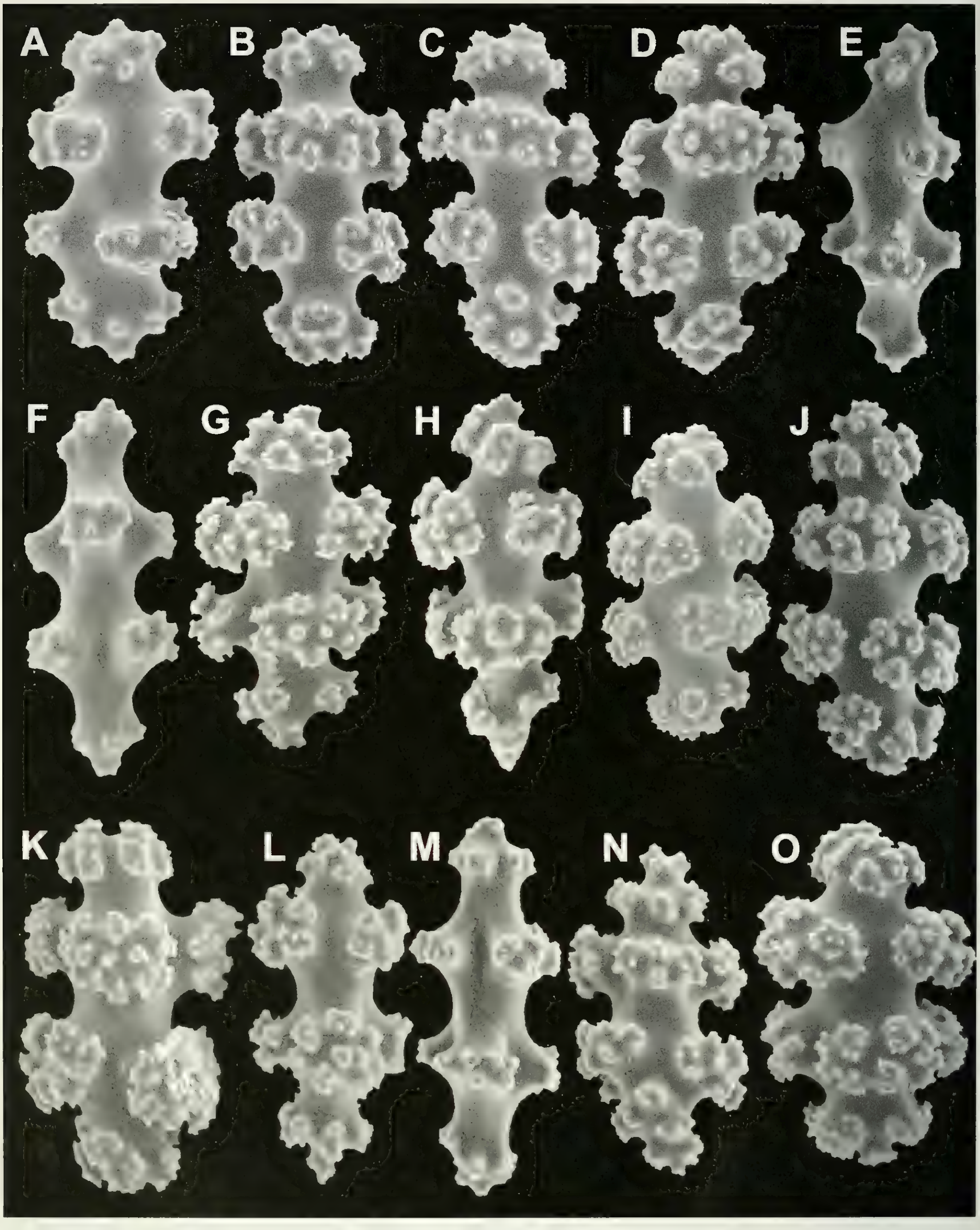

FIGURE 3. Holotype of *Pacifigorgia dampieri* sp. nov. Scanning electron micrographs of sclerites from the holdfast. A. 0.06 mm. B. 0.07 mm. C. 0.05 mm. D. 0.05 mm. E. 0.06 mm. F. 0.06 mm. G. 0.07 mm. H. 0.07 mm. I. 0.07 mm. J. 0.07 mm. K. 0.06 mm. L. 0.07 mm. M. 0.07 mm. N. 0.06 mm. O. 0.06 mm.

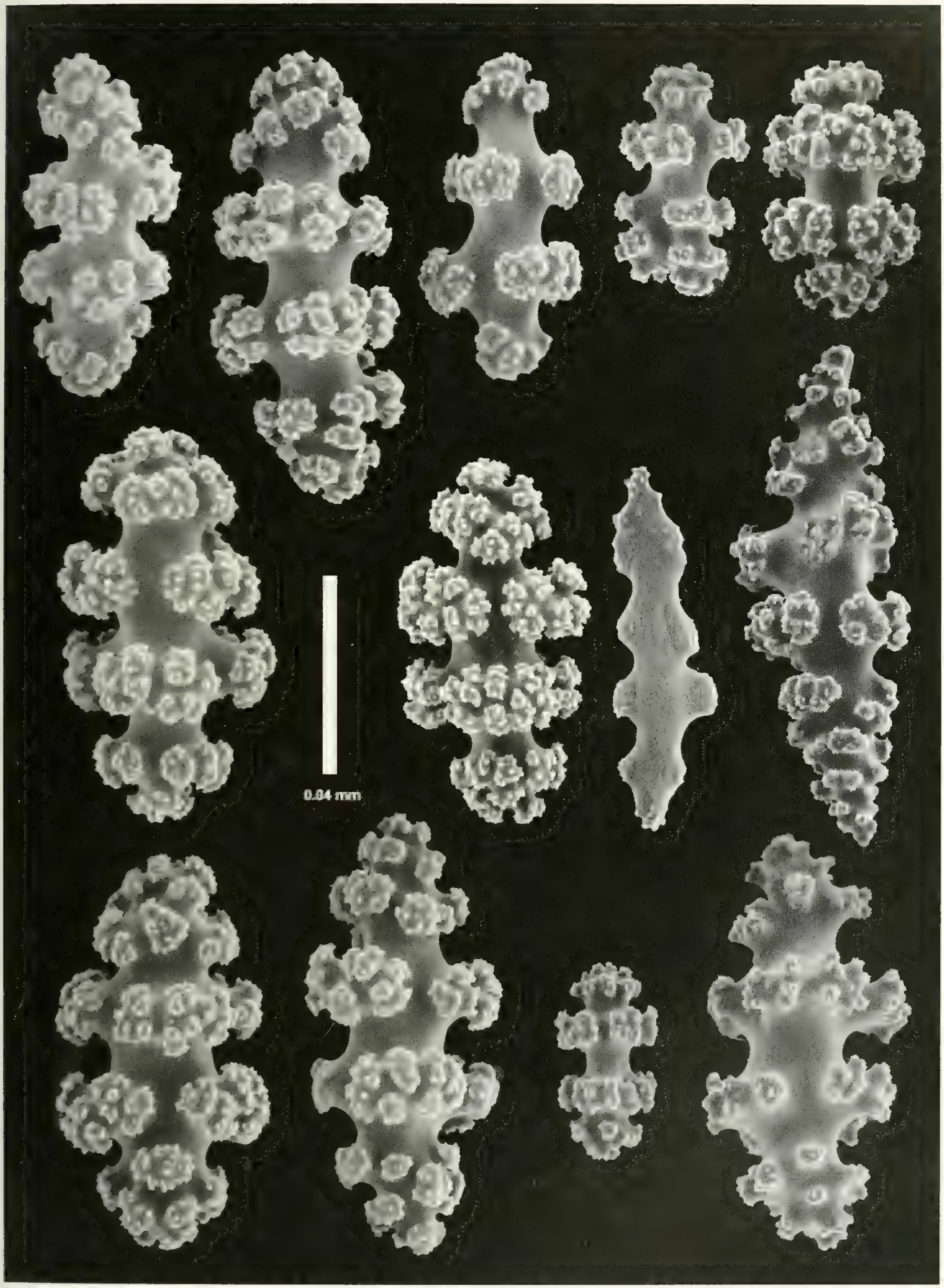

FIGURE. 4. *Pacifigorgia dampieri* sp. nov. (CASIZ 097022). Scanning electron micrographs of sclerites shown at the same scale; scale bar = 0.40 mm.

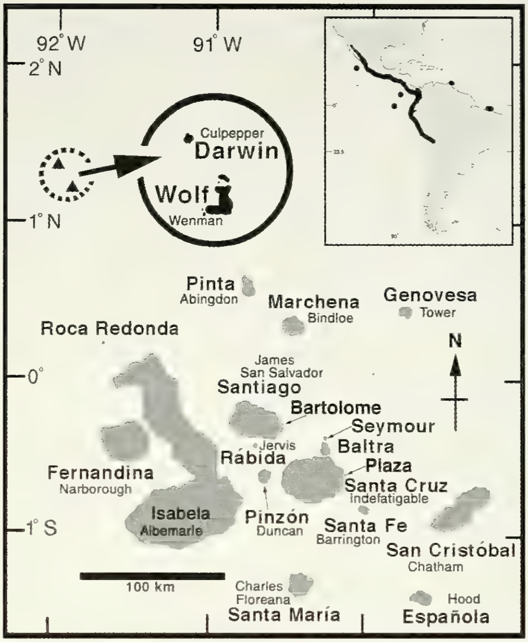

FIGURE 5. *Pacifigorgia dampieri* sp. nov. Map of geographic distribution; ▲ = collecting stations. Inset shows geographic range of the genus *Pacifigorgia* (in black).

Pacifigorgia darwinii (Hickson, 1928)

(Figs. 6–9, 24)

Gorgonia darwinii Hickson, 1928: 390–392. Stiasny, 1941:268–270.
Pacifigorgia darwinii: Breedy and Guzmán, 2002:808–813.

MATERIAL EXAMINED.— LECTOTYPE: BM 1930.6.17.10, Ecuador, Galápagos Islands, Isla Isabela, Tagus Cove, depth not recorded, 1923–1924, collected by C. Crossland. PARALECTOTYPES: BM 1936.8.30.1, 1961.2.6.148, 1961.2.6.150, same data as lectotype. BM 1936.8.29.1 (one of the original syntypes now designated as "Type" in the Darwin collection but more properly one of the paralectotype series), Ecuador, Galápagos Islands (specific island not recorded), depth not recorded, 1835, collected by C. Darwin (Beagle Collection No. 1306, 21 November 1901).

OTHER MATERIAL: CAS 097019, Ecuador, Galápagos Islands, Isla San Cristobal, Leon Dormido, 15–26 m depth (Station G2), 10 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", one whole specimen and one portion of another colony wet preserved in 75% ethanol. CAS 097031, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, 3–18 m depth (Station G9), 14 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", two whole wet specimens preserved in 75% ethanol. CAS 097032, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, 3–18 m depth (Station G9), 14 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", four whole wet specimens, preserved in 75% ethanol. CAS 097035, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, <18 m depth (Station G10), 14 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", one whole wet specimen, preserved in 75% ethanol. CAS 097039, Ecuador, Galápagos Islands, north shore of Isla Fernandina, <21 m depth (Station G13), 15 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", one whole wet specimen preserved in 75% ethanol. CAS 097054, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, <18 m depth (Station G10), 14 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", twelve whole wet specimens, preserved in 75% ethanol. CAS 097117, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, 3–18 m depth (Station G9), 14 May 1994, collected by G.C. Williams with SCUBA aboard "Mistral II", one whole wet specimen, preserved in 75% ethanol. CAS 097901, Ecuador, Galápagos Islands, Isla San Cristobal, 21 m depth, June 1993, depth not recorded, collected by P. Humann with SCUBA, one whole dried colony. CAS 105031, Ecuador, Galápagos Islands, Isla Floreana, Devil's Crown, 6 m depth, date not recorded, collected by P. Humann with SCUBA, one portion of a colony originally fixed in 10% formalin and wet preserved in 75% ethanol. CAS 147486, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, 9 m depth, 19 June 2001, collected by C. Hickman with SCUBA, one portion of a colony wet preserved in 75% ethanol. CAS 147487, Ecuador, Galápagos Islands, Isla Fernandina, Punta Espinosa, 21 m depth, 21 June 2001, collected by C. Hickman with SCUBA, one portion of a colony wet preserved in 75% ethanol. CDRS 03–86 and 03–77, Ecuador, Galápagos Islands, Islas Los Hermanos, 9 m depth, 18 January 2003, collected by C. Hickman. CDRS 01–95, Ecuador, Galápagos Islands, Isla Pinzon, 9 m depth, 22 June 2001, collected by C. Hickman. CDRS 1994, Ecuador, Galápagos Islands, Isla Isabela, Punta Vincente Roca, 18 m depth, 3 May 1994, collected by C. Hickman. CDRS 1991, Ecuador, Galápagos Islands, Isla Fernandina, Punta Espinosa, depth not recorded, 24 June 1991, collected by C. Hickman.

GENERAL DESCRIPTION.— The lectotype was designated, examined, and described in detail by Breedy and Guzmán (2002: 808). Also included in their description was a specimen studied here (CAS 097035). We, therefore, provide only a brief descriptive account.

The colonies examined are up to 250 mm, dark purple, with yellow or white oval rings, and have open and evenly reticulated branching. Most colonies are composed of 2–3 parallel fans. The mesh branches are up to 1.5 mm in diameter. The network is composed of polygonal, oblong, or sometimes round meshes, up to 13 mm in length and 3 mm in width (approximately 7 meshes/cm^2). The stem is short, not exceeding 5 mm in height, without distinct midribs. The free terminal branchlets are blunt and up to 10 mm in length. The oval mounds resulting from the retracted polyps are generally flat, and form yellow, cream, or white rings around the apertures of the polyps. These protuberances are mostly arranged in two longitudinal rows along most of the branches, and in multiple rows (4 or 5) on the thicker branches. The polyps are white with yellowish to pale pink sclerites arranged in points. The coenenchymal sclerites are mostly purplish red, whereas some are yellow and a few are bicolored. They are blunt spindles or capstans up to 0.09 mm long by 0.05 mm wide, and spindles with acute ends to 0.10 long and 0.04 mm wide. The anthocodial sclerites are flattened pale yellow rods up to 0.12 long and 0.02 mm wide, with scalloped or lobed margins.

The specimen figured (CAS 097035) is a flat, kidney-shaped fan with reticulations even and open throughout, 185 mm wide by 122 mm high (Fig. 5A). The network is composed of mostly rounded rectangular meshes (2–5 mm in diameter) to irregularly-shaped elongated ones (8–15 mm long by 1–4 mm wide) (Fig. 5B). The basal stem is very short, 5 mm in length. The retracted polyps form low rounded mounds in two opposite longitudinal rows along each face of the colony. The coenenchyme is dark reddish-purple, whereas the polyps mounds are mostly yellow (Fig. 5). Sclerites are mostly reddish purple (Fig. 5C), some are yellow, and a few are bicolored (red and yellow). Coenenchymal sclerites are mostly elongated spindles, some with tapering or distinctly pointed ends, 0.09–0.11 long (Figs. 5C, 6E–O), and mostly blunt eight radiates, 0.06–0.08 mm in length (Fig. 7). Some radiates lack ornate sculpture (Fig. 6A–D). Anthocodial sclerites are flattened rod-like sclerites with scalloped margins, up to 0.12 mm long (Fig. 6K).

DISTRIBUTION.— Southern islands of the Galápagos Archipelago (south of the Equator),

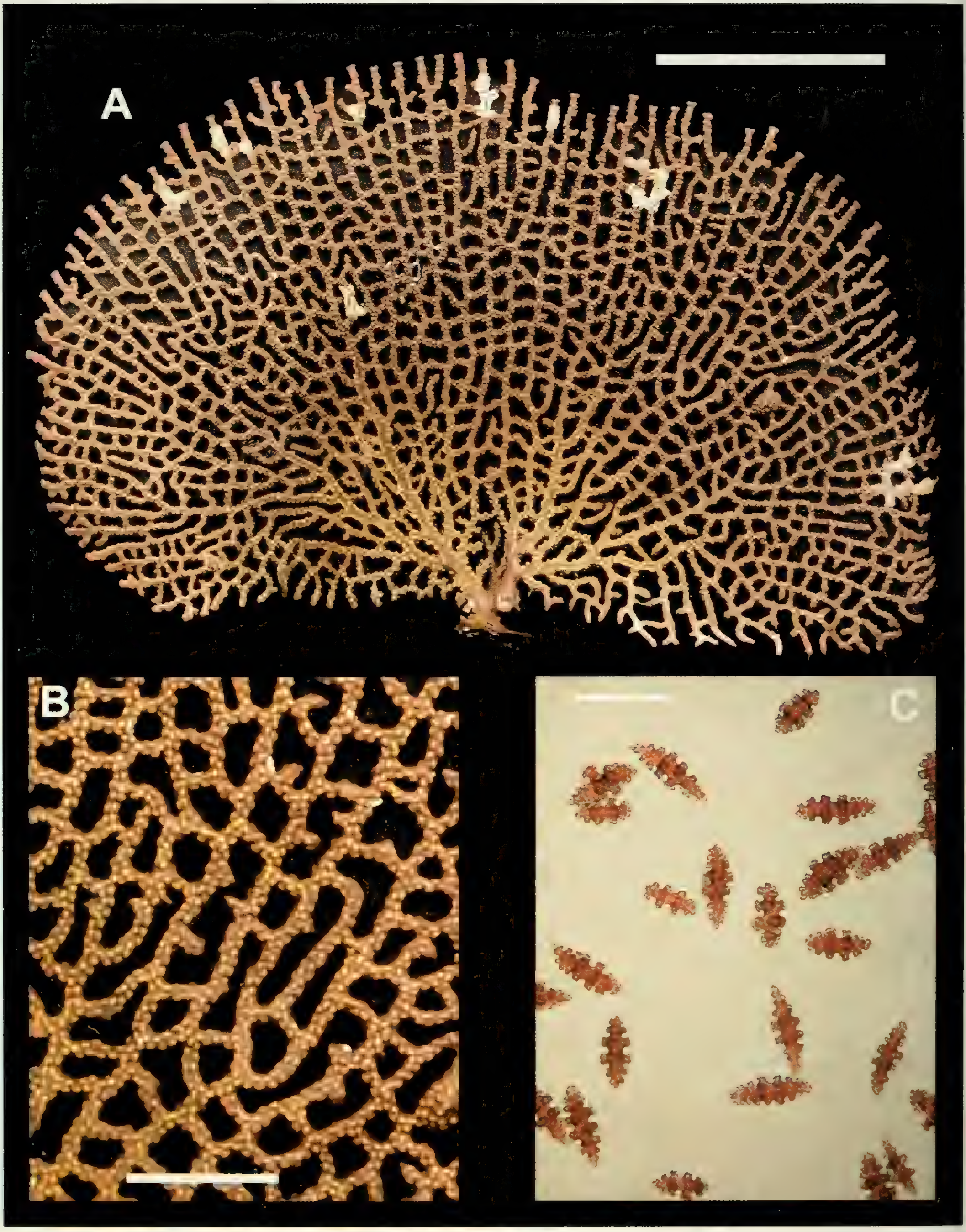

FIGURE 6. Non-type specimen of *Pacifigorgia darwinii* (CAS 097035) A. Whole colony, wet preserved; scale bar = 48 mm. B. Detail of branching pattern; scale bar = 13 mm. C. Micrograph of coenenchymal sclerites; scale bar = 0.15 mm.

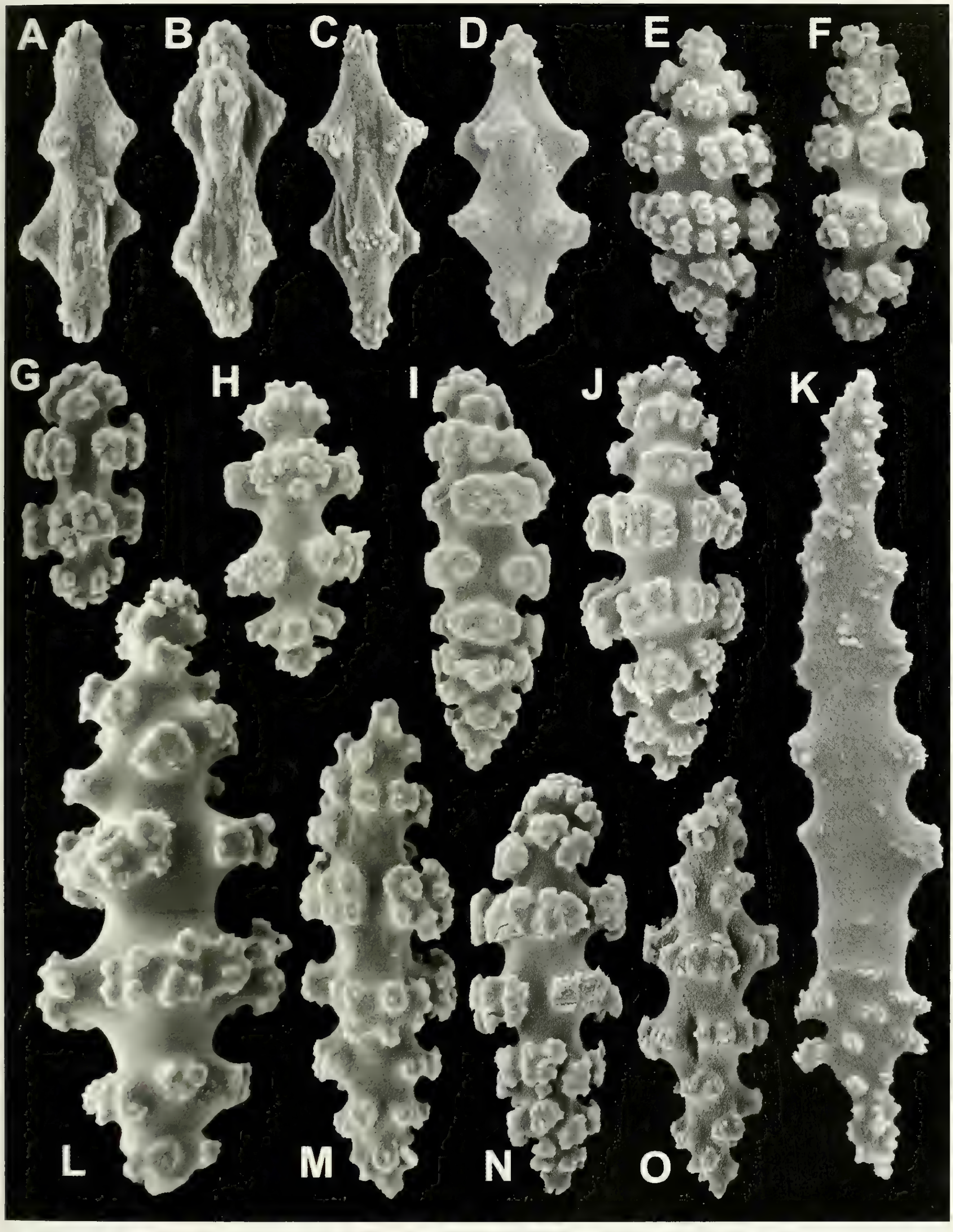

FIGURE 7. Non-type specimen of *Pacifigorgia darwinii* (CAS 097035). Scanning electron micrographs of sclerites from the tips of the ultimate branches. A. 0.06 mm. B. 0.04 mm. C. 0.06 mm. D. 0.07 mm. E. 0.09 mm. F. 0.09 mm. G. 0.05 mm. H. 0.06 mm. I. 0.10 mm. J. 0.10 mm. K. 0.12 mm. L. 0.10 mm. M. 0.10 mm. N. 0.10 mm. O. 0.11 mm.

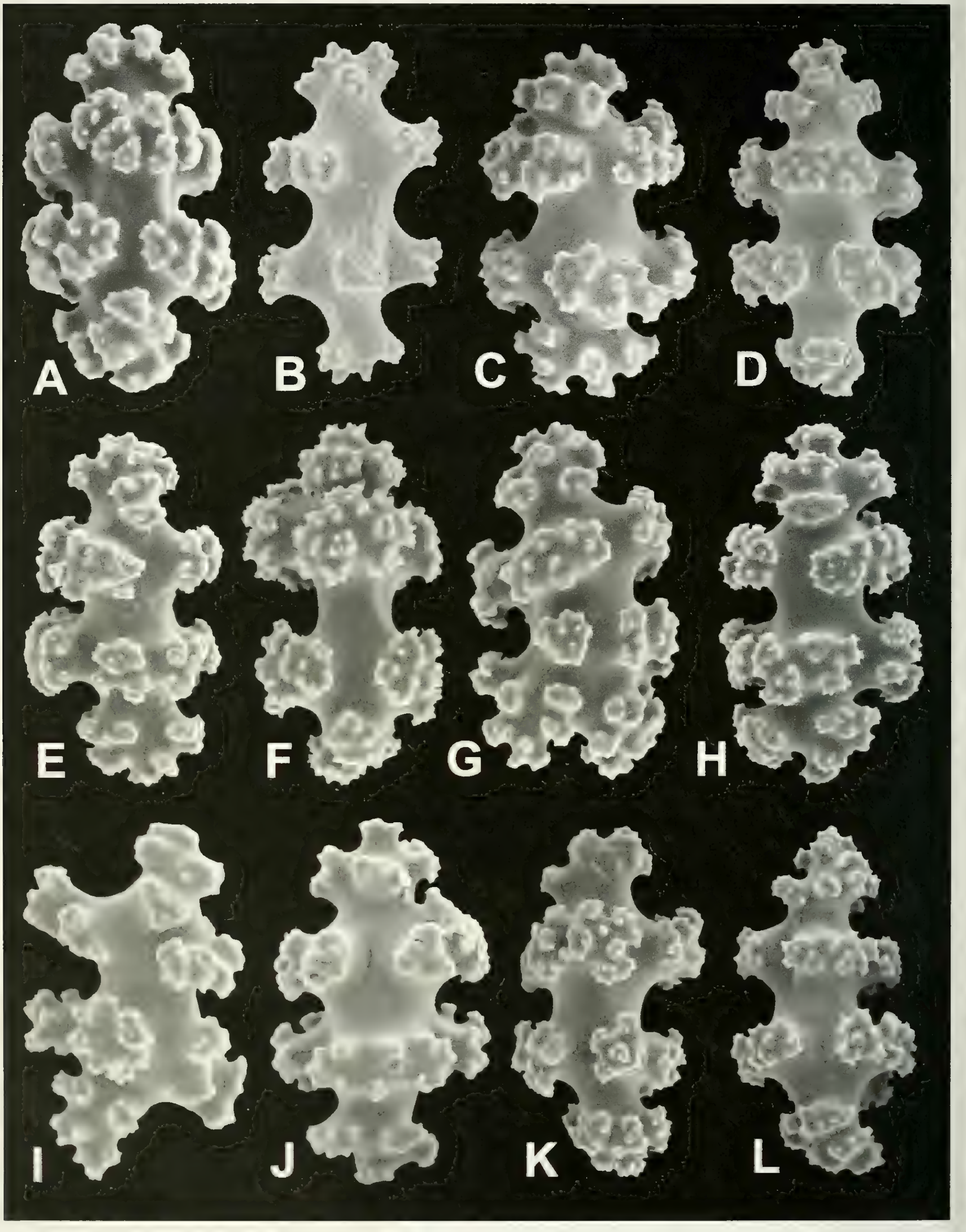

FIGURE 8. Non-type specimen of *Pacifigorgia darwinii* (CAS 097035). Scanning electron micrographs of sclerites from the holdfast. A. 0.06 mm. B. 0.06 mm. C. 0.06 mm. D. 0.08 mm. E. 0.07 mm. F. 0.06 mm. G. 0.07 mm. H. 0.07 mm. I. 0.06 mm. J. 0.06 mm. K. 0.07 mm. L. 0.07 mm.

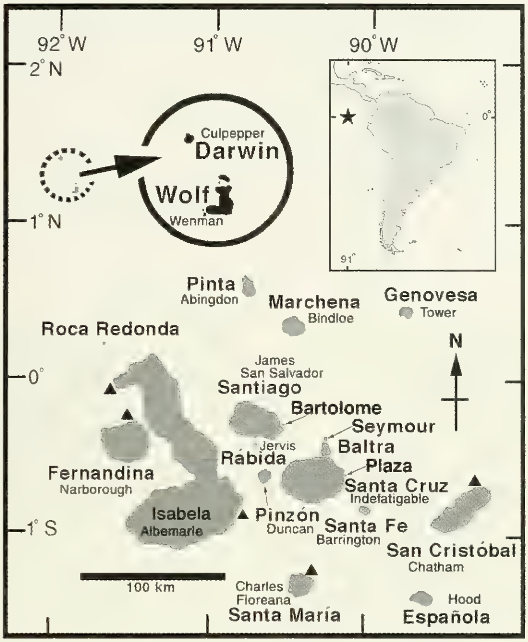

FIGURE 9. *Pacifigorgia darwini.* Map of geographic distribution; ▲ = collecting stations; ★ = location of Galápagos Islands.

including Isabela, Fernandina, Los Hermanos, Floreana, Gardner off Floreana or Gardner off Española (not specified), and San Cristobal; 3–26 m depth (Fig. 8). The presently known distribution forms a crescent-shaped arc from east to west in the southern part of the archipelago (Fig. 24).

REMARKS.— This species is the most common one of the genus around the islands. It is clearly distinct from the other taxa. We found some variation in the sclerites — there is a dominance of spindles with acute ends in some samples. This is the same situation with the other species found in Galápagos, which herein we describe. Also, the mound-like protuberances resulting from the retracted polyps varies from yellow to cream or white — San Cristobal (yellow, cream, or white); Isabela (cream or yellow); Fernandina (yellow); Floreana (white).

Pacifigorgia douglasii (Hickson, 1928)

(Figs. 10–11, 24)

Gorgonia darwinii var. *douglasii* Hickson, 1928:392–393.
Pacifigorgia douglasii (Hickson, 1928). Breedy and Guzmán, 2002:813–815.

PREFATORY NOTE.— Breedy and Guzman (2002:813) considered Hickson's *Gorgonia darwini* var. *douglasii* as a member of the genus *Pacifigorgia*, and raised the variation to specific status as a new combination. They believed the differences between *Pacifigorgia darwinii* and Hickson's taxon to be significant enough to justify raising the latter to species level. They designated the material cited below as lectotype. They also provided a description of the surviving material.

MATERIAL EXAMINED.— LECTOTYPE: BM 1961.2.6.161, 162, two microscope slides of sclerites only, Ecuador, Galápagos Islands, Isla Onslow, 8 m in depth, 1923–24, original material collected by Major Douglas.

DESCRIPTION.— See Breedy and Guzmán (2002:813–815) for a detailed description and evaluation. The sclerites are figured in the present paper (Fig. 10).

Distribution.— Reported from one locality, Onslow Island (off the north shore of Floreana), Galápagos Archipelago, 8 m depth, attached to a fishing line (Fig. 11).

Remarks.— We have not found a specimen of the colony that matches the lectotype sclerite preparation. These colonies appear to be missing and presumably all that remains of material representing this taxon are two microscope slides of sclerites.

We recently found in the NHM collection, a non-type specimen lot (BM 30.6.17.11) labeled as *Gorgonia darwinii* var. *douglasii*, containing three fragments of what we consider to be *Pacifigorgia darwinii*. One of the fragments represents the variety of *P. darwinii* with white rings, whereas the other two fragments are more representative of the typical form with yellow to cream

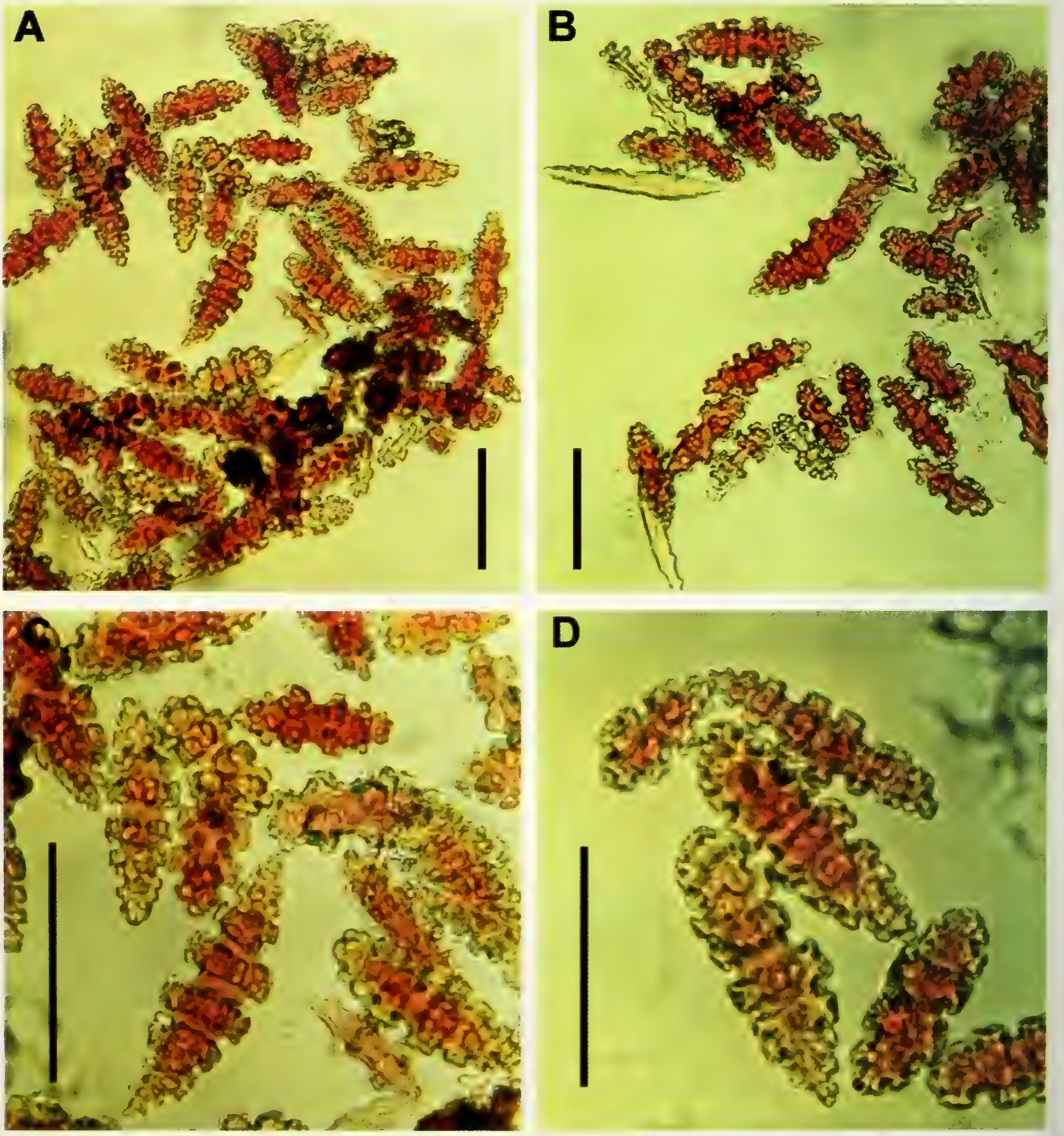

Figure 10. Type specimen of *Pacifigorgia douglasii*. A–D Micrographs of sclerites. Scale bars = 0.1 mm.

FIGURE 11. *Pacifigorgia douglasii.* Map of geographic distribution; ▲ = collecting stations; ★ = location of Galápagos Islands.

polyps mounds. Even though the morphology of the three fragments agrees in many respects to Hickson's description of *Gorgonia darwinii* var. *douglasii*, the sclerites are more consistent with those of *P. darwinii*. They differ in form and size from the sclerites on the lectotype slides (see the assessment of Breedy and Guzmán 2002). After examining many specimens, we conclude that the fragments can all be aligned with *P. darwinii*. There is not sufficient reason to separate the white-ringed variety from the typical form. It should therefore be viewed within the range of variability for the species.

Because of the depauperate nature of the type material, and the lack of any other specimen that matches Hickson's description, it is not possible to validate the taxonomic status of *Pacifigorgia douglasii*, and we must therefore consider this to be a dubious taxon. In addition, northern Floreana Island is also a collecting station for typical specimens of *Pacifigorgia darwinii* (Figs. 9, 24).

***Pacifigorgia rubripunctata* Williams and Breedy, sp. nov.**

(Figs. 12–16, 24)

MATERIAL EXAMINED.— HOLOTYPE: CAS 167958, Ecuador, Galápagos Islands, Isla Santa Cruz, Academy Bay, 3–6 m depth, 1964 (day and month not recorded), collected by Andre and Jacqueline De Roy. One whole wet specimen preserved in 75% ethanol. PARATYPE: CAS 147485, Ecuador, Galápagos Islands, Isla Rabida, 6 m depth, (Station 01–37), 17 June 2001, collected by Cleave Hickman. One whole specimen preserved in 75% ethanol.

OTHER MATERIAL: CAS 167959, same data as holotype, two dried fragments of colonies. CAS 053266, same data as holotype, one whole dried colony. CAS 101762, Ecuador, Galápagos Islands, Isla Española, Punta Suárez, 7.6 m depth, 4 March 1977, collected by John McCosker and party. Two whole wet specimens, originally preserved in formalin, later transferred to 75% ethanol. CAS 096904, Ecuador, Galápagos Islands, Isla Santiago, Sullivan Bay near Isla Bartolomé, depth not

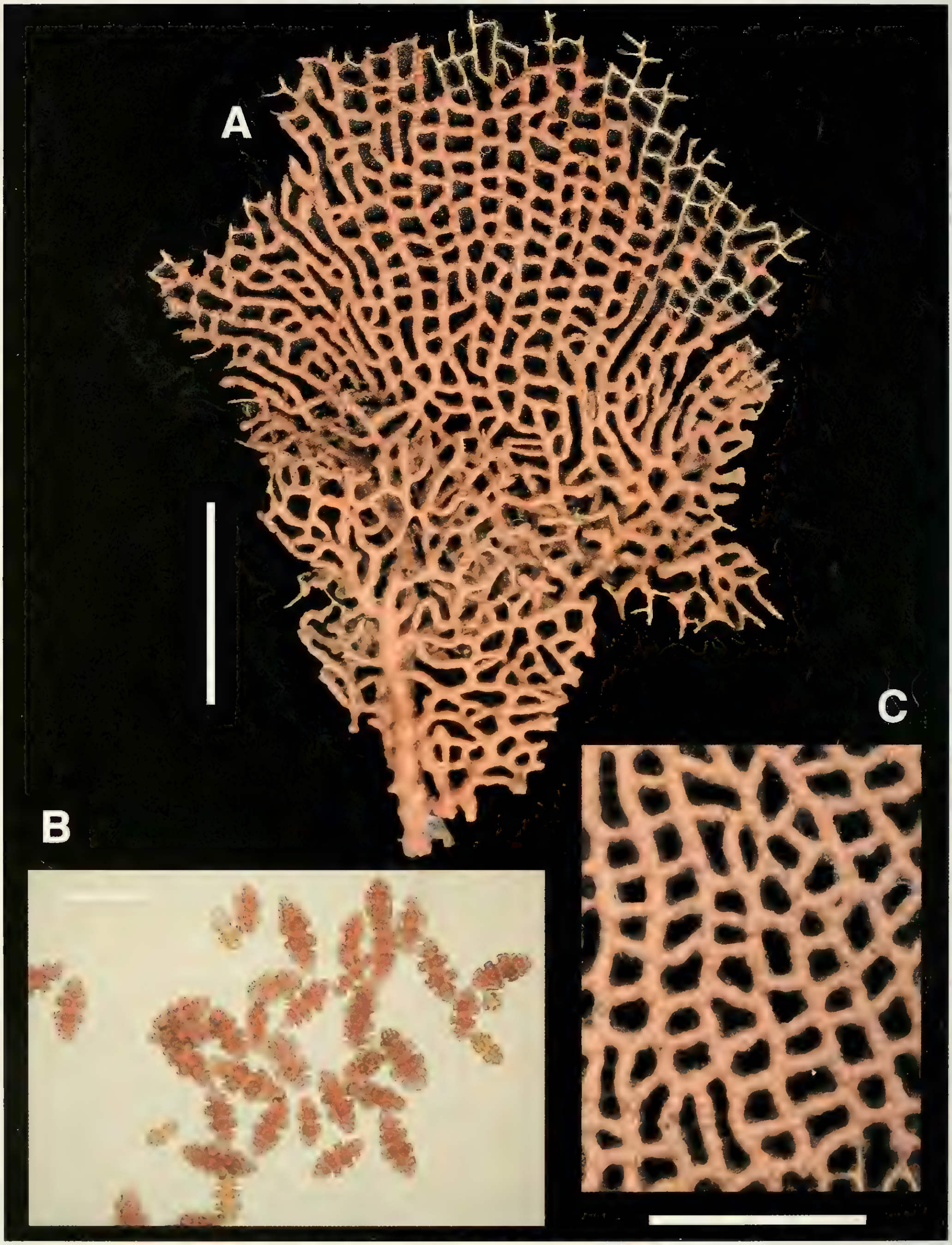

FIGURE 12. Holotype of *Pacifigorgia rubripunctata* sp. nov. A. Whole colony, wet-preserved; scale bar = 30 mm. B. Micrograph of coenenchymal sclerites; scale bar = 0.10 mm. C. Detail of branching pattern; scale bar = 20 mm.

recorded, 21 January 1938, collector not identified, one fragment of a colony wet preserved in 75% ethanol. CAS 147484, Ecuador, Galápagos Islands, Isla Rabida, 6 m depth, (Station 01–32), 17 June 2001, collected by Cleave Hickman. CAS 105033, Ecuador, Galápagos Islands, Nameless Islet off west coast of Isla Santa Cruz, 20 m depth, date not recorded, collected by Paul Humann, one whole specimen wet preserved in 75% ethanol. MCZ 36260 and MCZ 36262, Ecuador, Galápagos Islands, Isla Santa Cruz, Punta Astrada, 8–10 m depth, 1977, collected by S. Taylor.

GENERAL DESCRIPTION.— Colonies wider than high, up to 120 mm 9in height, and 150 mm in width, composed of a single primary fan and 2–3 smaller secondary fans. Secondary fans stick out from different parts of the main fan, and radiate in right angles, hence, they grow perpendicularly to the main fan. Colonies seem to have encrusting holdfasts. Color when dry is a light violet with red spots, which are sparsely or closely disposed, and bright reddish-orange polyp mounds. Wet preserved specimens are yellowish to white, spotted with red and purple, and polyp mounds reddish-orange, rarely yellowish.

Networks are regular and comprised of angular meshes. The meshes are up to 15 mm in length and 3 mm in width (density averages approximately 6 meshes/cm^2). Mesh branches up to 1.5 mm in diameter. No distinct midribs crossing the fans are observed, only thick short branches (up to 10 mm width) at the base. These extend for a short distance to one side of the fan, parallel to the substratum. Short stems raise the colony a little from the substratum. Terminal branchlets are short, up to 2 mm in length. Free twigs are very scarce. Polyp mounds are slightly raised, arranged in pairs in longitudinal rows, on the external part of the branches, and separated by branches of dark purple coenenchyme in the middle of the lines of polyps. Polyps are white with flattened anthocodial sclerites arranged in weak points.

Coenenchymal sclerites (Fig. 15) are mostly spindles with blunt ends, and radiates (capstans) with elongated ends, but a dominance of spindles with acute ends is also observed (e.g. CAS 105033). The sclerites are red, orange, and colorless with different predominance of colors, but some are bicolored. Spindles are long (up to 0.15 mm in length, and 0.04 mm in width) and with 4–8 whorls of tubercles, with both ends acute or blunt, or with one acute and the other blunt. Radiates (capstans) are wide (up to 0.09 mm in length, and 0.05 mm in width) with two whorls of tubercles and warty ends. A few crosses with acute or round ends (up to 0.09 long by 0.06 mm wide) are also present. Anthocodial sclerites are pale yellow rods (up to 0.10 mm in length, and 0.02 mm in width) with smooth or lobed margins (Fig. 15 shows all sclerites at the same scale).

DESCRIPTION OF HOLOTYPE.— Growth form and size (Fig. 12A, C). The holotype measures 120 mm in height by 94 mm in width. It is comprised of two similarly sized parallel fans that are joined by a common basal main stem. Only one of these fans can be seen in Fig. 12A. The main stem is flattened and measures 2 mm by 7 mm in transverse section. The holdfast portion is missing since the specimen was cut just above the holdfast to separate it from the substratum. The surviving portion of the main stem is approximately 40 mm in length and gives rise to an intricate and uniform network without conspicuous secondary branches. The networks are regular and comprised of meshes of variable shape. The meshes in the upper portion of one of the fans are mostly more or less square and arranged in longitudinal rows. Meshes of the upper portion of the other parallel fan vary from narrow and elongated to square or rectangular, and are not disposed in distinct rows. Meshes vary in size from 2 mm minimum width to 15 mm maximum length. The mesh branches are mostly 1.0–1.5 mm in width. The density of meshes varies from approximately 5–9 meshes/cm^2. The free tips of terminal branches are up to 5 mm in length.

Polyps (Fig. 12C): The polyp mounds formed by the retracted polyps are only slightly raised, often irregularly-shaped (deltoid to trapezoidal) as well as circular, with slit-like apertures. The mounds are distributed in four longitudinal rows (two rows on each face of a particular fan) along

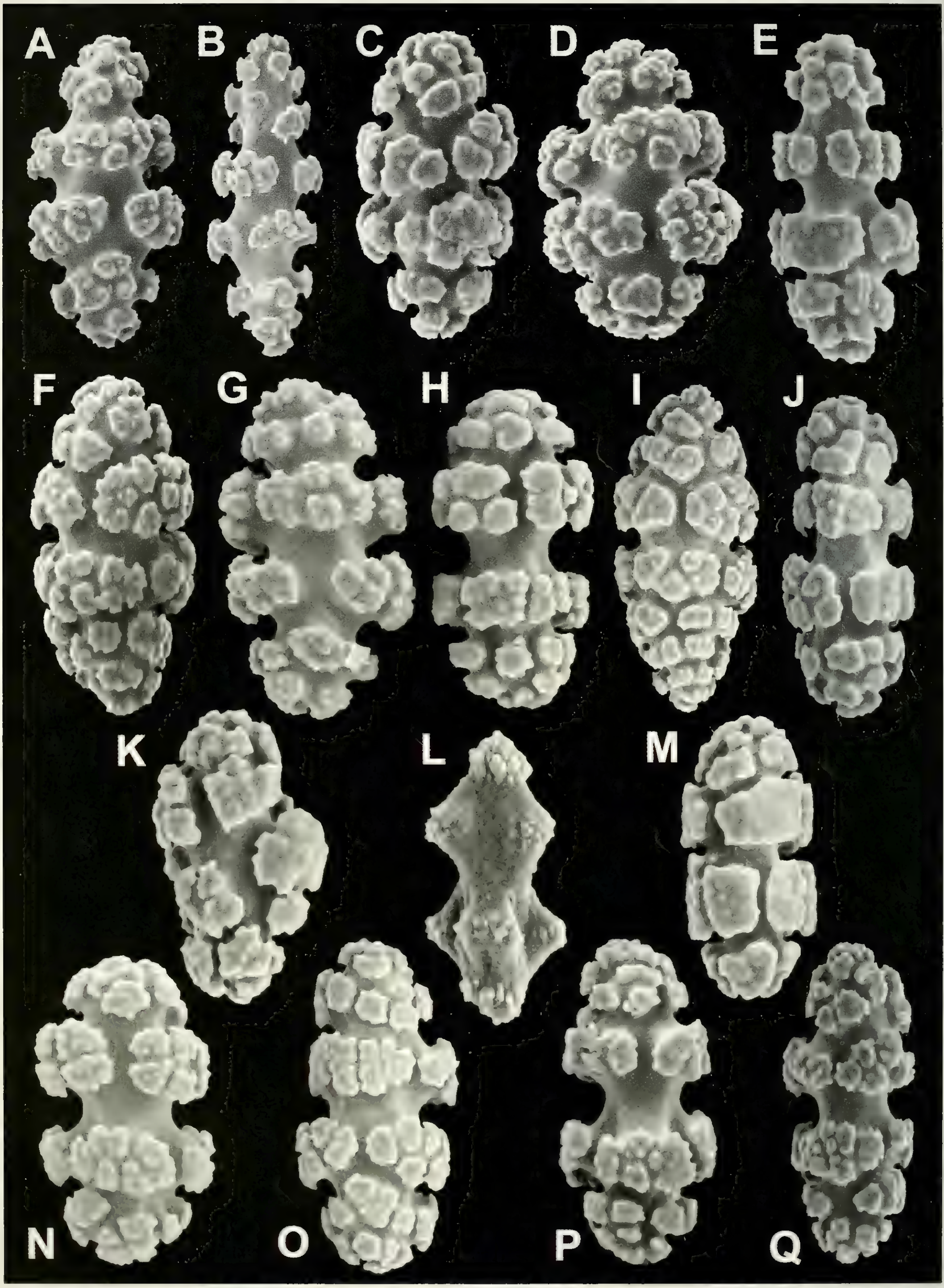

FIGURE 13. Holotype of *Pacifigorgia rubripunctata* sp. nov. Scanning electron micrographs of sclerites from the outermost branch tips. A. 0.08 mm. B. 0.09 mm. C. 0.06 mm. D 0.06 mm. E. 0.06 mm. F. 0.08 mm. G. 0.06 mm. H. 0.05 mm. I. 0.09 mm. J. 0.07 mm. K. 0.05 mm. L. 0.04 mm. M. 0.04 mm. N. 0.06 mm. O. 0.07 mm. P. 0.06 mm. Q. 0.08 mm.

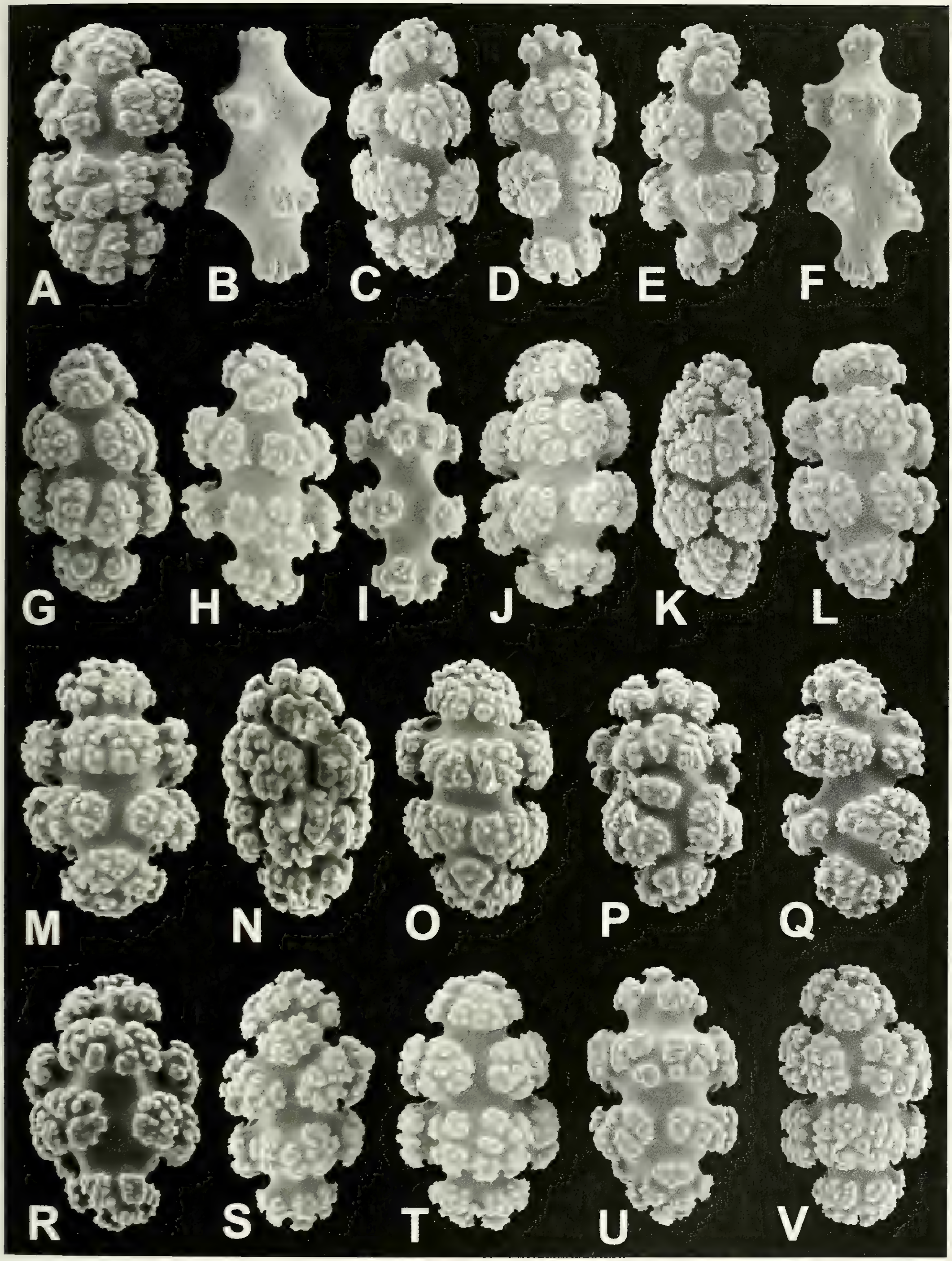

FIGURE 14. Holotype of *Pacifigorgia rubripunctata* sp. nov. Scanning electron micrographs of sclerites from the holdfast. A. 0.08 mm. B. 0.06 mm. C. 0.08 mm. D. 0.09 mm. E. 0.08 mm. F. 0.07 mm. G. 0.07 mm. H. 0.06 mm. I. 0.07 mm. J. 0.08 mm. K. 0.09 mm. L. 0.06 mm. M. 0.06 mm. N. 0.07 mm. O. 0.08 mm. P. 0.07 mm. Q. 0.08 mm. R. 0.07 mm. S. 0.08 mm. T. 0.07 mm. U. 0.08 mm. V. 0.09 mm.

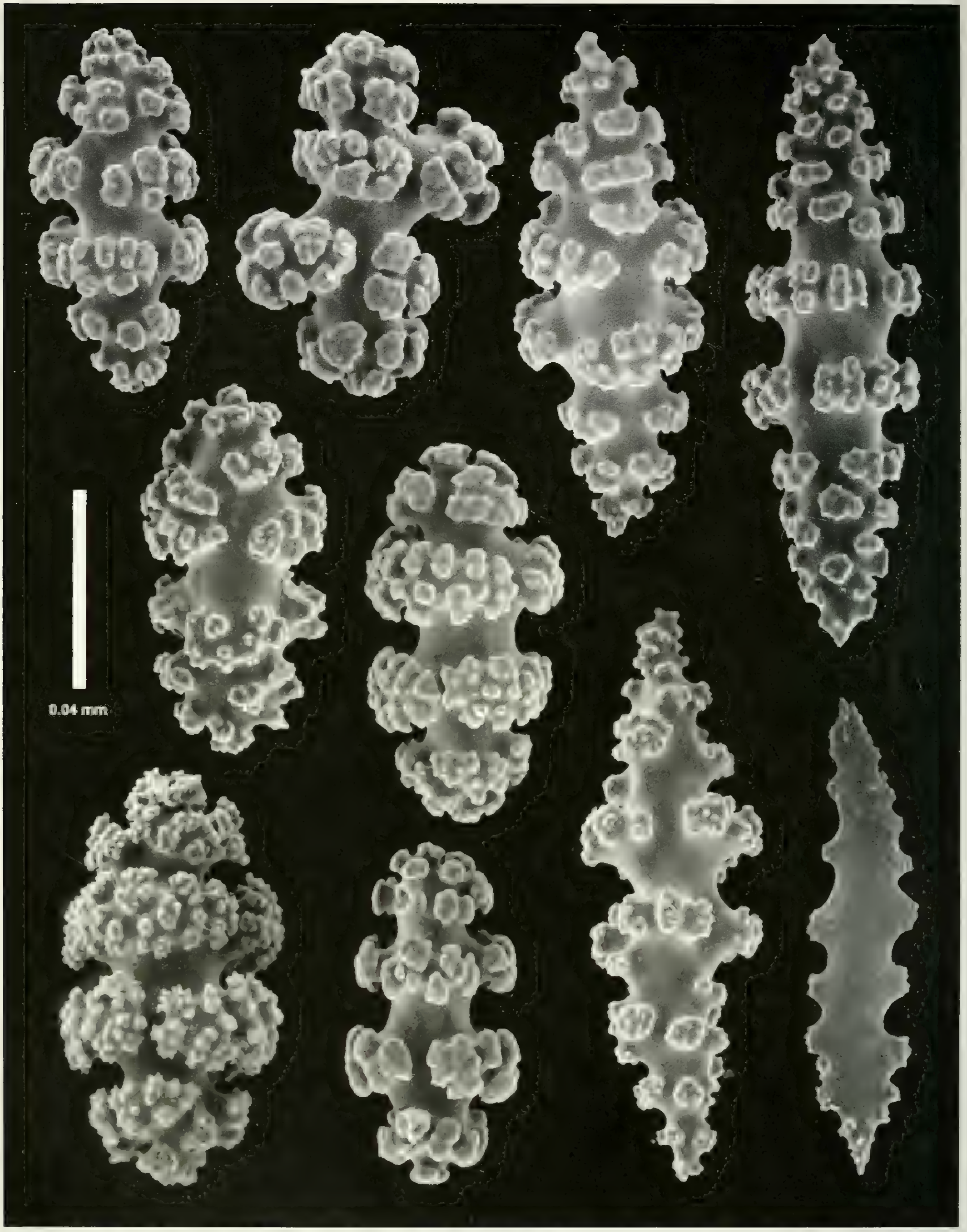

FIGURE 15. *Pacifigorgia rubripunctata* sp. nov. (CASIZ 147484). Scanning electron micrographs of sclerites shown at the same scale: scale bar = 0.40 mm.

FIGURE 16. *Pacifigorgia rubripunctata* sp. nov. Map of geographic distribution; ▲ = collecting stations; ★ = location of Galápagos Islands.

the mesh branches. Polyps have weak points sparsely disposed anthocodial sclerites that are elongated and flattened.

Sclerites (Figs. 12B, 13–15): Sclerites are red-purple, orange, or bicolored (orange at one end and colorless at the opposite end) (Fig. 12B). Coenenchymal sclerites are robust spindles or more elongated spindles with acute ends (0.08–0.11 mm long by 0.03–0.05 mm wide), and eight radiates (capstans) (0.04–0.08 mm long by 0.03–0.04 mm wide) (Figs. 13–14). A few cross-like sclerites are also present (approximately 0.08 mm long by 0.05 mm wide). Anthocodial sclerites are flattened rods with undulating margins (mostly $\leq$ 0.10 mm long).

Color (Fig. 12A, C): The coenenchyme throughout is a deep purplish red. The polyp mounds are orange, and contrast sharply with the surrounding coenenchyme. The polyps are white.

ETYMOLOGY.— The specific epithet of this new species is derived from the Latin *rubra* (red) and *punctatus* (spotted); in reference to the fine red-orange spots along the branches of most specimens, which are created by the retracted polyps.

DISTRIBUTION (Figs. 16, 24).— The range of this species is apparently restricted to a line extending from northwest to southeast, running through the center of the Galápagos Archipelago (Fig. 24); known from Islas Santiago, Bartolomé, Rábida, Santa Cruz, and Española (Fig. 16).

VARIATION.— A considerable amount of color variability is evident in this species. The coenenchyme varies from deep red or dark reddish purple to greyish-white, or yellow. The polyp mounds can vary from red to orange in most material, or pale yellow in one specimen (CAS 167959). The colors between the coenenchyme and the polyp mounds contrast sharply in all specimens.

***Pacifigorgia symbiotica* Williams and Breedy, sp. nov.**
(Figs. 17–24)

Material examined.— Holotype: CAS 097118, Ecuador, Galápagos Islands, Isla Darwin, Arch, 12–18 m depth, (Station G6), 13 May 1994, collected by Gary C. Williams with SCUBA, aboard "Mistral II". One whole wet specimen preserved in 75% ethanol. Paratype: CAS 097115, same data as holotype. One whole wet specimen preserved in 75% ethanol.

Other material: CAS 097041, same data as holotype. One whole wet specimen preserved in 75% ethanol. CAS 097948, Ecuador, Galápagos Islands, Isla Wolf, depth not recorded, 15 December 1898, collector not recorded, two dried fragments of colonies. CAS 097902, Ecuador, Galápagos Islands, Isla Wolf, 14 m depth, June 1993, collected by Paul Humann, one dried fragment of a colony.

General description.— Fans are stiff, planar or with smaller secondary fans. The main fans are wider than high (71–285 mm in width by 65–122 mm in height). Colonies have holdfasts that are strong and spreading (12–60 mm in maximum dimension). The main stem and primary branches are somewhat flattened and relatively wide (4–10 mm wide). This characteristic, along with the somewhat thickened mesh branches, gives the colonies a relatively rigid aspect.

The networks are intricate with open meshes. The meshes are highly variable in shape and size. They are often rectangular or deltoid, but very narrow and elongated ones as well as small circular ones are also evident. Meshes vary from 2–5 mm in width by 2–12 mm in length. Colonies usually have 6–8 meshes/cm^2. Mesh branches are relatively thick (1.5–2.5 mm in width). The thickened mesh branches make the meshes appear relatively small. The free terminal branchlets at the distal margin of the colonies are 2–8 mm in length, thick and blunt or truncated at the tips. The mound-like protuberances produced by the retracted polyps are relatively robust, hemispherical or mammiform, 1–2 mm in diameter, with ovoid or slit-like apertures. They cover most of the surface area of the mesh branches.

The coenenchymal sclerites are of two kinds. In the holdfast and main stem region, there is a predominance of relatively elongated eight radiates (0.06–0.08 mm long) with a relatively wide separation between the whorls of tubercles. In the mesh branches and the distal extremities of the colonies, the sclerites are girdled spindles, many of which have strongly attenuated ends (0.08–0.12 mm long); as well as compact, ovoid eight radiates (0.03–0.08 mm long). Some of the smaller radiates lack ornate tuberculation. The anthocodial sclerites are flattened, elongated rods with more or less scalloped or undulating margins (0.05–0.13 mm long). These are arranged in eight weakly disposed points. A crown is not apparent.

The color of the sclerites is mostly either dark red or bright yellow. However, some sclerites are bicolored — yellow and red. The superficial coenenchyme is deep reddish purple, whereas the polyp mounds are golden yellow to lemon yellow or orange-yellow. The polyps are white, with eight weak points of mostly yellow rod-like sclerites.

Description of holotype.— Growth form and size (Fig. 17A, C; 18). The holotype measures 98 mm high by 138 mm wide, composed of a single planar fan. An incipient secondary fan arises from near the distal terminus of the colony, and is parallel to it (22 mm high by 44 mm wide). The origin of this secondary fan is approximately 8 mm below the distal terminus of the main fan. The holdfast is spreading (23 mm wide by 28 mm long). The main stem is very short and flattened (approximately 6 mm long by 7 mm wide by 3 mm thick). This main stem gives rise to four primary branches, 12–18 mm long. An intricate network of mesh branches emanates from the distal regions of the primary branches. Networks are comprised of relatively small meshes with thickened mesh branches; approximately 6–8 meshes/cm^2. Meshes are highly variable and irregularly

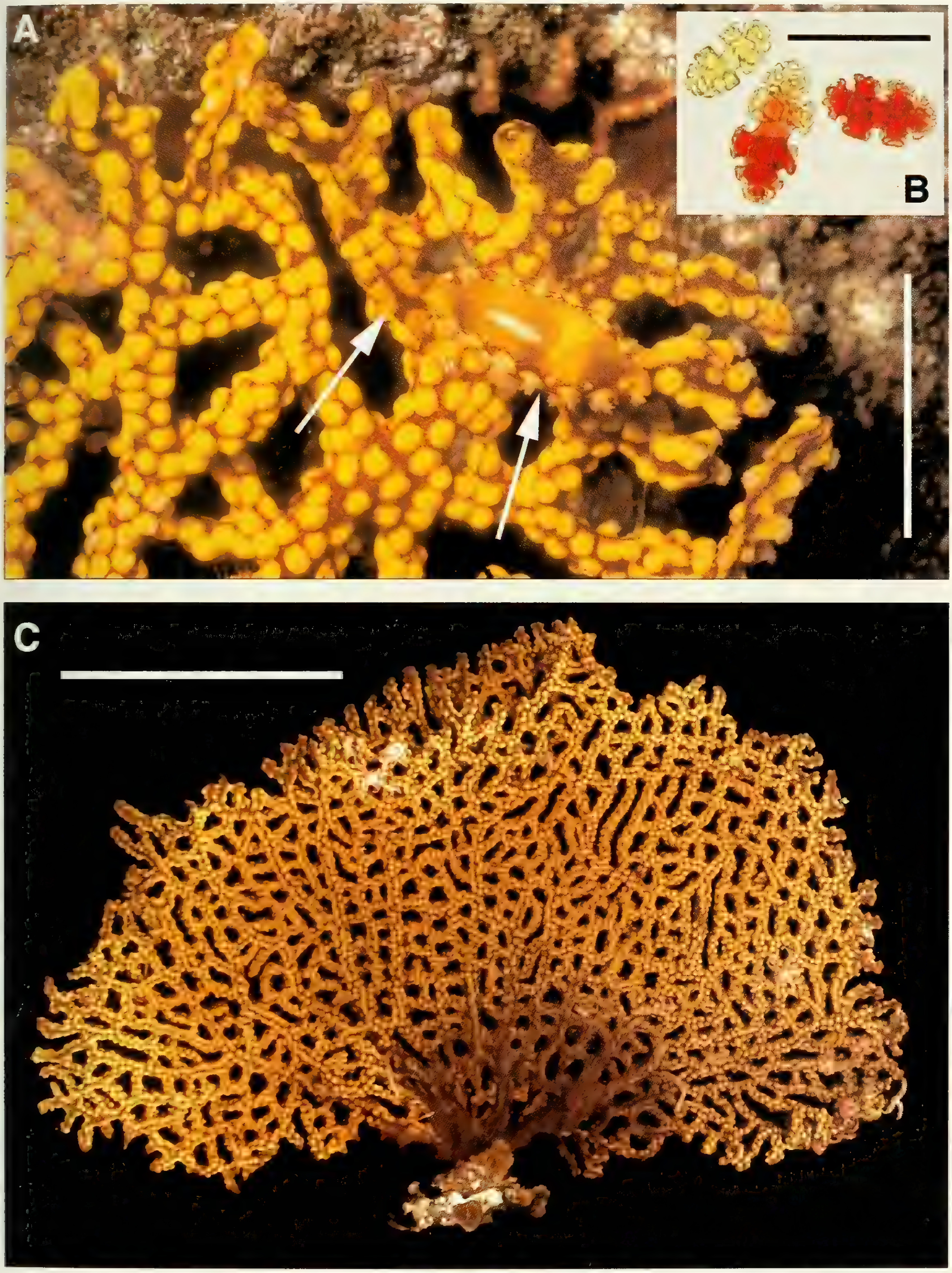

FIGURE 17. *Pacifigorgia symbiotica* sp. nov. A. Living coral with two epizoic mimics, a palaemonid shrimp (left arrow), and an ovulid gastropod (right arrow); scale bar = 10 mm. B. Three coenenchymal sclerites from the holotype showing variation in color; scale bar = 0.8 mm. C. Wet-preserved holotype; scale bar = 45 mm.

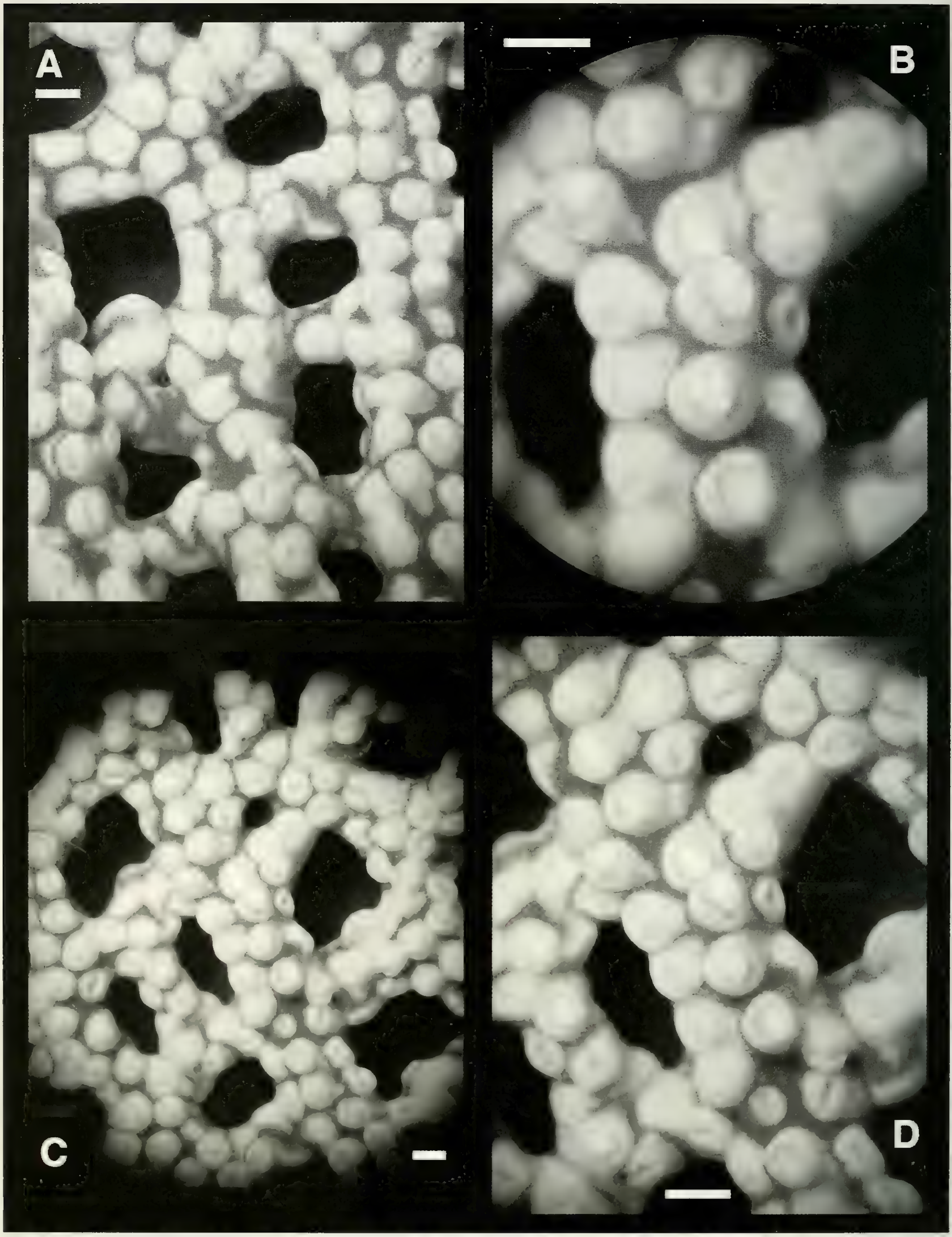

FIGURE 18. *Pacifigorgia symbiotica* sp. nov. A-D. Micrographs of colony external morphology from the preserved holotype - branching, reticulation, and retracted polyps. Scale bars = 1 mm.

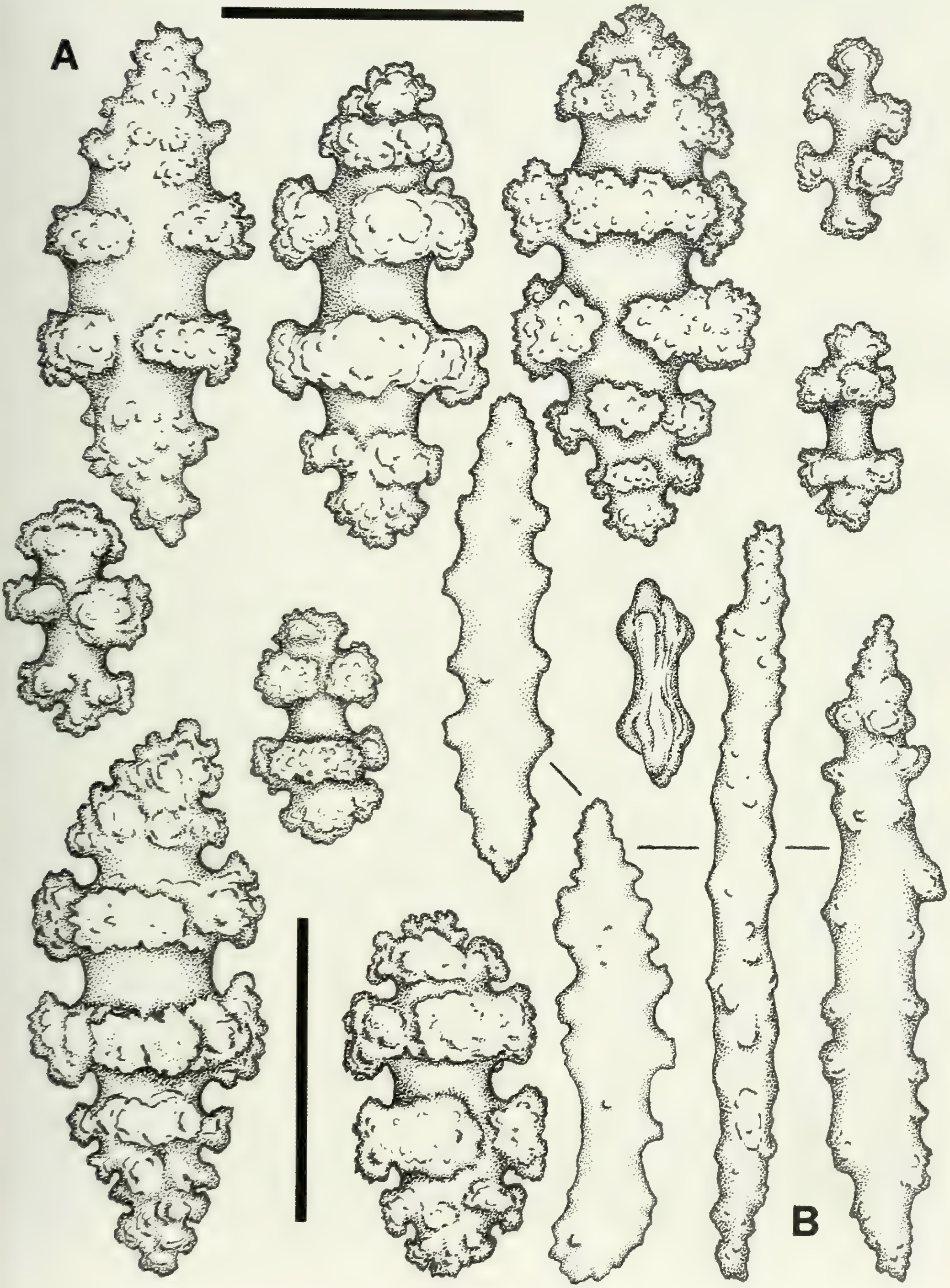

FIGURE 19. *Pacifigorgia symbiotica* sp. nov. A. Coenenchymal sclerites. B. Polyp sclerites. Scale bars = 0.05 mm.

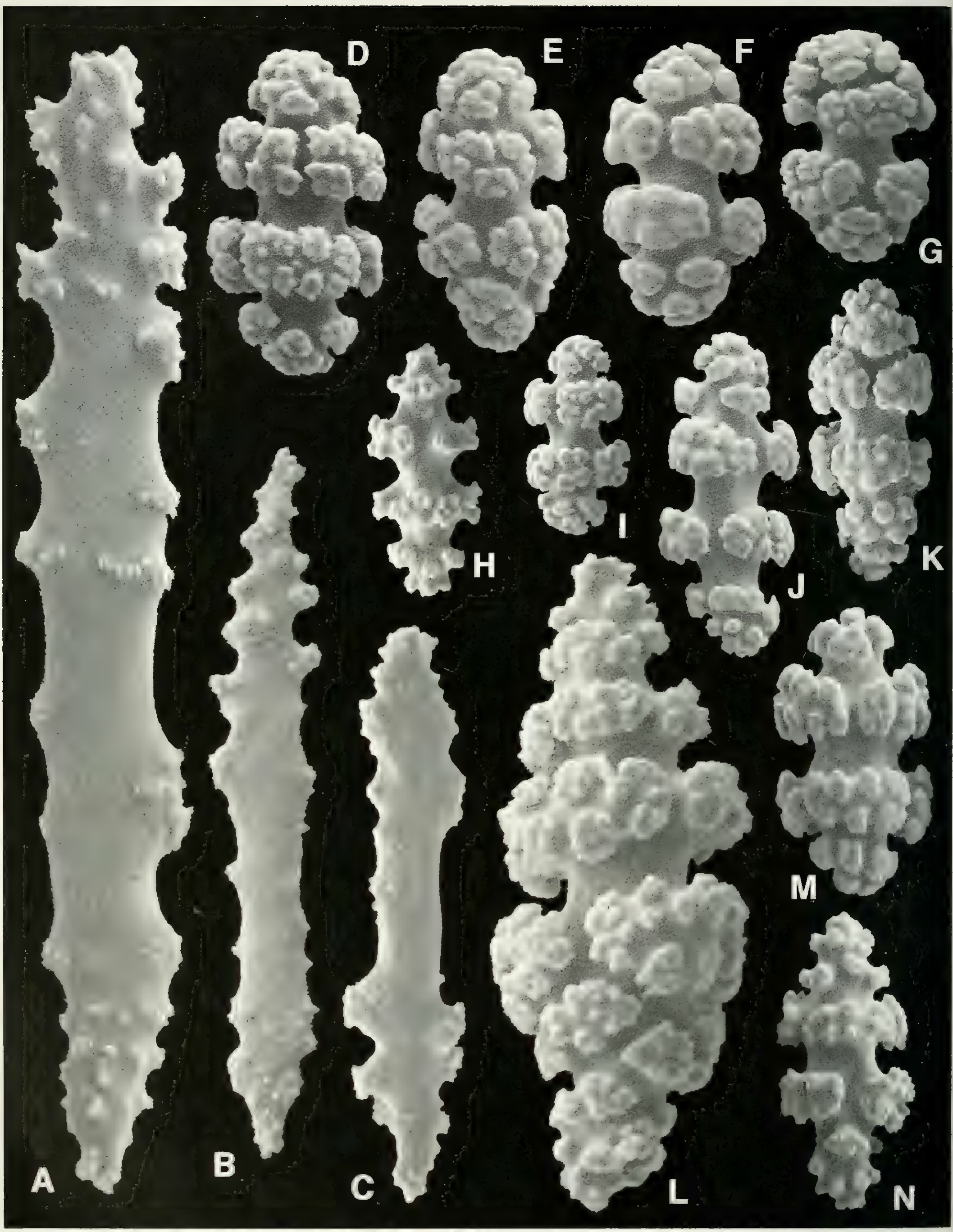

FIGURE 20. *Pacifigorgia symbiotica* sp. nov. Scanning electron micrographs of sclerites. A-C. Polyp sclerites. A. 0.14 mm. B. 0.12 mm. C. 0.10 mm. D-N. Coenenchymal sclerites. D. 0.06 mm. E. 0.06 mm. F. 0.06 mm. G. 0.05 mm. H. 0.06 mm. I. 0.06 mm. J. 0.09 mm. K. 0.08 mm. L. 0.10 mm. M. 0.07 mm. N. 0.08 mm.

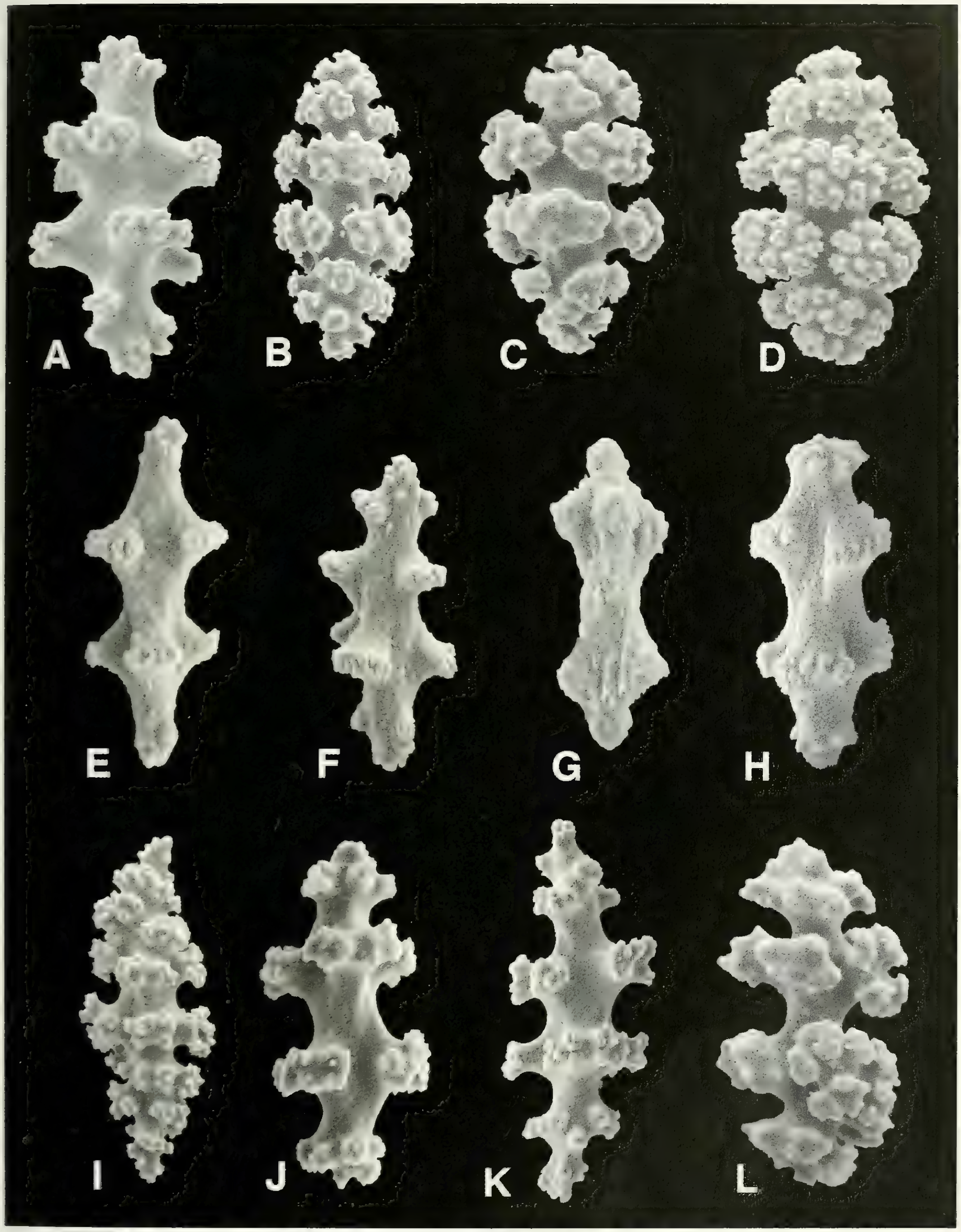

FIGURE 21. *Pacifigorgia symbiotica* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the branch tips. A. 0.07 mm. B. 0.08 mm. C. 0.07 mm. D. 0.07 mm. E. 0.06 mm. F. 0.06 mm. G. 0.03 mm. H. 0.05 mm. I. 0.12 mm. J. 0.06 mm. K. 0.11 mm. L. 0.06 mm.

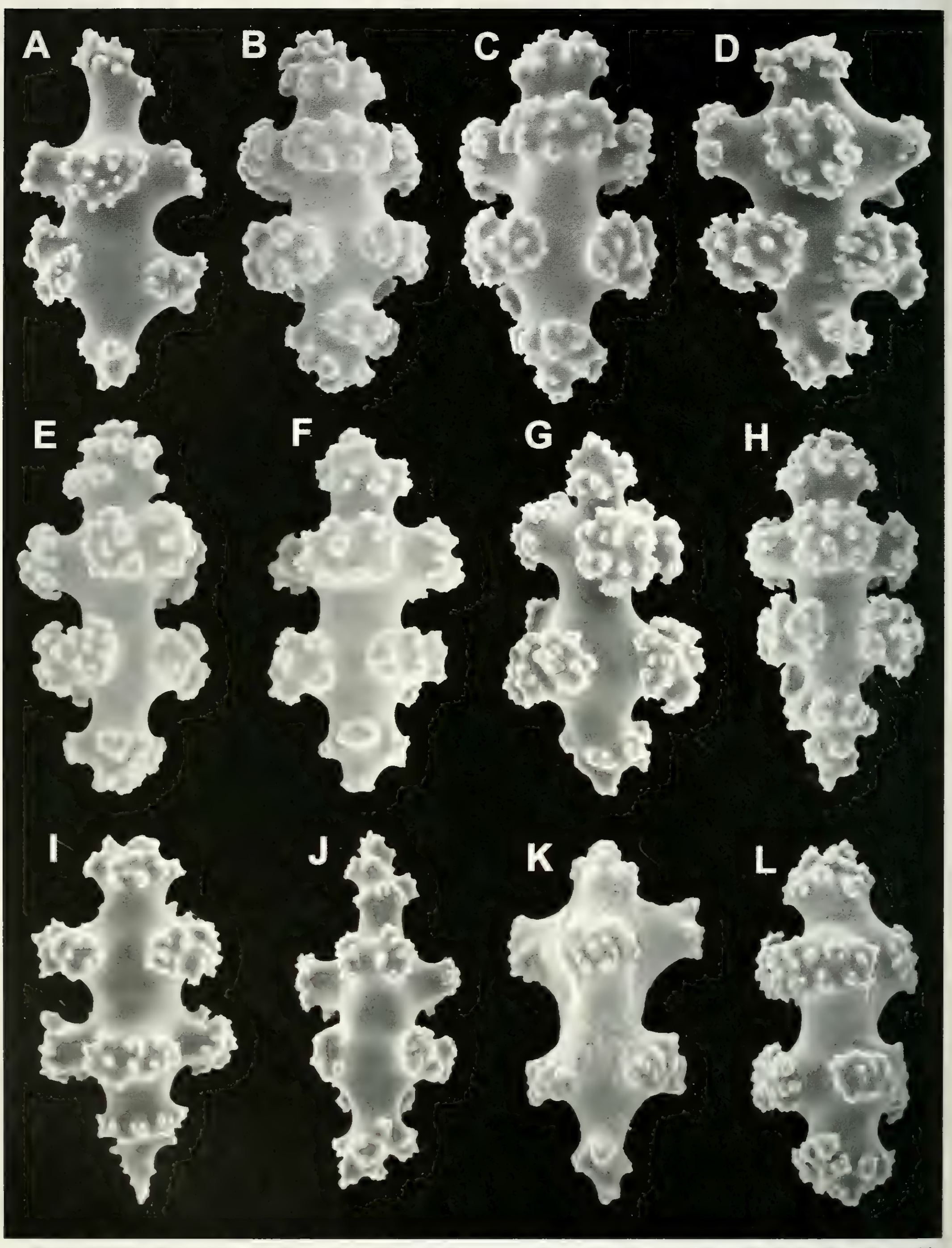

FIGURE 22. *Pacifigorgia symbiotica* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the holdfast. A. 0.06 mm. B. 0.08 mm. C. 0.07 mm. D. 0.06 mm. E. 0.07 mm. F. 0.07 mm. G. 0.06 mm. H. 0.07 mm. I. 0.07 mm. J. 0.08 mm. K. 0.06 mm. L. 0.07 mm.

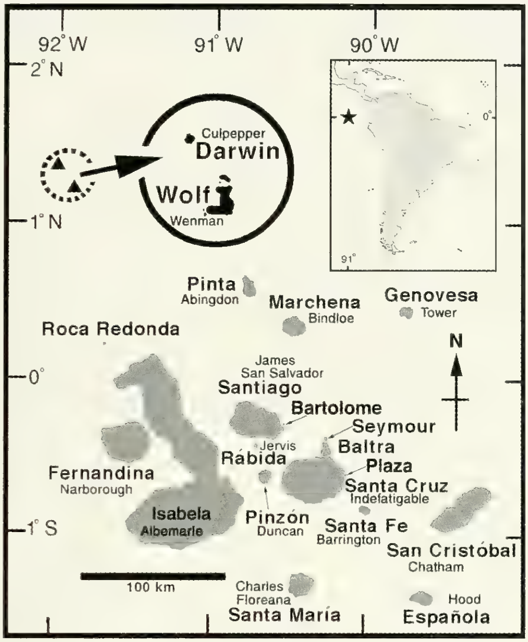

FIGURE 23. *Pacifigorgia symbiotica* sp. nov. Map of geographic distribution; ▲ = collecting stations; ★ = location of Galápagos Islands.

shaped: ovoid to rectangular (2–4 mm wide by 2–5 mm long), deltoid (1–2 mm wide by 3–4 mm long), or distinctly elongate (1–2 mm wide by 7–17 mm long). Mesh branches are relatively thick, mostly approximately 2 mm in diameter. Free terminal branches are thick and blunt with truncated tips, 3–8 mm long.

Polyps (Fig. 17A, 18). Polyp mounds are distinctive, mostly robust, hemispherical and mammiform, 0.8–1.0 mm in diameter, with ovoid or slit-like apertures. These are arranged in two longitudinal series along the mesh branches of each face of the fan. The polyps have eight weak points and no observable crown.

Sclerites (Figs. 17B, 19–22). The sclerites from the coenenchyme of the mesh branches and branch tips are girdled spindles, mostly wide in the middle with tapering and pointed ends (0.08–0.12 mm in length and 0.04–0.05 mm in width), as well as compact eight radiates (capstans) (0.05–0.08 mm long by 0.02–0.04 mm wide). Most of these are ornately tubercated (Fig. 20D–G). However, some are small (approximately 0.3 mm long) and are very sparsely ornamented (Fig. 21G). The sclerites of the holdfast region are radiates that are less compact, 0.06–0.08 mm in length (Fig. 22). Anthocodial sclerites are flattened rods with scalloped or undulating margins (0.08–0.11 mm long) (Figs. 19B, 20A–C).

Color (Fig. 17). The coenenchyme is a dark red-purple. Polyp mounds are bright yellow. The main stem and four primary branches do not contain polyps and are therefore deep reddish purple in color. Coenenchymal sclerites are red, yellow, or bicolored (red and yellow). Although anthocodial sclerites are mostly golden yellow, some are pale red.

ETYMOLOGY.— The specific epithet of this new species is derived from the Greek, *symbios* (living together); in reference to the remarkable mimicry and interactions of crustacean (caridean shrimp) and molluscan (ovulid snail) epizoites (Fig. 17A, arrows) that live on the surface of this new species of gorgonian coral.

DISTRIBUTION.— Apparently restricted to outlying Darwin and Wolf Islands, in the extreme northwestern fringe of the Galápagos Archipelago; 12–18 m in depth (Figs. 23–24).

DISCUSSION

The shallow-water (<50 m depth) gorgonian fauna of the Galápagos Islands is comprised of taxa in five genera of the two families Plexauridae (36% of the species) and Gorgoniidae (64% of the species). Of the eleven species that are considered valid, four of these (or 36%) belong to the genus *Pacifigorgia*. Marked morphological variability within each of the four species of *Pacifigorgia* is evident. Little is known of the geographic ranges of the various species, since only a limited number of collecting stations on a few islands have been sampled to date (Fig. 24).

TABLE 1. Species of *Pacifigorgia* considered valid.
(Type species: *Gorgonia stenobrochis* Valenciennes, 1846)

Species	Distribution
P. adamsii (Verrill, 1868)	Mexico to Panama
P. agassizii (Verrill, 1864)	Mexico to Panama
P. arenata (Valenciennes, 1846)	Mexico
P. bayeri Breedy, 2001	Costa Rica
P. cribrum (Valenciennes, 1846)	Mexico
P. dampieri sp. nov.	GalápagosIslands
P. darwinii (Hickson, 1928)	GalápagosIslands
P. elegans (Milne Edwards and Haime, 1857)	Trinidad to Brazil
P. engelmanni (Horn, 1860)	Mexico
P. exilis (Verrill, 1870)	Mexico to Panama
P. eximia (Verrill, 1868)	Costa Rica to Panama
P. gracilis (Kükenthal, 1924)	Mexico to Panama
P. irene Bayer, 1951	Costa Rica to Panama
P. media (Verrill, 1864)	Mexico to Nicaragua
P. pulchra (Verrill, 1870)	Mexico
P. rubinoffi Breedy and Guzman, 2003	Panama
P. rubripunctata sp. nov.	GalápagosIslands
P. rutila (Verrill, 1868)	Mexico
P. stenobrochis (Valenciennes, 1846)	Mexico to Peru
P. symbiotica sp. nov.	Galápagos Islands
P. tabogae (Hickson, 1928)	Panama

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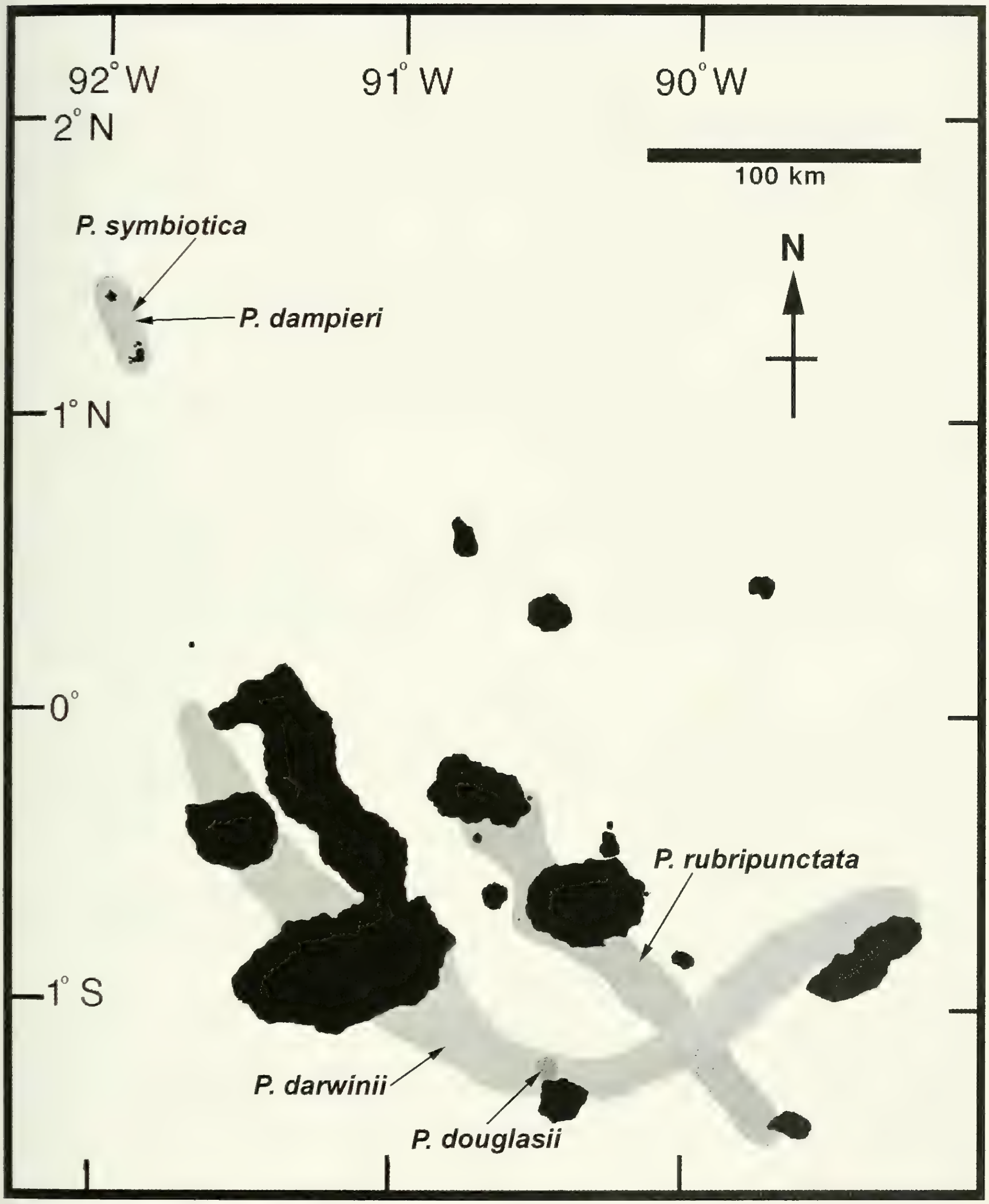

FIGURE 24. Range comparisons for the five species of the genus *Pacifigorgia* inhabiting the Galápagos Islands: *P. dampieri* sp. nov., *P. darwinii* (Hickson, 1928), *P. douglasii* (Hickson, 1928), *P. rubripunctata* sp. nov., and *P. symbiotica* sp. nov.

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Novelties and Nomenclatural Adjustments in the Neotropical Genus *Clidemia* (Melastomataceae: Miconieae)

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A new combination (*Clidemia quinquenervia* based on *Melastoma quinquenervium*) and 11 new species of *Clidemia* (*C. inopinata* from Mexico, Guatemala, and Honduras; *C. rodriguezii* from Costa Rica; *C. davidsei* from Costa Rica and Nicaragua; *C. allenii*, *C. coloradensis,* and *C. lanuginosa* from Costa Rica and Panama; *C. folsomii*, *C. pectinata*, *C. tenebrosa*, *and C. ventricosa* from Panama; and *C. evanescens* from Costa Rica, Panama, and Colombia) are proposed for the neotropical flora. Descriptions, diagnostic illustrations, distributional and phenological notes, and comparisons with probable relatives, are also provided together with a list of the species of *Clidemia* that have formicaria developed on the petioles, leaves, or at the branchlet nodes.

RESUMEN

Una nueva combinación (*Clidemia quinquenervia* basada en *Melastoma quinquenervium*) y once especies nuevas de *Clidemia* (*C. inopinata* de México, Guatemala, y Honduras; *C. rodriguezii* de Costa Rica; *C. davidsei* de Costa Rica y Nicaragua; *C. allenii*, *C. coloradensis,* y *C. lanuginosa* de Costa Rica y Panamá; *C. folsomii*, *C. pectinata*, *C. tenebrosa*, y *C. ventricosa* de Panamá; y *C. evanescens* de Costa Rica, Panamá, y Colombia) se proponen para la flora neotropical. Se proveen descripciónes, ilustraciones, notas sobre distribución y fenología, y discusiones sobre los afinidades entre las especies. Adémas se presenta una lista de las especies de *Clidemia* con formicarios desarrollados en los pecíolos, hojas, o en los nudos de las ramitas.

Clidemia D. Don, a berry-fruited genus of suffrutescent herbs or shrubs (rarely scandent or epiphytic) with over 180 species, ranges throughout tropical America. Among genera of the neotropical tribe Miconieae, *Clidemia* is closely related to and separated from *Miconia* only by the lateral or pseudolateral inflorescences. The Miconieae, as currently understood, consist of some 30 genera and over 1850 species. Because of its large size, definitive circumscription of the tribe and its constituent genera remain unresolved pending molecular data. This is also true of the current infrageneric classifications for the larger genera (i.e., *Clidemia, Ossaea* DC., *Leandra* Raddi, and *Miconia* Ruiz and Pavón). *Clidemia*, for example, has been divided into five sections based on characters such as floral merosity, occurrence of foliar dimorphism, production of formicaria, and persistence or dehiscence of calyx lobes following anthesis (Cogniaux 1888). The value of these characters in defining natural groupings is highly suspect but there are no published studies evaluating their taxonomic significance using modern techniques. Some of the sections of *Clidemia* have been accorded generic status in the past. Judd (1989) has recently resurrected one of these, *Sagraea*, for those species with truly axillary inflorescences and 4-merous flowers that lack an androecial fringe. He notes, however, that *Sagraea* has no apomorphic characters that can be used to distinguish it from other genera in the Miconieae. Judd (1989) has also proposed the genus *Pentossaea* W. Judd for seven species with axillary 5 (–6)-merous flowers and triangular apically acute petals. The diversity of Mesoamerican species attributable to *Clidemia* complicates the issue of recognizing generic segregates because there are species in the region with axillary inflorescences and 5-merous flowers that lack an androecial fringe (*C. davidsei* Almeda, *C. folsomii* Almeda, *C. mortoniana* Standl., *C. oblonga* Gleason, and *C. tenebrosa* Almeda); those with 4-merous flowers that have both axillary and pseudolateral inflorescences (*C. evanescens* Almeda); and those with 4-merous flowers, axillary inflorescences, and triangular apically acute petals [*C. sessiliflora* (Naudin) Cogn.]. Homoplasy and character reversals appear to have been recurrent themes in diversification of the Miconieae. Because of this and until other data can be brought to bear on the identification of monophyletic groups within the tribe, I see no defensible way of recognizing generic segregates or proposing new genera to accommodate the many character permutations exhibited by the diverse assemblage of taxa in this generic plexus.

In the course of preparing an account of the Melastomataceae for Flora Mesoamericana, I therefore have adopted a conservative approach. The 11 new species and one new combination proposed here have all been included in a broadly defined *Clidemia*. This approach is practical based on available information but it sheds little light on phylogenetic reality and underscores the considerable limitations in our current understanding of lineages within the Miconieae.

Clidemia was last treated for all of Mexico and Central America by Gleason (1939) who recognized 47 species for the region. Gleason's account was prepared before many areas in the region received any sustained systematic inventory of vascular plants. Many of the names used by Gleason are being relegated to synonymy and a few will be transferred to the genus *Miconia*. Including the taxa proposed here, I recognize 68 species of *Clidemia* in Mexico and Central America, 66 of which occur in the Mesoamerican region (i.e., Chiapas, Tabasco, and the Yucatan Peninsula south to the Panama/Colombia border). Fifty-five of the 66 Mesoamerican species occur in Costa Rica and Panama which, like *Miconia* (Almeda, 2000), makes these two countries the biodiversity stronghold for Mesoamerican species of *Clidemia*.

Species Descriptions

Clidemia allenii Almeda, sp. nov.

(Fig. 1)

Type.— Costa Rica: **Puntarenas**: Cantón de Osa. Golfo Dulce Area in the vicinity of Esquinas Experiment Station at sea level. 16 Apr. 1949. *P.H. Allen 5265* (holotype: CAS!; isotypes: AAU!, CR!, INB!, MEXU!, MO!, US!).

Ramuli teretes sicut petioli laminae subtus inflorescentia hypanthiaque pilis laevibus erectis dense vel modice armati et pilis stellatis modice vel sparse intermixtis. Lamina 6–23 × 4–10 cm elliptica apice acuminata vel attenuata basi rotundata et asymmetrica, 5–7-plinervata. Inflorescentia primum terminalis demum lateralis pauciramosa; flores 5-meri, bracteolis 1–6 × 0.25–0.5 mm, lobis interioribus 0.25 × 1.5 mm triangularibus vel late deltoideis, dentibus exterioribus setosis 2–4 mm eminentibus. Stamina isomorphica glabra, antherarum thecae 1.5–2 × 0.5 mm oblongae poro ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et ⅔ inferum apice glabro vel sparse setuloso.

Shrub or small tree 1.5–5 m tall. Internodes terete; upper branches, inflorescences, pedicels, hypanthia, and exterior calyx teeth moderately to copiously covered with smooth spreading hairs 1.5–3 mm long, sometimes underlain with a sparse to moderate understory of sessile stellate and stipitate-stellate hairs. Leaves of a pair ± equal to somewhat unequal in size; petioles 2–12 mm long; blades 6–23 × 4–10 cm, membranaceous, elliptic varying to elliptic-ovate, apex acuminate to attenuate, base oblique and mostly rounded, margin essentially entire and ciliate varying to obscurely denticulate distally, 5–7-plinerved with the innermost pair of primary veins diverging from the median vein 0.7–1.5 cm above the blade base, moderately covered adaxially with spreading simple hairs 1–2.5 mm long to nearly glabrous, moderately to sparingly covered abaxially with spreading simple hairs 1–3 mm long on the median vein and innermost primaries (especially toward the base) and sparsely underlain with deciduous sessile stellate and stipitate-stellate hairs varying to glabrate. Inflorescence 4–9 cm long, a pseudolateral modified dichasium sometimes divaricately branched from the base; bracts and bracteoles 1–6 × 0.25–0.5 mm, subulate to narrowly triangular, sparingly beset with smooth spreading hairs. Pedicels 0.5–1 mm long. Hypanthia (at anthesis), 4 mm long upward to the torus (vascular ring), cupulate to campanulate. Calyx tube 0.5 mm long, the calyx lobes 0.25 × 1.5 mm, ± rounded-triangular, hyaline and typically obscured by the copious indument; calyx teeth 5, 2–4 mm long, linear to subulate. Petals 5 in number, 4.5–5 × 1–2 mm, glabrous, pink or reportedly white in one population (*de Nevers 7207*), oblong to oblong-obovate. Stamens 10, isomorphic; filaments glabrous, 2–2.5 mm long; anthers 1.5–2 mm long, and 0.5 mm wide, yellow, linear-oblong, ± truncate at the apex with a ventrally inclined pore that is somewhat bent toward the dorsal side of the anther; connective conspicuously thickened dorsally and becoming dark when dry but neither prolonged nor modified. Ovary ⅔ inferior, 5-locular, apex elevated into a low ringlike collar with or without smooth hairs that surround the stylar scar. Style straight, 7 mm long, glabrous; stigma punctiform. Berry 5 × 5 mm, purple-black at maturity. Seeds 0.5 mm long, ± triangular in profile view, angulate and somewhat muriculate to papillate on the convex face.

PHENOLOGY.— Flowering material has been collected in February, April, and December; fruiting collections made in April, June, and December.

DISTRIBUTION.— An understory shrub or tree of primary forests in the Golfo Dulce region of southern Costa Rica from near Rincón on the Osa Peninsula east to vicinity of Chacarita with one known outlying population on the Santa Rita ridge in north-central Panama from sea level to 350m.

PARATYPES.— COSTA RICA: **Puntarenas**: Cantón de Osa. Bosque primario a la par de la Carretera Interamericana, 3 km. N de Chacarita, 08°59′00″N, 83°28′00″W, 28 June 1991, *Nepokroeff & Hammel 722* (CAS, CR, WIS); Cantón de Rancho Quemado, Fila Cantón de Osa. Bosque primario. Rincón, 8°46′N, 83°38′W, 7 Apr. 1990, *Quesada 591* (INB, MO); between Golfo dulce and Río Térraba, Dec. (w/out exact date) 1947, *Skutch 5394* (US). PANAMA: **Colón**: Santa Rita Ridge, Km 21.2, 9°20′N, 79°45′W, 24 Feb. 1986, *de Nevers 7207* (CAS).

DISCUSSION.— *Clidemia allenii* has basally oblique plinerved leaf blades (Fig. 1A); a prevailingly reddish indument of smooth spreading hairs on upper branches, leaf blades, inflorescences, hypanthia, and calyx teeth; hyaline calyx lobes; and a muriculate to papillate seed coat. It is variable in foliar size like other rain forest species of *Clidemia* and it also exhibits much variation in pubescence. All collections cited here have varying amounts of sessile-stellate or stipitate-stellate hairs as an understory on upper branches, petioles, primary elevated foliar veins, pedicels, and hypanthia. *Quesada 591* from Rincón on the Osa Peninsula of Costa Rica has nearly glabrous adaxial foliar surfaces and the indument of spreading hairs on abaxial leaf surfaces is also unusually sparse but the understory of stellate hairs on the elevated primary veins of abaxial foliar surfaces is especially dense. All other collections studied have a copious cover of spreading smooth hairs with a much sparser understory of stellate hairs. The single cited collection from Panama is reportedly a tree to 5 m with white flowers whereas the other Costa Rican collections are described as a shrub to nearly 3 m with pink flowers. In all other diagnostic features the collections from these

FIGURE 1. *Clidemia allenii* Almeda. A. habit. × ¼; B. representative leaf (abaxial surface). × ⅘; C. flower (at anthesis), × 5; D. petal (adaxial surface). × 5; E. stamen (profile view). × 12; F. mature berry. × 4; G. seeds. × 20. (A–F from the holotype.)

two countries are a close match and clearly conspecific.

Among congeners in Central America, *C. allenii* resembles *C. costaricensis* Cogn. & Gleason and *C. petiolaris* (Schltdl. & Cham.) Schltdl. ex Triana. All three species have pseudolateral inflorescences that are not paired at a node, a copious indument of smooth spreading hairs, unappendaged anther connectives, and a 5-locular ovary. In *C. costaricensis*, however, the mature leaf blades are not oblique at the base, the anther pores are dorsally (vs. ventrally) inclined, the ovary is completely inferior (vs. ⅔-inferior), and the seed coat is smooth. The widespread *C. petiolaris* differs from *C. allenii* in having (3–) 5-nerved (vs. 5–7-plinerved) leaf blades, an understory indument of sparsely and caducously appressed to incurved glandular hairs (vs. stellate hairs), petals that are consistently white, and anther connectives that are prolonged 0.25 mm dorso-basally.

ETYMOLOGY— This species is named for the late Paul H. Allen (1911–1963) who devoted a lifetime to the study of tropical American plants. Allen is best known for his pioneering book, The Rain Forests of Golfo Dulce (Allen 1956), which describes the region in southern Costa Rica where he collected the type of this species.

***Clidemia coloradensis* Almeda, sp. nov.**

(Fig. 2)

TYPE.— COSTA RICA: **Limón**: Almirante. Cerro Chiqui. Subiendo desde la base por el flanco norte, 09°43′40″N, 83°18′30″W, 1700 m, 18 Aug. 1995, *G. Herrera & W. Gamboa 8591* (holotype: CAS!, isotype: CR).

Ramuli teretes sicut foliorum venae primariae subtus inflorescentiaque dense strigosi pilis lavibus ca. 1–3 mm longis et dense persistenterque lanuginosa pilis gracillimis longis laxis intermixtis. Lamina 10–20 × 3.1–8.6 cm elliptica vel elliptico-ovata vel elliptico-oblonga apice acuta vel acuminata basi rotundato-obtusa vel subcordata, 5–7-nervata vel 5–7-plinervata. Inflorescentia primum terminalis demum lateralis; flores 5-meri, bracteolis 0.5–1 × 0.25–1 mm, lobis interioribus 0.75–1 × 1 mm orbicularibus, dentibus exterioribus subulatis 0.5–1.5 mm eminentibus. Stamina isomorphica glabra, antherarum thecae 1.5–2 × 0.5 mm oblongae poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5–loculare et omnino inferum apice glabro.

Monopodial shrub to 1 m tall. Internodes terete, the uppermost branches, inflorescence rachis and elevated primary veins on abaxial leaf surfaces copiously covered with smooth appressed tan or white hairs 1–3 mm long intermixed with or replaced by a lanate indument of dense woolly hairs. Leaves of a pair ± equal or slightly unequal in size; petioles 0.4–0.9 cm long; blades 10–20 × 3.1–8.6 cm, subcoriaceous and ± brittle when dry, elliptic to elliptic-ovate varying to elliptic-oblong, apex acute to acuminate, base obtuse to rounded or subcordate, margin ciliate, entire to inconspicuously crenulate, 5–7-nerved or if –plinerved then the innermost pair of primary veins diverging from the median vein 0.4–1.4 cm above the blade base, glabrous adaxially, the abaxial secondary veins sparsely to moderately covered with wrinkled woolly hairs mostly 0.5–1 mm long that are essentially replaced by minute glandular hairs on the actual surface. Inflorescence 3–12 cm long, a terminal pedunculate modified dichasium (sometimes appearing umbelliform) becoming pseudolateral with elongation of lateral branches; bracteoles 0.5–1 × 0.25–1 mm, triangular to triangular-ovate, apiculate and tipped with a trichome, ± concave on the adaxial surface. Pedicels (at anthesis) 0.5–1 mm long. Hypanthia 2.5 × 1.5 mm (at anthesis) campanulate but often becoming suburceolate and constricted apically into a short neck when in young fruit, moderately covered with minute ± appressed glandular hairs and a caducous mixture of lanate hairs about 0.25 mm long. Calyx tube obsolete, the calyx lobes 0.75–1 × 1 mm, semicircular to ± oblong, hyaline when dry but not obscured by the calyx teeth; calyx teeth 5 in number, 0.5–1.5 mm long, subulate to narrowly triangular, tipped with a smooth hair and sometimes with 1 to 3 other smooth appressed hairs on or at the base of each tooth. Petals 5 in number, 6–8 × 2–3 mm, glabrous, reportedly pink or magenta, oblong-obovate. Stamens 10, isomorphic; filaments 2 mm long, glabrous, linear-oblong;

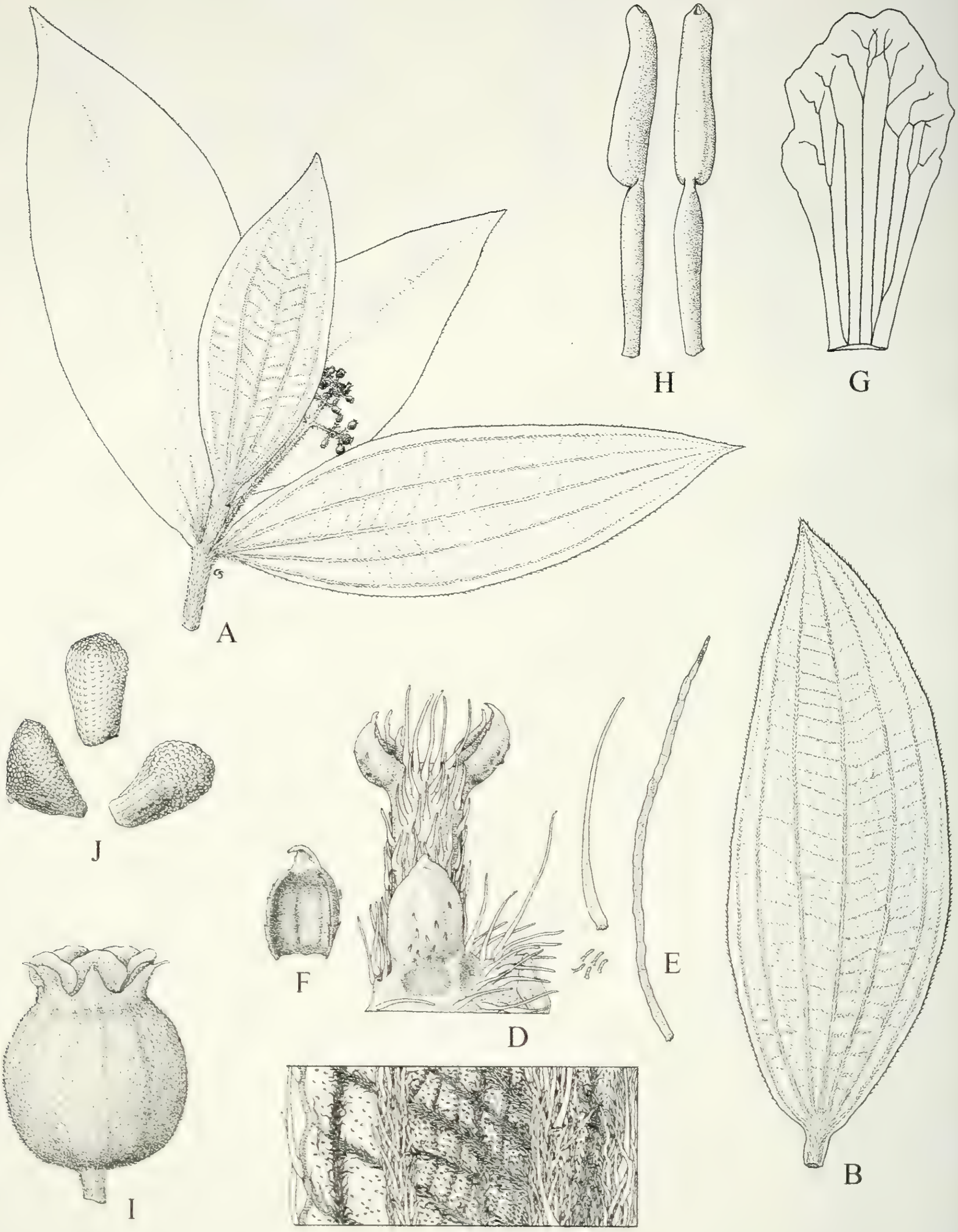


FIGURE 2. *Clidemia coloradensis* Almeda. A. habit, × ½; B. representative leaf (abaxial surface), × ½; C. enlargement of abaxial foliar surface, × ca. 3; D. portion of inflorescence rachis showing bracts and bracteoles, × ca. 12; E. smooth appressed hairs of abaxial leaf surface, × ca. 20; F. bracteole, × ca. 12; G. petal, × ca. 7; H. stamens, profile view (left) and dorsal view (right), × ca. 12; I. berry, × ca. 4; J. seeds, × 32. (A– F, I and J from *Almeda et al. 6437*; B from *Folsom & Collins 1814*; G and H from *Croat 37253*.)

anthers 1.5–2 × 0.5 mm, linear-oblong, yellow with a dorsally inclined apical pore; connective neither prolonged below the thecae nor appendaged. Ovary completely inferior, 5-locular, apex glabrous. Style 5–5.5 mm long, ± straight, glabrous; stigma capitate. Berry 5–8 × 6–7 mm when dry, turning pink then blue-purple when ripe. Seeds 0.5 mm long, ± triangular in profile view and ± obovoid in dorsal view, testa tuberculate.

Phenology.— Collected in flower during July and August, in fruit from January through April.

Distribution.— Locally common in primary cloud forests from southeastern Costa Rica to western Panama at 700–1700 m.

Paratypes.— Costa Rica: **Cartago**: Turrialba. Moravia. Cerro Tigre. Siguiendo por la quebrada innominada, bajando hasta Lago Ayil, 09°53′40″N, 83°22′55″W, 28 Mar. 1996, *Kuss 49* (CAS, CR). Panama. **Bocas del Toro**: Edwin Fabrega Dam and Reserve in Fortuna along the Continental Divide Trail, 12.9 km N of Sitio de Presa (Dam site) offices above the Dam, 08°45′04″N, 82°15′04″W, 7 Feb 1996, *Almeda et al. 7538* (CAS, PMA). **Bocas del Toro/Chiriquí border**: windswept cloud forest on slopes and valleys of the Cerro Colorado region, 27 Jan. 1989, *Almeda et al. 6437* (CAS, MO, PMA, US). Cerro Colorado, 11.2 km along ridge road from main road to Escopeta, 16 Aug. 1977, *Folsom 4879* (MO). **Chiriquí**: Cerro Colorado, along road to copper mine, 34.1 km beyond bridge over Río San Felix near town of San Felix, 15 July 1976, *Croat 37253* (CAS); Cerro Colorado top, Bocas Road, 17–18 Feb. 1977, *Folsom & Collins 1814* (CAS); between Pinolz and Divide on Chiriquí side. Caldera Trail, mostly mossy forest above the oak forest, 19 Apr. 1961, *Kirkbride & Duke 860A* (MO); between Quebrada Hondo and divide on Caldera Trail, 20 Apr. 1968, *Kirkbride & Duke 954* (MO, 2 sheets).

Discussion.— The slender or little-branched habit of *Clidemia coloradensis* and its deep forest habitat are typical of many formicarial species of this genus in the Mesoamerican region. *Clidemia coloradensis*, however, never appears to produce formicaria (ant domatia) of any kind. This species appears to flower during the rainy season which may account for the fact that few good flowering collections have been available for study.

Clidemia coloradensis is readily recognized by a distinctive combination of characters. The indument on upper internodes, the inflorescence axis, and elevated veins on abaxial foliar surfaces consists of smooth appressed hairs (1–3 mm long) intermixed with densely matted woolly hairs. The inflorescence is a long-pedunculate modified cluster of dichasia with ultimate units that often appear umbelliform. The calyx teeth are shorter than or only slightly exceeding the calyx lobes (Fig. 2I), the anther pores are dorsally inclined (Fig. 2H), the stigma is capitate, and the seed coat is tuberculate (Fig. 2J). The apiculate bracteoles that are concave on the adaxial side are also distinctive (Fig. 2F). Because of its distinctiveness, no close relatives in any part of the American tropics are evident at this time.

Etymology.—The specific epithet is derived from Cerro Colorado in western Panama where most of the fertile material of this species has been collected.

Clidemia davidsei Almeda, sp. nov.

(Fig. 3)

Type.— Costa Rica: **Puntarenas**: Cordillera de Talamanca; area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier; elev. 1500–1600 m, 9°02′N, 82°59′W, 6 Sep. 1984, *G. Davidse et al. 28374* (holotype: CAS!, isotypes: BM, CR, MO, PMA).

Ramuli teretes sicut petioli foliorum venae primarieae subtus inflorescentia hypanthiaque dense vel modice setosi (pilis 0.5–1 mm longis pro parte glanduliferis) et sparse cum pilis stellatis obsiti. Lamina 6.5–16.5 × 3–8.5 cm ovata vel elliptico-ovata apice acuminata basi rotundata vel obtusa, 5–7-plinervata. Inflorescentiae pauciflorae in foliorum superiorum axillis oppositis; flores 5-meri, bracteolis 0.5–1.5 × 0.25–0.5 mm; calycis tubus 0–0.25 mm, lobis 1.5–2 × 0.5 mm subulatis, dentibus exterioribus obsoletis. Stamina isomorphica glabra, antherarum thecae 1 × 0.4 mm oblongae poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et omnino inferum apicem versus sparsiuscule glandulis vel paullulo stellatis armatum.

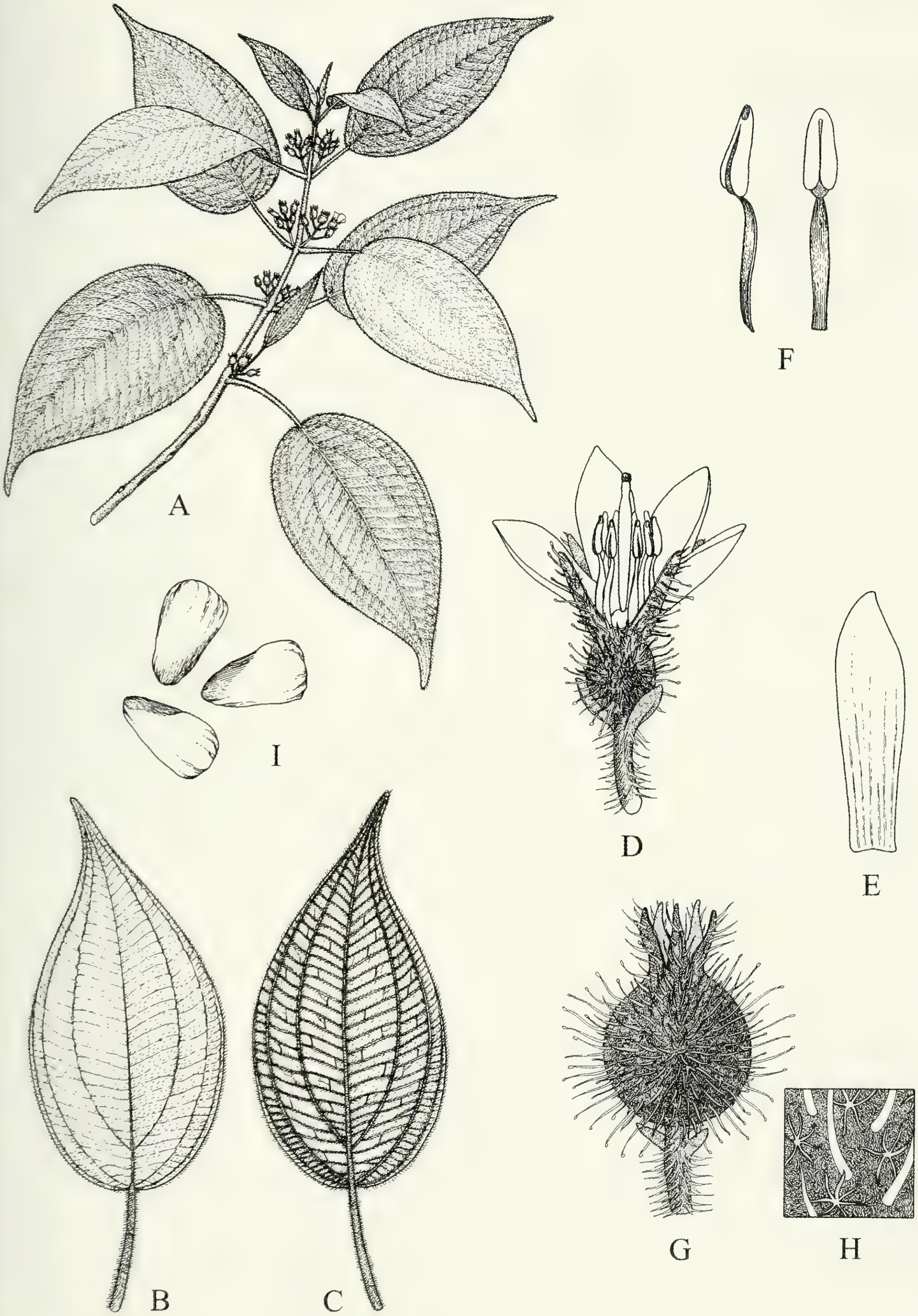
Lax shrub 1–3 m tall, the terete upper internodes, petioles, elevated primary veins of abaxial foliar surfaces, inflorescence, and hypanthia copiously to moderately covered with smooth (gland-tipped in part) spreading hairs 0.5–1 mm long with a ground layer of sessile stellate hairs. Leaves of a pair equal to somewhat unequal in size; petioles 1.3–5 (–6.2) cm long; blades 6.5–13.3 (–16.5) × 3–6.5(–8.5) cm, chartaceous and brittle when dry, ovate to elliptic-ovate, apex acuminate, base rounded to obtuse, margin entire to inconspicuously denticulate, 5–7-plinerved with the innermost pair of primary veins diverging from the median vein 3–7 mm above the blade base, the adaxial surface moderately covered with spreading smooth hairs and some glandular hairs 0.5–1 mm long intermixed with a scattering of stellate hairs on the actual surface and a concentration of stellate hairs on the impressed primaries toward the blade base, the secondary and higher order veins of the abaxial surface beset with smooth spreading hairs 0.5 mm long, the understory consisting of a very sparse scattering of stellulate hairs or the understory indument lacking. Inflorescence 1.5–2 cm long, axillary dichasia branched from the base or short-pedunculate and commonly paired at a node; bracteoles 0.5–1.5 × 0.25–0.50 mm, narrowly elliptic to oblong, apiculate and tipped with a short hair (otherwise glabrous). Pedicels (at anthesis) 0.5 mm long. Hypanthia 1–2 × 1.5 mm (at anthesis), campanulate to suburceolate. Calyx tube 0.25 mm long or obsolete, the calyx lobes 1.5–2 × 0.5 mm, subulate, beset with smooth spreading hairs like the hypanthium, calyx teeth lacking. Petals 5 in number, 2.5–4 × 0.5–1.5 mm, glabrous, white, ± oblong. Stamens 10, isomorphic, filaments 1.5 mm long, glabrous; anthers 1 × 0.4 mm, oblong, yellow with a dorsally inclined apical pore; connective thickened dorsally but neither prolonged below the thecae nor appendaged. Ovary 5-locular, completely inferior, apex sparsely and deciduously glandular or stellulate-puberulent, elevated into a low truncate cone at anthesis but becoming ± flat or rounded on maturing berries. Style 3 mm long, glabrous; stigma truncate to capitellate. Berry 4–5 × 4–5 mm when dry, blue-black or purple-black when ripe. Seeds 0.5 mm long, obovoid, testa ± smooth.

Phenology.— Collected in flower during January, March, July and August, and in October; in fruit from August through October, January and March.

Distribution.— Local and uncommon in cloud forests, river and lake margins, and forest clearings in southern Costa Rica with one outlying population in north-central Nicaragura at 1100–1750 m. The elevation on a single collection (*Williams et al. 28572*) is given as 3200 m. I suspect this report may be erroneous and should be regarded with suspicion until this species is recollected at that elevation again.

Paratypes.— Nicaragua: **Jinotega**: Las Alturas de Kilambé, 13°37′N, 85°40′W, 26 Mar. 1981, *Moreno & Sandino 7568* (CAS). Costa Rica: **Puntarenas**: Zona Protectora Las Tablas, slopes of Cerro Chai along Río Bellavista drainage on trail to Cerro Echandí, 15 Feb. 1991, *Almeda et al. 6637* (CAS, CR, MO); Finca Las Alturas, NW of the Lechería, 17 Feb. 1991, *Almeda et al. 6706* (CAS, CR); above coffee fincas along Río Coto Brus, near Coton, 23 km N of La Union on the Panama border, 9 Aug. 1974, *Croat 26604* (CAS, US); foothills of the Cordillera de Talamanca,

Figure 3. *Clidemia davidsei* Almeda. A. habit, × ½; B. representative leaf (adaxial surface), × ¾; C. representative leaf (abaxial surface), × ¾; D. flower (at anthesis), × ca. 10; E. petal, × ca. 11; F. stamens, ¾ dorsal view (left) and ventral view (right); G. berry, × 5; H. enlargement of berry surface, × ca. 9; I. seeds, × 30. (A – I from *Schnell 1046*.)


A
F
D
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I
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lower montane forest along the Río Bellavista, NW of Las Alturas, ca. 8°57′N, 82°51′W, 30 Aug. 1983, *Davidse 24318* (CAS, CR, MO); cloud forest above Wilson's finca, 6 km S of San Vito de Java, 14 Aug. 1967, *Raven 21763* (MO); cloud forest above Wilson's finca, 6 km S of San Vito de Java, 17 Aug. 1967 *Raven 21843* (CR, DUKE, MO); vicinity of Finca Las Cruces, San Vito de Java, 22–25 Aug. 1968, *Schnell 1046* (US); just S of San Vito de Java, W of Cruces for ca. 3 km along the road running along the Fila Cruces, 19 May 1984, *Taylor 3456* (DUKE); cloud forest near lake on ridge SW of Las Cruces, 21 July 1977, *Webster 21985* (CAS, DAV); cloud forest on ridge, 5 km S of San Vito, 11 May 1971, *Wilbur 14456* (DUKE). **San José**: on Panamerican highway N of San Isidro del General, 15 Oct. 1965, *Schnell 175* (US); Cordillera de Talamanca, about 25 km N of San Isidro del General along Panamerican highway, 29 Jan. 1965, *Williams et al. 28572* (US).

Discussion.— This species, which was first collected in 1965, is easily recognized by its indument of spreading hairs (gland-tipped in part) with a ground layer of stellate hairs (Fig. 3H), axillary dichasia that are commonly paired at a node (Fig. 3A), absence of exterior calyx teeth (Fig. 3G), inferior ovary, and smooth seed coat (Fig. 3I). Collections of *C. davidsei* examined for this study have been variously identified as *C. dentata* D. Don, *C. costaricensis* Cogn. & Gleason, and *C. petiolaris* (Schltdl. & Cham.) Schltdl. ex Triana. It is most like *C. dentata* in general aspect and foliar size. In *C. dentata* the inflorescence is pseudolateral, the calyx consists of a truncate rim that is obscured and exceeded in length by subulate exterior teeth, and the adaxial surface of the torus (vascular ring at the apex of the hypanthium) is adorned with 10 fimbriate scales that are absent in *C. davidsei*. The ovary of *C. dentata* is 5-locular like that of *C. davidsei* but it is ⅓-inferior (vs. completely inferior) and its seed coat is rugulate or granulate (vs. essentially smooth). Both *C. costaricensis* and *C. petiolaris* differ most notably from *C. davidsei* in having pseudolateral inflorescences that are never paired at a node and a calyx that is clearly differentiated into lobes and exterior teeth.

Costa Rican material of *C. davidsei*, which was all collected in the southwestern area of the country, is morphologically homogeneous. The single cited collection from Nicaragua, however, was puzzling and not placed in the recent treatment that I prepared for Flora de Nicaragua (Almeda 2001). It has slightly longer eglandular cauline trichomes (to 2 mm), longer petioles (to 6.2 cm), and larger leaf blades (16.5 × 8–8.5 cm) than the Costa Rica populations. In all other details it appears to be a good match for *C. davidsei* and is tentatively assigned to this species. Its status will require further consideration when better material comes to light.

Etymology.— This species is named for Gerrit Davidse (b. 1942), collector of the type, authority on the systematics of Poaceae, and a founding editor of the ambitious *Flora Mesoamericana* project.

Clidemia evanescens **Almeda, sp. nov.**

(Fig. 4)

Type.— Panama. **Coclé**: forested slopes above El Copé along abandoned road leading to the Continental Divide, elev. 700–850 m, 25 Feb. 1988, *F. Almeda et al. 5933* (holotype: CAS!; isotypes: AAU!, INB!, MO!, MEXU!, NY!, PMA!, US!).

Ramuli teretes sicut petioli foliorum venae primariae subtus inflorescentia hypanthiaque dense pilis asperis induti. Lamina 9–27 × 3.4–14.5 cm elliptica vel elliptico-ovata apice gradatim acuminata vel caudato-acuminata basi obtusa vel rotundata, 3–5-nervata. Inflorescentia primum terminalis demum lateralis pauciramosa vel in foliorum superiorum axillis; flores 4-meri, bracteolis 1.5–3 × 1–2 mm, calycis lobis interioribus 2–2.5 × 1.5 mm triangularibus, dentibus exterioribus 0.5–1.5 mm eminentibus. Stamina isomorphica glabra, antherarum thecae 1.5 × 0.5 mm oblongae poro dorsaliter inclinato; connectivum vix (0.1 mm) prolongatum, dente dorso-basali 0.5 mm glandulis 0.1 mm longis marginato. Ovarium 4-loculare et omnino superiorum apice dense glandulis inconspicuis induto.

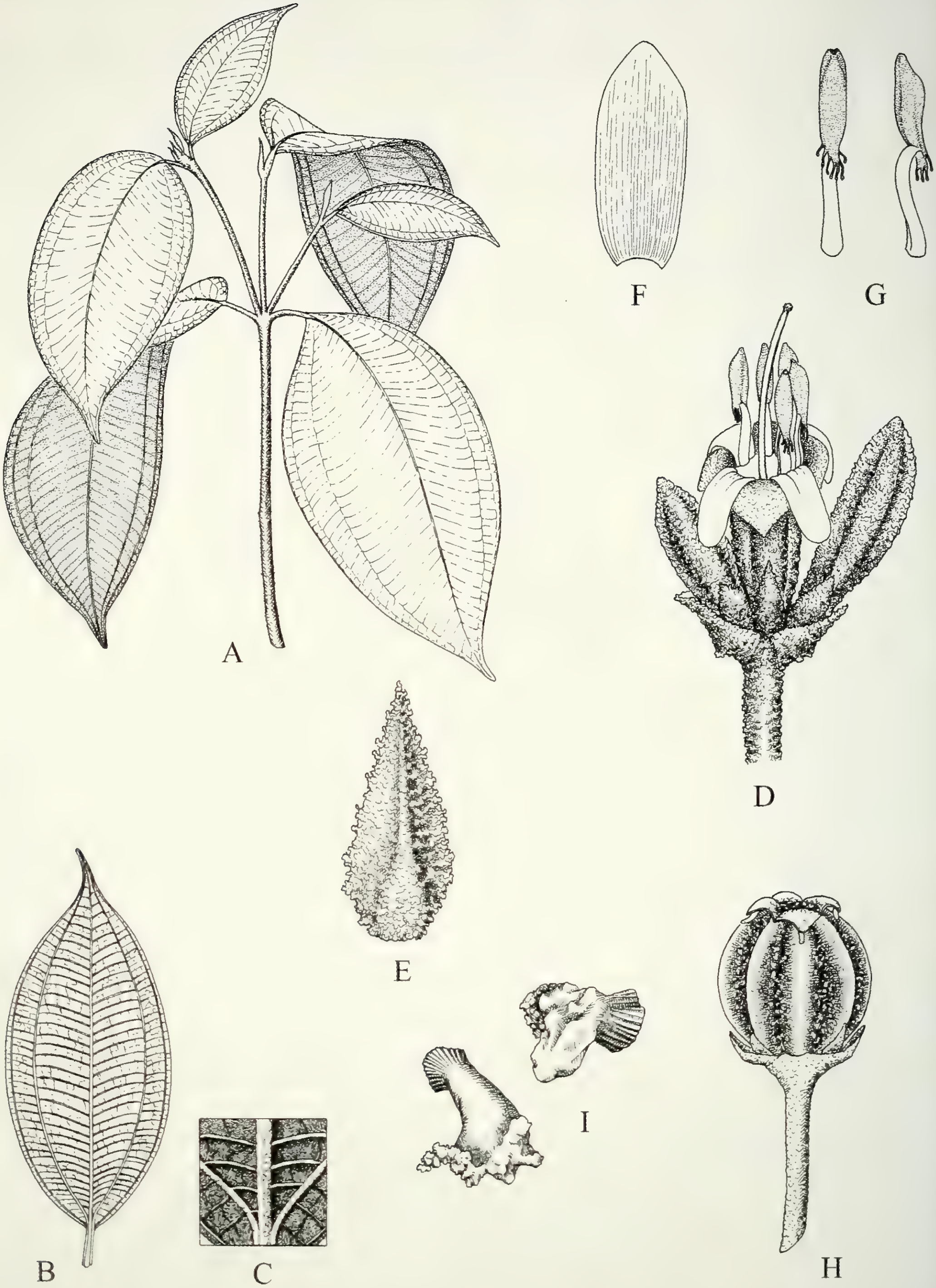
Shrub 0.5–4 m tall with the terete upper internodes, petioles, elevated primary and secondary veins on abaxial foliar surfaces, inflorescence rachis, bracteoles, hypanthia, and calyx lobes moderately to copiously covered with asperous-headed hairs. Leaves of a pair ± equal to somewhat unequal in length; petioles 1.5–4.7 cm long; blades 9–27 × 3.4–14.5 cm, subcoriaceous when dry, elliptic to elliptic-ovate, apex gradually acuminate to caudate-acuminate, base obtuse to rounded, margin essentially entire, 3–5-nerved, the secondary and higher order veins moderately to copiously beset with minute glands. Inflorescence 1–2.5 cm long, typically an axillary cluster of dichasia with branching initiated at the node or terminal with both lateral buds at a node elongating and overtopping the inflorescence; bracts and bracteoles 1.5–3 mm long and 1–2 mm wide at the base, triangular. Flowers 4-merous on pedicels 0.5–1 mm long that are obscured by subtending bracts and bracteoles. Hypanthia (at anthesis) subcylindric to narrowly campanulate. Calyx tube obsolete, the calyx lobes 2–2.5 × 1.5 mm, triangular, typically reflexed, calyx teeth 0.5–1.5 mm long, subulate. Petals 1.5–2 × 0.5–1 mm, glabrous, white, oblong, conspicuously reflexed at anthesis and early caducous. Stamens isomorphic; filaments 1.5 mm long, glabrous; anthers 1.5 × 0.5 mm, yellow or white, linear-oblong, ± truncate to somewhat emarginate at the apex with a dorsally inclined pore; connective prolonged dorso-basally into a deflexed gland-edged appendage 0.5 mm long. Ovary 4-locular, completely superior but tightly enveloped by the hypanthium, apex consisting of a shallow bowl-like depression with a slightly raised perimeter, copiously but inconspicuously glandular-puberulent. Style 6 mm long, glabrous; stigma punctiform to truncate. Berry 6 × 6 mm, bright orange at maturity, prominently 8-costate. Seeds 0.5 mm long, ± triangular in outline with an irregularly rugose testa and a foot-like projection at the narrow end.

Phenology.— Flowering and fruiting intermittently throughout the year.

Distribution.— Primary and secondary rain forests and cloud forests from north-central Costa Rica disjunctly to western Panama, and southwestern Colombia from 850–1900 m.

Paratypes.— Costa Rica: **Alajuela**: Reserva Biológica Monteverde, Río Peñas Blancas. Finca de Jesús Rojas, 10°18′N, 84°44′W, 4 Dec. 1989, *Bello 1540* (CAS, CR); Upala, Bijagua, El Pilón, subiendo por la margen derecha del Río El Roble hasta al Volcán Tenorio, 10°41′N, 85°00′20″W, 9 July 1988, *Herrera et al. 2037* (CAS, CR). Panama: **Coclé**: Alto Calvario above El Copé, ca. 6 km N of El Copé, Atlantic slope, along trail through forest W off old lumber trail leading to Las Ricas, Limón and San Juan, 8°39′N, 80°36′W, 23 June 1988, *Croat 68793* (CAS); El Copé, División continental arriba de Barrigón y el aserradero viejo. Camino de caballo a Coclesito, 27 Apr. 1992, *Peña et al. 469* (CAS, PMA). **Comarca de San Blas**: Cerro Brewster, 9°18′N, 79°16′W, 21 Apr. 1985, *de Nevers et al. 5452* (CAS); Cerro Habú, vicinity of peak, 78°49′W, 9°23′N, 19 Dec. 1980, *Sytsma et al. 2694* (CAS). **Chiriquí**: Edwin Fabrega Dam and Reserve in Fortuna. Quebrada Arena, 8°45′N, 82°05′W, 15 Jan. 1989, *Almeda et al. 6217* (CAS); Gualaca-Chiriquí Grande. 4.8 mi. beyond IRHE facilities at the Dam, 4 mi. N of bridge over Bayano Lake, 8°46′N, 82°16′W, 23 Sept. 1987, *Croat 68018* (CAS, MO). **Veraguas**: along trail to summit of Cerro Tute about ½ mile above the Escuela Agricultura Alto Piedra near Santa Fé, 29 Jan. 1989, *Almeda et al. 6490* (CAS, MO, PMA). Colombia: **Nariño**: Reserva Natural La Planada, municipio de Ricuarte, 18 Nov. 1993, *Restrepo 776* (US); La Planada Biological Reserve, ca. 7 km S of Chucunez, along trail to Pialapi beyond Quebrada La Calledita, 01°10′N, 77°55′W, 8 Aug. 1990, *Luteyn & Sylva 13943* (CAS, NY).

Discussion.— Among the 4-merous species of *Clidemia* that lack formicaria, *C. evanescens* is a standout because of its densely packed indument of roughened or asperous-headed hairs, conspicuously 8-ribbed hypanthia (Fig. 4H), small oblong petals (Fig. 4D, F), deflexed gland-edged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dorso-basal staminal appendages (Fig. 4G), completely superior ovary, and berries that are orange (vs. blue-purple) at maturity. The inflorescence position of this species is variable. It is typically an axillary cluster of dichasia with branching initiated at the vegetative node but at times it can be terminal with both lateral buds at a vegetative node elongating and overtopping the inflorescence.

Among congeners, *C. evanescens*, is most like *C. densiflora* (Standl.) Gleason and it seems likely that these two species are closely related. The latter also has 4-merous flowers, linear-oblong petals, anther connectives that are dorso-basally prolonged into a glandular appendage, and berries that are orange at maturity. In *C. densiflora*, the flowers are sessile (vs. pedicellate) and mostly fasciculate, the merely roughened hypanthial hairs are spreading but not tightly packed to conceal the actual surface as they are in *C. evanescens*. In addition to these differences, *C. densiflora* has modally smaller leaf blades [7–14(–18) × 2.5–5.5(–9) cm vs. 9–27 × 3.4–15 cm] and shorter petioles (0.3–0.8 cm vs. 1.5–4.7 cm).

ETYMOLOGY.— The specific epithet for this species is from the Latin word *evanescens,* meaning quickly disappearing or fading, in reference to the petals that fall away from the flowers quickly at anthesis.

Clidemia folsomii Almeda, sp. nov.

(Fig. 5)

TYPE.— PANAMA: **Veraguas**: along trail to summit of Cerro Tute about ½ mile above the Escuela Agricultura Alto Piedra near Santa Fé, 29 Feb. 1989, *F. Almeda et al. 6488* (holotype: CAS!; isotypes: AAU!, CAS!, INB!, MEXU!, MO!, PMA!).

Ramuli teretes sicut petioli laminae supra et subtus inflorescentia hypanthiaque pilis laevibus plerumque 1–2.5 mm longis pro parte glanduliferis modice obsiti et pilis stellatis modice vel sparse intermixtis. Lamina plerumque ad petioli apicem vesiculifera; vesicae 3.5–7.5 cm longae oblongae; lamina 11–26.5 × 7.5–21 cm cordata vel ovata apice caudato-acuminata 7–9-nervata vel 7–9-plinervata. Inflorescentia in foliorum superiorum axillis multiflorae; flores 5-meri bracteolis 0.5–1 × 0.25 mm; calycis tubus 1 mm altus, lobis interioribus 1.5 × 1.5 mm triangularibus, dentibus exterioribus subulatis setosis 1.5 mm eminentibus. Stamina isomorphica glabra, antherarum thecae 1–1.5 × 0.5 mm oblongae vel subulatae poro dorsaliter inclinato; connectivo non prolongato basi dorsaliter appendice hebeti ca. 0.2 mm longo descendenti armatum. Ovarium 5-loculare et omnino inferum apice modice glanduloso-puberulo.

Little-branched subshrub 1–2 m tall with terete internodes. Uppermost internodes, petioles, adaxial foliar surfaces, elevated primary veins on abaxial foliar surfaces, inflorescence rachis, bracts, bracteoles, pedicels, hypanthia, and calyx teeth moderately covered with smooth (mostly gland-tipped) spreading hairs 1–2.5 mm long with an understory of sessile or stipitate-stellate hairs. Leaves of a pair somewhat unequal in size, otherwise identical in all details and consistently bearing paired elongate formicaria 3.5–7.5 cm long extending from the blade base onto the upper portions of the petiole. Petioles 4–10 cm long, blades 11–26.5 × 7.5–21 cm, membranaceous and brittle when dry, cordate varying to ovate, apex caudate-acuminate, base broadly cordate, margin denticulate to crenulate (at least distally) varying to subentire, 7–9-nerved or -plinerved with the innermost primary pair diverging up to 2 cm above the blade base, the secondary and higher order veins moderately covered with ± sessile or subsessile stellate hairs. Inflorescence 6–13 cm long, axillary, laxly branched paniculiform dichasia typically paired at a node; bracteoles 0.5–1 mm long and 0.25

FIGURE 4. *Clidemia evanescens* Almeda. A. habit, × ca. ½; B. representative leaf (abaxial surface), × ¼; C. enlargement of abaxial foliar surface (midvein and innermost pair of primary veins), × ca. 2; D. portion of inflorescence (simple dichasium with flower at anthesis), × ca. 5; E. bracteole, × ca. 18; F. petal (adaxial surface), × ca. 14; G. stamens, dorsal view (left) and profile view (right), × ca. 10; H. berry, × 4; I. seeds, × ca. 48. (A – I from *Almeda et al. 5933.*)

mm wide at the middle, linear-oblong. Flowers 5-merous, subsessile or on pedicels to 1 mm long. Hypanthia (at anthesis) urceolate. Calyx tube ca. 1 mm long, the calyx lobes 1.5 × 1.5 mm, broadly triangular, collectively spreading and bowl-like; calyx teeth 1.5 mm long, subulate, exceeding and obscuring the calyx lobes. Petals 3–4.5 × 1.5–2.5 mm, glabrous, translucent white, pink, or white tinged with pink or purple, narrowly obovate to oblong. Stamens isomorphic; filaments 2 mm long, glabrous; anthers 1–1.5 × 0.5 mm, white, ± oblong to ± subulate in ventral view, emarginate at the apex with a dorsally inclined pore; connective thickened dorsally and prolonged dorso-basally into a blunt spur ca. 0.2 mm long. Ovary 5-locular, completely inferior; apex elevated into a low ± truncate dome surrounding the stylar scar, minutely glandular-puberulent like the adaxial vascular ring of the hypanthium. Style 5–6 mm long, glabrous; stigma punctiform to truncate. Berry 6 × 6 mm, blue at maturity. Seeds 0.5 mm long, obovoid to ± triangular in outline with a verruculose to rugulate testa.

PHENOLOGY.— Flowering and fruiting from November through June.

DISTRIBUTION.— Cloud forests, elfin forests, and stream banks in western Panama from 800 to 1300 m.

PARATYPES.— PANAMA: **Chiriquí**: vicinity of Fortuna Dam along trail from highway near Forestry Nursery down to Río Hornito, 8°45′N, 82°15′W, 27 Apr. 1988, *McPherson 12510* (CAS); distrito Boquete, Fortuna Dam site, 7 Feb. 1985, *van der Werff & van Hardeveld 6607* (CAS). **Coclé**: Cerro Gaital, east slope and ridges leading to the summit, 8°40′N, 80°07′W, 24 Feb. 1988, *Almeda et al. 5899* (AAU, CAS, INB, MEXU, MO, PMA); Alto Calvario, cloud forest above sawmill on continental divide, 5.2 miles above El Copé, 6 Dec. 1979, *Croat 49152* (CAS): Alto Calvario above El Copé, ca. 6 km N of El Copé, along trail which leads down to Las Ricas, Limón and San Juan, 22 June 1988, *Croat 68742* (CAS); Continental Divide above El Copé, 8°38′N, 80°39′W, 27 Nov. 1985, *de Nevers et al. 6407* (CAS); Cerro Gaital, elfin forest, 8°37′N, 80°6′W, 26 Nov. 1984, *de Nevers & Charnley 4388* (CAS); mountains N of El Valle de Antón, 28 May 1967, *Lewis et al. 1771* (MO); El Copé, División continental arriba de Barrigón y el aserradero viejo, camino de caballo a Coclesito, 27 Apr. 1992, *Peña et al. 467* (PMA); hills just N of El Valle, 14 Aug. 1971, *Wiehler & Dressler 71287* (US-2 sheets). **Panama**: Cerro Campana near the FSU field station trail up the mountain, 9 Aug. 1970, *Kennedy & Luteyn 435* (CAS, DUKE, US). **Veraguas**: trail to Reserva Biológica Serrania de Tute and the summit of Cerro Tute about 0.7 km beyond the Escuela Agricola Río Piedra just outside Santa Fé, 18 Feb. 1996, *Almeda et al. 7614* (CAS, PMA); 6.4 km outside Santa Fé on the road that passes the agriculture school, 5 May 1977, *Folsom 2955* (CAS); Cerro Tute, along ridge trail towards summit, 08°30′N, 81°07′W, 21 Mar. 1987, *McPherson 10743* (CAS).

DISCUSSION.— *Clidemia folsomii* is one of nearly 30 taxa (see Appendix I) in the genus *Clidemia* that produce formicaria or domatia to shelter ants. In *Clidemia,* these formicaria consist of paired inflated pouch-like outgrowths borne at the branch nodes, at the base of the leaf blade, on the petioles, or extending along a portion of the petiole and leaf blade. The ants that inhabit these domatia presumably defend the plants from herbivore attack but the exact nature of the symbiotic relationship has not been studied for the majority of *Clidemia* species (Benson 1985). Ants collected in the formicaria of one population of this species (*Almeda 5899*) were identified as *Solenopsis sp.* (subgenus *Diplorhoptrum)* by P.S. Ward. According to Ward, the ants collected in these domatia were probably nesting opportunistically; there are a number of generalist, arboreal ant species in this subgenus.

The size, shape, and placement of formicaria typically provide diagnostic features of taxonomic importance. The formicaria of *C. folsomii*, for example are elongate, produced at the very base of the leaf blade, and extend onto the distal half of the petiole (Fig. 5A, B). This together with the

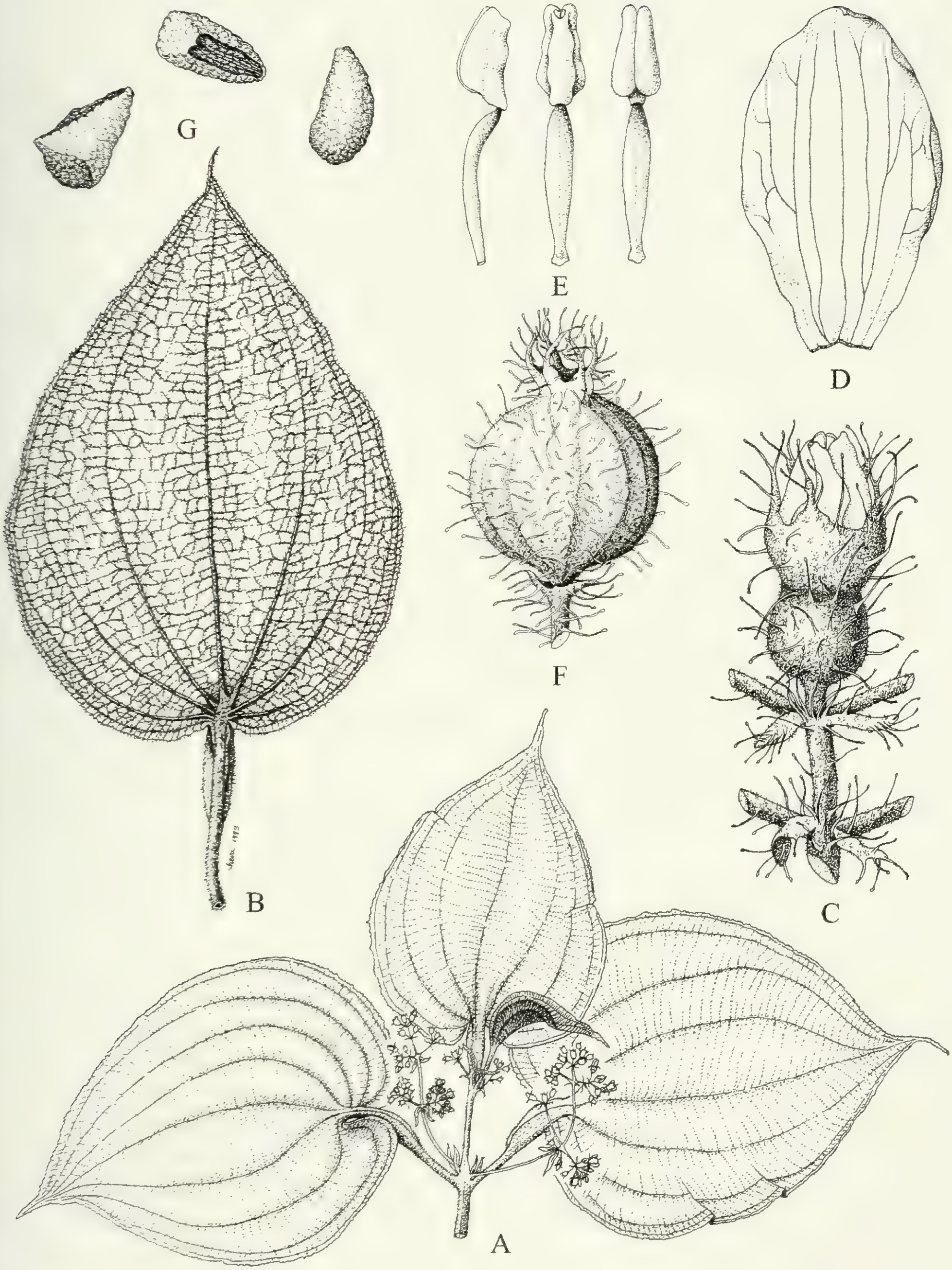

FIGURE 5. *Clidemia folsomii* Almeda. A. habit, × ¼; B. representative leaf (abaxial surface), × ca. ⅓; C. flower bud, × ca. 5; D. petal, × 12; E. stamens, profile view (left), dorsal view (middle), and ventral view (right), × ca. 12; F. berry, × 6, G. seeds, × 36. (A–F from *Almeda et al. 6488*; G from *Almeda et al. 5899*.)

large cordate leaf blades (Fig. 5B), axillary, paired, and laxly branched dichasia at each node (Fig. 5A), indument of spreading (mostly gland-tipped) hairs with an understory of stellate hairs, and well-developed calyx teeth (Fig. 5F) make this species unmistakable among congeners.

Morphologically, *Clidemia folsomii* does not appear to be particularly close to any of the other formicarial species in the genus. It is superficially most like *C. plumosa* (Desr.) DC., a non-formicarial species of Jamaica, Hispaniola and St. Thomas. Both species have elongate petioles, large cordate or ovate leaf blades, paired laxly branched dichasia at the upper nodes, a copious indument of spreading hairs, and elongate setose calyx teeth. In *C. plumosa,* the conspicuous pubescence consists of hairs that are eglandular (vs. mostly gland-tipped), the understory indument consists of small glands that look granular (vs. stellate hairs), and the flowers are 4-merous (vs. 5-merous).

ETYMOLOGY.— This species is named for James P. Folsom (b. 1950), student of neotropical Orchidaceae and veteran collector of Panamanian plants who first collected fertile material of this species in 1977.

Clidemia inopinata Almeda, sp. nov.

(Fig. 6)

TYPE.— MEXICO: **Chiapas**: Municipio La Trinitaria, Ejido Cuauhtemoc, Km 25, 20 Aug. 1984, *Méndez Ton 7868* (holotype: CAS!, isotype: MEXU!).

Ramuli rotundato-quadrangulati sicut petioli inflorescentiaque pilis laevibus erectis vel reflexis 2–8 mm longis. Lamina 7–24.5 × 4.2–13.5 cm ovata vel ovato-oblonga apice acuminata basi obtusa vel rotundata, supra modice longo-setosa pilis gracilibus laevibus 1–4 mm longis, subtus in nervis primariis et secundariis dense longo-setosa in nervulis superficieque modice vel sparse glandulosa, 5–7-nervata. Inflorescentia primum terminalis demum lateralis; flores 5-meri, bracteolis 3.5–8 × 2–3 mm. Calycis lobi interiores 0.75–1 × 0.75–1 mm suborbiculares, dentibus exterioribus 3 mm longis subulatis vel oblongis apice setiferis. Stamina isomorphica glabra, antherarum thecae 2.5 × 0.5 mm oblongae poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et ¾ inferum apice conico sparsissime glanduloso-puberulo.

Shrub 1–2 m tall. Internodes rounded-quadrate; uppermost branches, petioles, and inflorescence axes copiously hirsute with spreading to somewhat reflexed smooth hairs 2–8 mm long. Leaves of a pair ± equal to unequal in size; petioles 1.1–8 cm long; blades 7–24.5 × 4.2–13.5 cm, ovate to ovate-oblong, apex acuminate, base obtuse to broadly rounded, margin denticulate to serrulate and ciliate, 5–7-nerved, uniformly setose adaxially with smooth spreading hairs 1–4 mm long, the abaxial surface also copiously beset with spreading smooth hairs 1–3 mm long on the elevated primaries and higher order veins but only the primary and secondary veins sparingly underlain with minute deciduous glands. Inflorescence 4–9 cm long, a pseudolateral modified dichasium openly and divaricately branched from the base; bracts and bracteoles 3.5–8 × 2–3 mm, persistent, lanceolate to elliptic-lanceolate, glabrous on both surfaces with hirsute-ciliate margins. Pedicels 1–2 mm at anthesis lengthening to 3–4 mm on the infructescence. Hypanthia oblong to subcylindric, 4 mm long from the base to the torus (vascular ring), copiously covered with smooth spreading hairs 3–8 mm long underlain with a sparse cover of minute and inconspicuous glands. Calyx tube 0.25 mm long, the calyx lobes 0.75–1 × 0.75 mm, ± semicircular, glabrous and entire to subentire; calyx teeth 5 in number, 3 mm long or 4.5–6 mm long including the terminal hair, linear-oblong to subulate, beset with an indument like the hypanthium. Petals 5 in number, 5–7 × 2.5 mm, glabrous, white, oblong to oblong-obovate. Stamens 10, isomorphic; filaments glabrous, 2 mm long; anthers 2.5 × 0.5 mm, white, linear-oblong, ± emarginate at the apex with a dorsally inclined pore; connective conspicuously thickened dorsally and barely prolonged below the anther sacs and unappendaged. Ovary ¾-inferior, 5-locular, apex elevated into a low truncate ± crateriform cone with one or few spreading hairs and/or few minute glandular hairs. Style 5 mm long, straight, glabrous; stigma capitellate when receptive. Berry 6–8 × 4–5 mm, red to purple when mature. Seeds ca. 0.4 mm long, ovoid, the testa uniformly asperulate.

PHENOLOGY.— Flowering collections have been made from December through July; fruiting collections from April through January.

DISTRIBUTION.— Understory shrub of primary and secondary forests, forest margins, clearings, and disturbed sites near rivers from southeastern Mexico (Veracruz) disjunctly south through Guatemala to Honduras from 180–1230 m.

PARATYPES.— MEXICO: **Chiapas**: municipio of La Trinitaria, 10 km east northeast of Dos Lagos above Santa Elena, 19 Dec. 1980, *Breedlove 48832* (CAS); 15 km east-northeast of Dos Lagos above Santa Elena, 29 Dec. 1981, *Breedlove 56636* (CAS); municipio La Trinitaria, 10 km east-northeast of Dos Lagos above Santa Elena, 19 Jan. 1982, *Breedlove & Almeda 57505* (CAS); municipio La Trinitaria, km 25, camino Lagos de Montebello–Acayal, 3 May 1985, *Espejo et al. 1660* (MEXU). **Oaxaca**: municipio Santa María Chimalapa, San Antonio Nuevo Paraíso, 13 May 1995, *Torres 669* (CAS); municipio Sta. María Chimalapa, ca. 15 km ESE de Sta. María, 16°52′N, 94°34′30″W, 28 May 1987, *Hernández 2520* (US); "Río Uluapan", 8 km al E de San Bartolomé Ayautla, carretera Huautla–Jalapa de Díaz, Distr. Teotitlán, 20 July 1982, *Torres et al. 855* (CAS, MEXU); municipio Matías Romero, 7.2 km al O de Esmeralda, en la terracería La Laguna–Sarabia, luego 2.6 km al S por camino, 9 Mar. 1982, *Wendt et al. 3640* (CAS, US). **Tabasco**: municipio Huimanguillo, camino del ejido villa de Guadalupe a la torrey microondas, 6 Nov. 1994, *Guadarrama et al. 4132* (MEXU). **Veracruz**: municipio Catemaco, lado NE de Lago Catemaco en Cerros al E de Coyama, 26 Oct. 1971, *Beaman 5180* (CAS, MEXU); Bastonal–Sierra Santa Marta road, ca. 14 km E of Lago Catemaco, 29 May 1981, *Gentry et al. 32431* (CAS, MO); 11 km S de Tebanca, Camino a Bastonal, 26 Apr. 1982, *Ibarra 96* (CAS); municipio Hidalgotitlán, campamento La Laguna, along Río Las Cuevas and nearby pastures, 17°16′N, 94°31′W, 6 Mar. 1984, *Taylor 390* (CAS, F, XAL); municipio Hidalgotitlan, desde el Poblado 6 al sur por la brecha y la vereda al horcajo oriental del Río Cuevas, 17°15′N, 94°30′W, 17 July 1980, *Wendt et al. 2603* (CAS, US). GUATEMALA. **Alta Verapaz**: Chapultepec Farm, km 62 of Coban–Sebol Road, 25 May 1964, *Contreras 4801* (CAS, LL); 7 miles up road to Oxec along road which turns off Highway 7E between Tucurú and El Estor ca. 6 km NE of Panzós, 20 July 1977, *Croat 41649* (CAS, MO); 2 km al S de Jolomylix, Telemán, Panzós, Sierra de las Minas, 20 July 1988, *Martínez et al. 22958* (CAS, MEXU). **Izabal**: Montañas del Mico, 7–8 km W of Santo Tomás de Castilla on road to microwave tower, 19 Aug. 1988, *Stevens et al. 25598* (MEXU). HONDURAS. **Atlántida**: southern boundary of Lancetilla Valley (Near Tela), on ridge separating Lancetilla watershed from that to the SW of San Francisco, halfway to Cerro Peña Blanca, 15°41′30″N, 87°28′30″W, 9 Nov. 1988, *MacDougal et al. 3416* (CAS, MO). **Comayagua**: margins of Lake Yojoa near Pito Solo, 9 Aug. 1948, *Williams & Molina 14622* (MO). **Yoro**: along road from San José de Texíguat to Campo Nuevo in Cordillera Nombre de Dios, ca. 28 km SW of Tela–La Ceiba hwy. (#13), ca. 15°29′N, 87°27′W°, 27 Apr. 2000, *Daniel & Araque 9496* (CAS, EAP); slopes above E part of San José in the Río Leán Valley, between Río Texiguat and Río Guán Guán, slopes of Cordillera de Nombre de Dios, 6 Nov. 1988, *MacDougal et al. 3283* (CAS, MO).

DISCUSSION.— Diagnostic characters of *C. inopinata* include the openly and divaricately branched inflorescence (Fig. 6A), the conspicuous and persistent bracteoles (Fig. 6C), the deeply pigmented (blackish) hypanthia that are copiously covered with smooth spreading hairs (Fig. 6F) underlain with a sparse cover of minute inconspicuous glands, the white anther thecae, and the uniformly asperulate seed coat (Fig. 6G). *Clidemia fulva* Gleason has an aspect that is very reminis-

FIGURE 6. *Clidemia inopinata* Almeda. A. habit, × ⅓; B. representative leaf (abaxial surface), × ½; C. bracteole, × 6; D. petal (adaxial surface), × 8; E. stamens, profile view (left) and ventral view (right), × ca. 7; F. berry, × ca. 9; I. seeds, × ca. 56. (A from *Breedlove & Almeda 57505*; B from the holotype; D, E and G from *Breedlove 56636*; C and F from *Breedlove 48832*.)

cent of *C. inopinata* and the latter has typically been identified as the former. Both species share similar inflorescence architecture with persistent bracts and bracteoles, a copious indument of smooth spreading hairs, elongate calyx teeth, and white petals and anther thecae. In *C. fulva*, however, the leaf base is often unequal (vs. never unequal), pedicels on the infructescence are 4–8 mm long (vs. 3–4 mm), hypanthial hairs are 2.5–4 mm long (vs. 3–8 mm), the seeds are 0.75 mm long (vs. 0.4 mm), and the seed coat is smooth (vs. uniformly asperulate).

Clidemia fulva also has a more limited geographic and elevational distribution than *C. inopinata*. It occurs in Chiapas, Mexico, and in a limited region of adjacent Guatemala (Alta Verapaz, Izabal, and Peten) at elevations of 200–500 m.

ETYMOLOGY.— The epithet for this species is derived from the Latin word *inopinatus*, unexpected, alluding to the fact that it has long gone unrecognized under the name of a closely related species.

Clidemia lanuginosa Almeda, sp. nov.

(Fig. 7)

TYPE.— PANAMA: **Bocas del Toro**: Fortuna Dam area along continental divide trail bordering Chiriquí Province, 08°45′04″N, 82°15′04″W, elev. 1200–1300 m, 10 Mar. 1988, *F. Almeda et al. 6070* (holotype: CAS!; isotypes: INB!, MO!, PMA!).

Ramuli teretes sicut petioli inflorescentiaque modice pilis laevibus vel usque ad 3–5 mm obsiti et dense persistenterque lanuginosa pilis gracillimis laxis intermixtis. Lamina 8.5–22 × 5–12.5 cm ovata vel ovato-elliptica apice acuminata basi rotundata supra modice setosae pilis laevibus 3–6 mm longis, subtus in venis setosa et modice setulosa pilis caduco-glanduliferis, 7–9-plinervata; formicaria ca. 2–5.5 cm longa in laminarum basibus omnino immersa. Inflorescentia primum terminalis demum lateralis; flores 4 (–5)-meri, bracteolis 1–2 × 0.25 mm. Calycis lobi interiores 0.25 × 0.5–0.75 mm suborbiculares, dentibus exterioribus 0.5–4 mm longis subulatis apice setiferis. Stamina isomorphica glabra, antherarum thecae 1.75–2 × 0.2 mm subulatae poro dorsaliter inclinato; connectivo nec prolongatum nec appendiculatum. Ovarium (3–) 4 (–5)-loculare et omnino inferum apice glabro.

Little-branched subshrub 0.5–2 m tall, the terete upper internodes, petioles, and inflorescence rachis moderately covered with smooth spreading hairs 3–5 mm long with a dense understory of deciduous appressed somewhat woolly (often gland-tipped and crisped) hairs. Leaves of a pair equal to unequal in size, otherwise identical in all details and consistently bearing paired elongate inflated formicaria 2–5.5 cm long on the adaxial base of the blade; petioles 0.5–4 cm long; blades 8.5–22 × 5–12.5 cm, membranaceous and brittle when dry, ovate to ovate-elliptic, apex acuminate, base broadly rounded, margin subentire to denticulate, 7–9–plinerved, the paired primary veins arising at successive points above the blade base with the inner-uppermost primaries diverging from the median vein 2–4.5 cm above the blade base, the adaxial surface moderately and uniformly covered with smooth spreading hairs 3–6 mm long, the primary and higher order veins on the abaxial surface beset with smooth spreading hairs 2–5 mm long and an understory of minute deciduous glandular hairs. Inflorescence 2–8 cm long, a paniculiform dichasium that is initially terminal but then becomes pseudolateral with growth and elongation of lateral branches; bracteoles 1–2 mm long (including terminal hair) and 0.25 mm wide, subulate to oblong-subulate, sparingly beset with minute glandular hairs on the abaxial surface. Flowers 4 (–5)-merous on pedicels 0.5–1 mm long. Hypanthia (at anthesis) cylindric to cylindric-campanulate, sparsely covered with smooth spreading hairs 1–3 mm long and an understory of appressed glandular hairs. Calyx tube obsolete, the calyx lobes 0.25 × 0.5–0.75 mm, semicircular to rounded-triangular, tardily deciduous, hyaline, deciduously glandular-puberulent abaxially and glandular-ciliolate at the margins; calyx teeth 0.5–4 mm (excluding apical hair), subulate, sparingly beset with smooth spreading hairs 2 mm long and an understory of minute glandular hairs. Petals 2–4 × 1 mm, glabrous, white or pink, oblong to oblong-obovate. Stamens isomorphic; filaments 1.75–2 mm long, glabrous; anthers 1.75–2 × 0.2 mm, yellow, subulate with a dorsally inclined pore; connective thickened dorsally but not prolonged below the thecae and unappendaged. Ovary (3–) 4 (–5)-locular, completely inferior; apex elevated into a short cone (0.25 mm) and vaguely lobulate collar at anthesis that disappears on mature fruits. Style 4 mm long, glabrous; stigma punctiform to truncate. Berry 2.5–3 × 2.5–4 mm, blue at maturity. Seeds 0.5 mm long, triangular, the convex face somewhat angular with a densely tuberculate testa.

Phenology.— Flowering material has been collected from February through November; fruiting specimens have been collected in March, June, July, September, and November.

Distribution.— Local and uncommon, often in deep shade of cloud forests and rain forests from southeastern Costa Rica to Panama (Bocas del Toro east to Darién) at 300–1450 m.

Paratypes.— Costa Rica: **Limón**: Cantón de Talamanca, R.I. Talamanca, Cordillera de Talamanca, Alto Urén, 9°27′00″N, 82°59′30″W, 24 Sep. 1994, *Gallardo & Lépiz 281*, (INB); Cantón de Talamanca, R.I. Talamanca, Cordillera de Talamanca, Alto Urén, 9°21′35″N, 82°59′45″W, 13 Sep. 1992, *Gallardo 88* (INB); Reserva Indígena Talamanca, Sukut, desembocadura del Río Sukut en el Río Urén, camino al sureste, hacia Purisqui, 9°23′30″N, 82°58′00″W, 7 July 1989, *Hammel et al. 17571* (CAS, CR, INB, MO). Panama: **Bocas del Toro**: above Chiriquí Grande on a side road about 10 miles below the Continental Divide about 2 ½ miles east on that road, 8°55′N, 82°10′W, 19 Jan. 1989, *Almeda et al 6334* (CAS, PMA); road from Fortuna Dam to Chiriquí Grande, 10 miles from Continental Divide, 8°51′N, 82°10′W, 2 Aug. 1984, *Churchill 5933* (CAS): Oleoducto Road, near Continental Divide. Fortuna Dam area, 8°48′N, 82°12′W, 5 Feb. 1984, *Churchill et al. 4494* (CAS): después de la División Continental, en la carretera que va de Fortuna a Chiriquí Grande, 27 Aug. 1993, *Correa et al. 9854* (PMA); along road between Fortuna Dam and Chiriquí Grande, 7.3 mi. N of bridge over Fortuna Dam, 3.2 mi. N of Continental Divide, 8°45′N, 82°15′W, 10 Mar. 1985, *Croat & Grayum 60220* (CAS); road from Fortuna Dam to Chiriquí Grande, 3.1 mi. N of Continental Divide, 8°50′N, 82°15′W, 10 Mar. 1985, *McPherson 6770* (CAS); Edwin Fabrega Dam and Reserve in Fortuna. Trail to the hydrological station on the Río Hornito between Quebrada Nelson and Quebrada Mono, 7 Feb. 1996, *Almeda et al. 7521* (CAS, CR, MO, PMA); along road between Gualaca and Fortuna Dam, at 8.3 mi. NW of Los Planes de Hornito, 9 Apr. 1980, *Antonio 4150* (CAS); Fortuna, camino de Quebrada Bonita. Hacia el este del Río Chiriquí, 7 Apr. 1987, *Valdespino et al. 563* (CAS, PMA); Fortuna, plots 5–8 de Jaime Cavelier, frente al vivero del IRHE, 26 Apr. 1988, *Valdespino et al. 846* (CAS, PMA). **Chiriquí**: S. O. del campamento de Fortuna (Hornito), sitio de presa subiendo hasta la finca Pittií, bordeando el bosque y regresando por el lado S del campamento, 14 Aug. 1976, *Correa et al. 2424* (US); Fortuna Dam area, around creek to . of road drawing into Río Hornito S of reservoir, 8°43′N, 82°14′W, 14 June 1984, *Churchill 5375* (CAS); Fortuna Dam area, on Kaolin hill, just N of reservoir, 31 July 1984, *D'Arcy et al. 15902* (US). **Darién**: trocha Río Frio hacia la cima más allá de Rancho Tuque (3 horas de camino), 22 Sep. 1989, *Aranda et al. 949* (CAS, PMA). **Veraguas**: Distrito de Sante Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 July 1996, *Aranda et al. 2653* (CAS, PMA); in forest below summit of Cerro Arizona (Cerro Tute), above Santa Fé, 22 Apr. 1980, *Hammel & Kress 8569* (CAS); ridge east of Cerro Tute, NW of Santa Fé, 25 Oct. 1975, *Dressler 5203* (US); about 20 km NW of Santa Fé near the Continental Divide, 29 Mar. 1975, *Kennedy & Dressler 3417* (US); trail to Cerro Tute, above Escuela Agrícola Alto de Piedra, just W of Santa Fé, 8°32′N, 81°07′W, 5 June 1982, *Knapp and Dressler 5417* (CAS).

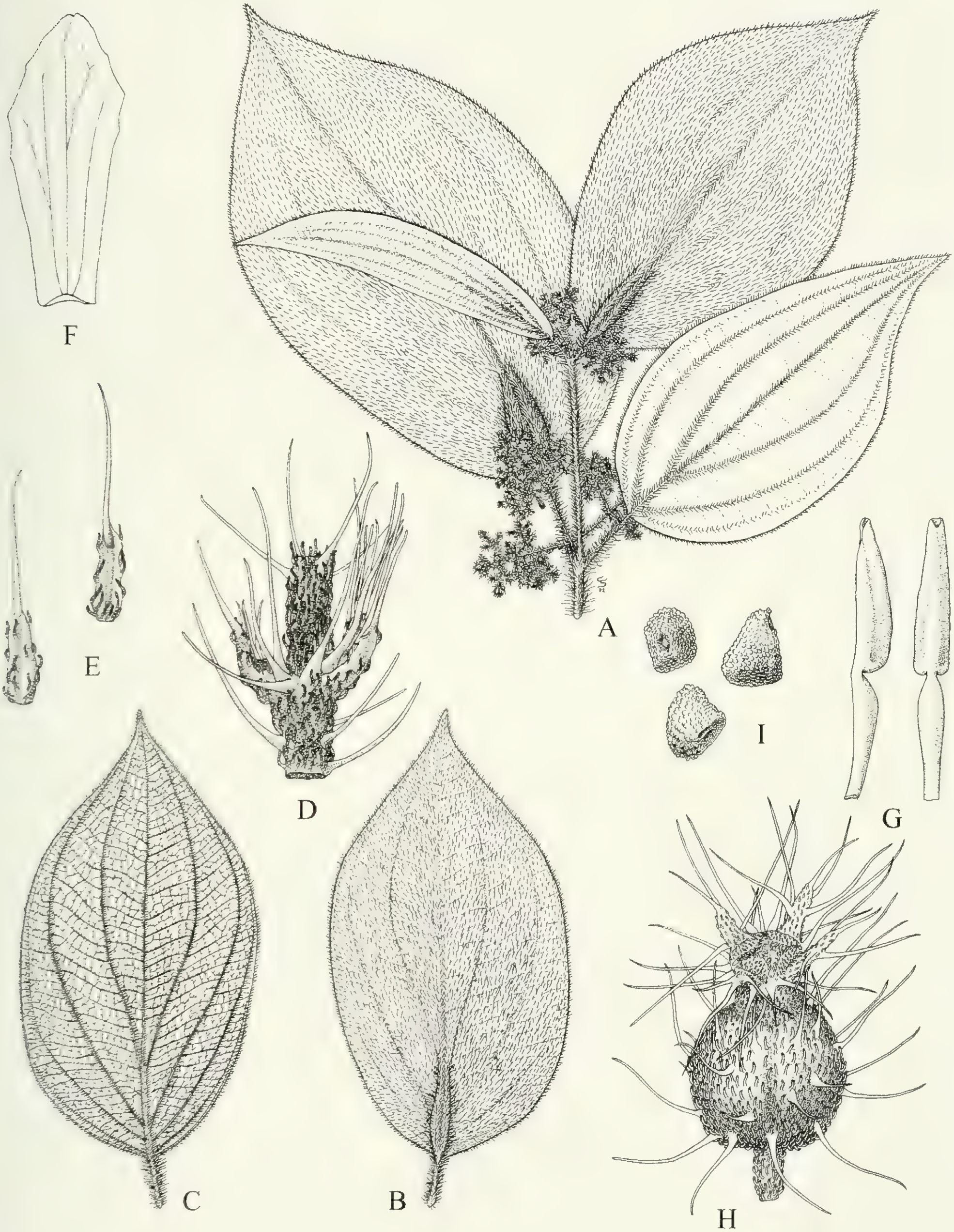

FIGURE 7. *Clidemia lanuginosa* Almeda. A. habit, × ca. ½; B. representative leaf (adaxial surface), × ⅓; C. representative leaf (abaxial surface), × ⅓; D. portion of inflorescence rachis, × 9; E. bracteoles, × 17; F. petal (adaxial surface), × 14; G. stamens, profile view (left) and dorsal view (right), × 11; H. berry, × ca. 9; I. seeds, ca. 56. (A – G from *Almeda et al. 6070*; H from *Churchill 5375*; I from *D'Arcy et al. 15902*.)

Discussion.— *Clidemia lanuginosa* is readily recognized by its 7–9-plinerved leaf blades with paired primary veins arising at successive points above the blade base (Fig. 7C), didymous formicaria (Fig. 7B) restricted to the adaxial base of the blade, and oblong, glandular-puberulent bracteoles that are tipped with a prominent apical hair (Fig. 7E). The indument on upper internodes, petioles, and the inflorescence is also distinctive. It consists of smooth spreading hairs 3–5 mm long with a dense understory of deciduous appressed woolly (often gland-tipped and somewhat crisped) hairs.

Clidemia lanuginosa is variable in characters that are typically constant in many other congeners. For example, the calyx lobes are persistent on some collections but tardily deciduous on others. Floral merosity and ovary locule number are also variable. The isomerous flowers of this species are typically 4-merous with a 4-locular ovary but the flowers on inflorescences of individual plants in populations from both Costa Rica and Panama can be prevailingly 4-merous with some that are 5-merous, and the ovary can vary from 3- to 5-locular. None of this variation appears to correlate with other vegetative or reproductive features.

Several collections from Cerro Tute, Panama, stand out because they have flowers that are consistently 5-merous with shorter calyx lobes and formicaria that occupy the blade base and about half of the distal portion of the petiole. These anomalous collections may represent a distinctive taxon; they are here excluded from the circumscription of *C. lanuginosa* pending additional study.

Etymology.—The specific epithet is derived from the Latin word, *lanuginosus*, woolly, to emphasize the copious understory of woolly hairs on upper internodes, petioles, and the inflorescence rachis.

Clidemia pectinata Almeda, sp. nov.
(Fig. 8)

Type.— Panama. **Bocas del Toro**: along oleoducto road between continental divide and Chiriquí Grande, 21 miles S of Chiriquí Grande, 8°50–55′N, 82°9–15′W, elev. 850 m, 3 May 1985, *Hammel 13748* (holotype: MO!).

Ramuli teretes sicut folia supra hypanthiaque glabri. Petioli 7–14.3 cm longi dense setosi pilis laevibus 4–9 mm longis. Lamina 20–20.5 × 10–13 cm ovato-elliptica apice breviter hebeti-acuminata vel hebeti-acuto basi rotundata, subtus sparse glanduloso-setulosa alioqui glabra, 7-plinervata. Inflorescentia primum terminalis demum lateralis. Pedunculus ad 18 cm longus cum pedicellis modice pilis glanduliferis inconspicuis obsitus; flores 5-meri; bracteolae 1–2 mm longae. Calycis tubus ca. 0.1 mm longus, lobis interioribus 0.5 × 1 mm oblatis, dentibus exterioribus 0.5 mm longis triangularibus. Stamina isomorphica glabra, antherarum thecae 2 × 0.25 mm oblongae poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare ¾ inferum apice glabro.

Shrub to 1.5 m tall with terete glabrous internodes, the nodes of uppermost branches and vegetative buds deciduously setose with smooth spreading hairs 2–6 mm long. Leaves of a pair essentially equal in size; petioles 7–14.3 cm long, glabrous on the abaxial surface but densely setose on the adaxial surface with smooth spreading hairs 4–9 mm long that appear pectinate (one-sided) and directed adaxially when dry; blades chartaceous and brittle when dry, 20–20.5 × 10–13 cm, entire but coarsely ciliate, ovate-elliptic, apex short-acuminate to acute, base broadly rounded, 7-plinerved, glabrous adaxially, the abaxial surface appearing glabrous but actually minutely and somewhat deciduously glandular-papillose. Inflorescence a pseudolateral, pendulous and long-pedunculate (to 18 cm long) corymbiform-umbelliform cluster of dichasia (3–4 cm long including secondary peduncles); the primary peduncle deciduously setose with smooth hairs 0.75–2 cm long; the

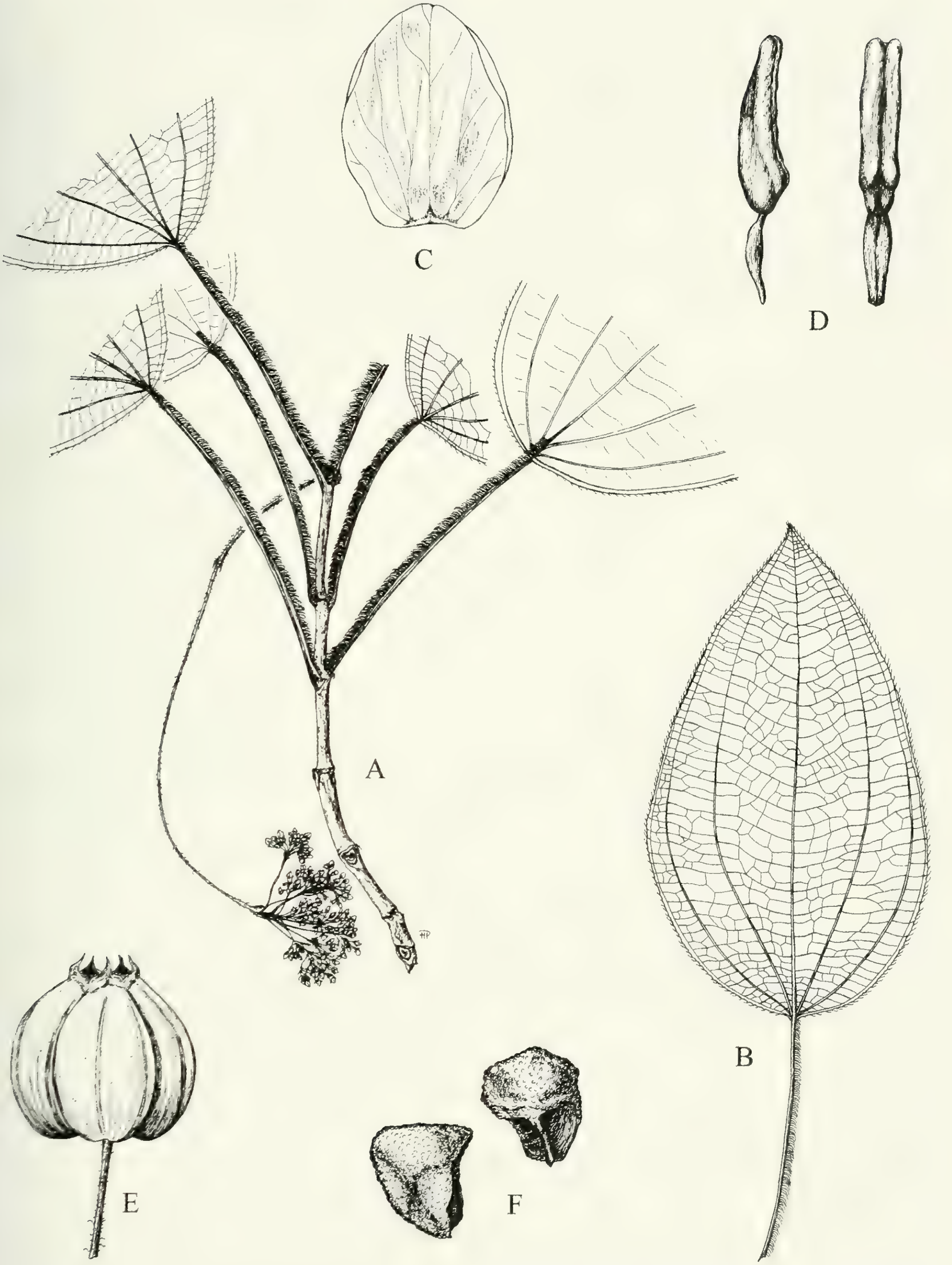

FIGURE 8. *Clidemia pectinata* Almeda. A. habit, ca. ½; B. representative leaf (abaxial surface), × ⅓; C. petal (adaxial surface), × 11; D. stamens, profile view (left) and ventral view (right), × 12; E. berry, × 4; F. seeds, × ca. 34. (A – D from the holotype; E and F from *Correa et al. 9855*.)

secondary peduncles, pedicels, and very young hypanthia sparsely to moderately beset with minute inconspicuous glands; bracts and bracteoles 1–2 mm long (including apical hair) and 0.25–0.5 mm wide, subulate, essentially glabrous. Flowers 5-merous on pedicels 1–2 mm long. Hypanthia (at anthesis) narrowly campanulate, beset with minute glandular hairs when young but essentially glabrous at maturity. Calyx tube ca. 0.1 mm long, the calyx lobes 0.5 × 1 mm, oblate, hyaline and glabrous; calyx teeth 0.5 mm long, triangular. Petals 3 × 2 mm, obovate, glabrous. Stamens isomorphic; filaments 1.5 mm long, glabrous, abruptly constricted distally just below the thecae; anthers 2 mm long, ca. 0.25 mm wide, oblong, truncate apically with a dorsally inclined pore; connective thickened dorsally but neither prolonged nor appendaged below the thecae. Ovary 5-locular, ¾-inferior, apex glabrous and smooth around the stylar scar. Style 3 mm long, straight and glabrous; stigma truncate. Berry 4 × 5 mm, reddish-purple and conspicuously lobed at maturity. Seeds 0.5–0.75 mm long, bluntly triangular and angular with a densely tuberculate testa.

PHENOLOGY.— Only two collections of the species are known; the May collection is in mature bud, the August collection is in mature fruit.

DISTRIBUTION.— Evidently local and rare in rain forests along stream banks on the Caribbean versant of western Panama in the region extending from Fortuna to Chiriquí Grande at 600–850 m.

PARATYPE.— PANAMA: Bocas del Toro: después de la División Continental en la carretera que va de Fortuna a Chiriquí Grande, 27 Aug. 1993, *Correa et al. 9855* (CAS, PMA, SCZ).

DISCUSSION.— *Clidemia pectinata* is perhaps the rarest and surely one of the most distinctive species of *Clidemia*. The combination of glabrous internodes (Fig. 8A), adaxial leaf blades, and mature hypanthia (Fig. 8E), pectinately pubescent petioles (Fig. 8B), and pendent long-pedunculate inflorescences (Fig. 8A) are unknown in any other species of *Clidemia*. The limited material available for study has precluded an assessment of variation and I was unable to relocate even sterile individuals of this species during field work in Panama in early 1996. Measurements of floral parts were taken on large but unexpanded flower buds of the holotype so even the size of most floral organs are likely to be larger when material is collected with expanded flowers.

ETYMOLOGY.— The epithet for this species is derived from the Latin word, *pectinatus,* i.e., with narrow close-set divisions like a comb. This refers to the posture and density of the petiolar hairs that are one-sided and directed adaxially when dry.

Clidemia quinquenervia (Mill.) Almeda, comb. nov.

BASIONYM: *Melastoma quinquenervium* Mill., Gard. Dict. ed. 8, sp. 15. 1768. *Octopleura quinquenervia* (Mill.) Triana, Trans. Linn. Soc. London 28:145. 1871. *Ossaea quinquenervia* (Mill.) Cogn., DC. Monogr. Phan. 7:1064. 1891. TYPE: Exact locality not legible, *Herb. Miller s.n.* (holotype: BM!).

Clidemia ? decurrens Beurl., Bid. Portobellos Flora. Kongl. Vetensk, Acad. Handl. 40:127. 1854. syn. nov. TYPE: Panama. Porto Bello, in silvis ad viam versus Panama, Apr. 1826, *Billberg 280* (holotype: S, photo: MO!).

Ossaea diversifolia (Bonpl.) Cogn., Bull. Acad. Roy. Sci. Belgique Ser. 3, 14:968. 1887. Basionym: *Melastoma diversifolium* Humb. & Bonpl., Melast. 138, t. 59. 1816. TYPE: Colombia. Río Magdalena, *Bonpland 1617* (holotype: P!; isotypes: P! - 3 sheets, US!).

For additional synonymy see Wurdack (1971:128).

Shrub 0.5–2 (–6) m, the terete upper internodes and branchlets, petioles, primary abaxial leaf veins, and inflorescence axes covered with a dense indument of stipitate or subsessile clavate asperous-headed hairs. Leaves of a pair somewhat unequal in size, blades 10–24 × 5–15 cm, broadly elliptic to ovate, 5–7 (–9)-plinerved, abruptly narrowed at the base and narrowly decurrent along the petiole, apex obtuse, acute, or short-acuminate, the margins ciliolate-denticulate, moderately to sparsely setulose or glabrate adaxially, sparsely and deciduously stellulate-furfuraceous and resinous-glandular on the secondary, higher order veins and blade surface abaxially. Inflorescence 2–4 cm long, a modified dichasium mostly divaricately branched from the base; flowers 5-merous on pedicels 0.25–0.5 mm long; the bracteoles mostly 0.5 mm long, subulate, persistent. Hypanthium bluntly 10-costate, deciduously resinous-glandular, occasionally with a sparse admixture of spreading simple hairs. Calyx vaguely undulate, ca. 0.25 mm long but concealed by the setulose exterior teeth that are 0.5–1 mm long. Petals 0.75–1.25 × 0.75–1 mm, obovate-oblong, densely papillose-furfuraceous on both surfaces with a projecting infra-apical, abaxial tooth. Filaments 1–1.5 mm long, anthers 1.5–2 mm long, yellow with a truncate to ventrally inclined apical pore; connective prolonged dorso-basally into a gland-edged spur ca. 0.25 mm long. Ovary 5-locular, completely inferior, apex somewhat depressed, minutely and deciduously resinous-glandular puberulent; berry 4–5 × 2.5 mm when dry, compressed, initially white to pink-purple but turning blue-black. Seeds 0.5 mm long, the testa smooth.

PHENOLOGY.— Flowering and fruiting throughout the year.

DISTRIBUTION.— Uncommon to locally common in gallery forests, semideciduous forests, rain forest margins, river or stream banks, pasture margins, and disturbed sites, often in deep or partial shade from Honduras south through southern Central America to Colombia, Venezuela, and Ecuador at 0–700(–1400) m.

REPRESENTATIVE SPECIMENS EXAMINED.— HONDURAS: **Gracias a Dios**: Ahuas Bila, 200 km SO de Puerto Lempira, orilla del Río Wankí, Coco o Segovia, 5–13 May 1985, *Nelson & Cruz 9345* (CAS). NICARAGUA: **Jinotega**: Macizos de Penas Blancas, 5 May 1976, *Neill 249* (CAS); Zelaya: Sector de Negro Wás, entre El Empalme y Rosita, ca. 13°45′ N, 84°25′W, 5 Sep. 1984, *Ortíz 2123* (CAS). COSTA RICA: **Cartago**: Atirro, 1894 (w/out exact date), *Donnell Smith 4775* (US). Heredia: La Selva, near Puerto Viejo, 21 May 1972, *Opler 826* (US). Limón. Ca. 5.5 km W of Limon off road to Siquirres, 27 July 1977, *Almeda et al. 3261* (CAS, CR); ca. 7 km SSW of Home Creek on the road to Bribri, 26 July 1977, *Almeda et al. 3256* (CAS, CR). **Puntarenas**: Cantón de Golfito, P. N. Corcovado, Peninsula de Osa, Estación Sirena, Sendero a Río Claro, 14 Oct. 1993, *Aguilar 2529* (CAS, INB, MO); disturbed sites above Golfito along the road to the television tower, 16 July 1977, *Almeda et al. 3094* (CAS, CR); Reserva Absoluta Cabo Blanco, Estación Cabo Blanco, 9°35′N, 85°06′W, 4 Nov. 1991, *Chavarría 305* (CAS, INB, MO); Punta Catedral, ca. 7 km SE of Quepos, 9°22.5′N, 84°09′W, 20 Aug. 1985, *Grayum & Sleeper 5896* (CAS, CR, MO); Nicoya Peninsula, canyons and ridges toward Punta Georgia, Punta Blanca trail, 23 Aug. 1995, *Sanders et al. 17706* (CAS, UCR); Reserva Biológica Carara, Sendero Quebrada Bonita-Bijagual, 9°46′10″N, 84°33′50″W, 8 Dec. 1989, *Zuñiga & Jiménez 18* (CAS, CR, INB). San José: Zona Protectora El Rodeo Ciudad Colón, 9°54′N, 84°16′W, *Varela 241* (CAS, INB, MO). PANAMA: **Bocas del Toro**: Lincoln Creek, 28 Jan. 1921, *Carleton 87* (US); Changuinola to 5 miles S at junction of Río Changuinola and Terebe, 17–19 Dec. 1966, *Lewis et al. 833* (F, MO, PMA). **Canal Area**: Madden Forest (Parque Nacional Soberanía), Las Cruces Trail, 3.6 mi N of Gamboa road turn-off, 23 July 1994, *Croat & Zhu 77060* (CAS, MO, PMA); Barro Colorado Island, Bat Cave, 18 Sep. 1982, *Schmalzel & Schupp 955* (CAS, MO). **Chiriquí**: vicinity of Puerto Armuelles, 28–31 July 1940, *Woodson & Schery 855* (MO). Coclé: forest on hills above road 18 km past Sardinilla on way to Nombre de Dios, 2 Aug. 1974, *Croat 26096* (MO). **Colón**: north of Diamante, ridge NW of abandoned mine on Quebrada de la Mina, 9°24′N, 79°35′W, 11 Jan. 1984, *Churchill & de Nevers 4216* (CAS, MO, PMA); 1–2 km from the Portobelo Highway up the Río Guanche, 9°30′N, 79°40′W, 17 Feb. 1982, *Knapp 3641* (CAS). **Comarca de San Blas**: Aligandi area along trail from ocean to waterfall on river, 7 Oct. 1978, *Hammel & D'Arcy 4989* (CAS, MO, PMA). **Darién**: de la estación de Cruce Mono hasta la quebrada Ipelisa (limite del parque), 28 Aug. 1990, *Aranda et al. 1517* (CAS, PMA); trail between Boca de Cupe and Río Piedras on the trail to Paca and Cana, 27 June

1959, *Stern et al. 733* (US). Los Santos/Veraguas border: mountains of S Azuero Peninsula near proposed route of road from El Cortezo to Arenas, 0–5 km SW of El Cortezo, 29 Oct. 1978, *Hammel 5461* (CAS, MO, PMA). **Panama**: area around Tortí Arriba, 31 Aug. 1977, *Folsom 5153* (CAS, MO, PMA); hills S of Guacuco, 8 km E of Ipetí, 78°20′W, 8°55′N, 18 Sep. 1982, *Hamilton & D'Arcy 1353* (CAS). **Veraguas**: Dto. De Montijo, Isla de Coiba, campamento de La Salina, subida hacia Río Negro, 21 Oct. 1995, *Martín & Ballesteros MB1345* (CAS, PMA). COLOMBIA: **Antioquia**: Quebrada Isaias, east of Turbo, 8 July 1946, *Haught 4946* (US). Bolívar: Boca Verde, Río Sinu, 13–14 Feb. 1918, *Pennell 4227* (US). **Chocó**: Río Ciego, 17 June 1967, *Duke 13290* (US); Corregimiento San Francisco, Vereda Coquital, Sitio "El Páramo, Quebrada Zardí, 8°23′N, 77°07′W, 22 May 1989, *Betancur et al. 1191* (US). **Cundinamarca**: San Antonio, 14 June 1948, *Haught 6241* (CAS). **Magdalena**: Parque Nacional Tayrona, along mule trail from Pueblito to Calabazo, ca. 11°19′N, 73°58′W, 26 Oct. 1972, *Kirkbride 2565* (US). **Tolima**: Mariquita, 10 Nov. 1938, *Haught 2429* (DS). VENEZUELA: **Portuguesa**: Distr. Guanare, 17 km NW of Tucupido by road, N slope of fila Las Palmas, 69°57′W, 9°01′N, 30 Oct. 1982, *Davidse et al. 21455* (CAS, MO, US). **Zulia**: Dto. Mara, cuenca del Río Guasare, alrededores del Destacamento Guasare No. 1 (La Yolanda), 10°52′10″N, 72°29′30″W, 9 Nov. 1982, *Bunting et al. 11977* (CAS). ECUADOR: **Napo**: Río Napo between Coca (Puerto Francisco de Orellana) and Armenia Vieja, 15 Nov. 1974, *Harling & Andersson 11986* (US). **Pastaza**: Río Pastaza, between Destacamento Chiriboga and Apachi Entza, ca. 76°55′–77°8′W, 2°20–32′S, 24 July 1980, *Øllgaard et al. 35173* (CAS).

DISCUSSION.— It is surprising that the generic placement of this species has not been adjusted until now since it was first proposed as a new species in 1768. It was described as *Clidemia* ? *decurrens* Beurl. in 1854 (see citation above) but students of neotropical Melastomataceae subsequently relegated Beurling's name to the synonymy of *Octopleura quinquenervia* or *Ossaea quinquenervia* without comment (Triana 1871; Cogniaux 1891; Wurdack 1980). Gleason (1939) makes no mention of it in his regional revision of *Clidemia*.

Among congeners, *C. quinquenervia* is closely allied to the rare Costa Rican endemic, *C. coronata* Gleason. Both species share a similar indument of asperous-headed hairs, densely papillose-furfuraceous petals, a completely inferior 5-locular ovary, and a smooth seed coat. Important distinctions between these species can be found in readily observed vegetative characters. In *C. coronata* the leaves are 5–7-nerved (vs. 5–9-plinerved), the blades are ciliate and ± entire (vs. ciliolate-denticulate) and the blade base is not decurrent on the petiole (vs. conspicuously so). Although both species also have anther connectives that are prolonged dorso-basally into appendages, the appendages on *C. coronata* are rounded and entire whereas those on *C. quinquenervia* are spur-like and gland-edged.

Clidemia rodriguezii Almeda, sp. nov.

(Fig. 9)

TYPE.— COSTA RICA: **Cartago**: Cantón de Paraíso, Cuenca del Reventazón. Orosí. Entrada a Tausito, aprox. 3 km después del cruce hacia la Estación Tapantí, 9°46′20″N, 83°47′10″W, 1400–1600 m, 15 Apr. 1998, *A. Rodríguez et al. 3239* (holotype: INB!; isotypes: CAS!, CR!, MO!, NY!, US!).

Ramuli quadrangulati; internodi alatis demum carinatis, nodis tumidus et carinatis. Petioli 6.3–12 cm long; lamina 6–23 × 11.7–16.2 cm ovata vel subcordata apice acuminata basi rotundata, 7–9-nervata, nervi subtus in axillis domatiis instructi. Inflorescentia lateralis in ramulis infra folia plerumque oriunda 1–1.5 cm longa multiflora; flores 4-meri, bracteolis 1.5–2 × 0.25–0.5 mm. Calycis tubus 1 mm longus, lobis interioribus 0.5 × 1 mm ovato-triangularibus, dentibus exterioribus 2 × 1 mm oblongis. Stamina isomorphica glabra, antherarum thecae 2 × 0.25 mm subulatae poro ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 4-loculare et omnino inferum glabrum.

Shrub 0.4–1.5 m tall, the glabrous cauline internodes thick and quadrate, distinctly alate when young becoming carinate with age with opposing faces 0.8–1.2 cm wide, the nodes bearing prominent expanded (0.25–0.75 mm) interpetiolar ridges. Very young nodes, vegetative buds, and young petioles (adaxial surface) copiously setose with smooth early deciduous hairs 0.5–1 mm long. Leaves of a pair equal to somewhat unequal, otherwise identical, bearing two pairs of vesicular domatia (2–4 mm long) on the abaxial blade base where the primary veins diverge from one another: petioles 6.3–12 cm long; blades, 16–23 × 11.7–16.2 cm, chartaceous and brittle when dry, ovate to subcordate, apex acuminate, base broadly rounded, margin ciliate-serrulate, 7–9-nerved, glabrous on the adaxial surface at maturity or with remnant tufts of smooth hairs along basal portions of the impressed primary veins, essentially glabrous abaxially. Inflorescence 1–1.5 cm long, a congested cluster of axillary dichasia, typically paired at each node below the leaves; rachis nodes persistently setose with flexuous hairs 0.5–1 mm long, the internodes glabrate and the pedicels copiously beset with minute stellulate or branched hairs; bracteoles 1.5–2 × 0.25–0.5 mm, oblong to narrowly triangular, glabrous except for a short terminal hair. Flowers 4-merous on pedicels 1.5–2 mm long. Hypanthia (at anthesis) suburceolate with a cylindric distal neck about 1 mm long, copiously stellulate-puberulent with an occasional scattering of smooth spreading flexuous hairs. Calyx tube 1 mm long, the calyx lobes 0.5 × 1 mm, ovate-triangular, fleshy, glabrous, erect and concealed by the calyx teeth; calyx teeth 2 × 1 mm, oblong, glabrous, widely spreading at anthesis and in fruit. Petals 2 × 0.75 mm, glabrous, white, oblong. Stamens isomorphic; filaments 2.5 mm long, glabrous; anthers 2 mm long, 0.25 mm wide, white, subulate with a ventrally inclined pore; connective somewhat thickened dorsally but neither prolonged nor appendaged below the thecae. Ovary 4-locular, completely inferior, apex glabrous and smooth. Style 5 mm long, glabrous; stigma punctiform. Berry 3–5 × 3–5 mm, purple at maturity. Seeds 0.5 mm long, ovoid to obovoid with a vaguely rugose testa.

PHENOLOGY.— Flowering material has been collected in April and August; fruiting specimens in March, April, and August.

DISTRIBUTION.— Rare and local in central and southeastern Costa Rica where it is known from the lower northern slopes of the Fila Matama, vicinity of Tapantí National Park, and the Parrita Valley north of Quepos at 700–1600 m.

PARATYPES.— COSTA RICA: **Limón**: Almirante. Fila divisoria entre la Cuenca superior del Río Xichiari y la cuenca superior del Río Boyei, 09°45′50″N, 83°19′45″W, 12 Aug. 1995, *Herrera 8446* (CAS, CR). **San José**: Cantón de Tarrazu. Faja Costeña del Valle de Parrita en el camino a Quepos. Fila San Isidro, luego del cruce a San Isidro, 09°33′25″N, 84°04′48″W, 26 Mar. 1995, *Morales & Ureña 3767* (CAS, INB).

DISCUSSION.— This little-collected species is characterized by a combination of many unusual characters. The uppermost internodes are quadrate, winged, and quite thick with opposing faces 0.8–1.2 cm wide (Fig. 9A). The nodes have prominent expanded interpetiolar ridges (Fig. 9A). The 4-merous flowers are borne in axillary congested dichasia that are typically paired at a node (Fig. 9A). The hypanthia are constricted distally into a conspicous neck (Fig. 9F). The exterior calyx teeth are foliaceous, adnate to and conceal the actual calyx lobes (Fig. 9C). Two pairs of vesicular domatia are produced at the abaxial blade base where the primary veins diverge from one another (Fig. 9B) but these are unusually small when compared to other domatia-bearing species in the genus.

In leaf shape and inflorescence architecture, *C. rodriguezii* is similar to and may be most closely related to *C. discolor* (Triana) Cogn., another species with 4-merous flowers and a 4-locular

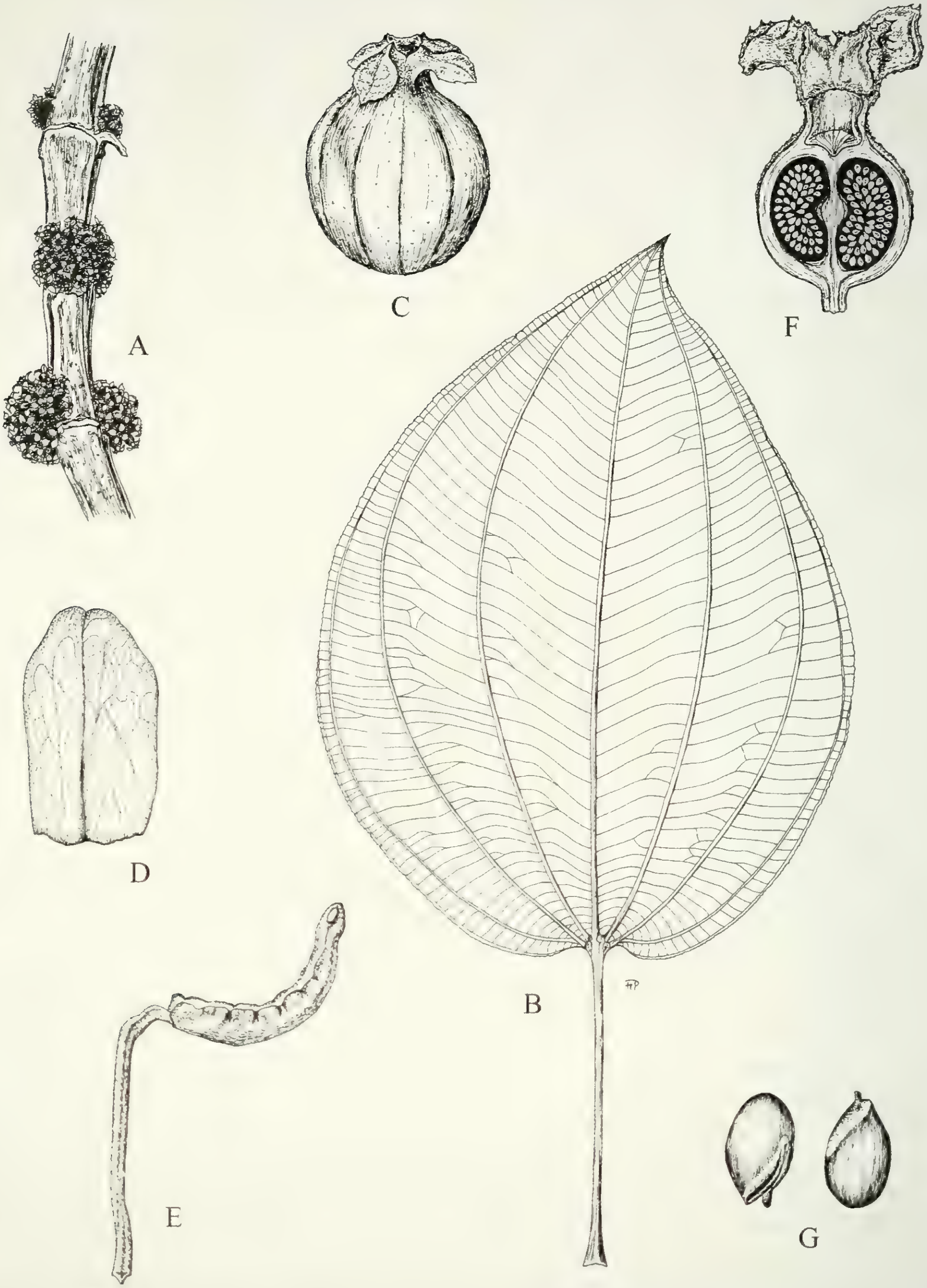

FIGURE 9. *Clidemia rodriguezii* Almeda. A. naturally defoliated branch with infructescences, × ca. 1; B. representative leaf (abaxial surface), × ½; C. berry, × ca. 7; D. petal, × 17; E. stamen (profile view), × ca. 17; F. immature berry (longitudinal section), × ca. 10; G. seeds, × ca. 32. (A – G from *Rodríguez et al. 3239.*)

ovary that is completely inferior. The latter has slender unwinged upper internodes that are rounded or rounded-quadrate and lack prominent interpetiolar ridges. The leaf blades of *C. discolor* also lack vesicular domatia at the abaxial base and the internodes of the inflorescence rachis are farinose-furfuraceous with an admixture of clavate glands (vs. glabrate to minutely stellulate).

Clidemia rodriguezii is also reminiscent of *C. epiphytica* (Triana) Cogn. Both species have 4-merous flowers, a 4-locular completely inferior ovary, and foliaceous calyx teeth that are adnate to and obscure the calyx lobes. The latter differs most notably in being a climbing vine with distinctly dimorphic leaf blades at each node that lack vesicular domatia.

ETYMOLOGY.— This species is named for Alexander Rodríguez G. (b. 1972), student of Costa Rican Asteraceae and collector of the type series. His collections were accompanied by excellent pickled material of flowers and fruits that facilitated the study and illustration of this species.

***Clidemia tenebrosa* Almeda, sp. nov.**

(Fig. 10)

TYPE.— PANAMA: **Coclé**: forested slopes above El Copé along abandoned road leading to the Continental Divide, 8°38′N, 80°38′W, 700–850 m, 24 Jan. 1989, *F. Almeda et al. 6392* (holotype: CAS!; isotypes: MO!, PMA!).

Ramuli primum obtuse sulcato-quadrangulati demum teretes sicut petioli folia inflorescentia hypanthiaque pilis laevibus (pro parte glanduliferis) dense induti. Lamina 22–44.5 × 10–16.5 cm elliptica vel ovato-elliptica apice gradatimque acuminato basi late acuta vel obtusa, subtus in venis primariis secundariisque sparse pilis glanduliferis induti et sparse vel sparsissime stellato-puberula, 7–9-plinervata; petioli liberi 2.5–5.5 cm longi; formicaria 4–7 cm longa ad petiolorum apices evoluta et in laminarum bases immersa. Inflorescentiae multiflorae in foliorum superiorum axillis oppositis; flores 5-meri, bracteolis 1.5–2 × 0.25 mm; calycis tubus ca 0.5 mm, lobis interioribus 0.75–1 × 1–1.5 mm triangularibus, dentibus exterioribus 4–5 mm longis subulatis. Stamina isomorphica glabra, antherarum thecae 1.5 × 0.5 mm oblongae vel subulatae poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et omnino inferum apice modice glanduloso-puberulo.

Monopodial or sparingly branched shrub 1–3 m tall with rounded-quadrate internodes. Upper internodes, petioles, both leaf surfaces, inflorescence rachis, pedicels, hypanthia and calyx teeth copiously covered with smooth (gland-tipped in part) spreading hairs 1.5–3 mm long. Leaves of a pair essentially equal in size and consistently bearing paired elongate formicaria 4–7 cm long extending from the adaxial blade base onto the distal portions of the petiole; petioles 3–8 cm long; blades 22–44.5 × 10–16.5 cm, chartaceous, flexuous when fresh and very brittle when dry, elliptic to ovate-elliptic, apex gradually acuminate, base rounded to obtuse, margin inconspicuously denticulate, 7–9-plinerved with the innermost pair of primary veins diverging from the median vein 2–3 cm above the blade base, the primary and higher order veins sparsely beset with a ground layer of minute glands sometimes sparingly intermixed with minute stellate hairs. Inflorescence 2–3.5 cm long, axillary congested dichasia that are paired at a node, the rachis, pedicels and hypanthia sparsely to moderately beset with a ground cover of tardily deciduous glands and stellulate hairs; bracteoles 1.5–2 × 0.25 mm (including the apical hair), subulate, inconspicuous and obscured by the surrounding indument of spreading hairs. Flowers 5-merous on pedicels 0.5–1 mm long. Hypanthia (at anthesis) subcylindric. Calyx tube ca. 0.5 mm long, the calyx lobes 0.75–1 × 1–1.5 mm, triangular, glandular-puberulent adaxially and along the margins; calyx teeth 4–5 mm long, subulate, greatly exceeding and obscuring abaxial surface of the calyx lobes. Petals 4–5 × 2–3.5 mm, glabrous, translucent white, obovate to oblong. Stamens isomorphic; filaments 2.5–3 mm

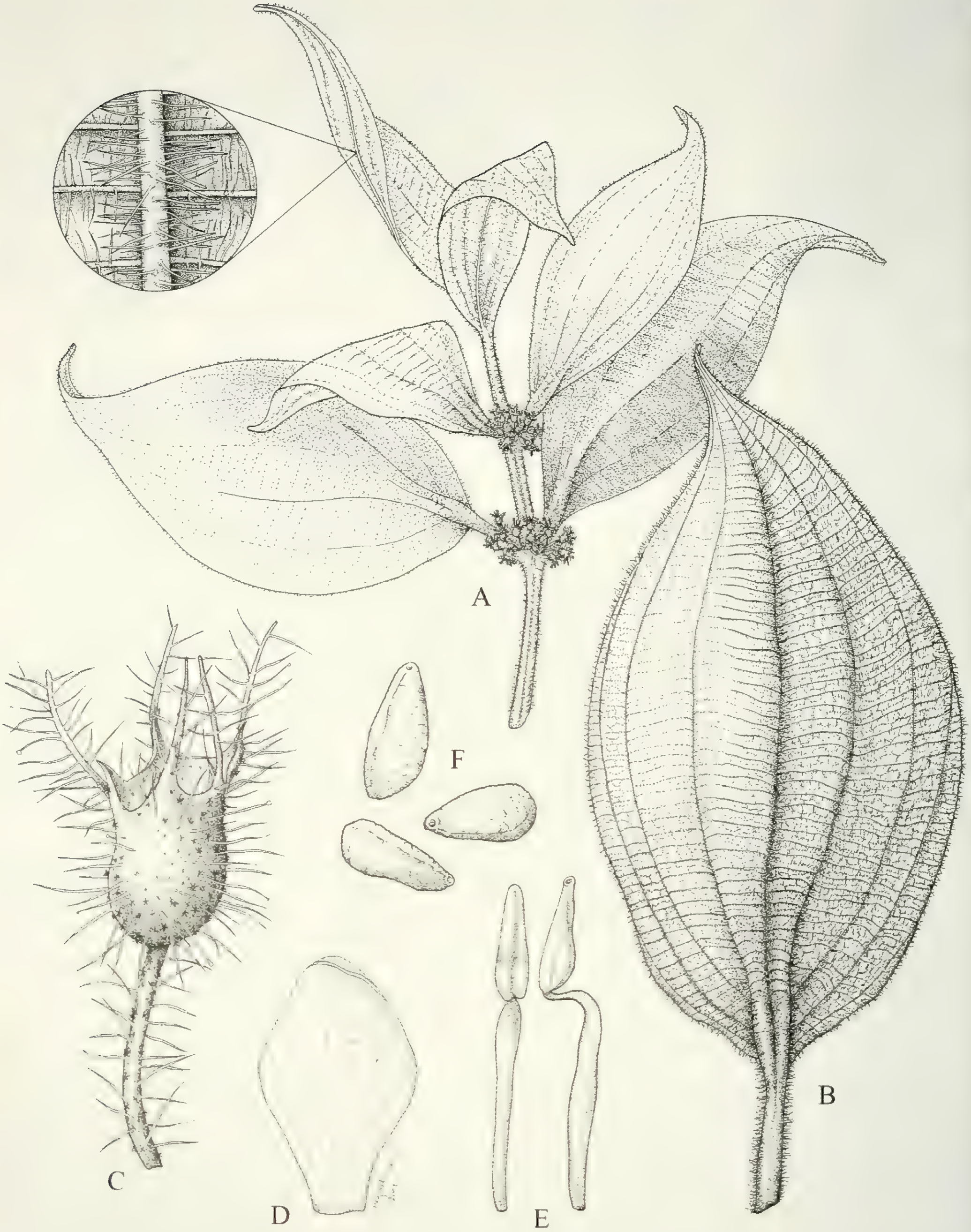

FIGURE 10. *Clidemia tenebrosa* Almeda. A. habit, × ⅓; B. representative leaf (adaxial surface), × ca. ⅓; C. immature berry, × 5; D. petal (adaxial surface), × 8; E. stamens, ventral view (left) and profile view (right), × 12; F. seeds, × ca. 38. (A and B from *Knapp 3734*; C from *Almeda et al. 6392*; D and E from *Croat 67552*; F from *Almeda et al. 7657*.)

long, glabrous; anthers 1.5 mm long, 0.5 mm wide, white, linear-oblong to subulate, truncate at the apex with a somewhat dorsally inclined pore; connective somewhat thickened dorsally but neither prolonged nor appendaged below the thecae. Ovary 5-locular, completely inferior, apex somewhat crateriform at anthesis, minutely glandular puberulent like the adaxial vascular ring of the hypanthium. Style glabrous, 6 mm long; stigma capitate. Berry 6 × 5 mm, blue at maturity. Seeds 0.5 mm long, obovoid with a smooth to vaguely rugulate testa.

PHENOLOGY.— Flowering material has been collected from January through March, July, September, and December; fruiting collections have been gathered in January, February, July, September, and December.

DISTRIBUTION.— Cloud forests of west-central Panama at 200–1100 m, typically in deep shade.

PARATYPES.— PANAMA: **Coclé**: forested slopes above El Copé along abandoned road leading to the Continental Divide, 25 Feb. 1988, *Almeda et al. 5935* (CAS); about 7–10.5 km beyond El Copé in Omar Torrijos National Park along end of rocky trail to Río Blanco and Limón beyond Alto Calvario, 21 Feb. 1996, *Almeda et al. 7657* (CAS, MO, PMA); vicinity of La Mesa, N of El Valle de Antón, along N slope of Cerro Gaital, 8°37′N, 80°08′W, 14 Jul. 1987, *Croat 67286* (CAS); Alto Calvario along summit of Continental Divide, 5.5 mi. N of El Copé, 8°39′N, 80°36′W, 13 Sep. 1987, *Croat 67552* (CAS); area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, 3 Feb. 1983, *Davidse & Hamilton 23514* (CAS); Atlantic drainage near Continental Divide at sawmill above El Copé, 7 Mar. 1982, *Hammel & Trainer 11314* (CAS); trail from Río Blanco del Norte to Caño Sucio, 8°44′N, 81°40′W, 21 Feb. 1982, *Knapp 3734* (CAS); between Caño Sucio and waterfall at base of Cerro Tife, ca. 4 hr. hike, 8°38′N, 80°36′W, 13 Dec. 1980, *Sytsma et al. 2557* (CAS). **Panamá**: sendero al Cerro Campana, 8°40′N, 79°55′W, 23 Sep. 1993, *Correa & Montenegro 10036* (PMA); Cerro Campana near the FSU field station trail up the mountain, 9 Aug. 1970, *Kennedy & Luteyn 435* (CAS, US); Altos de Campana, sendero del Tigre, 11 July 1998, *Montenegro & Galdames 1979* (CAS).

DISCUSSION.— *Clidemia tenebrosa* is like *C. collina*, *C. folsomii*, and *C. myrmecina* in having 5-merous flowers and formicaria positioned at the base of the blade but extending on to a portion of the petiole. Among these species, *C. tenebrosa* most closely resembles *C. collina.* Both species have plinerved leaf blades with at least the innermost pair of primary veins diverging from the midvein well above the blade base on the abaxial surface and a short inflorescence axis that is obscured by the dense indument. In *C. collina*, however, the leaf blades are prevailingly ovate varying to ovate-elliptic and mostly 9.5–21 cm long (vs. prevailingly elliptic varying to ovate-elliptic and 22–44.5 cm long), the inflorescence is pseudolateral but not paired at a node (vs. axillary and paired at a node), the understory indument on hypanthia is lacking or sparingly covered with minute deciduous glands (vs. a sparse to moderate cover of minute stellulate hairs and a scattering of minute glands), the anther thecae are yellow (vs. white), and the seed coat is densely tuberculate (vs. smooth to vaguely rugulate). The flowers and fruits of *C. tenebrosa* and other congeners with congested copiously hairy inflorescences are difficult to study once they are pressed and dried. This coupled with the highly fugacious nature of floral parts and brittleness of the inflorescence rachis typically make for specimens that are incomplete. To facilitate the preparation of specimens that are adequate for study, collectors should make every effort to preserve reproductive structures in a liquid medium in the field.

ETYMOLOGY.— The epithet for this species is derived from the Latin word, *tenebrosus*, dark, gloomy, or of shaded places, alluding to its shaded forest habitat.

Clidemia ventricosa Almeda, sp. nov.

(Fig. 11)

Type.— Panama: **Comarca de San Blas**: El Llano–Cartí road, 19.1 km from Interamerican Hwy., 9°19′N, 78°55′W, elev. 350 m, 5 Mar. 1985, *G. de Nevers et al. 4963* (holotype: CAS!; isotypes: CAS!, INB, KUNA, MEXU, MO, PMA).

Ramuli teretes sicut foliorum venae primariae subtus inflorescentia hypanthiaque pilis laevibus plerumque 3–7 cm longis induti. Lamina 11–23.5 × 4.1–8.5 cm ovato-elliptica vel ovata apice attenuata vel acuta basi rotundata, 5–7-nervata vel 5–7-plinervata; formicaria 1–2 cm longa ad petiolorum apices evoluta et raro in laminarum bases immersus. Inflorescentia primum terminalis demum lateralis; flores 5-meri, bracteolis 3.5–4.5 × 0.25–0.5 mm; calycis tubus 1 mm, lobis interioribus 0.5–0.75 × 1 mm triangularibus vel orbicularibus, dentibus exterioribus 2.5–3.5 mm longis subulatis. Stamina isomorphica glabra, antherarum thecae 3–4.2 × 0.5 mm subulatae poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 5-loculare et 2/3 inferum apice modice glandulosum-puberulo.

Sparingly branched shrub 0.5–1 m tall. The terete upper internodes, abaxial surface of petioles, and elevated primary veins on abaxial foliar surfaces copiously covered with appressed smooth hairs 3–7 cm long. Leaves of a pair equal to somewhat unequal in size; petioles 1–4 cm long with bulbous paired formicaria 1–2 cm long borne distally and sometimes barely extending onto the blade, the adaxial surface of the petioles and formicaria setose with spreading hairs 0.6–1.7 cm long; blades 11–23.5 × 4.1–8.5 cm, chartaceous, brittle when dry, oblong-ovate to elliptic-ovate, apex attenuate to acute, base rounded, margin entire, 5–7-nerved or if plinerved then the innermost pair of primary veins diverging from the median vein 0.5 cm above the blade base, the higher order veins and actual surface inconspicuously beset with scattered minute glands or nearly glabrous. Inflorescence 1.5–2 cm long, a pseudolateral congested modified dichasium, the rachis, hypanthia, and calyx teeth moderately setose with widely spreading hairs 0.4–1 cm long underlain by a scattering of very minute inconspicuous glands; bracts and bracteoles 3.5–4.5 × 0.25–0.5 mm (including the apical hair), subulate to oblong-subulate, inconspicuous and obscured by the surrounding setose indument. Flowers 5-merous on minutely glandular-puberulent pedicels 1–2 mm long. Hypanthia suburceolate at anthesis, prolonged distally into a cylindric neck 1 mm long above the ovary apex and below the vascular ring. Calyx tube 1 mm long, the calyx lobes 0.5–0.75 × 1 mm, rounded-triangular to semicircular, glandular-puberulent along the margins; calyx teeth 2.5–3.5 mm long (excluding the apical hair), greatly exceeding and somewhat obscuring abaxial surfaces of the calyx lobes, oblong to subulate. Petals 8 × 2.5 mm, glabrous, pink or reportedly yellowish with a tinge of purple at the tip (*Nee 10474*), oblong to narrowly obovate. Stamens isomorphic; filaments 3–3.5 mm long, glabrous, abruptly constricted at the junction with the thecae; anthers 3–4.2 × 0.5 mm, yellow, subulate with a dorsally inclined pore; connective thickened and somewhat ridged dorso-basally but neither prolonged nor appendaged below the thecae. Ovary 5-locular, 2/3-inferior, apex prolonged into a deciduously glandular truncate cone 1 mm long at anthesis. Style 9–9.5 mm long, glabrous, straight; stigma subcapitate to truncate. Berry 6–7 × 6–8 mm when dry, purple at maturity. Seeds 0.5 mm long, bluntly triangular in outline with a minutely asperulate testa.

Phenology.— The single known flowering collection was made in March; fruiting specimens have been collected from August through October.

Distribution.— Local and uncommon in low rainforests of north-central Panama, often in deep shade along creeks and in the vicinity of streams at 300–400 m.

Paratypes.— Panama: **Comarca de San Blas**: El Llano–Cartí road, 18 km from Interamerican Hwy., 9°19′N, 78°55′W, 7 Sept. 1984, *de Nevers 3877* (CAS); Nusagandi, El Llano-

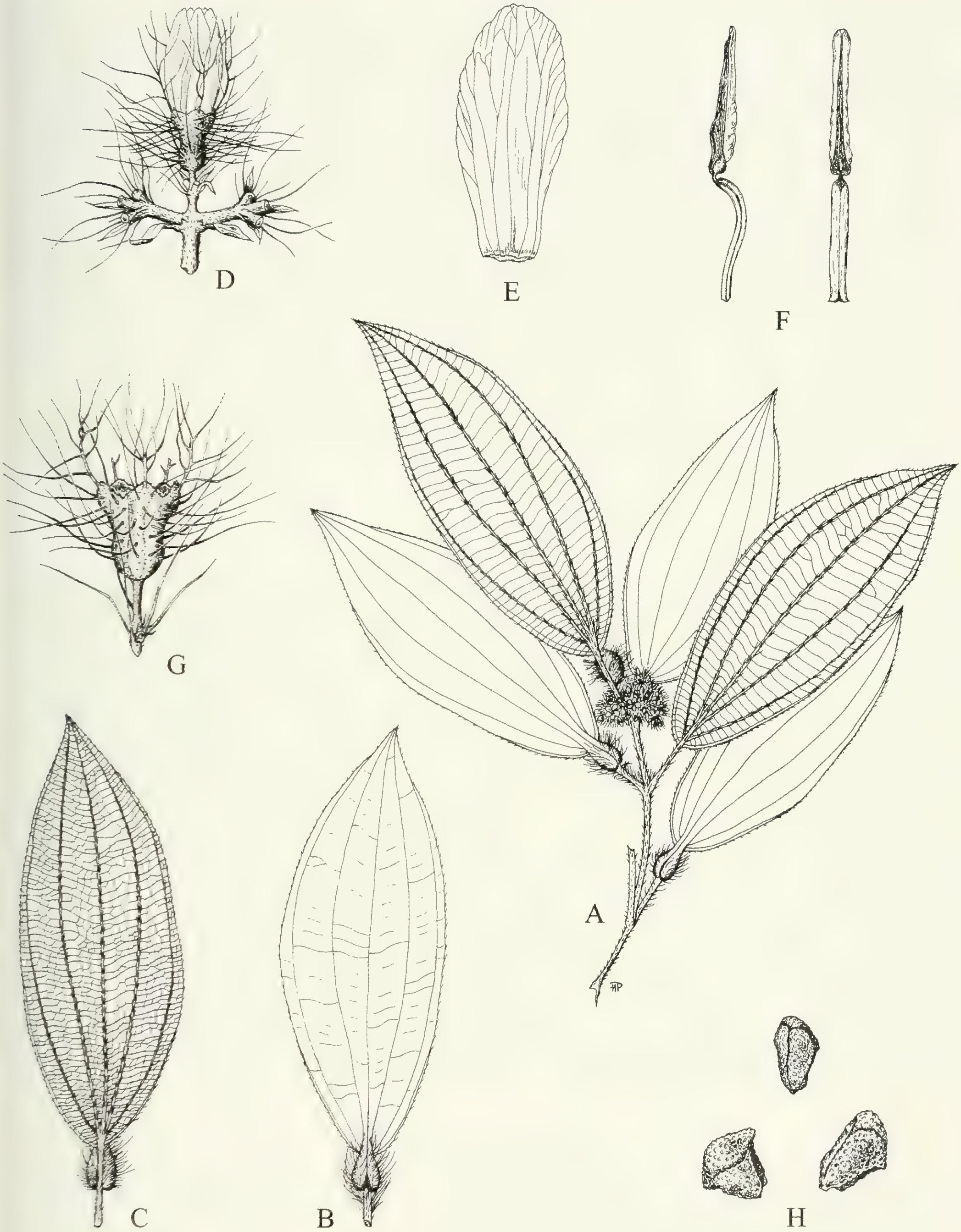

FIGURE 11. *Clidemia ventricosa* Almeda. A. habit, × ca. ⅓; B. representative leaf (adaxial surface), × ⅓; C. representative leaf (abaxial surface), × ⅓; D. flower (just prior to anthesis), × 2; E. petal (adaxial surface), × 5; F. stamens, profile view (left) and dorsal view (right), × 6; G. young fruiting hypanthium, × 2; H. seeds, × ca. 26. (A–G from *de Nevers et al. 4963*; H from *Folsom et al. 6182*.)

Cartí road, along a creek on the Atlantic slope, 9°19′N, 78°15′W, 10 Aug. 1984, *de Nevers & Gonzáles 3673* (CAS); El Llano–Cartí road, headwaters of Atlantic drainage, 9°19′N, 78°55′W, 29 Aug. 1984, *de Nevers & Gonzáles 3784* (CAS); El Llano–Cartí road, 9°19′N, 78°55′W, 1 June 1985, *de Nevers & Herrera 5821* (CAS). **Panamá**: road from El Llano to Cartí, 12.4 km N of Panamerican Hwy., 31 Oct. 1977, *Folsom et al. 6182* (CAS); wet forest along El Llano–Cartí road, 12 km N of Panamerican Hwy., 11 Mar. 1974, *Nee 10474* (MO, US).

DISCUSSION.— *Clidemia ventricosa* can be recognized by its glabrous adaxial foliar surfaces, mostly petiolar formicaria (Fig. 11B) that sometimes barely extend on to the blade base, smooth appressed hairs on the upper internodes, abaxial surface of the petioles, and elevated primary veins on abaxial foliar surfaces (Fig. 11C), pseudolateral congested dichasia (Fig. 11A), and widely spreading hairs on the inflorescence rachis, hypanthium, and calyx teeth (Fig. 11C). Among the Central American species of *Clidemia* with 5-merous flowers, only *C. taurina* and some populations of *C. pubescens* have petiolar formicaria like *C. ventricosa*. Both of these species are easily distinguished from *C. ventricosa* by their spreading or retrorse hairs on upper internodes and spreading hairs on elevated primary veins on the abaxial foliar surfaces.

ETYMOLOGY.— The epithet for this species is derived from the Latin word, *ventricosa*, swollen, in reference to the conspicuously bulbous ant domatia at the distal end of each petiole.

ACKNOWLEDGMENTS

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Appendix I

Species of *Clidemia* known to produce pouch-like ant domatia (formicaria) on some or all leaves, petioles, or branchlets nodes, and their geographic distributions.

C. *acostae* Wurdack — Ecuador
C. *ayangannensis* Wurdack — Guyana
C. *allardii* Wurdack var. *allardii* — Colombia, Ecuador, Peru
C. *allardii* Wurdack var. *maranonensis* Wurdack — Ecuador, Peru, Brazil
C. *ciliata* D. Don var. *elata* (Pittier) Uribe – Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru
C. *ciliata* D. Don var. *testiculata* (Triana) Uribe — Venezuela, Colombia
C. *collina* Gleason — Panama
C. *crenulata* Gleason — Belize, Guatemala, Honduras, Costa Rica, Nicaragua, Colombia, Ecuador
C. *foliosa* Gleason — Peru
C. *folsomii* Almeda — Panama
C. *heterophylla* (Desr.) Gleason — Colombia, Ecuador, Peru
C. *heptamera* Wurdack — Venezuela, Guyana
C. *inobsepta* Wurdack — Colombia, Ecuador
C. *juruensis* (Pilger) Gleason — Venezuela, Brazil, Peru
C. *killipii* Gleason — Colombia
C. *lanuginosa* Almeda — Costa Rica, Panama
C. *myrmecina* Gleason — Panama, Colombia
C. *neblinae* Wurdack — Venezuela
C. *pilosa* D. Don — Venezuela, Colombia, Ecuador, Peru
C. *pubescens* Gleason — Costa Rica, Panama
C. *rodriguezii* Almeda — Costa Rica (NB. The vesicular domatia of this species may be acarodomatia.)
C. *setosa* (Triana) Gleason — Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama
C. *spectabilis* Gleason — Nicaragua, Costa Rica, Panama
C. *sprucei* Gleason — Ecuador, Peru
C. *taurina* Gleason — Costa Rica, Panama
C. *tenebrosa* Almeda — Panama
C. *tococoidea* (DC.) Gleason — Venezuela, Brazil, Colombia
C. *ventricosa* Almeda — Panama

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Phylogenetic Systematics of *Okenia, Sakishimaia, Hopkinsiella* and *Hopkinsia* (Nudibranchia: Goniodorididae) with Descriptions of New Species from the Tropical Indo-Pacific

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The anatomy of eight species of *Okenia*, four species traditionally placed in *Hopkinsia* and one species of *Sakishimaia* was examined. The descriptions of previously described species, *Okenia pellucida, O. japonica, Hopkinsia rosacea, H. plana, H. pilosa, H. nakamotoensis* and *Sakishimaia kondoi* were expanded from prior morphological studies. Six new species of *Okenia* are described from the Indo-Pacific tropics. *Okenia brunneomaculata* is described from specimens collected from Indonesia and the Philippines. *Okenia purpureolineata* is known only from Okinawa in the Ryukyu Islands. *Okenia kendi* is described from specimens from Indonesia and the Philippines. *Okenia virginiae* is described from South Africa and is also known from Oman. *Okenia lambat* is described from the Philippines. *Okenia liklik* is described based on specimens from Papua New Guinea and the Philippines.

Preliminary phylogenetic studies reveal several important aspects about the relationships of these taxa. Collectively, these taxa appear to form a monophyletic clade. *Okenia mediterranea* is the most basal taxon in the present analysis and is the sister group to all of the other taxa. *Hopkinsia, Sakishimaia* and *Hopkinsiella* are nested within *Okenia* in the analysis presented. The characteristics employed to distinguish *Sakishimaia* and *Hopkinsiella* from *Hopkinsia* are not distinctly different or represent autapomorphies or symplesiomorphies. *Hopkinsia*, when *Sakishimaia* and *Hopkinsiella* are included, constitutes a monophyletic taxon. However, maintenance of *Hopkinsia* as a distinct taxon renders *Okenia* paraphyletic. On this basis, *Hopkinsia, Hopkinsiella* and *Sakishimaia* are considered as synonyms of *Okenia* to preserve the monophyly of this oldest taxon.

The Indo-Pacific Goniodorididae consist of species that have been placed in the genera *Ancula* Loven, 1846; *Goniodoris* Forbes and Goodsir, 1839; *Goniodoridella* Pruvot-Fol, 1933; *Hopkinsia* MacFarland, 1905; *Hopkinsiella* Baba, 1938; *Murphydoris* Sigurdsson, 1991; *Okenia* Menke, 1830; *Sakishimaia* Hamatani, 2001; *Spahria* Risbec, 1928 and *Trapania* Pruvot-Fol, 1931. These taxa have been sporadically studied for the last 100 years with additional species described in a wide variety of faunistic and systematic treatments. Recently, Rudman's (1987) monographic study of Indo-Pacific species of *Trapania* has significantly added to our knowledge of Indo-Pacific Goniodorididae. Few taxonomic studies have focused on the distinctions between the genera *Okenia*, *Hopkinsiella*, *Hopkinsia* and *Sakishimaia*. Bouchet and Ortea (1983) revised the systematic distinctions between the former three genera and concluded that *Okenia* and *Hopkinsia* represent distinct genera, whereas *Hopkinsiella* is regarded as junior synonym of *Hopkinsia*. Most recently, Hamatani (2001) described two new species from Japan, a species of *Hopkinsia* and a member of a new genus, *Sakishimaia*.

Recent investigations of tropical coral reef ecosystems throughout the Indo-Pacific tropics from South Africa, the Philippines, Indonesia, Papua New Guinea, the Marshall Islands, and the Hawaiian Islands have yielded specimens of six new species of *Okenia*. Description of these taxa is the focus of this investigation. The discovery of additional specimens *Okenia pellucida* Burn, 1967; *O. japonica* Baba, 1949; *Hopkinsia pilosa* Bouchet and Ortea, 1983; *Hopkinsia nakamotoensis* Hamatani, 2001 and *Sakishimaia kondoi* Hamatani, 2001 has permitted the amplification of these species. Anatomical examination of these taxa and preliminary phylogenetic analyses undertaken here require systematic revision of several goniodoridid taxa. All specimens examined here are housed in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ) and the South African Museum (SAM).

SPECIES DESCRIPTIONS

Okenia Menke, 1830

Type species: *Okenia elegans* (Leuckart, 1828), by monotypy.

Idalia Leuckart, 1828 (type species, *Idalia elegans* (Leuckart, 1828), by original designation).
Idaliella Bergh, 1881 (type species, *Idaliella elegans* (Leuckart, 1828), by original designation).
Idalina Norman, 1890 (type species, *Idalina elegans* (Leuckart, 1828), by original designation).
Cargoa Vogel and Schultz, 1970 (type species *Cargoa cupella* Vogel and Schultz, 1970, by original designation).
Hopkinsia MacFarland, 1905 (type species: *Hopkinsia rosacea* MacFarland, 1905, by monotypy). SYN. NOV.
Hopkinsiella Baba, 1938, (type species, *H. hiroi* Baba, 1938, by original designation). SYN. NOV.
Sakishimaia Hamatani, 2001, (type species, *S. kondoi* Hamatani, 2001, by original designation). SYN. NOV.

Okenia pellucida Burn, 1967

(Figs. 1F, 2–3)

Okenia pellucida Burn, 1967:52, pls. X–XI, figs. 1–3.

MATERIAL EXAMINED.— CASIZ 078645, seven specimens, Maalena Bay, Maui, Hawaiian Islands, 6 m depth, 4 June 1991, P. Fiene Severns. CASIZ 078493, 26 specimens, 1 dissected, Marang River Mouth, 16 km s. of Kuala Terengganu, Malay Peninsula, Malaysia, intertidal zone, 26 July, 1991, T.M. Gosliner. CASIZ 168016, two specimens, Sand Island, Palmyra Atoll, Oceania, 10 m depth, 27 May 2002, T.M. Gosliner.

DISTRIBUTION.— Australia (Burn 1967), United Arab Emirates (Behrens 2001), Hawaii (Gosliner, Johnson, and Bertsch 1986), Japan (Kurihara 1999) Palmyra Atoll and Malaysia (both from present study).

NATURAL HISTORY.— *Okenia pellucida*, together with its elongate egg masses, is found commonly on large masses of the ctenostomatous bryozoan, *Zoobotryon* sp.

EXTERNAL MORPHOLOGY.— The body is elongate (7–20 mm in length) with numerous elongate, rounded papillae situated along the notal margin and on the remainder of the notum. The body (Fig. 1F) is translucent white with numerous thin brown lines that form an interconnecting network on the notum. The rhinophores also contain patches of brown pigment. The rhinophores are elongate with 11 well–spaced lamellae. The gill consists of 8 bipinnate branches.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump directed dorsally. Numerous small, elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buc-

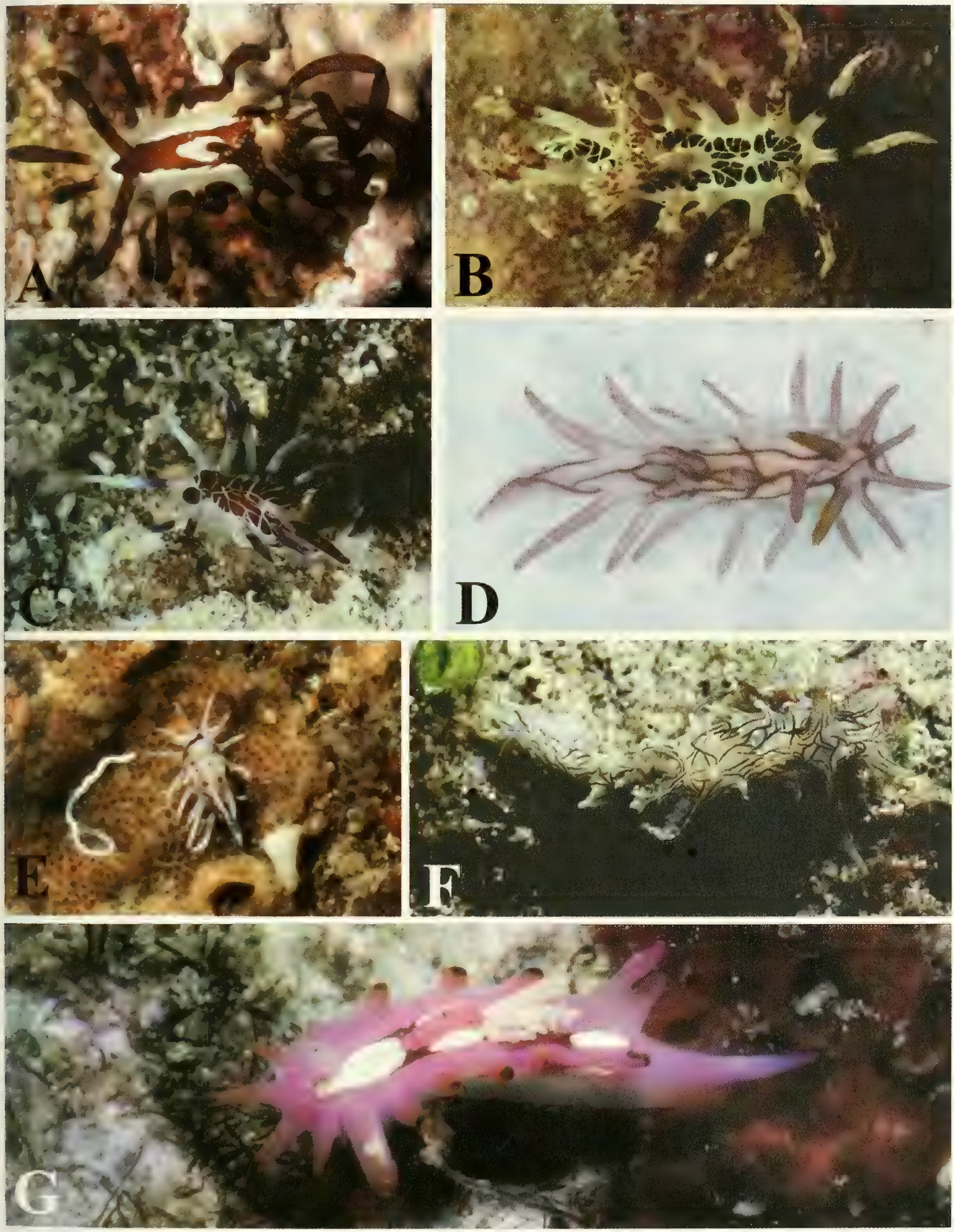


FIGURE 1. Living animals. A. *Okenia kendi* sp. nov., Sepok Point, Luzon, Philippines. B. *Okenia lambat* sp. nov. (CASIZ 084283), Devil's Point, Luzon, Philippines. C. *Okenia virginiae* sp. nov. (SAMA 35558), Vetchies Pier, Durban, South Africa. D. *Okenia purpureolineata* sp. nov., Seragaki Tombs, Okinawa, Japan, photo by R.F. Bolland. E. *Okenia brunneomaculata* sp. nov., Luzon, Philippines. F. *Okenia pellucida* Burn, 1967 (CASIZ 071398), Hawaii. G. *Okenia liklik* sp. nov., Barracuda Point, Madang, Papua New Guinea. All photos by T.M. Gosliner except as otherwise noted.

cal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is 16 × 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 2) are wide basally with an elongate acute bifid cusp. The masticatory margin of the inner lateral bears 17 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 2) with two short, blunt cusps along the outer edge.

Reproductive system (Fig. 3).— The preampullary duct is thin and elongate and expands into the elongate, sausage–shaped ampulla. The ampulla divides into a short oviduct that enters the female gland mass and a more elongate vas deferens. The proximal portion of the vas deferens is prostatic but relatively narrow. It curves and continues as an elongate loop that eventually widens slightly into the highly convoluted muscular, ejaculatory portion. The penial bulb is wide and conical. From it protrudes a rounded, fleshy penial papilla. The vagina is short and wide at its exit adjacent to the penis. More distally it narrows and continues as a thin duct that enters the base of the large, pyriform bursa copulatrix. From the base of the bursa is a second duct that joins with the smaller, more rounded receptaculum seminis. Near the base of the receptaculum the uterine duct separates from the duct joining the receptaculum and bursa and enters the female gland mass. The female gland mass consists of three portions, the albumen, membrane and mucous glands. The mucous gland is the largest of the nidamental glands.

Figure 2. *Okenia pellucida* Burn, 1967 (CASIZ 078493). Scanning electron micrograph of radular teeth.

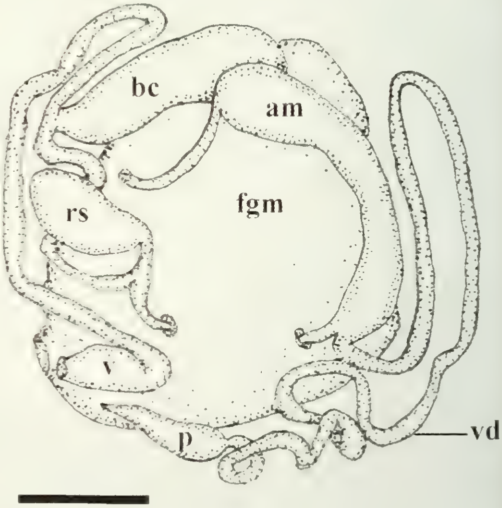


Figure 3. *Okenia pellucida* Burn, 1967 (CASIZ 078493). Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, rs = receptaculum seminis, v = vagina, vd = vas deferens; scale = 0.6 mm.

Discussion.— *Okenia pellucida* is immediately identifiable by its translucent white body color with a network of interconnecting thin brown lines. The present material agrees closely with that originally described by Burn (1967), with several exceptions. Burn did not describe the presence of oral glands surrounding the anterior end of the buccal mass. The original description included specimens with as many as 28 rows of radular teeth whereas the present material had only 16 rows. Burn also described the inner lateral teeth as having a smooth masticatory margin. The present material from Malaysia and specimens previously reported from the Hawaiian Islands (Gosliner, Johnson, and Bertsch 1986) have a series of triangular denticles along the masticatory margin. Despite these differences, the consistency in external anatomy, color pattern and reproductive anatomy suggest that all the material identified previously and from this study are conspecific. Recent records of this species support its wide ranging distribution from the United Arab Emirates to the Hawaiian Islands and Palmyra Atoll. This wide distribution of *Okenia pellucida* is not only facilitated by dispersal of planktotrophic larvae, but also by its association with the ctenostomatous bryozoan, *Zoobotryon* sp., which forms large masses carried by oceanic currents.

Okenia brunneomaculata Gosliner, sp. nov.

(Figs. 1E, 4–5)

Type material.— Holotype: CASIZ 168019, 20 m. depth, Ligpo Island, Calumpan Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 24 March 1993, T.M. Gosliner. Paratypes: CASIZ 085876, 4 specimens, 2 dissected, 20 m. depth, Ligpo Island, Calumpan Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 24 March 1993, T.M. Gosliner. CASIZ 083853, 1 specimen, 20 m. depth, Sepok Point, Maricaban Island, Batangas Province, Luzon, Philippines, 1–2 m depth, 26 February 1992, T.M. Gosliner. CASIZ 168017, three specimens, Tulamben, Bali, Indonesia, 21 October 2001, M.D. Miller. CASIZ 168018, two specimens, Tulamben, Bali, Indonesia, 21 October 2001, M.D. Miller.

Etymology.— The specific name, *Okenia brunneomaculata*, comes from the scattered brown spots found on the dorsal surface of the notum.

Distribution.— This species is known only from Luzon Island, Philippines and Bali, Indonesia (present study).

Natural History.— This species is found on ctenostomatous bryozoans on the undersides of the large foliose sponge colonies.

External morphology.— The living animals (Fig. 1E) are small, 4–6 mm in length. The preserved specimens are 2–3 mm. long. The body is moderately short and relatively high. There is a well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent white. There is a lateral band of chocolate brown and irregular spots of the same color scattered over the notum. There are 5–6 pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. Four to seven elongate papillae are scattered mid-dorsally anterior to the gill. A single mid-dorsal papilla is present posterior to the gill. The gill consists of 3–5 unipinnate branches. The rhinophores are elongate with 10 well–spaced lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and widens anteriorly The oral tentacles (Fig. 4A) are elongate and extend well beyond the margin of the foot.

Digestive system.— The buccal mass is thick and muscular with a rounded buccal pump directed posteriorly. There are no obvious oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth but no discrete jaw elements are visible. The cuticle expands as it enters the buccal pump. The radular formula is 14 × 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 5A) are broad basally with an acutely pointed cusp and 9–11 elongate denticles along the masticatory margin. The outer laterals are slightly smaller and reduced (Fig. 5B) with bifid cusp with two elongate projections along the outer side.

Reproductive system (Fig. 4B).— The preampullary duct is short and thin and expands into sausage–shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded segments. The distal end of the prostatic segment narrows into a short, curved ejaculatory portion that terminates in a narrow penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and elongate and connects directly to the large, spherical bursa copulatrix. At the base the bursa, the receptaculum duct emerges and parallels the vagina for some distance prior to joining the large, pyriform receptaculum seminis. The uterine duct emerges from near the base of the receptaculum and enters the female gland mass.

Discussion.— Several other species of *Okenia* have a whitish body color with brown markings: *O. angelensis* Lance, 1966; *O. zoobotryon* (Smallwood, 1910); *O. impexa* Marcus, 1957; *O. mija* Burn, 1967, *O. pellucida* Burn, 1967. All of these other species have much shorter notal papillae than does *O. brunneomaculata*. In *O. brunneomaculata*, the notal papillae are as long as the width of the body. The dorsal brown spots and bands of *O. brunneomaculata* are much larger than those found in the remaining species. The internal anatomy of *O. mija* remains unknown. Of the remaining species, *O. zoobotryon* and *O. angelensis* have outer lateral teeth that are short and rounded with bifid cusp (Marcus 1957; Valdés and Ortea 1995; Lance 1966). *Okenia brunneomaculata* and *O. impexa* have elongate outer laterals with a bifid cusp. In *O. impexa*, the outer lateral tooth has an additional basal denticle that is not present in *O. brunneomaculata*. *Okenia impexa* also has a single mid-dorsal papilla, whereas *O. brunneomaculata* has numerous dorsal papillae.

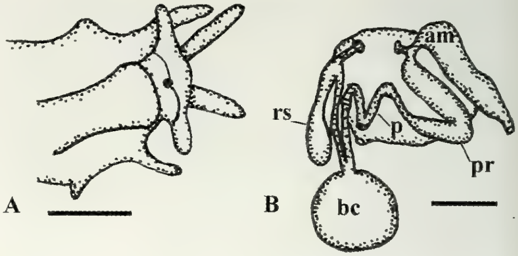


Figure 4. *Okenia brunneomaculata* sp. nov. (CASIZ 085876). A. Ventral surface of head; scale = 0.5 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.2 mm.

Figure 5. *Okenia brunneomaculata* sp. nov. (CASIZ 085876). Scanning electron micrographs of radular teeth. A. Inner lateral teeth. B. Outer lateral teeth. Scale = 2μm.

Okenia japonica Baba, 1949
(Figs. 6–7)

Okenia (*Okenia*) *japonica* Baba, 1949:45, fig. 45, pl. 15, fig. 52, Rudman and Darvell, 1990:39, pl. 2a.

Material examined.— CASIZ 070216, 1 specimen, 170 ft. [52 m] deep, Seragaki Beach, Okinawa, 22 April 1989, R.F. Bolland. CASIZ 099075, 1 specimen, 190 ft [58 m] deep, Seragaki Tombs, Okinawa, 12 March 1994, R.F. Bolland. CASIZ 105350, 2 specimens, 180 ft [55 m] deep, Seragaki Beach, Okinawa, 24 March 1994, R.F. Bolland. CASIZ 115378, 1 specimen, 190 ft [58 m] deep, Seragaki, Okinawa, 30 April 1989, R.F. Bolland. CASIZ 115382, 2 specimens dissected, 195 ft [59 m] deep, Seragaki, Okinawa, 11 April 1997, R.F. Bolland. RFB 2135B 180 ft [55 m] deep, Seragaki, Okinawa, 30 April 1989, R.F. Bolland.

Distribution.—This species is known from Sagami Bay and Kii, Japan (Baba 1949) and Hong Kong (Rudman and Darvell 1990) and is here recorded from Okinawa in the Ryukyu Islands.

Natural History.—*Okenia japonica* was collected on erect arborescent bryozoans in 50–60 m depth (R. Bolland, pers. commun.).

External morphology.—The living animals are 10–13 mm in length. The body is moderately elongate and relatively high. There is well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent white with a dense, uniform covering of opaque white. There are 6–7 pairs of elongate notal papillae along the sides of the body. The two anteriormost papillae are situated in front of the rhinophores and are anteriorly directed. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 4–5 unipinnate branches. The anteriormost branch is frequently bifid at the base. The rhinophores are elongate with 7–8 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is wider anteriorly. The oral tentacles (Fig. 6A) are broadly triangular and extend beyond the lateral margins of the foot.

Digestive system.— The buccal mass is thick and muscular (Fig. 6B) with a rounded buccal pump directed dorsally. Numerous, large,

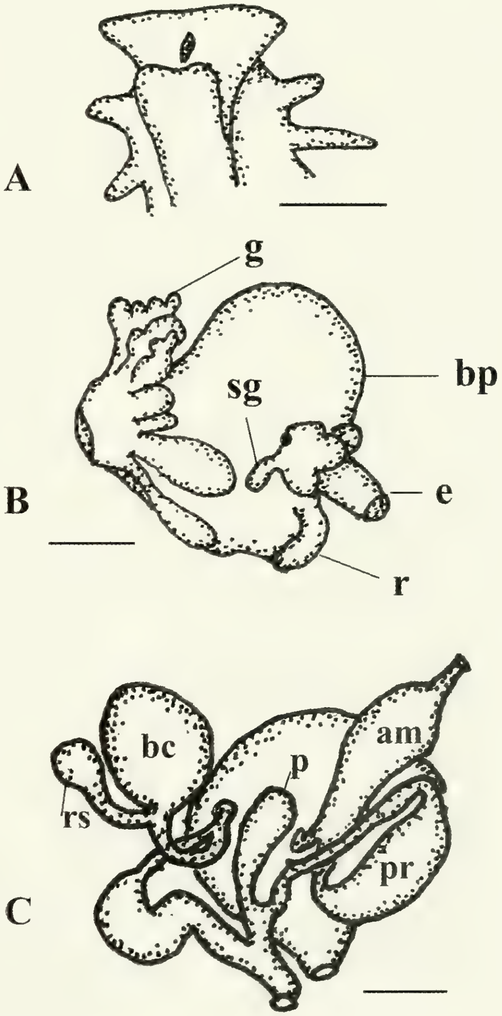


Figure 6. *Okenia japonica* Baba, 1949 (CASIZ115382). A. ventral view of head, scale = 1 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.25 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.2 mm.

elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is 20 × 1.1.0.1.1. The inner lateral teeth (Fig. 7) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears about 19–22 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 7) with a short cusp along the outer edge.

FIGURE 7. *Okenia japonica* Baba, 1949 (CASIZ 115382). Scanning electron micrograph of radular teeth; scale = 20 µm.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 6C).— The preampullary duct is short and thin and expands into an ovoid ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of a single, undivided portion. The distal end of the prostatic segment narrows into an elongate, straight ejaculatory portion that terminates near the base of the wide, elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and elongate basally and narrows more proximally. The narrow portion connects directly to the spherical bursa copulatrix and the smaller, pyriform receptaculum seminis. Near the middle of the narrow portion of the vagina, the uterine duct separates and enters the albumen gland.

DISCUSSION.— This species has been documented only once since its original description (Baba 1949; Rudman and Darvell 1990). The presence of a yellowish white body with fine opaque white markings is consistent between the original description and the present material. The number of notal appendages, the presence of a single medial papilla and a basally bifid anterior gill branch are also consistent between the original and present material. The denticulation and shape of the radular teeth are also very similar. The only difference noted is that Baba described 5–8 mm animals with 32–35 row of radular teeth whereas the present material (10–13 mm) has only 20 rows. The large oral glands were not noted by Baba nor was the reproductive anatomy described.

There is little doubt that the present material from deep water in Okinawa represents the same species originally described by Baba.

Okenia purpureolineata Gosliner, sp. nov.

(Figs. 1D, 8–9)

Type material.— Holotype: CASIZ 168020, 160 ft deep, Seragaki Beach, Okinawa, 2 June 1989, R.F. Bolland. Paratypes: CASIZ 099097, 1 specimen, 190 ft [58 m] deep, Seragaki Tombs, Okinawa 12 March 1994, R.F. Bolland. CASIZ 099085, 1 specimen, 175 ft [53 m] deep, Seragaki Tombs, Okinawa 18 February 1994, R.F. Bolland. CASIZ 070256, 1 specimen, dissected, 160 ft [49 m] deep, Seragaki Beach, Okinawa, 2 June 1989,, R.F. Bolland. CASIZ 070217, 1 specimen, 180 ft. [55 m] deep, Seragaki Beach, Okinawa, 30 April 1989, R.F. Bolland.

Etymology.— The species name, *Okenia purpureolineata*, is derived from the presence of longitudinal purple lines on the dorsal surface of the body.

Distribution.— This species is known only from Okinawa in the Ryukyu Islands (present study).

Natural History.— *Okenia purpureolineata* was collected on erect arborescent bryozoans in 49–60 m depth (R. Bolland, pers. commun.).

External morphology.— The living animals (Fig. 1D) are 10–12 mm in length. The body is moderately elongate and relatively high. There is a well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent purple. There is an irregular network of darker purple lines on the dorsal surface of the notum. Darker purple pigment is also present on the gill lamellae. The rhinophores are dark purple basally and red throughout most of their length. There are seven pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. Two medial papillae are present mid-dorsally anterior to the gill. The gill consists of 4–5 unipinnate branches. The rhinophores are elongate with 18–21 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is wider anteriorly. The oral tentacles are broadly triangular and extend beyond the lateral margins of the foot.

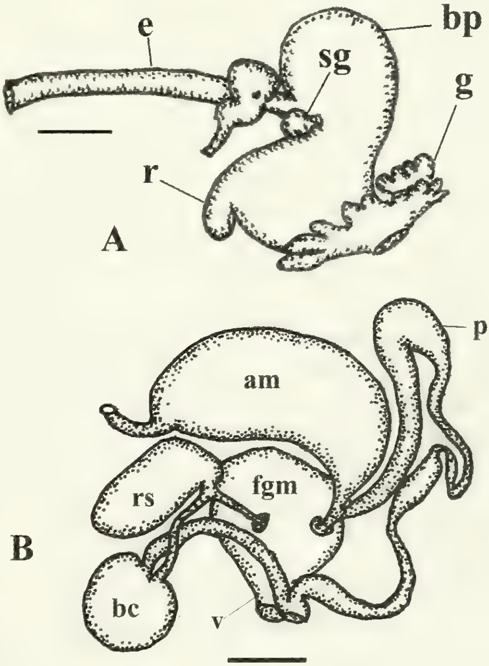


Figure 8. *Okenia purpureolineata* sp. nov. (CASIZ 070256). A. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.25 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.35 mm.

Digestive system.— The buccal mass is thick and muscular (Fig. 8A) with a rounded buccal pump directed posterodorsally. Numerous large, elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and

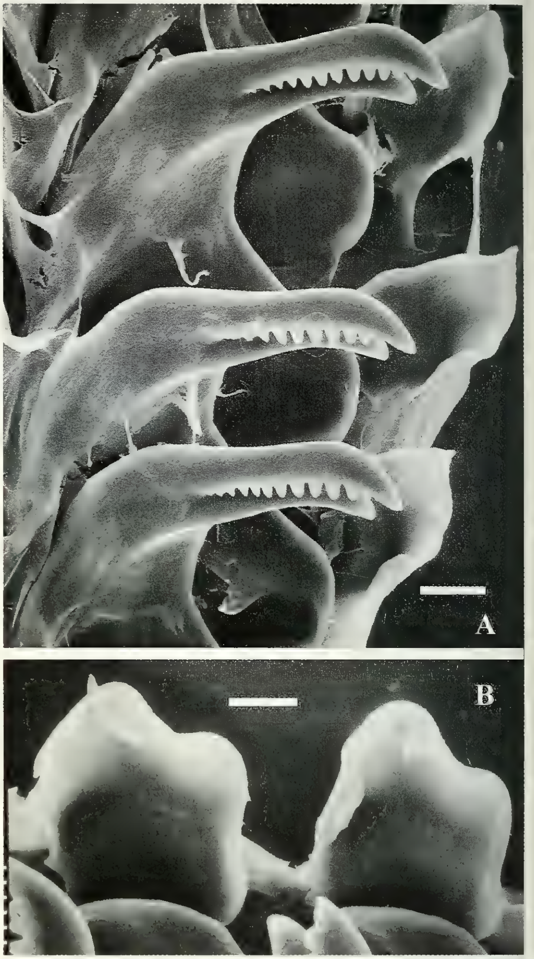


FIGURE 9. *Okenia purpureolineata* sp. nov. (CASIZ 070256). Scanning electron micrographs of radular teeth. A. View of half row of radular teeth; scale = 19 µm. B. Outer lateral teeth; scale = 12 µm.

extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is 28 × 1.1.0.1.1. The inner lateral teeth (Fig. 9A) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears 9–12 coarse, triangular denticles. The outer laterals are small and reduced (Fig. 9B) and quadrangular.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 8B).— The preampullary duct is short and thin and expands into a large sausage–shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and bilobed. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates at the top of the widest portion of the elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is narrow and elongate throughout its length. The proximal end of the vagina enters the spherical bursa copulatrix. At the base of the bursa another duct connects the large, pyriform receptaculum seminis. At the base of the receptaculum, the short uterine duct separates and enters the albumen gland.

DISCUSSION.— *Okenia purpureolineata* is similar to *O. japonica* in its external body shape. Both species occur sympatrically in relatively deep water from Okinawa. Although *O. japonica* is uniformly white in color, *O. purpureolineata* is purple with darker purple lines on the notum and red rhinophores. *Okenia purpureolineata* has two mid-dorsal papillae but only one is present in *O. japonica*. Both species have large oral glands surrounding the anterior end of the buccal mass, but there are more numerous glands in *O. purpureolineata*, that are smaller in size. The inner lateral teeth of *O. purpureolineata* have 9–12 large denticles along the masticatory border whereas there are 19–22 finer denticles on the inner laterals of *O. japonica*. In the reproductive system of *O. purpureolineata*, the receptaculum seminis and bursa copulatrix are well separated from each other whereas in *O. japonica* they are immediately adjacent to each other.

Okenia kendi Gosliner, sp. nov.

(Figs. 1A, 10–11)

Okenia sp. 2 Gosliner, Behrens and Williams, 1996:171, fig. 605.

Type material.— Holotype: CASIZ 110451, 1 specimen, Bethlehem, Caban Island, Batangas Province, Luzon, Philippines, 10 m depth, 24 April 1997, T.M. Gosliner. Paratypes: CASIZ 085880, 2 specimens, Babbit, Calumpan Peninsula, Batangas Province, Luzon, Philippines 25 March 1993, T.M. Gosliner. CASIZ 085892, 2 specimens, Layalayag, Maricaban Island, Batangas Province, Luzon, Philippines, 22 March 1993, T.M. Gosliner. CASIZ 085877, 2 specimens, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 23 March 1993, T.M. Gosliner. CASIZ 085883, 2 specimens dissected, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 26 March 1993, T.M. Gosliner. CASIZ 097397, 1 specimen, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 13 March 1994, T.M. Gosliner. CASIZ 105681, 1 specimen, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 26 February 1995, T.M. Gosliner. CASIZ 106593, 1 specimen, Bethlehem, Caban Island, Batangas Province, Luzon, Philippines, 15 m depth, 19 April 1996, T.M. Gosliner. CASIZ 093923, 2 specimens, Tandarusa Wreck and Pulau Kecil, Lembeh Strait, Manado, Sulawesi, Indonesia, 5–6 November 1993, P. Fiene Severns.

Etymology.— The specific epithet *kendi* is the Filipino word for candy, in reference to its appearance to a sweet confection.

Distribution.— This species is known from the Luzon Island, Philippines (Gosliner, Behrens, and Williams 1996) and Sulawesi, Indonesia (present study).

Natural History.— *Okenia kendi* is found on the underside of the large brown leafy sponge *Phyllospongia lamellosa* (Esper, 1799), on shallow reefs in 5–15 meters of water, where it feeds upon encrusting bryozoans (Gosliner, Behrens, and Williams, 1996).

External morphology.— The living animals (Fig. 1A) attain 30 mm in length. Preserved specimens range in size from 15–25 mm. The body is wide and dorso–ventrally flattened. There is a well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is translucent yellowish white. There is a broad mid-dorsal band of maroon pigment that runs from anterior to the rhinophores to the posterior end of the foot. The band divides around the mid-dorsal papillae and the two bifurcations rejoin each other posterior to the gills. The rhinophores and gill also have maroon pigment but also possess opaque white markings along their lengths. The medial and marginal papillae are maroon at the base and possess purple pigment more distally. There is a lateral line of maroon present on either side of the body between the notum and the foot. There are eight pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three unipinnate branches that are bifid or trifid at the base. The rhinophores are elongate with 31 congested lamellae. The anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and oral tentacles (Fig. 10A).

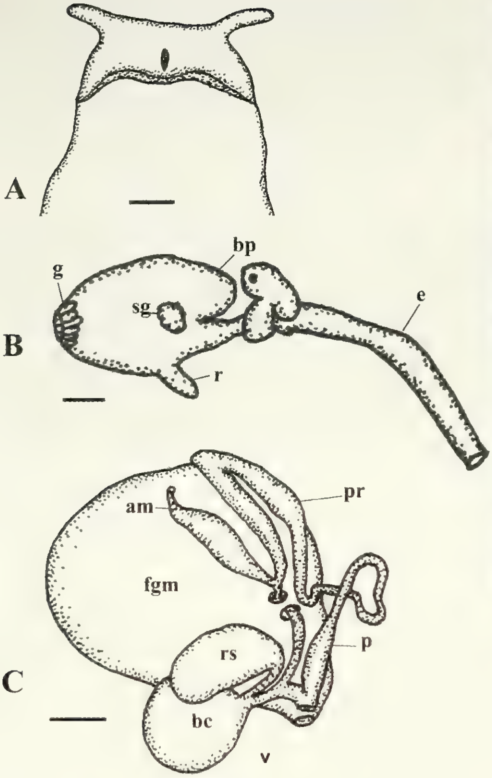


FIGURE 10. *Okenia kendi* sp. nov. (CSIZ 085883). A. ventral view of head; scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland, scale = 0.5 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.4 mm.

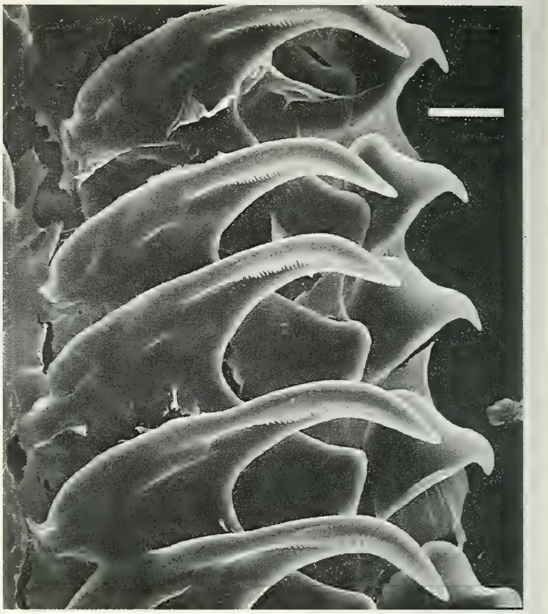


FIGURE 11. *Okenia kendi* sp. nov. (CASIZ 085883). Scanning electron micrograph of radular teeth; scale = 23 µm.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 10B) with a rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is 26 × 1.1.0.1.1. The inner lateral teeth (Fig. 11) are broad basally with an acutely pointed cusp and 35–38 elongate denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 11) with an elongate cusp along their outer side.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, immediately posterior to the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 10C).—The preampullary duct is short and thin and expands into an elongate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a wide, elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base of the vagina, the uterine duct separates and enters the albumen gland. From the base of the bursa copulatrix, a narrow duct connects the bursa with the large, pyriform receptaculum seminis.

Discussion.— Two described species of Indo-Pacific species of *Okenia* are similar in external appearance to *O. kendi. Okenia plebeia* (Bergh, 1902) and *Okenia barnardi* Baba, 1937, have a series elongate appendages along the notal margins and possess a single elongate mid-dorsal papilla. The color pattern of living specimens of *O. plebeia* is unknown. The radula of *O. plebeia* has a similar formula to that of *O. kendi*. with 27–28 rows of teeth. The inner lateral teeth of *O. plebeia* have approximately 30 denticles along the masticatory margin whereas *O. kendi* has 35–38 denticles. The outer lateral teeth of *O. plebeia* are rounded but those of *O. kendi* have a sharply pointed apical extension. The reproductive system of *O. plebeia* has a short prostate with a muscular portion that is four times the length of the penis. In *O. kendi*, the prostate is long and the muscular portion of the vas deferens is only about twice the length of the penis.

Okenia barnardi has a markedly different color pattern to that of *O. kendi*. It is light brown with a darker brown band near the notal margin that is punctuated by opaque white spots. An opaque white line is present dorsally on the posterior end of the foot. In contrast, *O. kendi* has a pattern of maroon blotches located on the notum. The anatomy of *O. barnardi* is largely undescribed. The radula was depicted in the original description (Baba 1937). The outer lateral teeth of *O. barnardi* have a rounded apex whereas there is a pronounced apical denticle on the outer laterals of *O. kendi*.

Okenia virginiae Gosliner, sp. nov.

(Figs. 1C, 12–13)

Okenia sp. Gosliner 1987: 92, fig. 159.
Okenia barnardi Debelius, 1996:196, upper photo, misidentification, not *O. barnardi* Baba, 1937.

Type material.— Holotype: SAM A35558, one specimen, dissected, Vetchies Pier, Durban, South Africa, 28 April 1982, T.M. Gosliner.

Etymology.— *Okenia virginiae* is named for my mother, Virginia Malaney Gosliner, in recognition of her nurturing my earliest interest in natural history.

Distribution.— This species is known from the Natal, South Africa (Gosliner 1987) and Oman (Debelius 1996).

Natural History.— *Okenia virginiae* was found on the underside of a small rock in 2 meters of water. The specimen when dissected was found to be parasitized by three trematodes.

External morphology.— The living animal (Fig. 1C) was 10 mm in length. It is 8 mm long in the preserved state. The body is wide and dorsoventrally flattened. There is well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is translucent white. There is a broad mid-dorsal band of brown pigment that runs from anterior to the rhinophores to the posterior end of the foot. It is interrupted by an irregular network of white pigment. The notal papillae, rhinophores and gill have irregular maroon bands along their length. There are 8 pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three unipinnate branches that are bifid or trifid at the base. The rhinophores are elongate with 21 congested lamellae. The

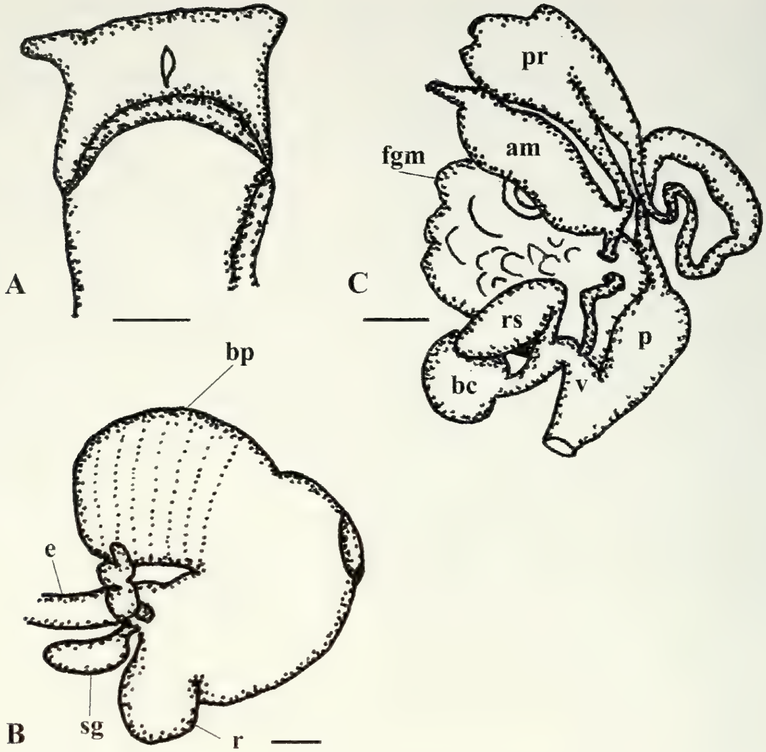


FIGURE 12. *Okenia virginiae* sp. nov. (SAMA 35558). A. ventral view of head scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.1 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.2 mm.

anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and elongate, triangular oral tentacles (Fig. 12A).

Digestive system.— The buccal mass is thick and muscular (Fig. 12B) with a rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates with a denticulate margin (Fig. 13B). The cuticle expands as it enters the buccal pump. The radular formula is 24 × 1.1.0.1.1. The inner lateral teeth (Fig. 13A) are broad basally with an acutely pointed cusp and 22–33 small, irregular denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 13A). They have a short cusp along their outer side.

Central nervous system.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, immediately posterior to the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure.

Paired buccal ganglia are situated ventral to the esophagus.

Reproductive system (Fig. 12C).— The preampullary duct is short and thin and expands into an elongate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base of the vagina, the uterine duct separates and enters the albumen gland. Distal from the base of the bursa copulatrix, a narrow duct connects the bursa with the large, pyriform receptaculum seminis.

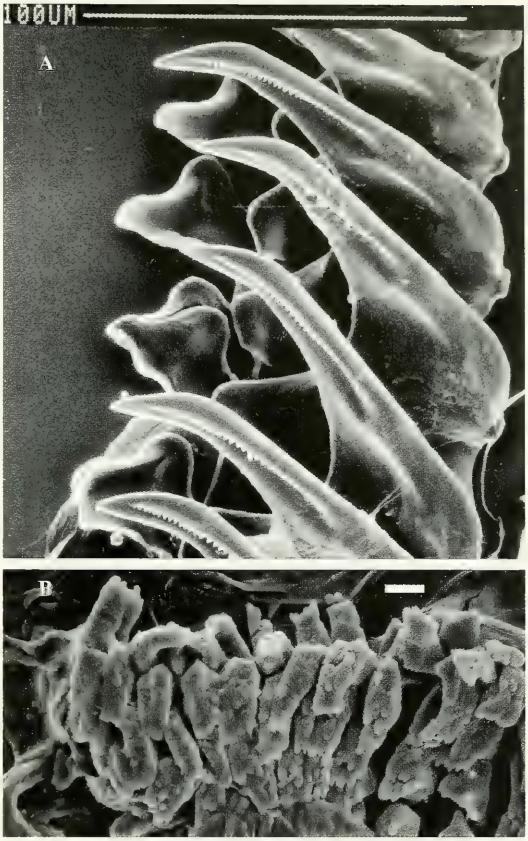


Figure 13. *Okenia virginiae* sp. nov. (SAMA 35558). Scanning electron micrographs. A. Half–row of radular teeth; scale = 100µm. B. Jaw rodlets; scale = 6 µm.

Discussion.— This species has been recently erroneously identified as *Okenia barnardi* (Debelius, 1996:196, upper photo). *Okenia virginiae* differs from *O. barnardi* in its color pattern by having dark brown pigment located in the center of the notum rather than submarginally and in having a network of white lines rather than opaque white spots. The outer lateral teeth are broad basally with a rounded apex in both *O. barnardi* and *O. virginiae*, in contrast to *O. kendi*, where the outer lateral teeth each have a pointed cusp. The reproductive anatomy of *O. barnardi* has not been described. *Okenia virginiae* has a reproductive system with a short vagina with the uterine duct entering the vagina near its base. This arrangement has not been described for any other member of the genus.

Okenia lambat Gosliner, sp. nov.

(Figs. 1B, 14–15)

Type material.— Holotype: CASIZ 084283, 1 specimen, dissected, Devil's Pt., Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 23 February 1992, T.M. Gosliner.

Etymology.— The specific epithet *lambat* is derived from the Filipino word for net, referring to the network of white markings that is visible through the brown notal pigment.

Distribution.— This species is known from the Luzon Island, Philippines (present study).

Natural History.— *Okenia lambat* has been found under a small stone in 10 meters of water.

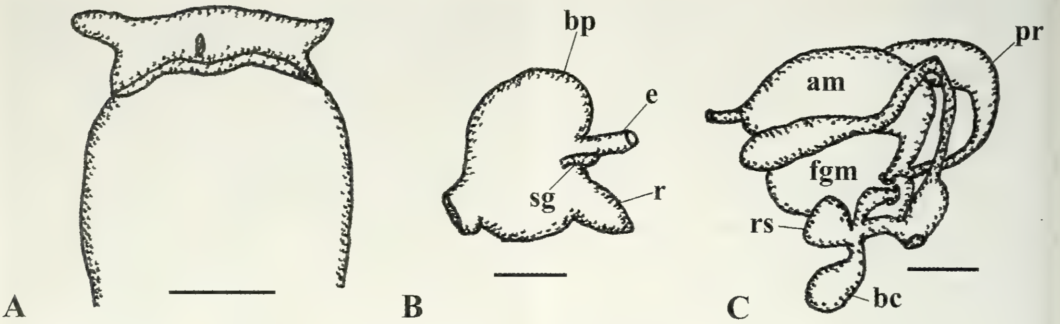


Figure 14. *Okenia lambat* sp. nov. (CASIZ 084283). A. ventral view of head, scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, sg = salivary gland; 0.2 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.1 mm.

External morphology.— The living animal (Fig. 1B) was 7 mm in length. Preserved, the specimen is 6 mm long. The body is wide and dorsoventrally flattened. There is a well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is opaque yellowish white. There is a broad mid-dorsal band of brown pigment that runs from anterior to the rhinophores to the posterior end of the foot. It is interrupted by an irregular network of white pigment. The notal papillae, rhinophores and gill have irregular maroon spots along their length. There are 8 pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three elongate, unipinnate branches. The two lateral branches are undivided and the anterior one is bifid to the base. The rhinophores are elongate with 18 congested lamellae. The anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and oral tentacles (Fig. 14A).

Digestive system.— The buccal mass is thick and muscular (Fig. 14B) with a massive rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is relatively short and extends posteroventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded rods. The cuticle expands as it enters the buccal pump. The radular formula is 18 × 1.1.0.1.1. The inner lateral teeth (Fig. 15A) are broad basally with an acutely pointed cusp and 18–19 denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 15B). They have an elongate cusp along their upper margin of the outer side and a rounded lobe basally.

Reproductive system (Fig. 14C).— The preampullary duct is short and thin and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is relatively narrow and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base of the bursa, the uterine duct separates from the vagina and enters the albumen gland. Also from the base of the bursa copulatrix, an additional narrow duct connects the bursa with the small, rounded receptaculum seminis.

Discussion.— *Okenia lambat* is very similar in its external appearance to *O. virginiae*. Both species have a series of lateral papillae with a single medial one and have dark brown dorsomedial pigment interrupted by a network of white lines. The general body color of *O. virginiae* is translucent white to cream whereas that of *O. lambat* is opaque yellowish white. Internally there are other differences that distinguish these taxa. In *O. lambat*, the masticatory margin-bearing denticles extend virtually to the apex of the primary cusp, in *O. virginiae* whereas the denticles terminate well short of the apex. The outer lateral teeth of *O. lambat* each bear an extended, acutely–pointed cusp, but in *O. virginiae* the cusp is much shorter and more rounded. Despite the fact that both *O. lambat* and *O. virginiae* are unique in having a much–shortened vagina, there are differences in the reproductive anatomy of the two species. In *O. lambat* the ejaculatory portion of the vas deferens is relatively short and is of uniform diameter throughout its length. In contrast, the elongate ejaculatory vas deferens of *O. virginiae* consists of a thin distal portion that expands into a wider portion that enters the penial bulb. In *O. lambat*, the uterine duct joins the vagina at the base of the receptaculum seminis whereas in *O. virginiae* it enters the genital atrium at the base of the vagina.

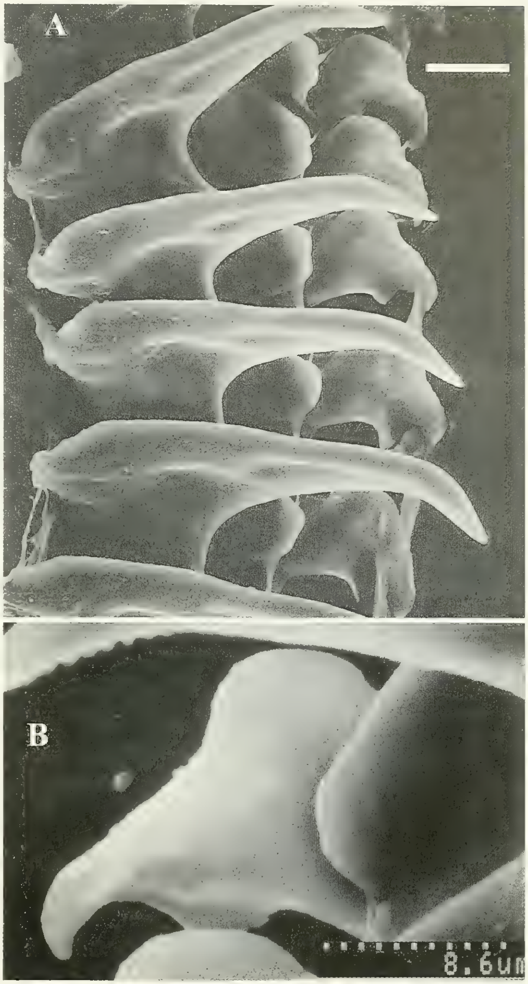


Figure 15. *Okenia lambat* sp. nov. (CASIZ 084283). Scanning electron micrograph of radular teeth. A. View of half row of radular teeth; scale = 13 μm. B. Outer lateral tooth; scale = 8.6μm.

Okenia liklik Gosliner, sp. nov.

(Figs. 1G, 16–17)

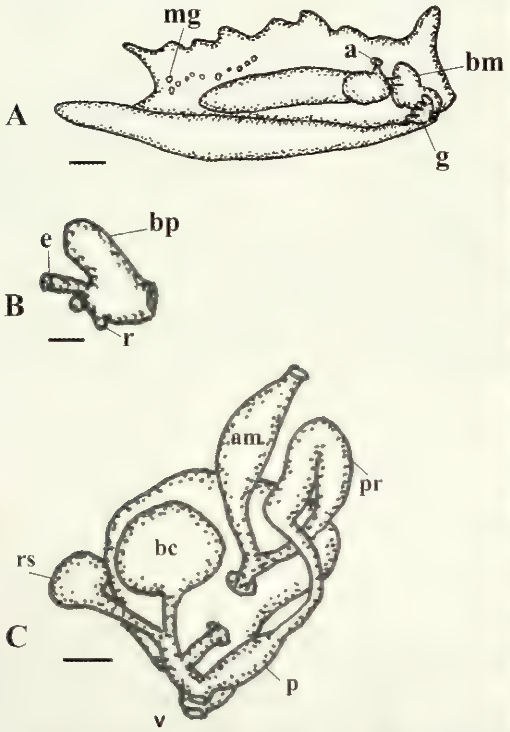
Type material.— Holotype: CASIZ 168021, one specimen, Barracuda Pt., Tab Island, Madang Lagoon, Madang, Papua New Guinea, 7 February 1988, R.C. Willan. Paratypes: CASIZ 168022, one specimen, Barracuda Pt., Tab Island, Madang Lagoon, Madang, Papua New Guinea, 7 February 1988, R.C. Willan. CASIZ 168023, one specimen, dissected, Bus Stop, Balayan Bay, Batangas, Luzon Island, Philippines, 10 m depth, 9 May 2001, Á. Valdés.

Etymology.— The specific epithet *liklik* is the Papuan pidgin word for small, in reference to the tiny body size of the mature specimens of this species.

Distribution.— This species has been found from Papua New Guinea and Luzon Island in the Philippines (present study).

External morphology.— The living animals (Fig. 1G) are small, 3–4 mm in length. The body is elongate and relatively high. There is a well–developed, continuous notal border. Immediately ventral to the notum is a series of small subdermal mantle glands situated in the posterior half of the body (Fig. 16A). The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly purplish pink. There is mid-dorsal band of chocolate brown that is interrupted by connected or three interrupted, irregular opaque white markings. The gill is uniformly opaque white. All but the posterior pair of papillae are tipped with an orange subapical marking and, in some cases, a chocolate brown apex. The posterior pair and the single medial papilla are purple with chocolate brown, but lack orange pigment. There are 8–9 pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. A single mid-dorsal papilla is present anterior to the gill. It has the form of a crenulate crest rather than a more typical digitiform papilla. The gill consists of 3 unipinnate branches. The rhinophores are elongate with 17–18 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is divided anteriorly.

Digestive system.— The buccal mass is thick and muscular (Fig. 16B) with a large rounded, elongate buccal pump directed posteriorly. There are a several elongate oral glands around the



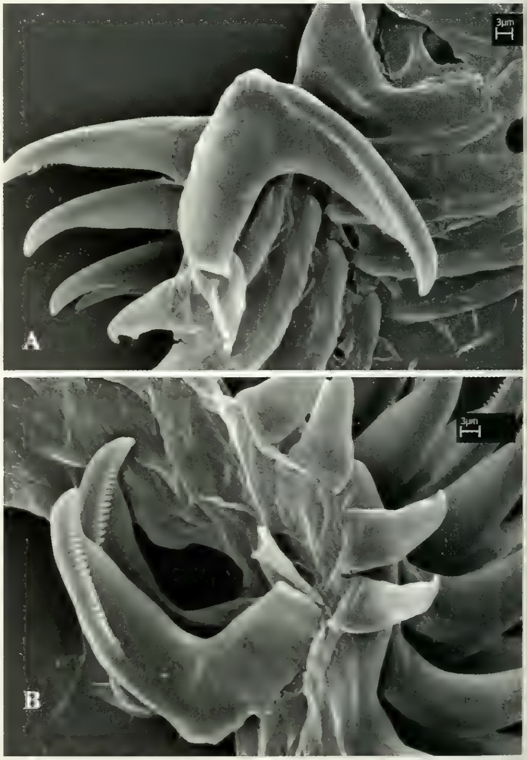


Figure 16 (left). *Okenia liklik* sp. nov. (CASIS 168023). A. Lateral view of preserved specimen, a =anus, bm = buccal mass, g = oral glands, mg = mantle glands; scale = 0.2 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac; scale = 0.1 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.1 mm.

Figure 17 (right). *Okenia liklik* sp. nov. (CASIS 168023). Scanning electron micrograph of radular teeth. A. Inner lateral teeth; scale = 3µm. B. Inner and outer lateral teeth; scale = 3µm.

mouth. The radular sac is relatively short and extends posteroventrally from the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. No distinct rodlets are evident around the opening of the buccal cuticle. The radular formula is 12 × 1.1.0.1.1. The inner lateral teeth (Fig. 17A, B) are broad basally with an acutely pointed cusp and 24–26 fine denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 17B) with a single acute cusp.

Reproductive system (Fig. 16C).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively narrow and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is wide and short and connects directly to the small, triangular bursa copulatrix. Near the base of the vagina, the short uterine duct separates from the vagina and enters the albumen gland. Also from the middle of the vaginal duct, an additional narrow duct connects the bursa with the large, rounded receptaculum seminis.

Discussion.— *Okenia liklik* has a distinctive purplish pink body color with orange, brown and opaque white markings. No other described species has been described as having glands situated near the posterior margin of the mantle. As in some other species of *Okenia*, such as *O. japonica* and *O. purpureolineata*, the body is elongate and narrow and large oral glands are present surrounding the mouth. The relatively large, unifid outer lateral teeth are more elongate than those found in other described species.

Okenia rosacea (MacFarland, 1905)

(Figs. 18–19)

Hopkinsia rosacea MacFarland, 1905:53; 1906:149, pl. 31, figs. 24,25, pl. 21, figs. 97–103.
Okenia rosacea (MacFarland, 1905) **comb. nov.**

Material examined.— CASIZ 072075, specimens, one dissected, Great Tide Pool, Pacific Grove, California, 1 June 1973, Gary McDonald.

Distribution.— This species was originally described from Monterey Bay, California (MacFarland 1905) has been found from Coos Bay, Oregon to Isla San Martin, Baja California (Behrens 1991).

Natural History.— This species feeds upon the cheilostomatous bryozoan, *Eurystomella* sp. (Behrens 1991).

Digestive system.— The buccal mass is large and the radular sac is elongate, extending well behind the posterior end of the muscular mass. The radular teeth of *Okenia rosacea* are distinctive. The inner laterals (Fig. 18) are elongate with a recurved apex forming a distinctive hook. The outer laterals are reduced to a small vestigial plate.

Reproductive system (Fig. 19).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the much wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental

Figure 18. *Okenia rosacea* (MacFarland, 1905). (CASIZ 072075) Scanning electron micrograph of inner lateral tooth; scale = 200 μm.

glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and elongate and connects directly to the large, saccate bursa copulatrix. Near the distal end of the vagina, the long uterine duct separates from the vagina and enters the albumen gland. Also from the distal end of the vaginal duct, an additional narrow duct connects to the small, saccate receptaculum seminis. Penial hooks were not observed.

Discussion.— *Okenia rosacea* is similar to *O. hiroi* (Baba, 1938) in its external anatomy and uniform pink coloration. The two species differ markedly in their radular anatomy: whereas *O. rosacea* has elongate, curved inner lateral teeth, those of *O. hiroi* are denticulate and hamate in shape. Only *O. rosacea* and *O. nakamotoensis* have elongate inner lateral radular teeth that terminate in a sharply curved apex. Those of *O. nakamotoensis* are even thinner and more elongate than those found in *O. rosacea*. Subsequent phylogenetic analysis shows that *Hopkinsia* is nested within *Okenia* and is therefore regarded as a synonym of the older taxon, *Okenia*.

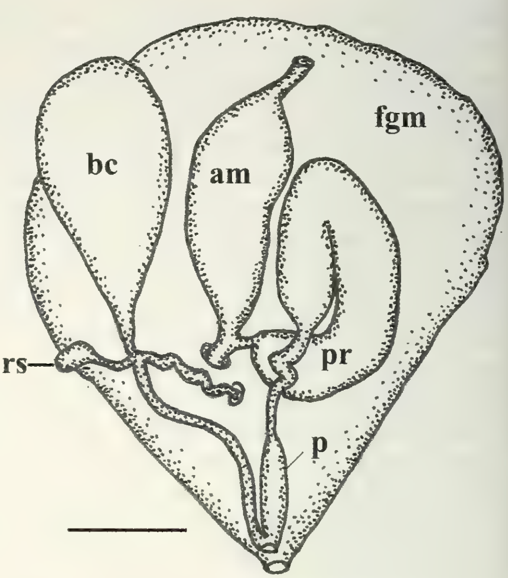


Figure 19. *Okenia rosacea* (MacFarland, 1905). (CASIZ 072075). Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis; scale = 1.0 mm.

Okenia plana Baba, 1960

(Figs. 20B, 21–22)

Okenia plana Baba, 1960:80, pl.7, figs 2a–d).
Hopkinsia plana (Baba, 1960), Bouchet and Ortea, 1983:231; Rudman and Darvell, 1990:37, pl.1f.

Material examined.— CASIZ 001026, six specimens, two dissected. Cooley's Landing, East Palo Alto, San Francisco Bay, California, 2 February 1977, D. Chivers. CASIZ 101373, five specimens, two dissected, Berkeley Fishing Pier, San Francisco Bay, California, 6 March 1963, L. Andrews. CASIZ 083837, 1 specimen, dissected, Seafari, Calumpan Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 17 February 1992, T.M. Gosliner.

Distribution.— This species was originally described from Japan (Baba, 1960) and later recorded from Hong Kong (Rudman and Darvell 1990), California (Steinberg 1963; Behrens 1991), New Zealand and Australia (Rudman 1998). The present specimen extends the range to the Philippines. The specimens from California represents a human introduction (Behrens 1991).

Natural History.— In the Philippines this species was found under coral rubble in about 6 meters of water. Specimens introduced into San Francisco Bay have been observed on the encrusting cheilostomatous bryozoan, *Membranipora* sp., growing on arborescent algae (present study).

External morphology.— The living animals (Fig. 20B) attain 10–15 mm in length. Preserved specimens were 4–9 mm long. The body is broad and ovoid. There is no distinct notal border. The foot is short and does not extend beyond the oval of the general body. The body is uni-

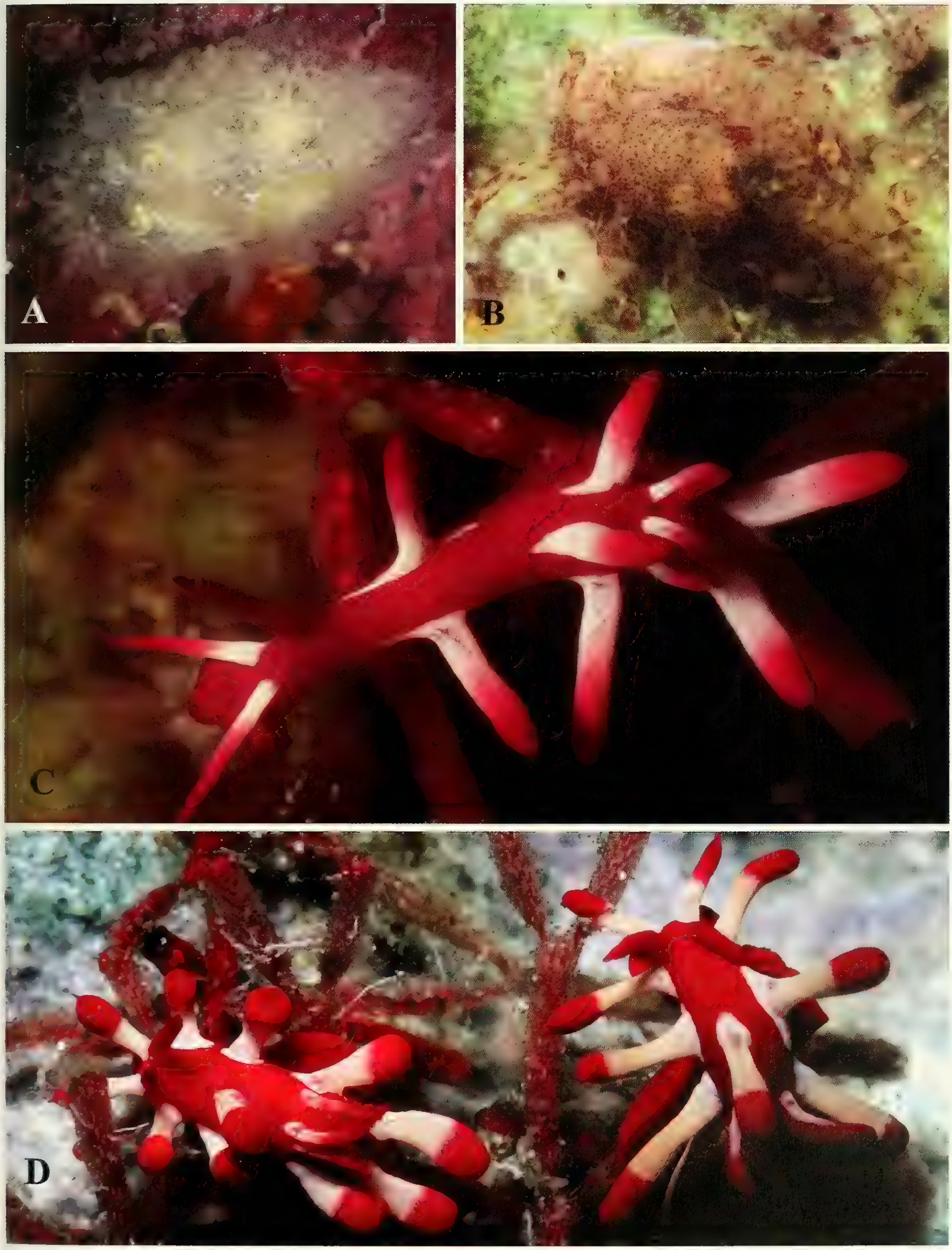


FIGURE 20. Living animals. A. *Okenia pilosa* (Bouchet and Ortea), 1983 (CASIZ 109784), Barracuda Point, Madang, Papua New Guinea. B. *Okenia plana* Baba, 1960 (CASIZ 083837), Anilao, Luzon, Philippines. C. *Okenia kondoi* (Hamatani, 2001), Balicasag Island, Bohol, Philippines. D. *Okenia nakamotoensis* (Hamatani, 2001), Balicasag Island, Bohol, Philippines, photo by G. Williams. All photos by T.M. Gosliner except as otherwise noted.

formly translucent yellowish white with the exception of small brown spots scattered over the surface of the notum and occasional opaque white spots. The notal papillae, rhinophores and gill all possess larger brown and yellow blotches. There are 5 pairs of elongate papillae scattered on either side of the dorsal surface of the body. A single medial papillae is present mid-dorsally anterior to the gill. The gill consists of 9–11 unipinnate branches. The rhinophores are relatively short with 12–15 congested lamellae. The anterior end of the foot is deeply indented anteriorly forming a v–shaped edge that encloses the mouth (Fig. 21A). The oral tentacles are indistinct but are separated from the foot by a groove. The genital aperture is situated on the right side of the dorsal surface of the body approximately a third of the length of the body posterior to the head.

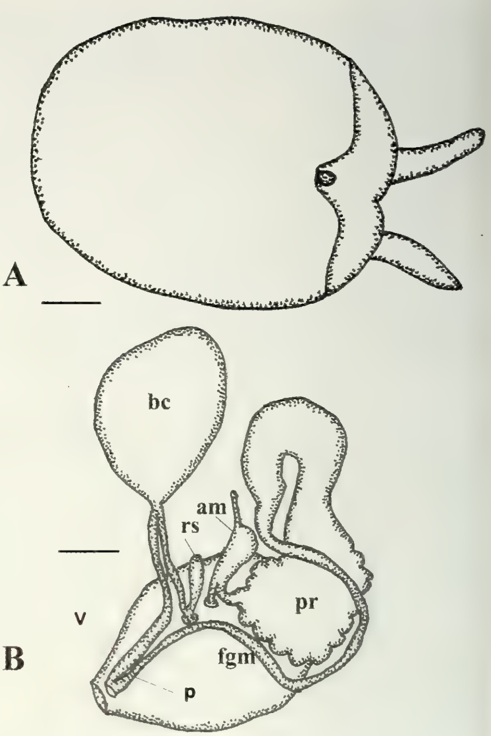


FIGURE 21. *Okenia plana* Baba, 1960. A. Ventral view of preserved specimen, (CASIZ 083837); scale = 0.6 mm. B. Reproductive system, (CASIZ 001026), am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.5 mm.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is relatively short. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is 21–29 × 1.1.0.1.1. in two specimens examined. The inner lateral teeth (Fig. 22) are thin and elongate and with a straight apex. They are devoid of denticles. The outer laterals are small and reduced with two pointed denticles along the outer margin, occasionally with 2–3 smaller denticles along the edge.

REPRODUCTIVE SYSTEM (Fig. 21B).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the narrow vas deferens that expands into a massive, lobate prostatic portion. The oviduct enters the highly folded female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. More distally the lobate prostatic segment of the vas deferens narrows somewhat into a second glandular section that is relatively wide and consists of two folded sections. The distal end of the prostatic segment narrows into an elongate, thin, curved ejaculatory portion that terminates in a narrow penis. There is no distinct penial papilla. The thin vaginal duct exits adjacent to the penis. It is elongate and narrow and connects directly to the large, spherical bursa copulatrix. Near the base of the bursa, another elongate duct enters the small pyriform receptaculum seminis. Also from the base of the receptaculum, the short uterine duct enters the large female gland mass.

DISCUSSION.— *Okenia plana* lacks the pink color of *O. rosacea* and *O. hiroi* and is uniformly

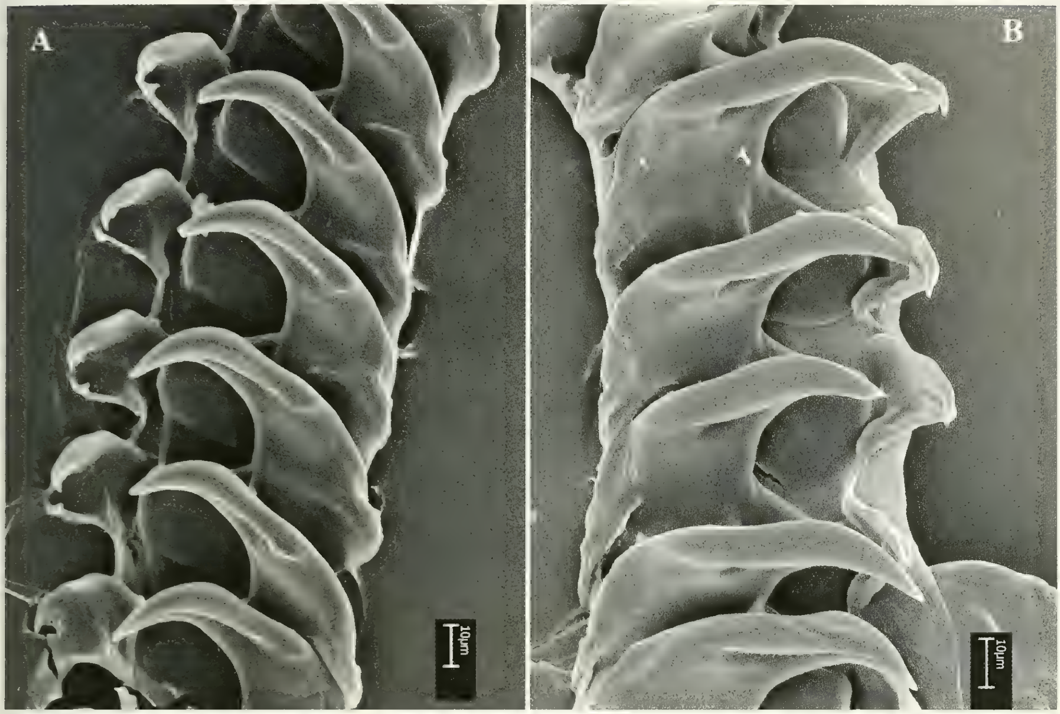


FIGURE 22. *Okenia plana* (Baba, 1960). Scanning electron micrographs of radular teeth. A. Half row of radular teeth of specimen from San Francisco Bay (CASIZ 001026); scale = 10μm. B. Half row of radular teeth of specimen from the Philippines (CASIZ 083837); scale = 10μm

yellowish white with black spots and opaque white markings on the notum and notal papillae. Its color pattern is similar to that found in *O. pilosa* Bouchet and Ortea, 1983. The two species differ in the arrangement of the notal papillae and in their radular anatomy. In *O. plana* there are almost always five pairs of marginal notal papillae and a single mid-dorsal papilla, whereas in *O. pilosa* there are 35–40 scattered papillae over the surface of the notum. In *O. plana* the inner lateral teeth are short and evenly arched, whereas in *O. pilosa* the primary cusp is far more elongate. In *O. plana*, the outer lateral tooth has two primary denticles with occasional 2–3 smaller denticles. In *O. pilosa* the outer lateral teeth have up to 14 denticles along their outer margin.

There is little anatomical difference in the Californian and Philippine specimens examined here. The primary difference is in the color pattern. The specimens from California have larger, darker brown spots that are more regularly distributed over the surface of the notum and notal papillae. There is little difference in the shape and denticulation of the radular teeth. The reproductive anatomy of this species has not previously been described. The most distinctive features of the reproductive anatomy are the lobed prostate, the extremely narrow ejaculatory portion of the vas deferens and the thin vagina.

Okenia pilosa (Bouchet and Ortea, 1983)

(Figs. 20A, 23–24)

Hopkinsia pilosa Bouchet and Ortea, 1983:227, figs 1–7; Rudman and Darvell, 1990:36, pl.1e.
Okenia pilosa (Bouchet and Ortea, 1983) **comb. nov.**

MATERIAL EXAMINED.— CASIZ 109784, 10 m depth, Barracuda Point, Tab Island, Madang

Lagoon, Madang, Papua New Guinea, 4 November 1996, T. M. Gosliner.

Distribution.— This species was originally described from New Caledonia (Bouchet and Ortea 1983) and later recorded from Hong Kong (Rudman and Darvell 1990). The present specimen extends the range to Papua New Guinea.

Natural History.— This species is found under coral rubble in about 6 meters of water.

External morphology.— The living animals (Fig. 20A) reach 13 mm in length. The preserved specimen was 11 mm long. The body is broad and ovoid. There is no distinct notal border. The foot is short and does not extend beyond the oval of the general body. The body is uniformly translucent white with the exceptions of a network of opaque white and yellow pigment on the notum and rhinophores. The gill rachises are also translucent yellow. Scattered brown spots are present on the notum. There are 35–40 elongate papillae scattered over the dorsal surface of the body. A single medial papilla is present mid-dorsally and is situated immediately anterior to the gill. The gill consists of 12 bipinnate branches. The rhinophores are relatively short with 7–8 congested lamellae. The anterior end of the foot is deeply indented anteriorly forming a v–shaped edge that encloses the mouth (Fig. 23A). The oral tentacles are indistinct but are separated from the foot by a groove. The genital aperture is situated on the right side of the dorsal surface of the body approximately a third of the length of the body posterior to the head.

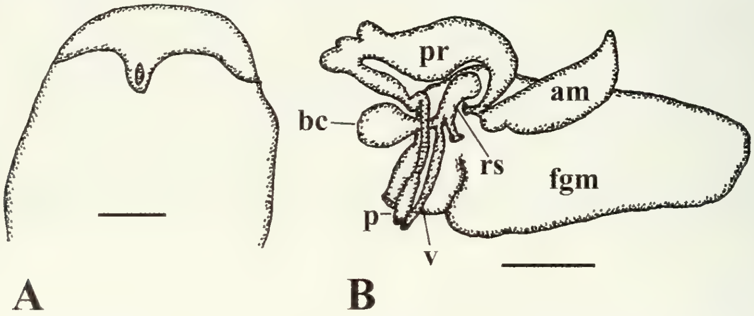


Figure 23 *Okenia pilosa* (Bouchet and Ortea, 1983) (CASIZ 109784). A. Ventral view of preserved specimen; scale = 1.0 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.4 mm.

Digestive system.— The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is relatively short. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is 19 × 1.1.0.1.1. The inner lateral teeth (Fig. 24) are thin and elongate and with a straight apex. They are devoid of denticles. The outer laterals are small and reduced with an approximately 14 denticles along the masticatory margin.

Reproductive system (Fig. 23B).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively wide and consists of two convoluted, folded portions. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is elongate and narrow and connects directly to the small, spherical bursa copulatrix. Near the base of the bursa, a short duct enters the pyriform receptaculum seminis. Also from the base of the receptaculum, the short uterine duct enters the large female gland mass.

Discussion.— As in *Okenia plana*, a translucent body color with mottled brown spots and opaque white pigment makes the living animals of *O. pilosa* exceedingly cryptic when encountered on their host bryozoans. The anatomical distinctions between these two taxa are reviewed in the discussion following *O. plana*.

In their original description of *H. pilosa*, Bouchet and Ortea (1983) revised the systematics of taxa included in *Hopkinsia*. They transferred *Okenia plana* Baba, 1960 and *Hopkinsiella*, with its monotypic species, *H. hiroi*, to *Hopkinsia*. They noted that radular differences between *Hopkinsia rosacea* and *Hopkinsiella hiroi* were of specific value rather than generic value. They noted that the primary feature that distinguishes *Hopkinsia* from *Okenia* is the absence of a distinct pallial ridge in the former. Bouchet and Ortea stated that members of the two genera feed on different prey with species of *Hopkinsia* feeding on Bryozoa whereas species of *Okenia* feed on tunicates. However, it is evident from many studies, including the present work, that several species of *Okenia* are also specialists on bryozoans rather than tunicates (Burn 1967; Rudman and Darvell 1990; present study). Subsequent phylogenetic analysis supports the inclusion of all of these taxa within a single monophyletic taxon, *Okenia*.

Figure 24. *Okenia pilosa* (Bouchet and Ortea), 1983 (CASIZ 109784). Scanning electron micrograph of radular teeth; scale = 10μm.

Okenia nakamotoensis (Hamatani, 2001)

(Figs. 20D, 25–26)

Okenia sp. 1 Gosliner, Behrens and Williams, 1996: 171, fig. 604.
Hopkinsia nakamotoensis Hamatani, 2001:151, fig. 1 A–E.
Okenia nakamotoensis (Hamatani, 2001) **comb. nov.**

Material examined.— CASIZ 096238, 5 specimens, 2 dissected, Balacasag Island, Bohol, Philippines, 29 m. depth, 21 March 1994, T. M. Gosliner. CASIZ 096244, 2 specimens, Balacasag Island, Bohol, Philippines, 34 m. depth, 22 March 1994, T. M. Gosliner. CASIZ 117028, 1 specimen, 20 m depth, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, 28 March 1992, S. Johnson. CASIZ 120736, 3 specimens, Cement Ship Pinnacle, Enewetak Atoll, Marshall Islands, 21 August 1983, S. Johnson. CASIZ 120732, 4 specimens, 1 dissected, Enewetak Atoll, Marshall Islands, 5 June 1983, S. Johnson. CASIZ 120733, 5 specimens,15 m depth, R. Buoy Pinnacle, Kwajalein

Atoll, Marshall Islands, 18 June 1982, S. Johnson. CASIZ 120734, 5 specimens, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, 22 June 1982, S. Johnson. CASIZ 120735, 7 specimens, 1–20 m depth, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, J. Johnson. CASIZ 093922, 5 specimens, unnamed reef near Koon Island, East Banda Sea, Indonesia, 17–30 m depth, 14 November 1993, P. Fiene Severns.

Distribution.— This species is known from the Kuroshima Island, Japan (Hamatani 2001) Indonesia, Bohol and Cebu Islands (Philippines) and Enewetak and Kwajalein Atolls (Marshall Islands) (Gosliner, Behrens, and Williams 1996; present study).

Natural History.— This species is found on outer reef faces in 10–30 meters of water, where it feeds upon the bright red bryozoan, *Tropidozoum cellariforme* Harmer, 1957 (Gosliner, Behrens, and Williams 1996).

External morphology.— The living animals (Fig. 20D) attain 20 mm in length. Preserved specimens range in size from 3–13 mm. The body is elongate and wide. There is no distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body is uniformly red with the exceptions of the gill rachises and the base of the notal papillae, which are pinkish white. The gill lamellae and apices of the notal papillae are the same color as the remainder of the body. There are five pairs of elongate notal papillae along the sides of the body. Two of these are situated anterior to the rhinophores. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 3–4 unipinnate branches. The rhinophores are elongate with 13–20 congested lamellae. The anterior end of the foot is rounded and forms a projection anterior to the mouth. The oral tentacles are fused to form an oral veil. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.

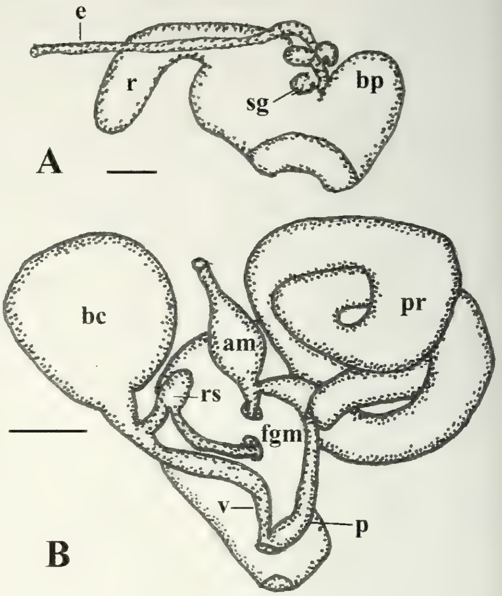


Figure 25. *Okenia nakamotoensis* (Hamatani, 2001) (CASIZ 096238). A. Buccal mass, bp = buccal pump, e = esophagus, sg = salivary gland, r = radula sac; scale = 1.0 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.5 mm.

Digestive system.— The buccal mass is thick and muscular (Fig. 25A) with a rounded buccal pump situated anteriorly. The radular sac is elongate and is approximately equal in length to the rest of the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is 16 × 1.1.0.1.1. The inner lateral teeth (Fig. 26A) are extremely thin and elongate and with a hooked apex (Fig. 26B). They are devoid of denticles. Some of the older teeth are eroded and have a simple rounded or irregularly fractured apex. The outer laterals are small and reduced (Fig. 26C) with an anteriorly directed cusp.

Central nervous system.— The ganglia of the central nervous system are highly concentrated and surround the esophagus. The cerebral and pleural ganglia are largely fused. A sessile eye

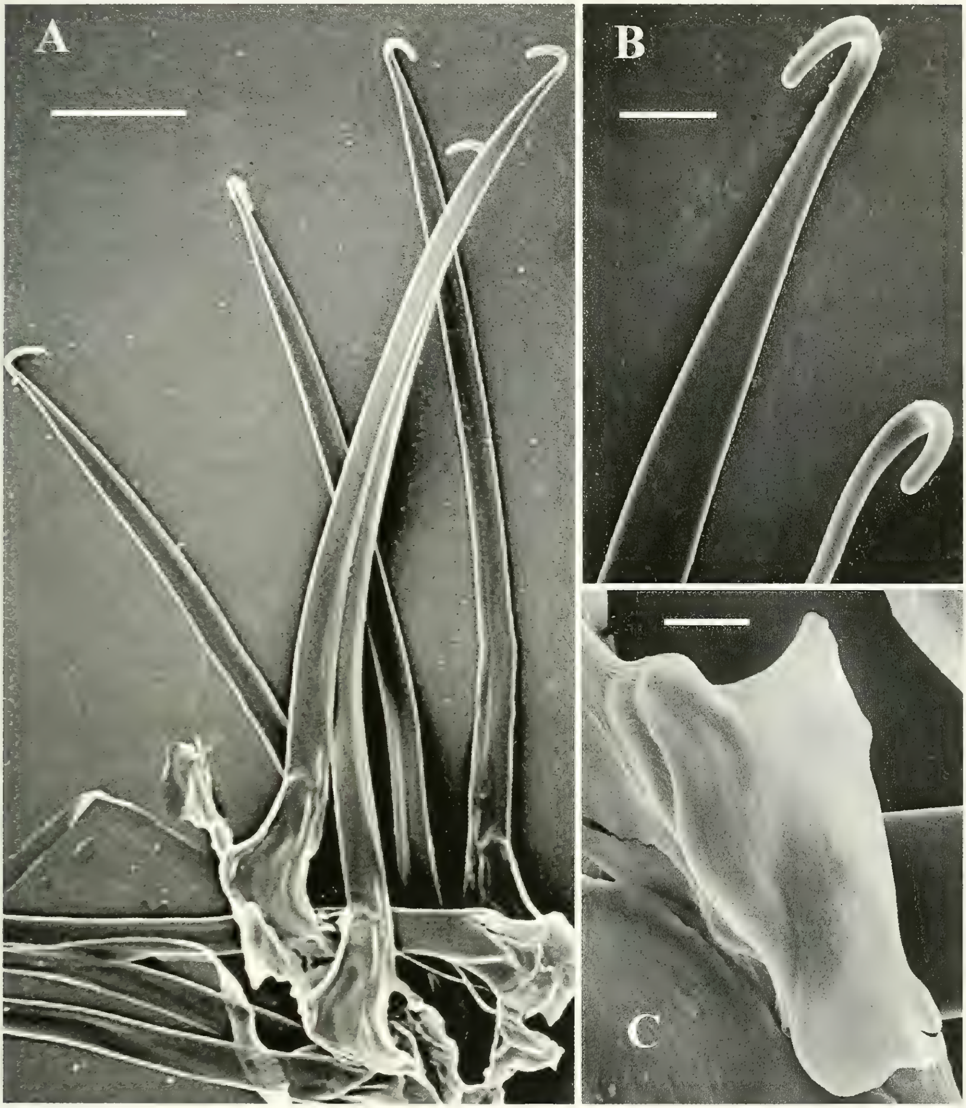


FIGURE 26. *Okenia nakamotoensis* (Hamatani, 2001) (CASIZ 096238). Scanning electron micrographs. A. Inner lateral teeth, scale = 150 µm. B. Apices of inner lateral teeth; scale = 34 µm. C. Outer lateral tooth; scale = 20 µm.

is present at the base of either cerebral ganglion The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 25B).— The preampullary duct is short and thin and expands into an ovoid ampulla. The ampulla divides into a short, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of approximately three coils. The distal end of the prostatic segment narrows into a short, straight ejaculatory portion that terminates in an indistinct, but slightly wider penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The thin elongate vagina exits adjacent to the penis. It connects to the large, spheroid bursa copulatrix. From the base of the bursa a short duct connects to the small, serial receptaculum seminis. From the proximal end of the receptaculum the uterine duct joins with the female gland mass.

Discussion.— The original description of *O. nakamotoensis* (Hamatani, 2001) includes illustrations of the external anatomy, the buccal mass and the radular teeth. All of these features, as originally described, are consistent with the present material from the Marshall Islands and the Philippines. The shape of the inner lateral teeth closely resembles that described for the type species of the genus *Hopkinsia*, *O. rosacea*. In both taxa, the inner laterals are thin and elongate with a hook–shaped apex, although the teeth are thinner and more elongate in *O. nakamotoensis* than in *O. rosacea*. *Okenia nakamotoensis* differs externally from *O. rosacea*. It is bright red with white pigment situated basally on the notal appendages and red apices whereas *O. rosacea* is uniformly pink in color. Also, *O. rosacea* has more numerous randomly distributed notal appendages while *O. nakamotoensis* has five pairs of lateral appendages and a single mid-dorsal appendage anterior to the gill. The reproductive systems of the two species are similar in configuration with several notable differences. Although the ampulla of *O. rosacea* is larger than that found in *O. nakamotoensis*, the prostatic portion of the vas deferens of *O. nakamotoensis* is more highly convoluted, consisting of several loops, than that of *O. rosacea*.

Okenia kondoi (Hamatani, 2001)

(Figs. 20C, 27–28)

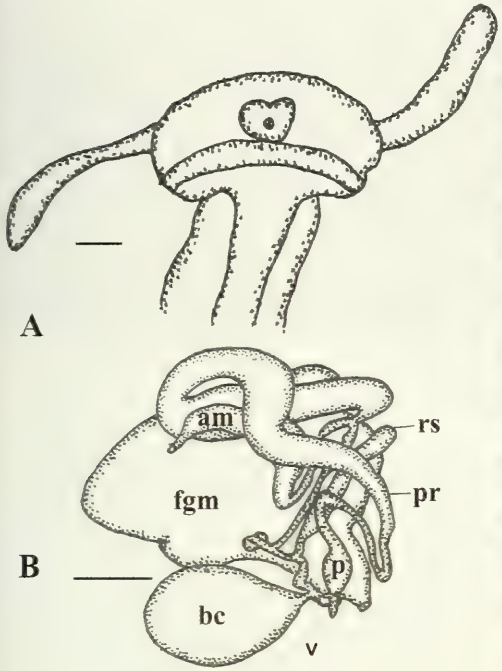
Sakishimaia kondoi Hamatani, 2001:153, Fig 2a–e.
Okenia kondoi (Hamatani, 2001) **comb. nov.**

Material examined.— CASIZ 158272, 5 specimens, Balacasag Island, Bohol, Philippines, 29 m. depth, 21 March 1994, T.M. Gosliner. CASIZ 106551, 7 specimens, 1 dissected, Agus Point, Mactan Island, Cebu, Philippines, 20 m. depth, 27 April 1996, M. Miller and T.M. Gosliner. CASIZ 158273, 4 specimens, CASIZ 120732, 4 specimens, Enewetak Atoll, Marshall Islands, 5 June 1983, S. Johnson.

Distribution.— This species is known from the Kuroshima Islands, Japan (Hamatani, 2001), Bohol and Cebu Islands (Philippines) and Enewetak and Kwajalein Atolls (Marshall Islands) (Gosliner, Behrens, and Williams 1996; present study).

Natural History.— This species is found together with *O. nakamotoensis* on outer reef faces in 10–30 meters of water, where it feeds upon the bright red bryozoan, *Tropidozoum cellariforme* Harmer, 1957.

External morphology.— The living animals (Fig. 20C) attain 20 mm in length. Preserved specimens range in size from 3–13 mm. The body is elongate and narrow. There is no distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body is uniformly red with the exceptions of the gill rachises and the base of the notal papillae, which are pinkish white. The gill lamellae and apices of the notal papillae are the same color as the remainder of the body. There are four pairs of elongate notal papillae along the sides of the body. Two of these are situated anterior to the rhinophores and are more thin and elongate than the more lateral ones. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 3–5 unipinnate branches. The rhinophores are elongate with 10–20 congested lamellae. The anterior end of the foot expands into two rounded lobes that are united as a small hood that surrounds the mouth (Fig. 27A). The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.



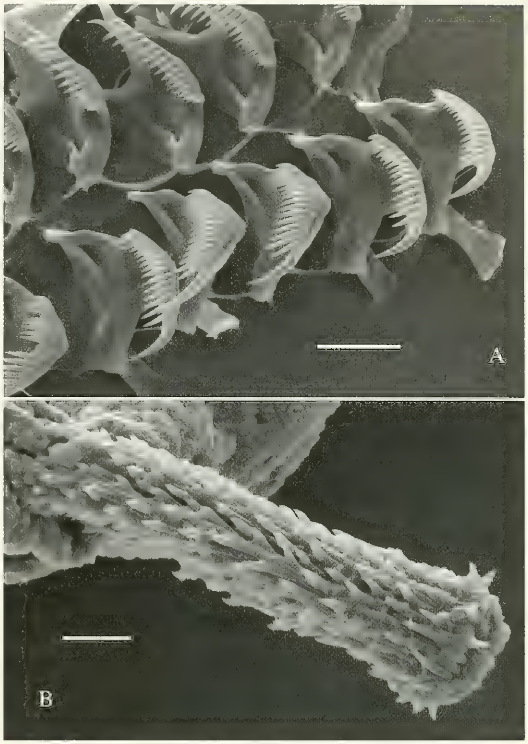


FIGURE 27 (left). *Okenia kondoi* (Hamatani, 2001) (CASIZ 106551). A. ventral view of head; scale = 0.2 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.3 mm.

FIGURE 28 (right). *Okenia kondoi* (Hamatani, 2001) (CASIZ 106551). Scanning electron micrographs. A. Radular teeth; scale = 35 μm. B. Penial armature; scale = 100 μm.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is short and protrudes only slightly from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. Lobate oral glands are present at the anterior end of the buccal mass around the mouth. The radular formula is 25 × 1.1.0.1.1. The inner lateral teeth (Fig. 28A) are truncate with a broad base and an elongate masticatory margin. The tooth contains 16–17 elongate denticles. The outer laterals are small and reduced to elongate, fan–shaped, quadrangular plates.

REPRODUCTIVE SYSTEM (Fig. 27B).—The preampullary duct is short and thin and expands into an elongate, cylindrical ampulla. The ampulla is curved and divides into an elongate, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the rounded, elongate receptaculum seminis. The lobate female gland mass consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded adjacent portions. The distal end of the prostatic segment narrows into a long, curved ejaculatory portion that terminates in a distinct conical penis. Protruding from the penial bulb is a cuticular portion bearing rows of chitinous hooks (Fig. 28B). The thick short base of the massive bursa copulatrix functions as the vagina. Near its base is a short duct that bifurcates and joins the albumen gland and the elongate receptaculum seminis.

Discussion.— Hamatani (2001) described *Sakishimaia* as a distinct genus based on the presence of a cylindrical slender body, absence of a pallial margin and velum and the absence of second (outer) lateral teeth. Scanning electron micrographs of the radula of *O. kondoi* (Fig. 28A) clearly show the presence of outer lateral teeth. The only characteristic unique to *O. kondoi* is the more body shape that is more elongate than species of *Hopkinsia*. This feature is shown to represent an autapomorphy for this taxon. The phylogeny presented here indicates that *O. kondoi* is nested within *Hopkinsia,* which in turn is nested within *Okenia*. Consideration of *Sakishimaia* as a distinct genus renders *Hopkinsia* paraphyletic. Similarly maintaining *Hopkinsia* makes *Okenia* paraphyletic. Thus, I consider it more prudent to consider *Sakishimaia* as a synonym of *Okenia* to maintain the monophyly of this taxon.

PHYLOGENETICS

To date, no phylogenetic analysis has been undertaken for members of the genera *Okenia, Hopkinsia, Hopkinsiella and Sakishimaia*. In the absence of phylogenetic studies there has been no objective test of the monophyly of these taxa. Recent works including these taxa (Bouchet and Ortea 1983; Hamatani 2001) have based systematic revisions exclusively on traditional rather than phylogenetic criteria. It is therefore important to conduct a preliminary phylogenetic analysis of members of these taxa. To facilitate such an analysis, morphological and anatomical studies were undertaken. Most data used to construct the matrix for phylogenetic analysis are derived from the morphological studies presented here. In addition to the species specifically discussed here, specimens of *Okenia angelensis* Lance, 1966 were examined (CASIZ 072351, 4 specimens, one dissected, Morro Bay, California, May-June 1981, David Behrens). Morphological description for other species were taken from the literature to represent morphological variation and geographical breadth. Specifically, anatomical details for the following taxa were derived from the following morphological studies: *Diaphorodoris luteocincta* (Schmekel and Portmann, 1982), *Goniodoris nodosa* (Thompson and Brown, 1984), *Okenia impexa* (Marcus, 1958; Schmekel and Portmann 1982), *O. zoobotryon* (Marcus, 1957, as *O. evelinae*; Valdés and Ortea 1995), *O. quadricornis* (Valdés and Ortea, 1995), *O. elegans* (Valdés and Ortea, 1995), *O. aspersa* (Schmekel and Portmann, 1982), *O. mediterranea* (Valdés and Ortea, 1995) and *O. hiroi* (Baba, 1938).

To determine the phylogenetic relationships of species of *Okenia, Hopkinsia, Hopkinsiella* and *Sakishimaia*, twenty morphological characters and one biological character were examined for 23 taxa, including *Diaphorodoris luteocincta* and *Goniodoris nodosa* as outgroup taxa. These taxa were chosen primarily because their anatomy is reasonably well described. These taxa also represent an excellent sample of the morphological variation that is known to exist in these taxa and also represent global geographical coverage of the known distribution of the Goniodorididae. All characters were treated as unordered. The following characters were considered:

1. *Body shape*: In the outgroup taxa and in many species of *Okenia* and *Hopkinsia* the body is short and ovoid (0). In some species of *Okenia* and *Sakishimaia kondoi* the body is narrow and elongate (1).
2. *Mantle between notum and foot*: In the outgroup and species of *Okenia*, the lateral margins of the body provide a surface distinct from the notum and foot (0). In these taxa, the genital opening is situated on this lateral surface of the right side of the body. In species of *Hopkinsia* and *Sakishimaia*, there is no distinct lateral surface and the notum slopes to the foot (1). In these taxa, the genital opening is on or near the lateral margin of the notum.
3. *Notal ridge*: In the outgroup taxa the notal edge is demarcated by a distinct thickening of tissue around its

entire margin (0), whereas all of the ingroup taxa lack any thickening around the mantle margin (1).

4. *Mid-dorsal crest*: In the outgroup taxa and *Okenia mediterranea*, there is a distinct mid-dorsal longitudinal crest that extends between the rhinophores and gill (0). In the remaining taxa, no thickening of tissue is present (1).
5. *Caudal crest*: The outgroup taxa, *O. mediterranea* and *O. quadricornis* have a caudal crest extending along the middle of posterior portion of the foot (0). This feature is absent in the remaining taxa studied here (1).
6. *Oral tentacle shape*: In *Diaphorodoris luteocincta* and several species of *Okenia*, the oral tentacles are rounded in shape (0). In other species, including *Goniodoris nodosa* and most species of *Okenia*, the oral tentacles are triangular and tentacular (1), whereas in species of *Hopkinsia* and *Sakishimaia*, the oral tentacles are fused with the mouth region to form an oral veil (2).
7. *Buccal pump*: In most species examined here, including the outgroup taxa and most of the ingroup taxa, the buccal pump portion of the buccal mass is moderately expanded (0), whereas in *Okenia virginiae* and *O. lambat* it is greatly expanded into a massive structure (1).
8. *Radular sac*: In the outgroup and vast majority of the ingroup taxa, the radular sac is much shorter than the rest of the buccal mass (0) whereas in *Hopkinsia rosacea* and *H. nakamotoensis* it is almost as long or longer than the buccal mass (1).
9. *Marginal papillae*: In the outgroup taxa, the margin of the notum may be undulate or irregular, but distinct lateral papillae are absent (0). In all of the ingroup taxa, elongate lateral papillae extend outward from the sides of the body (1).
10. *Mid-dorsal papillae*: In the ingroup taxa there are numerous conical papillae evenly distributed over the surface of the notum. This arrangement is also found in some species of *Okenia* and *Hopkinsia pilosa*. Mid-dorsal papillae are absent in *O. aspersa* and *O. quadricornis* (1). *Okenia purpureolineata* is unique in having two mid-dorsal papillae anterior to the gill (2). In many species of *Okenia*, *Hopkinsia* and *Sakishimaia*, there is a single mid-dorsal papillae anterior to the gill (3).
11. *Rhinophoral lamellae*: In the outgroup taxa and the vast majority of ingroup taxa, the rhinophores are characterized by having crowded lamellae along most of their length (0). In *Okenia angelensis, O. impexa, O. pellucida, O. zoobotryon* and *O. brunneomaculata* the rhinophoral lamellae are well separated from each other (1).
12. *Inner lateral tooth shape*: In the outgroup and most ingroup taxa the inner lateral teeth have a broad shape with a thick pointed cusp (0). In *Hopkinsia rosacea* and *H. nakamotoensis* the inner lateral teeth are highly modified and much elongated (1).
13. *Inner lateral tooth denticulation*: The ingroup taxa, *Hopkinsia hiroi*, and many species of *Okenia* the masticatory margin of the inner lateral tooth bears numerous fine teeth (0). Some species of *Okenia* and *Sakishimaia* (*O. impexa, O. pellucida, O. zoobotryon, O. brunneomaculata, S. kondoi*) have inner lateral teeth with fewer, coarser denticles (1). In *Hopkinsia rosacea, H. pilosa, H. plana* and *H. nakamotoensis* the inner lateral teeth entirely lack denticles (2).
14. *Inner lateral tooth apex*: In the outgroup taxa and the vast majority of ingroup taxa the apex of the inner lateral tooth is gently curved with an acute apex (0). In *Hopkinsia rosacea* and *H. nakamotoensis*, the apex of the inner laterals are sharply curved with a rounded apex (1).
15. *Outer lateral tooth*: The shape of the outer lateral teeth varies considerably in the taxa considered. In the outgroup and most of the ingroup taxa the outer laterals have a single apex (0). In *Okenia impexa* and *O. brunneomaculata* the outer lateral teeth have a deeply divided tooth with two sharp projections (1). The outer lateral tooth of *Hopkinsia rosacea* and *H. nakamotoensis* is greatly reduced in size to a tiny plate (2). The outer lateral tooth of *Sakishimaia kondoi* is flat and quadrangular in shape (3). The outer lateral tooth of *Hopkinsia plana* and *H. pilosa* is multidenticulate (4).
16. *Oral glands*: In the outgroup taxa and the vast majority of ingroup taxa studied here, there are minute oral glands at the anterior base of the buccal mass, adjacent to the mouth (0). Large oral glands are present in *Okenia japonica, O. liklik* and *O. purpureolineata* (1). The development of oral glands remains unknown for *Okenia aspersa, O. zoobotryon* and *Hopkinsia hiroi* (?).
17. *Ampulla length*: The ampulla provides the hermaphroditic duct from the ovotestis to the genital aperture. It also serves as an endogenous sperm storage organ. In the outgroup taxa and many ingroup taxa, the ampulla is elongate (0). In *Okenia japonica, O. virginiae, O. impexa, O. brunneomaculata, O. lambat, O.*

purpureolineata, H. pilosa, H. plana, H. rosacea, H. nakamotoensis and *Sakishimaia kondoi*, it is short (1). The form of the ampulla is not known for *O. aspersa* or *O. quadricornis* (?).

18. *Receptaculum seminis*: In the outgroup and the vast majority of ingroup taxa the diameter of the receptaculum seminis is about the same size as the bursa copulatrix (0) whereas in species of *Hopkinsia* and *Sakishimaia kondoi*, the diameter of the receptaculum seminis is much smaller than the bursa copulatrix (1). The form of the receptaculum seminis is not known in *Okenia quadricornis, O. aspersa, O. zoobotryon* or *Hopkinsia hiroi* (?).
19. *Uterine duct*: In the outgroup taxa and the majority of ingroup taxa the uterine duct is proximal to the receptaculum seminis (0). In *O. japonica, O. virginiae, O. lambat, O. kendi* and *O. liklik*, the uterine duct emerges from the vagina (1). The uterine duct position is unknown for *Okenia quadricornis, O. aspersa* or *Hopkinsia hiroi* (?).
20. In the outgroup taxa and the vast majority of the ingroup taxa, the vagina is long (0). In *Okenia virginiae, O. lambat* and *O. kendi*, the vagina is short (1). The length of the vagina is unknown for *Okenia quadricornis, O. aspersa, O. zoobotryon* or *Hopkinsia hiroi* (?).
21. Members of the taxa studied either feed on bryozoans (0) or tunicates (1). Food associations are unknown for *Okenia liklik* (?).

In order to determine phylogenetic relationships, the following data were entered into a data matrix using MacClade 3.01 (Table 1). This analysis was performed using PAUP 3.1.1, for the data matrix. All characters were treated as un–ordered and unweighted. A Heuristic search using stepwise addition from 1000 random starting trees was undertaken using the DELTRAN option, resulting in 200 trees with a length of 41, a consistency index of 0.683 and retention index of 0.824. The strict consensus of these trees is shown in Figure 29. Bremer support analysis was conducted to test the robustness of the tree.

DISCUSSION

The preliminary phylogeny presented here is moderately well supported, given the number of characters. Bremer support values are included in Figure 29. Most nodes have a Bremer support value of 1. The two most basal nodes have a Bremer support value of at least 2. Additionally, the clade that contains *Hopkinsia rosacea* and *H. nakamotoensis* also has a value of at least 2. Further analysis was not possible, owing to the large number of trees that were produced (more than 60,000) after adding trees with two more steps. Adding a third step to the tree lengths far exceeded the computing ability of the computer dedicated to phylogenetic analysis. The greater robustness of these basal clades is especially important for the subsequent systematic conclusions that are discussed.

The phylogenetic hypothesis presented in Figure 29 suggests several important aspects regarding the phylogeny of *Okenia*, *Hopkinsia, Hopkinsiella* and *Sakishimaia*. These taxa collectively form a monophyletic taxon characterized by two synapomorphies (presence of marginal papillae and absence of a notal ridge). *Okenia mediterranea* is the sister taxon to all the remaining members of the ingroup. Several large monophyletic clades are formed by species traditionally included in *Okenia*. This first clade contains the European Atlantic taxa, *O. elegans*, *O. aspersa* and *O. quadricornis* and is the sister group to all the remaining taxa. This clade is supported by an ecological synapomorphy, that all these taxa feed on tunicates rather than bryozoans. It is also interesting to note that Valdés and Ortea (1995) considered *O. aspersa* and *O. quadricornis* as the same species. This issue needs to be more fully studied with comparative material from Atlantic and Mediterranean waters. Members of this clade have short, rounded oral tentacles, as in the outgroup taxon *Diaphorodoris luteocincta*. *Okenia leachi* (Alder and Hancock, 1854) may also be a member of this clade. It also has rounded oral tentacles and feeds upon tunicates, but its anatomy remains largely unknown.

TABLE 1. Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	body	mant	notal	mid-(	caud	oral	bucc	radul	marg	mid (	rhind	inner	inner	inner	seco	oral	ampu	rece	uteri	vagir	feedi
Diaphorodoris luteocincta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniodoris nodosa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 / 1
Okenia angelensis	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Okenia quadricornis	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	?	?	?	?	1
Okenia elegans	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Hopkinsiella hiroi	0	1	1	1	1	2	?	?	1	0	0	0	0	0	0	?	?	?	?	?	0
Okenia impexa	0	0	1	1	1	1	0	0	1	3	1	0	1	0	1	0	1	0	0	0	0
Okenia japonica	1	0	1	1	1	1	0	0	1	3	0	0	0	0	0	1	1	0	1	0	0
Okenia mediterranea	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Okenia pellucida	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Hopkinsia pilosa	0	1	1	1	1	2	0	0	1	0	0	0	2	0	4	0	1	1	0	0	0
Hopkinsia plana	0	1	1	1	1	2	0	0	1	3	0	0	2	0	4	0	1	1	0	0	0
Okenia aspersa	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	?	?	?	?	?	?
Hopkinsia rosacea	0	1	1	1	1	2	0	1	1	0	0	1	2	1	2	0	1	1	0	0	0
Okenia zoobotryon	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
Okenia virginiae	0	0	1	1	1	1	1	0	1	3	0	0	0	0	0	0	1	0	1	1	0
Okenia lambat	0	0	1	1	1	1	1	0	1	3	0	0	0	0	0	0	1	0	1	1	0
Okenia kendi	0	0	1	1	1	1	0	0	1	3	0	0	0	0	0	0	0	0	1	1	0
Okenia liklik	1	0	1	1	1	1	0	0	1	3	0	0	0	0	0	1	1	0	1	0	?
Okenia brunneomaculata	0	0	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0
Hopknsia nakamotoensis	0	1	1	1	1	2	0	1	1	3	0	1	2	1	2	0	1	1	0	0	0
Sakashimaia kondoi	1	1	1	1	1	2	0	0	1	3	0	0	1	0	3	0	1	1	0	0	0
Okenia purpureolineata	1	0	1	1	1	1	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0

The sister group of these three species contain three distinct clades. The first of these, supported by two apomorphies (tentacular oral tentacles, sparse rhinophoral lamellae) contains *O. angelensis*, *O. zoobotryon*, *O. pelllucida* and the sister species, *O. impexa* and *O. brunneomaculata. Okenia impexa* and *O. brunneomaculata* share two synapomorphies, coarse denticles on the inner lateral tooth and a bifid outer lateral tooth. Additionally, all of these taxa have a translucent white body color with varied brown markings. They also all appear to feed upon ctenostomatous bryozoans. It appears that *O. mija* Burn, 1967 may also be a member of this clade. Its internal anatomy remains largely unknown, but it has a similar color pattern, feeds on ctenostomatous bryozoans and has sparse rhinophoral lamellae. Collectively members of this clade inhabit a wide geographical area and include subtropical and tropical Atlantic, Eastern Pacific and Indo-Pacific taxa. Understanding the detailed phylogeny of this clade may also shed some additional light on the historical biogeography of this taxon.

The second clade is supported by three synapomorphies (absence of a distinct lateral surface of the body, oral tentacles fused with the mouth region to form an oral veil and the presence of a short ampulla). *Sakishimaia kondoi* is nested within the species traditionally placed within *Hopkinsia. Hopkinsiella hiroi* is basal within this clade, but lacks any autapomorphies. *Hopkinsia rosacea* and *H. nakamotoensis* are sister species, a relationship that is supported by five synapomorphies. These taxa are all Pacific in their distributions, from the Indo-Pacific tropics and subtropics and temperate Japan and California.

The third clade is restricted to the Indo-Pacific tropics and adjacent subtropical waters of Japan. It is supported by three synapomorphies, the presence of tentacular oral tentacles, the presence of a single mid-dorsal papillae and the presence of short ampulla. This clade is divided into two sister clades. One of these, contains *Okenia liklik*, *O. purpureolineata* and *O. japonica*. These three species have an elongate body and large oral glands. These taxa are restricted to the margins of the western Pacific. The other subclade contains *O. kendi*, and the sister species, *O. lambat* and *O. virginiae*. This clade is supported by the presence of a short vaginal duct and a uterine duct that emerges from the vagina. *Okenia barnardi* Baba, 1937, also appears to be a member of this clade. This is suggested by its body shape, arrangement of lateral papillae and the presence of a single medial papillae anterior to the gill. The anatomy of this species remains largely undescribed.

Several systematic conclusions are evident from this phylogenetic analysis. On the basis of this preliminary phylogeny, *Sakishimaia* must be considered to be a junior synonym of *Hopkinsia*, since it is nested within *Hopkinsia* and maintaining it would render *Hopkinsia* paraphyletic.

The monophyly of the ingroup is supported when only single outgroup taxa are included (either *Diaphorodoris luteocincta* or *Goniodoris nodosa*) and the other taxon is included in the ingroup. The monophyly of *Hopkinsia* (including *Sakishimaia kondoi*) is well supported. However, *Okenia* is paraphyletic when *Hopkinsia* is maintained, as the latter taxon is nested well within *Okenia*. One possible systematic solution is to create a series of subgeneric names in order to maintain *Hopkinsia*. This does not seem to add any information not already contained in the phylogeny and adds unnecessary names to the nomenclature. A second solution is to include all of the ingroup taxa within a single monophyletic taxon, *Okenia*. In this case, *Hopkinsia, Hopkinsiella* and *Sakishimaia* would be junior synonyms of *Okenia*.

It is with regret that I feel compelled to adopt this latter solution. *Hopkinsia* is a much beloved name that honors the founding of the Hopkins Marine Station of Stanford University and was erected by Frank Mace MacFarland, former Stanford Professor of Biology and President of the California Academy of Sciences. Nevertheless, it is the most simple solution that preserves monophyly and does not create a nomenclature that is unnecessarily complicated. Therefore, *Hopkinsia, Hopkinsiella* and *Sakishimaia* are here considered as junior synonyms of *Okenia*.

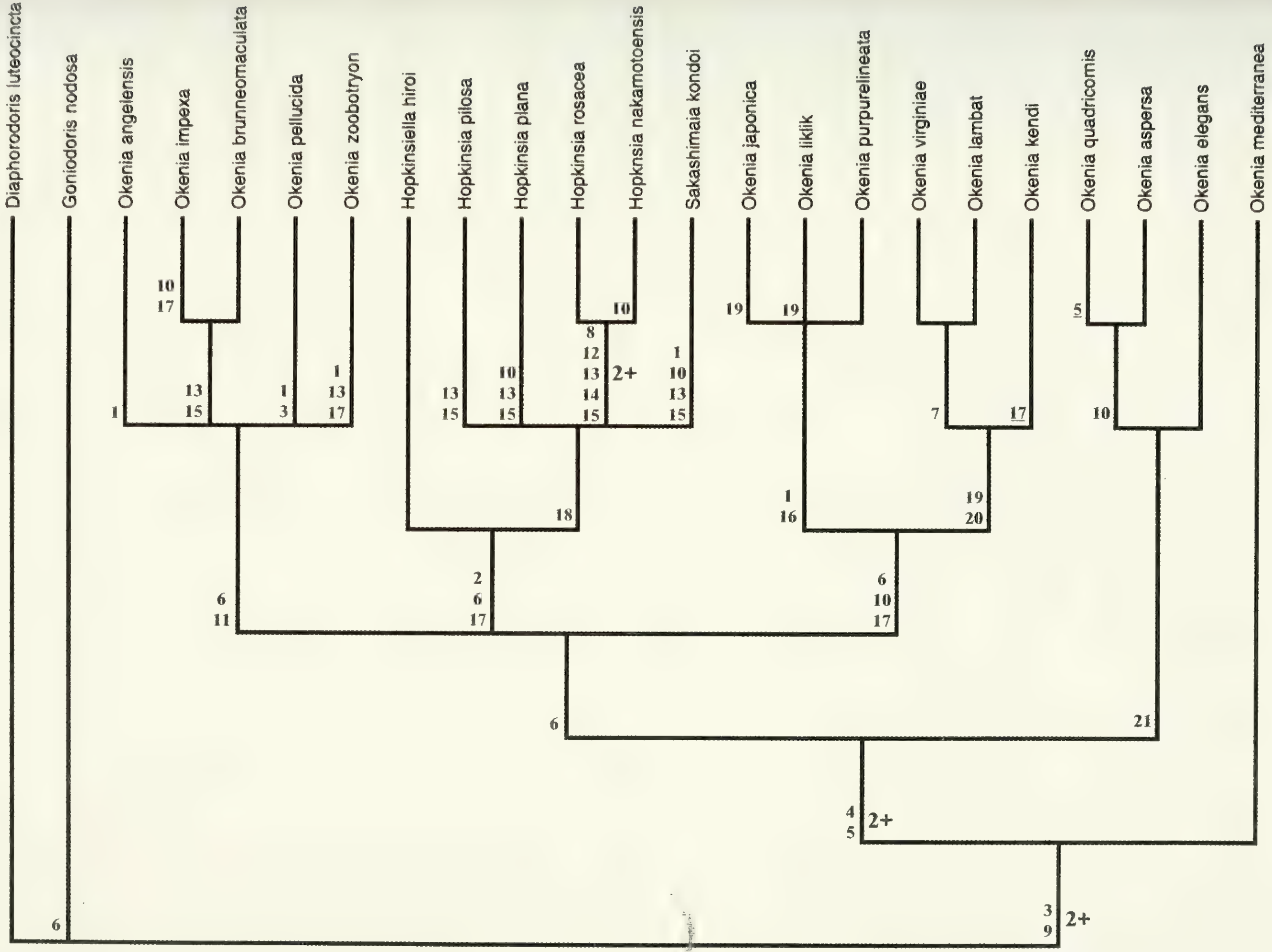


FIGURE 29. Strict consensus tree of preliminary phylogeny. Apomorphies are indicted by character numbers included in the analysis. Characters which exhibit reversal are underlined. Bremer support values for each node are indicated as large numerals on the right side of each node. Bremer values not indicated on figure are 1.

At least 12 additional described species of *Okenia* have not been fully studied for the anatomical characters included in this study. At least four undescribed species of *Okenia* are known to occur in the eastern Pacific tropics and two undescribed species are known from Australian waters. These taxa should be examined and incorporated into subsequent phylogenetic studies. Additional phylogenetic studies of the remaining goniodoridid and onchidoridid genera are also to necessary to produce a broader understanding of the phylogeny and systematics of these poorly understood dorid nudibranchs.

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Eptatretus lakeside sp. nov., a New Species of Five-Gilled Hagfish (Myxinidae) from the Galápagos Islands

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We describe *Eptatretus lakeside* sp. nov. from a deepwater (762 m) specimen trapped off Fernandina Island, Galápagos Islands. The new species differs from all known *Eptatretus* in having: five pairs of gill pouches; 3-cusp multicusps in anterior and posterior rows; 6 unicusps in each anterior and posterior row; 36 total cusps; 19 tail pores; 88 total pores; palatine tooth triangular; and body coloration pinkish-orange. A key to the species of Galápagos hagfishes is provided.

The myxinoid fauna of the Galápagos Archipelago was unknown until 1995 when the California Academy of Sciences (CAS) / Harbor Branch Oceanographic Institute (HBOI) expedition made numerous deepwater collections using the submersible *Johnson Sea-Link*. During that cruise, three species of *Eptatretus*, *E. grouseri*, *E. mccoskeri*, and *E. wisneri* were trapped and all were described as new (McMillan 1999). A subsequent expedition in 1998 involving CAS, HBOI, and the National Museum of Natural History (USNM), again using the submersible *Johnson Sea-Link*, captured additional specimens of hagfishes, including a single remarkable specimen of *Eptatretus*, which is described herein as new.

Hagfishes are rare in the eastern tropical Pacific but abundant in the temperate and subtemperate eastern Pacific. In fact, the extensive deepwater collections off Central America and the Galápagos made by the U.S. Fish Commission Steamer *Albatross* in 1891 (Garman 1899) resulted in but one hagfish specimen. It was captured over a rocky bottom in 730 fathoms (1335 m) in the southern end of the Gulf of Panama and described as *Myxine circifrons* Garman, 1899. In contrast to the *Albatross*, the successful capture of hagfishes by the recent expeditions can be explained by the difficulty that the *Albatross* expedition had in trawling over unusually rocky terrain, and by the undeniable benefits provided by manned submersibles in exploring and collecting in complex deepwater habitats.

Currently, there are 30 recognized species of *Eptatretus*, 12 of which are known from the eastern Pacific (McMillan and Wisner 1984; Wisner and McMillan 1988, 1990; McMillan 1999). Undoubtedly more species remain to be discovered.

MATERIALS AND METHODS

The type of the new species as well as the holotypes of all other hagfishes from the Galápagos Islands are deposited in the Department of Ichthyology of the California Academy of Sciences (CAS), San Francisco. Other type specimens examined are deposited in the Scripps Institution of Oceanography (SIO), La Jolla, and National Museum of Natural History (USNM), Washington, D.C.

Methods of measuring and counting follow those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). The names of anatomical structures follow Wisner and McMillan (1995) and Mok (2001). Length of the specimens (in mm) is given as total length (TL), the distance from the front of the rostrum to the end of the caudal finfold. All other measurements are given in percentage of TL. Counts of gill pouches (GP), gill apertures (GA), and cusps are taken for both sides, whereas slime pore counts are from the left side. Measurements and counts are given in Table 1 and compared with data of all other *Eptatretus* species previously known from the Galápagos Islands. We provide drawings from the anterior and posterior sets of cusps, including the palatine tooth, which are not usually useful characters to identify hagfish species, but in this case they aid in distinguishing species. We provide a key to the *Eptatretus* species from the Galápagos Islands, which was modified from McMillan (1999).

Eptatretus lakeside Mincarone and McCosker, sp. nov.

(Figs. 1, 3; Table 1)

Material examined.— Holotype: CAS 201880 (field number JM-155), an immature female, 275 mm TL, from off Cabo Douglas, NW Fernandina Island, Galápagos Islands, 00°17′30″S, 91°39′36″W, 762 m depth, collected on 17 July 1998 by David Pawson and Godfrey Merlen, using a baited metallic minnow trap, deployed while aboard the submersible R/V *Johnson Sea-Link* (JSL Dive 3101).

Diagnosis.— *Eptatretus lakeside* can be distinguished from its congeners by a combination of the followings characters: five pairs of gill pouches; 3-cusp multicusps in anterior and posterior rows; 6 unicusps in each anterior and posterior rows; 36 total cusps; 19 tail pores; 88 total pores; palatine tooth triangular; and body coloration pinkish-orange.

Description of the Holotype.— Body subcylindrical and slender, slightly deeper than wide at prebranchial, branchial, and trunk regions and strongly compressed at tail. Rostrum bluntly rounded; nasopharyngeal duct cylindrical, tube-like, slightly projecting. One pair of conspicuous nasal-sinus papillae on the inner dorsal surface of the nasal sinus. Three pairs of barbels on the head, the first two pairs about equal in size and adjacent to the nasopharyngeal duct; the third pair is immediately adjacent to the oral cavity. Ventral finfold (VFF) conspicuous, 2 mm high, beginning 25 mm behind the last gill aperture and extending backward to the cloaca. Caudal finfold quite thin and rounded, extending around tail to dorsal surface, ending about over cloaca.

Total length 275 mm; prebranchial length 68 mm; branchial length 17 mm; trunk length 145 mm; tail length 50 mm; body width at prebranchial region 14 mm; body depth at mid-trunk including VFF 20 mm; body depth excluding VFF 18 mm; body depth over cloaca 15 mm; tail depth 17 mm. Three-cusp multicusps in anterior and posterior rows of cusps; 6 unicusps in each anterior and posterior row; total cusps 36. Cusps long, slender, and pointed; palatine tooth triangular (Fig. 3). A segmentally arranged row of slime pores on each side, extending from beyond head to behind cloaca. Prebranchial pores 15; branchial pores 4; trunk pores 50; tail pores 19; total pores 88. Four branchial pores are intercalated with five gill apertures on both sides. No slime pore associated with the pharyngocutaneous duct. Five pairs of gill pouches corresponding to five pairs of gill apertures. Last branchial duct confluent with the pharyngocutaneous duct on the left side. First pair of gill pouches lies posterior to end of dental muscle; ventral aorta branches at the second gill pouch.

Body color in alcohol pinkish; barbels and face the same color as body; eyespots present but inconspicuous; ventral finfold pale; caudal finfold with a narrow pale margin. In life, the specimen was pinkish-orange.

Distribution.— Known only from the Galápagos Islands.

FIGURE 1. Dorsal view of preserved holotype of *Eptatretus lakeside* (CAS 201880; 275 mm TL).

ETYMOLOGY.— Named *lakeside*, a noun in apposition. We take great pleasure in honoring the Lakeside Foundation of California, which has generously supported the work of the senior author and many other foreign scholars.

Key to Galápagos Species of *Eptatretus*

1a. Five or six gill pouches and apertures on each side. 2
1b. Eight gill pouches and apertures on each side 3

2a. Body coloration pinkish-orange; 3/3 multicusp pattern; 36 total cusps; 88 total pores . . . . *Eptatretus lakeside*, new species
2b. Body coloration dark brown; 3/2 multicusp pattern; 44–48 total cusps; 71–79 total pores . . . . *Eptatretus grouseri* McMillan, 1999

3a. Prebranchial length 24–26 % of TL; 3/3 multicusp pattern; 48–51 total cusps; 14–15 prebranchial pores . . . . *Eptatretus mccoskeri* McMillan, 1999
3b. Prebranchial length 19–23 % of TL; 3/2 multicusp pattern; 44 total cusps; 9 prebranchial pores . . . . *Eptatretus wisneri* McMillan, 1999

COMPARISON.— Three five-gilled species of *Eptatretus* were previously known: *E. grouseri* McMillan, 1999 from the Galápagos Islands, *E. profundus* (Barnard, 1923) from South Africa, and *E. eos* Fernholm, 1991 from the Tasman Sea. All have a 3/2 multicusp pattern, whereas *E. lakeside* has 3/3. *Eptatretus lakeside* also differs from *E. grouseri* in the following characters, respectively:

FIGURE 2. Left lateral view of preserved *Eptatretus grouseri* (CAS 201882; 420 mm TL).

number of unicusps on each row (6 *vs*. 8–10); total cusps (36 *vs*. 44–48); tail pores (88 *vs*. 71–79); shape of palatine tooth (triangular and depressed *vs*. conic [Fig. 3]); and its body coloration (pinkish-orange [Fig. 1] *vs*. dark brown [Fig. 2]). Also, the teeth of *E. lakeside* are more slender and more elongate than those of *E. grouseri* (Fig. 3). *Eptatretus lakeside* differs from *E. profundus* in the following characters, respectively (based on the redescription of the holotype of *E. profundus*

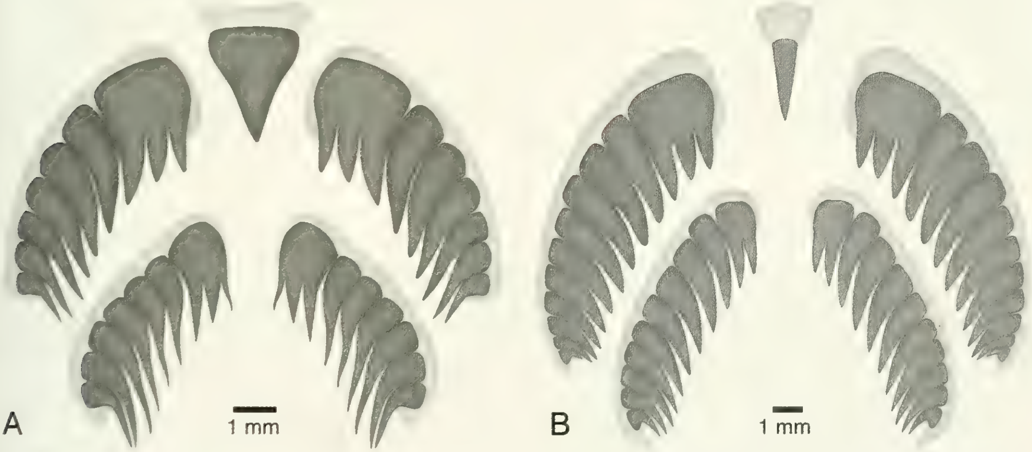

FIGURE 3. Dentition of (A) *Eptatretus lakeside* (CAS 201880, 275 mm TL), and (B) *Eptatretus grouseri* (CAS 201882, 420 mm TL).

TABLE 1. Measurements and counts of *Eptatretus* from the Galápagos Islands.

	E. lakeside	*E. grouseri*		*E. mccoskeri*	*E. wisneri*
	Holotype	Holotype	Non-types (2)	Holotype	Holotype
Total length TL (mm)	275	370	315–420	310	355
		Measurements in % of TL			
Prebranchial length	4.7	20.3	21.0–22.2	25.8	18.9
Branchial length	6.2	8.1	6.3–6.5	10.0	12.1
Trunk length	50.9	57.0	54.0–55.7	48.4	51.3
Tail length	18.2	14.6	16.9–17.5	15.8	17.7
Body width	5.0	5.9	5.4–6.3	7.3	6.5
Body depth					
Inc. ventral finfold	7.2	6.8	7.9–9.0	8.2	8.0
Exc. ventral finfold	6.4	6.8	7.9–8.8	8.2	7.7
Over cloaca	5.4	5.7	6.4–6.5	7.3	6.5
Tail	6.0	6.8	7.6–7.9	8.9	8.3
		Counts			
Cusps					
Multicusps	3/3	3/2	3/2	3/3	3/2
Anterior unicusps*	6+6	9+9	9–10	10+10	9+9
Posterior unicusps*	6+6	8+8	9–9	9+10	9+9
Total cusps	36	44	46–48	51	46
Slime pores, left side					
Prebranchial	15	12	11–12	13	9
Branchial	4	4	5–5	7	7
Trunk	50	46	42–48	43	43
Tail	19	15	13–14	10	14
Total pores	88	77	71–79	73	73
Gill apertures*	5+5	5+5	5–6	8+8	8+8
Gill pouches*	5+5	5+5	5–6	8+8	8+8

* Left + right count.

by Strahan 1975): number of unicusps on each row (6 *vs.* 8); tail pores (19 *vs.* 15); and its body coloration (pinkish-orange *vs.* dark brown). Despite the multicusp condition, *E. eos* shares some characters with *E. lakeside*: both have a pinkish body coloration; a long tail (about 18% of TL); an elongated tube-like nostril (longer in *E. eos*); and the same number of unicusps (six). However, *E. lakeside* differs from *E. eos* in the number of prebranchial pores (15 *vs.* 26), trunk pores (50 *vs.* 75–77), tail pores (19 *vs.* 26–27), and total pores (88 *vs.* 128–130) (based on the original description of the holotype of *E. eos* by Fernholm 1991). The other two *Eptatretus* species from the Galápagos Islands, *E. mccoskeri* and *E. wisneri*, can be easily separated from *E. lakeside* by their having eight pairs of gill pouches and a brownish-black body coloration. The triangular shape of the palatine tooth is probably an autapomorphy of *E. lakeside* (Fig. 3A). *Nemamyxine kreffti* McMillan & Wisner, 1982, is the only other hagfish that has a similar palatine tooth, but its tooth is more depressed and has a rounded point (Mincarone 2001). In most hagfish species the palatine tooth has a conical shape like a bird's claw (Fig. 3B).

The Galápagos species of *Eptatretus*, albeit based on a very limited sample size, appear to be stratified by depth. The only known *E. mccoskeri* were trapped at 215 m on a seamount SE of San Cristobal Island on the eastern edge of the archipelago. The other species were captured off Fernandina Island (F), along the western edge of the archipelago, and from Seymour (S) Island (= James) in the center of the archipelago. They were trapped at the following depths: *E. wisneri*, 512–563 m (F); *E. grouseri*, 648–722 m (F and S); and *E. lakeside*, 762 m (F).

Remarks.— The location of capture, Cabo Douglas, is located along the NW corner of Fernandina Island and drops steeply into deep water (more than 1000 m depth at a distance less than 2 km from shore). The specimen was collected using a galvanized metal minnow trap baited with fish flesh and set from the submersible at 0845 and retrieved approximately one hour later. The bottom was nearly flat with a slight downward slope (<10°) and covered with fine gray sediment and occasional lava boulders (~ 0.5 m in diameter) in the vicinity of other large lava reefs. The temperature at depth was 8°C and there was a current of ~0.3 knot. The habitat is further described by Iwamoto and McCosker (2001) who described a new macrourid, *Coryphaenoides gypsochilus*, from that site. Also observed at and near that locality were several pelagic holothurians (*Pelagothuria nanatrix* Ludwig), hagfishes (*Eptatretus grouseri* McMillan and *E. wisneri* McMillan), catsharks (*Apristurus* spp.), combtooth dogfish (*Centroscyllium nigrum* Garman), chimaeras (*Hydrolagus* spp.), witch-eels (*Facciolella equatorialis* (Gilbert)), viperfish (*Chauliodus sloani* Bloch and Schneider), grenadier (*Nezumia loricata loricata* (Garman)), cardinalfish (*Epigonus merleni* McCosker and Long), batfishes (*Dibranchus erinaceus* (Garman)), ateleopodids (*Guentherus altivelis* (Osório)), bythitids (*Diplacanthopoma jordani* (Garman)), and an undescribed scorpionfish (*Phenacoscorpius* sp.).

Comparative Material.— *Eptatretus grouseri*: CAS 86428, holotype, 370 mm TL, Punta Espinosa, Fernandina Island, Galápagos Islands, 00°14′36″S, 91°26′36″W, 722 m; SIO 97–77, paratype, 138 mm TL, taken with holotype; CAS 201882, 2 specimens, 315–420 mm TL, Seymour Island, Galápagos Islands, 00°21′42″S, 90°15′00″W, 648 m, 25 July 1998, *Johnson Sea-Link* (JSL Dive 3113). *Eptatretus mccoskeri*: CAS 86431, holotype, 310 mm TL, San Cristobal Island, Galápagos Islands, 01°06′19″S, 89°06′56″W, 215 m; SIO 97–75, paratype, 290 mm TL, taken with holotype; USNM 344905, paratype, 284 mm TL, taken with holotype. *Eptatretus wisneri*: CAS 86429, holotype, 355 mm TL, Cabo Hammond, Fernandina Island, Galápagos Islands, 00°27′56″S, 91°37′33″W, 563 m; SIO 97–76, paratype, 316 mm TL, Galápagos Islands, 00°17′30″S, 91°38′54″W, 512 m.

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A New Species of Finless Snake Eel (Anguilliformes: Ophichthidae) from Ascension Island, with Comments on *Ichthyapus acutirostris*

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***Ichthyapus insularis*, new species, is described from the intertidal of Ascension Island. It differs from its widespread Atlantic congener, *I. ophioneus*, in its vertebral number and tail length, and from all other *Ichthyapus* in its vertebral number, body proportions, and preopercular pore condition. The identity of *I. acutirostris* Brisout de Barneville (1847), the generic type, is aligned with specimens from Japan.**

In preparing the ophichthid section of the Fishes of the Western North Atlantic, Eugenia Böhlke, Jim Böhlke, and I examined a myriad of finless ophichthids (McCosker et al. 1989) and discovered that one species, *Ichthyapus ophioneus*, was widely distributed from Bermuda to Brazil, and that its only Atlantic congener was an undescribed species from Ascension Island. In preparation for the forthcoming ophichthid chapter of FAO's Fishes of the Eastern Central Atlantic, I now describe that new species. In preparing this description, I believe that I have helped to solve the long-lasting conundrum, "what is the identity of *Ichthyapus acutirostris* Brisout de Barneville (1847)?"

MATERIALS AND METHODS

Type specimens of the new species are deposited in the Department of Ichthyology of the California Academy of Sciences (CAS), San Francisco. Measurements are straight-line (point to point) and made with dial calipers and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths; head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus. Vertebral counts (which include the hypural) are taken from radiographs. Preanal vertebrae are counted until mid-anus. Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985).

Ichthyapus insularis McCosker, sp. nov.

(Figs. 1–2; Tables 1–2)

MATERIAL EXAMINED.— HOLOTYPE: USNM 214480, an immature male, 427 mm TL, from Southwest Bay, Ascension Island, in 0–1 m, collected by S. Olson on 12 July 1970. PARATYPES: USNM 375444, 8(227–423 mm TL), collected with the holotype. CAS 218803, 387 mm TL, collected with the holotype. ANSP 158903, 2 (166–244 mm TL), from southwest side of English Bay, Ascension Island (07°53′48″S, 14°23′06″W), collected among rocks and sand by W.D. Anderson on 16 July 1980.

Diagnosis.— An elongate, finless species of sphagebranchin (*sensu* McCosker 1977) ophichthine with: tail 57–60% and head 9–11% of total length; 4 preopercular pores and 5 pores in supratemporal canal; teeth conical, uniserial on jaws and vomer; body mostly colorless in preservative; and mean vertebral formula -45-123.5, total vertebrae 121–126.

Counts and Measurements of Holotype (in mm).— Total length 427; head 46.8; trunk 130.2; tail 250; body depth at gill openings 11.5; body width at gill openings 11.1; body depth at anus 9.8; body width at anus 9.6; snout 6.5; tip of snout to rictus 15.0; eye diameter 1.2; interorbital distance 2.8; gill opening length 7.3; isthmus width 2.2. Vertebral formula -44-121. 120 lateral-line pores, 8 in branchial region, 46 pores before the anus.

Description of the Holotype.— Body elongate, nearly cylindrical throughout, snout and tail tip sharply pointed, depth at gill openings 37 in TL. Branchial basket notably wider and deeper than body. Head and trunk 2.4 in TL; head 9.1 in TL, 2.8 in trunk. Snout sharply pointed, its underside flattened and bisected by a groove nearly to anterior nostrils. Lower jaw short, included, upper and lower lips meet when mouth is closed. Mouth moderately elongate. Rictus well behind rear margin of eye. Eye minute, 12.1 in upper jaw and 39 in head, its center above middle of upper jaw. Anterior nostril non-tubular, a convoluted opening on underside of snout, about midway between tip of snout and tip of lower jaw when mouth is closed. Posterior nostril with an irregular rim, opening inside of mouth. Branchial openings low, ventral, with a median fold forming a pouch; branchial region expanded, creating a bulbous region in posterior half of head.

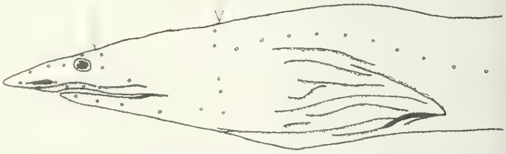

Figure 1. Lateral view of the holotype of *Ichthyapus insularis* (USNM 214480, 427 mm TL). Arrows indicate locations of the median interorbital and the temporal pores.

Head pores (Fig. 1) conspicuous. Single median interorbital and temporal pores. Supraorbital pores 1 + 4, infraorbital pores 5 + 2, supratemporal pores 5, lower jaw pores 4, preopercular pores 4. (The head pores of the 11 paratypes are nearly identical to those of the holotype, save 2 with 5 rather than 4 right lower jaw pores and 1 with 6 rather than 5 supratemporal pores.) 120 lateral-line pores, 8 before gill opening, 46 before anus.

Teeth (Fig. 2) uniserial, small, conical and sharp. Intermaxillary with a chevron of 11 teeth, followed by a short gap and a linear row of 13 vomerine teeth. Jaw teeth nearly subequal, small and close-set, 24–28 teeth in upper jaw and 22–26 teeth in lower jaw.

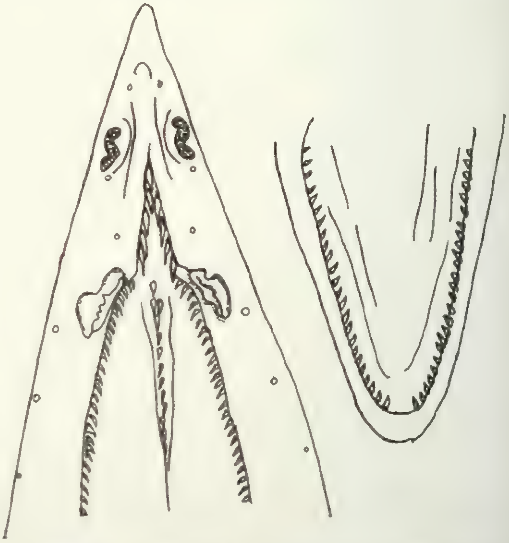

Figure 2. Dentition of the holotype of *Ichthyapus insularis* (USNM 214480, 427 mm TL) (upper jaw, left; lower jaw, right). The lips have been slightly retracted to expose the teeth and posterior nostrils.

Body mostly colorless in isopropanol. Faint brown pigment smudges surround the second and third supraorbital pores and overlaying the nape and cheeks; a faint brown posteriorly-directed "v" arises behind posterior mid-orbit and extends to the interorbital pore.

Size.— The largest specimen examined is 427 mm, an immature male. None of the specimens appears (examined radiographically, but not by dissection) to be a mature female.

Etymology.— From the Latin *insularis*, of an island, in reference to its apparently endemic location.

Distribution.— Known only from Ascension Island.

Table 1. Counts and proportions (in thousandths) of the holotype and 11 paratypes of *Ichthyapus insularis*. TL= total length. HL= head length.

	Mean	*Range*
TL (mm)	—	166–427
HL/TL	99	90–110
Head and trunk/TL	415	401–426
Tail/TL	585	401–426
Depth at gill opening/TL	25	20–29
Upper jaw/HL	307	267–338
Snout/HL	154	139–167
Eye/HL	25	19–29
Interorbital/HL	65	54–74
Gill Opening/HL	138	113–166
Isthmus/HL	43	32–61
Preanal vertebrae	45	44–46
Total vertebrae	123.5	121–126

Remarks.— Inasmuch as species of *Ichthyapus* lack fins and, particularly in preservative, display little or no differences in coloration, the most useful characters to differentiate species seems to be the preopercular pore (POP) condition, vertebral number, and body/tail proportions. Those characters show limited variation as demonstrated by an examination of 77 specimens of *I. ophioneus* that had a range of total vertebrae from 125–139, and the POP condition of 75 specimens was 4 and only two had 3 pores (McCosker et al. 1989). On that basis, *Ichthyapus insularis* appears to be most similar to *I. ophioneus* (Evermann and Marsh), a widespread western Atlantic species from Bermuda, Bahamas, Florida, the Greater Antilles, and St. Helena Island. The two, however, differ in their vertebral number (121–126 vs. 125–139) and the comparative length of head and trunk to total length (.40–43 vs. .36–40). Specimens of the new species were compared to and separable from *I. ophioneus* from St. Helena Island. And, although not visible on all specimens, the faint dorsal head coloration of *I. insularis* is lacking in all specimens examined of *I. ophioneus*. The new species can be differentiated from its Pacific and Indian Ocean congeners on the basis of characters listed in Table 2.

The only recent treatment of Ascension Island shorefishes is that of Lubbock (1980). In it he mentions but did not examine an Ascension Island specimen of "*Sphagebranchus ophioneus* found washed up on the beach by the Shackleton-Rowett expedition." I have not examined that specimen either, but I believe that it will prove to be *I. insularis*.

Lubbock listed 71 shorefish species at Ascension and found 11 to be endemic. Recognizing that *I. insularis* is indeed endemic, the degree of endemism of his ichthyofaunal list is thereby elevated to 12 species or 17%. More recent collecting at Ascension and the reidentification of many museum specimens (for example, two additional ophichthids, *Callechelys bilinearis* and *Phaenomonas longissima*, are now known from Ascension) will undoubtedly modify Lubbock's analysis.

Comparative Material Examined.— 1062 specimens of *Ichthyapus ophioneus*, 50–479 mm TL, from 86 lots from Bermuda, Bahamas, Florida, West Indies, Cuba, Puerto Rico, Lesser Antilles, Panama, Belize, Venezuela, Brazil and St. Helena, including the holotypes of *Sphagebranchus ophioneus* (USNM 49526) and *Sphagebranchus conklini* (FMNH 57731). Those specimens are listed in McCosker et al. (1989:325).

On the Identity of *Ichthyapus acutirostris*

The provenance of the type specimen of *Ichthyapus*, *I. acutirostris* Brisout de Barneville (1847), is unknown in that the type specimen (MNHN 2119, two were described, but only one

TABLE 2. Characteristics of the species of *Ichthyapus*. Abbreviations are: 1, this study; 2, McCosker and Castle 1986; 3, Blache and Bauchot 1972; 4, Hatooka et al. 1995; 5, Randall and McCosker 1975; 6, McCosker et al. 1989; 7, McCosker 2002; POP = preopercular pore condition; body is the proportion of head and trunk (in hundredths); * = holotype.

	POP	*Vertebrae*	*Body/TL*	*Source*
I. acuticeps	4	101–108	47–50	1,2
*I. acutirostris**	3	133	40	1,3
I. Japan	3	129–133	42–44	4
I. Easter Island	3	130–134	42–45	5
I. insularis	4	121–126	41–43	1
I. ophioneus	4	125–129	35–40	6
I. selachops	4	137–144	38–40	1
I. "*vulturis* complex" (except Hawaii)	4	120–130	39–41	1
I. vulturis (Hawaiian archipelago)	3 or 4	120–124	39–43	1,7

remains) lacks locality information other than "Haute-Mer, Océan équatorial." The specimen was collected by "M. Rang" (Monsieur Paul-Charles-Alexandre-Léonard Rang, 1793–1843), a French malacologist who collected primarily in the tropical Atlantic but also visited India, Madagascar (Bauchot et al. 1990:121), and Japan (P. Béarez, in litt., 7 Jan. 2004). There is no indication the he traveled to the South Pacific.

Since its description, *Ichthyapus acutirostris* has been ascribed to specimens from St. Helena Island (Cadenat and Marchal 1963) and from Baja California, Mexico (Blache and Bauchot 1972). The type of *I. acutirostris* has 133 vertebrae and three preopercular pores (POP). It thereby does not agree with any Atlantic species. Blache and Bauchot compared the type specimen to a specimen of *Ichthyapus* from Baja California (MNHN 1893-58) and suggested that the two were conspecific. I have examined both specimens and find the latter to be *Ichthyapus selachops* (Jordan and Gilbert 1882), a widespread eastern Pacific species known from Baja California to Ecuador, which has 137–144 vertebrae (n = 17) and four POP. (Table 2 lists the POP and vertebral condition of all known *Ichthyapus*.)

The only species with three POP are *I. acutirostris*, some specimens of Hawaiian *I. vulturis* (the relationship of Hawaiian *I. vulturis* to those across the Indo-Pacific requires further analysis), and specimens of *Ichthyapus* from Easter Island (identified as *I. vulturis* by Randall and McCosker 1975) and Japan (identified as *I. vulturis* by Hatooka et al. 1995). Vertebral numbers of all Hawaiian *I. vulturis* are lower than those of *I. acutirostris*, and on that basis I presume that their identity would reside with specimens now known either from Easter Island or Japan. In that the collector never visited the south Pacific (few if any collections had been made at or near Easter Island before the 20th century) but had traveled to Japan (aboard the *Levant* and after 1836), I suggest that the remaining holotype of *I. acutirostris* is of the same species as the two specimens identified by Hatooka et al. (1995) from Japan. A comparison of the proportions, pore patterns, and dentition as seen in the illustration of the Japanese specimen (Hatooka et al. 1995, fig. 2) with the illustrations of the holotype of *I. acutirostris* (Blache and Bauchot 1972, figs. 14–15) demonstrates that they are identical. *Ichthyapus vulturis* is known from Japan. I have examined a specimen from Ogasawara Islands (BPBM 35175, 99 mm TL) that has 120 vertebrae and four POP. The identity of the Easter Island specimens remains undetermined. And finally, although species of *Ichthyapus* live in shallow water and are easily captured with rotenone and occasionally captured by dredge sampling, it is possible that additional unknown taxa remain that could be identified with *I. acutirostris*.

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A Synopsis of *Justicia* Section *Mesoamericanae* (Acanthaceae)

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Four morphologically and palynologically similar species of *Justicia* from southern Mexico and Central America are treated as a new section of the genus, *Justicia* sect. *Mesoamericanae*. *Justicia calliantha* (Honduras), *J. nicaraguensis* (Nicaragua), *J. sulfurea* (Guatemala and El Salvador), and *J. torresii* (Mexico) share a similar inflorescence structure, floral form, and pollen type but differ from one another in vesture, size and color of the corolla, and calyx length.

With estimates of 600 species worldwide, *Justicia* is the largest genus of Acanthaceae and the largest genus of the family in the Mesoamerican region. At least 97 species have been reported from this region between the Isthmus of Tehuantepec and the eastern border of Panama (Daniel 1995, 1997, 2001, in press, unpublished). Phylogenetic relationships among species of *Justicia* and related genera were discussed by McDade et al. (2000), and additional sampling of taxa and molecular markers in the Justicieae are underway.

In an infrageneric study of *Justicia*, based on a worldwide subset of species, Graham (1988) recognized 16 sections and seven subsections. Additional sections in the genus have been recognized by Hansen (1987), Hilsenbeck (1990), Ensermu Kelbessa (1990), Immelman (1992), and Daniel (2003). The descriptive activity at the infrageneric level subsequent to Graham's (1988) account attests both to the importance of her treatment and to the morphological diversity in the genus that remained (and still remains) to be placed into a taxonomic framework. Numerous American species cannot be accomodated in any of the sections that have been previously recognized (e.g., see Daniel 1999, 2002; Daniel and Wasshausen 1990) and Graham (1988) treated numerous species as "peripheral" to her infrageneric taxa. Herewith, a group of morphologically similar and predominately Mesoamerican species of *Justicia* that cannot be accomodated in existing infrageneric taxa of that genus is accorded sectional status.

Justicia section *Mesoamericanae* T.F. Daniel, sec. nov.

TYPE. *Justicia sulfurea* (Donn. Sm.) D.N. Gibson.

Herbae perennes vel frutices; inflorescentia in axillis foliorum, pedunculata, brevispicata vel breviracemosa vel fasciculata, floribus 1–5, sessilibus vel brevipedicellatis; calyx 4-lobus, lobis aequalibus vel subaequalibus; corolla flava, aurantiaca, vel rubra, tubo ampliato gradatim apicem versus, fauce indistincta; stamina thecis basi ecalcaratis; pollinis granae 2-aperturatae; capsula 15–33 mm longa, pubescens trichomatibus glandulosis; semina tuberculata.

Perennial herbs to shrubs. Young stems multistriate with greenish striations. Inflorescence of pedunculate short-spikes, racemes, or subcapitate clusters of flowers from axils of leaves, spikes or clusters solitary or paired at nodes. Flowers sessile to short-pedicellate, 1–5 per inflorescence; calyx 4-lobed, lobes equal to subequal in size; corolla yellow, orange, or red, tube gradually expanded distally, lacking a distinct throat, ± equal to or longer than lips; thecae lacking basal appendages; pollen 2-aperturate, apertures flanked on each side by 2(–3) rows of ± circular insulae, insulae and interapertural regions reticulate. Capsules 15–33 mm long, pubescent with glandular (and often eglandular as well) trichomes; seeds 4, sublenticular, covered with ± conical tubercles.

Section *Mesoamericanae* consists of 4 species that occur from southern Mexico (lat. 17°51′N in Oaxaca) to northern Nicaragua (lat. 13°45′N in Atlántico Norte). Each of the species is relatively restricted in distribution and their distributions are not known to overlap. The species occur in a diversity of biotic communities. Macromorphological and palynological characters of the section are shown in Figures 1 and 2, respectively.

The section is distinguished by the combination of axillary, pedunculate, and few-flowered inflorescences; more or less equally 4-lobed calyces; relatively large corollas with the tube gradually expanded distally; diaperturate pollen; and glandular pubescent capsules. The greenish (turning brown with age) seeds bearing prominent tubercles may also be characteristic of the section, but seeds remain unknown for two of the species.

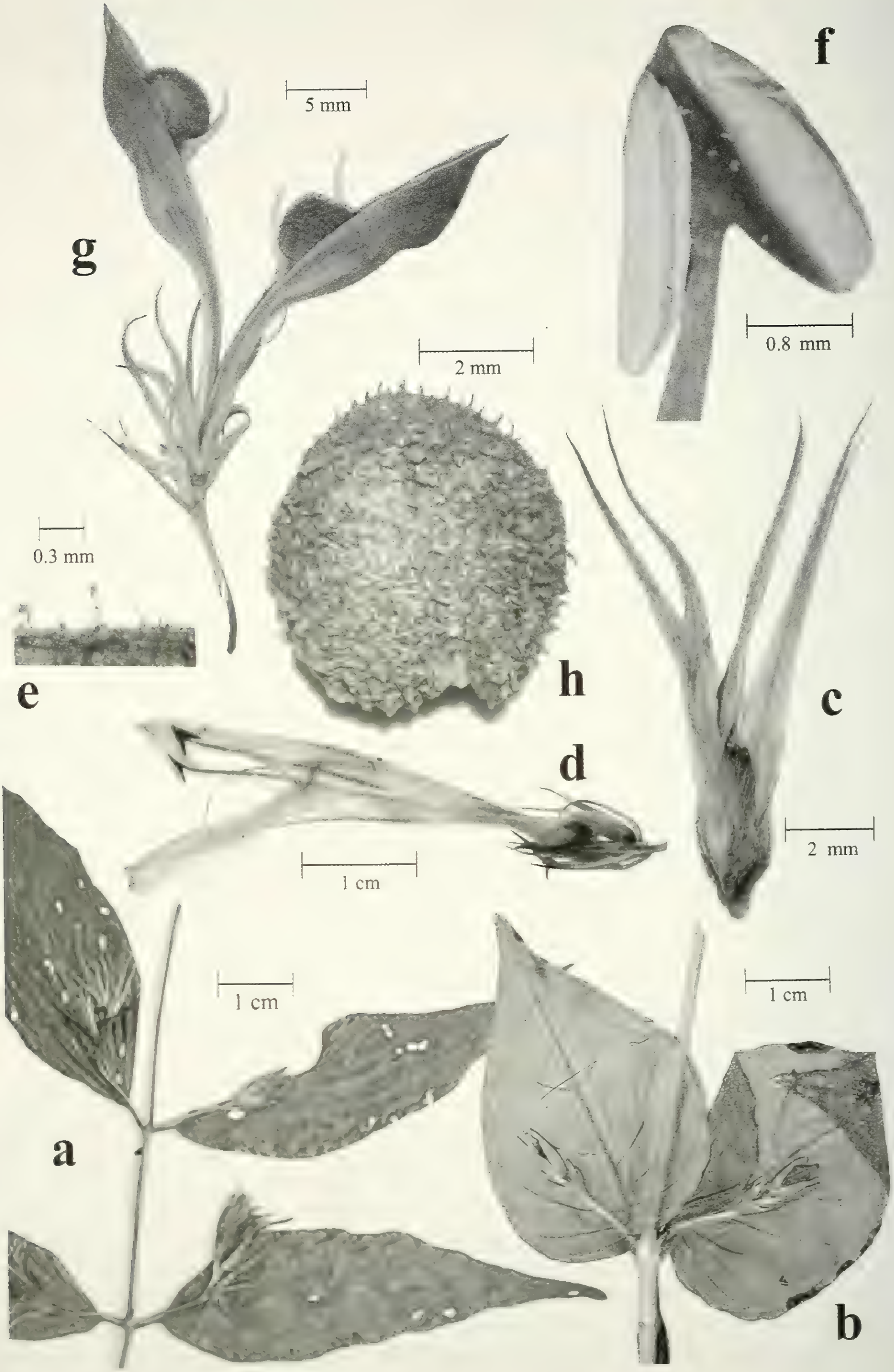
The inflorescence is a few-flowered spike or raceme of alternate, sessile, single-flowered dichasia subtended by two bracteoles in the axil of a bract. The flowers are sessile (spikes) to short-pedicellate (racemes). The fertile portion of the spikes is often reduced with the rachis between bract-bearing nodes very short or nearly absent. When the rachis is not evident, the spikes appear as pedunculate clusters of flowers and the distinction between bracts and bracteoles is then difficult to discern. The entire inflorescence is sometimes partially or entirely enclosed by revolue leaves.

Diaperturate pollen in *Justicia* is secondarily bilateral in symmetry and somewhat more complicated to describe that radially symmetric pollen (see Daniel 1998). Pollen in section *Mesoamericanae* has a P:E in apertural view of 1.404 to 2.021 and a P:E in interapertural view of 3.711. Because the ratio of the longer equatorial axis to the shorter equatorial axis is 1.90 (based on grains of *J. torresii* only), the pollen can be characterized as globose-oblong (Walker and Doyle 1975). Pollen among the four species of section *Mesoamericanae* is remarkably uniform in sculptural characteristics (Fig. 2).

Using Graham's (1988) key to and descriptions of sections of *Justicia*, plants treated here would appear most similar to species in section *Drejerella* (Lindau) V. Graham (i.e., with inflorescences short-pedunculate and consisting of fewer than seven flowers and with red to yellow flowers 24 to 63 mm long). Species of section *Mesoamericanae* differ from those in section *Drejerella* by having a 4 (vs. 5)-parted calyx, somewhat longer inflorescence peduncles (0.5–2 vs. less than 1 cm long), and 2 (vs. 3)-aperturate pollen. Pollen of species in section *Mesoamericanae* (Figure 2) conforms to that described and figured by Graham (1988) as her type 7. Such pollen is encountered in at least four of Graham's sections. One of these, section *Chaetothylax* (Nees) V. Graham, contains some species with 4-parted calyces. However, species in that section differ by having highly modified anthers (i.e., thecae oblique, unequal in size, and the lower with a basal appendage) and white, pink, blue, or wine-red corollas. The other sections with similar pollen (*Orthotactus* (Nees) V. Graham, *Plagiacanthus* (Nees) V. Graham, and *Simonisia* (Nees) V. Graham) all have 5-parted calyces and differ in various other characters as well.

Key to Species of *Justicia* sect. *Mesoamericanae*

1a. Corolla red, externally pubescent with glandular and eglandular trichomes; Honduras. . . . . 1. *J. calliantha*
1b. Corolla yellow or orange, externally pubescent with eglandular trichomes only. 2


g
5 mm
f
0.8 mm
2 mm
0.3 mm
e
h
c
d
1 cm
2 mm
1 cm
1 cm
a
b

2a. Cauline trichomes mostly antrorse to antrorsely appressed; calyx 11–14 mm long; thecae 2.5–3.2 mm long; Mexico. . . . . 4. *J. torresii*
2b. Cauline trichomes mostly retrorse; calyx 5–10 mm long; thecae 1.5–2.5 mm long; Central America. 3

3a. Corolla yellow, (17–) 22–29 mm long, lobes of lower lip 1.7–2.5 mm long; Guatemala and El Salvador. . . . . 3. *J. sulfurea*
3b. Corolla orange, 31–41 mm long, lobes of lower lip 3–4.5 mm long; Nicaragua. . . . . 2. *J. nicaraguensis*

1. *Justicia calliantha* Leonard, Ceiba 1:113. 1950.

TYPE.— HONDURAS: **Francisco Morazán**: Río Yeguare near San Francisco, 800 m, rocky knolls, 24 November 1946, *L. Williams & A. Molina R. 10971* (holotype: US!; isotype: EAP!).

Perennial herbs or shrubs to 2 m tall or long, sometimes weak and clambering. Young stems subterete to subquadrate, evenly or bifariously pubescent with flexuose to retrorse eglandular trichomes 0.2–1 mm long. Leaves petiolate, petioles to 18 mm long, blades ovate to broadly ovate to cordate, 25–103 mm long, 16–56 mm wide, 1.1–1.9 times longer than wide, (rounded to) acute to acuminate at apex, truncate to rounded to cordate at base, surfaces pubescent (mostly along major veins) with erect to flexuose eglandular trichomes, margin entire. Inflorescence peduncles 5–17 mm long, evenly pubescent with erect to flexuose eglandular trichomes 0.1–1 mm long, flower clusters 1 per axil, 1–5-flowered, sometimes with a short rachis evident among flowers, rachis (if present) pubescent like peduncles. Bracts opposite to alternate, (lance-ovate to) subulate, 3–5.3 mm long, 0.5–1.3 mm wide, abaxial surface pubescent with an understory of erect eglandular and/or subglandular to glandular trichomes to 0.1 mm long and an overstory of erect to flexuose eglandular (and sometimes glandular) trichomes 0.2–0.5 mm long, margin similarly pubescent. Bracteoles (see discussion) subulate, 3.5–6 mm long, 0.5–7 mm wide, abaxial surface and margin pubescent like bracts. Flowers sessile to short pedicellate (i.e., pedicels to 2 mm long). Calyx 6–9.5 mm long, lobes lanceolate, 4–8 mm long, 0.8–1.3 mm wide, abaxially pubescent with an understory of erect subglandular to glandular trichomes to 0.1 mm long and an overstory of erect to flexuose glandular and eglandular trichomes 0.2–0.3 mm long. Corolla red, 29–34 mm long, external surface pubescent with erect to flexuose glandular and eglandular trichomes 0.1–0.3 mm long, tube 15–18 mm long, 2.8–3 mm in diameter near midpoint, upper lip 13–18 mm long, 2-lobed, lobes to 0.5 mm long, lower lip 16–19 mm long, lobes 0.5–3.3 mm long, 0.8–3 mm wide, central lobe largest. Stamens 14–16 mm long, filaments glabrous (at least distally), thecae 2–3.2 mm long, subparallel to perpendicular, unequally inserted (overlapping by 1.9–2 mm), unequal in size (distal theca larger), both thecae dorsally pubescent with eglandular trichomes. Style 26–31 mm long, proximally pubescent with eglandular trichomes, distally glabrous, stigma unequally 2-lobed, 1 lobe 0.2 mm long, other lobe rudimentary. Capsule 15–20 mm long, externally pubescent with erect to retrorse glandular and eglandular trichomes to 0.2 mm long, head ellipsoid with medial constriction, 9–13 mm long. Seeds 3.8–4.8 mm long, 3.5 mm wide, surfaces and margin covered with stout subconic tubercles, tubercles papilose and usually with some minute spiny projections less than 0.05 mm long.

FIGURE 1. Macromorphological characteristics of *Justicia* sect. *Mesoamericanae*. a. Leaves and inflorescences of *J. nicaraguensis* (*Stevens 6848*). b. Leaves and inflorescences of *J. calliantha* (*Molina R. 649*). c. Calyx of *J. torresii* (*Torres C. & Cortes A. 11472*). d. Fertile portion of inflorescence with flower of *J. torresii* (*Torres C. & Cortes A. 11472*). e. Pubescence of external surface of corolla of *J. calliantha* (*Molina R. 649*). f. Anther of *J. torresii* (*Daniel s.n.*). g. Inflorescence with capsule of *J. torresii* (*Torres C. & Cortes A. 11472*). h. Seed of *J. torresii* (*Torres C. & Cortes A. 11472*).

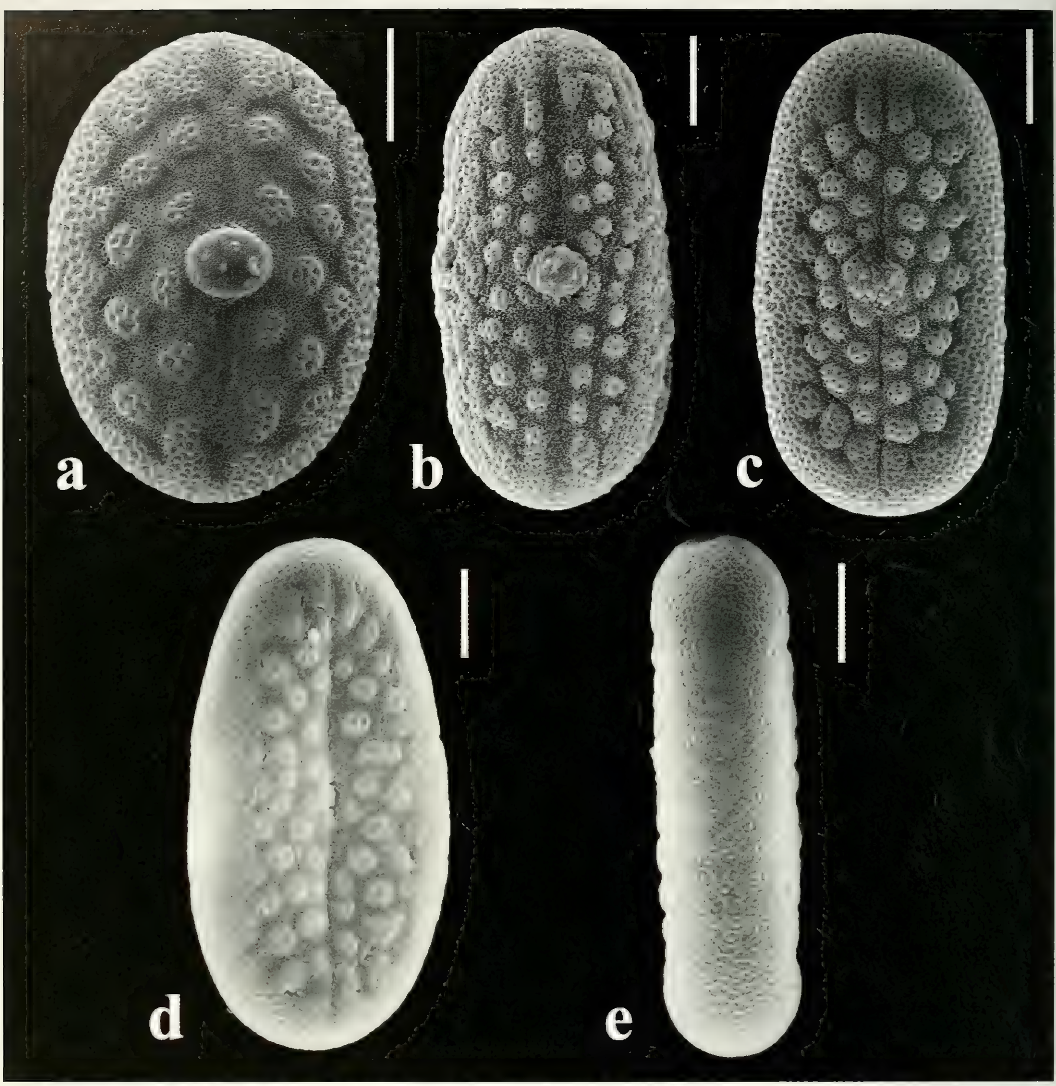


FIGURE 2. Representative pollen of *Justicia* sect. *Mesoamericanae*. a. *J. calliantha* (*Molina 18571*), apertural view. b. *J. nicaraguensis* (*Pipoly 6289*), apertural view. c. *J. sulfurea* (*Molina R. & Molina 27794*), apertural view. d. *J. torresii* (*Torres C. & Cortes A. 11472*), apertural view. d. *J. torresii* (*Torres C. & Cortes A. 11472*), interapertural view. Scales = 12 µm.

PHENOLOGY.— Flowering: November-March; fruiting: December-March.

DISTRIBUTION AND HABITATS.— Endemic to Honduras (Fig. 3) where plants occur in oak forests, thornscrub, and along streams at elevations from 600 to 1050 meters.

ILLUSTRATION.— Ceiba 1:114. 1950.

ADDITIONAL SPECIMENS EXAMINED.— HONDURAS: **Comayagua**: Los Jícaros, 5 km SE de Lamaní, *B. Holst 626* (EAP). **El Paraíso**: Quebrada Jagua, below Guayabillas, *A. Molina R. 649* (F, GH, MO); Río Yeguare drainage, Río Lizapa, *A. Molina R. 5034* (F, GH); Las Casitas, *P. Standley et al. 620* (EAP, F); Quebrada Dantas, ca. 10 km N of Yuscarán, *L. Williams 17206* (F, GH). **Francisco Morazán**: Mpio. Tegucigalpa, ca. 4 km SE de Tegucigalpa, orilla del Río Las Canoas, *J. Linares 1880* (MO); riveras del Río Yeguare, ca. 14°N, 87°W, *A. Molina R. 1794* (GH, MO); along Río Guacerique between Los Laureles and Las Tapias, NW of Tegucigalpa, *A. Molina R. 18571* (F, NY); Río Yeguare near El Zamorano, *P. Standley 66* (F); Río Yeguare E of El Zamorano, Santa Clara, *P. Standley 15438* (F, GH).

Geographically and morphologically, this species is closest to *J. nicaraguensis*. They can be distinguished by the characters in the following couplet:

1a. Corolla red, externally pubescent with glandular and eglandular trichomes, lower lip 16–19 mm long; young stems subterete to subquadrate, evenly to bifariously pubescent; leaves 1.1–1.9 times longer than wide, truncate to rounded to cordate at base; bracts 3–5.3 mm long; thecae pubescent; capsule 15–20 mm long.. . . . . *J. calliantha*

1b. Corolla orange, externally pubescent with eglandular trichomes only, lower lip 11–13 mm long; young stems quadrate to quadrate-sulcate, unifariously pubescent; leaves 2.2–4.5 times longer than wide, usually acute at base; bracts 6.5–11 mm long; thecae glabrous; capsule 33 mm long. . . . . *J. nicaraguensis*

2. *Justicia nicaraguensis* Durkee, Novon 9:508. 1999.

TYPE.— NICARAGUA: **Atlántico Norte** ("Zelaya"): along trail from Cerro Saslaya to San José del Hormiguero, between Caño Majagua and Caño Sucio, tall evergreen forest, ca. 13°45′N, 84°59′–85°00′W, 600–800 m, 10 March 1978, *W. Stevens 6848* (holotype: MO; isotype: CAS!).

Perennial herbs or shrubs to 4 m tall, sometimes clambering or vinelike. Young stems quadrate to quadrate-sulcate, unifariously pubescent with mostly retrorse (varying from flexuose to antrorse) eglandular trichomes and sometimes with a few scattered (mostly antrorse or upward pointing) eglandular trichomes as well, trichomes 0.3–0.6 mm long. Leaves petiolate, petioles to 5 mm long, blades lance-ovate to ovate to ovate-elliptic, 40–101 mm long, 16–35 mm wide, 2.2–4.5 times longer than wide, acuminate to long-acuminate at apex, (rounded to) acute (often asymmetric) at base, surfaces pubescent with antrorse to antrorsely appressed eglandular trichomes restricted to midvein (dense on adaxial surface, sparse on abaxial surface), margin entire to subsinuate. Inflorescence peduncles 7–11 mm long, ± evenly pubescent with (erect to) antrorse to flexuose (to retrorse) eglandular trichomes (0.05–) 0.3–0.6 mm long and sometimes distally with erect glands 0.05–0.2 mm long as well, flower clusters 1 per axil, 2–5-flowered, rachis sometimes evident among flowers, sparsely pubescent with eglandular trichomes like those of peduncle. Bracts lanceolate to narrowly elliptic to linear, 6.5–11 mm long, 1–1.7 mm wide, abaxial surface pubescent with antrorse eglandular trichomes 0.3–0.5 mm long (often sparse) and erect to flexuose glandular trichomes 0.05–0.2 mm long (often more prevalent distally), margin prominently ciliate with erect to flexuose eglandular trichomes to 0.8 mm long. Bracteoles lanceolate to narrowly elliptic, 6–11 mm long, 0.8–1.4 mm wide, abaxial surface and margin pubescent like bracts. Flowers sessile. Calyx 9–10.5 mm long, lobes subulate, 6.5–9 mm long, 0.8–1 mm wide, abaxially pubescent like bracts. Corolla orange, 31–41 mm long, externally pubescent with flexuose eglandular trichomes 0.2–0.7 mm long, tube 20–28 mm long, 1.7–2.5 mm in diameter near midpoint, upper lip 10.5–11 mm long, entire, lower lip 11–13 mm long, lobes 3–4.5 mm long, 1.6–2.5 mm wide. Stamens 11 mm long, filaments glabrous (at least distally), thecae 1.7–2.2 mm long, subparallel to sagittate, equally to subequally inserted, subequal in size, glabrous. Style 25–36 mm long, glabrous (at least distally), stigma 0.2 mm long, lobes not evident. Capsule 33 mm long, pubescent with erect to flexuose glandular trichomes 0.05–0.1 mm long. Seeds not seen.

PHENOLOGY .— Flowering and fruiting: March.

DISTRIBUTION AND HABITATS.— Endemic to Nicaragua (Atlántico Norte; Fig. 3) where plants occur in evergreen primary forest and in disturbed secondary forest at elevations from 300 to 800 meters.

Illustration.— Ann. Missouri Bot. Gard. 9:509. 1999.

Additional specimens examined.— Nicaragua: **Atlántico Norte** ("Zelaya"): Finca S of La Pimenta, ca. 13°45′N, 84°59′W, *J. Pipoly 6289* (CAS, MO); trail from Cerro Saslaya to San José del Hormiguero, between Caño Sucio and Loma Mollejones, ca. 13°45′N, 84°58–59′W, *W. Stevens 7015* (MO).

In addition to its orange corollas, this species differs from others in the section by its larger capsules with glandular (only) trichomes.

3. *Justicia sulfurea* (Donn. Sm.) D.N. Gibson, Fieldiana, Bot. 34:74. 1972. *Dianthera sulfurea* Donn. Sm., Bot. Gaz. 35:6. 1903.

Type.— Guatemala: **Santa Rosa**: Cerro Redondo, 1200 m, September 1893, *E. Heyde & E. Lux 6215* (lectotype, designated by Gibson in 1972: US!; isolectotypes: A!, F!, GH!, MO!).

Perennial herbs to 2 m. Young stems subquadrate, unifariously (to ± bifariously) pubescent with mostly retrorse (occasionally flexuose to antrorse, especially at upper nodes) eglandular trichomes 0.3–0.8 mm long. Leaves petiolate, petioles to 4 mm long, blades lance-ovate to ovate, 25–113 mm long, 8.5–31 mm wide, 2.5–4.4 times longer than wide, acuminate to long-acuminate at apex, truncate to rounded to acute to subcordate (often asymmetric) at base, surfaces pubescent with flexuose to antrorsely appressed eglandular trichomes (restricted to major veins on adaxial surface and concentrated on major veins but disposed throughout on abaxial surface), margin entire to subsinuate. Inflorescence peduncles 6–20 mm long, evenly pubescent (or with trichomes ± unifariously disposed) with flexuose to antrorse to retrorse eglandular trichomes 0.4–0.8 mm long, spikes or flower clusters 1 per axil, 1–4-flowered, rachis (if present) nearly glabrous or with sparse glandular or eglandular trichomes 0.05–0.2 mm long. Bracts subulate to lance-subulate, 4.5–7.5 mm long, 0.5–0.9 mm wide, abaxial surface and margin pubescent with erect to flexuose to antrorse to antrorsely appressed eglandular trichomes 0.3–1.3 mm long, sometimes with flexuose glandular trichomes 0.1–0.3 mm long as well. Bracteoles subulate to lance-subulate, 5–8 mm long, 0.5–0.7 mm wide, abaxially and marginally pubescent like bracts. Flowers sessile to subsessile (i.e., pedicels to 1 mm long). Calyx 5–8 mm long, lobes subulate to lance-subulate, 4.5–6.7 mm long, 0.3–1.3 mm wide, abaxially pubescent like bracts and usually with flexuose glandular trichomes (sometimes inconspicuous) 0.1–0.3 mm long present as well. Corolla yellow, (17–) 22–29 mm long, externally pubescent with flexuose eglandular trichomes 0.2–1 mm long, tube (11–) 16–20 mm long, 2.3–3 mm in diameter near midpoint, upper lip (6–) 9–12 mm long, entire, lower lip (6–) 10.5–13 mm long, lobes 1.7–2.5 mm long, 1.5–3 mm wide. Stamens 11–14 mm long, filaments glabrous (at least distally), thecae 1.5–2.5 mm long, sagittate to subperpendicular, subequally inserted, subequal in size, lower theca glabrous, upper theca sometimes with a few eglandular trichomes near base (e.g., *Molina R. & Molina 27794*). Style 26–29 mm long, pubescent near base with eglandular trichomes, glabrous distally, stigma 0.3–0.4 mm long, lobes not evident. Capsule (immature?) 14 mm long, pubescent with erect glandular (and a few eglandular) trichomes 0.05–0.1 mm long. Seeds not seen.

Phenology .— Flowering: September-October; fruiting: January.

Distribution and habitats.— Known from central and southeastern Guatemala (Baja Verapaz and Santa Rosa) and western El Salvador (Ahuachapán) where plants occur in moist thickets along rivers and on rocky slopes in disturbed forests at elevations from 1140 to 1500 meters (Fig. 3).

ILLUSTRATION.— None found.

ADDITIONAL SPECIMENS EXAMINED.— GUATEMALA: **Baja Verapaz**: Pachirax River, Sierra Chuacús, 6 km from Rabinal, road to Guatemala City, *A. Molina R. & A. R. Molina 27794* (EAP, F); Cachil, *A. Molina R. & A. R. Molina 27834a* (EAP). EL SALVADOR: **Ahuachapán**: without locale, *S. Padilla V. 640* (US); Sierra Apaneca, region of Finca Colima, *P. Standley 20141* (GH, NY, US).

Gibson (1972, 1974) noted that this rarely collected species was known to her only from the type collection. Other collections resembling the type have since been collected or located. The most recent known collection of *J. sulfurea* was made in 1972 by the Molinas in Guatemala.

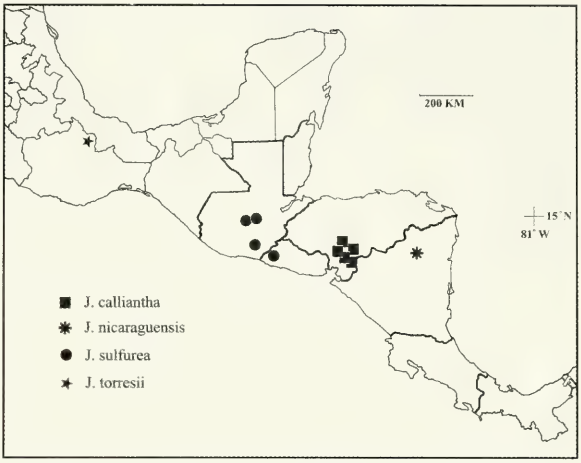


FIGURE 3. Map of a portion of Middle America showing distributions of species of *Justicia* sect. *Mesoamericanae*.

Molina & Molina 27794 has considerably fewer glandular trichomes in the inflorescence (i.e., restricted to calyx lobes where inconspicuous) than does the type (i.e., glands present and usually conspicuous on bracts, bracteoles, and calyx). Also in *Molina & Molina 27794*, the eglandular trichomes on the abaxial surface and margin of bracts, bracteoles, and calyx lobes are erect to flexuose and 0.6–1.3 mm long whereas in the type, the eglandular trichomes on these structures are flexuose to antrorsely appressed and 0.3–0.7 mm long. *Standley 21041* from El Salvador more closely resembles the type in these pubescence characters.

4. *Justicia torresii* T.F. Daniel, Contr. Univ. Michigan Herb. 18:280. 1993.

TYPE.— MEXICO: **Oaxaca**: Distr. Tuxtepec, Mpio. Santa María Jacatepec, camino a Cosolapa San Antonio, Ejido de San Felipe Tilpa, 13.3 km SW de La Reforma, 17°51′N, 96°03′W, 20 February 1988, *R. Torres C. & L. Cortes A. 11472* (holotype: CAS!; isotype: MEXU!).

Perennial herbs to 4.5 dm tall. Young stems subquadrate, pubescent with flexuose to antrorse to antrorsely appressed to retrorse eglandular trichomes 0.3–0.5 mm long, trichomes ± evenly, unifariously, or bifariously disposed. Leaves petiolate, petioles to 6 mm long, blades ovate to lance-ovate, 25–85 mm long, 12–43 mm wide, 1.6–3.3 times longer than wide, (acute to) acuminate at apex, rounded to acute at base, surfaces pubescent (mostly along major veins) with cauline type trichomes. Inflorescence peduncles to 20 mm long, pubescent with cauline type trichomes, spikes (1–) 2–3 (–5)-flowered, rachis (if present) pubescent with antrorse eglandular trichomes 0.2–0.4 mm long. Bracts narrowly lanceolate to lance-linear to lance-subulate, 6–17 mm long, 0.8–1.5 mm wide, abaxial surface pubescent with cauline type trichomes and distally with glands (sometimes sparse) 0.1–0.2 mm long as well, margin ciliate with (flexuose to) antrorse to antrorsely appressed eglandular trichomes 0.2–0.8 mm long. Bracteoles lance-subulate to subulate, 5–13 mm long, 0.5–1.5 mm wide, abaxial surface and margin pubescent like bracts although the glands usually more conspicuous. Flowers sessile to subsessile (i.e., pedicels to 0.5 mm long). Calyx 11–14 mm long, lobes lance-subulate, 9-13 mm long, 1.4–1.6 mm wide, abaxially pubescent like bracts. Corolla yellow, (33–) 36–46 mm long, externally pubescent with flexuose eglandular trichomes 0.2–0.7 mm long, tube (23–) 26–31 mm long, upper lip 10–16 mm long, entire, lower lip 10–17 mm long, lobes 1.4–4 mm long, 1.5–3 mm wide. Stamens 12–14 mm long, filaments glabrous, thecae 2.5–3.2 mm long, sagittate, subequally inserted, subequal in size, glabrous. Style 35–39 mm long, sparsely pubescent proximally, glabrous distally, stigma subspheric, 0.3–0.4 mm long. Capsule 24–28 mm long, pubescent with erect to retrorse, glandular and eglandular trichomes 0.1–0.3 mm long, head ellipsoid with a slight medial constriction, 16–18 mm long. Seeds 4, green turning brown, 5–6 mm long, 5–5.5 mm wide, surface and margin covered with stout subconic and subflexuose tubercles to 0.5 mm long, tubercles striate and covered with minute spiny projections less than 0.05 mm long.

Phenology .— Flowering and fruiting: February.

Distribution and habitats.— Endemic to southern Mexico (Oaxaca; Fig. 3) where plants occur in lowland rain forest at an elevation of 300 meters.

Illustration.— Contr. Univ. Michigan Herb. 19:281. 1993.

Additional specimens examined.— MEXICO: **Oaxaca**: seeds of type (*R. Torres C. & L. Cortes A. 11472*) grown at San Francisco Conservatory of Flowers in 1990-1991, *T. Daniel s.n.* (CAS, DUKE, ENCB, K, MEXU, MICH, MO, NY, RSA, TEX, US).

The two species of section *Mesoamericanae* with yellow flowers appear particularly similar to one another, and additional collections may eventually show them to represent a single, variable species. Unfortunately, seeds remain unknown for *J. sulfurea*. These two species can be distinguished by the characters in the following couplet:

1a. Bracts 4.5–7 mm long; calyx 5–8 mm long; corolla 27.5–29 mm long; thecae 1.5–2.2 mm long; style 26–29 mm long. . . . . *J. sulfurea*
1b. Bracts 6–17 mm long; calyx 12–14 mm long; corolla (33–) 36–46 mm long; thecae 2.5–3.2 mm long; style 35–39 mm long. . . . . *J. torresii*

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Nucella megastoma, A New Late Pliocene Muricid Gastropod from Northern California

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***Nucella megastoma* new species from the Merced Formation of San Mateo County and the Wilson Grove Formation of Sonoma County, both late Pliocene of California, is distinguished by the presence of a labral tooth, strong alternating spiral cords, and a large aperture. This rocky-shore predatory muricid gastropod co-occurred with several other muricids, including four species of *Nucella* without a labral tooth and a labral-tooth-bearing species of *Acanthinucella*.**

Nucella is a species-rich genus of northern-hemisphere ocenebrine muricid gastropods with a relatively well-documented history dating back to the late Oligocene (Collins et al. 1996; Marko and Vermeij 1999; Vermeij 2001). Species-level taxonomy based on shell characters is problematic in this group owing to the great variation — much of it the result of phenotypic plasticity — in such features as the number and expression of spiral cords, thickness of the outer lip, expression of denticles on the inner side of the outer lip, spire height, and length of the siphonal canal. It is therefore with considerable surprise that a hitherto undescribed species of this genus should come to light. Although only two specimens of this new form are available, they are so distinctive that the formal proposal of a new species for them is warranted. Here we describe it as *Nucella megastoma* sp. nov.

Geological Setting

The new species comes from the Merced Formation of San Mateo County and the Wilson Grove Formation of Sonoma County, both in north-central coastal California. The Merced Formation ranges in age through much of the Pliocene and Pleistocene (Ingram and Ingle 1998). Its molluscan fauna (Glen 1959; Yancey 1978) contains several intertidal muricids, including *Acanthinucella spirata* (de Blainville 1832), *Nucella analoga* (Forbes 1950) (see below), *N. emarginata* (Deshayes 1839) in the broad sense, and *N. lamellosa* (Gmelin 1791); but our new species *N. megastoma* was not previously reported as part of this fauna. [Glen also reports *N. lima* (Martyn) and *Ocenebrina interfossa* (Carpenter) from the "Merced" Formation at Pillar Point, but Powell (1998) following Wiley (1983) and Wiley and Moore (1983) refer the outcrops at Pillar Point to the Purisima Formation.] The Wilson Grove Formation is of late Miocene to late Pliocene age (Powell et al. 2003), but the locality from which we report *N. megastoma* was determined on paleontological grounds to be of late Pliocene age (Powell et al. 2003). At this locality, the new species (reported by Powell et al. 2003, as *Acanthinucella* sp.) co-occurs with *Nucella trancosana* (Arnold 1908). These and several other rocky-shore gastropods are found alongside other molluscs that are inferred to have lived at shelf depth offshore (Powell et al. 2003). It is likely that *N. megastoma* lived in an exposed rocky-shore setting, where species are not normally preserved as fossils. Fossilization of such rocky-shore species depends on transport to environments where sedimentation permits fossil preservation.

SYSTEMATICS

Family Muricidae Rafinesque, 1915
Subfamily Ocenebrinae Cossmann, 1903

Genus *Nucella* Röding, 1798

TYPE SPECIES: *N. lapillus* (Linnaeus, 1758) (see Kool and Boss 1992)

Nucella megastoma Vermeij and Powell, sp. nov.

(Figs. 1a–d)

Acanthinucella sp., Powell et al. 2003, Table 11.

DIAGNOSIS.— Medium-sized *Nucella* with low spire, rounded last whorl, high alternating spiral cords, a broad aperture, thin outer lip without denticles on inner side, and strong labral denticle at apertural end of external spiral groove located above basalmost spiral cord.

DESCRIPTION OF HOLOTYPE.— Shell medium-sized, height 26.8 mm (apex broken off), spire low (aperture height:shell height ratio 0.85); preserved teleoconch consisting of three whorls, of which the last one is large, rounded, and inflated, without shoulder angulation and without basal constriction on right (outer-lip) side; axial sculpture absent except for growth increments; spiral sculpture of last whorl consisting of nine high, sharply rounded, primary cords; adjacent cords separated by distinct secondary cord; a secondary cord also present between suture and first primary cord; widest point of shell located at fourth cord from suture; aperture wide, its height:width ratio 2.1; outer lip thin, its inner side without denticles; anterior of outer lip with distinct labral tooth formed at apertural end of external spiral groove situated between the two most basal primary cords; columella rounded, smooth, without parietal tooth at adapical end; umbilical slit absent; siphonal fasciole high, sharply rounded.

HOLOTYPE: CAS Geology 69251: height (incomplete) 26.8 mm, diameter 23.3 mm, aperture height 22.0 mm, aperture width 10.8 mm, outer-lip thickness 1.0 mm.

TYPE LOCALITY: Seven Mile Beach, San Mateo County, California, Merced Formation (late Pliocene).

DESCRIPTION OF PARATYPE.— Shell height 37.4 mm (incomplete); similar to holotype except that the spiral sculpture on the last whorl consists of seven primary cords, which have no secondary cord between them except on the abapertural side.

PARATYPE: CAS Geology 69252: height 37.4 mm, diameter 33.7 mm, aperture height 28.0 mm, aperture width 14.0 mm, outer-lip thickness 1.6 mm.

LOCALITY OF PARATYPE: north side of River Road, 0.2 miles north of Trenton, 0.3 miles east of intersection of River Road and Trenton-Healdsburg Road, Sonoma County, California; Wilson Groove Formation (late Pliocene).

REMARKS.— Although the two available specimens differ somewhat in sculpture, notably in the expression of secondary cords, they share the presence of a labral tooth, a broad aperture, a basally constricted whorl on the apertural side of the last whorl, and seven to nine strong primary cords alternating with secondary cords. These distinctive features indicate a single species-level taxon in the genus *Nucella*.

Living intertidal ocenebrine muricids with a labral tooth in the northeastern Pacific mostly belong to the genera *Acanthinucella* Cooke, 1918, and *Mexacanthina* Marko and Vermeij, 1999. These genera differ from *Nucella megastoma* by generally having a shoulder angulation and by the usual presence of deeply recessed denticles on the inner side of the outer lip. In *Mexacanthina*, moreover, the conspicuous labral tooth has a more basal position than in *N. megastoma*, in which the tooth is situated above the lowest cord instead of below the lowest cord. In *Acanthinucella*, several spiral cords are situated below the tooth-bearing groove (see Marko and Vermeij 1999; Vermeij 2001). Data from mitochondrial gene sequences show that *Acanthinucella*, which appears in California during the "Margaritan" stage of the late Miocene as *A. norma* (Nomland 1917), is part of a South American clade (Marko and Vermeij 1999) dating back to the late Oligocene (Vermeij 2001; DeVries and Frassinetti 2003). *Mexacanthina* is a Pleistocene to Recent genus whose labral tooth is inferred to have evolved independently from that in either *Acanthinucella* or *Nucella* (Marko and Vermeij 1999). *Nucella*, a late Oligocene to Recent genus with origins in the northeastern Pacific (Amano et al. 1993), consists mainly of species without a labral tooth, but *N. packi* (Clark 1918) from the late Oligocene of California and some specimens of *N. analoga compressa* (Dall 1915) have a labral tooth (Vermeij 2001).

Nucella megastoma is best compared to three Recent species of the genus from the northeastern Pacific. *Nucella lima* (Gmelin 1791), a common species in Alaska, is like *N. megastoma* in having a low spire, alternating spiral cords, and a broad aperture with a thin outer lip. There are typically nine or ten primary cords, but a labral tooth of the type seen in *N. megastoma* is never present. *N. canaliculata* (Duclos 1932), another common northern species, has nine to 11 high spiral cords and much smaller secondary cords. Its aperture is more elongate than that of *N. lima* and *N. megastoma*, and a labral tooth is rarely present. In a few specimens in the Vermeij collection from Attu (Aleutian Islands, Alaska), a barely perceptible labral tooth is situated at the apertural end of a spiral groove between the two most basal primary cords. J. H. McLean (pers. commun. to Vermeij, July 2003) distinguishes between a northern *N. canaliculata* and the more southerly *N. analoga* (Forbes 1850), which ranges from Vancouver Island (British Columbia) to central California. Vermeij's examination of specimens confirms McLean's interpretation. *N. analoga* has 16 to 18 low, somewhat flat-topped cords, usually without secondaries, on the last whorl. A labral tooth is absent. In populations from central California, which Dall (1915) named as the form *compressa*, one or more of the abapical crenations on the outer lip is enlarged to form a labral tooth. This form has 11 to 13 cords without secondaries on the last whorl, and is in Vermeij's view distinct from typical *N. analoga*. All these taxa — *N. canaliculata*, *N. analoga*, and the form *compressa* — which were formerly regarded as belonging to the single taxon *N. canaliculata*, differ from *N. megastoma* by being slightly basally constricted and by having a higher spire.

At its type locality (Seven Mile Beach, San Mateo County, in the Merced Formation), *N. megastoma* co-occurs with *N. analoga*. The available specimens of *N. analoga* from this locality and from other localities in the Merced Formation lack a labral tooth and are indistinguishable from Recent examples (Fig. 1, e–f).

Three fossil species of *Nucella* resemble *N. megastoma*. The most similar fossil species to *N. megastoma* is *N. packi* (Clark 1918) from the San Ramon Sandstone (late Oligocene) of Contra Costa County, California. This species is thick-shelled and low-spired, and has 15 low cords without secondaries, as well as traces of a labral tooth at the apertural end of an external groove between the two most basal cords (Amano et al. 1993; for assignment to *Nucella* see Marko and Vermeij 1999; Vermeij 2001). *N. packi* differs from *N. megastoma* by having a slightly constricted base, more numerous and lower spiral cords, and by having denticles deeply recessed on the inner side of the outer lip. The early to middle Miocene *N. tokudai* (Yokoyama 1932), known in California

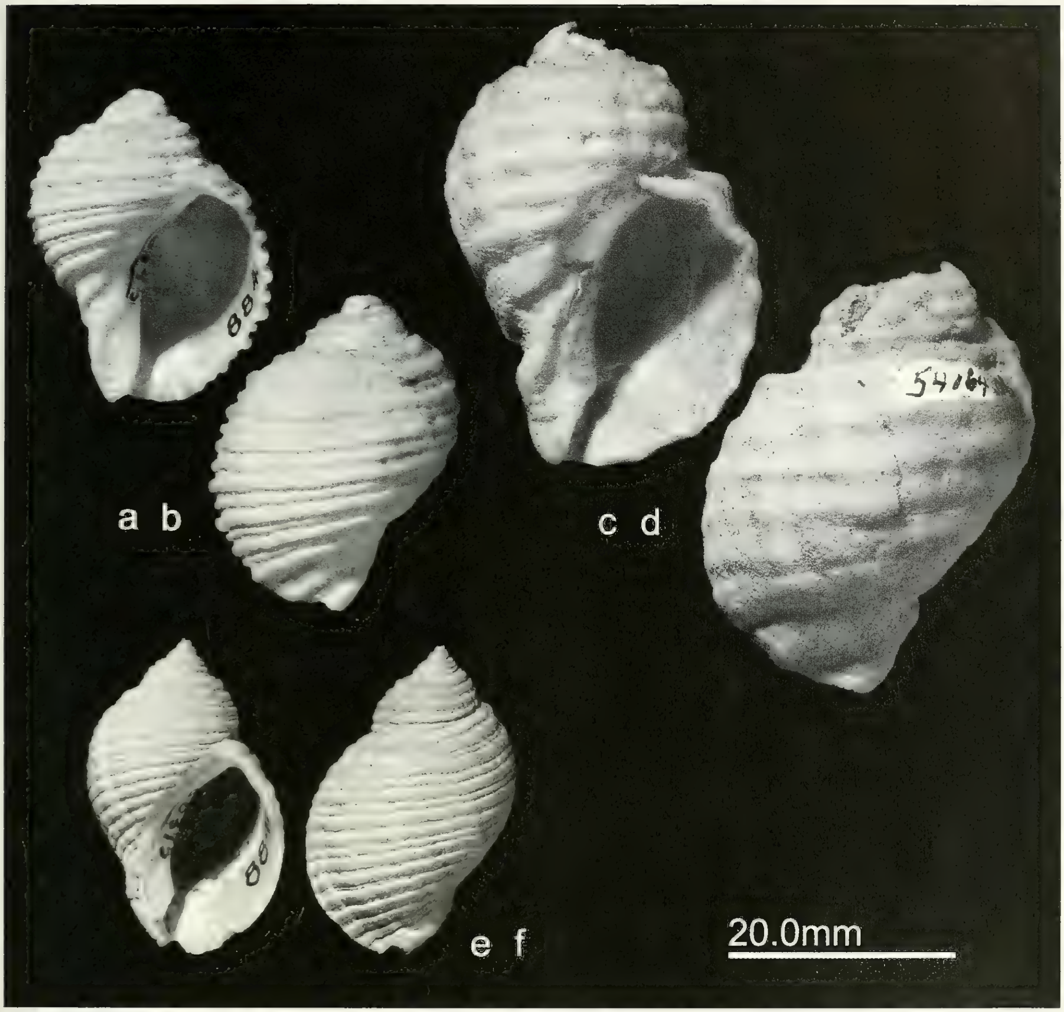

FIGURE 1. a–b, *Nucella megastoma*, sp. nov., holotype, Merced Formation. c–d, *Nucella megastoma* sp. nov., paratype, Wilson Grove Formation. e–f, *Nucella analoga* (Forbes, 1850), Merced Formation at Seven Mile Beach, San Mateo County, California.

also as *Thais (Stramonita) carrizoensis* Loel and Corey 1932, is a low-spired species that differs from *N. megastoma* by having more numerous primary cords (11 to 19 versus seven to nine), having denticles inside the outer lip, and lacking a labral tooth (see Amano et al. 1993 for detailed discussion of this species and its relation to *N. packi*, with which *T. (S.) carrizoensis* had been synonymized by Addicott 1970). Finally, the Pliocene *N. trancosana* (Arnold 1908) is characterized by a very thick shell, 13 or more very low (often obsolete) spiral cords, and denticles on the inner side of the outer lip. A labral tooth is absent (see also Addicott 1969). *N. trancosana* is not known from the Merced Formation (Glen 1959; Yancey 1978) but does co-occur with *N. megastoma* in the Wilson Grove (Powell et al. 2003) Formation.

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Grenadiers (Gadiformes, Teleostei) of Walters Shoals, Southwestern Indian Ocean, with Description of a New "West-Wind Drift" Species

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During cruise 17 of the *Vityaz'*, numerous specimens of a new species of *Caelorinchus, C. vityazae*, were collected off Walters Shoals in the Indian Ocean south of Madagascar. The new species is here described from 32 specimens collected at five different localities within the southeastern Atlantic and southwestern Indian Ocean in the biogeographical area defined by Collette and Parin (1991) as the West Wind Drift Island Province. *Caelorinchus vityazae* is a member of the *C. fasciatus* species group whose 14 members are confined primarily to temperate waters of the southern hemisphere, with most species found off Australia and New Zealand. The new species can be distinguished from others of the clade by the combination of having 10-11 prominent saddle marks, a naked underside of head, and a sharply pointed terminal snout scute. Of the 22 other species of grenadiers recorded from Walters Shoals, most are widespread in the southern hemisphere or circumglobal.

Collette and Parin (1991) reported on the shallow-water fishes of Walters Shoals, an oceanic seamount about 400 nautical miles south of Madagascar they considered as one of a chain of seven islands and seamounts having close faunal affinities. The chain stretches from Gough Island in the South Atlantic to Amsterdam and St. Paul islands in the southern Indian Ocean; most of the chain lies along the edge of the relatively stable eastward-flowing subantarctic surface current called the West Wind Drift (WWD). In recognition of the faunal affinities within the chain, Collette and Parin named the area West Wind Drift Islands Province.

The Soviet research vessel *Vityaz'* occupied a series of deepwater bottom-trawl stations off Walters Shoals during cruise 17, the same cruise on which Collette and Parin made their shallow-water collections. Parin et al. (1993) have reported on fish and invertebrate from the Shoals. Among the fishes, they recorded 19 species of grenadiers taken at depths between 525 and 2050 m. One of grenadiers collected from Walters Shoals represents an undescribed species of *Caelorinchus* that is known only from collections made at five localities within the WWD Island Province; it appears to represent a species endemic to that province. A number of other Walters Shoals grenadiers have distributions that coincide with the circumglobal boundaries of the West Wind Drift, which suggests that whatever physical, chemical, biological, or other factors that define the limits of the water mass have an affect on the distribution of these grenadiers.

We provide here a description of the new *Caelorinchus* and a list of other grenadiers taken on Walters Shoals, along with comments on their distributions.

MATERIALS AND METHODS

Most of the specimens reported here were provided through the courtesy of N. V. Parin, chief scientist for the 1988–89 *Vityaz* cruise 17 to Walters Shoals. The grenadiers received by the California Academy of Sciences (CAS) from that cruise were collected mostly by M. E. Anderson and the second author (YNS). Other specimens of the new species were examined through the courtesy of curators at LACM, MNHN, USNM, ZISP, and ZMMGU. Abbreviations for museum depositories follow Leviton et al. (1985 and 1988) except for the P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, formerly IOAN, now IORAS, and the Zoological Institute of the Russian Academy of Sciences, formerly ZIL, now ZISP. The reader is referred to Iwamoto (1990a) and Iwamoto and Merrett (1997) for generic diagnoses and species synonymies; complete reference citations to original descriptions of the genera and species treated here are available in Eschmeyer's *Catalog of Fishes* (1998).

Counts and measurements were taken following procedures established for grenadiers by Gilbert and Hubbs (1916), and later modified by Iwamoto (1970) and Iwamoto and Sazonov (1988). In the Specimens Examined section for all species other than the new *Caelorinchus*, the museum catalog number is followed in parentheses by the number of specimens and the range in size in mm head length (HL) or mm total length (TL), or both. For *Vityaz* collections, only the station number and depth of capture are given, but additional collection information is provided in Table 1.

TABLE 1. Abbreviated data set for stations at which grenadiers were captured on Walters Shoals during *Vityaz* cruise 17.

sta. 2668; 33°1.2′S, 44°36.8′E; 1010 m; 8 Dec. 1988.
sta. 2670, 33°01.6′S, 44°49.2′E; 1100–1090 m; 8–9 Dec. 1988.
sta. 2671; 32°55′S, 45°00′E; 1200–1175 m; 12 Dec. 1988.
sta. 2672; 32°53′00S, 45°11′30″E; 1310–1265 m; 9 Dec. 1988.
sta. 2673; 32°45′S, 45°30′E; 1750–1700 m; 12 Dec. 1988.
sta. 2674; 33°16′42″S, 43°41′05″E; 900–920 m; 12 Dec. 1988.
sta. 2686; 33°04′12″S, 43°52′05″E; 653–660 m; 12 Dec. 1988.
sta. 2706; 33°1′00″S, 44°30′00″E; 970–980 m; 15 Dec. 1988.
sta. 2707; 33°1′48″S, 44°23′36″E; 910–925 m; 15 Dec. 1988.
sta. 2708; 33°07.5′S, 44°04.0′E, 785–760 m; 15 Dec. 1988.
sta. 2721; 33°25′18″S, 43°37′30″E; 1000–1030 m; 12 Dec. 1988.
sta. 2735; 33°36′00″S, 44°32′00″E; 930–950 m; 19 Dec. 1988.
sta. 2736; 33°58′06″S, 45°01′00″E; 1030–1050 m; 19 Dec. 1988.
sta. 2742; 34°41′48″S, 45°28′00″E; 1518–1750 m; 20 Dec. 1988.
sta. 2764; 33°16′42″S, 43°41′00″E; 920–900 m; 24 Dec. 1988.
sta. 2765; 33°09′S, 43°41′E; 870–880 m; 24 Dec. 1988.
sta. 2772; 31°59′00″S, 45°11′00″E; 1950–2050 m; 25 Dec. 1988.

WALTERS SHOALS GRENADIERS

Fifteen species of bathygadid and macrourid grenadiers were captured on Walters Shoals during *Vityaz* cruise 17. Two species of *Caelorinchus* could not be identified with any known species; one of these is here described as new, the other requires further study and comparison with other specimens before it can be described. Other vessels have collected grenadiers on Walters Shoals, including the former Soviet vessels *Zvezda Kryma* (in 1976 and 1977) and *Professor Mesiatzev* (in 1979), and the French vessel *RV Marion Dufresne* (in 1976). They recorded seven other grenadiers, giving a total of 22 species known from Walters Shoals. Five of the 22 (*Cetonurus globiceps,Coryphaenoides armatus, Kuronezumia bubonis, Malacocephalus laevis,* and *Odontomacrurus murrayi*) are circumglobal in distribution, but most of the remainder are widespread southern hemisphere species.

Family Bathygadidae

1. *Bathygadus cottoides* Günther, 1878

Specimens examined.— IORAS 167 (2 spec.); *Vityaz* sta. 2671, 1200–1175 m. IORAS uncat. (4 specimens, 105–210 mm TL); *Vityaz* sta. 2672, 1310–1265 m. IORAS 169 (35, 73–163 TL); *Vityaz* sta. 2673, 1750–1700 m. IORAS 521 (1, 129 TL), *Vityaz* sta. 2674, 1500–1600 m. IORAS uncat. (14, 137–205 TL); *Vityaz* sta. 2742, 1518–1750 m. IORAS 170 (1 spec.); *Vityaz* sta. 2748, 765–750 m.

Distribution.— South Africa east to Australia and New Zealand; depth range about 1000–1600 m (Iwamoto and Anderson, 1994:3–4; Iwamoto and Graham, 2001:421).

2. *Bathygadus favosus* Goode and Bean, 1886

Specimens examined.— IORAS uncat. (1, 430 TL); CAS 66517 (1, 75.2 HL, 413+ TL); *Vityaz* sta. 2672, 1310–1265 m.

Distribution.— North Atlantic and southeast Atlantic from Gulf of Guinea south to Cape Town, South Africa; depth range from 768–2745 m (Iwamoto 1970:348; Iwamoto and Anderson 1994:5).

3. *Gadomus capensis* (Gilchrist and von Bonde, 1924)

Specimens examined.—IORAS uncat. (6 spec.); CAS 66519 (5 spec.); *Vityaz* sta. 2668, 1010 m. IORAS uncat. (86, 180–370 TL); *Vityaz* sta. 2670, 1100–1090 m. IORAS 526 (6, 240–410 TL); *Vityaz* sta. 2671, 1200–1175 m. CAS ex66517 (28.5 HL, 195 TL); *Vityaz* sta. 2672; 1310–1265 m. IORAS 1743 (1 spec.); *Vityaz* sta. 2706, 970–980 m. IORAS uncat. (2 spec.), CAS 66519 (5 spec.); *Vityaz* sta. 2736, 1030–1050 m. IORAS 531 (1 spec.); *Vityaz* sta. 2742, 1750–1800 m.

Distribution.— Southern Africa, from Table Bay to Mozambique; Madgascar Plateau; Walvis Ridge, se. Atlantic; in 850–1480 m (Iwamoto and Anderson 1994:5).

Family Macrouridae

4. *Asthenomacrurus victoris* Sazonov and Shcherbachev, 1982

Distribution.— Indian Ocean, Japan, and Australia, in about 1650–3500 m (Iwamoto and Graham, 2001).

Remarks.— Recorded by Parin et al. (1993), but no specimens from *Vityaz* cr. 17 were available for examination.

5. *Caelorinchus vityazae* Iwamoto, Shcherbachev, and Marquardt, sp. nov.

(Figs. 1–2)

"*Caelorinchus* sp. *sensu* Iwamoto and Anderson, 1994": Duhamel, 1999: tables 1 and 2.

Specimens examined.— Holotype: CAS 66493 (64 mm HL, 277 mm TL); 33°16'42"S, 43°41'00"E, 900–920 m, *Vityaz* cr. 17, sta. 2764, 24 Dec. 1988. Paratypes (33 specimens): **Indian**

Ocean: Walters Shoals: IORAS 179 (4 spec.), CAS 66494 (3, 46–55 HL); *Vityaz* sta. 2686, 650–660 m. IORAS 174279 (1 spec.); *Vityaz* sta. 2706, 980 m. CAS 66485 (69 HL, 269 TL); *Vityaz* sta. 2707, 910–925 m. IORAS 529 (1 spec.); *Vityaz* sta. 2670, 1600–2000 m. IORAS 1741 (1 spec.); *Vityaz* sta. 2733, 1100–1090 m. USNM 30786O (7, 53–74 HL); *Vityaz* sta. 2735, 850–740 m. CAS 218975 (2, 67–69 HL); same data as for holotype. LACM 44770-1 (1, 56.2 HL, 230 mm TL); *Vityaz* sta. 2708, 785–760 m. MNHN 2000–1476 (2, 17.5–48.2 HL, 85–188+ TL); 33°11.4'S, 44°00.4'E, 620–635 m, *Marion Dufresne* cr. MD08, sta. 6, CP47, 16 March 1976. **Southwest Indian Ridge**: MNHN 1996-228 (1, 71.9 HL, 310 TL); 41°24'S, 42°54'E, 556–440 m, *Kerguelen de Tremarec,* 26 Feb 1996. **Amsterdam and St. Paul Islands**: MNHN 1989-1139 (1, 48.7 mm HL, 185+ mm TL); 38°48.65'S, 77°36.14'E, 410–450 m, *Marion Dufresne* cr. 50, CP 209, sta. H22, 18 July 1986. MNHN 1989-1140 (1, 42.4 HL, 181 TL); 38°38'S, 77°29'E, 510–485 m, *Marion Dufresne* cr. 50, sta. 33, CP 149, 22 Jul 1986. **South Atlantic: Discovery Tablemount**: ZMMGU P-15650 (3, 39–44 HL); 42°30.5'S, 01°33'W, 400 m, *Prof. Mesiatzev* cr. 8, trawl 155, 10 Dec. 1979. **Bank Gulf**: ZISP uncat. (11, 49.0–68.5 HL); 39°37'S, 06°38.2'W, *Evrika* cr. 3, 190–335 m.

DIAGNOSIS.—A species of *Caelorinchus* with the following combination of characters: snout moderate (orbit diameter 0.88–1.16 into snout length), tipped with a sharp terminal scute, area dorsally behind leading edge of snout fully scaled, anterolateral margin of snout incompletely supported by bone; underside of head naked; body scales between origin of second dorsal fin and lateral line with 9–13 parallel rows of small, slender spinules; anterior dermal window of light organ short, extending forward about midway between anal-fin origin and pelvic-fin insertion; swim bladder deeply bilobed anteriorly; a distinctive banding pattern along body.

DESCRIPTION OF HOLOTYPE (paratype data in parentheses).— Head length about 25% total length (23–34%), about 1.5 times (1.5–1.8) greatest body depth. Width of body across pectoral bases about 75% (60–80%) greatest body depth. Snout tipped with a short but sharply pointed scute. Snout length greater than postorbital length, 1.9 times (1.6–2.0) interorbital width. Orbit large, elliptical, 1.7 times (1.6–2.0) broad, flat interorbital region. Subopercle terminates ventrally in slender tip that extends slightly beyond preopercle. Interopercle completely hidden behind preopercle. Upper jaw extends posteriorly to below middle of orbit. Mouth relatively small, rictus restricted posteriorly by lip folds; lips thick. Chin barbel short, slender, about one-third of orbit. Gill membranes broadly connected to isthmus, without a free posterior fold. Upper margin of operculum completely restricted by membrane; opercular opening ventrally extends forward to below posterior portion of preopercle.

Teeth all small, in bands in both jaws. Premaxillary band short and broad, its length approxi-

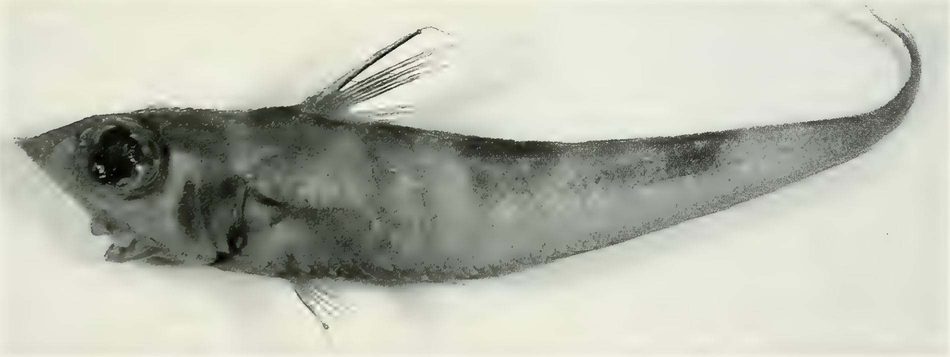

FIGURE 1. *Caelorinchus vityazae* sp. nov. Lateral view of paratype (CAS 66494, 54.8 mm HL, 212+ mm TL), from Walters Shoals, captured at a depth of 653–660 m.

mately 40% length upper jaw (30–50%); outer series of teeth slightly enlarged. Dentary band narrower, longer, and tapered posteriorly, about equal to rictus length.

First dorsal fin height about two-thirds head length; length of base about equal to interspace between first and second dorsal fins. Leading edge of second spinous ray smooth, its tip thin, extending slightly beyond adjacent segmented ray. Pectoral fin extends posteriorly to above anal-fin origin. Outer ray of pelvic fin with filamentous distal tip, extending posteriorly to above second ray of anal fin.

Body scales large and adherent, large scales below origin of second dorsal fin covered with 9–11 (9–13) parallel rows of short slender spinules. Predorsal scales with slightly elevated medial ridge of spinules and differing in that manner from other body scales. Ridges on head marked by stout, coarsely spinulated modified scales. Underside of head completely naked. Area dorsally behind both leading horizontal edges of snout fully covered with small spiny scales. Nasal fossa mostly scaly, but small naked area anteriorly with a thin anteroventral naked strip connecting to suborbital ridge. Suborbital ridge formed of stout, coarsely spined scales, with two rows of stout scales extending from below anterior margin of orbit to end of preopercle.

Pyloric caeca slender, short, length of longest about two-thirds of orbit diameter, 18 total (12–19, $x = 16.2$, n = 6). Light organ relatively small, length about $^5/_6$ths of orbit diameter, located immediately anterior to anus. Anterior dermal window of light organ in shallow, narrow depression before anus, extending forward to about midway between anal-fin origin and pelvic-fin insertion, not reaching pelvic girdle. Swim bladder large, separated by a narrow constriction into anterior and posterior chambers, the anterior chamber divided by a deep medial cleft forming two large lobes, with each lobe containing two gas glands each connected to a short, broad rete.

Color. As many as 11 saddle markings along dorsal half of body. First, third, fifth, and seventh saddles most prominent. Markings fade ventrally (generally more prominent in smaller individuals. Abdominal region bluish-black, color extending from above anterior portion of anal fin to region of pectoral and pelvic fins, but not along shoulder girdle and anteriorly on chest. Head relatively pale save the following: gill cover blue-black, most anterior rim of orbit dark (dark pigment encircling orbit in some, mostly younger, specimens, although darkest and most distinct along anterior margin); inside of mouth and anterior portion of lips blue-black. Underside of head pale to light dusky (dark dusky near tip of snout in some paratypes). Pectoral fin dusky, pale at base. First dorsal fin uniformly dark dusky except for long spinous ray, which is white (blackish in some smaller paratypes, dark to base in some, with thin pale basal margin in others). Pelvic fin uniformly light dusky except outer ray white (some paratypes with darker rays). Anal fin dusky anteriorly, becoming paler posteriorly. Lips pale, gums dark.

Counts and measurements (holotype first, followed by range in paratypes in parenthesis). 1D. II,8 (II,8–10); P. i15(i14–i19, usually i15–i18); V.7. Scales below origin of 1D. 4.5 (4.5–5.5); below middle of 1D. 4.5 (3.5–4.5); below origin of 2D. 4.5 (4.0–4.5); lateral line scales over distance equal to predorsal length 25 (24–30). Gill rakers first arch (mesial) 2+6 (8–10 total); second arch (lateral) 0+7 (6–8 total), (mesial) 2+6 (8–10 total).

Total length 269 mm (85–320 mm); head length 69 mm (17.5–76.8 mm). Following in percent of head length: snout length 38 (33–38); preoral length 32 (31–38); internasal width 22 (21–26); interorbital width 20 (19–23); orbit diameter 33 (33–40); suborbital width 18 (15–18); postorbital length 32 (26–32); orbit to preopercle distance 33 (27–36); upper jaw length 27 (24–30); premaxillary teeth-band length 7 (6–13); barbel length 10 (7–13); first gill-slit length 12 (11–16); preanal length 147 (137–163); outer pelvic ray to anal-fin origin 43 (33–47); body depth 63 (55–67); body width at pectoral base 58 (45–63); interspace between 1D. and 2D. 20(15–29); height 1D. 62 (58–77); length P. 49 (46–59); length V. 46 (37–58); length anterior dermal window 7 (4–10)

Etymology.— Named after the research vessel *Vityaz* on which many of the type specimens were captured.

Distribution.— Endemic to the West Wind Drift Islands Province; known from Bank Gulf and Discovery Tablemount in the South Atlantic, and Walters Shoals and St Paul and Amsterdam islands in the western Indian Ocean. Depth range 653–950 m.

Comparisons.— *Caelorinchus vityazae* is one of 14 spp. belonging to a clade that we call the *C. fasciatus* group. Species in the group share the following combination of characters: (1) snout short, usually blunt, its leading margin when viewed from above usually forming an obtuse angle in most species, its length about equal to or (usually) shorter than large orbit; (2) lateral and medial processes of nasal bone not connected laterally ("anterolateral margin not supported by bone"); (3) a well-developed fossa of light organ immediately anterior to anus, extending forward, depending on species, to midway between anus and pelvic fins, to as far forward as slightly beyond bases of pelvic fins (e.g., *C. mirus*); (4) body scales large, with 12 to more than 20 parallel rows of small spinules in largest scales of adults; (5) swim bladder divided into a single posterior chamber and a deeply bilobed anterior chamber; (6) prominent multiple saddle bands along body in most species. Species in the group include: *C. amydrozosterus* Iwamoto and Williams, 1999, *C. aspercephalus* Waite, 1911.*C. australis* Richardson, 1839, *C. biclinozonalis* Arai and McMillan, 1982, *C. bollonsi* McCann and McKnight, 1980, *C. cookianus* McCann and McKnight, 1980, *C. fasciatus* (Günther, 1878), *C. maurofasciatus* McMillan and Paulin, 1993, *C. mirus* McCulloch, 1926, *C. mystax* McMillan and Paulin, 1993, *C. parvifasciatus* McMillan and Paulin, 1993, *C. simorhynchus* Iwamoto and Anderson, 1993, an undescribed species from Western Australia, and the new species here described.

Caelorinchus aspercephalus, C. australis and *C. biclinozonalis* also have a relatively pointed snout like that of the new species, but they differ, among other characters, in having a scaly underside of head and much different body markings (faint oblique saddles directed slightly anteroventrally in *C. aspercephalus*, thin horizontal stripes in australis and only two saddle marks in biclinozonalis). The other remaining species of the group have the tip of the snout armed with a coarse, blunt, trifid scale; in the new species the terminal scute consists of a somewhat-elongate, sharp, medial prong flanked by much smaller, blunt prongs (Fig. 2); as a consequence of the elongate medial prong, the snout viewed dorsally forms an acute angle, rather than an obtuse one. Additionally, *C. simorhynchus* lacks saddle markings; *C. bollonsi* has saddles in specimens less than about 30 cm, but lacks them in adults; it also has a black anal fin, small patches of scales on the underside of the head above the lower jaw articulation, and 27–38 pyloric caeca (characters from McMillan and Paulin 1993:827). *Caelorinchus parvifasciatus* has faint saddle marks posteriorly on the tail, the dorsal surface of the snout behind the leading edge usually has a naked area on both sides, and the pyloric caeca count is 22–28. The unusually large fossa of the light organ in *C. mirus*, and the black spots on the pelvic fin and on the base of the pectoral fin are distinctive for that species. In *C. cookianus* the saddles are uniformly dark and there are slight differences from the new species in the shape of the pale

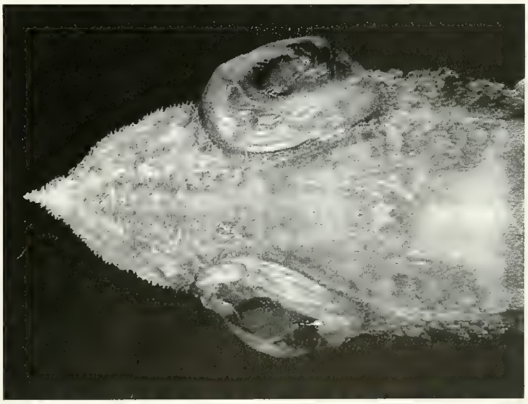

Figure 2. *Caelorinchus vityazae* sp. nov. Dorsal view of head of paratype (CAS 66494, 54.8 mm HL), showing shape of snout and details of terminal scute.

interspaces; the pyloric caeca count of 19–27 (*fide* McMillan and Paulin 1993:827) is also slightly higher. *Caelorinchus maurofasciatus* and *C. fasciatus* are closely similar in appearance and morphometry to the new species, but differ slightly in pigmentation of the dorsal and anal fins and in the shape and prominence of the saddle marks on the body. *C. amydrozosterus* has a clear naked area on each side of the dorsal snout surface, saddle markings that are oriented in the opposite direction, and a larger dermal window of the light organ. *Caelorinchus mystax* has a deep, blunt snout, anal fin with a black distal margin, and more than 100 pyloric caeca.

6. *Caelorinchus karrerae* Trunov, 1984

Specimens examined.— IORAS 1779 (1 spec.); *Vityaz* sta. 2670, 1100–1090 m. CAS 66486 (10, 52–65 HL, 236–275 TL); *Vityaz* sta. 2668, 1010 m. CAS 66488 (10, 53–63 HL, 220+–271 TL); *Vityaz* sta. 2670, 1100–1090 m. IORAS 1744 (1 spec.); *Vityaz* sta. 2706, 980 m. CAS 66490 (14, 21–55 HL, 90+–251+ TL); *Vityaz* sta. 2707, 910–925 m. IORAS 196 (1 spec.); *Vityaz* sta. 2708, 785–760 m. IORAS 537 (12 spec.); *Vityaz* sta. 2733, 775–750 m. IORAS 197 (5 spec.); *Vityaz* sta. 2734, 850–740 m. CAS 66492 (57 HL, 224+ TL); *Vityaz* sta. 2764, 920–900 m.

Distribution.— Southeastern Atlantic (off Namibia, South Africa, Discovery Tablemount); Indian Ocean (Walters Shoals, Amsterdam and St-Paul Islands, Mascarene Bank, West Australian Ridge [= Broken Ridge]); about 900–1200 m (Trunov 1984; Iwamoto and Anderson 1994)

Remarks.— A quick comparison of specimens of this species and *C. innotabilis* from Australia and New Zealand revealed no significant difference between them, suggesting a possible synonymy of the nominal species. If so, the species is distributed on both sides of the southern tip of South America, across the South Atlantic and Indian oceans to New Zealand.

7. *Caelorinchus* sp. 1B

Specimens examined.— IORAS 1817 (6 spec.), *Vityaz* sta. 2668, 1010–1010 m. IORAS 535 (14 spec.) and IORAS 1798 (5), *Vityaz* sta. 2671, 1200–1175 m. IORAS 1818 (6) and CAS 66426 (2, 109–123 HL, 370–400+ TL); *Vityaz* sta. 2672, 1310–1265 m. IORAS 520 (2 spec.), *Vityaz* sta. 2736, 1050–630 m.

Distribution.— Indian Ocean and possibly southwestern Pacific, 1020–1760 m

Remarks.— This is likely to be an undescribed species closely related to *C. labiatus*. It is currently under study.

8. *Cetonurus globiceps* (Vaillant, 1884)

Specimens examined.— IORAS 233 and CAS 66465 (2, 83–94 HL, 330+–380 TL), CAS 66484 (3, 68–79 HL, 294+–305+ TL); *Vityaz* sta. 2672, 1310–1265 m.

Distribution.— Widespread in Atlantic, southern Africa, Indian Ocean, southern Australia, and New Zealand, in depths of 970–1600 m (Sazonov and Shcherbachev 1985).

Remarks.— Also recorded from Walters Shoals by Shcherbachev (1987).

9. *Coryphaenoides armatus* Hector, 1874

Distribution.— Worldwide, usually at depths of about 2,000–4,000 m (Wilson and Waples 1983).

Remarks.— Not taken by *Vityaz*, but recorded by Shcherbachev (1987).

10. *Coryphaenoides dossenus* McMillan, 1999

Specimens examined.— IORAS 187 (1, 214 TL); *Vityaz* sta. 2671, 1200–1175 m. IORAS uncat. (1, 24 HL, 141 TL); *Vityaz* sta. 2706, 970–980 m.

Distribution.— Widespread in southern hemisphere, from eastern South Atlantic, Indian Ocean, Tasman Sea, Coral Sea, in depths of about 700–1600 m, but most commonly in around 900–1200 m.

Remarks.— Additional records are documented in Shcherbachev and Iwamoto (1995:310)

11. *Coryphaenoides filicauda* Günther, 1878

Specimens examined.— IORAS uncat. (2, 86+–230 TL); *Vityaz* sta. 2673, 1450–1700 m.

Distribution.— Circumglobal in southern hemisphere, in depths of about 1600 to more than 5000 m (Iwamoto and Sazonov 1988).

12. *Coryphaenoides grahami* Iwamoto and Shcherbachev, 1991

Specimens examined.— CAS 73237 (1 paratype, 55 HL, 340+ TL); 33°56.8′S 45°27.8′E, 1270–1280 m, *Zvezda Kryma* cr. 6, tr. 90, 31 Jul 1976.

Distribution.— Widespread, from Atlantic off southern Africa, in southern Indian Ocean, and Tasman Sea off southeastern Australia, in depths of 1050–1300 m.

Remarks.— Not taken during *Vityaz* cruise 17, but recorded from Walters Shoals by Iwamoto and Shcherbachev (1991:210) from other vessel collections.

13. *Coryphaenoides mcmillani* Iwamoto and Shcherbachev, 1991

Specimens examined.— CAS 73236 (paratype, 45 HL, 225+ TL), *Vityaz* sta. 2670, 1100–1090 m. IORAS 518 (paratype, 32+ HL, 166+ TL), *Vityaz* sta. 2672, 1310–1265 m.

Distribution.— Southern Ocean from South Atlantic on Whale Ridge (off South Africa) to New Zealand, in 950–1400 m.

14. *Coryphaenoides murrayi* Günther, 1878

Specimens examined.— CAS 218976 (1, 21.0 HL, 133 TL); V-2742, 1518–1750 m.

Distribution.— Western Indian Ocean, southeastern Australia, New Zealand and Fiji, in depths of 1196–2350 m (Iwamoto and Shcherbachev 1991; Iwamoto and Graham 2001).

15. *Coryphaenoides serrulatus oceanus* Iwamoto and Shcherbachev, 1991

Specimens examined.— ZISP 49797 (holotype, 89 HL, 482+ TL), IORAS (2 paratypes, 71–89 HL, 402–480+TL) and CAS 66432 (paratype, 54 HL, 303 TL); *Vityaz* sta. 2706, 970–980 m. IORAS 538 (5 spec.), CAS 66468 (7 paratypes, 58–71 HL, 332–415 HL); *Vityaz* sta. 2668, 1010 m. IORAS (116, 240–470); *Vityaz* sta. 2670, 1100–1090 m. IORAS 1799 (5 spec.); *Vityaz* sta. 2671,1200–1175 m. IORAS 539 (1 paratype, 39 HL, 234 TL) and CAS 66481 (1 paratype, 45 HL, 290 TL); *Vityaz* sta. 2707, 910–940 m. CAS 66464 (1 paratype, 56 HL, 282+ TL); *Vityaz* sta. 2764, 920–900 m. IORAS 188 (20 paratypes, 35–66 HL, 213–388 TL); *Vityaz* sta. 2765, 870–880 m. IORAS 189 (1 spec.); *Vityaz* sta. 2767, 240–300 m. ZMMGU P-17638 (56 HL, 337 TL); 33°08'S, 44°15'E, 870–888 m, *FIOLENT* cr. 11, tr. 18, 14 Apr. 1979. ZMMGU P-17655 (82 HL, 420 TL); 32°19'S, 44°30'00"E, 1210–1240 m, *Zvezda Kryma* cr.7, tr. 50, 22 Jan. 1977.

Distribution.— Widespread, in southern Indian Ocean; 870–1255 m.

Remarks.— Also recorded from Walters Shoals by Shcherbachev (1987) and Iwamoto and Shcherbachev (1991).

16. *Coryphaenoides striaturus* Barnard, 1925

Specimens examined.— CAS 66463 (5, 21–71 HL, 95+–398 TL); *Vityaz* sta. 2672, 1310–1265 m. IORAS (4, 28–65 HL, 183–353 TL); *Vityaz* sta. 2673, 1750–1700 m. IORAS 519 (1 spec.); *Vityaz* sta. 2674, 1500–1600 m. CAS 66427 (1, 91 HL, 493 TL), CAS 66428 (1, 54 HL, 303+ TL), IORAS (3, 26–65 HL, 149+–334 TL); *Vityaz* sta. 2742, 1518–1750 m. I0RAS (3, 45–57 HL, 245+–341 TL), CAS 66471 (1, 79 HL, 450 TL); *Vityaz* sta. 2772, 1950–2050 m. ZMMGU P-17619 (2, 39–47 HL, 240–280 TL); 32°12'S, 43°15.5'E, 1460–1470 m, *Prof. Mesiatzev* cr. 7, tr. 135, 14 Jun 1979. ZMMGU P-17620 (2, 67–76 HL, 345+–400 TL); 32°19'S, 44°03'E, 1210–1240 m, *Zvezda Kryma* cr. 7, tr. 50, 21 Jan 1977.

Distribution.— Widespread, from southeastern Atlantic, across southern Indian Ocean, to southern Australia and New Zealand, in depths of 823–2020 m.

Remarks.— A relatively common species, with more Walters Shoals records documented in Iwamoto and Shcherbachev (1991).

17. *Haplomacrourus nudirostris* Trunov, 1980

Specimens examined.—CAS 66501 (1 juvenile); *Vityaz* sta. 2670, 1100–1090 m

Distribution.— Southern hemisphere from southwest coast of Africa, through Indian Ocean to Australia, and into western South Pacific off New Zealand and New Caledonia, in about 800–1600 m (Iwamoto and Graham 2001:473).

18. *Kuronezumia bubonis* (Iwamoto, 1974)

Specimens examined.— CAS 66502 (1, 45 HL, 258+ TL spec.); *Vityaz* sta. 2721, 1000–1030 m.

Distribution.— Widespread in tropical to subtropical waters of western Atlantic, Hawaii, South China Sea, southern Indian Ocean, New Zealand, and eastern Australia (Iwamoto and Graham 2001).

19. *Malacocephalus laevis* (Lowe, 1843)

Specimens examined.— CAS 66509 (1, 43 HL, 305+ TL); *Vityaz* sta. 2706, 970–980 m. MNHN 2000–175 (51 HL, 290+ TL); 33°11.4'S, 44°00.4'E, 620–635 m, *Marion-Dufresne* sta. C, cr. MD08, CP47, 16 March 1976.

Distribution.— Worldwide in tropical to temperate seas in about 200–1000 m (Iwamoto and Graham 2001).

20. *Mesobius antipodum* Hubbs and Iwamoto, 1977

Specimen examined.— ZMMGU P.14717 (1, 108 HL, 513+ TL); 32°25'S, 43°46.4'E, 1030 m.

Distribution.— Cool temperate waters from South Atlantic to southern Australia and New Zealand, in 700–1300 m (Iwamoto and Graham 2001).

Remarks.— Not taken by *Vityaz*; recorded by Shcherbachev (1987) and Shcherbachev et al. (1979).

21. *Odontomacrurus murrayi* Norman, 1939

Distribution.— Atlantic and Indo-West Pacific; bathypelagic, in depths from 300 m to more than 2000 m (Parin et al., 1993).

Remarks.— Not taken by *Vityaz*'; recorded by Shcherbachev (1987).

22. *Sphagemacrurus pumiliceps* (Alcock, 1894)

Specimens examined.— IORAS 542 (1 spec.); *Vityaz* sta. 2672, 1310–1265 m.

Distribution.— Widespread in Indo-West Pacific in 500–1840 m (Iwamoto and Graham 2001).

Discussion

The *Caelorinchus fasciatus* Group

All species of the *Caelorinchus fasciatus* species group (to which *C. vityazae* belongs) are residents of the subtropical and subantarctic (warm-temperate and antiboreal, respectively, of Ekman, 1953) waters of the southern hemisphere. Their distribution patterns more or less coincide with the West Wind Drift (or Circumpolar) current that encircles the globe at mid to high latitudes of the Southern Ocean. The depth distributions of these *Caelorinchus* species are shallow for grenadiers, with a few found occasionally in shallow coastal waters as well as along the outer shelf and upper continental slope. *Caelorinchus biclinozonalis*, for example, has been recorded from only four meters depth (Arai and McMillan, 1982), *C. aspercephalus* from depths as shallow as 33 m, and *C. australis* from 37 m (McCann and McKnight 1980). *C. aspercephalus* has what is possibly the shallowest depth range of all grenadiers, 33–335 m. None of the species of this clade are known from depths beyond 1000 m. These rather limited depth distributions doubtlessly subject members of this clade to much the same environmental factors that affect other shallow-water marine organisms of mid- to high-latitude waters of the southern hemisphere. It is, therefore, not surprising that most of the *C. fasciatus* species group have relatively limited geographic distributions that show general concordance with surface water masses.

Caelorinchus simorhynchus is the sole African member of the clade, having a distribution from Namibia (19°52′S, 12°20′E) in the Atlantic, south around the Cape of Good Hope to off Cape St. Francis (34°54′S, 24°18′E) in the Indian Ocean. *C. fasciatus* has the broadest distribution, from the southwestern Atlantic west to New Zealand and Australia. It is known from off both sides of the southern tip of South America, from off Chile (41°40′S) south and east across the Straits of Magellan (at about 53°S) to the Falkland Islands (about 53°S, 31°W), and north along the Patagonian coast of Argentina. The species is known from off the South Island of New Zealand and only off the southeastern coast of Australia (despite published records to the contrary; see Iwamoto and Graham 2001:443). The 10 remaining species (of 14) are found in Australia and New Zealand. Four of these are endemic to New Zealand: *C. biclinozonalis*, *C. bollonsi*, *C. cookianus*, and *C. mystax*, with *C. parvifasciatus* possible a fifth species (see Iwamoto and Graham 2001:454). There are four (and possibly five) species endemic to Australia: *C. amydrozosterus* (western Australia), *C. australis* (southeastern Australia, including NSW, Tas., Vic., and SA), an undescribed species from WA, and *C. mirus* (east, south and west coasts: Qld., NSW, Tas., Vic., SA, and WA). A population of *C. parvifasciatus* that is possibly different from that of New Zealand is confined to southeastern Australia (NSW, Tas., Vic.). *C. maurofasciatus* is widespread across southern Australia (WA, SA, Vic., Tas., NSW) and New Zealand. Thus, rather surprisingly, only two and possibly three species of the group are common to both Australia and New Zealand. The large number of species (more than 100) in the genus and the relatively limited distributions of most suggest that historical and environmental factors that led to speciation events within the grenadiers have had a greater effect on *Caelorinchus* than in any other of the 30 plus grenadier genera.

Biogeographical Affinities of Walters Shoals Grenadiers

Duhamel (1999:fig. 2) sketched a zone of biogeographic affinities in the neretic ichthyofauna that stretches in a narrow band across the southern hemisphere. Included in this zone is the WWD Island Province. That Walters Shoals is part of the WWD Island Province is somewhat anomalous in that the seamount is not in itself within the waters of the West Wind Drift, but is instead bathed by the warm, south-to-southwestwardly-flowing waters of the subtropical branch of the South Equatorial Current (see Fig. 3). Water temperatures of 19–23°C in the austral summer were recorded over Walters Shoals by Collette and Parin (1991) during the *Vityaz* cruise, categorizing the waters as distinctly warmer than those off islands typical of the Province (Duhamel, *in litt.*, January 2004). The shoals lie well to the north of the Subtropical Convergence (STC) (see Fig. 3), which defines the northern boundary of the West Wind Drift and more or less coincides with the 14–15°C surface isotherms during summer and 10–12°C during winter (Ekman 1953:212). The shoals are probably affected by the seasonal and yearly oscillations of the boundary. Despite these counter-intuitive factors, Walters Shoals maintains a strong West Wind Drift element to its fauna. Collette and Parin (1991) found 35–40% of the shallow-water fish fauna of Walters Shoals to be endemic to the WWD Island Province; the primary affinities appeared to be with subtropical faunas, and to a lesser extent, to tropical ones. Parin et al. (1993) took a broader look at the shallow-water fauna, including in their analysis the invertebrates as well as fish. They concluded that the source faunas for Walters Shoals were tropical western Indian Ocean as well as southernmost South Africa and islands of the West Wind Drift. On the continental slope and in midwaters, they found that subtrop-

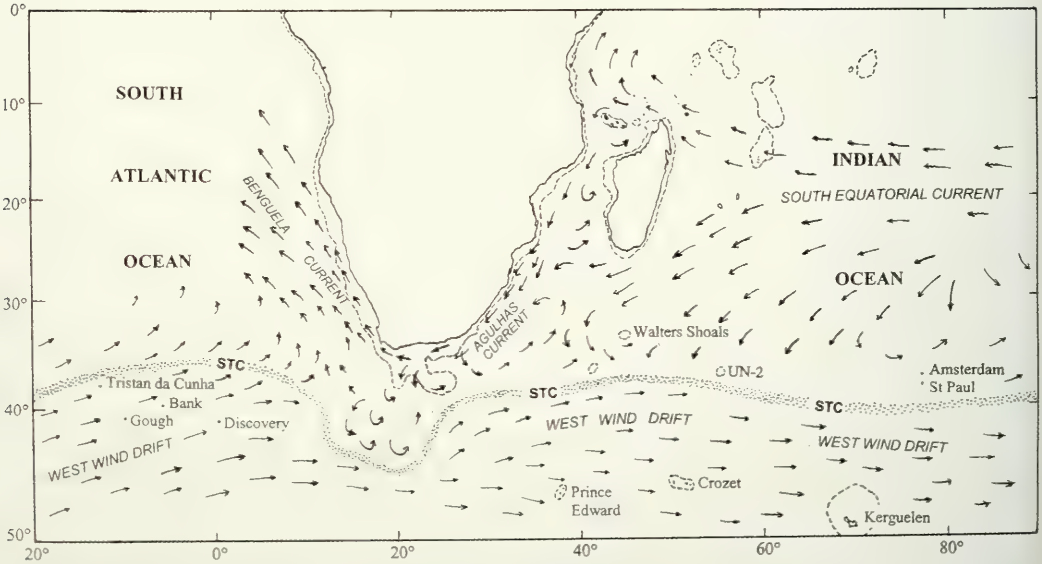

FIGURE 3. Current patterns in the region of the West Wind Drift Islands Province (drawn from various sources). Current patterns and Subtropical Convergence (STC) around southern Africa drawn according to map by Shillington (1986: fig. 4). The Subtropical Convergence roughly follows the 14–15°C summer isotherms (Ekman 1956:212) and separates the warm temperate subtropical region from the cool-temperate subantarctic region.

ical, antitropical, and southern peripheral species predominated. We have found the upper- and mid-slope grenadier fauna of Walters Shoals to be fairly well in accord with those from subtropical and subantarctic water masses of the southern hemisphere. Oscillations of the STC as well as the large counter-clockwise currents that break off from the WWD farther to the east of Walters Shoals and eventually form a gyre that merges with the South Equatorial and Subtropical currents may account for the diversity of the grenadiers of the WWD Island Province. Assuming dispersal by pelagic-stage eggs, larvae, and prejuveniles, it is not difficult to envision settlement onto Walters Shoals of juvenile grenadiers that originated from the WWD water mass. A more-precise delimitation of the water masses with the various distributions of species overlain might provide a better understanding of the causes of these distributions.

Duhamel (1999) recorded and analyzed the deepwater ichthyofauna of Saint Paul and Amsterdam islands from specimens procured by the French vessels *R/V Marion-Dufresne* (July 1986) and *F/V Austral* (July 1996). Of the 48 species in 21 families represented, the Macrouridae was the richest family in terms of species (12 spp.), although not in abundance or biomass, which categories were dominated by berycids and oreosomatids. Duhamel found a high incidence of commonality in the fauna with those from southern Africa (91% in common) and southern Australia and New Zealand (82%), but low (12%) commonality with that from South America.

The Kerguelen and Crozet islands lie farther south than Walters Shoals and other islands of the WWD Island Province, and are inside the Antarctic Convergence (the surface water at Kerguelen in the summer is around 5°C and around 2°C in winter [Ekman 1953:218]). The grenadier composition of these two islands (see Duhamel 1997; Iwamoto 1990b) reflect the Antarctic water and this Southern Ocean location. Of the species Duhamel listed, *Macrourus carinatus* and *Coryphaenoides lecointei* are subantarctic to Antarctic in distribution and were not taken in waters of the WWD Island Province; *Cynomacrurus piriei* is a circumglobal bathypelagic species that is generally confined to waters inside of the Antarctic Convergence; and "Coryphaenoides armatus and *C. filicauda*, found in common with Walters Shoals, are very deep species which occur worldwide or in the southern hemisphere. The succession of thermic fronts (Subtropical Convergence STC, Subantarctic front and Polar front) separate the WWD province from the Southern Ocean. The species which occur in both regions are only the deep-sea ones, which are not under the influence of surface frontal systems." (Duhamel, *in litt.* January 2004)

A list of the grenadiers of the WWD Island Province is provided in Table 2. Records for some of the species are based strictly on the literature and may not be accurate, as we have not critically examined all the specimens documenting these distributions. A few changes have been made to the identifications of certain species. *Coryphaenoides carapinus*, for example, is listed here as *C. filicauda*. Specimens from the WWD region appear to be the latter species, based on recent examination of many specimens from southern Australia, but the two are not considered synonyms. *Lucigadus ori* and *L. nigromaculatus* are treated as the same for this table, although they are each still considered distinct (but difficult-to-differentiate) species. The listing of *Coryphaenoides murrayi* from Crozet Island is based on MNHN 1985-901 (see Iwamoto 1990b:200, fig. 12), but that identification may not be correct. Walters Shoals has by far the most grenadier species of the Province (22), which probably reflects its geographical position well to the north of other islands of the Province, and perhaps also because it has had more successful trawl hauls made on its slopes.

Walters Shoals grenadiers are compared in Table 3 with those from Amsterdam and St-Paul (ASP), southern Africa, the south coast of Australia (see Gomon et al. 1994), and New Zealand. Eleven of the 14 spp. (or 79% of the spp.) from ASP were also taken off Walters Shoals; this represented 48% of the Walters Shoals grenadiers. It is likely that more collecting off ASP would result in more species found in common, as slope bottoms of oceanic elevations such as represented here

TABLE 2. Tentative list of grenadiers of the West Wind Drift Island Province and Crozet and Kerguelen islands. Records for some of the species are based on the literature and may not be accurate.

	Gough and vicinity	*Bank and vicinity*	*Discovery*	*Walters Shoals*	*St. Paul and Amsterdam*	*Crozet*	*Kerguelen*
Bathygadidae							
Bathygadus cottoides				+			
Bathygadus favosus				+(1)			
Gadomus capensis				+			
Macrouridae							
Asthenomacururs victoris				+			
Caelorinchus kaiyomaru	+(6)	+(8b)	+(8b,9,12)				
Caelorinchus karrerae			+(8b)	+	+(3,11)		
Caelorinchus matamua			+(9)				
Caelorinchus pseudoparallelus		+(8a)	+(8a,9)				
Caelorinchus vityazae	+	+	+(9,12)	+	+(3,11)		
Caelorinchus sp. B			+(8b,12)	+	– ?		
Cetonurus globiceps				+(1,10)	+(3,11)		
Coryphaenoides armatus				+(1)		+(14)	
Coryphaenoides dossenus				+(4)	+		
Coryphaenoides fernandezianus							+(3)
Coryphaenoides filicauda				+	+(3,11)	+(3)	+(3)
Coryphaenoides grahami				+(5)			
Coryphaenoides lecointei							+(3)
Coryphaenoides mcmillani				+(5)	+(3,11)		
Coryphaenoides mediterraneus?					+(3,11)		
Coryphaenoides murrayi				+		+(3)	+(3)
Coryphaenoides serrulatus				+(1,5)	+(3,11)		
Coryphaenoides striaturus			+(12)	+(1,5)	+		
Cynomacrurus piriei			+(9)				+(13)
Haplomacrourus nudirostris		+(6)		+(10)			
Kumba maculisquamis		+(7)					
Kuronezumia bubonis				+(1)			
Kuronezumia leonis			+(9)				
Lucigadus ori/nigromaculatus					+(3,11)		
Macrourus carinatus/holotrachys			+(9,12)			+(3)	+(3)
Malacocephalus laevis				+(1)	+(11)		
Mesobius antipodum			+(9)	+(1,2)	+(11)		
Nezumia propinqua?					+(3,11)		
Odontomacrurus murrayi				+(1)	+(11)		
Sphagemacrurus pumiliceps				+(1)			

TABLE 3. Number of grenadier species from Walters Shoals (WS) found in common with southern Africa (So. Afr.), Amsterdam and Saint Paul islands (A & SP), south coast of Australia (So. Austr.), and New Zealand (New Zeal.).

	So. Afr.	*A & SP*	*So. Austr.*	*New Zeal.*
Family Bathygadidae				
Bathygadus cottoides	+	-	+	+
Bathygadus favosus	+	-	-	-
Gadomus capensis	+	-	-	-
Family Macrouridae				
Asthenomacrurus victoris	-	-	-	+
Caelorinchus innotabilis/karrerae	+	+	+	+
Caelorinchus vityazae	-	+	-	-
Caelorinchus sp. B	-	-	-	+?
Cetonurus globiceps	+	+	+	+
Coryphaenoides armatus	+	-	-	+
Coryphaenoides dossenus	+	+	+	+
Coryphaenoides carapinus/filicauda	+	+	+	+
Coryphaenoides grahami	+	-	-	+
Coryphaenoides mcmillani	+	+	-	+
Coryphaenoides murrayi	-	-	+	+
Coryphaenoides serrulatus	-	+	+	+
Coryphaenoides striaturus	+	+	+	+
Haplomacrourus nudirostris	+	-	+	+
Kuronezumia bubonis	+	-	-	+
Malacocephalus laevis	+	+	+	+
Mesobius antipodum	+	+	+	+
Odontomacrurus murrayi	+	+	+	+
Sphagemacrurus pumiliceps?	+	-	-	-
No. of grenadiers in fauna	46	14	40	73
No. of species in common	17	11	12	18
WS spp. represented (%)	77%	48%	52%	82%
% WS spp. in fauna	37%	79%	30%	25%

FOOTNOTE REFERENCES FOR TABLE 2 (left). (1) Shcherbachev (1987); (2) Shcherbachev, Sazonov and Piotrovsky (1979); (3) Duhamel (1997), except *C. dossenus, C. striaturus* and *Nezumia* sp.; *C. murrayi* from Crozet as *Coryphaenoides* sp.; (4) Shcherbachev and Iwamoto (1995); (5) Iwamoto and Shcherbachev (1991); (6) Trunov (1980); (7) Trunov (1981); (8) Trunov (1984); (9) Trunov (1986); (10) Iwamoto and Anderson (1994); (11) Duhamel (1999); (12) Golovan and Pakhorukov (1983); *Caelorinchus* sp. B as *C. occa*; (13) Duhamel, *in litt.*, January 2004; (14) Iwamoto (1990b).

are notably difficult to trawl. Duhamel (1999:189) remarked on the "low number of successful trawls (26) in relation to the high number of damaged nets (five broken beams and falled [sic.] nets; all bottom trawls stopped after less than ten minutes)." It is likely that completion of many more successful hauls in both areas will result in a higher percentage of species in common. As might be expected, the list showed a high commonality of the species with the moderate-sized fauna (46 spp.) of southern Africa — 17 of the 23 Walters Shoals spp. (77%) in common. Two WWD Island Province species not also found off southern Africa may be endemic to the Province — *Caelorinchus vityazae* and possibly the *Nezumia* sp. cf. *propinqua* taken by the *Marion Dufresne*. There was markedly less commonality with the moderate-sized fauna from the south coast of Australia (12 of 40 spp., or 30%). If the grenadiers from Tasmania and New South Wales were also included with those from the south coast of Australia, there would have been a much higher percentage in common with the grenadiers of Walters Shoals. Surprisingly, New Zealand had 82% (18 spp.) of the Walters Shoals grenadiers represented, although those 18 spp. constituted less than one-quarter of that large fauna of about 73 spp. The more southerly position of New Zealand as compared with Australia's south coast may account for the pronounced difference, in that the WWD impinges more directly onto the former area.

That many of the shallow-water fishes of Walters Shoals are also found off the islands Tristan da Cunha, Gough, Saint Paul and Amsterdam, and the seamount UN-2 (= Austral Seamount) seems somewhat perplexing. A logical explanation is that they are located within the northern oscillatory region of the WWD and therefore have been subjected to elements of subtropical as well as subantarctic faunas. These conditions probably obtain with the grenadier fishes of Walters Shoals and Amsterdam and St. Paul islands (see Duhamel 1999), which reflect mixed provenances. The grenadiers of the WWD Island Province are predominantly widespread subtropical, worldwide, or confined to the southern hemisphere; examples of the last are *Caelorinchus karrerae, Coryphaenoides dossenus, C. striaturus, C. grahami, C. mcmillani,* and *Kuronezumia leonis.* A smaller group of species is more or less confined to waters of the WWD (*Coryphaenoides murrayi, C. subserrulatus, Caelorinchus kaiyomaru*). One Walters Shoals species (*Gadomus capensis*) is otherwise known only from southern Africa (see Iwamoto and Anderson, 1994), whereas a second species (*Lucigadus ori*) is known only from southern Africa and southwestern Australia (one specimen; see Iwamoto and Williams, 1999). Among grenadiers, only the new *Caelorinchus* and a possible new *Nezumia* species from Amsterdam Island appear to be endemic to the WWD Island Province, so far as current collections reveal. It is apparent that much more collecting in this faunistically interesting region, especially in the southeastern Atlantic around Tristan da Cunha, Bank Gulf, and Gough, will be necessary before we will be able to come to a more thorough understanding of its biogeography.

CONCLUSION

Walters Shoals has the most diverse grenadier fauna of all islands and seamounts of the WWD Island Province. Its diversity is attributed to its location well to the north of the Subtropical Convergence where its surface waters are primarily of subtropical origin. That it contains a significant WWD component to its grenadier fauna may be a result of oscillations within the WWD and to dispersal via the current by long-lived pelagic grenadier eggs and larvae. The faunal nexus among grenadiers between the oceanic elevations of the WWD Island Province is supported by the presence of *Caelorinchus vityazae* in five of these elevations. This new species belongs to a species group within the large genus *Caelorinchus*, whose members are almost solely confined to waters in or immediately north of the WWD. The broad connection between grenadiers across the mid to higher latitudes of the southern hemisphere, from the South Atlantic to New Zealand, is seen by the relatively high commonality of the faunas of widely separated regions bathed by the waters of the WWD.

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Two New Species of Scincid Lizards (Squamata) from the Massif de Kopéto, New Caledonia

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Field research in the ultramafic peaks of northwest New Caledonia has resulted in the discovery of two new species of scincid lizard from the Massif de Kopéto. One is a surface active species of moderate size that on the basis of genetic and morphological criteria is recognized as the sister species to *Lioscincus steindachneri* Bocage (the type species of the genus). The other species belongs to the genus *Nannoscincus*, a group of diminutive, elongate, small-limbed, burrowing species. Both are so far only known from relatively high elevation closed forest on the Massif de Kopéto, an area actively mined for nickel. Both species are considered to be of particular conservation concern due to their apparently restricted distribution, and the potential threat to their preferred habitat from mining activities.

Prior to the 1980s, the herpetofauna of New Caledonia was very poorly known. Virtually all of the systematic and distributional data available were derived from the research of Roux (1913) or earlier workers, and additional small collections of material were made only sporadically in the intervening decades, resulting in the description of only a few new taxa (see review in Bauer and Sadlier 2000). During the period between 1980–2000 many new lizard species and several new genera were discovered and described, bringing the number of recognized lizard taxa in New Caledonia to 68, of which 61 are endemic (Bauer and Sadlier 2000). This increase resulted largely from an extensive program of targeted field research that sampled humid and sclerophyll forests as well as maquis vegetation at all elevations. Much of this field research focused on the rich lizard fauna found in the humid closed forests of the axial mountain chain that runs nearly the full length of the main island, the Grand Terre. Recent expeditions to mid- and high-elevation sites within the major forest blocks have led to the description of many new taxa with highly restricted distributions (e.g., Bauer et al. 1998, 2000; Sadlier et al. 1998; Sadlier and Bauer 1999, 2000), indicative of the extensive microendemism that characterizes most of the New Caledonian herpetofauna (Bauer and Sadlier 1993, 2000; Bauer 1999).

Despite this effort, much of New Caledonia remained herpetologically unexplored. In particular, the series of large, isolated ultramafic peaks on the northwest side of the island constituted one of the most poorly known areas in New Caledonia. These massifs are substantially drier than the axial ranges on metamorphic rock that parallel them to the east (Paris 1981; Sautter 1981) and they support a rich and distinctive flora (Jaffré 1974; Jaffré and Latham 1974). They are mostly covered by maquis shrubland, a vegetation formation that has evolved to cope with the toxic, mineral-rich

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soils, but at higher elevations have remnant patches of moist forest, characterized by numerous emergent Araucaria (Jaffré 1980; Morat et al. 1986; Jaffré et al. 1987).

In 2001 a field program was initiated in Province Nord, Grande Terre, to determine the lizard species composition and conservation significance in various habitats, including the remnant moist forests on the major ultramafic peaks in the northwest. These are, from south to north, the Massif du Boulinda (1330 m), the Massif de Kopéto (1083 m), the Massif de Koniambo (940 m), the Massif d'Ouazangou-Taom (1092 m), Mont Kaala (1079 m), Dôme de Tiébaghi (599 m), and Sommet Poum (414 m). Although maquis vegetation extends to the tops of nearly all these peaks, small and highly fragmented forest patches also remain despite often intensive mining activity. All of these massifs were visited by one or more of the authors during the period 2001–2003. This survey effort resulted in a number of significant finds, all of which indicate the lizard fauna of these ultramafic peaks has a complex evolutionary history similar to that of the fauna of the humid forests of the central and north-eastern ranges of New Caledonia.

Among the more interesting lizards obtained in the course of this research were specimens of two new species of skink in the genera *Lioscincus* and *Nannoscincus*, both of which were collected from, or in the immediate vicinity of, small patches of remnant high elevation (>700 m) forest on the Massif de Kopéto (Fig. 1), on the west of the Grande Terre.

FIGURE 1. Map of New Caledonia showing location of Massif de Kopéto, type locality for *Lioscincus vivae*, sp. nov. and *Nannoscincus manautei* sp. nov.

The Massif de Kopéto, and the contiguous peak Paéoua (1144 m), are separated from the Massif de Koniambo to the north by the broad valleys of the Koné and Pouembout Rivers, from the Massif du Boulinda to the south by the deep valley of the Népoui River, and from the axial ranges by the low-lying, hill country around Forêt Plate. This area has been discussed and figured by Holloway (1979). Like other northwestern massifs, the vegetation of Kopéto exhibits distinct elevational stratification (Jaffré 1974; Jaffré and Latham 1974). Elevations above 700 m are characterized by maquis vegetation dominated by species of *Costularia, Hibbertia, Knightia, Dicranopteris, Gahnia*, and *Grevillea*, but patches of humid forest are also present (Fig. 2). These may be dominated by podocarps, myrtaceous or lauraceous trees, or by species of *Casuarina, Metrosideros, Nothofagus*, or *Araucaria*. The 20-year mean annual rainfall for the summit region of the Massif de Kopéto is 1830 mm (982–3288 mm), with a marked wet season from December to March (60% of annual rainfall, monthly mean 270.4 mm vs dry season monthly mean of 93.5 mm). Clouds to ground level enshroud the summit for 20% of the time. Temperatures average around 20°C, with extremes rarely dropping below 10°C or exceeding 30°C.

MATERIAL AND METHODS

MORPHOLOGY.— Specimens examined were from the collections of the Australian Museum (AMS), California Academy of Sciences (CAS), and Muséum National d'Histoire Naturelle, Paris

FIGURE 2. Isolated closed forest patch on the Massif de Kopéto typical of habitat in the area from which the types of *Lioscincus vivae*, sp. nov. and *Nannoscincus manautei*, sp. nov. were collected.

(MNHN). Radiographs were prepared using a Eresco AS2 X-ray machine to determine phalangeal formulae and the number of presacral vertebrae and postsacral vertebrae (complete original tails only) with exposures of 40 sec at 40 kV.

The full suite of morphological characters listed below was scored for each specimen. The following mensural features were recorded: snout to vent length (SVL), measured from tip of snout to caudal edge of anal scales; axilla to groin distance, measured from middle of base of forelimb to base of hindlimb; forelimb to snout length, measured from tip of snout to middle of base of forelimb; hindlimb length, measured from middle of base of hindlimb to tip of fourth toe including nail; tail length unless otherwise stated is measured from caudal edge of anal scales to tip of tail, on complete original tails only as determined by radiographs. Body measurements are expressed as percentages of snout to vent length in the taxon accounts.

Head scalation generally follows Taylor (1935) as described and figured by Sadlier (1986). The following meristic characters were recorded: midbody scale rows = number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scales = number of scales in a paravertebral row from first scale posterior to parietal scale (including nuchals) to last scale at level of vent opening; fourth finger and toe scales = number of dorsal scales on fourth digit of hand and foot, distal scale contains claw; basal scale is last largely undivided scale at, or proximal to, a point level with intersection of the third and fourth digits (variably present as a single large scale common to the base of the fourth, third, and second fingers in some *Nannoscincus*), basal scale of fourth toe broadly contacts basal scale of adjacent third toe; fourth finger and toe lamellae = number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides and the mean value used. Means of variable mensural and meristic features are reported with their standard deviations.

Molecular Analysis.— As part of a broad-scale phylogenetic study of the endemic reptiles of New Caledonia, we obtained mitochondrial and nuclear DNA sequences (514 bp of ND2 and 830 bp of rag-1) from the majority of New Caledonian skink species (including all but one genus) and representatives of related lygosomine skink lineages from Australia, New Zealand, and Africa. This phylogenetic analysis includes representatives of all *Lioscincus* species with the exception of *L. greeri*. ND2 sequences are available for all *Nannoscincus* except *N. exos*. Molecular data were analyzed within maximum parsimony and Bayesian frameworks using PAUP* v4 b10 (Swofford 2000) and MrBayes v3 (Hulsenbeck and Ronquist 2001), respectively. Support for nodes on the optimal topologies was assessed using bootstrap and Bayesian posterior probability values.

Systematics

Reptilia: Squamata: Scincidae

Lioscincus vivae Sadlier, Bauer, Whitaker, and Smith, sp. nov.

(Figs. 3–7)

Type material.— Holotype: Muséum National d'Histoire Naturelle, Paris (MNHN) 2003.1003 (formerly AMS R163227): Adult female; New Caledonia, Province Nord, Massif de Kopéto, Mont Vert, 21°10′22.4″S 165°02′14.6″E (altitude 720m), collected by A. H. Whitaker and V.A. Whitaker, 25 October 2002. Paratypes: Australian Museum (AMS) R163228: Adult female; same collection data as holotype. AMS R163122: Adult male; New Caledonia, Province Nord, Massif de Kopéto, Mont Vert, 21°10′22.0″S 165°02′10.9″E (altitude 720m), collected by A.H. Whitaker and V.A. Whitaker, 20 June 2002. California Academy of Sciences (CAS) 226163: Juvenile; New Caledonia, Province Nord, Massif de Kopéto, Papainda 21°10′33″S 165°01′04″E (altitude 860m) collected by T. Jackman, A. Bauer, R. Sadlier, S. Smith, and G. Watkins-Colwell, 21 January 2003.

Etymology.— The specific epithet is a matronym honoring Vivienne ("Viv") Whitaker, who collected the holotype and two of the paratypes and who made a major contribution to our field research in northwestern Grand Terre. The name is feminine and is formed in the genitive singular.

Diagnosis.— *Lioscincus vivae*, sp. nov. can be distinguished from all other members of its genus except *L. steindachneri* by the following combination of characters: frontoparietals fused; anterior loreal elliptical and in narrow contact with upper labials; lower eyelid with an obvious, centrally located semi-transparent disc; each parietal scale bordered by an upper secondary temporal scale and two more or less similar sized scales not noticeably larger than adjacent dorsal scales; body scales smooth.

Lioscincus vivae, sp. nov. is readily distinguished from *Lioscincus steindachneri* in having: anterior loreal contacting upper labials (vs usually present as a semilunar scale positioned off postero-dorsal edge of enlarged nasal scale and failing to contact labials); labials below eye separated from contact with lower eyelid by a complete subocular row of scales (vs fifth upper labial scale contacting lower eyelid); more paravertebral scale rows (62–65 vs 57–60); color pattern distinctly two-toned with a white midlateral stripe anteriorly with a white midlateral stripe on head and neck (males) or full length (females) of body (vs a pattern of transverse bars with no white midlateral stripe).

Description (based on holotype and thee paratype specimens including one adult male, two adult females, and one juvenile; measurements are for adult specimens only).— *Measurements*: SVL 53.5–55.0 mm; distance from axilla to groin 50.9–54.5% of SVL ($\bar{x}$ = 52.6); distance from forelimb to snout 40.0–43.0% of SVL ($\bar{x}$ = 41.9); hindlimb length 50.9–52.3% of SVL ($\bar{x}$ = 51.4);

tail length 210.9% of SVL (estimated from individual with most complete tail).

Scalation (Fig. 3): Nasals widely separated; frontonasal broader than long; prefrontals large and narrowly separated to narrowly contacting; supraciliaries usually 7 (fused to give 5 on left and 6 on right in AMS R163228); supraoculars four; frontoparietals fused; interparietal distinct; parietals each bordered by a upper secondary temporal scale and two more or less similar sized scales not noticeably larger than the adjacent dorsal scales; upper labials 7; lower labials 6; loreals two, anterior loreal contacting the upper labials narrowly; complete subocular row of 9–12 scales ($\bar{x}$ = 10.25 ± 0.29) between preocular and pretemporal scales; primary temporal single; upper and lower secondary temporals single; tertiary temporals one (50%), or two; postlabials two; postmental contacting first and second lower labial; chinshields 3, first pair in broad contact; body scales smooth, midbody scale rows 32–34 ($\bar{x}$ = 32.75 ± 0.96); paravertebral scales 62–65 ($\bar{x}$= 62.75 ± 1.5); scales on top of fourth finger 12–14 ($\bar{x}$ = 12.75 ± 0.96); lamellae beneath fourth finger 23–24 ($\bar{x}$ = 23.4 ± 0.48); scales on top of fourth toe 17–19 ($\bar{x}$ = 18.0 ± 1.00); lamellae beneath fourth toe 41–47 ($\bar{x}$ = 43.5 ± 1.91).

Coloration (in life): There is marked sexual dimorphism between the adult male and the adult females, with the juvenile similar in coloration to adult females.

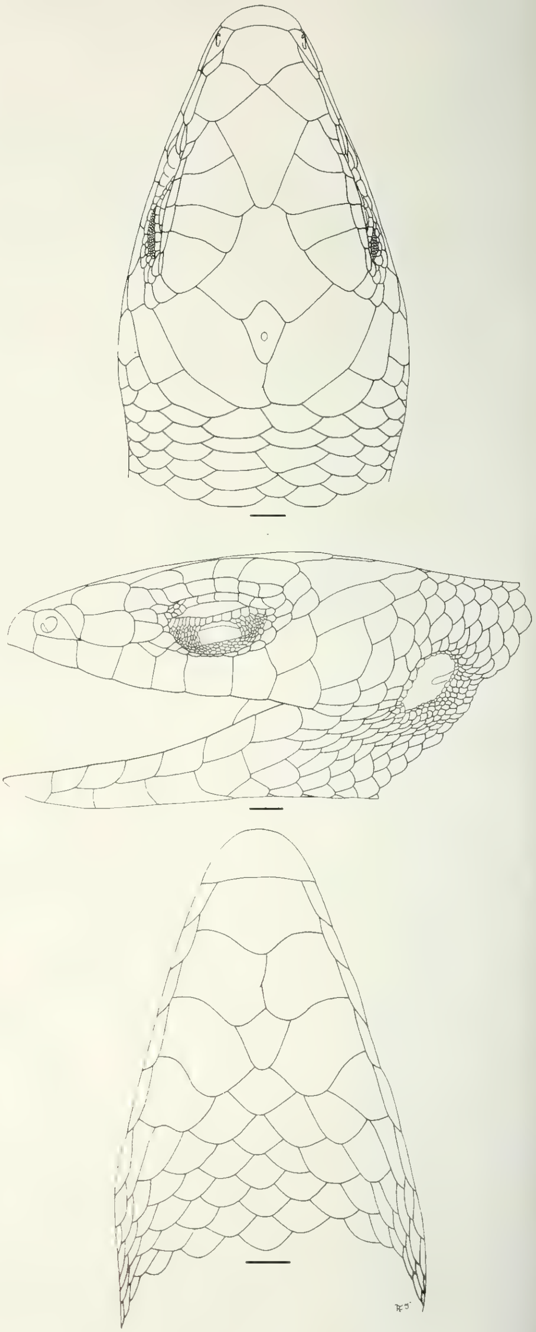

FIGURE 3. Dorsal (upper), lateral (middle), and ventral (lower) views of the headshields of holotype of *Lioscincus vivae*, sp. nov. (MNHN 2003.1003). Scale bar = 1 mm.

Adult male (Figs. 4–5): Dorsal surface of body and tail uniform reddish brown, with indistinct paler middorsal stripe two half scales wide (noted at time of capture but not evident in accompanying photograph). Head gray-brown with numerous scattered dark spots on the dorsal headshields. Dorsolateral margin with a concentration of fine dark longitudinal flecks from just above the ear to just past the hindlimb. Lateral surface of anterior half of body two-toned, mid brown above (not as red as dorsal surface) and pale gray below. Bold white midlateral stripe with narrow black margin above passing through the labials to the ear, and recommencing behind the ear but fading

FIGURE 4 (above). Lateral view of a paratype of *Lioscincus vivae*, sp. nov. (AMR 163122) in life showing adult male color pattern and the long tail characteristic of the species.

FIGURE 5 (right). Lateral view of the head a paratype of *Lioscincus vivae*, sp. nov. (AMR 163122) in life.

towards the forelimb. Remainder of the lateral surface of the body (between the fore- and hindlimbs) grading from brown to gray (breaking into obscure pale blotches) towards the ventral surface. Side of head with numerous dark scattered spots to the headshields, and median and posterior labials each with large dark spots centered where the white midlateral stripe passes. Undersurface white, the throat and chest with fine, scattered, dark flecks.

Adult females (Figs. 6–7): Dorsal surface reddish brown (as for adult males, but lacking middorsal stripe). Bold, white, dorsolateral stripe (2/3 scale width), dark-edged (broken) above from in front of the forelimb to just past the hindlimb. Lateral surface two-toned, dark brown above (darker than dorsal surface) and gray below, separated by a bold, broad (1.5–2 scales width), white, midlateral stripe passing through the labials to the ear, and recommencing behind the ear and passing above the forelimb to the hindlimb, and approximately a third of the way along the tail. The midlateral stripe is dark-edged above and below. Undersurface white, throat and chest with fine, scattered, dark flecks. In life the ventral surface has a faint yellow flush around the anal scales. Buccal cavity and tongue very pale, lacking any obvious dark pigmentation (condition not recorded for male and juvenile specimens).

Coloration of the single juvenile paratype is typical of adult females.

FIGURE 6 (above). Lateral view of the holotype of *Lioscincus vivae*, sp. nov. (MNHN 2003.1003) in life showing typical adult female color pattern.

FIGURE 7 (right). Lateral view of the head of the holotype of *Lioscincus vivae*, sp. nov. (MNHN 2003.1003) in life.

Osteology. Presacral vertebrae 28 (n = 1) or 29 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4, respectively.

DISTRIBUTION AND HABITAT.— Known only from above 700 m on the Massif de Kopéto, from two sites approximately 2 km apart. Two individuals (MNHN 2003.1003 and AMS R163228) were collected amongst logs, ferns, and grasses on the margin of a narrow road through low, closed forest on a steep slope at Mont Vert, and another (AMS R163122) from beneath a stone in adjacent high elevation maquis. The juvenile specimen (CAS 226163) from Papainda was collected from a rock crevice in a road cutting in closed forest at the ecotone with maquis shrubland. The range of *L. vivae* may also include the Paéoua massif, as Paéoua and Kopéto share a similar habitat, are contiguous and together are isolated from all other neighboring peaks.

RELATIONSHIPS.— The new species is very distinctive in appearance and genetic data clearly identify it as the sister species to *Lioscincus steindachneri* (type species for the genus). The relationship is supported by high bootstrap values and Bayesian posterior probabilities (100% and 1, respectively) in our analyses of all genera, and by a shared suite of unique apomorphies discussed above. ND2 mitochondrial sequence divergence between *L. vivae* and *L. steindachneri* (13.5%) is equivalent to mean pairwise congeneric species divergence within other New Caledonian skink genera (e.g., *Tropidoscincus* 11.5%, *Sigaloseps* 14.4%, *Marmorosphax* 12.1% and *Caledoniscincus* 12.9%). Phylogenetic analyses of genetic data from all New Caledonian genera indicate a revised *Lioscincus* will result in some taxa being assigned to new genera (Smith et al., unpublished data in preparation). The generic allocation of *L. vivae*, as the sister to the type species, however, will be unchanged.

Nannoscincus manautei Sadlier, Bauer, Whitaker, and Smith, sp. nov.

(Figs. 8–9)

Type material.— Holotype: MNHN 2003.1001 (formerly AMS R163229): Adult female; New Caledonia, Province Nord, Massif de Kopéto, Papainda, 21°10′38.5″S 165°01′15.4″E (elevation 800 m), collected by A.H. Whitaker and V.A. Whitaker, 25 October 2002. Paratype: AMS R163123: Adult female; same locality and collectors as holotype, 22 June 2002.

Etymology.— The specific epithet honors our friend and colleague Joseph Manauté, now of the Direction des Resources Naturelles de la Province Sud (Service des Parcs et Réserves Terrestres). When working for the Direction du Développement Economique et de l'Environnement (Service del'Environnement) of the Assemblée de la Province Nord, Joseph was a strong proponent of the herpetological surveys that revealed this and many other new species. He remains a strong supporter of both scientific investigation and conservation in New Caledonia. The epithet is masculine and is formed in the genitive case.

Diagnosis.— *Nannoscincus manautei* sp. nov. can be distinguished from all other members of the genus by the following combination of characters: frontoparietals fused; loreal single; left oviduct lost in females; lower labials five; lower eyelid with a semitranslucent window; ear opening minute; body scales smooth; adult dorsal color uniform brown; ear opening positioned three scales posterior to lower secondary temporal; longitudinal scale rows around the body 18–20; presacral vertebrae 32–33; phalangeal formula for pes 2.3.4.4.3.

The first five characters readily distinguish *N. manautei* from *N. gracilis, N. slevini*, and a new species from Pic Ningua in the southern ultramafic block, all of which have divided frontoparietals, two loreals (the anterior semilunar and usually failing to contact the labials), a right and left oviduct, and a 'scaled' lower eyelid.

Nannoscincus manautei shares the apomorphic character states of a single loreal, loss of the left oviduct, and reduction to five lower labials with a group of six other species (*N. mariei*; *N. greeri*; *N. rankini*; *N. humectus*, *N. hanchisteus*, and *N. exos*).

Three species, *N. humectus*, *N. hanchisteus*, and *N. exos*, have smooth body scales like *N. manautei*. The relatively uniform adult coloration of *N. manautei*, lacking obvious differentiation between dorsal and lateral surfaces, distinguishes it from these species, all of which are noticeably two-toned in having a distinctly lighter dorsal and darker lateral surface. *Nannoscincus manautei* can be further distinguished from *N. hanchisteus* and *N. exos* by the positioning of the ear opening three (vs two) scales posterior to the lower secondary temporal, and from *N. humectus* by having fewer lamellae beneath the 4th toe (12–13 vs 15–19) and fewer longitudinal scale rows around the body (18–20 vs 20–24).

The smooth body scales of *N. manautei* will distinguish it from *N. greeri*, *N. mariei*, and *N.*

rankini all of which have 3–4 fine striations down the body scales. *Nannoscincus manautei* most closely resembles *N. mariei* and *N. rankini*, both of which are relatively uniformly colored as adults. It can be further distinguished from *N. mariei* by the presence of a "windowed" (vs "scaled") lower eyelid, fused (vs paired) frontoparietals, and the presence of a small external ear opening (lacking in *N. mariei*), and from *N. rankini* by the positioning of the ear opening three (vs two) scales posterior to the lower secondary temporal and in having fewer longitudinal scale rows around body (18–20 vs 22–24).

Description (based on holotype and paratype).— Measurements: SVL 31.0–34.0 mm; distance from axilla to groin 64.7–66.1% of SVL ($\bar{x} = 65.4$); distance from forelimb to snout 32.2–32.3% of SVL ($\bar{x} = 32.25$); hindlimb length 20.6–21.0% of SVL ($\bar{x} = 20.8$); tail length 103.2% of SVL or more (estimated from individual with most complete tail).

Scalation (Fig. 8): Nasals large and moderately separated; frontonasal broader than long; prefrontals very small and widely separated; supraciliaries seven, with the first supraciliary contacting frontal (thereby excluding contact between the prefrontal and first supraocular); frontal short almost as broad as long; supraoculars four; frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; upper labials six; lower labials five; primary temporal single; upper and lower secondary temporals single; tertiary temporals two; postlabials two; post temporals three (number of scales positioned posterior to lower secondary temporal and ear opening); postmental contacting first and second lower labial; chinshields three, first pair in broad contact; body scales smooth, midbody scale rows 18–20; paravertebral scales 53–56 ($\bar{x} = 54.5$); scales on top of fourth finger 4–5 ($\bar{x} = 4.3 \pm 0.57$), scales at base of second, third, and fourth fingers variable, ranging from a single scale at the base of each digit, to two scales of

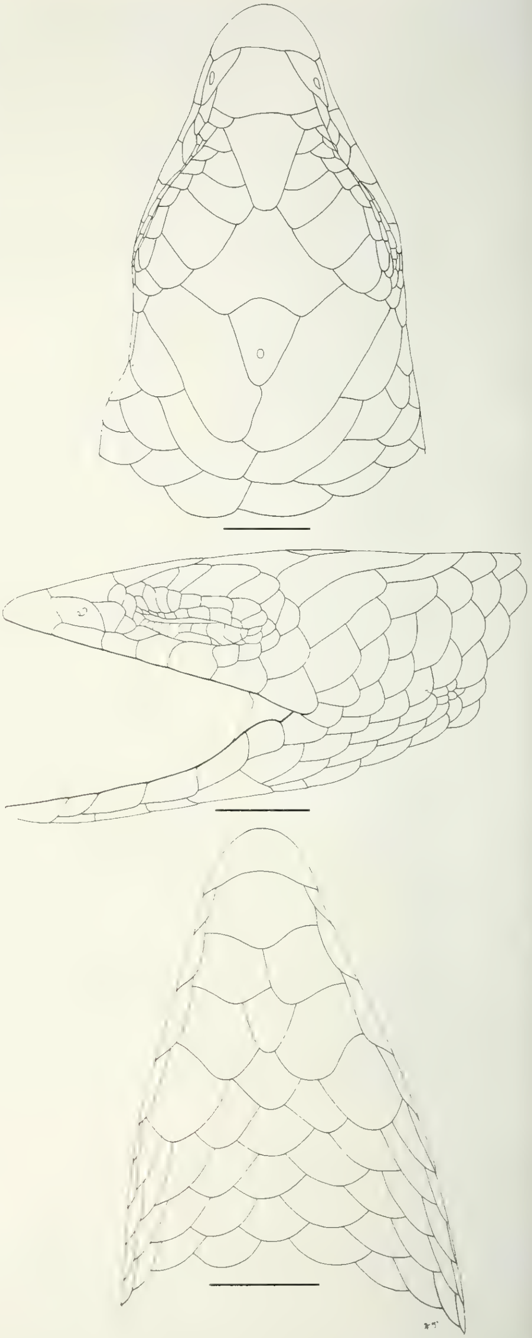

FIGURE 8. Dorsal (upper), lateral (middle), and ventral (lower) views of the head shields ofholotype of *Nannoscincus manautei*, sp. nov. (MNHN 2003.1001). Scale bar = 1 mm.

equal size, to a small scale at the base of the second digit and an enlarged scale common to base of the third and fourth digits; lamellae beneath fourth finger 4; scales on top of fourth toe 6; lamellae beneath fourth toe 12–13 ($\bar{x} = 12.5 \pm 0.5$).

Coloration (in life; Fig. 9): Dorsal color mid brown overall, head and nape with pale spots centered on individual head shields and scales of the nuchal area, extending to upper labials on holotype. Lateral surface similar to dorsal uppermost, becoming progressively paler towards to the venter. Dark markings along the ventrolateral margin between the forelimbs and jaw concentrated towards the center of each scale, and forming one to two obscure brown stripes running back obliquely from the rear and underside of the jaw. Lower labials with dark brown markings across the middle of each scale separated by lighter interspaces, dark markings extending to adjacent chinshields. Ventral surface pale with a concentration of scattered brown markings at edges and regular brown markings to the edge of the throat region.

Osteology: Presacral vertebrae 31–32 ($x = 31.5 \pm 0.7$); phalangeal formula for manus and pes 2.3.4.4.3 and 2.3.4.4.3, respectively.

Distribution and Habitat.— Known only from a single site above 700 m on the Massif de Kopéto. Both holotype and paratype were collected under logs and rocks embedded in a deep humus layer and overlain by thick leaf litter in a patch of moist closed forest characterized by emergent *Araucaria*. Another *Nannoscincus*, presumed to be the same species, was seen beneath a log in similar habitat approximately 1.8 km to the east. As for *Lioscincus vivae*, the range of *N. manautei* may also include the Paéoua massif.

Relationships.— *Nannoscincus* is a member of the Australasian *Eugongylus* group of lygosomine skinks (Greer 1979). It is distinguished from other genera in the group by a combination of morphological synapomorphies that includes: fusion of the atlantal arches and intercentrum of the first cervical vertebra into a single element; an elongate body with 29 or more presacral vertebrae; phalanges of digits of the forelimbs reduced, with a phalangeal formula of 2.3.4.4.3 or less for the manus (Sadlier 1990; Bauer and Sadlier 2000).

The generic status of a single Australian species referred to the genus, *N. maccoyi*, has recent-

Figure 9. Dorsal view of a paratype (AMS R163123) of *Nannoscincus manautei*, sp. nov., in life.

ly been re-evaluated (Sadlier et al., in review), leaving ten species, all endemic to the New Caledonian mainland, in two distinct species groups. One of these, the "*gracilis*" group (Sadlier 1990) includes *N. gracilis*, *N. slevini*, and an undescribed species from Pic Ningua, one of the northernmost peaks in the southern ultramafic block of New Caledonia. The species in this group are all superficially similar in that they have very elongate bodies and a markedly two-toned color pattern. They also share a suite of distinctive apomorphic characters, two of which, a reduction in the number of phalanges of the third and fourth fingers to yield the pedal phalangeal formula 2.3.3.3.3 and a generally highly elevated number of presacral vertebrae, are unique within *Nannoscincus*. The monophyly of the "*gracilis*" group is supported by moderate bootstrap support (67%) and high posterior probability (1) in analyses of mitochondrial DNA sequence data (Smith et al, unpublished data, in preparation).

The other group is a clade of six species (*N. mariei*; *N. rankini*; *N. greeri*; *N. hanchisteus*; *N. humectus*; and *N. exos*) characterized by three morphological synapomorphies (loss of the left oviduct in females; reduction in number of lower labial scales to five; and loss of the anterior loreal scale), and is referred to as the "*mariei*" species group (Sadlier et al. 2002). These features are also present in the species of *Nannoscincus* described here, which is, therefore, considered a member of the "*mariei*" group. It is superficially most similar to *N. rankini*, which is believed to be endemic to Mont Aoupinié, approximately 25 km east of Kopéto, in the more mesic central chain of mountains. ND2 divergence between *Nannoscincus manautei* and other members of the *mariei* group species, has a mean of 13.5% (vs 13.2% for comparisons among previously described members of the *mariei* group). However, mitochondrial ND2 sequence data analyzed using parsimony and Bayesian criteria (Swofford 2000; Hulsenbeck and Ronquist 2001) do not support the monophyly of the "*mariei*" group, but rather suggest they form a poorly resolved basal cluster of species within the genus. A further phylogenetic analysis of the genus *Nannoscincus* is currently being prepared for publication.

CONSERVATION

Nannoscincus manautei is known from a single location and *Lioscincus vivae* from two locations on the Kopéto massif. Both are likely to be found in other high elevation (>700 m) forest patches on, and associated with, the Kopéto-Paéoua massif. The individual size of these forest patches is extremely small. They are scattered across the top of the mountains, mostly on south-facing slopes, and often in and adjacent to gullies.

Our investigations on the northwestern ultramafic massifs have revealed that most of these peaks support endemic species of lizards that do not occur on adjacent mountains. Such is possibly the case with the species described here. Despite searches of comparable habitat on the Massif du Boulinda to the south and the Massif de Koniambo to the north, no additional sites for either species was located. On the next major massif to the east, Mont Aoupinié, *N. manautei* is replaced by the high-altitude species *N. rankini*, and it is very unlikely to occur in low altitude forests in the vicinity of Massif de Kopéto where it is replaced by other *Nannoscincus* species (nearest known localities *N. humectus* and *N. gracilis* at Forêt Plate, 500–600 m and 9 km to the northeast, or *N. hanchisteus* at Pindaï, <60 m and 18 km to the southwest). No comment is possible on the likelihood that *L. vivae* occurs at elevations significantly below 700 m.

The nickel mining operation on Kopéto is one of the most sophisticated and intensive in the region. The remnant areas of high altitude closed forest on the mountain have all been disturbed to different degrees by access roads, by the construction of containment ponds and waste rock dumps (often in gullies), and by wind-blown dust or excess run-off from actively mined surfaces (Fig. 10). Given the steep terrain and the small size of the remaining forest patches, mining activity through

FIGURE 10. Patch of gully forest (bottom center) on the Massif de Kopéto illustrating disruption of adjacent forest associated with recent mining activity (left).

or immediately adjacent to these forests has the potential to alter a significant proportion of the overall area of the habitat remaining for these lizard species.

Because of their apparently highly restricted distribution, the small size and fragmented nature of the remaining moist forest habitat on the Massif de Kopéto, and the potential threat to this habitat from established mining activities in areas immediately adjacent to the known habitat, both species would be ranked as Critically Endangered under the modified IUCN classification system used for the New Caledonian herpetofauna (total area of occupancy <100 km^2, a single population and an apparent continuing decline in area, extent and/or quality of habitat) (Sadlier and Bauer 2003).

The survey effort in closed forests of the Kopéto massif undertaken in 2001–2003, or for that matter on any of the ultramafic massifs in the northwest of the island, can only be regarded as preliminary (about 1–3 calendar days or 2–8 person days per massif). Given the limited time spent surveying the individual peaks in this region it is possible these new species could have a somewhat wider range than is currently indicated, in which case their conservation status would need to be reviewed.

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Phylogenetic Relationships of the Genus *Ptyctolaemus* (Squamata: Agamidae), with a Description of a New Species from the Chin Hills of Western Myanmar

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A new species of *Ptyctolaemus* is described from the Chin Hills, Chin State, western Myanmar. Specimens were found on the slopes of Mount Victoria between elevations of 709 m and 1,940 m in areas of secondary forest in close proximity to human habitation. The new species differs from *P. gularis*, by having a more developed nuchal crest in males, shorter limbs, larger and more heterogeneous dorsal body scales, and a shorter tail. *P. phuwuanensis* can be distinguished from *P. gularis* and the new species by the presence of femoral pores and a distinct gular region. A molecular phylogenetic analysis of *P. gularis, P. phuwuanensis*, the new species of *Ptyctolaemus* from Chin State, and other species in the draconine clade indicates that *P. phuwuanensis* is sister to all other draconine agamids and we recommend the recognition of the genus name *Mantheyus* for *P. phuwuanensis* in light of these results. *Ptyctolaemus* from Chin State and *P. gularis* are related but significantly different genetically and morphologically representing separate species.

Two species of *Ptyctolaemus* are currently recognized. *Ptyctolaemus gularis* (Peters, 1864) currently known from northeastern India (Boulenger 1890; Wall 1908; Smith 1935; Mathew 1995; Pawar and Birand 2001), Xizang Autonomous Region [Tibet], China (Huang 1980), Kachin State, Myanmar (Smith 1940), Sagaing Division, Myanmar (California Academy of Sciences specimens), and Chin State, Myanmar (Shreve 1940; Moody 1980), and *P. phuwuanensis* Manthey and Nabhitabhata, 1991, is known from northeastern Thailand and western central Laos (Manthey and Nabhitabhata 1991; Ananjeva and Stuart 2001). After examining specimens of *P. phuwuanensis*, Ananjeva and Stuart (2001) provided a number of characters, including the presence of femoral glands and a unique gular fold morphology that lead them to place *P. phuwuanensis* in the new genus *Mantheyus*. Hallermann and Böhme (2003) objected to the placement of *M. phuwuanensis* into a monotypic genus stating that Ananjeva and Stuart (2001) did not provide autapomorphic characters distinguishing *M. phuwuanensis* from *P. gularis* and thus did not demonstrate that *Mantheyus* represented an isolated evolutionary lineage without close relatives. Hallermann and Böhme (2003) argued that femoral glands are a plesiomorphic character and the similarity of the gular folds represented a possible synapomorphy for *P. gularis* and *M. phuwuanensis* and therefore regarded *Mantheyus* as a junior, subjective synonym.

In March 2001, while surveying Nat Mat Taung National Park and surrounding areas of the southern Chin Hills, Chin State, Myanmar, the Myanmar Herpetological Survey team collected eight individuals (seven adults and one juvenile) belonging to the genus *Ptyctolaemus*. After comparing these specimens with the holotype of *P. gularis* as well as other specimens from India and northern Myanmar, we determined that the specimens from the Chin Hills represent a new species. The external comparisons were followed by a molecular phylogenetic analysis of the genus utilizing tissue samples of *Ptyctolaemus* from Chin State, *P. gularis* from northern Myanmar, and *P. phuwuanensis* from Laos. Because the type locality of *P. gularis*, given in Peters (1864) as "Calcutta", is thought to be in error (Jerdon 1870; Zhao and Alder 1993), we analyzed the mensoral data of the Chin State specimens, the holotype of *P. gularis* and other specimens of *P. gularis* from India and northern Myanmar, using principal component analysis. This allowed us to determine which species of *Ptyctolaemus* are most similar to the holotype of *P. gularis* and should be recognized as the nominal species.

MATERIALS AND METHODS

All California Academy of Sciences (CAS) specimens were hand collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Samples of liver tissue were taken from selected specimens and stored in 95% ethanol. Latitude, longitude and elevation were recorded using a Garmin 12 Global Positioning System receiver (datum WGS 84).

Comparative material was obtained from the Institute of Systematic Zoology, Humboldt University, Berlin (ZMB); the Natural History Museum (British Museum), London; Field Museum of Natural History; Museum of Comparative Zoology, Harvard University; National Museum of Natural History, Smithsonian Institution; Myanmar Biodiversity Museum, Hlawga; and California Academy of Sciences (see material examined section). Museum symbolic codes follow Leviton et al. (1985) except for the ZMB, the Wildlife Heritage Trust, Colombo, Sri Lanka (WHT), Bombay Natural History Society (BNHS), and the, newly established, Myanmar Biodiversity Museum (MBM). The codes BNHS-AMB, MBM-JBS, MVZ-RM, WAM-ERP are followed by the field numbers for Aaron M. Bauer, Joseph B. Slowinski, J. Robert Macey, and Eric R. Pianka, respectively, for uncataloged specimens being deposited at the designated institutions.

The following measurements were obtained from all specimens of *Ptyctolaemus gularis* and *Ptyctolaemus* from Chin State examined in the study (limb lengths were taken from the right side unless noted otherwise): snout-vent length (SVL); tail length (TailL); head length (HeadL), distance from tip of snout to rear border of right angle of jaw; head width (HeadW), widest point in the temporal region, anterior to the tympanum; upper arm length (UarmL), from elbow to forelimb insertion; forearm length (ForeaL), from base of palm to elbow; hand length (HandL), from base of palm to end of fourth finger (not including the claw); thigh length (ThighL), from knee to thigh insertion; crus length (CrusL), from base of heel to knee; foot length (FootL), from heel to end of fourth toe; fourth toe length (4^{th}Toe), from base or fourth toe to toe tip (not including the claw); and ratios of TailL/SVL, HeadW/HeadL, HeadW/SVL, HeadL/SVL, UarmL/SVL, ForeaL/SVL, ThighL/SVL, and CrusL/SVL.

Data for the following meristic characters were recorded: supralabials (SupL), number of enlarged scales bordering left and right margin of upper lip (not including rostral scale); infralabials (InfL), number of enlarged scales bordering left and right margin of lower lip (not including mental scale); number of nuchal crest spines (NuchalC), enlarged mid-dorsal crest scales from posterior portion of the head to the posterior portion of the nape; number of scales around midbody (MidB); number of ventral scale rows (VentSR), scale rows between posterior margin of gular and anterior edge of vent; and number of subdigital lamellae on the right fourth toe (SDL).

Scale counts and observations of external morphology were made using a dissecting microscope. Measurements, except for TailL, were made with digital calipers with a 0.01 mm precision and rounded to the nearest 0.1 mm. Tail lengths were measured using a measuring tape with a precision of 1 mm.

Genomic DNA was extracted from liver using the Qiagen QIAamp tissue kit. Amplification of genomic DNA was conducted using a denaturation at 94°C for 35 s, annealing at 50°C for 35 s, and extension at 70°C for 150 s with 4 s added to the extension per cycle, for 30 cycles with Life Technologies (Gibco) Taq polymerase. Negative controls were run on all amplifications to check for contamination. Amplified products were purified on 2.0% Nusieve GTG agarose gels and reamplified under the conditions described above. Reamplified double-stranded products were purified using the Qiagen Qiaquick Purification kit. Cycle-sequencing reactions were run using ABI Prism Big Dye Terminator version 3 DNA Sequencing Kit (Perkin-Elmer) with a denaturation at 95°C for 15 s, annealing at 50°C for 1 s, and extension at 60°C for 4 min for 35–40 cycles. Sequencing reactions were run on a MJ Research Basestation or ABI PRISM® 3100 Genetic Analyzer.

Amplifications of the mitochondrial ND1 gene to the COI gene from genomic DNA were done with three primer combinations. All samples were amplified with L3914 in combination with H4980. *Ptyctolaemus phuwuanensis* was amplified with L4437 in combination with H6159. *P. gularis* and the new species were amplified with L4437 in combination with H5934a. Both strands were sequenced using L3914, L4160, L4437, L4882a, L4882b, H4980, L5549b, L5638b, H5934a, and H6159.

Most primers are as described by Macey et al. (1997a) except L3914, which is erroneously reported in Macey et al. (1998a) as L3878. Additional primers used include L4160 (Kumazawa and Nishida 1993), L4882a (Schulte et al. 1998), L4882b (Macey et al. 2000), L5549b (Schulte et al. 2003), and H6159 (Weisrock et al. 2001). Primer numbers refer to the 3' end on the human mitochondrial genome (Anderson et al. 1981), where L and H denote primers whose extension produces the light and heavy strands, respectively. Voucher specimen information and GenBank accession numbers for newly reported sequences are provided in the material examined section. Aligned DNA sequences are available in TreeBASE (Study accession S1056; Matrix accession number M1800).

DNA sequences were aligned initially by eye. Positions encoding part of ND1, all of ND2, and part of COI were translated to amino acids using MacClade 4.06 (Maddison and Maddison 2003) for confirmation of alignment. Alignments of sequences encoding tRNAs were based on secondary structural models. Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes using these models. Unalignable regions were excluded from phylogenetic analyses using the same regions excluded by Macey et al (2000).

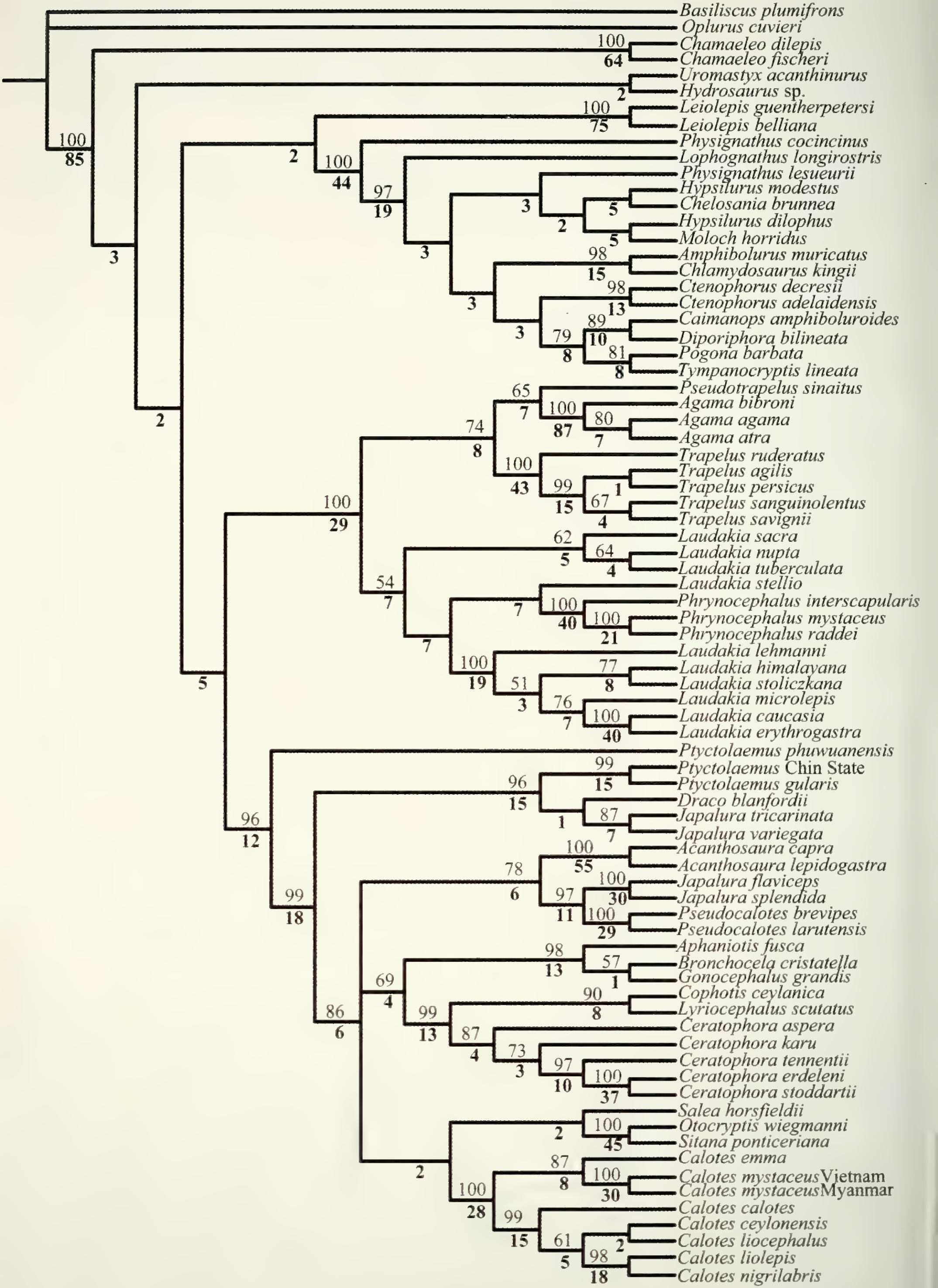
Phylogenetic trees were estimated using PAUP* beta version 4.0b10 (Swofford 2002) with a heuristic search featuring TBR branch swapping and 500 random taxon additions using maximum parsimony (MP). Bootstrap resampling (Felsenstein 1985a) was applied to assess support for individual nodes using 1000 bootstrap replicates with 100 random taxon additions per replicate. Decay indices (= "branch support" of Bremer 1994) were calculated for all internal branches using TreeRot.v2c (Sorenson 1999). In our evaluation of branch support strength, we consider a bootstrap value of 95% and above as strongly supported (Felsenstein and Kishino 1993), 95–70% as moderately supported, and below 70% as poorly supported. Maximum-likelihood (ML) analyses were also performed. Simultaneous optimization of ML parameters and phylogenetic hypotheses for this data set was computationally impractical; therefore, ModelTest v3.06 (Posada and Crandall 1998) was used to find the best fitting model of sequence evolution for the tree from unweighted parsimony analysis. Posada and Crandall (2001) found that the starting tree did not significantly influence the estimated parameters found by ModelTest. The best fitting model parameters were fixed, and then used in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. Bootstrap analysis of the maximum-likelihood tree was computationally intractable.

Bayesian analysis was used to estimate a phylogenetic tree using many of the default values in MrBayes 3.04 (Huelsenbeck and Ronquist 2001). All analyses were initiated from random starting trees and run for 40,000,000 generations using four incrementally heated Markov chains. Values of the likelihood model were estimated from the data and initiated using flat priors. Trees were sampled every 100 generations resulting in 400,000 saved trees. To ensure that Bayesian analyses reached stationarity, the first 200,000 saved trees were discarded as "burn-in" samples. Sampled trees were used to generate a 50% majority-rule consensus tree in PAUP* and the percentage of trees having a particular clade represented that clade's posterior probability (Huelsenbeck and Ronquist 2001).

Wilcoxon signed-ranks (WSR) tests (Felsenstein 1985b; Templeton 1983) were used to examine statistical significance of the shortest tree relative to alternative hypotheses. This test determines whether the most parsimonious tree is significantly shorter than an alternative tree or whether their differences in length are statistically indistinguishable (Larson 1998). Wilcoxon signed-ranks tests were conducted as two-tailed tests (Felsenstein 1985b). Tests were conducted using PAUP* (Swofford 2002), which incorporates a correction for tied ranks. Goldman et al. (2000) criticized the application of the WSR test as applied in this study. Therefore, nonparametric Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa 1999), as advocated by Goldman et al. (2000), also were performed to test the shortest tree relative to the shortest alternative hypotheses using 10,000 resampling estimated log-likelihood (RELL) approximations in PAUP* to compare with the results of WSR tests. Parameter values were estimated on the ML trees using the likelihood criteria under the GTR + I + G model of sequence evolution. Buckley (2002) found the SH test to be a conservative model-based hypothesis test and, in general, to have low Type 1 and Type 2 error relative to the SOWH test (Goldman et al. 2000) and Bayesian posterior probabilities.

Alternative phylogenetic hypotheses for WSR and SH tests were tested using the most parsimonious phylogenetic topologies compatible with a particular constraint. To find the most parsimonious tree(s) compatible with a particular phylogenetic hypothesis, phylogenetic topologies were constructed using MacClade 4.06 (Maddison and Maddison 2003) and analyzed as constraints using PAUP* (Swofford 2002) with a heuristic search of 500 random addition of sequences.

Multivariate statistical analyses were applied to specimen measurements of *Ptyctolaemus gularis*, from India, northern Myanmar (Sagaing Division and Kachin State), and the holotype, and *Ptyctolaemus* from Chin State using 11 morphological variables: tail length, head length, head width, upper arm length, lower arm length, hand length, upper leg length, lower leg length, foot length, length of the four toe, and number of midbody scales. Specimen MCZ 44747 was not included because it contained missing data (the skull had been removed). All variables were ln-transformed. To examine shape differences between *P. gularis* and the Chin State *Ptyctolaemus* and remove the effects of size on morphometric variables, each variable was regressed on SVL and residuals were calculated. Principal components analysis (PCA) was performed on the variance-covariance matrix of the residuals. A discriminant function analysis (DFA) was employed using the same 11 variables to examine interspecific differentiation. All analyses were conducted using the statistical package PAST (Hammer et al. 2001). These complementary analyses were performed to


Basiliscus plumifrons
Oplurus cuvieri
100 Chamaeleo dilepis
64 Chamaeleo fischeri
Uromastyx acanthinurus
2 Hydrosaurus sp.
100 Leiolepis guentherpetersi
75 Leiolepis belliana
100 Physignathus cocincinus
85 2 100 Lophognathus longirostris
44 Physignathus lesueurii
97 Hypsilurus modestus
19 3 5 Chelosania brunnea
2 Hypsilurus dilophus
5 Moloch horridus
3 3 98 Amphibolurus muricatus
15 Chlamydosaurus kingii
98 Ctenophorus decresii
3 13 Ctenophorus adelaidensis
89 Caimanops amphiboluroides
3 79 10 Diporiphora bilineata
8 81 Pogona barbata
8 Tympanocryptis lineata
65 Pseudotrapelus sinaitus
7 100 Agama bibroni
2 74 80 Agama agama
8 87 7 Agama atra
100 Trapelus ruderatus
Trapelus agilis
43 99 1 Trapelus persicus
100 15 67 Trapelus sanguinolentus
29 4 Trapelus savignii
62 Laudakia sacra
5 64 Laudakia nupta
4 Laudakia tuberculata
54 Laudakia stellio
7 7 100 Phrynocephalus interscapularis
40 100 Phrynocephalus mystaceus
21 Phrynocephalus raddei
7 Laudakia lehmanni
100 77 Laudakia himalayana
5 19 51 8 Laudakia stoliczkana
3 76 Laudakia microlepis
7 100 Laudakia caucasia
40 Laudakia erythrogastra
Ptyctolaemus phuwuanensis
99 Ptyctolaemus Chin State
96 15 Ptyctolaemus gularis
15 Draco blanfordii
96 1 87 Japalura tricarinata
12 7 Japalura variegata
100 Acanthosaura capra
78 55 Acanthosaura lepidogastra
100 Japalura flaviceps
99 6 97 30 Japalura splendida
18 11 100 Pseudocalotes brevipes
29 Pseudocalotes larutensis
98 Aphaniotis fusca
57 Bronchocela cristatella
69 13 1 Gonocephalus grandis
4 90 Cophotis ceylanica
86 99 8 Lyriocephalus scutatus
6 13 87 Ceratophora aspera
4 73 Ceratophora karu
3 97 Ceratophora tennentii
10 100 Ceratophora erdeleni
37 Ceratophora stoddartii
Salea horsfieldii
2 100 Otocryptis wiegmanni
45 Sitana ponticeriana
87 Calotes emma
2 8 100 Calotes mystaceus Vietnam
100 30 Calotes mystaceus Myanmar
28 Calotes calotes
99 Calotes ceylonensis
15 61 2 Calotes liocephalus
5 98 Calotes liolepis
18 Calotes nigrilabris

determine whether morphological variation provided a basis for detectable structure between the two forms, and to identify with which group the holotype, and thus the name belong.

RESULTS

The three new mitochondrial DNA sequences range in size from 1706–1721 bases and were aligned with 30 draconine ingroup and 45 acrodont and iguanid outgroup sequences from Macey et al. (1997a–b, 1998b, 2000) and Schulte et al. (2002) for a total of 1972 aligned positions. Sequences reported here were inferred to be authentic mitochondrial DNA, based on the criteria of Macey et al. (1997a). All sequences show strong strand bias against guanine on the light strand, a characteristic of the mitochondrial genome but not the nuclear genome and there were no stop codons after translation to amino acids using MacClade. In the phylogenetic analysis of 1434 unambiguous sites in 78 aligned sequences, 1147 (946 ingroup only) were variable and 1051 (795 ingroup only) are phylogenetically informative (parsimony criterion). Of the 1972 aligned positions, 538 positions were judged unsuitable for phylogenetic analysis because of questionable alignment.

Analysis of DNA sequence data produced three overall most-parsimonious trees each 12,777 steps in length (Fig. 1). Phylogenetic relationships were overall congruent with the hypothesis of Macey et al. (2000). The clade containing *Ptyctolaemus phuwuanensis* and all previously sampled members of Draconinae is recovered with strong support (96% bootstrap, decay index 12). The sister taxon relationship between *P. phuwuanensis* and the remaining draconine taxa also is recovered with strong support (99% bootstrap, decay index 18). The remaining taxa form two clades, one containing species in the genera *Ptyctolaemus, Draco,* and *Japalura* that is strongly supported (96% bootstrap, decay index 15) and the other forming a weakly supported group (86% bootstrap, decay index 6) with all other taxa sampled. The monophyly of the clade comprised of *Ptyctolaemus gularis* and the Chin State *Ptyctolaemus* is well supported with a bootstrap of 99% and decay index of 15. Topological differences between the parsimony tree presented here and in Macey et al. (2000) within Draconinae and among outgroups are restricted to weakly supported nodes in both trees. In addition, all strongly supported relationships recovered in our analysis are consistent with the phylogeny of Macey et al. (2000).

Hierarchical likelihood-ratio tests, as implemented in ModelTest, find that the most complex model (GTR + I + G) best explains the DNA sequence data and topology of the overall most-parsimonious tree. Model parameters are as follows: $\alpha = 0.5902$; proportion of invariant sites = 0.1382; substitution rates R(a) = 0.268, R(b) = 3.355, R(c) = 0.315, R(d) = 0.238, and R(e) = 1.000; and estimated base frequencies A = 0.418, C = 0.325, G = 0.063, and T = 0.193. A single optimal tree is found using maximum likelihood (Fig. 2) with a negative log likelihood of 51384.41. All groupings that received strong heuristic support (> 95% bootstrap, decay index > 10) from parsimony analyses occurred in the tree recovered by ML analyses.

Results from Bayesian analyses were congruent with those of ML and MP for all strongly supported nodes under MP, however, due to recent critiques regarding the interpretation of posterior probability values as overestimates of a node credibility (Buckley 2002; Suzuki et al. 2002) and by request of a reviewer these results are not presented.

Both MP and ML analyses recovered *Ptyctolaemus* as a nonmonophyletic group as recognized by Ananjeva and Stuart (2001). The WSR tests applied to the molecular data showed that the short-

◄— FIGURE 1. Phylogenetic relationships among agamid lizards based on maximum parsimony analysis of molecular data (length = 9047 steps). Bootstrap values are presented above branches and decay indices are shown in bold below branches on the phylogram.

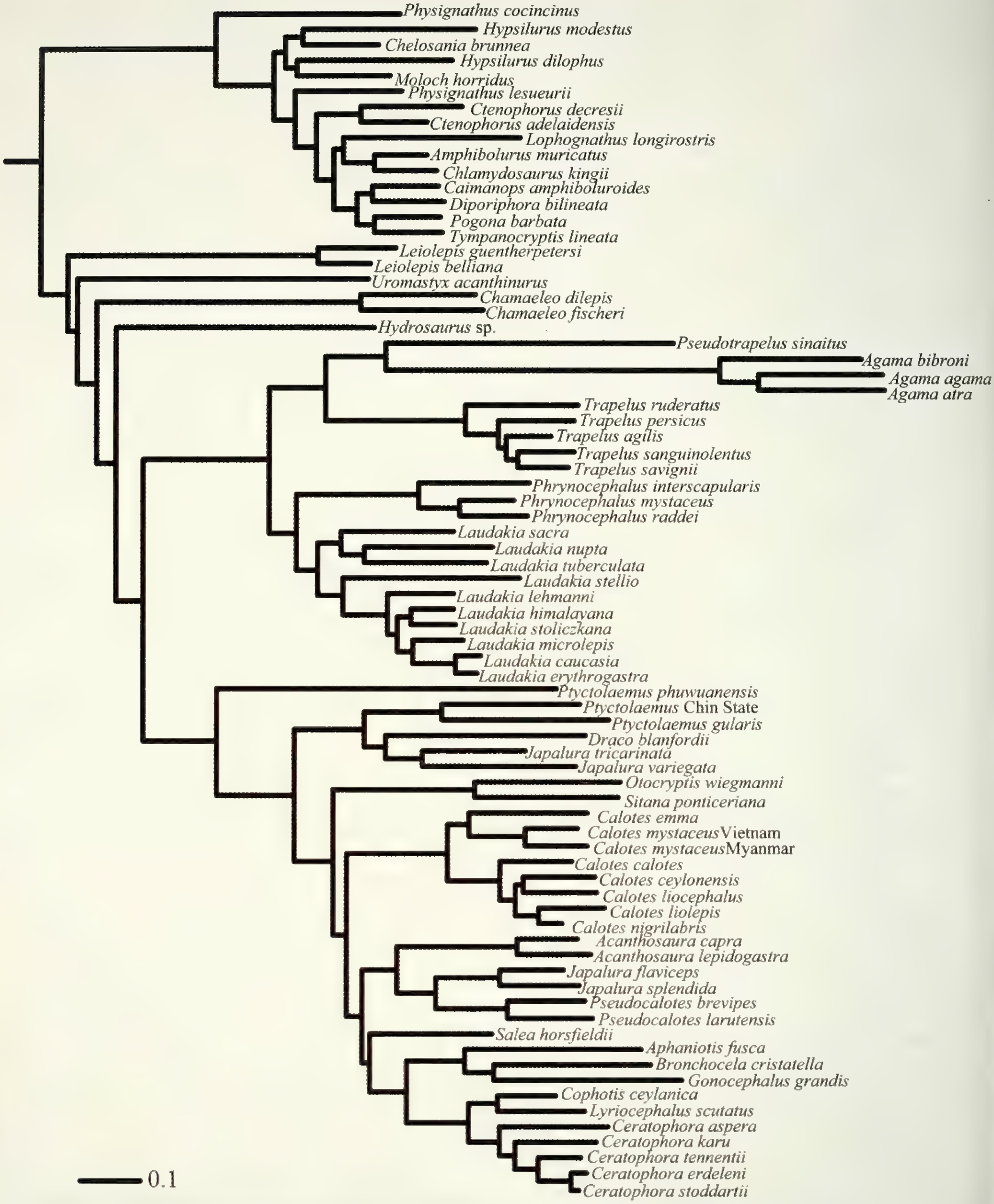


FIGURE 2. Phylogenetic relationships among agamid lizards based on maximum likelihood analysis using GTR + I + G model (mean -log-likelihood = 51384.41). Outgroups are identical to those presented in figure 1 and are not presented. The above tree is a phylogram.

est alternative tree showing *Ptyctolaemus* constrained to be monophyletic is significantly longer than the three overall shortest trees (n = 114; Ts = 4485; P < 0.001*). The SH test applied to the molecular data also rejected the alternative hypotheses of *Ptyctolaemus* monophyly (D ln L = 70.13; P < 0.001*) in favor of the overall shortest tree. We also tested the monophyly of the agamid clade Draconinae. The WSR tests applied to the molecular data showed that the three overall most parsimonious alternative trees showing Draconinae nonmonophyletic were not significantly longer than the three overall shortest trees (n = 110–142; Ts = 3386–5500; P < 0.253–0.324). The SH test did reject the alternative hypothesis of draconine nonmonophyly (D ln L = 24.4–25.06, P < 0.023–0.03*) in favor of the overall shortest trees showing monophyly.

Results of principal components analyses (PCA) using size-adjusted morphometric variables are presented in Table 1. The first two axes represent 80.9% of the variation. The first PC axis loads highest for tail length, hind limb measurements, and upper arm length. The highest loading for PC axis 2 is for midbody scale row number. PC axes 1 and 2 are plotted in Fig. 3. According to the PCA, *P. gularis* differs morphometrically from the Chin State *Ptyctolaemus* with no overlap.

According to discriminant function analysis (DFA), the two *Ptyctolaemus* species have almost no overlap in body shape. The classification procedure correctly classified 96.8% of specimens under their own species. All individuals of the Chin State *Ptyctolaemus* were classified correctly and one specimen of *P. gularis* (CAS 226687), the smallest specimen measured, was misclassified. Hotelling's T^2 test conducts a t-test on the canonical variates of the DFA. This test was highly significant with P < 0.0004* and correctly placed the type (ZMB 5004) of *Ptyctolaemus gularis* with other specimens identified as this species.

TABLE 1. Loadings and percentage of explained variance for the first two principal component axes based on size-adjusted morphometric variables. Analysis applied to 11 morphometric variables.

Variable	*PC 1*	*PC 2*
TailL	0.857	0.104
HeadL	0.499	0.305
HeadW	0.607	0.135
UarmL	0.931	-0.169
ForeaL	0.685	0.008
HandL	0.757	-0.282
ThighL	0.933	0.125
CrusL	0.958	0.057
FootL	0.91	-0.286
4thToe	0.888	-0.324
MidB	0.783	0.512
Eigenvalue	0.074	0.006
% of total variance	74.58	6.35

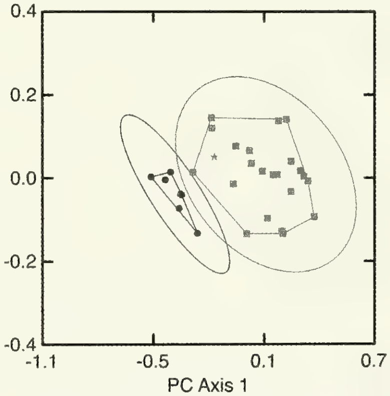


FIGURE 3. Position of adult *Ptyctolaemus* from Chin State and *P. gularis* specimens in morphospace based on the first two principal component axes from size-corrected body measurements. The first factor correlates with tail length, head width, all limb lengths, and midbody scale number. The second factor correlates with midbody scale number. Squares denote *P. gularis* specimens, circles denote *Ptyctolaemus* from Chin State specimens and the star indicates the type specimen of *P. gularis*. Ninety-five percent confidence ellipses and convex hulls are presented around specimens of each species.

DISCUSSION

Analysis of DNA sequence recovers *Ptyctolaemus phuwuanensis* as the sister taxon to all other sampled species of draconine agamids. Results of statistical hypothesis tests applied to these mtDNA sequences strongly reject the hypothesis that *Ptyctolaemus,* as circumscribed by Hallerman and Böhme (2003), is monophyletic. As such, *P. phuwuanensis* represents a distinct evolutionary line without close relatives. The uncorrected pairwise percent sequence divergence between *P. gularis* and the Chin State *Ptyctolaemus* is 21.16%. This level of sequence divergence is greater than the maximum uncorrected sequence divergences between sampled species with *Acanthocercus* (13.12%), *Calotes* (20.31%), and *Ceratophora* (16.48%). Pairwise sequence divergence between *P. phuwuanensis* and the other species of *Ptyctolaemus* ranges from 30.14–30.57% providing genetic evidence that this taxon is quite different from the former two species.

Honda et al. (2000a) using mitochondrial DNA recovered a monophyletic Draconinae containing a clade of *P. phuwuanensis* as the sister taxon to *Draco*. However, in another phylogenetic study of the Draconinae, Honda et al. (2000b), also found *P. phuwuanensis* sister to all other draconine genera included in the analysis. In both analyses, the position of *P. phuwuanensis* was weakly supported using bootstrap analyses and *P. gularis* was not sampled.

Hallerman and Böhme (2003) recommended that *Mantheyus phuwuanensis* be a junior, subjective synonym of *Ptyctolaemus.* They suggested there was insufficient evidence for nonmonophyly of species within *Ptyctolaemus,* interpreting the femoral pores present in *P. phuwuanensis* as a plesiomorphic trait and the presence of parallel, longitudinal folds as an autapomorphy of the genus.

These characters require reinterpretation in the context of the phylogenetic hypotheses presented here. We agree that the presence of femoral pores in *P. phuwuanensis* is a plesiomorphy and that these pores may have been lost once in the common ancestor of all other draconine agamids. However, as noted by Ananjeva and Stuart (2001), the morphology of the gular region in *P. phuwuanensis* (Fig. 4A) is distinct from *P. gularis* (Fig. 4B). The Chin State *Ptyctolaemus* (Fig. 4C) is similar to *P. gularis* and equally distinct from *P. phuwuanensis. Ptyctolaemus phuwuanensis* has a well defined gular sac surrounded by a "U"-shaped fold; this fold is encompassed by a second "U"-shaped fold. In addition, a transverse gular fold is formed by the posterior portion of the outer fold being connected on either side to the oblique folds in front of the shoulders and continuing dorsally and posteriorly from the shoulder. The gular folds of *P. gularis* and the Chin State *Ptyctolaemus* are formed by the collapsing of the gular pouch and surrounding skin in an accordian-like fashion, causing a pleating of the gular skin. The gular

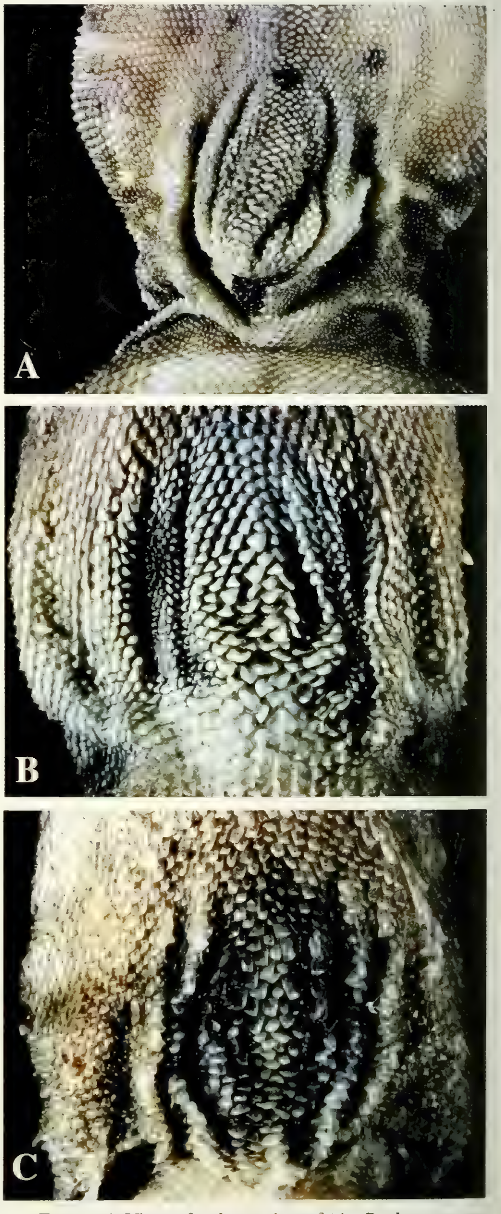


FIGURE 4. View of gular region of (A) *P. phuwuanensis*, FMNH 262582; (B) *P. gularis*, CAS 225592; and (C) *Ptyctolaemus* from Chin State, CAS 227489.

folds of *P. gularis* and of the Chin State *Ptyctolaemus* have longitudinal gular pleating curving medially at the posterior end. Thus, the parallel, longitudinal folds do not appear to be a homologous, shared derived trait for this genus and represent two independent alterations of the gular region. This is not surprising, given that the gular region of iguanian lizards has been modified numerous times independently in chamaeleons, *Anolis,* corytophanines, amphibolurine agamids, *Polychrus,* and within the Draconinae (common ancestor of *Sitana* and *Otocryptis*). Therefore, we recommend *P. phuwuanensis* be removed from synonymy and placed in the genus *Mantheyus* in accordance with Ananjeva and Stuart (2001).

SPECIES DESCRIPTION

Ptyctolaemus collicristatus Schulte and Vindum, sp. nov.

Ptyctolaemus gularis, Shreve 1940, Proc. New England Zool. Club 18:24.
Ptyctolaemus gularis, Moody 1980, Ph.D. Dissertation, Univ. Michigan, Ann Arbor, p. 308.

DIAGNOSIS AND CAMPARISONS.—The only clear character that distinguishes the genus *Ptyctolaemus* from other genera of the subfamily Draconinae (sensu Macey et al. 2000) or Group V agamids (sensu Moody 1980) of mainland southeast Asia is that the males of *P. gularis* have longitudinal gular folds on either side of the midline with the posterior portion of the folds curving medially on each side of the throat. However, these folds are only evident when the gular pouch is in a relaxed position (as in preserved specimens). The folds are formed when the gular pouch is relaxed in an accordion-like fashion, the folds become more pronounced because the scales within the folds are darkly pigmented.

The only other species with gular folds is *Mantheyus phuwuanensis*, however it has rounded “U”-shaped folds encompassing the gular sac. *M. phuwuanensis* also differs from *Ptyctolaemus* and all other draconines by the presence of femoral pores (Ananjeva and Stuart 2001).

The new species can be distinguished from *P. gularis* by having a more prominent nuchal crest (Fig. 5) comprised of larger, flattened, triangular, scales, consisting of fewer scales in adult males (15–16 versus 17–30 scales); a shorter tail, with an average TailL:SVL ratio of 1.99 versus 2.24 (Fig. 6); stouter and shorter limbs (Fig. 6); and more heterogeneity among dorsal and lateral scales.

HOLOTYPE.— CAS 227489 (Figs. 5–10), from Myanmar, Chin State, Min Dat District, Min Dat Township, 21°22′20.1″N, 93°58′34.6″E, 1,482 m, collected by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 7 April 2001.

DESCRIPTION OF HOLOTYPE.— Adult male with a SVL of 91.3 mm; TailL 182 mm (see Table 2 and 3 for additional measurements and meristic characters and Table 4 for body proportions).

Rostral scale 2.9 times as wide as high, about 1.4 times higher than touching upper labials, bordered behind by two supralabials and six postrostrals, medial two postrostrals being largest; supraciliary edge sharp; canthus rostralis moderately sharp, less so toward nostral; nasals extending slightly beyond vertical plane of canthus rostralis; scales on snout irregular in shape and size, slightly imbricate; series of seven, enlarged, keeled scales form an inverted ‘Y’-shaped pattern on middle of snout, first three anterior scales on midline, pointing posteriorly, posterior to third scale are two scales on either side directed diagonally toward superciliary ridge; inner border of supraocular region with a semicircular series of slightly larger, feebly keeled scales, at closest point one head scale separates left and right series; scales within semicircular series smaller and feebly keeled; most upper head scales with one hair receptor on posterior end of scale keel; small, slightly conical, postorbital scale; slightly circular group of enlarged, keeled, scales on either side of occiput; seven supralabials on left and 9 on right; orbit 6.0 mm in horizontal diameter; distance

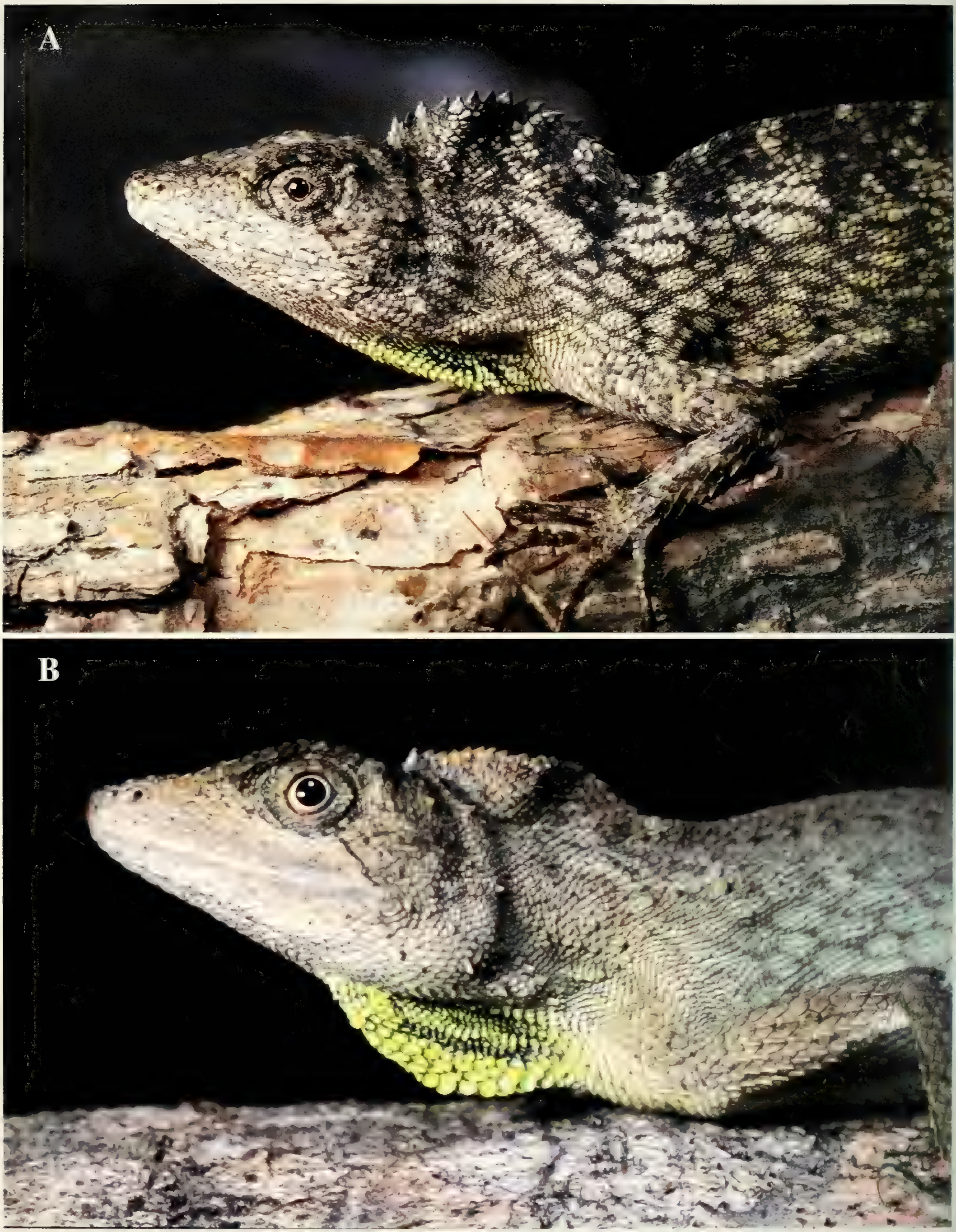


FIGURE 5. (A) View of anterior portion of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489, and (B) *P. gularis*, CAS 221433. Photographed by Hla Tun and Dong Lin, respectively.

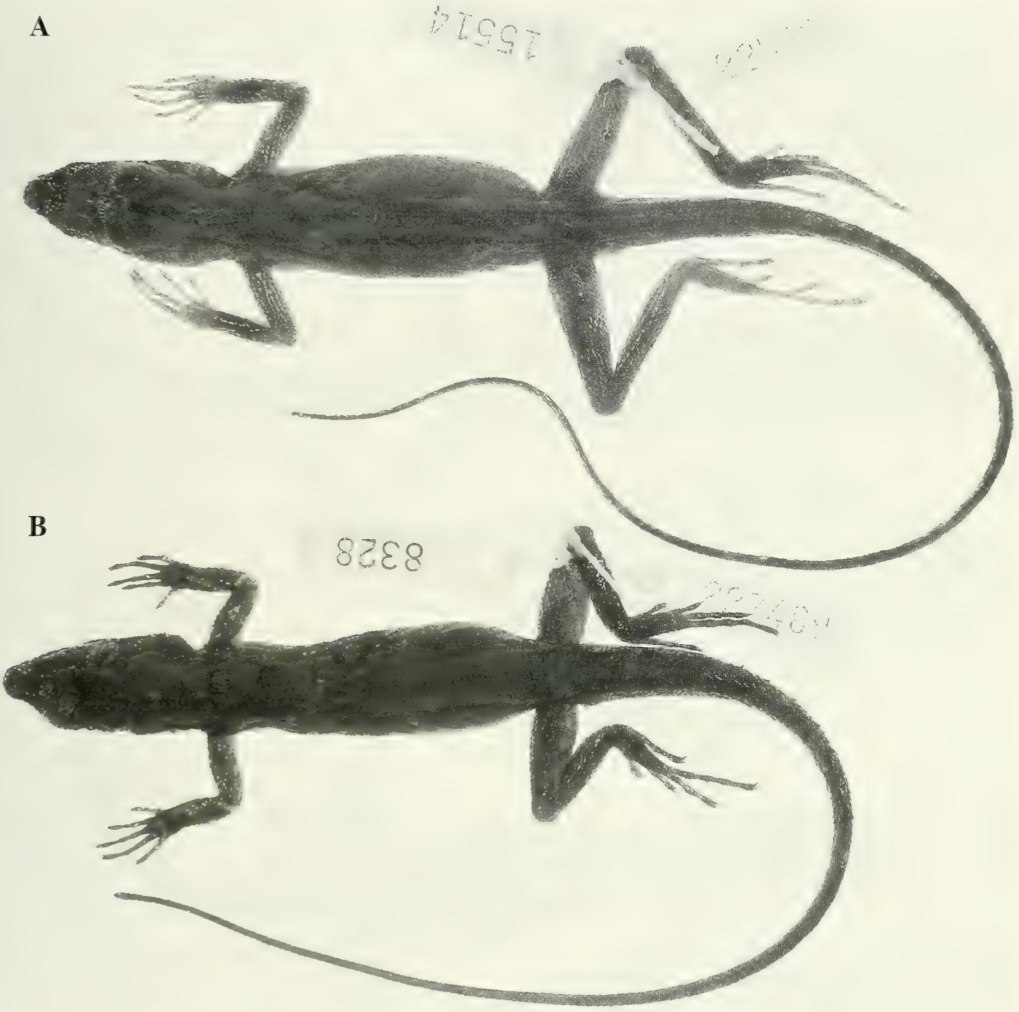


FIGURE 6. Dorsal views of (A) *Ptyctolaemus gularis*, CAS 225592, and (B) holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Dong Lin.

from anterior edge of orbit to nostril 6.7 mm, and 10.6 mm to tip of rostral scale; tympanum concealed, covered with smooth, slightly imbricate scales, scales equal in size to adjacent scales; two enlarged scales posterior and horizontal to orbit, keeled and elevated; temporal area with three enlarged, slightly conical, scales, first between circular group of scales adjacent to occiput and horizontal enlarged scales posterior to orbit, second and third horizontal and posterior to first, on right side scales one and two are separated by three scales and second and third separated by one scale, on left, first and second scale are separated by four scales, and scales two and three are touching.

Mental scale triangular, wider than long, slightly narrower than rostral; mental followed by an infralabial on either side and two rectangular shaped postmentals which contact first infralabials and length of mental except for posterior tip of mental where postmentals are separated by one small gular scale medially; posterior to postmentals are three chin shields on each side that run par-

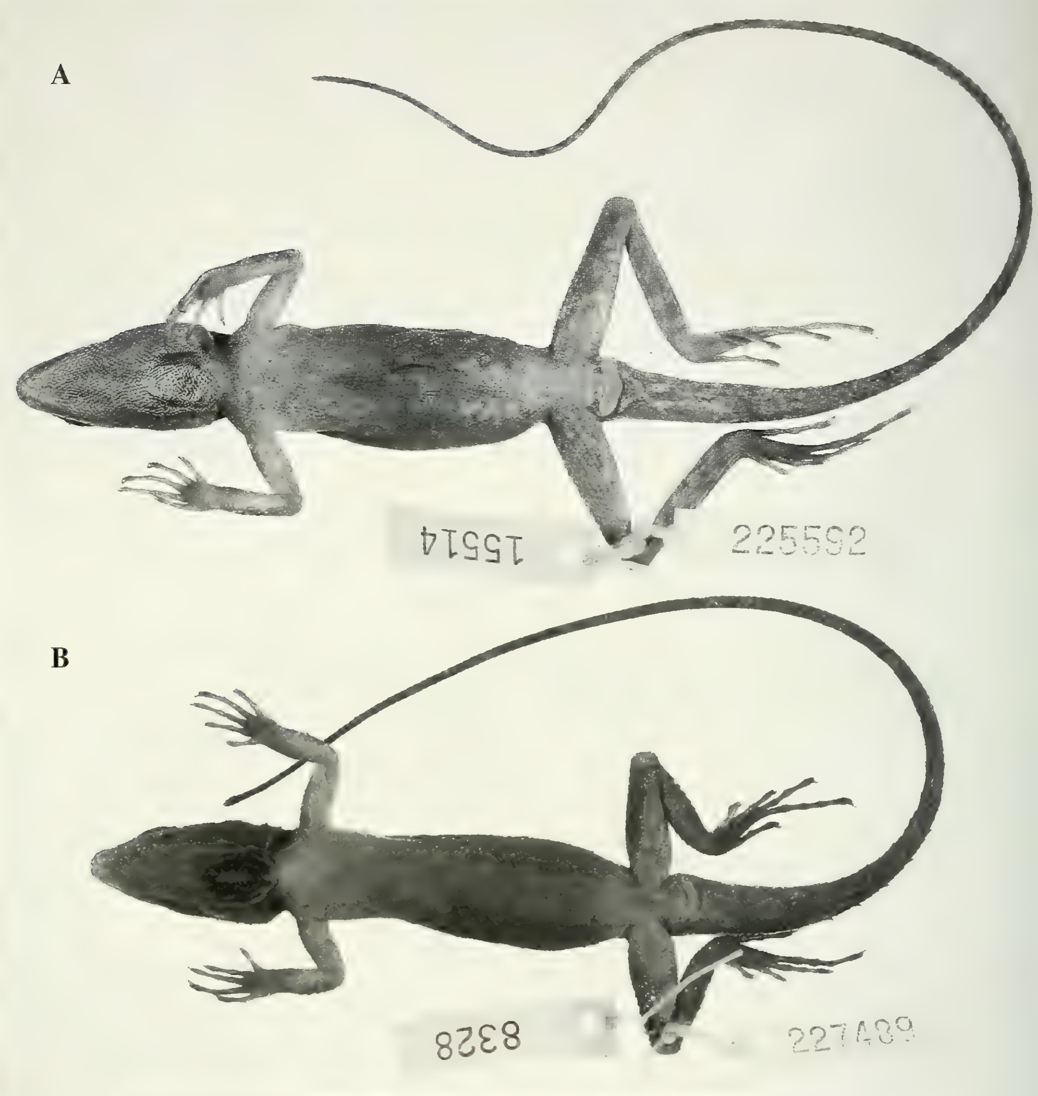


FIGURE 7. Ventral views of (A) *Ptyctolaemus gularis*, CAS 225592, and (B) holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Dong Lin.

allel to infralabials, anterior portion of first chin shield touching first infralabial, remaining portion of first chin shield and following two chin shields are separated from infralabials by one scale row; eight infralabials on either side. Gular scales anterior to gular pouch small (smaller than ventral scales), rounded, imbricate and slightly mucronate, most terminating with hair-bearing receptors; scales of gular pouch slightly triangular and smooth, becoming larger toward center, most with hair-receptors on tip; three distinct raised gular folds on either side of midline; folds curve toward midline posteriorly.

Nuchal crest composed of 16 erect, compressed, triangular scales, each scale notched on posterior side below apex, notch contains one hair-bearing receptor; longest nuchal scale extends vertically 1.4 mm from its base; skin of nuchal crest and dorsal crest lax, with ability to be flattened laterally and erected (Fig. 5). Scales between angle of jaw and shoulder with feebly keeled, imbricate scales, interspersed with three large, keeled scales; small oblique curved fold in front of shoulder; axial scales granular.

Dorsal scales strongly keeled, imbricate, pointing backwards; mid-dorsal scales smaller than bordering dorsal scales; lateral scales heterogeneous, majority of scales much smaller than dorsals, feebly keeled or not keeled, slightly imbricate, interspersed with enlarged strongly keeled scales; lateral scales pointing backwards and down.

Ventrals larger than lateral scales, equal in size to largest dorsals and enlarged interspersed lateral scales, strongly keeled, imbricate, mucronate, pointing backwards.

Limbs moderate, covered dorsally with strongly keeled, imbricate, slightly mucronate scales; ventral surface of forelimbs with smaller feebly keeled, imbricate, scales; ventral surface of hind limbs with feebly keeled, imbricate and slightly mucronate scales; relative length of digits (right hand; measurements in mm in parentheses): IV (8.5) > III (7.9) > II (6.1) > V (5.2) > I (3.8); (right foot): IV (13.3) > III (9.4) > V (9.0) > II (6.6) > I (4.2); subdigital lamellae on fingers bicarinate with a few tricarinate on base of third and fourth fingers; subdigital lamellae of toes tricarinate and bicarinate: I and II bicarinate, III bicarinate, base with enlarged and rounded keels along leading edge, IV and V tricarinate becoming bicarinate distally; 21 and 22 subdigital lamellae under third and fourth fingers, respectively, and 22 and 28 under third and fourth toes, respectively.

Tail slightly compressed laterally, covered with homogenous, strongly keeled, imbricate, mucronate scales.

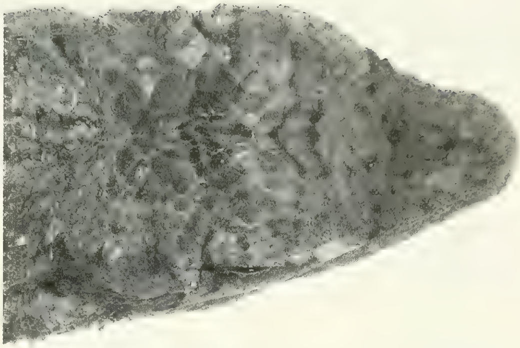


FIGURE 8. Dorsal view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

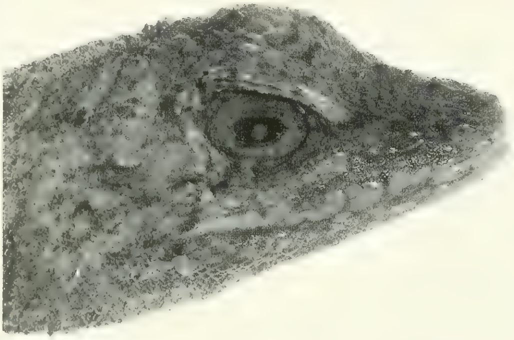


FIGURE 9. Lateral view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

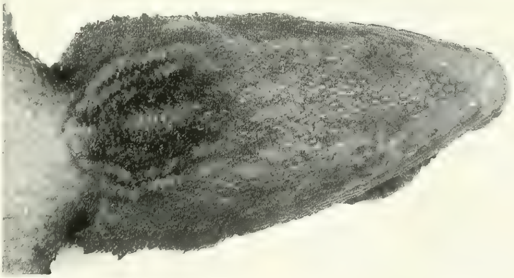


FIGURE 10. Ventral view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

COLORATION IN ALCOHOL. Dorsum has a dull, grayish brown appearance. Snout a uniform gray brown; two faint, irregular, light brown bars bordered by darker brown bars, extending perpendicular to head axis, between anterior and posterior superciliary scales; two brown parallel stripes radiating posteriorly and diagonally from eye, anterior, stripe reaching jaw angle, posterior stripe shorter; gular scales anterior to gular pouch light

TABLE 2. Sex and mensural data (in mm) for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis* (* indicates measurement was taken from left side).

	Sex	SVL	TailL	HeadL	HeadW	UarmL	ForeaL	HandL	ThighL	CrusL	FootL	4thToe
Ptyctolaemus collicristatus												
CAS 227489 Holotype	M	91.3	182	24.7	13.2	11.9	12.4	11.8	19.7	16.4	22.7	13.3
CAS 219991	M	82.8	174	22.9	11.9	10.3	13.2	11.4	19.5	16.2	21.7	13.4
USNM 559811	M	79.7	157	21.5	11.9	10.7	11	12.1	17.6	15.4	22.5	12.5
CAS 220560	M	78.4	167	22.1	11.5	10.9	11.9	12.2	18	16.7	21.3	13.5
MBM-JBS 8195	M	77.3	137	21.5	11.5	9.7	10.9	11.3	18.3	15.5	22.7	13.3
MCZ 44747	M	47	83			6.5	7.2	6.6	11.3	9.7	13.9	7.5
CAS 220561	F	81.3	171	22.3	11.8	10	11.4	10.7	17.7	15.3	20.2	11.8
MBM-JBS 8312	F	71.1	148	19.9	10.9	9.1	9.9	10.4	16	14.2	19.6	11.8
Ptyctolaemus gularis												
CAS 225592	M	87.4	213	25.3	13.7	15	14.1	15.6	27.2	24.8	27.4	16.5
BM 1974.847	M	81.5	198	25	12	12.7	12.2	13.5	25.3	21.8	27.8	16.7
CAS 224733	M	79.8	209	23.9	12.6	13.4	13.3	13.6	22.9	21.1	26.4	14.6
CAS 226690	M	79.6	191	22.6	12.9	12.7	12.8	12.9	22.4	20.9	23.5	13.6
CAS 224704	M	76.5	188	23	12	12.3	12.6	12.6	20.1	19.5	25.2	14.3
CAS 224431	M	78	183	23.8	12.1	12.9	12	13.2	22.1	18.6	24.8	14.1
BM 1974.849	M	74	181	22.4	11.9	11.4	11.6	11	23.4	20.4	23	14.5
CAS 221433	M	73.2	177	21	11.8	118	12	12.8	21.1	19.3	25.5*	14.8*
FMNH 42675	M	72.5	181	22.1	11.5	12.7	13	11.7	22.7	21.8	24.8	14.1
BM 1946.8.1.14	M	70.7	161	22.2	11.3	11.5	12.3	10.3	20.3	18.4	23.1	13
ZMB 5004 Holotype	M	65.7	153	18.6	10.9	9.1	10.1	10.4	17.8	14.6	18.9	11.8
USNM 123425	M	56.1	124	15.9	9.2	7.6	7.6	9	15.4	13.8	17.4	9.8
CAS 226687	M	45.1	100	12.7	7.5	6.6	7.8	8.2	13.1	11.5	14	8.9
MBM-JBS 17893	F	77.9	201	22.1	12.5	11.9	11.9	12.6	24	20.6	26.1	15.8
BM 1974.846	F	75	177	20.9	10.9	10.3	10.1	10	19.4	18.7	20.9	11.8
BM 1974.848	F	72.1	170	18.2	11.1	11.4	10.7	11.4	20.9	20	24	14.2
CAS 224652	F	71.4	169	20.5	11.9	10.6	11.2	11.2	19.6	18.2	21.9	12.5
MBM-JBS 18089	F	71	162	22.3	11.8	10	11.6	10	20.2	17.5	21.1	12.5
CAS 226688	F	70.2	184	20.2	11.4	11.1	12.6	11.5	21.2	19.1	22.7	14.4
CAS 226689	F	66.9	157	18.8	11.1	9.8	10.4	10.8	18.4	16.6	20	12.2
CAS 221297	F	62.1	144	18.4	10.1	10.7	9.1	12	18.6	17.8	22.2	13.5
CAS 221296	F	61.7	162	18.7	10.2	11.2	12.1	11.2	19.4	18.4	23.2	13.7
CAS 221515	F	58	143	18.2	10.2	8.9	9.6	9.7	15.3	16.2	19.3	11.7
CAS 226691	F	48.8	125	12.5	8.7	8.6	8.3	8.5	14.2	13.5	16.9	10.8

TABLE 3. Sex and meristic characters for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis*.

	SEX	MidB	VentSR	NuchalC	SupL (L/R)	InfL (L/R)	SDL
Ptyctolaemus collicristatus							
CAS 227489 Holotype	M	82	77	16	7/9	8/8	28
CAS 219991	M	78	64	15	8/8	8/7	28
USNM 559811	M	87	80	15	8/9	8/8	29
CAS 220560	M	76	84	15	8/7	8/8	34
MBM-JBS 8195	M	83	75	15	8/7	8/8	30
MCZ 44747	M	75	74	15	7/7	8/8	28
CAS 220561	F	76	74	15	9/8	8/9	30
MBM-JBS 8312	F	85	81	15	10/8	9/9	30
Ptyctolaemus gularis							
CAS 225592	M	111	81	30	8/8	9/8	34
BM 1974.847	M	106	77	20	9/9	9/9	38
CAS 224733	M	104	75	22	8/8	7/8	32
CAS 226690	M	111	73	18	8/8	8/7	31
CAS 224704	M	102	74	24	8/9	8/9	31
CAS 224431	M	101	72	21	8/8	7/7	36
BM 1974.849	M	108	73	19	9/9	9/9	37
CAS 221433	M	89	66	21	8/8	7/8	30*
FMNH 42675	M	96	80	22	9/8	9/9	30
BM 1946.8.1.14	M	91	78	24	7/8	8/8	33
ZMB 5004 Holotype	M	90	76	24	7/8	9/8	34
USNM 123425	M	81	75	18	8/9	9/9	30
CAS 226687	M	100	68	17	8/7	8/8	31
MBM-JBS 17893	F	96	67	18	9/10	10/9	35
BM 1974.846	F	90	79	16	8/8	8/8	30
BM 1974.848	F	89	75	17	8/9	8/8	34
CAS 224652	F	96	72	14	7/8	7/8	30
MBM-JBS 18089	F	88	75	15	8/8	8/8	33
CAS 226688	F	102	70	20	8/8	9/9	35
CAS 226689	F	86	84	15	7/7	8/8	30
CAS 221297	F	92	70	14	7/7	7/9	33
CAS 221296	F	94	73	15	7/7	8/7	34
CAS 221515	F	94	76	16	8/9	8/9	32
CAS 226691	F	81	71	15	8/8	8/8	34

TABLE 4. Sex and body proportions for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis*.

	SEX	SVL:TailL	HeadW:HeadL	HeadL:SVL	HeadW:SVL	UarmL:SVL	ForeaL:SVL	ThighL:SVL	CrusL:SVL
Ptyctolaemus collicristatus									
CAS 227489 Holotype	M	1.99	0.54	0.27	0.14	0.13	0.14	0.23	0.18
CAS 219991	M	2.1	0.52	0.28	0.14	0.12	0.16	0.24	0.2
USNM 559811	M	1.97	0.55	0.27	0.15	0.13	0.14	0.22	0.19
CAS 220560	M	2.13	0.52	0.28	0.15	0.14	0.15	0.23	0.21
MBM-JBS 8195	M	1.77	0.54	0.28	0.15	0.13	0.14	0.24	0.2
MCZ 44747	M	1.77				0.14	0.15	0.24	0.21
CAS 220561	F	2.1	0.53	0.27	0.14	0.12	0.14	0.22	0.19
MBM-JBS 8312	F	2.08	0.55	0.28	0.15	0.13	0.14	0.24	0.2
Ptyctolaemus gularis									
CAS 225592	M	2.44	0.54	0.29	0.16	0.17	0.16	0.31	0.28
BM 1974.847	M	2.43	0.48	0.31	0.15	0.16	0.15	0.31	0.27
CAS 224733	M	2.62	0.53	0.3	0.16	0.17	0.17	0.29	0.26
CAS 226690	M	2.4	0.57	0.28	0.16	0.16	0.16	0.28	0.26
CAS 224704	M	2.46	0.52	0.3	0.16	0.16	0.17	0.26	0.25
CAS 224431	M	2.35	0.51	0.31	0.16	0.17	0.15	0.28	0.24
BM 1974.849	M	2.45	0.53	0.3	0.16	0.15	0.16	0.32	0.28
CAS 221433	M	2.42	0.56	0.29	0.16	0.16	0.16	0.29	0.26
FMNH 42675	M	2.5	0.52	0.3	0.16	0.18	0.18	0.31	0.3
BM 1946.8.1.14	M	2.28	0.51	0.31	0.16	0.16	0.17	0.29	0.26
ZMB 5004 Holotype	M	2.33	0.58	0.28	0.17	0.14	0.15	0.27	0.22
USNM 123425	M	2.21	0.57	0.28	0.16	0.14	0.14	0.28	0.25
CAS 226687	M	2.22	0.59	0.28	0.17	0.15	0.17	0.29	0.26
MBM-JBS 17893	F	2.58	0.56	0.28	0.16	0.15	0.15	0.31	0.27
BM 1974.846	F	2.36	0.52	0.28	0.14	0.14	0.13	0.26	0.25
BM 1974.848	F	2.36	0.61	0.25	0.15	0.16	0.15	0.29	0.28
CAS 224652	F	2.37	0.58	0.29	0.17	0.15	0.16	0.27	0.25
MBM-JBS 18089	F	2.28	0.53	0.31	0.17	0.14	0.16	0.28	0.25
CAS 226688	F	2.62	0.56	0.29	0.16	0.16	0.18	0.3	0.27
CAS 226689	F	2.35	0.59	0.28	0.17	0.15	0.16	0.28	0.25
CAS 221297	F	2.32	0.55	0.3	0.16	0.17	0.15	0.3	0.29
CAS 221296	F	2.63	0.54	0.3	0.16	0.18	0.2	0.31	0.3
CAS 221515	F	2.47	0.56	0.31	0.17	0.15	0.17	0.26	0.28
CAS 226691	F	2.56	0.69	0.26	0.18	0.18	0.17	0.29	0.28

brown (darker than ventrals); scales in center of gular pouch lighter than anterior gular scales; scales between gular folds gray or with dark brown spotting, giving appearance of fold recesses being dark brown or black. Dorsal portion of body with a base color of grayish brown; dorsal crest scales chocolate brown; lateral scales gray brown with black spotting; enlarged interspersed lateral scales with dark brown on trailing edge, less so ventrally. Dorsal portion of limbs are brown, more so than body (dorsal); posterior portion of thighs lighter brown; ventral surface of limbs, hands, feet, cream colored (lighter than gular scales anterior to gular pouch). Dorsal portion of tail like body; ventral basal third of tail light brown becoming darker brown toward tip.

COLOR IN LIFE (Fig. 5). Based on color transparency (Fuji Provia 100 AF film) of anterior portion of body. Head a uniform pale grayish brown; iris yellow-brown; two parallel brown stripes radiating diagonally from eye, darker anterior stripe reaching posterior margin of jaw, posterior stripe about half the length of anterior stripe; gular pouch bright yellow medially with greenish-yellow and dark brown laterally. Dorsal portion of body mottled or forming irregular dark brown saddles on pale grayish brown; flanks with a base color of grayish brown anteriorly becoming a yellowish brown posteriorly; brown reticulations on flanks from above shoulder continuing posteriorly. Forelimbs mottled with light and dark brown.

VARIATION.— Body measurements, meristic characters and body proportions for holotype and paratypes of *Ptyctolaemus collicristatus* sp. nov. are presented in Tables 2–4, respectively. Coloration is determined from alcohol preserved specimens. Paratypes are similar to holotype in most respects except as noted below.

CAS 219991 (adult male); four equal-sized postrostrals; series of four enlarged, keeled scales form an inverted 'Y'-shaped pattern on middle of snout, first two anterior scales on midline, pointing posteriorly, posterior to second scale is one scale on either side directed diagonally toward superciliary ridge; temporal area with two enlarged, slightly conical, scales, first between circular group of scales adjacent to occiput and horizontal enlarged scales posterior to orbit, second horizontal and posterior to first, separated by three or four scales. Three chin shields posterior to postmentals on each side that run parallel to infralabials, first two chin shields separated from infralabials by one scale row, third separated by two scales. Nuchal crest composed of 15 erect, compressed, triangular scales, longest nuchal scale extends vertically 0.75 mm from its base. Midventral incision from tissue removal.

Dorsal body appears dull, grayish brown. Snout a uniform gray brown; barring on head similar to holotype except posterior bar reduced to dark brown mottling in parietal area; lateral scales gray brown with black spotting on trailing edge of most scales.

CAS 220560 (adult male); five postrostral scales with medial scale being largest; 'Y'-shaped pattern on snout comprised of six enlarged scales, three medial to each other followed by one diagonal scale on left and two on right side. Postmental is followed by five enlarged chin shields on either side; gular folds indistinct, probably from being extended and flattened during formalin fixation. Nuchal crest pronounced, largest nuchal crest scale 1.3 mm. Midventral incision from tissue removal.

Overall body coloration similar to holotype; only anterior stripe radiating from eye distinct; dorsum interspersed with dark brown scales, vague pattern of four saddles.

CAS 220561 (adult female); five postrostral scales with medial being largest; 'Y'-shaped pattern on snout consists of five enlarged keeled scales, three along midline and posterior two, smaller and less pronounced, pointing diagonally toward superciliary ridge. Postmentals separated by two scales posterior to mental; three enlarged chin shields on left side, two on right; gular pouch indistinct, two gular folds on either side of midline. Nuchal crest low, largest scale 0.56 mm. Midventral incision from tissue removal.

Superoculars light with perpendicular dark bars on anterior and posterior edge; two brown stripes radiating from eye, anterior stripe reaching below angle of jaw by 7 scales, posterior strip reaching four scales behind orbit; area between orbit and upper labials light tan; gular pouch uniform cream colored with a few light brown scales, scales in folds cream colored; flanks with a reticulated pattern of dark brown on light brown; ventral coloration uniform light tan or cream colored except for posterior portion of tail being darker.

USNM 559811 (adult male); ‘Y’-shaped pattern on snout consists of seven raised scales, three along midline and two scales on either side of third scale pointing diagonally toward superciliary ridges, anterior scale of diagonal scales smaller than posterior; five postrostral scales. Postmentals separated by two scales medially; four enlarged chin shields on left side and three on right; two gular folds on either side of midline. Largest nuchal crest scale 0.73 mm. Midventral incision from tissue removal.

Overall appearance is light brown gray. Upper head coloration uniform, head without barring over superciliary scales; dorsal scales of body darker brown than lateral scales; gular pouch with dark brown and gray scales in folds; ventral coloration uniform cream colored.

MBM-JBS 8195 (adult male); five postrostral scales with medial scale being largest; ‘Y’-shaped pattern on snout comprised of five enlarged scales, three medially followed by one diagonal scale on each side. Postmentals touching, followed by three enlarged chin shields on either side; gular pouch with two folds. Largest nuchal crest scale 1.1 mm.

Only one faint gray bar across anterior superoculars is present.

MBM-JBS 8312 (adult female); six postrostral scales, distal and medial scales largest; ‘Y’-shaped pattern on snout comprised of seven enlarged scales, three medially followed by two diagonal scales on each side. Three enlarged chin shields present on either side; three indistinct gular folds on each side.

Head has faint barring, posterior edge of anterior bar dark, posterior bar darkest in parietal area. Body is mostly light gray with dorsal scales darker than lateral scales.

MCZ 44747 (subadult male); ‘Y’-shaped pattern on snout comprised of five enlarged scales, three medially, followed by one diagonal scale on each side. Two gular folds.

General coloration of dorsum is light brown with five light bars on back. Flanks have reticulated pattern.

CAS 220033 (juvenile), SVL 29.5 mm, TailL 61 mm; five postrostral scales; ‘Y’-shaped pattern on snout consists of five enlarged scales, three along midline and one on either side of third scale pointing diagonally. Two gular folds on either side of midline. Fifteen enlarged nuchal crest scales.

Upper head with two wide dark brown bars, anterior bar between middle portion of superciliaries, posterior bar, ‘V’-shaped, outer margins crossing posterior portion of superciliaries; two stripes radiating diagonally from eye, anterior stripe continuing on to neck. Gular cream colored, speckled with black or dark brown. Dorsum with three indistinct brown saddles, one on neck and two on anterior portion of body; body grayish. Limbs mottled with light and dark brown.

SEXUAL DIMORPHISM.— The main external morphological difference between males and females is the distinct gular pouch in males whereas in females the pouch is absent, although faint gular folds are still present. Males also have a more developed, higher, nuchal crest.

ETYMOLOGY.— The specific epithet is derived from the Latin “collum” meaning neck and “cristatus” meaning crested and refers to the nuchal crest.

NATURAL HISTORY AND DISTRIBUTION.— *Ptyctolaemus collicristatus* has thus far only been found on the slopes of Mt. Victoria, Chin State, Myanmar (Fig. 11). Although thorough surveys in Chin State have not been conducted, recent (July–August, 2003) surveys carried out by the

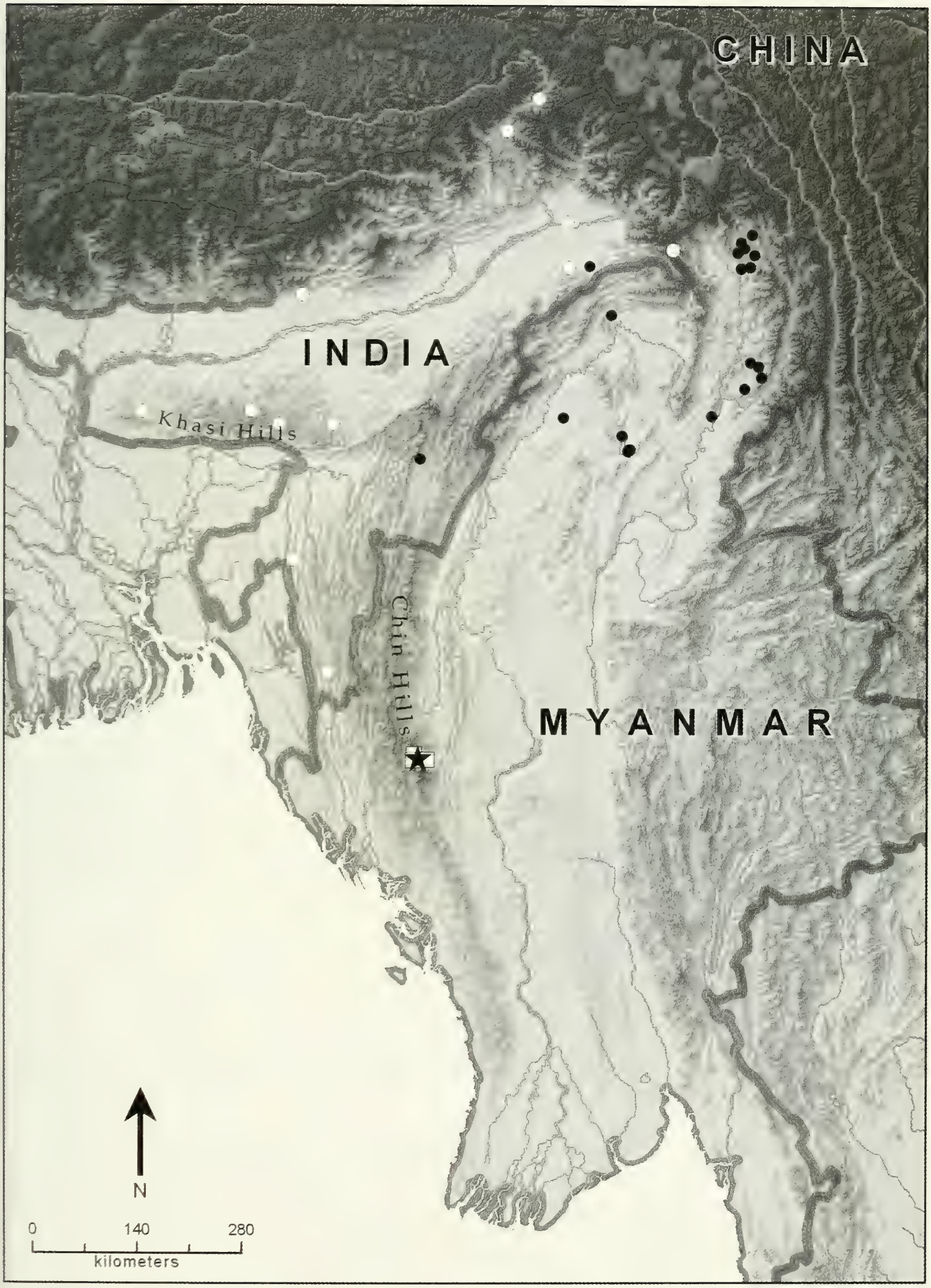


FIGURE 11. Map showing the distribution of *P. collicristatus*, sp. nov. (open squares with the type locality represented by a star) and *Ptyctolaemus gularis* (closed circles represent specimens examined; open circles represent literature records [Boulenger 1890; Wall 1908; Huang 1980; Mathew 1995; Pawar and Birand 2001]). Map prepared by Michelle S. Koo.

Myanmar Herpetological Survey team in the vicinity of Hakha (northern Chin State) failed to find individuals of either species of *Ptyctolaemus*. All specimens of *P. collicristatus* were found in dry mountain forest with deciduous hardwoods and pine between elevations of 790 m and 1,940 m. All specimens were found in areas of secondary forest in close proximity to human habitation. Two specimens were found on trees approximately 2 m above ground, the others were active on the ground.

The CAS specimens of *P. gularis* from Kachin State and Sagaing Division were collected in subtropical evergreen forest, in vegetation, 1–4 m above ground. Smith (1940) also reported that specimens from Kachin State were found in trees and bushes.

The distribution of *P. gularis* in southern northeastern India (Fig. 11) is in close proximity to *P. collicristatus*. These localities represent visual observations (Pawar and Birand 2001) and can not been confirmed by the authors.

Although the Myanmar Herpetological Survey has only made two excursions into Chin State, the collections have resulted in three new species of lizards (*Calotes chincollium* Vindum, 2003; *Cyrtodactylus gansi* Bauer, 2003 and *Ptyctolaemus collicristatus*, sp. nov.). Preliminary examination of other specimens from these collections includes a possible five new species of anurans. The number of new and possibly endemic species supports the idea that the formation of the Indo-Burman Range caused disruption of gene flow among closely allied populations resulting in subsequent vicariant speciation (Vindum et al. 2003).

MATERIAL EXAMINED

Ptyctolaemus collicristatus sp. nov.— PARATYPES (7 specimens). All (except for MCZ specimen) collected from Myanmar, Chin State, Min Dat District, Min Dat Township. **CAS 220560–61**, **USNM 559811**, **MBM-JBS 8312**, 21°22′20.1″N, 93°58′34.6″E, 1,482 m: CAS 220560 collected 16 March 2001, by Kyi Soe Lwin; CAS 220561 collected 18 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; USNM 559811, collected 19 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; MBM-JBS 8312, collected 5 April 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; CAS 219991, from Baw Khue Plantation, 21°23′ 20.9″N, 93°52′20.0″E, 1,940 m, collected 19 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; **MBM-JBS 8195**, 21°26′4.6″N, 93°49′29.6″E, 1,663 m elevation, collected 23 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; **MCZ 44747** from Burma [Myanmar], Chin Hills, Mt. Victoria, 1,400 m elevation, collected 1 July 1938 by G. Heinrich.

ADDITIONAL MATERIAL EXAMINED

Geocoordinates in brackets were added retrospectively and should not be considered original data supplied by the collector(s).

Mantheyus phuwuanensis.— FMNH 262581–82, Lao People's Democratic Republic, Bolikhamxay Province, Thaphabat District, Phou Khao Khouay National Biodiversity Conservation Area, That Leuk Waterfall, 18°23′42″N, 103°04′17″E, 200 m.

Ptyctolaemus collicristatus sp. nov.— CAS 220033, Myanmar, Chin State, Min Dat District, Min Dat Township, Nat Ma Taung National Park, Hee Laung Village, 21°22′07.6″N, 93°49′04.0″E, 709 m.

Ptyctolaemus gularis.— ZMB 5004 (HOLOTYPE), type locality unknown; BMNH 1946.8.1.14, India, Manipur, 22.5 km N of Imphal, Kanglatongbi [24°59′N; 93°54′E]; BMNH 1974.846 Myanmar, N Chengyang [if N'Chang Yang = 25°50′N, 97°48′E], 62 m; BMNH 1974.847 Myanmar, Hkawng Ga [25°58′N, 98°00′E], 1,311 m; BMNH 1974.848 Myanmar, Tara Hka [26°09′N, 97°52′E], 366 m; BMNH 1974.849 Myanmar, Mahtum [26°06′N, 97°58′E], 1,220 m; CAS 221296–97, Myanmar, Kachin State, Putao District, Machanbaw Township, between Alonga and Ahtonga, 27°16′51.3″N, 97°45′31.8″E; CAS 221433, Myanmar, Kachin State, Putao District, Naung Mon Township, Aureinga camp, 27°17′49.8″N, 97°51′58.1″E; CAS 221515, Myanmar, Kachin State, Putao District, Naung Mon Township, Rabaw, 27°26′28.4″N, 97°55′07.5″E; CAS 224431, Myanmar, Kachin State, Putao District, Nagmung Township, Hkakabo Razi National Park, between Pannandin Village and Shin San Ku camp, 27°41′07.7″N, 97°53′38.6″E, 1,188 m; CAS 224652, Myanmar, Kachin State, Putao District, Nagmung Township, Nagmung Town, 27°31′22.5″N, 97°47′56.1″E, 569 m; CAS 224704, Myanmar, Kachin State, Putao District, Nagmung Township, between Kasanku Village and Hton Hlar Village, 27°35′31.3″N, 97°45′25.4″E, 573 m; CAS 224733, Myanmar, Kachin State, Putao District, Nagmung Township, Ma Za camp, 27°28′06.8″N, 97°42′59.5″E, 976 m; CAS 225240, Myanmar, Kachin State, Putao District, Nagmung Township, Au Yin Ga camp, 27°17′51.4″N, 97°51′57.1″E; CAS 225592, Myanmar, Sagaing Division, Hkamti Township, Htamanthi Wildlife Sanctuary, beside Natesu stream, 25°28′46.0″N, 95°37′13.5″E; CAS 226687, Myanmar, Kachin State, Hukaung Valley Wildlife Sanctuary, 26°42′40.8″N, 96°11′35.6″E, 308 m; CAS 226688, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′20.5″N, 96°24′16.1″E, 253 m; CAS 226689, Myanmar, Kachin State, Mohynyin Township, Indawgyi Wildlife Sanctuary, Kyar Phu stream, 25°04′28.4″N, 96°23′30.8″E, 268 m; CAS 226690, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, 25°05′55.5″N, 96°25′11.0″E, 652 m; CAS 226691, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, 25°15′44.6″N, 96°19′20.1″E, 172 m; MBM-JBS 17893, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′31.5″N, 96°24′06.0″E, 246 m; MBM-JBS 18089, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′25.2″N, 96°24′18.2″E, 263 m; FMNH 42675, Myanmar, Kachin State, Myitkyina District, Myitkyina [25°30′N, 97°24′E]; USNM 123425, India, 12 mi E Ledo [27°18′N, 95°56′E].

MATERIAL EXAMINED IN PHYLOGENETIC ANALYSES

Newly reported sequences are: *Mantheyus phuwuanensis,* Lao PDR, Bolikhamxay Province, Thaphabat District, Phou Khao Khouay National Biodiversity Conservation Area, near That Xay waterfall, 18°27’N, 103°10’E, 300 m (FMNH 255495; GB AY555836); *Ptyctolaemus gularis,* Myanmar, Kachin State, Putao District, Naung Mon Township, Rabaw, 27°26′28.4″N, 97°55′07.5″E (CAS 221515, GB AY555838), *P. collicristatus,* Myanmar, Chin State, Min Dat District, Min Dat Township, Nat Ma Taung National Park, Baw Khue Plantation, 21°22′20.1″N, 93°58′34.6″E (USNM 559811, GB AY555837). Several corrections are made to the identifications as reported in Macey et al. (2000). *Calotes emma* (MVZ 222144) is *Calotes mystaceus*; *Calotes versicolor* (MVZ 224102) is *Calotes emma*; sequences reported as *Bronchocela cristatella* and *Aphaniotis fusca* should be switched, that is AF128495 is *Bronchocela cristatella* and AF128497 is *Aphaniotis fusca*. Previously reported sequences used here are reported in Macey et al. (1997a,b, 1998b, 2000) and Schulte et al. (2002): *Basiliscus plumifrons* (MVZ 204068, U82680); *Oplurus cuvieri* (MVZ-RM10468, U82685); *Uromastyx acanthinurus* (MVZ 162567, U71325); *Chamaeleo dilepis* (CAS 168922, AF128460); *Chamaeleo fischeri* (CAS 168965, U82688); *Physignathus cocincinus* (MVZ 222159, U82690); *Lophognathus longirostris* (WAM-ERP-R29940, AF128462); *Physignathus lesueurii* (SAMA R33417, AF128463); *Hypsilurus modestus* (AMS R122434, AF128464); *Chelosania brunnea* (AMS R140288, AF128465); *Hypsilurus dilophus* (AMS R122449, AF128466); *Moloch horridus* (SAMA R38770, AF128467); *Amphibolurus muricatus* (SAMA R34770, AF128468); *Chlamydosaurus kingii* (SAMA R34531, AF128469); *Ctenophorus decresii* (SAMA R31008, AF128470); *Ctenophorus adelaidensis* (SAMA R40929, AF128471); *Caimanops amphiboluroides* (WAM R104419, AF128472); *Diporiphora bilineata* (QM J46161, AF128473); *Pogona barbata* (SAMA R41126, AF128474); *Tympanocryptis lineata* (SAMA tissue collection R35B06, voucher may be lost, AF128475); *Leiolepis guentherpetersi* (MVZ 222157, AF128461); *Leiolepis belliana* (MVZ 215497, U82689); *Hydrosaurus* sp. (TNHC 54902, AF128476); *Agama agama* (CAS 199007, AF128504); *Agama atra* (CAS 193436, AF128505); *Agama bibroni* (MVZ-FC501201, voucher frozen whole, AF128506); *Pseudotrapleus sinaitus* (BMNH 1996.201, AF128507); *Trapelus ruderatus* (NHMG Re. ex. 5212, AF128508); *Trapelus agilis* (NHMG Re. ex. 5210, AF128509); *Trapelus persicus* (NHMG Re. ex. 5211, AF128510); *Trapelus sanguinolentus* (CAS 179758, AF128511); *Trapelus savignii* (MVZ RM10471, AF128512); *Laudakia nupta* (NHMG Re. ex. 5209, AF128513); *Laudakia tuberculata* (ZIL 20697.1, AF128514); *Laudakia sacra* (CAS 170554, AF128515); *Laudakia stellio* (MVZ-RM10494, AF128516); *Phrynocephalus interscapularis* (CAS 179151, AF128517); *Phrynocephalus mystaceus* (CAS 179754, AF128518); *Phrynocephalus raddei* (CAS 179770, U82691); *Laudakia lehmanni* (CAS 183009, AF028677); *Laudakia himalayana* (CAS 183016, AF028676); *Laudakia stoliczkana* (CAS 167878, AF128519); *Laudakia microlepis* (NHMG Re. ex. 5135, AF028678); *Laudakia caucasia* (CAS 184650, AF028683); *Laudakia erythrogastra* (CAS 184400, AF028680); *Draco blanfordii* (MVZ 222156, AF128477); *Japalura tricarinata* (CAS 177397, AF128478); *Japalura variegata* (ZIL 20922, AF128479); *Aphaniotis fusca* (TNHC 57874, AF128497); *Bronchocela cristatella* (TNHC 57943, AF128495); *Gonocephalus grandis* (TNHC 56500, AF128496); *Cophotis ceylanica* (WHT 2061, AF128493); *Lyriocephalus scutatus* (WHT 2196, AF128494); *Ceratophora aspera* (WHT 1825, AF128491); *Ceratophora karu* (WHT 2259, AF128520); *Ceratophora tennentii* (WHT 1633, AF128521); *Ceratophora erdeleni* (WHT 1808, AF128522); *Ceratophora stoddartii* (WHT 1512, AF128492); *Acanthosaura capra* (MVZ 222130, AF128498); *Acanthosaura lepidogaster* (MVZ 224090, AF128499); *Japalura flaviceps* (MVZ 216622, AF128500); *Japalura splendida* (CAS 194476, AF128501); *Pseudocalotes brevipes* (MVZ 224106, AF128502); *Pseudocalotes larutensis* (previously reported as *Pseudocalotes flavigula* – TNHC 58040, AF128503); *Salea horsfieldii* (BNHS-AMB5739, AF128490); *Otocryptis wiegmanni* (WHT 2262, AF128480); *Sitana ponticeriana* (WHT 2060, AF128481); *Calotes emma* (MVZ 224102, AF128489); *Calotes mystaceus* Vietnam (MVZ 222144, AF128487); *Calotes mystaceus* Myanmar (CAS 204848, AF128488); *Calotes calotes* (WHT 1679, AF128482); *Calotes ceylonensis* (WHT 1624, AF128483); *Calotes liocephalus* (WHT 1632, AF128484); *Calotes liolepis* (WHT 1808, AF128485); *Calotes nigrilabris* (WHT 1680, AF128486).

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Short Communications

The Argus Moray, *Muraena argus*, Added to the California Fauna.— A remarkable moray eel (family Muraenidae) was recently photographed by scuba diver Chris Menjou at Catalina Island, Southern California. It is undoubtedly *Muraena argus* (Steindachner) and represents the first record of it north of Magdalena Bay, Baja California Sur, Mexico (24°32.5′N, 112°04.8′W). The eel was encountered on 11 October 2003 at 1400 hrs along the western boundary of the marine park at Casino Point, north of Avalon Harbor (33°20.7′N, 118°19.0′W). It was living among large, algae-covered rocks at 12 m. Maximum reported size of *M. argus* is 120 cm; Menjou described its head as slightly less than "fist-sized," indicating that it was probably an adult. *Muraena argus* is unique among eastern Pacific morays in having elongate, tubular posterior nostrils, a white freckling on a black background, and bright yellow eyes; the only other California moray, *Gymnothorax mordax* (Ayres), is brown and lacks tubular posterior nostrils. *Muraena argus* is also known from Alijos Rocks (off Baja California Sur), the Gulf of California; Cocos Island; Malpelo Island; the Galápagos and Isla La Plata, Ecuador; and Lobos de Afuera, Peru (as *M. albigutta* Hildebrand), from shallow water to 60 m (McCosker and Rosenblatt 1975; Robertson and Allen 2002). Its appearance in California may be related to the extreme 1982–1984 or 1997–1998 El Niño events which brought numerous larvae, juveniles, and adults of eastern tropical Pacific fishes to California (Lea and Rosenblatt 2000).

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Figure 1. Argus moray, *Muraena argus*, photographed at Catalina Island by Chris Menjou.

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VASCULARIZATION OF THE SECOND DORSAL FIN OF NUPTIAL MALE *ETHEOSTOMA SQUAMICEPS* (PERCIDAE: TELEOSTEI).— Nuptial male darters of the *Etheostoma squamiceps* species group possess modified second dorsal fins during the reproductive season. In May 2002 we discovered that nuptial male spottail darters from two streams in Illinois and Kentucky had extensive vascularization of the second dorsal fin, a feature hitherto unreported for the species. Accumulation of red blood cells in the fleshy knobs of the second dorsal fin produced a marked orange-red color in some of the male darters. Nuptial male *E. crossopterum* from a stream in Kentucky did not exhibit the vascularization in the second dorsal fin.

Darters of the subgenus *Catonotus* exhibit sexual dimorphism during the reproductive season; the males develop fleshy knobs on the first or second dorsal fins, enhanced color patterns, swollen heads, and/or fleshy ridges on some body scales (Mayden 1985; Braasch and Mayden 1985; Page et al. 1992). The second dorsal fin of male darters of the *Etheostoma squamiceps* species group become modified, resulting in fins with specific pigment patterns and shapes, especially at the tips of the fin rays. These modified fins are the most useful morphological features for distinguishing darters in the group (Page et al. 1992). Dorsal fin knobs and pectoral fin spots of darters from the three clades within *Catonotus* have been hypothesized to serve as egg mimics that increase the likelihood of females choosing to spawn with males (Page and Bart 1989; Porter et al. 2002). Although many studies have been done on members of the *E. squamiceps* species group (Braasch and Mayden 1985; Page et al. 1992; Bandoli 2002 and references therein), an additional difference in the second dorsal fin of *E. squamiceps* was noticed recently.

MATERIALS AND METHODS.— *Etheostoma squamiceps* were collected with a seine from Coefield Creek (near town of Franklin Mines, Crittenden Co., KY), and we kept 4 nuptial males that exhibited orange-red color in the tips of the second dorsal fin. *Etheostoma squamiceps* also were collected from Hogthief Creek (Co. Rd. 3 bridge near junction with Co. Rd. 12, 6 km N of Elizabethtown, Hardin Co., IL), and we kept 3 nuptial males for comparison with the Coefield Creek specimens. *Etheostoma crossopterum* were collected from Ferguson Creek (S.R. 70 bridge crossing, 4.5 km E of Smithland, Livingston Co., KY), and 5 nuptial males were kept for comparison. Darters from each of the three sites were captured on 4 May 2002, returned to the laboratory, and their fins were examined (while alive) with a dissecting microscope on the same day. Photomicrographs were taken of the second dorsal fin of a live male *E. squamiceps* from Coefield Creek on 6 May 2002 (deposited in California Academy of Sciences, CAS 216888, n = 2 males) and other specimens from the sites were frozen for genetic analyses as part of a separate project.

RESULTS.— Of the darters captured in Coefield Creek, four adult males exhibited bright orange-red coloration at the tips of the second dorsal fin rays in addition to the usual nuptial condition. Bright coloration was not evident in fins of male *E. squamiceps* from Hogthief Creek at the time of capture. Extensive vascularization of the second dorsal fin was observed in all male *E. squamiceps* from both Coefield and Hogthief creeks using light microscopy but was more pronounced in some specimens from Coefield Creek due to greater amount of coloration, which first caught our attention in the field. The color appeared orange to the naked eye at the time of collection, but when observed with a light microscope, the color appeared red. Accumulation of red blood cells in the fleshy knobs produced the marked coloration (Fig. 1). The circulation of blood through the fin membranes and into the fin knobs was observed in live fishes with a microscope, revealing the accumulation of blood in the fin knobs; hence, the color of the knobs was not due to carotenoids. The second dorsal fin of *E. crossopterum* did not exhibit any obvious vascularization as seen in the fins of *E. squamiceps*, and thus serves as an additional difference between nuptial males of the two species.

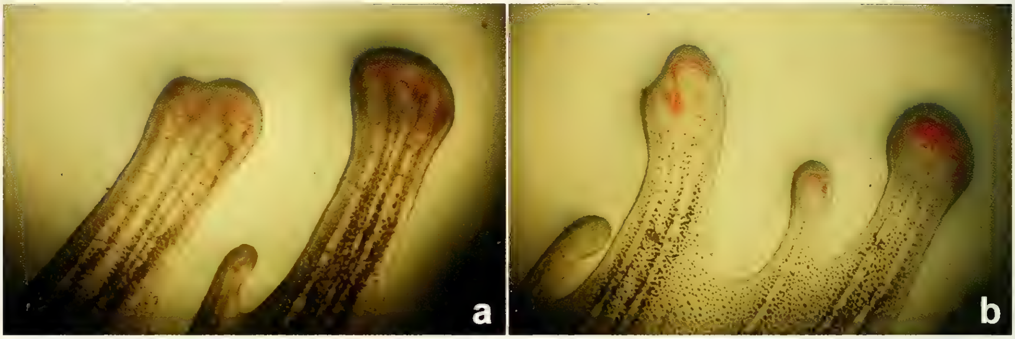

FIGURE 1. Fleshy knobs at tips of second dorsal fin rays of *Etheostoma squamiceps* (71.3 mm SL, nuptial male, CAS 216888), showing extensive vascularization of the fin (a and b are different portions of the same fin).

DISCUSSION.— Further study of the fins of live males of this group of darters might reveal that other species have highly vascularized second dorsal fins during the reproductive season, especially those species with fleshy knobs on the second dorsal fin (*E. chienense*, *E. oophylax*, *E. neopterum*, and *E. pseudovulatum*), and might provide a synapomorphy for some or all of the species of the fleshy-knob clade (Page et al. 1992). However, in the most recent phylogenetic study of the subgenus *Catonotus*, *E. squamiceps* did not cluster with three other fleshy-knob species (Porterfield et al. 1999); therefore, the vascularization may be an autapomorphic character in *E. squamiceps*.

The knobs on the second dorsal fin are believed to serve as egg mimics that attract females to the nest site (Page and Bart 1989; Page et al. 1992). The extensive vascularization of the second dorsal fin of *E. squamiceps* might provide coloration that makes the white knobs resemble the color of eggs and thus more effectively mimic eggs, especially because the knobs of this species are small in comparison to the other fleshy-knob species. Two of the other fleshy-knob species have yellow knobs that resemble eggs more closely due to the coloration (Page et al. 1992). Porter et al. (2002) did not consider *E. squamiceps* as a species possessing egg mimics. Female *E. squamiceps* spawn with larger males significantly more often than with smaller males as determined in laboratory trials (Bandoli 1999); however, fin knob development was not evaluated, and the role of the knobs as egg mimics has yet to be determined for this species. The fin vascularization noted in this paper provides another morphological difference between nuptial males of *E. squamiceps* and *E. crossopterum* and an opportunity to further evaluate the function of the vascularization with regard to spawning success and brood care.

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THE ADVERTISEMENT CALL OF *BRACHYTARSOPHRYS FEAE* (BOULENGER 1887) (ANURA: MEGOPHRYIDAE).— Little is known about the natural history or calling behavior of the five species of frogs currently placed in the genus *Brachytarsophrys* (*B. feae, B. carinensis, B. intermedius, B. platyparietus*, and *B. chuannanensis*). Because of their rarity, these animals have received little attention in the historical literature. In March 2002, while conducting a survey in Kachin State in northern Myanmar, we encountered and recorded chorusing *Brachytarsophrys feae*. To the best of our knowledge, to date, this is the only analyzed recording of any frog belonging to this genus to be reported in the literature.

The males of *Brachytarsophrys feae* (Fig. 1) were found in evergreen montane forest at an elevation of 1,085 m. All individuals were found under rock overhangs which formed small caves in the middle of shallow slow flowing streams. In all instances, the opening to the cave faced downstream, and the substrate was gravel or cobble. Individuals were found in regions where the stream was densely covered by canopy. The stream width was about 1.5 meters, and the banks were heavily vegetated. Five males were heard calling at one locality near Ngar War Village, Hkakabo Razi National Park, Kachin State, Myanmar (27°50′03.5″N, 97°45′40.8″E). The call of one individual (SVL 116.2 mm) was recorded at 2145 hrs. during

FIGURE 1. *Brachytarsophrys feae*, Northern Myanmar. Photo by Hla Tun.

heavy rain. The air temperature was 13°C and the stream temperature was 14°C.

Calls were recorded *in situ* by KSL using a Sony WM DC6 Professional recorder. Ambient temperature, relative humidity and general weather conditions were recorded along with microhabitat and habitat data. Individuals were collected and photographed and latitude and longitude were recorded using a Garmin 12 GPS with the datum set to WGS 84. Animals were euthanized and then fixed in 10% buffered formalin before being transferred to 70% ethanol. Specimens are deposited in the California Academy of Sciences (CAS). Calls were digitized and analyzed using Raven 1.1 software (Cornell Bioacoustics Lab) on a Macintosh G4.

Four advertisement calls were evaluated (CAS 228507). The spectrogram depicts calls consisting of four to five notes. The notes vary in the number of harmonics, from two to seven in our sample (Fig. 2C). The dominant frequency lies at 1378 Hz, with harmonics at 4134 Hz, 6890 Hz, 9646 Hz, 12403 Hz, 15159 Hz, 17915 Hz and 20671 Hz. As is evidenced by plotting frequency (in KHz) against intensity (in arbitrary units) (Fig. 2E), there is an inverse relationship between frequency and intensity, the energy of the note lying primarily in the lower frequencies. It is interesting to note that the rate of change in intensity between successive harmonics decreases. Notes also display some frequency modulation, with a small frequency dip in the fundamental frequency and lower range harmonics (Fig. 2D) at the beginning of the note.

Call duration ranged from 2.256–3.5488 s. Within a call, notes lasted between 0.34–0.474 s (n = 18) and occurred at intervals ranging from 0.293–0.482 s. Captured in the recording are two non-overlapping calls emitted by other individuals (Fig. 2B at 18 s and 1.40 mins). While the latter call evoked an almost immediate response (call four) from our target male (lapse time of 6 s), in the former case 34 seconds lapsed before eliciting a response (call three of our target male). Due to our

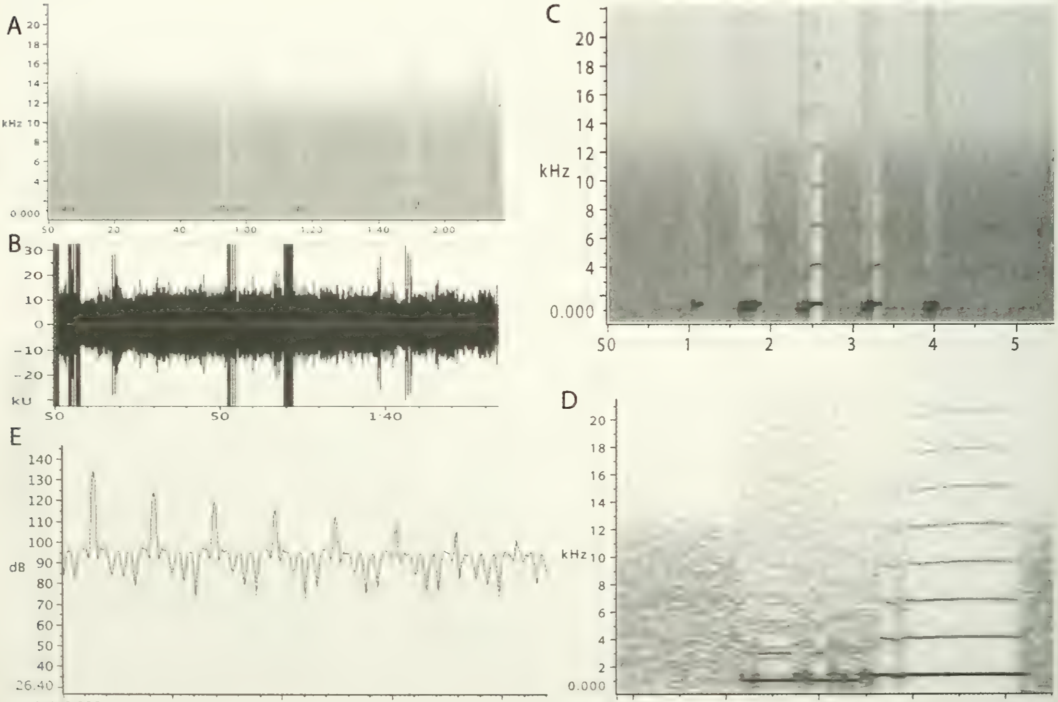

FIGURE 2. A. spectrogram of calls (time vs. frequency) B. waveform of calls (amplitude vs. time) C. spectrogram of call two (time vs. frequency) D. spectrogram of note three call two (time vs. frequency) E. power graph (frequency vs. dB).

small sample size we can not differentiate whether this is a true call-timing shift or if calls in this instance were by random chance non-overlapping. Interestingly, the first response call (call three of our target male) contained notes with seven added harmonics suggesting that *B. feae* may add additional elements to its call in response to the non-overlapping calls of their neighbors. By selectively exceeding the acoustic energy of its competitors, the male may attract females while still conserving energy (Schwartz 2001). In our limited experience with this species, chorusing was only heard during the rain. On nights when it was not raining, individuals did not even emerge from their rock burrows. The coordination of chorusing with abundant background noise may help disguise the location of the chorus from potential predators (Grant et al. 1998).

DISCUSSION.— The calls of *B. platyparietus* are unknown, and the calls of *B. feae B. carinensis, B. intermedius, and B. chuannanensis* have not received much attention in the literature. Taylor (1962) characterized the call of *B. carinensis* as "introduced on a querulous note followed by a loud raucous call repeated five or six times with slight pauses between", and Smith (1921) summed up the call of *B. intermedius* simply as "loud, harsh croakings". Similar to Taylor's (1962) report on the call of *B. carinensis*, and Smith's (1921) report on the call of *B. intermedius*, the call of *B. feae* is quite loud and can be heard from a distance. Smith (1940) described the call of *B. feae* as follows "This frog had a piercing cry, not unlike a small Kloxon (horn). For each performance it filled its lungs in three distinct breaths, opened its mouth, paused a little, and then gave vent to a continuous harsh screeching until its wind had gone." To our interpretation, the call more closely resembled barking.

The few accounts of habitat preferences consist of *B. carinensis* "ensconced among rocks in a stream" (Taylor 1962), *B. intermedius* found in "some deep crevice between the rocks or boulders of the streams" (Smith 1921), *B. chuannanensis* found in "streams usually hiding in openings in stone or mud-caves" (Fei et al. 2000), and lastly, *B. platyparietus* found under rocks along the sides of streams (Rao Ding-Qi, pers. commum.).

The only behavioral account comes from Bourret's (1942) observation that the males of *B. carinensis* were "very irritable". This can also be said of the males of *B. feae*. It appears that *B. feae* males are territorial and it is surmised from field observations that they defend their territory. Although no combat was witnessed, KSL noted that when the call was imitated the male would advance rapidly from his cave.

It is hoped that eventually, this call can be comparatively evaluated with those of its congeners. In light of the fact that *Brachytarsophrys* species appear to inhabit similar microhabitats, it would be informative to evaluate the call characteristics coupled with environmental factors within a phylogenetic framework.

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